Fishery closures, more than predator release, increased resilience of nearshore fish and invertebrates to the Deepwater Horizon oil spill

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Abstract

Introduction

Unexpected responses after a high-intensity low-duration stressor can arise because focal populations are embedded in a larger ecosystem of human and ecological interactions. Toxicological studies alone that focus on single species are often insufficient to predict population or community level impacts. More than a decade after the 2010 Deepwater Horizon Macondo well blowout, we are developing a clearer picture of the impact of the oil spill on saltmarsh ecosystems. For marsh fishes and large-bodied invertebrates (i.e., crabs and shrimp), there has been a largely consistent finding of significant impacts at the individual- or organismal-level but, unexpectedly, no impact at the population-level (Fodrie et al. 2014). Several hypotheses have been proposed to explain this apparent paradox. First, even small-bodied marsh fishes are capable of detecting and dispersing away from patches of crude oil (Martin 2017). Second, short generation times of small-bodied marsh fishes and high intrinsic rates of population increase translate to a potential for rapid recovery (Vastano et al. 2017, Jensen et al. 2019). Third, many fish and invertebrates are caught as target species or bycatch in commercial and recreational fisheries, and temporary closure of these fisheries may have offset mortality from the oil spill (van der Ham and de Mutsert 2014). Finally, fishes and invertebrates may have experienced predatory release as some of their important predators, such as picivorous birds and dolphins, were impacted by the spill (Short et al. 2017). While the first two hypotheses have received much devoted research, the final two remain largely untested across a diversity of saltmarsh taxa.

The nearshore waters of the northern Gulf of Mexico contain extremely productive fisheries, with commercial and recreational catches exceeding all other areas in the United States (Chesney et al. 2000, Adams et al. 2004, Lellis-Dibble et al. 2008). Valuable fisheries in Gulf Coast estuaries drive local economies and are deeply embedded in local culture (Jacob et al. 2013, Savolainen et al. 2014). Commercial species such as oysters (*Crassostrea virginica*), various species of Penaeid shrimps, blue crabs (*Callinectes sapidus*), and gulf menhaden (*Brevoortia patronus*) are harvested and exported globally, while abundant recreationally-important species such as red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), and flounders (*Paralichthys* spp.) promote thriving tourism revenues for Gulf residents.

The 2010 Deepwater Horizon oil spill, however, had negative impacts on local and regional fishing communities that may have been strong enough in turn to impact population dynamics of fished species. Two weeks following the collapse of the drilling platform, the National Oceanographic and Atmospheric Administration (NOAA) initiated closures on nearshore fishing to prevent human ingestion of oil-contaminated seafood. These closures ranged from around 17,000 km2 (approximately the area of Connecticut) in May 2010 to more than 88,000 km2 later in June 2010 (approximately the area of Maine), representing over a third of Gulf of Mexico federal waters (Lubchenco et al. 2012). Despite the capping of the wellhead in July and the gradual reduction in closure area, the spill has been implicated in commercial losses of $4.9 billion and recreational losses of $3.5 billion in the years following the spill (Sumaila et al. 2012). However, the indirect, ecological consequences of this cessation of fishing remains uncertain and may mask any negative impact due to oil’s toxicity (Schaefer et al. 2016).

An alternative consideration for reconciling the conflicting individual- and population-level responses observed for marsh fishes and large-bodied invertebrates is a release from predation following high predator mortality (Fodrie et al. 2014). Specifically, exposure to crude oil released from the Deepwater Horizon induced substantial mortalities and dispersal of piscivorous predators including bottlenose dolphin (*Tursiops truncatus*) (Venn-Watson et al. 2015), and seabirds, wading birds, and other marsh-associated shorebirds (Haney et al. 2014). In some cases, reduced survival rates were observed up to three years following the oil spill (Schwacke et al. 2013, McDonald et al. 2017). These species typically exert top-down control on coastal nekton communities and their reduced abundances potentially generated a degree of release from predatory controls. Predation release has already been attributed to the large Gulf Menhaden recruitment class observed following the spill (Short et al. 2017). However, estimating the total loss of predatory biomass is hampered by the resolution of surveys and a lack of direct measurements of the mortality processes. Thus, any attempts to do so likely underestimate the total. This is because indirect effects that may decrease lifespans and reproductive potential (Peterson et al. 2003) are difficult to quantify, but impart considerable pressures on individuals and populations.

