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Exploring effects of hypoxia on fish and fisheries in the northern Gulf of Mexico using a dynamic spatially explicit ecosystem model

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ABSTRACT

The formation of an extensive hypoxic area off the Louisiana coast has been well publicized. However, determining the effects of this hypoxic zone on fish and fisheries has proven to be more difficult. The dual effect of nutrient loading on secondary production (positive effects of bottom-up fueling, and negative effects of reduced oxygen levels) impedes the quantification of hypoxia effects on fish and fisheries. The objective of this study was to develop an ecosystem model that is able to separate the two effects, and to evaluate net effects of hypoxia on fish biomass and fisheries landings. An Ecospace model was developed using Ecopath with Ecosim software with an added plug-in to include spatially and temporally dynamic Chlorophyll *a* (Chl *a*) and dissolved oxygen (DO) values derived from a coupled physical–biological hypoxia model. Effects of hypoxia were determined by simulating scenarios with DO and Chl *a* included separately and combined, and a scenario without fish response to Chl *a* or DO. Fishing fleets were included in the model as well; fleets move to cells with highest revenue following a gravitational model. Results of this model suggest that the increases in total fish biomass and fisheries landings as a result of an increase in primary production outweigh the decreases as a result of hypoxic conditions. However, the results also demonstrated that responses were species-specific, and some species such as red snapper (*Lutjanus campechanus*) did suffer a net loss in biomass. Scenario-analyses with this model could be used to determine the optimal nutrient load reduction from a fisheries perspective.

1. Introduction

Nutrient rich waters flowing from the Mississippi River into the Gulf of Mexico result in high primary productivity in this coastal area (Turner et al., 2006). Bacterial decomposition of this organic matter in combination with summer stratification has led to the occurrence of an extensive area of low bottom oxygen since at least the early 1970s (Rabalais and Turner, 2006). While often referred to as the 'dead zone', the effect on living marine resources of this annually reoccurring area of hypoxic bottom waters off the coast of Louisiana is not necessarily lethal.

Hypoxia refers to oxygen levels of 2 mg/l or lower, which can lead to decreased feeding and growth rates, changes in activity level, avoidance behavior, and death in fish and shellfish (Bell and Eggleston, 2005; Robert et al., 2011; Goodman and Campbell, 2007). The exact level of dissolved oxygen that results in effects on physiology or behavior is species-specific, which can results in community structure shifts and changes in species interactions (Essington and Paulsen, 2010). Indirect effects occur through predator–prey relationships; fish could be affected not by hypoxia, but by the response of their prey or predators to hypoxia, and the effects could be either positive or negative (Altieri, 2008; Pierson et al., 2009; Eby et al., 2005). Effects on fisheries may be even more complicated, as catch per unit effort (CPUE) could decrease when the abundance of target species is reduced by hypoxia, or could increase due to aggregation of target species at the edge of the hypoxic zone, which may enhance their susceptibility to be caught (Craig, 2012).

A significantly obscuring mechanism is the fact that the same nutrient enriched waters that are the main cause of bottom hypoxia (Rabalais and Turner, 2001), are responsible for the high primary

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and secondary production in this region (Gunter, 1963; Nixon and Buckley, 2002; Chesney et al., 2000). It is likely due to these complications, that holistic effects of hypoxia on the fisheries ecosystem of the northern Gulf of Mexico have remained elusive (Rose, 2000; Rose et al., 2009).

The purpose of this study is to analyze effects of hypoxia on fish and fisheries through ecosystem model simulations, and to provide a tool that can be used in management scenario analyses pertaining to Mississippi River nutrient load reductions and coastal fisheries management. To this purpose an Ecospace model was developed using Ecopath with Ecosim (EwE) software that was enabled to receive spatio-temporal primary productivity and dissolved oxygen output from a coupled physical–biological hypoxia model developed by Fennel et al. (2011). Since a reduction in hypoxia would entail a reduction in nutrients that enter the Gulf of Mexico, it is important to incorporate the effects of nutrient enrichment on phytoplankton (and changes therein) in an ecosystem model that studies effects of hypoxia and scenarios that may reduce this hypoxia. Output of the Fennel et al. (2011) model of dissolved oxygen (DO) as well as Chl *a* was used as forcing functions in the Ecospace model to account for both effects. Similar approaches to incorporate effects of biogeochemistry on foodweb models, often referred to as End-to-End modeling, have been used in other studies (see e.g. Libralato and Solidoro, 2009).

