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## Using Ecosystem-Based Modeling to Describe an Oil Spill and Assess the Long-Term Effects

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Using Ecosystem-Based Modeling to Describe an Oil Spill and Assess the Long-Term Effects

by

Lindsey N. Dornberger

A dissertation submitted in partial fulfillment  
of the requirements for the degree of  
Doctor of Philosophy in Marine Science  
with a concentration in Marine Resource Assessment  
College of Marine Science  
University of South Florida

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## **Abstract**

The goal of the research conducted in this dissertation was to define and test methods to incorporate oil spill effects into an ecosystem-based assessment model. It was instigated by the Deepwater Horizon oil spill, an unprecedented oil spill in the United States for both depth and volume, with unknown implications for the health of the region. Using an ecosystem-based assessment model like Atlantis, with integrated oil spill dynamics, was the ideal candidate to predict long-term impacts such as decreased abundance or population recovery time. However no previous methodology existed for doing so in any ecosystem-based assessment model. Therefore, first I conducted a literature review to gather data across fish species on lesion frequency and fish body growth impacts from oil exposure. The two data sets were then fitted to four different dose-response models, and an effect threshold log-linear “hockey-stick” model was selected as the best fit and most parsimonious for both lesions and growth. Next, I conducted a similar analysis comparing macrofaunal and meiofaunal abundances to oil exposure concentrations in the Gulf of Mexico collected after Deepwater Horizon. I confirmed that these data had the domed relationship between invertebrate abundances and oil concentration observed in previous invertebrate oil studies. This domed relationship indicates that abundance increases at low to moderate oil levels, and declines at high oil levels. To drive this relationship in an Atlantis ecosystem model, three scenarios were tested in combination with oil toxicity: 1) Mississippi nutrient loading, 2) increased detritus from marine oil snow sedimentation and flocculent accumulation, and 3) predators altering their behavior to avoid oil exposure. At the Atlantis polygon resolution, only scenario 2, increased detritus from marine oil snow



sedimentation and flocculent accumulation, generated the domed relationship for invertebrate abundances. Lastly, the “hockey-stick” model for fish mortality and growth was applied to both fishes and invertebrates in combination with scenario 2 for an integrated long-term assessment of the Gulf of Mexico. Newly available fish exposure data were used to generate an uptake-depuration model for this assessment. The combined effect forcings on vertebrates and invertebrates proved to have more severe long-term implications on population size and recovery than simulations with only fish forcings. Large demersal fishes, including elasmobranchs, were the most severely impacted by large biomass declines in the model spill region. Sensitivity analyses indicated that there was the potential for no recovery during 50 years of simulation in the spill region for many functional groups. Analysis of the synergy between fishing mortality  $F$  and toxicity from an oil spill identified that some guilds are more sensitive in an oil spill simulation to varied  $F$  than others. Snappers are the most sensitive to increased fishing mortality, while groupers respond the most to a reduction in fishing mortality. The invertebrate guild and small pelagic fishes responded the least to different values of  $F$ . Changing  $F$  also had implications for guild recovery – some guilds only fully recovered to control scenario biomass when  $F$  was reduced. A few functional groups were unable to survive with the combined effects of oil toxicity and increased  $F$ , and went extinct before the end of the 50-year simulation. Overall, this work provided the first framework for initial integrated modeling of oil spill impacts in an ecosystem-based assessment model, a potentially important component to future ecosystem-based fisheries management. The “hockey-stick” dose response model is applicable beyond Atlantis modeling, and can be tuned to fit specific events based on available data. I have also identified the importance of including marine oil snow sedimentation and flocculent accumulation to accurately drive the response of benthic invertebrates. Findings from the

combined vertebrate and invertebrate simulations should help inform research efforts in the Gulf of Mexico and future oil spill response efforts.

## **Chapter One: Introduction**

Ecosystem-based fisheries management (EBFM) has been hailed as the future of fisheries management for decades (Knecht & Cicin-Sain, 1993; Grumbine, 1994; Griffis & Kimball, 1996; Costanza et al., 1998; Link & Browman, 2014; Marshall et al., 2017; Levin et al., 2018). It offers a holistic approach to resource management with the goal of sustaining ecosystem health (Pikitch et al., 2004), accounting for population drivers beyond single species dynamics. These drivers can include competition, predation, anthropogenic impacts, and environmental conditions. EBFM is also a useful tool for managing multiple fisheries with interacting target species, and accounts for the compounding effects of fishing and environmental factors to maximize system health (Pikitch et al., 2004; Plagányi & Butterworth, 2004).

EBFM is widely acknowledged as a necessary tool for modern fisheries management (Pikitch et al., 2004; Murawski, 2007; Engler, 2015; Patrick & Link, 2015), but the scope of EBFM makes implementation more difficult than a single species approach (Browman & Stergiou, 2004; Plagányi & Butterworth, 2004; Curtin & Prellezo, 2010; Cowan et al., 2012). EBFM requires the ability to accurately collect and analyze more data than is needed for single species efforts (Hilborn, 2011; Cowan et al., 2012; Walther & Möllmann, 2014). In addition, it is constrained by the ability of the managing body to accurately interpret results, understand the limitations of outputs, and appropriately implement into policy the outputs of EBFM (Leslie et al., 2008; Jennings and Rice, 2011; Berkes 2012). Despite international calls for EBFM implementation (Ministry of the Environment, 1997; Ecosystem Principles Advisory Panel, 1999; World Summit on Sustainable Development, 2002; United Nations Environment

Programme, 2006), common misconceptions regarding EBFM still exist (Murawski, 2007; Patrick & Link, 2015) and implementation is not wide-spread.

Where feasible, the benefits of using EBFM are clear. EBFM additionally works to reconcile the needs of other human sectors of the system, including tourism, water management, and oil and gas activity and related potential spill events. As oil exploration and drilling move into deeper water and new environments, the ability to understand the impact of an oil spill is a prime example of an event with ecosystem level implications. Using ecosystem-based assessment tools to determine the impacts of these events could provide the same beneficial insights as using EBFM instead of a single species approach. Ecosystem-based models are useful, but underutilized, tools to assess impacts of an oil spill. Not only can these models be tuned to match the current state of the system, but they can project possible future states, test different management strategies, and predict potential outcomes of disturbance events (Christensen & Walters, 2004; Plagányi & Butterworth, 2004; Fulton et al., 2011, 2014). Importantly, ecosystem models can help amalgamate and synthesize research after oil spills (Okey & Wright 2004; Ainsworth et al. 2018).

Mass data collection and research efforts were instigated in response to the unique and extensive Deepwater Horizon (DwH) oil spill, which make it an ideal candidate for end-to-end ecosystem modeling efforts. On April 20<sup>th</sup>, 2010, the MC252 Macondo well site (also known as DwH) blew out after the platform exploded, killing 11 people. As previously used methods of halting the flow of oil failed (Lubchenco et al., 2012), unprecedented amounts of oil were released into the GoM from a depth of 1500 meters. Eventually the wellhead was capped on July 15<sup>th</sup>, 2010. Over the course of 87 days, Griffiths (2012) estimates 4.6 million barrels of oil flowed into the GoM, though according to the US v. BP trial (2015) that value is 3.19 million

barrels. Both estimates set the DwH event as the largest oil spill in US history, and it is also unprecedented both for its depth (greater than 1000m) and the use of dispersants at the wellhead (Kujawinski et al., 2011). This combination of factors resulted in a deep-sea plume of oil within which up to 35% of the released hydrocarbons were trapped (Griffiths, 2012; Ryerson et al., 2012) with unknown persistence time (Peterson et al., 2012).

Satellite imagery revealed that oil covered a surface area of 68,000 square miles (Norse & Amos, 2010). The surface oil interacted with marine snow and mineral particles to form heavy aggregates (Passow et al., 2012; Daly et al., 2016) that resulted in a rapid pulse of sedimentation – a process now known as Marine Oil Snow Sedimentation and Flocculent Accumulation (MOSSFA, Daly et al., 2016) -- that exceeded background levels (White et al., 2012; Montagna et al., 2013; Valentine et al., 2014; Brooks et al., 2015; Chanton et al., 2015; Romero et al., 2015). It appears that 0.5-47% of the oil spilled reached the seafloor through this process (Valentine et al., 2014; Chanton et al., 2015; Romero et al., 2017), the value range being a result of different regional deposition.

These different components of the oil spill covered a vast extent of the northern GoM ecosystem, with the potential for wide-reaching ecological impacts. Toxicological impacts have been found in communities ranging from microbial and planktonic (Bælum et al., 2012; Almeda et al., 2013, 2014) to fishes (Murawski et al., 2014; Tarnecki & Patterson, 2015; Herdter et al., 2017) and to charismatic megafauna and top predators (US Fish and Wildlife Service, 2011, Henkel et al., 2012; Haney et al., 2014). The massive research response to the DwH event provides the opportunity to collaborate across disciplines and use the data collected in an ecosystem-based modeling effort. Ainsworth et al. (2018) reported on impacts on fishes from the DwH oil spill based on an Atlantis model. Toxic effects on fish health and growth were added to

the model following Dornberger et al. (2016), as well as emergency fisheries response closures, in order to estimate potential long-term effects of the oil spill in the GoM ecosystem. Other research efforts are also ongoing to use ecosystem models to describe the DwH event, including another Atlantis model of the northern GoM (Gosnell, S., unpublished data) and an Ecopath with Ecosim model of the GoM (Rohal, M., unpublished manuscript).

This dissertation focuses on informing ecosystem-based modeling efforts of oil spills and describes potential long-term impacts and recovery time from the DwH event. Chapter 2 describes methods for modeling how individual organism-level fish health effects of oil exposure contribute to effects a population level across a continuous exposure spectrum. Here, I explored the dose-response relationship of oil exposure on both body growth and mortality, using lesion prevalence as a measure of declined health that would result in a higher mortality rate. The coauthors of this publication provided helpful insights on methods improvement and overall feedback. This manuscript was published in the journal *Marine Science Pollution Bulletin* (Dornberger et al., 2016). Towards a holistic approach, I designed Chapter 3 to first assess the relationship between benthic invertebrate abundance and oil exposure, and then determine if the resulting relationship could be driven in Atlantis using external forcings. After confirming that benthic invertebrate abundances sampled in the GoM indicated a domed shaped relationship with oil (data from Montagna et al., 2013), three forcing scenarios were tested in combination with toxicity in Atlantis. I determined that it was feasible to drive both abundance increases and toxicity in benthic invertebrate populations, using detrital forcings to represent MOSSFA organic enrichment. For the final chapter, the results from Chapters 2 & 3 were input into the Atlantis model for a combined higher and lower trophic level view of the DwH impacts on the system. Oil toxicity parameters and sediment exposure estimates of fishes and invertebrates were varied

in sensitivity analysis, and four different fishing efforts assessed to observe the combined impact of fisheries management and oil impacts.

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## **Chapter Two: Developing a polycyclic aromatic hydrocarbon exposure dose-response model for fish health and growth**

### 2.1 Note to reader

Appendix A - *Developing a polycyclic aromatic hydrocarbon exposure dose-response model for fish health and growth* presents research published in the journal *Marine Pollution Bulletin*. A full reprint is available in Appendix A with permission from Elsevier. The original text is available here: <https://doi.org/10.1016/j.marpolbul.2016.05.072> . All authors (Lindsey Dornberger, Cameron Ainsworth, Stephen Gosnell, and Felicia Coleman) worked together equally to conceptualize this manuscript. Literature review and data collection were designed by LD and SG. Analytical methods, including model design and testing, were developed by LD, CA, FC, and SG, and were conducted by LD. LD wrote the manuscript and generated all tables and figures. All authors edited the manuscript during the preparation and publication process.

### 2.2 Research overview

I generated a continuous, multi-species dose-response model for fishes exposed to petrogenic polycyclic aromatic hydrocarbons (PAHs). First, I conducted a comprehensive literature review and collected published data sets describing the health effects of petrogenic PAH exposure on fishes. I selected two health effects for dose-response modeling: growth and mortality. Before testing dose-response models, I compared the exposure medium of the collected data sets by generating the ratio of the effect observed to the log of the exposure value. I compared the source effect across nested mixed-effect models fit using  $X^2$  tests. For mortality, exposure mediums were not significantly different, so the data could be combined for dose-

response model analysis. Growth analysis indicated the sediment and water exposure mediums were not significantly different and could be combined, however food exposure was significantly different and had to be assessed separately. I fit four models (linear, step-wise, exponential, and “hockey-stick) to all three data sets using nonlinear least squares. Then I used Akaike Information Criterion to identify the most parsimonious model for both mortality and growth. The “hockey-stick” model was the best fit and most parsimonious in all settings. The results of this chapter were used to describe oil spill simulations in the Atlantis modeling framework.



## **Chapter Three: Simulating oil-driven abundance increases and toxicity in benthic marine invertebrates using the Atlantis modeling framework**

### **3.1 Introduction**

Between April 20<sup>th</sup> and July 15<sup>th</sup>, 2010, the Deepwater Horizon (DwH) oil spill in the Gulf of Mexico (GoM) released an estimated 4.6 million barrels of oil (Griffiths, 2012). Mitigation actions taken to reduce the impact of the spill included significant releases of freshwater from the Mississippi River, surface oil burns, and dispersant applications at the surface and wellhead (Kujawinski et al., 2011; Lubchenco et al., 2012; McNutt et al., 2012). The freshwater outflow from the Mississippi River -- a large source of sediment and particulates in the region (Corbett et al., 2006; Bianchi et al., 2007) -- was elevated above normal levels between May and October 2010 in an attempt to flush oil from the Mississippi delta and coastline (Bianchi et al., 2011; Kourafalou & Androulidakis, 2013). The increased Mississippi flow contributed to significant deposition of sediment and hydrocarbons near the De Soto Canyon and in other areas (White et al., 2012; Montagna et al., 2013; Valentine et al., 2014; Brooks et al., 2015; Chanton et al., 2015; Romero et al., 2015). The mass sediment flux to the seafloor is from marine oil snow formation during and after the spill (Brooks et al., 2015) through a pathway now known as *Marine Oil Snow Sedimentation and Flocculent Accumulation* (MOSSFA; Daly et al., 2016). Indeed, 0.5-47% of the oil spilled sedimented to the seafloor (Valentine et al., 2014; Chanton et al., 2015; Romero et al., 2017) in a spotty distribution across the continental shelf, slope, and onto the deep ocean seafloor. This key pathway is important in extrapolating effects to unsampled areas, and in determining the impacts of this spill on the

benthic community in the GoM. Potential effects include direct toxicity from crude oil and its by-products, smothering, shading, and anoxia. With the potentially large volume of oil that reached the seafloor, chronic effects could occur in the sediment, as well as in demersal communities due to resuspension of oil from disturbance events.

Montagna et al. compared effects of oil release on meiofauna and macrofauna communities at the DWH wellhead and at natural seeps in the same vicinity. What they found were diversity reductions in soft-bottom benthic meiofauna and macrofauna in the 24 km<sup>2</sup> surrounding the DWH wellhead, with more moderate effects observed as distance from the wellhead increased. They correlated this effect with oil indicators and distance from the wellhead. No comparable correlation was found associated with natural hydrocarbon seeps. A follow-up study conducted the subsequent year revealed persistent contamination and continued declines in richness and biodiversity (Montagna et al., 2017). This result suggests that the system had persistent community structure shifts within that time frame of these two studies.

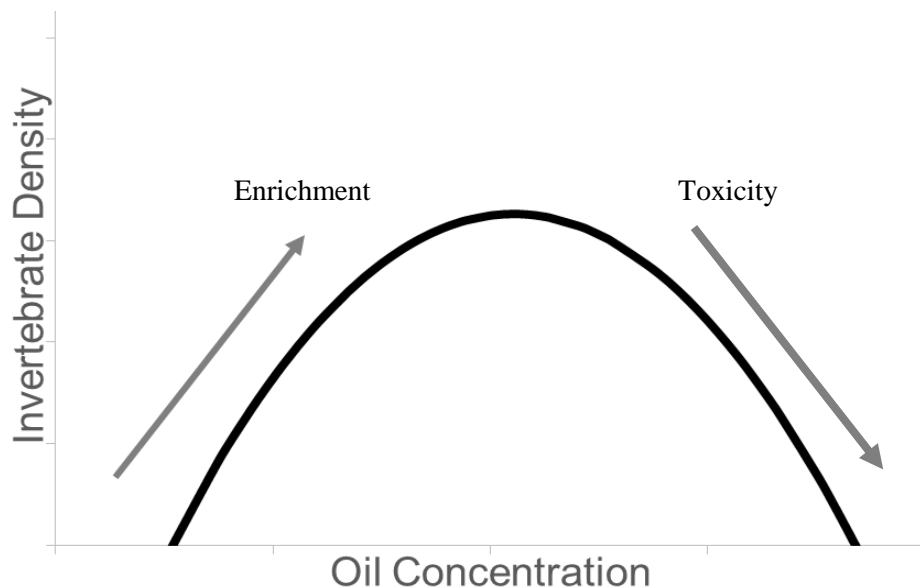
These benthic habitats are important repositories of biodiversity (Hessler & Sanders, 1967; Grassle & Maciolek, 1992), and changes in community structure can have effects across the marine food web. The direct and indirect effects of oil exposure on benthic-dwelling organisms varies with species group and habitat, with sessile and relatively sedentary organisms more affected in soft sediment habitats, and more mobile invertebrates affected most on rocky shorelines (Suchanek, 1993). Fishes are negatively affected by oil toxins, such as polycyclic aromatic hydrocarbons (PAHs), which can reduce growth and fecundity in fishes, and are correlated with increased prevalence of lesions and cancers (Collier et al., 2013; Murawski et al., 2014; Vignet et al., 2014; Brown-Peterson et al., 2015; Hedgpeth & Griffitt, 2016; Herdter et al., 2017). Oil spills add to the chronic oil toxicity burden as oil settles in the sediment and

resuspension of contaminated sediments occurs from disturbance (Latimer et al., 1999; Yang et al., 2008; Roberts, 2012).