Ecosystem models allow us to integrate both the direct impacts of stressors and the indirect impacts of stressors that are mediated through food web interactions. In this respect, they have been used to study the impact of stressors such as oil spills (Ainsworth et al. 2018, Lewis et al. n.d.), hypoxia (de Mutsert et al. 2017), ocean acidification (Marshall et al. 2017), and fishing (Koehn et al. 2017) on populations and communities. The ability of ecosystem models to account for predator-prey interactions, population dynamics, fisheries, and, in some cases, biophysical forcing makes them valuable tools for strategic management and can give scientists and managers a high-level understanding of major risks and drivers in an ecosystem. Their ability to account for all food web interactions, including ones that may not be apparently influential, makes ecosystem models particularly useful for generating new hypotheses and ruling out implausible ones (cite).

In this study we use mass-balance food web models coupled with a generalized equilibrium model to examine whether fishery closures, predator mortality, or both can plausibly explain the persistence of nearshore fish and invertebrates following Deepwater Horizon. Furthermore, we explore this question by quantifying 1) only direct impacts of fisheries and predators and 2) both the direct impacts and impacts mediated through all food web interactions. This allows us to understand the added benefit of using the more holistic food web model to study these questions.

Methods

We developed a mass-balance food web model to quantify both the direct and indirect impacts of fishery closures and predator mortality on five major fish and invertebrate groups in Barataria Bay, Lousiana, USA: Panaeid shrimp; blue crabs; Atlantic croaker, spot, and silver perch; red drum; and gulf menhaden. To explore direct impacts of fishery closures and predator mortality, we asked what proportion of total mortality of these five groups (both juvenile and adult life stages) came from 1) fisheries, 2) sea birds, and 3) dolphins. We then applied a generalized equilibrium model (Essington and Munch 2014) to explore the indirect effects that account for impacts of fisheries, sea birds, and dolphins on all food web interactions. This tool allows us to ask the following question of our mass-balance model: “how much will the biomass of a species change from an X% change in the mortality of a predator species (or an X% change in fishing effort)?” While dynamic non-equilibrium food web models can also explore these indirect effects, they require extensive tuning of functional response parameters, which have little to no data available to inform parameter values. Because the generalized equilibrium models are fast to compute and are meant to be applied within a “neighborhood” of equilibrium, we can easily simulate many different flexible functional response scenarios to better understand a range of possible results.

*Developing a mass-balance model*

We parameterized our food web model using the Rpath package (Lucey et al. 2020), an implementation of the Ecopath (Christensen and Pauly 1992) modeling framework in R (R Core Team 2020). Ecopath models are snapshots of food webs that assume equilibrium mass balance; that is, all biomass produced from the net result of consumption and respiration equals all mortality from predation, fisheries, and other sources. We did not include migration or biomass accumulation in our model. Food web dynamics in Ecopath are governed by a master equation:



In equation (1), *Bi* is the biomass of functional group *i*, *PBi* is the production to biomass ratio of group *i* (under mass balance, this is equal to total mortality), *EEi* is the ecotrophic efficiency or proportion of total production removed by predators and fisheries within the model domain, *Ci* is the fisheries catch (including bycatch and discards), *QBj* is the consumption to biomass ratio for predator *j*, *DCji* is the diet composition, or proportion by mass of prey *i* in the diet of predator *j*, and *n* is the total number of functional groups. A functional group is a species, species life stage, or group of species, that have similar life history characteristics and roles in the ecosystem. All biomasses are in g/m2 (equivalent to metric tons/km2) and all rates are annual. Ecopath is able to solve the resulting system of *n* linear equations for *n* unknowns, which means that the user leaves one parameter undefined for each functional group. In practice, this is often the ecotrophic efficiency (*EE*).