The ecosystem model developed for this study takes a holistic approach by simulating species interactions, while accounting for changes in biomass as well as spatial distribution changes, and by explicitly simulating fisheries with dynamic fleets. The model allows for simulations of all direct and indirect effects on fish and fisheries, in an environment where hypoxia and primary productivity fueling can be evaluated together and separately. While this ecosystem model contains sixty groups to provide a representative simulation of the ecosystem, the main focus of this paper is on a select group of species that are of economic or ecological significance. These species are Gulf menhaden (*Brevoortia patronus*), which is largest fishery in Louisiana by weight; brown, white and pink shrimp (*Farfantepenaeus aztecus*, *Litopenaeus setiferus*, and *Farfantepenaeus duorarum*), together comprising the largest fishery by value; red snapper (*Lutjanus campechanus*), a popular sportfish; Atlantic Croaker (*Micropogonias undulatus*), the most dominant forage fish in the model area; and jellyfish, a group of organisms of interest because of previous documented responses to hypoxia in other areas.

2. Methods

2.1. Data preparation

Fisheries independent survey data from the SEAMAP program of the Gulf States Marine Fisheries Commission (seamap.gsmfc.org) was used to determine which species were representative of the area, and to determine the biomass of each species present in the model area. Initial biomass in the base model was based on the average biomass of each group (species or functional group) from 2005 to 2008. Fishing was represented by including shrimp trawls, recreational fishing, snapper/grouper fishery, crab pots, menhaden fishery, squid fishery, and longlines as 'fleets' in the model. Annual landings of model groups by these fleets were based on NOAA Fisheries Annual Commercial Landings Statistics (st.nmfs.noaa.gov), and trip ticket data from the Louisiana Department of Wildlife and Fisheries. These data were used to develop the Ecopath model.

Landings data from 1950 to 2010, and SEAMAP data collected in the model area from 1982 to 2010 were used to calculate annual landings and biomass (t/km^2) respectively for each group in the model for which these data were available. In addition, an oxygen forcing function was developed from data collected during Lumcon cruises from 1998 to 2007 (D. Obenauer, personal communication), and a nutrient forcing function from NO_x data collected in the Mississippi River by USGS from 1950 to 2010 (toxics.usgs.gov) to simulate nitrogen load into the coastal area from the Mississippi River. These time series and forcing functions were used for model calibration in Ecosim.

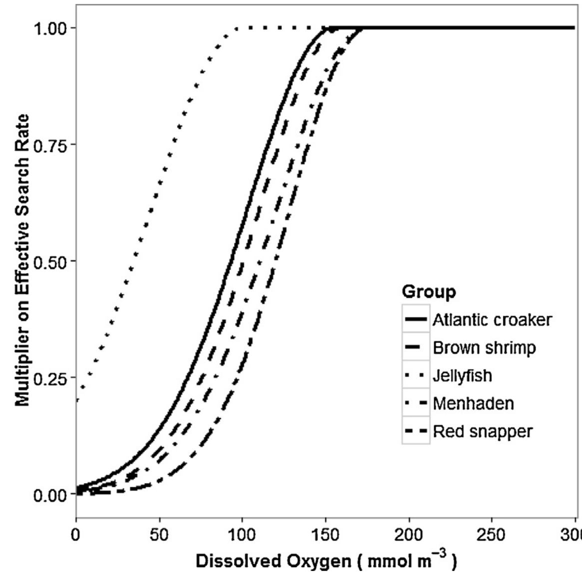

Fig. 1. Oxygen response curves of selected species.

In EwE, a nutrient forcing function serves as a multiplier on primary production. In order for groups to respond to the level of dissolved oxygen, empirically derived sigmoidal oxygen response curves were developed. These curves were developed by determining catch rates at each level of dissolved oxygen, using all SEAMAP data where dissolved oxygen was measured during collections. The tolerance curves were then used as a multiplier on effective search rate in Ecosim (and Ecospace, using a plug-in described in Section 2.5) as described in Christensen et al. (2008) and de Mutsert et al. (2012), to affect biomass of each specific group (Fig. 1).

2.2. Model preparation

The EwE modeling suite was used to build the model (www.ecopath.org). The virtual representation of the ecosystem was developed in Ecopath, the static model of the EwE modeling suite. Groups in the model represent single species as well as species aggregated in functional groups. Where deemed necessary to represent ontogenetic diet changes or size-selective fisheries, species were split into multiple life stages. For those species, the initial biomass of only one life stage was derived from empirical data, and the biomass of other stages were determined using a *von Bertalanffy* growth model. Some functional groups were represented with multiple life stages as well. This resulted in 60 groups (Table 1). Parameters included for each group to develop a mass-balanced Ecopath model in addition to biomass (B), were the P/B (production/biomass) ratio, Q/B (consumption/biomass) ratio, and the total fisheries catch rate (Y) for the groups that are fished. Parameters were derived from other Gulf of Mexico food web models (Walters et al., 2008; de Mutsert et al., 2012) or fishbase (fishbase.org).

Two master equations must be satisfied to correctly parameterize the Ecopath model. The first equation describes the production of each functional group as a set of n linear equations for n groups:

$$\left(\frac{P_i}{B_i}\right) \cdot B_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot \left(\frac{Q_j}{B_j}\right) \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \qquad (1)$$

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