Some populations of organisms may actually benefit from oil exposure through organic enrichment of the food web (Jewett et al., 1999) or other mechanisms. Studies of natural oil seeps reveal toxic effects of exposure on benthic invertebrates within seeps, but microbial and meiofaunal enrichment at seep peripheries (Montagna & Spies, 1985; Montagna et al., 1986, 1987). These findings led to the exploration of toxicity vs. enrichment in relation to oil. The pioneer experiment by Spies et al. (1988) examined dose-responses of meiofauna and macrofauna abundance in sediments containing various concentrations of oil with supplemental kelp. They found a pronounced domed response in macrofauna, with abundance highest at low concentrations of oil, and declining as oil concentrations increased (Figure 3.1). They determined that direct oil exposure had little effect on meiofaunal abundance, though other studies had shown loss of individuals from oil (Ustach, 1979; McLachan & Harty, 1982; Frithsen et al., 1985).

Additional studies have found similar domed-shaped relationships (Figure 3.1) in relation to natural oil seeps (Montagna et al., 1986; Palmer et al., 1988; Montagna et al., 1995). A leading explanation is that in the presence of oil, the abundance of oil-degrading microbes increases, providing additional food for meiofauna, which, in turn, are food to macrofauna (Olsgard & Gray, 1995; Steichen et al., 1996; Peterson et al., 1996; Jewett et al., 1999). Top-down shifts through fish physiological (e.g., reduced growth and fecundity, increased mortality; cite papers) and behavioral (e.g., avoidance, migration; Rice et al., 1976; Gray, 1990; Martin, 2017; Ainsworth et al., 2018) responses to oil exposure could indirectly boost benthic invertebrate abundances through predation release or diet shifts. Specific to the GoM and DwH, common fish

invertivores of interest include grunts (family Haemulidae), porgies (family Sparidae), snappers (family Lutjanidae), and triggerfish (family Balistidae) (Dance et al., 2011).



*Figure 3.1 A conceptual model of the potential domed relationship between invertebrate abundance and environmental oil concentration*

This study aimed first to explore whether a domed relationship (Figure 3.1) existed between benthic invertebrates in the GoM and the DwH oil. To do so, I examined sediment core data (Montagna et al., 2013) from the northern GoM (nGoM). Secondly, I tested the possible relationships between benthic invertebrate abundance and sediment oil concentration in an end-to-end ecosystem model. The model framework selected for this study was Atlantis (Fulton, 2001; Fulton et al., 2004a, b, 2005, 2007), which is being used by others in simulations of GoM ecosystem response to the DWH event (Ainsworth et al., 2018), and in ongoing work to model the Ixtoc oil spill (Ortega-Ortiz, J., unpublished manuscript).

I use Atlantis to examine the conditions that could create an increase in invertebrate macro- and meio-faunal abundances at low to intermediate oil concentrations. Three hypotheses

are tested: 1) Mississippi nutrient loading, based on the flushing of the Mississippi river (Bianchi et al., 2011) stimulated primary production at the surface (O'Connor et al., 2016); 2) increased detritus from MOSSFA (Brooks et al., 2015; Romero et al., 2015) stimulated the benthic food web; and 3) predators altering their behavior to avoid oil exposure (Rice et al., 1976; Gray, 1990; Martin, 2017; Ainsworth et al., in 2018) reduced predation mortality on invertebrates. Scenario 1 would stimulate a primary production based food web, scenario 2 would stimulate a detritus based food web, and scenario 3 would be a release of top-down pressure on the system. Each scenario was tested individually to determine if one scenario alone could have been the driver of the dome-shaped population response of macro- and meio-fauna, or if a combination of factors were necessary. Finally, toxicity was applied based on the dose-response model of Dornberger et al. (2016), following the methods of Ainsworth et al. (2018) in combination with each scenario.

### 3.2 Methods

#### *3.2.1 Analysis of benthic invertebrate relationship*

I used the data from Montagna et al. (2013, Supplementary Table 1), which includes cores from 68 stations in the nGoM assessed for meiofaunal and macrofaunal abundances, and other biotic and chemical data, such as total petrogenic hydrocarbons (TPH). These data were used to compare invertebrate abundances against TPH values to determine what relationships exist.

First, I examined the relationship between depth and benthic invertebrate abundances. Abundances were log transformed and regressed against depth using linear model least squares residuals. Because the negative correlations were significant (meiofauna:  $R^2 = 0.09$ ,  $p < 0.05$ ; macrofauna:  $R^2 = 0.24$ ,  $p < 0.0001$ ), I then examined two other key environmental variables: TPH and barium. TPH was the measured oil exposure variable, and barium was another potential

oil-related variable that could be used to describe the domed relationship, as it is found in relation to offshore drilling operations (Kennicutt et al., 1996). TPH and barium were tested against each other, and each were tested against depth, for redundancies in explanatory variables. The correlation between these variables was tested using the Spearman rank correlation coefficient (SRCC). Because TPH and barium were significantly positively correlated ( $\rho = 0.48$ ,  $p < 0.001$ ), I used TPH alone in model building. Depth was not correlated with oil variables, so, partial residuals were generated to remove the determined depth effect, as if depth were held constant across the data set. To preserve the appropriate scale for the abundances, the y-intercept from the depth regression was added to the depth-controlled data (Rex et al., 2006).

Then, to test the dome relationship, the depth controlled benthic invertebrate abundances were fit to four TPH models, using data points where TPH values were measured and present

$$1. \text{ constant, } \log(\textit{abundance}) = a \quad \textit{Eq. 3.1}$$

$$2. \text{ linear, } \log(\textit{abundance}) = \log(\textit{TPH}) + a \quad \textit{Eq. 3.2}$$

$$3. \text{ exponential, } \log(\textit{abundance}) = b * e^{(\log(\textit{TPH}*c))} \quad \textit{Eq. 3.3}$$

$$4. \text{ quadratic, } \log(\textit{abundance}) = b * \log(\textit{TPH})^2 + c * \log(\textit{TPH}) + a \quad \textit{Eq. 3.4}$$

Here,  $a$  represents log of abundance with no oil effect, and  $b$  and  $c$  are modifiers for the rate of change of abundance. Models 1-3 were selected as potential simpler models to describe the relationship between benthic invertebrate abundance and TPH. All models were built and fitted in R using linear model least squared residuals or non-linear least squares for both macro- and meiofauna data sets. The models were then assessed for parsimony using AIC (Akaike, 1973, 1974).

### 3.2.2 *Atlantis simulations*

Atlantis is a spatially explicit, three-dimensional, deterministic, end-to-end ecosystem model operating at 12-hour time steps (Fulton, 2001; Fulton et al., 2004a, b, 2005, 2007). The model is coupled to a hydrodynamic model that provides currents, temperature, and salinity. Hydrodynamics for the GoM model are provided by the American Seas model based on the National Research Laboratory developed NCOM model (Martin, 2000). These dynamics affect nutrient cycling, primary production, and organism physiology and distribution. Several nutrients are tracked, although nitrogen is the model's main currency (Link et al., 2011). Atlantis polygon geometry is determined based on bioregional features and fisheries management areas. Depending on depth, there are up to six water column layers per polygon, and a sediment layer. Atlantis uses 91 functional groups: 61 age-structured (AS) vertebrates and invertebrates, 19 non-age-structured invertebrates, 6 primary producers, 2 bacteria and 3 detritus. Each functional group is constrained by sub-models describing consumption, production, respiration, reproduction, and movement. Vertebrates and some exploited invertebrates are tracked by numbers and body weight, while non-exploited invertebrates are only tracked as biomass pools. The 23 invertebrate functional groups are: protists, crustose coralline algae, toxic dinoflagellates, infaunal meiobenthos\*, small zooplankton, large zooplankton, jellyfish, squid, sponges\*, sessile filter feeders\*, herbivorous echinoderms\*, stony corals\*, octocorals\*, oysters\*, bivalves\*, blue crab\*, stone crab\*, crabs and lobsters\*, carnivorous macrobenthos\*, brown shrimp\* (AS), white shrimp\* (AS), pink shrimp\* (AS), and other shrimp\* (AS). Groups with an asterisk were considered benthic associated invertebrate functional groups in Atlantis for the purposes of this study. The three detrital groups are labile, refractory, and carrion. Functional groups can contribute to detrital and nutrient pools through waste excretion, sloppy feeding, and mortality.

The detrital groups can also be defined as part of any functional groups' diet. A more in-depth review of the system equations is available in Link et al. (2011). The GoM implementation of Atlantis is described in Ainsworth et al. (2015).

To drive abundance increases in scenarios 1 and 2, point source inputs were used. For scenario 1: Mississippi nutrient loading was targeted to increase in the six polygons surrounding the Mississippi River Delta by about a factor of six, based on the observations of Bianchi et al. (2011). The silica, nitrate, and ammonium concentrations were increased when compared to non-enriched Atlantis simulations. For scenario 2: increased detrital deposition from MOSSFA had an increase in detrital loads on the seafloor by a factor of about 2-5 in the seven polygons closest to the wellhead (Brooks et al., 2015). The nutrient and detrital values were held for the duration of the oil spill, then returned to normal. For scenario 3 (predators altered behavior to avoid oil): benthic fish (predators) were removed from oiled polygons. To do so, spatial forcing files were created following the methods of Ainsworth et al. (2018) that set a spatial mortality effect proportional to the oil concentration. This approach kills predators in the system instead of relocating them to non-oiled areas, but it should result in a similar effect as predator behavioral changes would have on mortality rates of benthic invertebrates. The predator mortality forcing lasted for the duration of the oil spill. Functional groups were considered a benthic predatory fish if their diet consisted of 20% or more from the benthos.

Each of these three scenarios were used in Atlantis individually, in the absence of oil toxicity, to determine if they were capable of inducing benthic invertebrate abundance increases. Abundance increase was determined by comparing the scenarios to a control simulation at the polygon level. Once determined that a scenario could independently cause abundance increases, it was used in conjunction with oil concentration estimates from Lagrangian oil transport model



(Paris et al., 2012; Aman & Paris, 2013). Toxicity spatial forcing was generated for the 17 benthic associated invertebrate functional groups, following the hockey-stick methods of Dornberger et al. (2016) and Ainsworth et al. (2018). This hockey-stick function assumes that oil concentrations below a defined threshold will have no impact on the population, and above that threshold mortality will increase log-linearly. Since the initial dose-response hockey-stick relationship was developed for fishes, multiple iterations of each scenario containing toxicity were run, varying the threshold that determines when toxicity effects begin to occur. Thresholds tested were 100 ppb, 200 ppb, 300 ppb, 500 ppb, 1000 ppb, 2000 ppb, and 3000 ppb. The water column far field oil model was compared to sedimentary oil data (Romero et al., 2015, 2017) to create an approximate oil concentration in the sediment covering the entire oil field (Ainsworth et al., 2018). They demonstrated that the concentration factor could vary up to 1000, which was the factor used in this study. No toxicity was applied to fish functional groups to avoid confounding effects from predator death (except when used as the method for simulating predators altering their behavior to avoid oil exposure). This reductionist approach will allow us to identify more easily the mechanics at work in the invertebrate response to oil. Simulations in Atlantis lasted for one year. All scenario results were assessed using September and October 2010 outputs from Atlantis, to match the timeframe that the sediment core abundance data were collected (Montagna et al., 2013).

### 3.3 Results

#### *3.3.1 Benthic invertebrate abundance and TPH relationship*

The results of fitting the established linear model of abundance by depth (reviewed by Rowe, 1983; Rex et al., 2006) indicated that for this data set, depth had a significant ( $R^2 = 0.23$ ,  $p < 0.001$  for macrofauna, and  $R^2 = 0.09$ ,  $p < 0.05$  for meiofauna) relationship with log

abundance of both groups, consistent with past research. Correlating TPH versus Barium, the SRCC value was 0.48 and the p value < 0.001, which is why barium was excluded from further modeling efforts. For TPH and depth, the SRCC value was -0.02 and the p value was 0.87, indicating that they are not correlated variables and would act independently on abundance.

The results from the linear and nonlinear least squares fitted models for TPH against both macrofaunal and meiofaunal depth controlled abundances selected the quadratic equation as the best fit with the lowest sum of squared residuals, as well as the most parsimonious based on the AIC results (Table 3.1). The increase in macrofauna and meiofauna was apparent at low-medium oil concentrations, suggesting a domed relationship exists between oil concentration and benthic invertebrate abundance (Figure 3.2). Figure 3.2 shows abundance partial residuals after removing the depth effect, with the intercept added back to values for scale preservation.

*Table 3.1 Sum of squared residuals (SS) and AIC results for macrofauna and meiofauna invertebrate abundances.  $\omega$ AIC is the Akaike weight, which can be interpreted as the probability that the model would be the best fit under repeated sampling among all the models tested (Pechenik 1987).*

Model	Macrofauna			Meiofauna		
	SS	AIC	$\omega$ AIC	SS	AIC	$\omega$ AIC
Constant	2.542	-10.243	2.97E-05	6.310	41.313	1.22E-04
Linear	2.539	-8.311	1.13E-05	5.195	32.811	0.00859
Exponential	2.423	-10.929	4.19E-05	5.898	39.674	2.78E-04
Parabola	1.631	-31.089	1	4.197	23.296	1

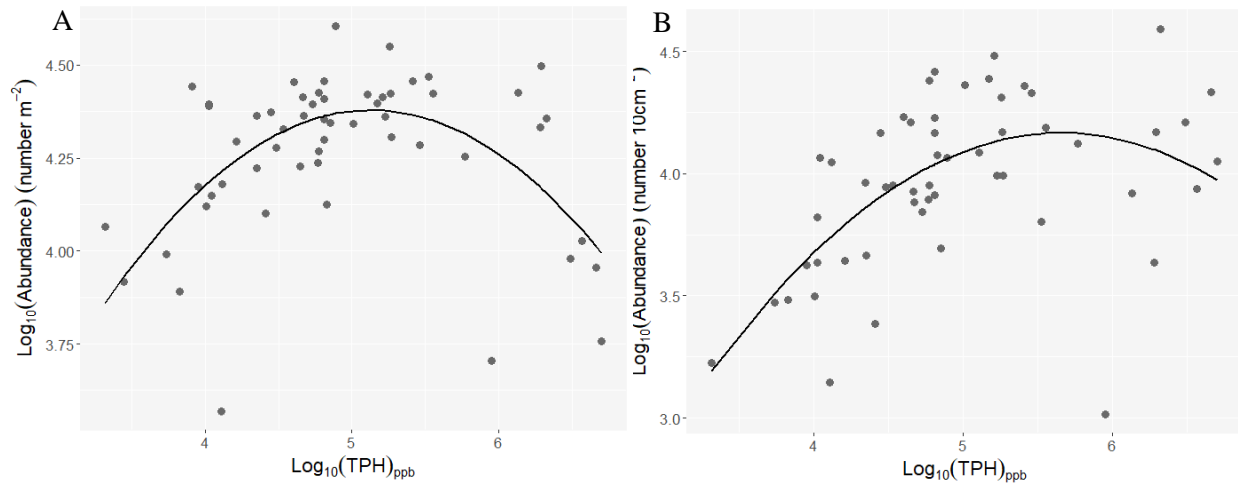


Figure 3.2 Benthic invertebrate abundances against sediment total petrogenic hydrocarbon sediment concentrations, with best fit quadratic models. Effects of depth were removed. A) Macrofaunal abundances in numbers per square meter. B) Meiofaunal abundances in numbers per 10 square centimeters. Raw data from Montagna et al. (2013)

### 3.3.2 Atlantis simulations

Comparison between the three scenarios and a control Atlantis simulation indicated that each forcing function methodology was suitable to achieve the desired scenarios in the model. For scenario 1, nutrients were elevated from 2 – 20 x control levels, in scenario 2, detrital levels were 3.5 - 6.5 x control levels, and in scenario 3, benthic predatory fish densities were reduced by 4 -290 t·km<sup>-2</sup>. Benthic invertebrate abundance increases occurred in each scenario, to varying degrees. Of the three scenarios, the smallest effect averaged across polygons was observed in scenario 1 (~0.01 t·km<sup>-2</sup> relative to an average abundance of 344 t·km<sup>-2</sup> in the control scenario) (Figure 3.3). Scenario 2 had the strongest average effect, showing a much larger response than the other two scenarios (Figure 3.3). For scenario 2, the abundance of the oyster functional group was not used to calculate this average, as it had a much stronger abundance increase than other groups. The average abundance of benthic invertebrates, excluding oysters, in the control was 133 t·km<sup>-2</sup>. Data are not shown.