Ecopath also allows for separation of functional groups into more than one life history stage, referred to as “stanzas.” In this case, the user defines the production to biomass ratio for all life stages, the von Bertalanffy growth rate parameter, and the consumption to biomass ratio and biomass for a single “leading” stanza that is best informed by data. Ecopath then fills in the remaining parameters by assuming a stable age distribution and a cubic relationship between length and biomass.­

Our mass-balance model is generally based on Barataria Bay and the broader Mississippi Delta (Fig. 1). Most parameters are based on de Mutsert et al. (2017) which described the estuarine waters around the Mississippi Delta and was, importantly, parameterized for a baseline prior to the Deepwater Horizon oil spill. However, a new assessment of resident dolphins in Barataria Bay has since been completed indicating dolphins are over an order of magnitude more abundant than originally thought (McDonald et al. 2017). In addition, we included several more predatory species in our model than de Mutsert et al. (2017): gars, stingrays, and diving birds (previous seabird densities were based only on pelicans). This led to difficulty balancing the model, and there was not enough biomass of certain fish species to sustain predator populations. This is likely due to predator biomasses being based on assessments, which are close to a full census, while fish biomasses were based on fishery-independent surveys conducted by the Louisiana Department of Wildlife and Fisheries (LDWF) with much lower catchabilities. In order to balance the model, we increased biomasses of X from de Mutsert et al. (2017). Alternatively, we tried quadrupling biomass of all species sampled by LDWF surveys (i.e., assume 25% catchability across all functional groups with biomasses informed by LDWF sampling), but this led to an overabundance of fish species, and the lower trophic levels that fish consumed became unbalanced.

Saving in case this is useful: (Loesch et al. 1976) found 25-33% catchabilities for many species in this habitat.

*Direct impacts of fishing and predation*

We first quantified the total fraction of mortality to each of our five functional groups (both juvenile and adult stanzas for: Panaeid shrimp; blue crabs; Atlantic croaker, spot, and silver perch; red drum; and gulf menhaden) that arose from 1) fishing, 2) dolphins, 3) pelicans, and 4) diving birds (generally gulls, terns, and frigate birds). We chose the five key functional groups because research has shown that the abundance of these fish and invertebrate groups was relatively steady following the oil spill and they represent some of the most important functional groups in the system, both ecologically and socially (Fodrie et al. 2014, Ward et al. 2018). If fishing or predation is a key component of mortality for these groups, we would expect these fish and invertebrate populations to increase in abundance following the substantial declines in fishing effort and predator abundance following the spill. Because few population increases occurred, if fishing or predation is a key component of mortality for these groups, we consider this evidence that oil-induced mortality did occur, but was simply compensated for by temporary reductions in other mortality sources. This approach uses the food web model as a repository of information on plausible stocks and flows of biomass, but does not take advantage of its network structure.

The mortality rate of group *i* from fishing is calculated as: . The mortality rate of group *i* induced exclusively by predation from group *j* is calculated as: . Because each fish and invertebrate group has a different natural productivity, we standardized these mortality rates by dividing by *PBi*. This gave us a metric for the total proportion of annual mortality arising from each source.

*Generalized equilibrium model*

One benefit of food web models is they account for all energy pathways when considering the impacts of stressors to the system (Fleeger 2020). For example, lower marine mammal abundance may benefit small-bodied fishes due to reduced predation, but if marine mammals also consume larger mesopredators of small-bodied fishes, the net result of lower marine mammal abundance becomes unclear. While the previous analysis provided a coarse examination of how populations may respond directly to changing fishing and predation patterns, we wanted to also consider these indirect pathways.

Rather than project a single possible manifestation of the food web forward through time with high uncertainty, we instead focused on how the food web would respond to perturbations within the neighborhood of its current assumed equilibrium. We did this assuming uncertainty in 1) predator-dependence of the feeding functional response, 2) prey-dependence of the feeding functional response, and 3) density-dependence of the mortality not captured by fishing or predation. We note that in Ecosim, the standard process for projecting Ecopath models through time, users do not have the option to define all of these terms.