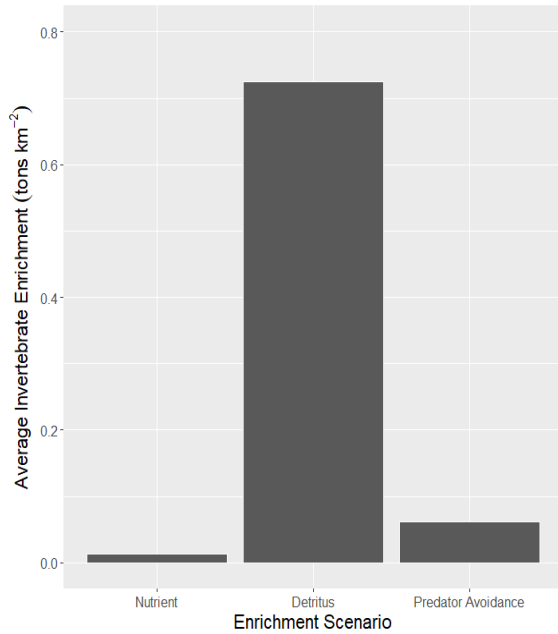


Figure 3.3 Average benthic invertebrate functional group abundance increases in scenarios 1-3 with no toxicity. The averages were calculated using the six common polygons where direct forcing occurred in each scenario. The oyster functional group was removed from the detritus scenario as an outlier.

In the three scenarios combined with toxicity, it became apparent that low threshold toxicity overwhelmed any abundance increases that had occurred without mortality forcing from oil toxicity. Of all of the 100 ppb, 200 ppb, 300 ppb, 500 ppb, 1000 ppb, 2000 ppb, and 3000 ppb threshold simulations, only scenario 2 (MOSSFA) at 3000 ppb demonstrated both increased abundances in some polygons, and toxicity effects in others (Figure 3.4). Figure 3.4 shows total benthic invertebrate biomass differences between each scenario and the control scenario. Blue polygons indicate a net increase in biomass, red polygons a net decrease, as a result of the scenario drivers. Additional scenario 1 simulations were run increasing the nutrient loading, up to thousands of times greater than control levels, however still no enrichment was apparent when toxicity was present.

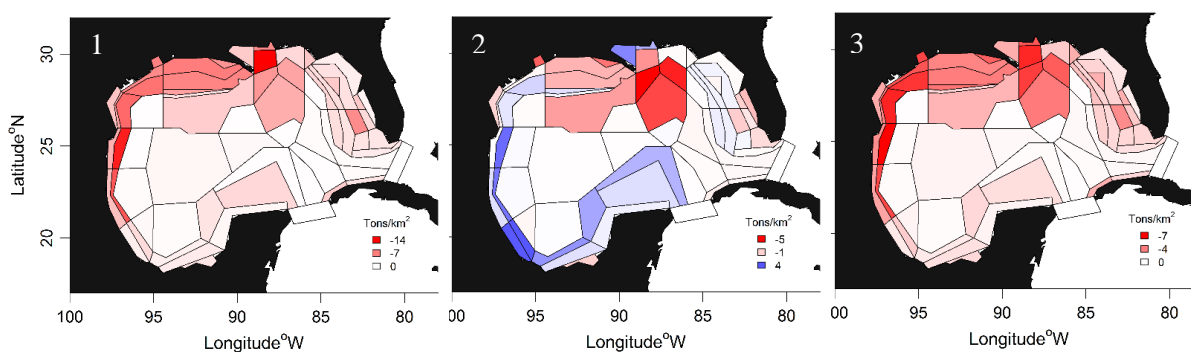


Figure 3.4 Benthic invertebrate density differences in oil scenarios 1-3 compared to a control simulation. 1) Mississippi nutrient loading and toxicity, 2) Increased detritus from MOSSFA and toxicity, oyster functional group removed as an extreme outlier, 3) Predators altered behavior to avoid oil exposure and toxicity. Results are summed across functional groups, from October 2010 in the 3000 ppb threshold simulation.

Though scenario 3 indicated slightly higher biomass increases in oil free simulations (Figure 3.3), it also did not have any polygons with net abundance increases when oil toxicity was present (Figure 3.4). Additional scenarios were run removing all fishes from the oiled region, not just benthic predators; however, both increases and declines in abundance were still not present at the polygon level except in one functional group, infaunal meiobenthos. Based on these results, only scenario 2 produced polygons representing both sides of the domed relationship. An apparent combination of increased productivity at low-med oil concentrations and toxicological mortality at high oil concentrations across benthic invertebrate functional groups is evident in scenario 2. In scenario 2, across the model, a general shift in predation occurred towards benthic invertebrates, stimulated by the addition of detritus. Within this trend however, consumption of shrimps is reduced, as the majority of their predators' (such as mullet, demersal fish, and larger crustaceans) diets shifted to other benthic invertebrate prey resources. As stimulation of the benthic detrital food web moves across the model through neighboring polygons, the blue polygons in the southwest GoM in scenario 2 are mostly a result of these shrimp biomass increases. Oysters were removed from Figure 3.4, as their biomass increase was orders of magnitude greater than other functional groups. As the only scenario indicating both

increases and decreases in abundance based on oil concentration, scenario 2 invertebrate functional groups' biomass was plotted against simulated oil exposure to determine if the expected dome shape was present. It is distinct for some groups (Figure 3.3). Other groups indicated a reverse parabola.

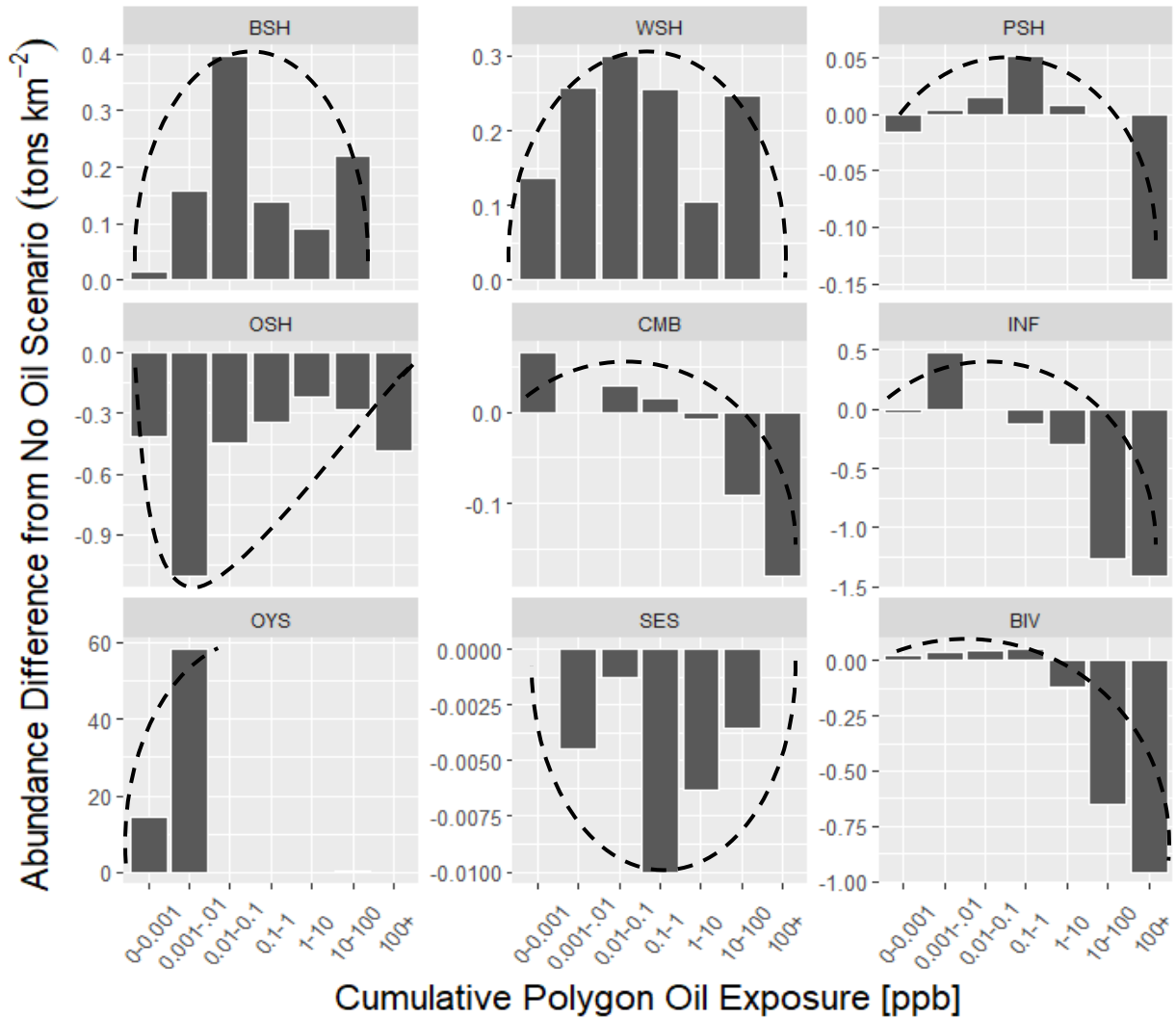


Figure 3.3 Example functional group abundance differences in detritus enrichment oil scenario. BSH – Brown Shrimp, WSH – White Shrimp, PSH – Pink Shrimp, OSH – Other Shrimp, CMB – Carnivorous Macrobenthos, INF – Infaunal Meiobenthos, OYS – Oysters, SES – Sessile Filter Feeders, BIV – Bivalves. Results from October 2010 in the 3000 ppb threshold scenario.

### 3.4 Discussion

This study aligns with previously published results indicating that exposure to low to intermediate oil levels can cause increases in some benthic invertebrate populations (Spies et al., 1988; Steichen et al., 1996; Olsgard & Gray, 1995; Peterson et al., 1996; Jewett et al., 1999). I confirmed the previously described domed relationship between benthic invertebrate abundance and oil exposure existed in the GoM after the DWH oil spill for two benthic invertebrate groups. The delayed abundance peak in the meiofaunal data set compared to the macrofaunal dataset is likely a function of top-down predation pressure on meiofauna from macrofauna.

This research was the first to examine that relationship using an ecosystem model. The three scenarios examined here (1: nutrient loading from the Mississippi, 2: increased detritus from MOSSFA, and 3: predator behavioral changes to avoid oil) were chosen to represent potential changes to the system resulting specifically from the DWH oil spill that would stimulate abundance increases in the benthos. I demonstrated that benthic invertebrate abundance increases were possible using either nutrient, detrital, or predator oil avoidance forcings. However, note that the current means of modeling predator oil avoidance make it impossible to differentiate between predator death and oil avoidance. In a true oil avoidance scenario, predators would relocate to different polygons within the model in order to evade oil. Within the limitations of the Atlantis software, benthic predators had to be completely removed from the system using the mortality forcing. The mortality and subsequent decay of the predators results in increased nutrients in polygons affected, which could be confounding the effects of predators altering their behavior to avoid oil exposure and potentially adding a second forcing through nutrient enrichment (Figure 3.3).

By combining the nutrient or detrital enrichment or predator oil avoidance forcing functions with a toxic oil field, the viability was determined for each forcing effect as the sole driver of the increased population abundance at low-med oil concentrations. Addition of nutrients at the Mississippi River delta had the smallest effect on invertebrate populations, and never produced a domed relationship in Atlantis, even at the highest nutrient levels. For this reason, scenario 1 must be eliminated as a potential driver of benthic invertebrate abundance increases in the Atlantis GoM oil spill model. This suggests that surface nutrient source input alone is not likely to explain the observed effects on benthic invertebrates from the DwH oil spill.

For scenario 3, only benthic predators were removed from initial testing to avoid confounding food web effects. Although benthic predator removal caused slightly greater increases in invertebrate abundance than scenario 1, it did not produce a domed relationship. In additional test simulations, extending the predator removal to include all fish functional groups produced increases in a single functional group, infaunal meiobenthos, while all other benthic invertebrates only showed decreases in abundance (mortality). These results indicate that benthic predators altering their behavior to avoid oil exposure is not the sole driver of benthic invertebrate abundance increases. Enrichment of the detrital food web appears to be the best candidate as a potential driver of benthic invertebrate population increase. This fits with other research indicating that increased oil provides food for microbes, which in turn provide food for meiofauna, then macrofauna (Steichen et al., 1996; Olsgard & Gray, 1995; Peterson et al., 1996; Jewett et al., 1999).

The environmental forcing functions nearly matched detritus levels sampled in the GoM (Brooks et al., 2015), and the functional group abundance increases supported the pattern seen in



the data from Montagna et al. (2013) for both macrofauna and meiofauna. However, not all macrofaunal functional groups had low oil biomass increases. The sessile filter feeders functional group indicated a reverse parabola, suggesting that there are additional food web interactions. Oysters, which had a uniquely large abundance increase, could be outcompeting the other sessile filter feeding functional group, which would otherwise benefit from increased detritus in the water. This is supported by the oyster and sessile filter feeder parameters in Atlantis GoM: oysters have a production rate (P/B) of 1.2, and a daily growth rate of 0.22%, versus sessile filter feeder's production rate of 0.8 and daily growth rate of 0.16%. Alternatively, benthic predator populations that consume the sessile group could be growing in response to increased resources from the increased detritus, and preying upon the sessile group. It should be noted that our oyster dynamic does not match observed trends. There is a documented loss of oysters since the DwH oil spill that has been attributed to low salinity from Mississippi flushing (Powers et al. 2017), an event that is not captured here. Other potential factors not represented in these simulations include bioaccumulation, the potential chemical effects of dispersants, benthic oxygen limitation, and the by-products of the surface oil burns (Kujawinski et al., 2011; Lubchenco et al., 2012; McNutt et al., 2012).

MOSSFA research has been an important component in understanding the ecosystem response to the DwH oil spill, and these results indicate that MOSSFA could provide a pathway for enrichment of benthic invertebrate abundance. In the GoM, it is possible that any or all three of these factors contributed to the relationship between benthic invertebrates and TPH. The Deepwater Horizon oil spill has shown us how oil interactions in deltaic systems can result in MOSSFA, an express pathway for surface oil to reach the benthos. In such cases, stimulation of

the detritus food web may be common and result in unintuitive and non-linear influences on benthic fish and invertebrate populations already affected by direct oil toxicity.

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## **Chapter Four: A synthesis of top down and bottom up impacts of the Deepwater Horizon oil spill using ecosystem modeling**

### ***4.1 Introduction***

The Deepwater Horizon (DwH) oil spill in the Gulf of Mexico (GoM) resulted in the largest response effort to an oil spill in US history (Levy & Gopalakrishnan, 2010; Barron, 2012), as well as a coordinated research effort by many scientists across different government agencies and research institutions to assess the state of the system (Deepwater Horizon Project Tracker, 2018). Two of the largest research collaboration efforts were initiated by NOAA's Natural Resource Damage Assessment process (NRDA) (Lubchenco et al., 2012) and the Gulf of Mexico Research Initiative (GoMRI) (Colwell et al., 2014). [Put NOAA/ NRDA first –that group started long before GoMRI.] . The NRDA process for the DwH event was the largest federal response ever undertaken, with the primary directive to determine how the event affected the GoM's natural resources, as well as the impact on human use of those resources (Lubchenco et al., 2012). The GoMRI offered competitive research grants to collaborative consortia with two goals in mind: first, to study the DwH event and its effects on the system, and second to create improvements for oil spill mitigation, detection, and remediation (Colwell et al., 2014).

These efforts have resulted in hundreds of publications describing the effects of the DwH event on various components of the system. Publications range from topically specific studies, like single species impacts, to literature reviews (e.g. Beyer et al., 2016; Daly et al., 2016). Targeted assessments provide vital information at the species level, however using single species assessments alone to attempt to determine the impact of the DwH on the health of organisms is a

limited approach, as community interactions and synergistic effects are not accounted for. There is the potential for non-linear dynamics and interactions between affected components. An ecosystem-based approach to assessing DwH can help to address these interactions (reviewed by Curtin & Prellezo, 2010), and would be a key step towards integrating the knowledge gained from research efforts.

Using oil spill data in a holistic, end-to-end ecosystem model can provide meaningful insights that inform future oil spill response efforts, as well as the end goals of both GoMRI and NRDA. Ainsworth et al. (2018), for instance, used data from DwH response efforts and other oil related studies in an Atlantis model to characterize ecosystem behavior and predict long-term effects of the oil spill on the northern Gulf of Mexico, particularly as it related to fish populations. Whereas Ainsworth et al. (2018) tested top-down effects of the oil spill on fish abundance and mortality, this study represents a synthesis of bottom-up and top-down effects across a broader range of taxa.

Bottom-up effects relate to the accumulation of detrital biomass on the seafloor as a result of marine oil snow sedimentation and flocculent accumulation (MOSSFA). MOSSFA is a transport pathway for surface oil to reach the seafloor through aggregation of oil and marine snow and subsequent rapid sinking, as was observed in the GoM after the DwH spill (Passow, 2014; Brooks et al., 2015; Romero et al., 2015). This significantly impacted the distribution of oil, and spurred researchers to examine the ecological consequences of MOSSFA on pelagic and benthic communities (Daly et al., 2016). This bottom-up driver is extremely important for DWH (Brooks et al. 2015; Daly et al., 2016; Romero et al., 2017) and representing this significant pathway of oil to the benthic community is therefore key to accurately modeling an ecosystem level response to the oil spill. In addition to MOSSFA bottom-up drivers, I used a dose-response hockey-stick

model (Dornberger et al., 2016) to drive benthic invertebrate mortality at high oil concentrations, which in combination with MOSSFA generates a domed relationship between benthic invertebrate abundance and oil (Chapter 3 Dornberger).

Research into the cumulative effects of various human stressors on fish populations has been identified as a major gap in our knowledge (Sala et al., 2003; Pew Ocean Commission, 2003; U.S. Commission on Ocean Policy, 2004; Crain et al., 2008, 2009). In particular, Crain et al. (2008) note that the absence of controlled studies assessing the combined effects of fishing and other stressors on fish populations is a particular concern. Controlled field experiments of this type are inherently difficult to perform, requiring that they be addressed using different means (Crain et al. 2009). For instance, using established ecosystem-based modeling efforts, one could not only identify the potential cumulative effects of fishing and an oil spill, but it could elucidate the synergistic effects of multiple stressors across a community of fished populations, providing critical insights for both scientists and managers. My objective in this study is to do just that, using an Atlantis ecosystem-based fishery model.

## 4.2 Methods

### *4.2.1 Atlantis*

Atlantis is a deterministic, end-to-end ecosystem model with a spatially explicit three-dimensional framework (Fulton, 2001; Fulton et al., 2004a, b, 2005, 2007). It operates at 12-hour time steps. Atlantis uses an irregular polygon structure reflecting bioregional features, and political and regulatory boundaries. Each polygon has a sediment layer and up to 6 water column layers, depending on depth of the area described by the polygon. Depth strata are consistent across polygons (z-coordinate system).

Atlantis is also coupled to a hydrodynamic model that includes currents, temperature and salinity per polygon and depth layer. For the GoM Atlantis model, the coupled hydrodynamic data are provided by the American Seas model, which is based on the National Research Laboratory developed NCOM model (Martin, 2000). Nutrient cycling and subsequent primary productivity, as well as organism distribution, are all affected by the hydrodynamic inputs. Nitrogen is used as the measure of functional group biomass and the model's main currency (Link et al., 2011), though several other nutrients are also tracked.

The GoM Atlantis model uses a total of 91 functional groups: 61 age-structured vertebrates and invertebrates, 19 non-age-structured invertebrates, 6 primary producers, 3 types of detritus, and 2 bacteria. All vertebrates and some exploited invertebrates that are age-structured are tracked in Atlantis by body weight in mg N, and number of individuals. Non-exploited invertebrates are only tracked as biomass pools in mg N. Carrion detritus, labile detritus, and refractory detritus are the three detrital functional groups. Any functional group can add to detrital and nutrient pools through mortality, waste excretion, and remnants from feeding behavior. The detrital groups can also be consumed as a defined part of any functional groups' diet. A full review of the modeling system and equations is available in Link et al. (2011). The specific GoM implementation of Atlantis and model fitting is available in Ainsworth et al. (2015). For this research project, Atlantis simulations were run for 50 years, from 2010 to 2060.

#### *4.2.2 Environmental drivers of the oil spill*

Oil concentration estimates were provided by a probabilistic framework for oil droplet-tracking based on an open-source Lagrangian stochastic model, the Connectivity Modeling System (CMS) (Paris et al., 2012, 2013; Aman & Paris, 2013). The most recent CMS simulations of the Deepwater Horizon blowout are described in an article in preparation (Paris & Perlin,

unpublished manuscript). Implementation of these oil data in Atlantis follows the methods of Ainsworth et al. (2018). Briefly, oil estimates were provided at 1/12th degree grid points and in four depth layers, averaged across 0-20m, 20-50m, 50-200m, and 200m-2000m. Dose-response calculations were made at the grid point scale and averaged over all Atlantis polygons, adjusting for the proportion of grid points per polygon that do not contain oil. Transient biomass dynamics were allowed to settle in the first 110 days of the simulation before introducing oil forcing to the model, which then lasts for 167 days.

There is not enough available sediment oil data from the field to use directly in the model as the oil driver for the sediment layer in simulations. In addition, the precise distribution, concentration, and extent of DwH oil on the seafloor is unknown. Romero et al. (2015, 2017) provided sediment core concentrations, which were then compared to estimated time- and depth-integrated water column concentrations from CMS, to establish a ratio between sediment and water column concentrations (Ainsworth et al. 2018). Using an estimated ratio between sediment oil concentrations and modeled oil values allows for the generation of an estimated, continuous sediment concentration map used to drive sediment oil toxicity. The sediment-to-water column ratio (K) is potentially up to 1000:1 (Ainsworth et al. 2018), so a K of 1000 was used as an upper limit of sensitivity analyses, along with 30%K, and 60%K values or K = 1000, 700, and 400. K plays a critical role in the impact of the oil spill on benthic organisms.

Metabolic processing of oil for all fish and benthic invertebrates was accounted for by calculating uptake and depuration rates based on data from fish exposure studies. Miller et al. (2017) exposed red drum to a CEWAF solution at 1 ppm (TPH) using Corexit 9500 and Louisiana Sweet crude oil for four days. Following the exposure, they moved the fish to tanks of untreated, clean seawater for six days. During their experiment, two fish were sacrificed every



day for the exposure period, then every other day during the recovery, through day ten. This sampling was used to generate average liver total PAH concentrations for each day sampled (Miller et al. 2017). The four days of exposure values were used to calculate a linear regression uptake value based on 1 ppm exposure, resulting in an uptake of 2.13 ppm/day. This exposure to uptake ratio calculates to 0.47. This can be used to estimate the uptake rate at any exposure level assuming a linear relationship. To reflect uptake in Atlantis, current oil exposure values were divided by 0.47 to generate the exposure-specific linear uptake rate  $\mu$ . To calculate depuration rate, the peak average liver concentration and subsequent concentrations at 2, 4, and 6 days post exposure were used to calculate an exponential decay formula. When external exposure ends, the estimated decay formula returns the body load to 1% of peak levels through depuration in about 10 days (parameter  $p$  in the decay Equation 4.1 = -0.46). In the Atlantis simulations, these rates are used for both water column and sediment exposure. These rates were combined with the oil concentration estimates to calculate an exposure concentration,  $[oil]_{exposed}$ .

$$[oil]_{exposed} = \left[ Oil_{t-1} + \left( \frac{Oil_t}{\mu} \right) \right] * e^p \quad Eq. 4.1$$

To drive simulated MOSSFA in the system, point source inputs for detrital loading were used. Detrital concentrations were targeted to increase by a factor of about 2 – 5 x in the seven polygons closest to the wellhead, based on observations of increased detritus after the DWH event (Brooks et al., 2015). The elevated detrital input values were held for the duration of the oil spill forcing (167 days), then inputs were lowered to normal values.

#### 4.2.3 Biological drivers of the oil spill

To drive oil effects on organism health, dose-response models that were evaluated for mortality and growth in a previous publication were used (Dornberger et al. 2016). Four models were fit by maximum likelihood estimation and compared using an Akaike information criterion

(AIC). For both mortality and growth, the “hockey-stick” equations best explained the relationship between oil exposure and fish health and growth. The applied version of this hockey-stick equation is shown in equation 1, where it has been adjusted to only calculate the modifier to a generic response if oil exposure is past the threshold value.

$$R_t = a * \text{Log} \left( K * \frac{[oil]_{exposed}}{[oil]_{thresh}} \right) * \omega^{-1} \quad \text{if } [oil]_{exposed} \geq [oil]_{thresh} \quad \text{Eq. 4.2}$$

$R_t$  is the response modifier for either growth or mortality at time  $t$ , and  $a$  is the fitted slope ( $m_{mortality} = 0.2885$ ,  $m_{growth} = 0.1051$ ).  $\omega$  represents the average exposure period from the studies used to derive the dose-response relationships (15 days), so the inverse was used to determine an average daily effect.  $[oil]_{thresh}$  is the threshold below which oil has no effect on the response. The mortality threshold has a large impact on the magnitude of the effect modifier, so sensitivity analyses included three variants of  $[oil]_{thresh}$  for fishes: 362, 635, and 907 ppb based on validation and sensitivity done in Ainsworth et al. (2018), and two for benthic invertebrates: 1,000 and 3,000 ppb based on invertebrate analyses (Chapter 3 Dornberger). The hockey-stick shape produces higher effect values at higher concentrations. Hence, in order to scale growth down from 100% to a reduced rate as oil exposure increases, the growth response modifier  $G_t$  is subtracted from 1. The growth threshold for both water and sediment exposure was estimated to be 2.94 ppb for fishes. Sensitivity analysis of this threshold would be of little value since it is a very low oil concentration. No growth modifier was applied to invertebrates.

Since some organisms are not constrained exclusively to the sediment or water column, a weighted response modifier is calculated for each group accounting for relative benthic association of the group. The total modifier  $R_{oil}$  for both growth and mortality at a given time step takes the relative modifiers for the water column  $R_{pelagic}$  and sediment  $R_{benthic}$ , scaling them

by the proportion  $B$  of the affected group's diet that comes from benthic food sources. Note the symbol change, e.g. that  $R_t = R_{pelagic}$  at time  $t$  when the exposure medium is the water column.

$$R_{oil} = R_{pelagic} * (1-B) + R_{benthic} * B \quad Eq. 4.3$$

The more heavily a group's diet depends on a pelagic or benthic food source, the more its response modifier will reflect the pelagic or benthic medium, respectively. The mortality modifier  $M_{oil}$  is then applied in M1, which summarizes natural mortality from non-predation sources as

$$M1 = m_l + m_q + M_{oil} \quad Eq. 4.4$$

where  $m_l$  and  $m_q$  are linear and quadratic mortality, which are regular tuning parameters in Atlantis. The growth modifier  $G_{oil}$  and M1 are both applied to equation 4, the instantaneous rate of change of biomass ( $B$ , in mg N) for each polygon, depth layer and age class of functional group  $i$ .

$$\frac{dB_i}{dt} = [Rec_i + T_{IMM,i} - T_{EM,i} - M1_i - \sum_j P_{i,j} - F_i] * G_{oil} [G_{i,s} + G_{i,r}] \quad Eq. 4.5$$

$Rec_i$  is recruitment of new individuals into the age class.  $T_{IMM,i}$  is immigration of group  $i$  and  $T_{EM,i}$  is emigration,  $F_i$  is fisheries mortality, and  $P_{i,j}$  is predation term of predator  $j$  on group  $i$ .  $G_{i,s}$  is growth in structural nitrogen per individual and  $G_{i,r}$  is growth in reserve nitrogen per individual, which are functions of consumption, growth rate, and assimilation efficiency. No oil avoidance behavior modifier was applied.

Recruitment impacts were also included following the methods of Ainsworth et al. (2018). They used the results of a larval distribution map and surface oil comparison from DwH conducted by Chancellor (2015) to approximate the net recruitment impact from loss of larvae. They assumed that all larvae exposed to oil were killed.

The oil spill emergency fishery closures were implemented as spatiotemporally dynamic marine protected areas. The timing of the closures was reported by the National Centers for Environmental Information (2016). In Atlantis, the proportion of each polygon that overlapped a closure during the scheduled period was closed to the appropriate fishing fleet(s). This effectively simulates the local emergency closures; however, it does not include reallocation of fishing effort elsewhere. The closure dynamics were updated on a daily time step, and were included for the full duration of the emergency fisheries closures.

To determine the effects of a toxic oil spill combined with theoretical varied fishing mortalities, the sensitivity of the system stressed by oil was also simulated by varying fishing mortality in three additional worst case sensitivity scenarios. In these scenarios, the fleet specific relative Fishing mortality  $F$  of each functional group was scaled by 0.5, 2, and 10. These varied  $F$  values were in combination with the worst case sensitivity scenario parameters of 1000 K, fish mortality threshold of 362, and invertebrate mortality threshold of 1000. Fishing mortality  $F$  by functional group and fleet was originally fit to historical catch as described in Ainsworth et al. (2015). All scenario parameters are listed in Table 4.1.

*Table 4.1 List of all parameter values used in Atlantis sensitivity and modified fishing simulations. The number following the column title is the total number of simulations run using a combination of the below parameter values. K is the sediment to water column ratio.  $[oil]_{thresh}$  is the oil concentration where mortality for that type of organism begins based on the hockey-stick dose-response model. The fishing mortality modifier is the scalar used to adjust MFC matrices in theoretical fishing simulations*

<b>Parameters</b>	<b>Sensitivity Analyses (18)</b>	<b>Fishing Mortality and Oil (3)</b>
K	400, 700, 1000	1000
Fish $[oil]_{thresh}$	362, 635, 907	362
Benthic invertebrate $[oil]_{thresh}$	1000, 3000	1000
Fishing mortality modifier	-	0.5, 2, 10

#### 4.2.4 Analysis

For consistency and cross comparison, analytical grouping by polygon and guild matched that of Ainsworth et al. (2018). All results presented here are averaged across 13 highly impacted polygons (Figure 4.1) unless stated otherwise. These 13 polygons roughly correspond to the area targeted for injury assessment efforts (Deepwater Horizon Natural Resource Damage Assessment Trustees, 2016). Results from Atlantis functional groups were averaged into nine guilds: snappers (Family: Lutjanidae), groupers (Family: Serranidae), Sciaenidae, elasmobranchs, large pelagic fish, small pelagic fish, small demersal and reef fish, large demersal fish, and invertebrates. The composition of these guilds are listed in Table 4.2. Guilds were used for clarity in assessing impacts across a broader range of species in the ecosystem than specific functional groups. In Atlantis, functional group is the term used to track pre-defined populations and can be either species specific or multiple related species. The Atlantis functional groups' species compositions are presented in Ainsworth et al. (2015).

*Table 4.2 List of Atlantis functional groups contained within each guild.*

<b>Guilds</b>	<b>Atlantis Functional Group Names</b>
Snappers	Red snapper, Vermilion snapper, Lutjanidae
Groupers	Gag grouper, Red grouper, Scamp, Shallow Serranidae, Deep Serranidae
Large pelagics	Yellowfin tuna, Bluefin tuna, Little tunny, Other tuna, Swordfish, White marlin, Blue marlin, Other billfish, Greater amberjack, Jacks, King mackerel, Spanish mackerel
Small pelagics	Spanish sardine, Menhaden, Pinfish, Small pelagic fish
Small demersal & reef	Small reef fish, Small demersal fish
Sciaenidae	Black drum, Red drum, Sciaenidae
Elasmobranchs	Blacktip shark, Benthic feeding sharks, Large sharks, Filter feeding sharks, Small sharks, Skates and rays
Large demersal	Flatfish, Other demersal fish
Invertebrates	Brown shrimp, White shrimp, Pink shrimp, Other shrimp, Blue crab, Stone crab, Crabs and lobsters, Stony corals, Octocorals, Sponges, Carnivorous macrobenthos, Infaunal meiobenthos, Herbivorous echinoderms, Oysters, Bivalves, Sessile filter feeders

Outputs from Atlantis were analyzed across sensitivity analyses and compared to the results of Ainsworth et al. (2018) to determine the effects of including invertebrate mortality, MOSSFA detrital loading, and varying fishing mortality.

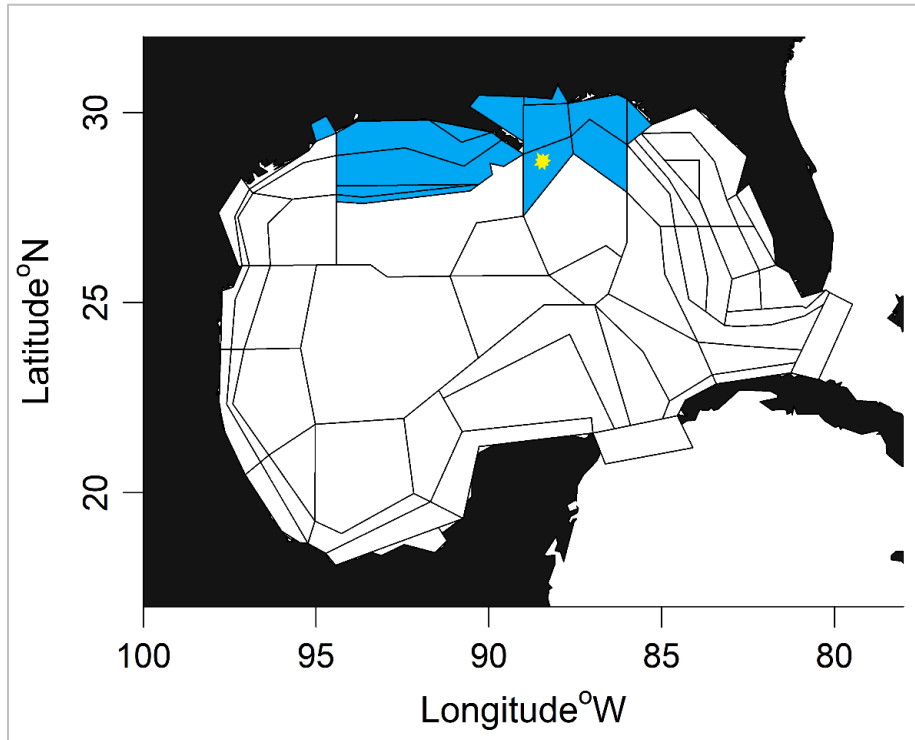


Figure 4.1 Polygon geometry for Atlantis GoM. Shaded polygons represent the polygons used for oil spill analysis. The star is the relative location of the Deepwater Horizon site.