To overcome this limitation, we used our Ecopath model to parameterize the generalized equilibrium model described in Essington & Munch (2014). We calculated the derivative of biomass of each fish or invertebrate functional group with respect to total fishing mortality and the derivative of biomass with respect to the per capita growth rate of each predator group. The generalized model describes a system near equilibrium (total biomass produced equals total mortality), so we can quantify how populations may respond to perturbations. The generalized equilibrium model assumes that the per capita rate of population change of group *i*, *ri*,as a function of the vector of biomass for all functional groups, ***B***,is:

In equation (2), the first term describes biomass gains from consumption, the second term describes biomass loss from predators, and the third term is other mortality (not fishing or predation). *GCEi* is the gross conversion efficiency of group *i*, or the production to consumption ratio (*GCEi = PBi*/*QBi*). The parameter *γi* dictates the density-dependence of the other mortality (e.g., disease, predation and fishing outside model domain, senescence) and is drawn from a random distribution (Table 1). *M0,i* scales the other mortality and is solved for using the Ecopath biomass and mortality rate accounted for by the ecotrophic efficiency term. Notably, the generalized equilibrium model described by equation (2) does *not* include a dynamic relationship between juvenile and adult functional groups.

The functional response *fij(Bi, Bj)* in equation (2) describes the per prey consumption rate of prey *i* by predator *j* and is approximated as:

where *αij* is the effective search and capture rate of predator *j* on prey *i*, *θij* describes the prey dependence (from *θij* = 1 as a linear response to 0 as a fully saturated response), and *εij* describes the predator dependence (also between 0 and 1). The parameters *θ* and *ε* are drawn randomly from distributions for each predator-prey pair (Table 1), and *α* is solved for using the values at Ecopath equilibrium for biomass and predator consumption.

Given equation (2), the rate of total population change can be described as:

where *Ci* is again catch of group *i*. In order to determine the ecosystem’s expected reaction to predator mortality and fishery closures we calculated two quantities: 1) where *E* is relative fishing effort compared to the effort at mass balance equilibrium (i.e., we calculate the derivative at *E* = 1) and 2) for *j* as the index for pelicans, diving birds, and dolphins. This second partial derivative will tell us the influence of pelicans, birds, and dolphins on population dynamics. To calculate these derivatives, we introduce ***J****r(****B****)* as the Jacobian of the per capita production rate, or the matrix of all partial derivatives . Then, based on calculations summarized in Essington & Munch (2014):

And

where ***s*** is the selectivity vector such that *siE = Fi* and *Fi* is the fishing mortality rate of group *i*. This allows us to assess a proportional decrease in fishing across functional groups, accounting for the fact that some species experience higher fishing mortality rates than others. We standardize these derivatives by biomass of the fish or invertebrate functional groups, and, in the case of the response to predator declines, with respect to predator productivity. This yields a proportional change in biomass of the prey group for a proportional change in fishing effort or predator productivity. Here, we report the change in biomass per 10% change in fishing effort or predator productivity, to balance 1) the fact that the quantities we calculate are to be interpreted within a “neighborhood” of equilibrium with 2) the major proportional changes observed following the oil spill, particularly with respect to fishing (100% decline lasting one year).

Results

Our Ecopath model contains five functional groups for primary producers, 31 functional groups for consumers, (14 of which are broken up into juvenile and adult life stages), and one detrital group (Table 2). Trophic levels ranged from one (primary producers) to 3.86 (adult sharks) with an average trophic level of 2.46 and a biomass-weighted average of 3.10.

Fishing was a major source of direct mortality for the adult stanza of the menhaden (), blue crab (), and panaeid shrimp () functional groups (Fig. 2). While the fishing mortality rate on the federally managed stock of panaeid shrimp in the Gulf of Mexico is much higher than represented in our model (cite stock assessments), the bulk of the Gulf shrimp fishery occurs farther offshore than the estuarine waters modeled here. This also means that the heavy bycatch mortality rates many fish species experience as a result of the Gulf shrimp fishery are also outside the domain of this model.

Only dolphins exerted a significant amount of direct predation mortality on the species we examined (Fig. 2). Dolphins inflicted particularly high mortality for the functional group representing Atlantic croaker, spot, and silver perch, where dolphins accounted for approximately 50% of the mortality of both the adult and juvenile life stages. Dolphins also represented an important mortality source for adult menhaden and juvenile red drum. While the species here represent important diet items for some seabird species, seabirds are not abundant enough in our model to exert substantial mortality on the populations.