## 4.3 Results

### *4.3.1 Population impacts*

In Figure 4.2, guild biomass divided by (relative to) control no oil spill simulation guild biomass is shown over the course of the 50-year simulations. The average biomass across all sensitivity simulations, with  $K$  and  $[oil]_{thresh}$  variation, is shown as the solid black line. The shaded area represents the range of outcomes from sensitivity analysis on sediment concentration factor  $K$  and mortality  $[oil]_{thresh}$  for fishes and invertebrates. The results for snappers, groupers, Sciaenidae, and large demersal fishes agree with the trends from the oil spill simulations

observed in Ainsworth et al. (2018), though the relative declines vary slightly. Relative changes qualitatively match remotely operated vehicle observations (W. Patterson, Pers. Comm.) in Ainsworth et al. (2018), which indicated as much as a 75% decrease in small reef fish and a 70% decrease in some large reef fish post spill. Small pelagics, small demersal and reef fish, and Sciaenidae exhibit declines during the spill period followed closely by recovery. However, the responses begin to differ around years 5 to 10. Small demersal & reef fishes and Sciaenidae average above the no spill scenario from about year 2016 on, while the small pelagics guild declines again and maintains biomass at roughly half the no spill scenario. This trend in small pelagics is driven by the “small pelagic” functional group within the guild. The small pelagic

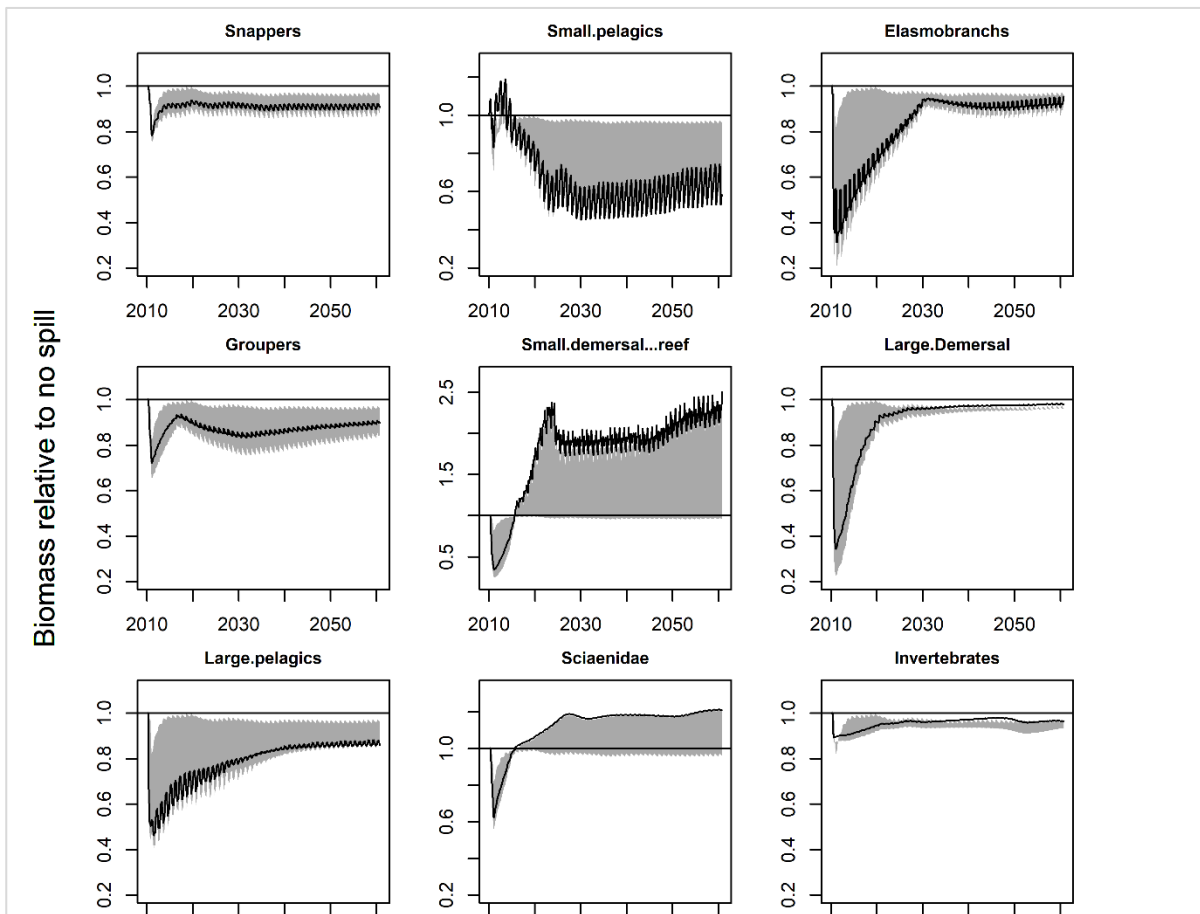


Figure 4.2 Relative biomass trajectories of Atlantis guilds. Biomasses were averaged across 12 impacted polygons and divided by the biomass from the no oil scenario. The shaded area represents the range of outcomes from sensitivity analysis on sediment concentration factor  $K$  and mortality  $[oil]_{thresh}$  for fishes and benthic invertebrates. The solid black line shows the average biomass across all 18 sensitivity runs.

functional group goes virtually extinct after roughly 20 years due to fishing and increased predation pressure. In the small pelagic guild, species specific functional groups menhaden and pinfish recover in 20 and 5 years, respectively.

When including oil effects on both fishes and benthic invertebrates, increased benthic invertebrate abundance is no longer evident at the invertebrate guild and polygon level in October 2010 (6 months after first spill), across all sensitivity analyses. However, a few functional groups within the benthic invertebrate guild do exhibit both increases and declines at the polygon level during the window of greatest impact (7-16 months): infaunal meiobenthos, sponges, sessile filter feeders, carnivorous macrobenthos, and blue crab.

Including benthic invertebrate mortality and MOSSFA forcings changes the recovery dynamics of functional groups in the worst case scenario compared to previous simulations seen in Ainsworth et al. (2018). However, there is still no distinguishable relationship between guild biomass minima and recovery time (Figure 4.3). Of the functional groups included in the guild analysis within the highly impacted polygons, 27 did not recover to within 99% of original biomass levels in the worst case scenario, roughly 51% of groups examined. In the best case scenario, 10 functional groups did not recover.

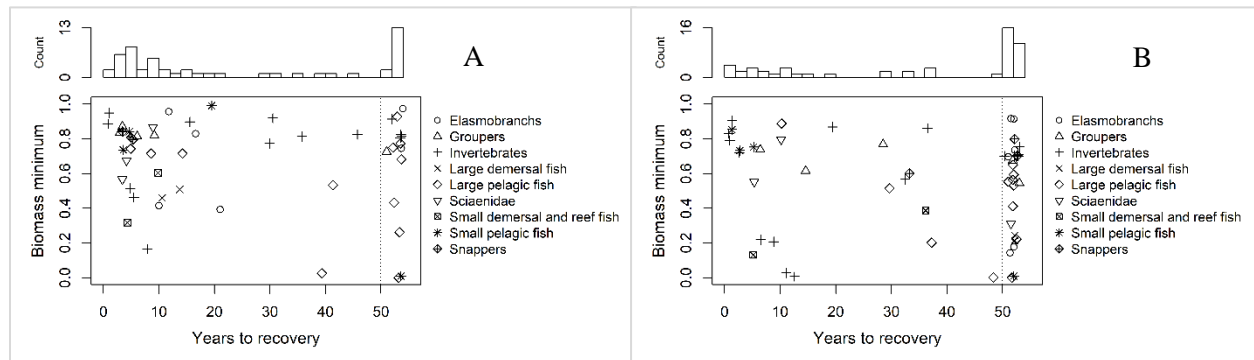


Figure 4.3 Best case and worst case functional group recovery time and biomass minimum. A) The “best case” scenario, with sediment concentration factor  $K$  of 400, fish mortality threshold at 907ppb, and invertebrate mortality threshold at 3000ppb. B) The “best case” scenario, with sediment concentration factor  $K$  of 1000, fish mortality threshold at 362ppb, and invertebrate mortality threshold at 1000ppb. All functional groups that constitute a guild are shown. The count of functional groups by recovery time are shown in the count graph above.



### 4.3.2 Diet changes

For six of the eight fish guilds, per capita consumption rate declined in the worst case oil scenario (Figure 4.4). For seven of the eight guilds, the benthic invertebrate proportion of the predators' diet increased in the oiled scenario, though only five of the predator guilds' diet constitutes at least 1% invertebrates (Figure 4.4). Of the guilds whose diets shifted to contain a

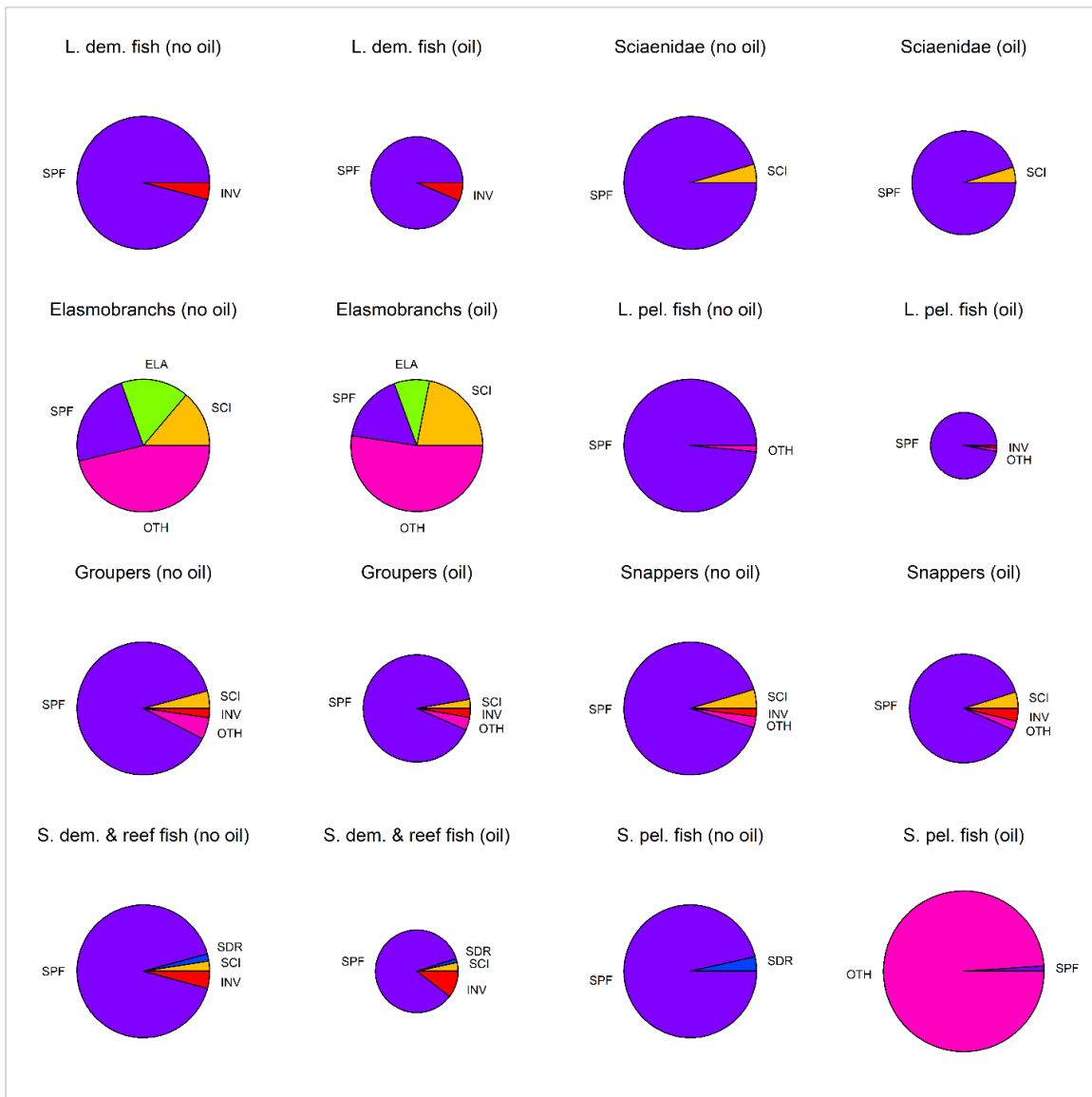


Figure 4.4 Guild per capita consumption rate on prey. The area of each graph is proportional to the predator's per capita consumption rate. Only prey groups constituting >1% of the predator guild's diet are shown. The diet snapshot is taken from day 300 of the simulation, when oil effects were pronounced. Labels: Large demersal fish (LDF), Sciaenidae (SCI), Elasmobranchs (ELA), Large pelagic fish (LPF), Groupers (GRP), Snappers (SNP), Small demersal and reef fish (SDR), Small pelagic fish (SPL), Invertebrates (INV), other prey items (OTH).

higher proportion of invertebrates, three guilds also reduced the proportion of their diet dependent on small pelagic fish.

#### 4.3.2 Combined oil and varied fishing mortality scenarios

Relative biomass differences in the varied  $F$  scenarios from the base fishing scenario, for the nine guilds averaged across the 13 heavily impacted polygons, are shown in Figure 4.5. The guilds most sensitive to fishing changes combined with “worst case” scenario oil were snappers, groupers, and small demersal & reef fish. Snappers were most affected in the  $F \times 10$  scenario. Groupers had the largest positive response to a release of fishing pressure. The guilds least affected by changes in  $F$  were small pelagics and benthic invertebrates.

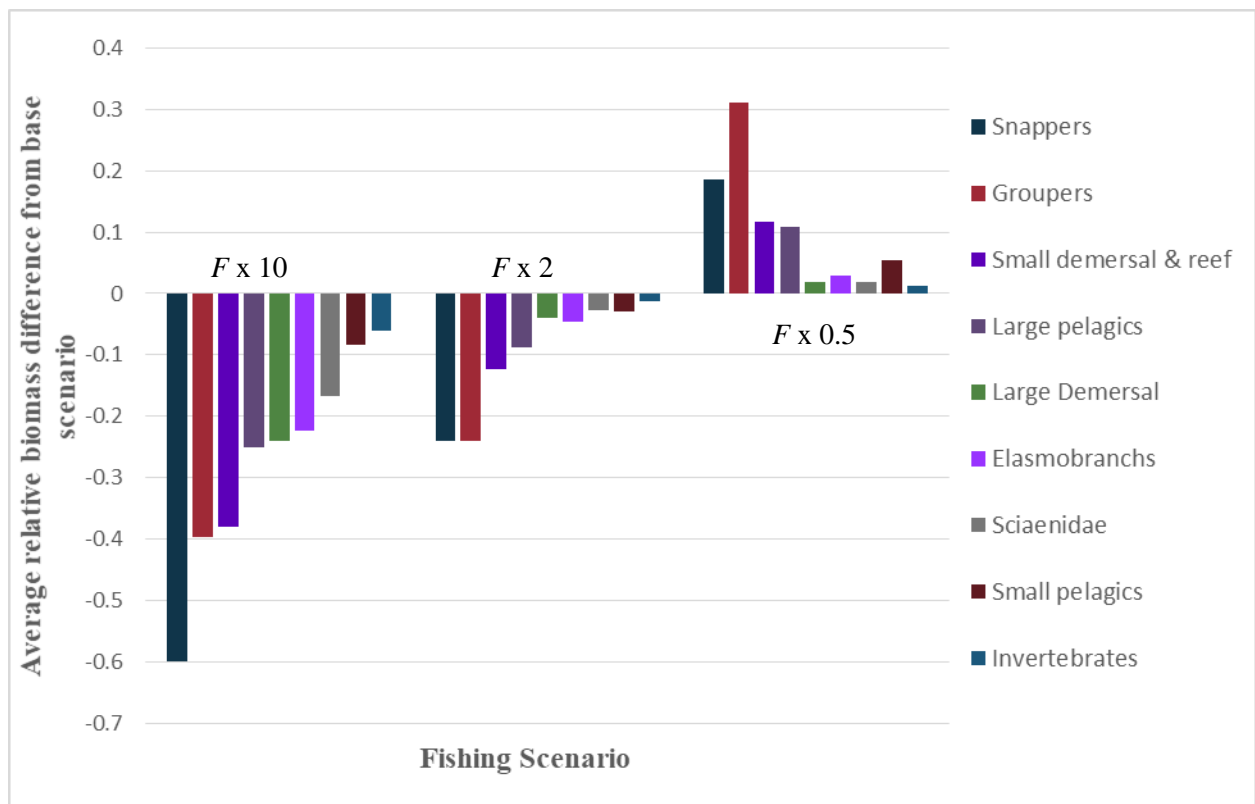


Figure 4.5 Average relative biomass changes from the base  $F$  scenario for Atlantis exploited guilds across three varied  $F$  scenarios.  $F \times 10$ ,  $F \times 2$ , and  $F \times 0.5$  means increasing fishing mortality on all exploited groups by 10, 2, and 0.5 times, respectively. All scenarios have MOSSFA detritus forcing and the “worst case” oil parameters of  $K = 1000$ , fish threshold = 363, and benthic invertebrate mortality threshold = 1000.

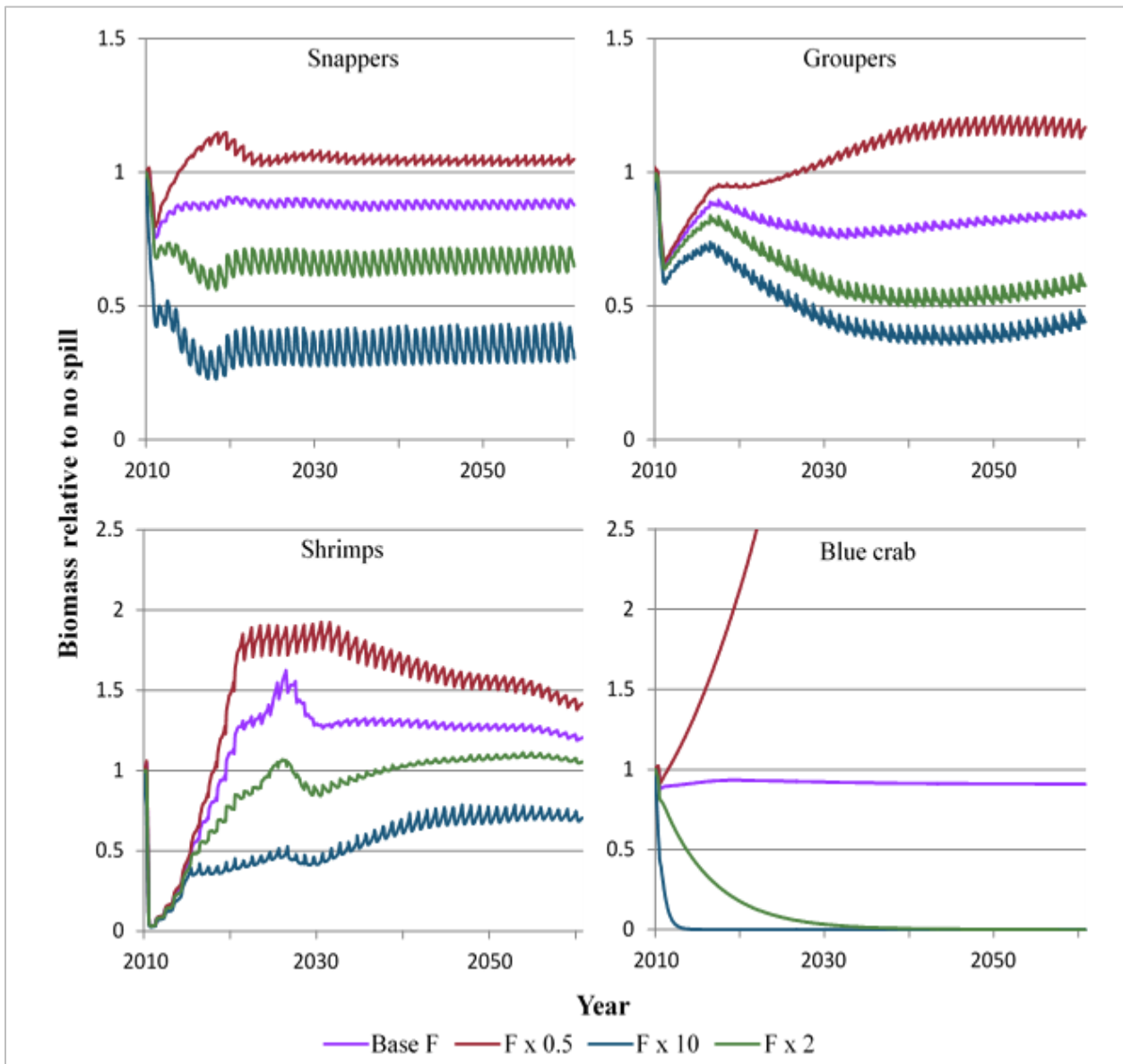


Figure 4.6 Example groups of functional group relative biomass changes from no oil across three varied  $F$  and one base  $F$  scenarios.  $F \times 10$ ,  $F \times 2$ , and  $F \times 0.5$  means increasing fishing mortality  $F$  by a factor of 10, 2 and 0.5 across all fishing gears and species, respectively. Snappers and Groupers are both guilds, Shrimps are a sub-guild within the Invertebrate guild, and Blue crab is a functional group. The Blue crab  $F \times 0.5$  relative biomass reached 70 times that of no oil, so the y-axis was limited to 2.5 for visibility of other scenarios' relative biomass.

In general, snappers, groupers, large pelagics, small pelagics, small demersal & reef, and Sciaenidae all exhibited lower biomass minima when  $F$  was increased during the oil spill simulation. Representative example guilds from this list are shown in Figure 4.6. All guilds had different biomass trajectories with varied  $F$  relative to the no oil scenario, and some reached

reduced or elevated equilibrium states from the base  $F$  scenario. Snapper biomass oscillated around 0.35 relative to no oil for the  $F \times 10$  scenario, and 1.5 for the 0.5  $F$  scenario (Figure 4.6). Groupers reached a new equilibrium around 1.2 relative to no oil for the 0.5  $F$  scenario (Figure 4.6). Both guilds indicate that while the oil spill had an initial effect on biomass, the long-term biomass stabilization was dependent upon fishing effort, not magnitude of decline from the oil spill.

As a guild, benthic invertebrates indicated minor shifts in varied  $F$  scenarios. However, shrimps (brown shrimp, pink shrimp, white shrimp, other shrimps), blue crab, and lobsters were more heavily impacted by changes in  $F$  (Figure 4.6). In the  $F \times 10$  scenario, blue crab and lobsters exhibit similar trends, and go extinct after 8-10 years. Shrimps eventually reach a new reduced equilibrium about 0.75 relative to no oil, though in all scenarios they initially indicate a severe decline in biomass. The long-term trends in shrimps indicate that while  $F$  plays a role in biomass stabilization, other food web dynamics that occur as a result of the oil spill allow the biomass to grow larger than in the control scenario for all scenarios except  $F \times 10$ .

#### 4.4 Discussion

The addition of benthic invertebrate mortality and MOSSFA detrital loading induces a few significant changes in projections from previous Atlantis DwH simulations (Ainsworth et al., 2018). In the “worst case” scenario, where fishes and invertebrates are most heavily impacted by the oil spill, over half of the examined functional groups never recover to pre-spill biomass in the targeted polygons. Although 10 functional groups do not recover in the “best case” scenario, the majority of these are less affected than in the “worst case” scenario. Most of these groups have a biomass minimum between 60% and 90% of the control no-oil scenario. This suggests that less

severe oil spills cause fewer heavily reduced populations, and proportionally more functional groups reach a new stable state biomass that is slightly reduced from pre-spill conditions.

Across scenarios, the most heavily impacted guilds are large demersal fishes (including elasmobranchs). The loss of these fishes is similar to that found in Ainsworth et al. (2018), but the magnitude of the biomass declines are more severe. This indicates that despite organic enrichment resulting from MOSSFA, toxic effects and starvation from prey population declines in demersal and reef-associated predators are still a concern. The combined effects of commercial fishing efforts and toxic effects from the oil spill prevent recovery in these groups. Further, Ainsworth et al. (2018) indicated that the most affected species were small bodied reef and demersal fishes, not the large demersal fishes found in this study. While the initial trends for the small demersal & reef fish guild match across studies, they diverge around the year 2020.

In this study, small demersal & reef fishes, though initially hit hard, increase in biomass after 2020 and maintain an elevated population size. This is possibly due to a combination of top-down and bottom-up impacts: initial benthic MOSSFA organic supplementation allowed their prey resource biomass to grow, and reduction of large fish predation pressure due to oil toxicity (e.g., the loss of large demersal fishes). The loss of these large predators could account for the rebound of small demersal & reef fishes.

Atlantis projections for large pelagic fish have not been realized in observations and sampling. Atlantis predicts large population declines in this guild due to the overlap of the sub-surface plume with migration corridors. However, oil avoidance is an important behavior in vertebrates (Rice et al., 1976; Gray, 1990; Martin, 2017; Ainsworth et al., 2018) that is currently not taken into account. Therefore, the results here likely overestimate the effect on migratory fishes like the large pelagic guild. Developing the ability to influence migration among Atlantis

polygons temporarily during large biologically-significant events could improve upon this and would provide better insights for this guild. Species-specific oil uptake rates (equation 1), limiting the maximum exposure a functional group would experience, could effectively differentiate species' abilities to avoid contaminated areas.

The diet of several guilds relies more on benthic invertebrate prey sources in the oiled scenario target polygons. This could also be a result of MOSSFA-driven benthic enrichment, which would indicate that the detrital forcing behavior is capturing the pathway of organic matter to the benthic community. Overall, benthic invertebrates are less affected in the oil simulations than fish guilds, though the benthic invertebrate guild never recovers to pre-spill biomass in any of the sensitivity scenarios. Some benthic invertebrate functional groups show the domed relationship of MOSSFA enrichment vs. toxicity at the polygon level, but the loss of this relationship at the guild level could be due to polygon resolution. It is possible on a smaller scale this relationship exists, but when combined with all oil forcings and averaged over such a large area and across functional groups the effect is lost. There are other benthic and MOSSFA related parameters not included here that could also play an important role. Notably, the uptake-depuration model used here was developed based on a single species of fish exposed to oil in water tanks. The representation of impacts on the benthos would be better described if an uptake-depuration model could be developed based on sediment exposure, and separately for different fishes and invertebrates. The other environmental MOSSFA factors that could be explored in future simulations include benthic smothering (hypoxia), changing redox conditions, and resuspension of contaminated sediments during storm events.

The combination of benthic invertebrate and fish forcings has resolved one issue seen in the benthic invertebrate only simulations (Chapter 3 Dornberger). For those MOSSFA simulations,

the oyster functional group was removed as an extreme outlier based on enrichment compared to a control scenario, as their population exploded in targeted polygons. In this work, with the combined vertebrate and invertebrate simulations, oyster behavior responds similarly to other invertebrate groups. There is a decline during the oil spill followed by gradual recovery in most 50-year sensitivity simulations. This aligns with the initial documented loss of oysters that occurred immediately after the oil spill and response efforts (Powers et al. 2017). I note here that Powers and his colleagues attributed the decline to low salinity from Mississippi flushing as a method to purge oil from the delta after the spill, which is not directly forced here. Oyster dynamics likely stabilized in the combined forcing scenario due to a combination of improved detritus dynamics and food web interactions. Detritus inputs were adjusted to stabilize long-term model dynamics, building up to target detritus values, and the trophic cascade from toxic effects on large demersal fishes increased pressure on oysters. De Mutsert et al. (2017) modeled oyster dynamics in the GoM post-DWH, with outputs fitting catch data well but not biomass. They note that successful modeling of oysters requires additional environmental data, and used a new spatiotemporal environmental model in Ecopath with Ecosim.

The other significant findings of this study are related to the synergistic effects of fishing and oil. A change in fishing pressure can make the difference between recovering post-spill, or not. Atlantis suggests that in targeted polygons, some of the affected guilds (e.g. snappers and groupers) will not recover without release from pre-spill fishing pressures. In fact, some guilds' long-term biomass is determined by the relative  $F$  value, not the magnitude of the decline due to the oil spill event. This is an important topic to explore, especially relative to red snapper population and management in the eastern GoM. The recent stock assessment (Southeast Data, Assessment, and Review, 2018) indicated that a population decline in this region was possible

and that the stock should be monitored closely, although the authors noted that the predicted decline could be due to poor model parameterization. Additionally, groupers show more resilience to release from fishing pressure in the presence of oil than do other guilds and exhibit the largest net gain in biomass compared to the baseline fishing scenario. This indicates a non-linear relationship between the combined effects of fishing and oil on grouper abundance.

Shrimps and crabs were also significantly affected by changes in fishing pressure. Surprisingly, the rate of recovery for the shrimp group was relatively similar across scenarios, but stabilized at different biomass levels. Shrimps dynamic indicates that while the oil spill and fishing have an effect on biomass, other food web dynamics resulting from the oil spill and fishing efforts allow shrimps to grow in biomass relative to the control. Conversely, crabs were very sensitive to changes in fishing mortality, experiencing population explosions when fishing pressure was reduced, or crashed when pressure was increased. Sensitivity to small changes in  $F$  could be a model artifact acting through impacts on age class bottlenecks.

Some fish groups are minimally affected by changes in fishing. Across the three fishing sensitivity scenarios, the least responsive to changes in  $F$  was small pelagics. This could be due to their large natural mortality as prey items for fish guilds in this region. When fishing pressure is reduced, top-down effects of predation pressure could be keeping the small pelagic fish from growing in biomass. When fishing is increased, the small pelagic fish are harvested but the corresponding release from predation pressure minimizes the relative biomass lost. While the emergency fisheries closures were included in these simulations, subsequent spatial reallocation of fishing effort was not. This has implications for the results of this study. The impact of fishing mortality  $F$  might be underestimated, or the impact of increased  $F$  in the sensitivity analyses. If fishermen moved outside of the closures to fish in areas that are not their normal target regions,



this would not be captured in simulation. If that were included, biomass impacts and catch estimates could differ.

This study provides additional important insights into the potential long-term implications of the DwH oil spill. The combined forcing of fish and benthic invertebrate health effects and MOSSFA detrital loading have proven to have a significant effect on Atlantis outputs. Since 1.8-14% of oil released is estimated to have reached the benthos (Valentine et al., 2014), and a key pathway of that oil transport has been identified in MOSSFA (Brooks et al., 2014, Daly et al., 2016), accurate representation of benthic organisms and environmental forcings are important to capturing the dynamics of this habitat. Additionally, the potential combined effects of changes in fishing effort and oil spill scenarios could be important for fisheries management. This study also suggests that for heavily affected areas, decreasing fishing pressure by 50% for a few years could allow some populations to return to pre-spill levels in that same time span, while continued fishing results in no recovery over a 50-year simulation. While the economic impacts of this type of policy decision are not examined here, it is a concept worth exploring in future research and considering as a mitigation response for future spills. Indirect food web and synergistic effects have significance both for injury assessment and recovery planning in large scale ecosystem disturbances like DwH.

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## **Chapter Five: Conclusion**

The research conducted for this dissertation aimed to describe methods for incorporating observed oil spill impacts into an end-to-end ecosystem model, Atlantis, and test their efficacy. Ecosystem-based assessment tools like Atlantis are currently underutilized in relation to predicting impacts of oil spills. However, ecosystem-based fisheries management (EBFM) is the way forward for fisheries management (Knecht & Cicin-Sain, 1993; Grumbine, 1994; Griffis & Kimball, 1996; Costanza et al., 1998; Link & Browman, 2014; Levin et al. 2018; Marshall et al. 2017). Thus, it is imperative that we gain the ability to use ecosystem-based assessments of anthropogenic events to support holistic management. I effectively created a basic conceptual framework for implementing oil spill effects into any ecosystem-based assessment model. I successfully integrated this framework into Atlantis, a spatially explicit trophodynamic ecosystem model, to project potential long term impacts of the Deepwater Horizon (DwH) oil spill in the Gulf of Mexico (GoM). My DwH work informs potential research focuses of future efforts in the GoM, as well as the implications of future oil spills and their corresponding mitigation efforts.

In Chapter 2, I developed a dose-response model to describe the population level health effects of oil exposure on fishes (Dornberger et al., 2016). Multi-species data were gathered from a literature review of studies assessing two facets of fish health: growth and the development of lesions & tumors. While not necessarily a direct cause of mortality, lesions and tumors are indicative of an overall decline in health. I used this as a proxy for mortality based on the association between reduced health or behavioral changes and the increased risk of mortality



from predation, disease, parasitism, or competition (Moore & Dywer, 1974; Moles & Norcross, 1988). Exposure medium was also considered and tested, indicating for lesion data that all mediums produced similarly proportional responses, but for growth, food based exposure was significantly different from water or sediment and had to be treated separately. These lesion and growth data sets were then compared to oil exposure levels, and a continuous dose-response model generated for each to specify the population level impact at any given exposure. The identified best fit model for all data sets, a “hockey-stick” model with an effect threshold and log linear response (Dornberger et al., 2016), matches models previously built to describe single-species lesion frequency (Johnson et al., 2002). The “hockey-stick” shape of the identified dose-response model is also qualitatively informative, as it indicates there is a threshold of exposure below which there is no detectable population level response. This is supported by early toxicological studies into the effects of oil on marine organisms (summarized in Moore & Dwyer, 1974). This dose-response model provides an important foundation with which to predict growth and mortality population level responses, and can be used in any ecosystem-based modeling efforts of an oil spill scenario.

In Chapter 3, I assessed the relationship between benthic invertebrate abundances and oil exposure in the GoM from sediment cores collected in 2010. This work confirmed the previously defined benthic invertebrate abundance domed response to oil (Montagna & Spies, 1985; Montagna et al., 1986, 1987; Spies et al., 1988; Olsgard & Gray, 1995; Steichen et al., 1996; Peterson et al., 1996; Jewett et al.; 1999) existed in the GoM after the DwH oil spill for meiofauna and macrofauna. Once confirmed, to drive this relationship for the DwH oil spill I tested potential external forcings in Atlantis. Driving this response in Atlantis was a novel concept, so three potential abundance stimulating scenarios were chosen: 1) Mississippi nutrient

loading from the flushing mitigation efforts (Bianchi et al., 2011), stimulating primary productivity as a pathway to benthic invertebrate abundance increases; 2) increased detritus from MOSSFA (Brooks et al., 2015; Romero et al., 2015) stimulating the detritus based food web as a pathway to benthic invertebrate abundance increases; 3) predators altering their behavior to avoid oil exposure (Rice et al., 1976; Gray, 1990; Martin, 2017; Ainsworth et al., in 2018) reducing top-down pressure from predation as a means of benthic invertebrate abundance increases. These scenarios were combined with an invertebrate mortality dose-response model to create the domed relationship of increased abundance at low-moderate oil levels and decreased abundance at high oil levels. The results indicated that at the resolution of Atlantis polygons, only scenario 2 (MOSSFA) was able to drive the domed relationship. This is an important finding for future oil spill modeling efforts, as it identifies a key environmental contributor to food web dynamics, and also supports the results post-DwH identifying MOSSFA as an important component of this oil spill (Daly et al., 2016).