The more integrative generalized equilibrium model confirmed results from the direct mortality sources, but also illustrated cases where indirect interactions may be important factors. Adult blue crab and adult menhaden showed large positive responses to reductions in fishing effort, and adult panaeids showed small positive responses, all with relatively low uncertainty, consistent with the results from only the direct impacts (Fig. 2b). Adult and juvenile croaker, spot, and perch showed large positive responses coincident with reductions in dolphin survival, though there was more uncertainty, also in alignment with the direct mortality results (Fig. 2a). As with the direct analysis, seabirds were not a major factor. Thus, when direct impacts are substantial, they tend to dominate over indirect impacts, and quantifying only direct impacts is a useful first-order exploration.

Our inability to accurately quantify functional responses leads to high uncertainty in how groups less impacted by direct mortality will respond to oil spill-induced changes in the ecosystem. Surprisingly, for six functional group stanzas, the median response to decreased dolphin survival was actually a decrease in biomass, presumably due to release of key mesopredators (Fig. 2a). Five functional group stanzas also had negative median responses to reduced fishing pressure, due to similar indirect effects (Fig. 2b). However, for many of these groups, the 50% simulation interval also includes positive responses. In fact, the 80% simulation interval (not plotted because its wide range obscures the bar heights) contains zero for all ten functional group stanzas and all three predators with the exception of a slight positive response of adult menhaden to diving bird mortality. In response to fishing, only blue crabs and menhaden, the two targets of major commercial fisheries within the model area, and adult red drum, which has no direct fishing mortality in this model (recreational catch targets juveniles), had 80% simulation intervals that did not overlap zero. Thus, with the single exception of adult red drum, while some parameter combinations simulated qualitatively “significant” responses to changing fishing pressure, these responses were highly variable and depended on the particular set of functional responses.

Discussion

Both predator release and fishery closures can explain compensatory responses of certain nearshore fish and invertebrate populations to the Deepwater Horizon oil spill, and such populations may have experienced oil-induced mortality that was masked by these ecosystem processes; however, fishery closures were likely the more significant factor. Based on the direct analysis, fishing and consumption by top predators both accounted for up to ~50% of mortality of different groups; based on the integrative analysis, 10% changes in fishing effort led to larger responses than 10% changes in predator survival. Considering that the oil spill caused much larger changes in fishing effort than in predator survival, we conclude that, while both mortality sources may be responsible for some compensatory responses of fish and invertebrate populations to the Deepwater Horizon oil spill, fishing likely played a stronger role.

* Model caveats- uncertainty we found that is buried in other models
* There is a paper that concluded that a bumper year class of menhaden was due to predator release specifically from pelicans. Need to explain that.
* Other ecosystem modeling in response to oil spill (Atlantis model, a study from the NRDA in some weird modelling software the EPA uses)
* Other approaches that could be used to answer this question. Benefits of this approach. (The importance of functional responses in driving some results seems like an important revelation.)
* Your ideas?
* Grand conclusion. Last paragraphs are the worst. Go back to hypotheses, where this this paper leave us?

Other notes with more recent citations:

Zooplankton community also had no noticeable changes beyond natural variability (Daly et al. 2021)

“Knowledge of indirect effects is essential to improve understanding of the potential for chemical harm in natural systems. For example, indirect effects may confound laboratory-based ecological risk assessment by enhancing, masking, or spuriously indicating the direct effect of chemical contaminants.” (Fleeger 2020)

“The nektonic food web in this region is flexible to disturbance and likely has redundant energy pathways explaining the reported ecosystem resilience to the DWH spill. We show that an ENA, when applied to multiple levels of ecosystem hierarchy, may aid understanding of marine food web resilience.” (Lewis et al. n.d.)

Found increase in nekton biomass during the years immediately following the spill and community composition change related to increase in specific species, coastal AL and MS, mechanisms unclear. (Martin et al. 2020)

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