In Chapter 4, I combined the results from Chapters 2 & 3 to run integrated modeling efforts with effects on vertebrates and benthic invertebrates in the Atlantis framework. I also tested the combined effects of fishing mortality and oil spill impacts to determine potential compounding effects. This advances upon the work of Ainsworth et al. (2018) and provides important insights into the potential impacts and synergies in the system. Adding MOSSFA and benthic invertebrate toxicity forcings had an effect on the diet of a few guilds of fishes. Several guilds had a proportional increase of invertebrates in their diet during the peak impact period of the oil spill. With the addition of MOSSFA and benthic invertebrate toxicity, Atlantis indicates DwH has the potential to significantly impact biomass in the region for over 50 years. In the “worst case” sensitivity scenario, over half of the assessed functional groups do not recover in 50

years. Optimistically, in the “best case” sensitivity scenario with minimal oil impacts, fewer functional groups do not recover. In this scenario, the majority of functional groups that do not recover in the 50 year period have a higher biomass minimum than in the “worst case” scenario. This would indicate that in a “best case” scenario, many unrecovered groups have equilibrated at a new steady state slightly reduced from a control level, compared to the “worst case” scenario where many groups have severe biomass reductions. Also, these simulations captured the documented decline in oyster populations (Powers et al., 2017), and projections for eastern GoM red snapper populations match the recent stock assessment (Southeast Data, Assessment, and Review, 2018). Overall, I suggest that the most affected guilds by biomass in the oil spill region are large demersal fishes and elasmobranchs.

This work also emphasizes the importance of fishing mortality,  $F$ , during oil spill recovery. The ability to jointly test the effects of fishing pressure and oil spill impacts at an ecosystem level supports the call to move towards EBFM. In Atlantis, a reduction in fishing effort allows for the recovery of guilds that would otherwise not recover. Both fishes and commercially targeted invertebrates indicate the potential for this interaction. This indicates that, in some cases, the combined pressures of an oil spill and continued fishing efforts may be too daunting an obstacle for the population to independently overcome. When a targeted species is struggling to recover after an oil spill, whether it is DwH or a future event, these findings suggest that reducing fishing pressure has the potential to aid in generating species recovery.

Overall, in this dissertation I have successfully used an ecosystem-based assessment model to incorporate data from the DwH oil spill and conduct an ecosystem assessment. As suggested by many international fisheries policy recommendations (Ministry of the Environment, 1997; Ecosystem Principles Advisory Panel, 1999; World Summit on Sustainable

Development, 2002; United Nations Environment Programme, 2006), EBFM should be utilized where possible to manage fish stocks. The ability to implement anthropogenic impact events, like oil spills, into ecosystem-based assessment models to support EBFM is an additional step towards providing holistic, consistent insights into managed systems. The results of this research provide a basis for further ecosystem-based oil spill modeling efforts, highlight the importance of including secondary effects of a spill, like MOSSFA, and indicate potential long-term impacts of DwH.

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## Appendix A: Developing a polycyclic aromatic hydrocarbon exposure dose-response model for fish health and growth

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# Developing a polycyclic aromatic hydrocarbon exposure dose-response model for fish health and growth



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## ABSTRACT

One of the more important steps in understanding the ecosystem-level effects of anthropogenic disturbances on resident species is developing an accurate representation of the lethal and sub-lethal effects of these stressors. We develop methods for describing the impacts of oil on growth and mortality rates in fishes. We conducted a literature search to determine potential relationships between direct and indirect effects of exposure to oil, based on the frequency of lesions and body growth reduction. Data examining these effects with different exposure mediums were assessed and then input into four potential response models (a linear, step-wise, hockey-stick, and exponential model). We assessed the models using the Akaike Information Criterion. The most parsimonious and best fit model was the hockey-stick. This analysis will aid in identifying where future research on the impact of oil on fish should focus and also aid the development of ecosystem models on impacts of oil spills.

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## 1. Introduction

As the quantity and type of chemicals humans introduce into aquatic environments grows, a better understanding of species responses to exposures and factors that modulate it must be developed. As the number of oil extraction operations and corresponding oil spills increase, the specific need to understand how oil can impact organisms, especially fish, has become even more acute. The intensity of crude oil toxicity depends on the species or life stages involved, as well as the concentration and composition of the oil (Mosbech, 2002; McCay et al., 2004; Incardona et al., 2011a; McKenna et al., 2013). Exposure effects are further modified by the local climate, habitat, currents, and oil spill response efforts (Moore and Dwyer, 1974; Tjeerdema et al., 2013; Almeda et al., 2014).

Understanding both lethal and sub-lethal exposure effects is important to building a comprehensive view of the impacts from an oil spill. Direct mortality from hydrocarbons in oil is observed across a range of species (Rice et al., 1984; Lee and Page, 1997; Carls et al., 1999; Brown-Peterson et al., 2015), and sub-lethal effects are observed in some organisms (Moore and Dwyer, 1974; Lee and Page, 1997; Brown-Peterson et al., 2015). These toxic sub-lethal effects can include changes in behavior and predator-prey dynamics, growth impediment, and increased susceptibility to disease and parasitism (Moore and

Dwyer, 1974). Sub-lethal effects may interact and persist after acute toxicological impacts have subsided. Exposure to oil can slow growth, decrease recruitment to the fishery, and increase susceptibility to predation (Moles & Norcross, 1998). The size-spectrum theory suggests that at a given age, larger individuals have a higher chance of survival due to lower predatory densities (Hare and Cowen, 1997), thus even a small decline in the ability of a juvenile fish to grow or store lipids can have a severe impact on their chance of survival (Meador et al., 2006). This suggests that growth reduction can have an indirect mortality effect on a population. Fecundity may also be affected by a decline in growth, as larger females produce larger eggs with larger yolk sacs, leading to faster larval growth (Kennedy et al., 2007).

Within the oil exposure literature, a large body of research has focused on the effects of polycyclic aromatic hydrocarbons (PAHs), key components of oil, on certain fish species. PAHs are thought to be major components in the toxicity of oil, partially because their metabolites have oxidative and carcinogenic properties (Moore and Dwyer, 1974; Lin and Tjeerdema, 2008; Incardona et al., 2011a). Brown et al. (1973) found a higher prevalence of stomach, skin, and liver tumors, especially hepatic neoplasms, in 16 species of fishes correlated with the presence of two PAHs (naphthalene and benzo[a]anthracene), crude oil, and other toxicants (e.g. chlorinated hydrocarbons) in the water column of the Fox River in Wisconsin. There is also strong evidence supporting a causal relationship between exposure to sediment PAHs and liver neoplasms and other liver lesions in marine species (Myers et al., 1991). A statistical analysis of these lesions supports a

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morphologically identifiable progression ultimately leading to hepatic neoplasms, or liver tumors (Myers et al., 1991). The most supported causative PAHs for liver lesions are higher in weight, often pyrogenic (Vethaak et al., 1996; Myers et al., 1998). Burning oil in response to a spill increases the relative amount of higher weight PAHs in the system, increasing the risk of these lethal impacts.

Predicting the impacts of oil spills on fish populations is further complicated by the lack of data relating direct exposure concentrations to changes in life rates. Many studies, dating back to Moore and Dwyer (1974) have approximated the oil threshold at which a risk of health impacts begins, but not the shape of the organismal or population response. Some studies only compare oiled with non-oiled sites, and do not consider the degree of exposure (Khan and Nag, 1993; Jewett et al., 1995; Marty et al., 2003). Others use biliary fluorescent aromatic compounds (FACs) as an indicator of oil exposure, which have been documented in the laboratory to have a positive correlation with exposure dose (Collier and Varanasi, 1991). However, there are many factors that influence these FAC concentrations and caution should be used when interpreting these results from field investigations (Lee and Anderson, 2005). These examples highlight the difficulty in defining the relationship between oil exposure concentration and organismal response.

Dose-response curves, which predict how organisms and populations respond to increasing toxin exposure, offer a chance to connect lethal and sub-lethal impacts of oil. They also may be integrated into ecosystem models in order to predict long-term changes in food webs due to spills. The goal of this article is to parameterize best fit dose response models relating petrogenic PAH or oil exposure values to growth and mortality rates, which can then be used to predict responses of organisms to oil spills. Developing dose-response curves will allow direct estimates of oil impacts on organisms to be developed and tested. However, dose-response curves may take multiple shapes. To assess our current knowledge of how oil exposure may impact species, we gathered data on petrogenic PAH exposure and impacts on fish species from the literature and tested best fits against several common response models. This assessment and modeling exercise will also aid in identifying gaps in current empirical studies and target future work.

## 2. Methods

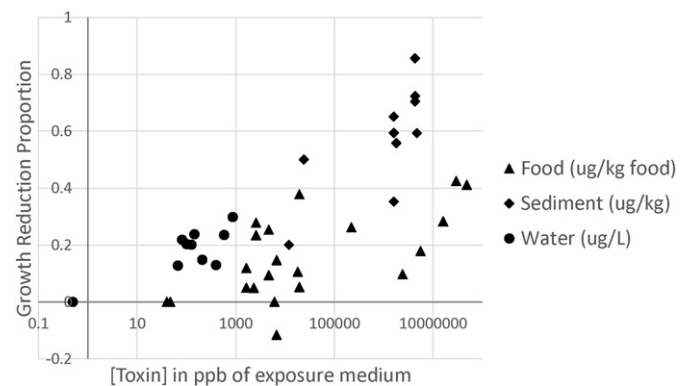
### 2.1. Literature search

Given the paucity of data related directly to oil exposure on juveniles and adults, we conducted a literature search to identify studies where an impact on organism health or growth was correlated with PAH exposure. We recognize the existence of literature on oil effects on larvae and embryos (e.g. Incardona et al., 2005, 2008, 2011b, 2015; Carls et al., 2008), however they were not included in this study as there is a difference in response during this stage as well as many ecosystem models do not explicitly model this life stage. Our search was initially guided by the review of PAH impacts on fishes by Collier et al. (2013), however many of the studies reviewed were pyrogenic in nature, therefore the search was expanded upon to locate other relevant studies focused on petrogenic sources. Lee and Page (1997) provide another review of oil spill impacts on sub-tidal regions, however many field studies relating to the Exxon Valdez spill are unable to quantify oil exposure. While we originally intended to develop different dose-response curves for juvenile and adult fishes, and for pelagic, demersal and epibenthic habitat use, it is not possible at this time due to limited ecotoxicological data. Thus, we grouped all relevant data found in the literature search into one general fish grouping for the purpose of establishing the shape of the dose-response curve (although we note that the overall magnitude of effect is established through other means and may reflect differential PAH uptake rates due to habitat use). Ecotoxicological studies in progress by Gulf of Mexico Research Initiatives (GOMRI) researchers (see

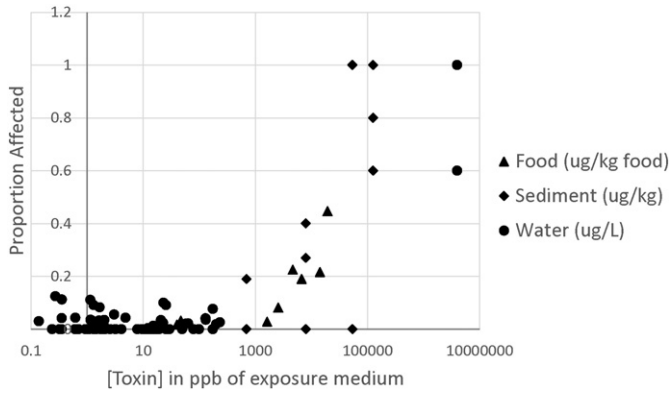
<http://gulfresearchinitiative.org/consortia/>), may soon provide data necessary to discriminate between different life stages and habitat use.

From the results of our literature review, we tested the relationship between PAH exposure and lesion and tumor frequency (a proxy for mortality) as well as growth for several reported species. Lesion frequency was chosen as a proxy for mortality due to the documented progression from lesions to tumors (Myers et al., 1991), indicating an overall decline in the health of the fish. We do not assume direct mortality from this decline in health, but rather an increase in likelihood of mortality from any source due to reduced health and behavioral changes (Moore and Dwyer, 1974; Moles & Norcross, 1988). Overall, four studies were used relating to lesion or similar pathology frequency data, located on the liver, pancreas, gills, or externally, and seven studies were used relating to growth reduction. To examine the growth response after PAH exposure, the species included were Pink Salmon (*Oncorhynchus gorbuscha*), Inland Silversides (*Menidia beryllina*), Yellowfin Sole (*Limanda aspera*), Rock Sole (*Lepidopsetta bilineata*), Pacific Halibut (*Hippoglossus stenolepis*), Chinook Salmon (*Oncorhynchus tshawytscha*), Turbot (*Scophthalmus maximus*), Zebrafish (*Danio rerio*), Southern Flounder (*Paralichthys lethostigma*) (Moles and Rice, 1983; Gundersen et al., 1996; Moles and Norcross, 1998; Meador et al., 2006; Morales-Nin et al., 2007; Vignet et al., 2014; Brown-Peterson et al., 2015). Literature growth values were not uniform in units reported, so available data were converted to reflect a proportional reduction in biomass growth rate. This was done through a data transformation, which divided each individual growth response by a reference rate (which is represented by the growth rate under the lowest PAH concentration tested). This resulted in a low value for organisms exhibiting slow growth. All values were then subtracted from one to represent the proportional difference in growth from the reference rate. Using this method, all growth rate data points fall between 0 and 1, where a value of 0 would be no reduction in growth relative to the reference rate and 0.5 would be 50% reduction in growth. Exposure concentrations were also not uniform, and included petrogenic hydrocarbons, total PAH, fuel oil concentration, total aromatic hydrocarbons, and tPAH50 (sum of 50 aromatic hydrocarbons). Units were converted to  $\mu\text{g/L}$  water,  $\mu\text{g/kg}$  wet sediment, or  $\mu\text{g/kg}$  food pellet.

For lesion frequency some of the species included were Zebrafish (*Danio rerio*), Southern Flounder (*Paralichthys lethostigma*), and Alligator Gar (*Atractosteus spatula*) (Larcher et al., 2014; Brown-Peterson et al., 2015; Omar-Ali et al., 2015). The final data set included came from a



**Fig. 1.** All literature data used in the analyses relating PAH exposure to growth reduction. The x-axis is shown on a log scale of toxicant concentration in ppb for different exposure mediums ( $\mu\text{g/L}$  water,  $\mu\text{g/kg}$  wet sediment, or  $\mu\text{g/kg}$  food). Toxicant concentrations were reported as total petrogenic hydrocarbons, total PAH, fuel oil concentration, total aromatic hydrocarbons, or tPAH50 (total concentration of 50 PAH) (Moles and Rice, 1983; Gundersen et al., 1996; Moles and Norcross, 1998; Meador et al., 2006; Morales-Nin et al., 2007; Vignet et al., 2014; Brown-Peterson et al., 2015). The y-axis is a proportional reduction in growth for each data point, obtained by comparing it to the control or lowest-exposure data point in that study. The legend illustrates the exposure medium.



**Fig. 2.** All literature data used in the analyses relating PAH exposure to lesion frequency. The x-axis is shown on a log scale of PAH concentration in ppb for different exposure mediums ( $\mu\text{g/L}$  water,  $\mu\text{g/kg}$  wet sediment, or  $\mu\text{g/kg}$  food). Toxicant concentrations were reported as total PAH, oil concentration, tPAH50 (total concentration of 50 PAH), or oil in ppb for water (Paris et al., 2012; Larcher et al., 2014; Murawski et al., 2014; Brown-Peterson et al., 2015; Omar-Ali et al., 2015). The legend illustrates the exposure medium.

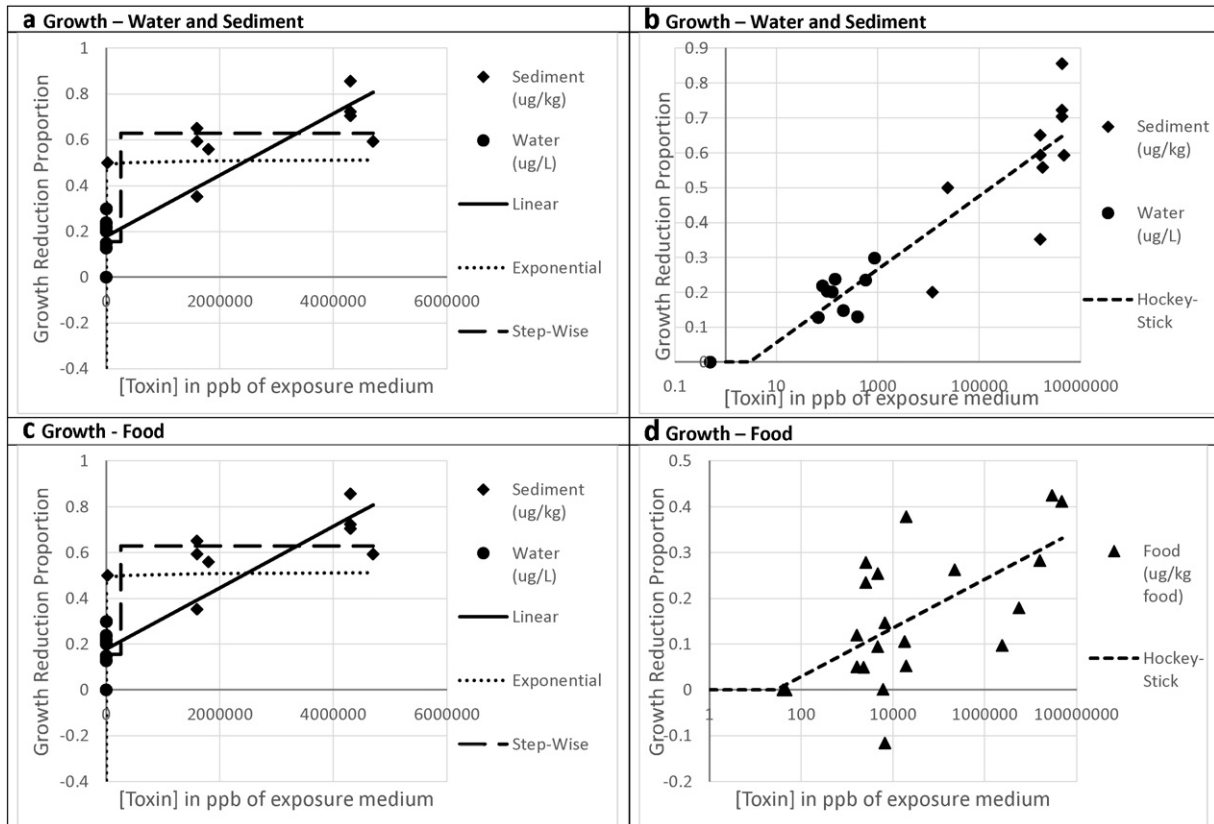
combination of Murawski et al.'s (2014) report on external lesions in a suite of 103 species caught via long-lining with Paris et al. (2012) far-field oil plume model to predict oil exposure at catch locations. These values from the oil plume model were reported in ppb in the water column; the other studies used had different exposure concentration reports of total PAH, oil concentration, and tPAH50, and the units were converted to either  $\mu\text{g/L}$  water,  $\mu\text{g/kg}$  wet sediment, or  $\mu\text{g/kg}$  food pellet. The lesion frequency data were reported as a proportion of the population with lesions at various exposure values. Pathologies included in this analysis were fin rot, external skin lesions, duct carcinoma, hepatocellular

necrosis, hepatopancreatic necrosis, eosinophilic inclusions in exocrine pancreas, reduced exocrine pancreas, epithelial proliferation of the gills, and swollen or fused lamellae of the gills.

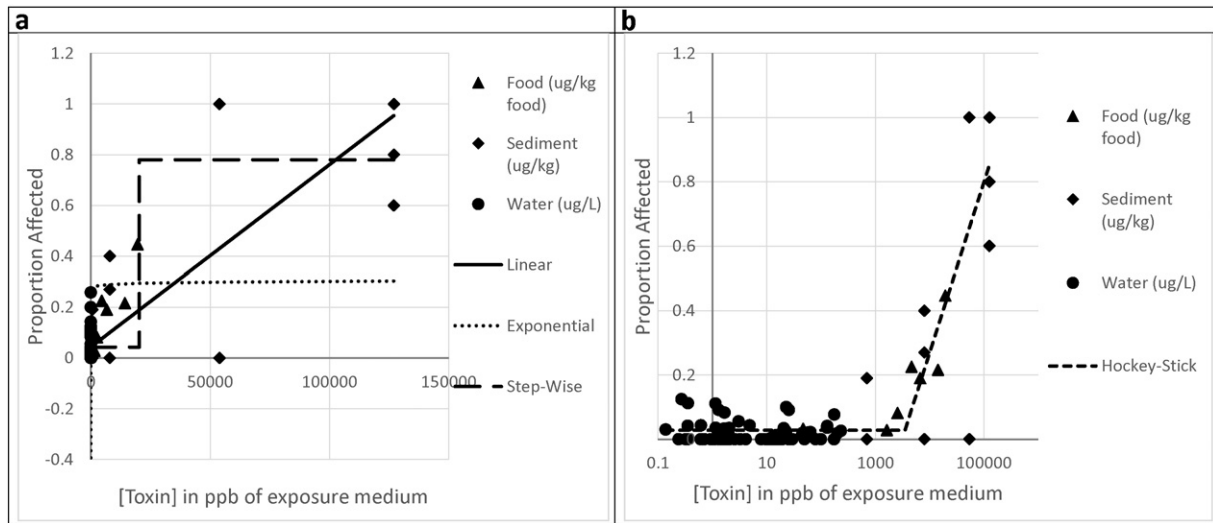
We also attempted to use a red snapper growth data set (Herdter, 2014) collected from the GOM in relation to the Deepwater Horizon blowout. Initially these data were compared to predicted water column oil concentrations provided by the far-field oil plume model created by Paris et al. (2012), however after analysis no relationship existed. At this time, the data are not applicable, but ongoing analysis is underway to compare the fish data sets to sediment core PAH concentrations (Romero et al., 2014) and may be added to future work.

2.2. Analysis of exposure route

Due to the limited availability of studies describing both an organismal impact correlated with an exposure dose, we were unable to include only one route of oil exposure in this analysis. Doing so would severely limit the breadth of our work and the already limited applicable data. We recognize that there are different bioavailabilities of toxins from oil depending on the exposure medium, however we considered the possibility that the broad range of exposure values and the large number of fish used in this analysis might minimize the effect of differing bioavailabilities. To assess if the different exposure mediums resulted in different intensities of effect, the ratio of the effect observed to the log of the exposure value for that effect was calculated for each data point in both the growth and lesion data sets. The exposure values were log transformed to reduce the effect of the large variability present in exposure values. The impacts of exposure medium on these data were assessed using a mixed-effects model that included exposure medium as a categorical, fixed variable. Since given studies may have contributed multiple data points, a random effect for study was also



**Fig. 3.** Growth data from literature data sets for different exposure mediums with fitted models. The four models are a linear model, exponential, step-wise, and hockey-stick model using log transformed PAH data. Three of the models are shown in a for water and sediment exposure and c for food exposure (exposure medium indicated by marker type). Since the hockey-stick model uses log transformed data, it is shown on a separate graph in b for water and sediment exposure and d for food exposure with a log-scale PAH concentration axis.



**Fig. 4.** Lesion frequency data from literature data sets for all exposure mediums with fitted models (exposure medium indicated by marker type). The four models are a linear model, exponential, step-wise, and hockey-stick model using log transformed PAH data. Since the hockey-stick model uses log transformed data, it is shown on a separate graph in b with a log-scale PAH concentration axis.

included in the model. The effect of source was considered by comparing nested models (each fit by maximum likelihood) using  $X^2$  tests (Zuur et al., 2009) in the lme4 package in R (Bates, 2010). If the model results were insignificant, it supported that the medium of exposure did not significantly change the organismal response, and thus the different types of data were combined for dose-response model analysis. If responses were found to differ significantly among exposure medium, we carried out posthoc tests using Holm’s correction in the multcomp package in R (Hothorn et al., 2008) to determine which mediums substantially differed from others. Significantly different exposure mediums were assessed separately for dose-response models.

2.3. Dose-response models

We evaluated four possible shapes using model-selection procedures to describe the relationship between PAH concentration and organism mortality and growth. The four models are:

1. a general linear model (Gad, 1998)

$$R = m * [PAH] + R_{\theta} \tag{1}$$

2. an exponential function (Gad, 1998):

$$R = [PAH]^a - R_{\theta} \tag{2}$$

3. a step-wise function (Gad, 1998) when

$$R = \begin{cases} R_{\theta} & \text{if } [PAH] < [PAH]_{thresh} \\ R_l & \text{otherwise} \end{cases} \tag{3}$$

4. a “hockey stick” function (Horness et al., 1998; Johnson et al., 2002) when

$$R = \begin{cases} R_{\theta} & \text{if } [PAH] \leq [PAH]_{thresh} \\ R_{\theta} + m * \log([PAH]/[PAH]_{thresh}) & \text{otherwise} \end{cases} \tag{4}$$

**Table 1**  
Fitted parameters values (with standard error in parentheses) for each growth model based on Reduced Gradient Algorithm solutions using Solver.

Growth data analyses				
Model	Equation	Parameter 1	Parameter 2	Parameter 3
<i>Water and sediment exposure</i>				
Linear	$R = m * [PAH] + R_{\theta}$	$m = 1.34E-7 (1.84E-8)$	$R_{\theta} = 0.1783 (0.0354)$	–
Exponential	$R = [PAH]^{a-R_{\theta}}$	$a = 0.00397 (0.03922)$	$R_{\theta} = 0.5510 (0.113)$	–
Step-wise	$R = \begin{cases} R_{\theta} & \text{if } [PAH] < [PAH]_{thresh} \\ R_l & \text{otherwise} \end{cases}$	Threshold = 255,416 (490–806,000 <sup>a</sup> )	$R_{\theta} = 0.15606 (0.03517)$	$R_l = 0.62877 (0.04974)$
Hockey-stick	$R = \begin{cases} R_{\theta} & \text{if } [PAH] \leq [PAH]_{thresh} \\ R_{\theta} + m * \log([PAH]/[PAH]_{thresh}) & \text{otherwise} \end{cases}$	Threshold = 2.942 (4.132)	$R_{\theta} = 3.57E-8 (0.0422)$	$m = 0.1051 (0.011)$
<i>Food exposure</i>				
Linear	$R = m * [PAH] + R_{\theta}$	$m = 7.91E-9 (2.15E-9)$	$R_{\theta} = 0.0104 (0.0259)$	–
Exponential	$R = [PAH]^{a-R_{\theta}}$	$a = 0.00328 (0.0098)$	$R_{\theta} = 0.8514 (0.1049)$	–
Step-wise	$R = \begin{cases} R_{\theta} & \text{if } [PAH] < [PAH]_{thresh} \\ R_l & \text{otherwise} \end{cases}$	Threshold = 203,407 (1309.5–4,000,000 <sup>a</sup> )	$R_{\theta} = 0.10047 (0.02997)$	$R_l = 0.2789 (0.05842)$
Hockey-stick	$R = \begin{cases} R_{\theta} & \text{if } [PAH] \leq [PAH]_{thresh} \\ R_{\theta} + m * \log([PAH]/[PAH]_{thresh}) & \text{otherwise} \end{cases}$	Threshold = 28.422 (148.7)	$R_{\theta} = -1.19E-6 (0.113)$	$m = 0.0531 (0.0122)$

<sup>a</sup> Indicates a 95% confidence interval was calculated and is reported in the parentheses instead of standard error.

**Table 2**

Fitted parameters values (with standard error in parentheses) for each lesion model based on Reduced Gradient Algorithm solutions using Solver.

Lesion data analysis				
Model	Equation	Parameter 1	Parameter 2	Parameter 3
Linear	$R = m * [PAH] + R_0$	$m = 7.174E-6$ (4.859E-7)	$R_0 = 0.04344$ (0.01286)	–
Exponential	$R = [PAH]^a - R_0$	$a = 0.004793$ (0.010321)	$R_0 = 0.754541$ (0.050793)	–
Step-wise	$R = \begin{cases} R_0 & \text{if } [PAH] < [PAH]_{thresh} \\ R_1 & \text{otherwise} \end{cases}$	Threshold = 20,340.99 (3617.5–36,787 <sup>a</sup> )	$R_0 = 0.04308$ (0.01187)	$R_1 = 0.78$ (0.03792)
Hockey-stick	$R = \begin{cases} R_0 & \text{if } [PAH] \leq [PAH]_{thresh} \\ R_0 + m * \log([PAH]/[PAH]_{thresh}) & \text{otherwise} \end{cases}$	Threshold = 3521 (836.3)	$R_0 = 0.02812$ (0.01118)	$m = 0.5297$ (0.05212)

<sup>a</sup> Indicates a 95% confidence interval was calculated and is reported in the parentheses instead of standard error.

where  $R$  represents a generic organismal response (either a change in growth or mortality),  $R_0$  is the background concentration at which populations exhibit this response, and  $R_1$  is the constant affected population response above the PAH threshold.  $[PAH]_{thresh}$  is the PAH concentration at which the response of the population changes, and  $m$  is the rate of change in the population response. The linear model (1) assumes a linear increase in population-level effect proportional to PAH concentration, while the exponential function (2) assumes that physiological stresses compound in a multiplicative way leading to increased effects at higher PAH concentrations. The step-wise function (3) assumes the organism can process low concentrations of oil with minimal or low impact but that above a threshold PAH concentration there is a higher constant population-level effect. The hockey stick function (4) assumes that the organism can process low concentrations of oil with minimal impact, and above a threshold PAH concentration, population-level effects increase log-linearly (Horness et al., 1998; Johnson et al., 2002). We used a Generalized Reduced Gradient algorithm in Solver to fit each of the four models to the growth data set (separated into just food exposure and a combined sediment and water exposure). Upon graphical inspection, the lesion data set had two data points that were three orders of magnitude larger in exposure value than the next largest exposure, and these were removed from further analysis before models were fitted following the growth data set methods. These fits were refined and standard error calculated using nonlinear least squares in R for Eqs. (1), (2), and (4). Eq. (3), the step-wise model, was refined using the rpart package in R, and through bootstrapping the 95% confidence interval (95% CI) for the step-wise thresholds were calculated (Felsenstein, 1985). We then used the Akaike Information Criterion (AIC) to assess model fit (Akaike, 1973, 1974).

### 3. Results

The results of the literature search conducted for growth and lesion frequency are shown in Figs. 1 and 2 respectively. Analysis of the impacts of medium indicated that there was a significant difference in exposure medium for the growth data ( $X^2_2 = 16.154$ ,  $p = -0.0003$ ).

Post-hoc analysis revealed a significant difference between food exposure and both sediment and water ( $z = -3.393$ ,  $p = 0.00208$ ;  $z = -3.160$ ,  $p = 0.0032$  respectively). There was no significant difference between exposure via water or sediment for growth ( $z = 0.043$ ,  $p = 0.96$ ). Therefore, the sediment and water exposure data were combined, and the food exposure data analyzed separately. For the lesion data set, the analysis indicated that there was no significant difference between exposure mediums based on the average lesion rate per log unit exposure in each medium ( $X^2_2 = 0.0317$ ,  $p = 0.86$ ). Therefore, all exposure mediums were combined for the lesion data set dose-response analysis.

After the four dose-response models were fitted to the combined lesion and separated growth data, they were plotted over the data points as shown in Figs. 3 and 4. Eq. (4), the hockey-stick model, is shown on a separate, log scaled graph as it log transforms the data, while the other four models are not on a log scaled axis so the true shape of the curve is displayed. The fitted parameter estimates are shown in Tables 1 and 2, along with their standard error or 95% CI.

The results from the Generalized Reduced Gradient algorithm and nonlinear least squares for both growth reduction and lesion frequency show that Eq. (4), the hockey-stick model, is the best fit with the lowest sum of squared residuals for all data sets (Tables 3 and 4). It is also the most parsimonious based on the AIC results for all data sets, the combined lesion and separated growth sets.

### 4. Discussion

It is clear that of the four models assessed, for these data, the hockey-stick model is both the best fit and most parsimonious regardless of exposure medium. For growth effects, the selection based on fit and parsimony of the hockey-stick model suggests that there is a decline in growth after a threshold is met, though our analysis suggests this threshold occurs at low toxin concentrations. For mortality effects, the selection of the hockey-stick relationship suggests that fish are able to tolerate low concentrations of PAHs in the environment without exhibiting a visible mortality impact. The implications of this are that

**Table 3**

Sum of squared residuals (SS) and Akaike Information Criterion (AIC) results for past literature obtained growth data for both exposure medium groupings. K is the number of parameters included in each model.  $\Delta AIC$  is the difference between the AIC value of the current model and that of the lowest AIC value of all tested models.  $\omega AIC$  is the Akaike weight, a normalized relative likelihood for the model. Akaike weights can be interpreted as the probability that under repeated sampling and testing, the model with a value of 1 would be the best fit among the models considered (Pechenik, 1987).

Model	SS	K	AIC	$\Delta AIC$	$\omega AIC$
<i>Sediment and water based exposure</i>					
Linear	0.478081772	2	–84.49	18.94	7.71E–05
Exponential	2.44036734	2	–46.997	56.433	5.57E–13
Step-wise	0.435358403	3	–83.98	19.45	5.98E–05
Hockey-stick	0.186889223	3	–103.43	0	1
<i>Food based exposure</i>					
Linear	0.356497425	2	–94.408	0.708	0.701875
Exponential	1.18927207	2	–63.714	31.402	1.52E–07
Step-wise	0.375429365	3	–87.386	7.73	0.020963
Hockey-stick	0.268269217	3	–95.116	0	1

**Table 4**  
Sum of squared residuals (SS) and Akaike Information Criterion (AIC) results for literature obtained lesion data. K is the number of parameters included in each model.  $\Delta$ AIC is the difference between the AIC value of the current model and that of the lowest AIC value of all tested models.  $\omega$ AIC is the Akaike weight, a normalized relative likelihood for the model. Akaike weights can be interpreted as the probability that under repeated sampling and testing this model would be the best fit among the models considered (Pechenik, 1987).

Model	SS	K	AIC	$\Delta$ AIC	$\omega$ AIC
Linear	1.813785951	2	−447.44	38.12	5.28E−09
Exponential	18.71181147	2	−190.73	294.83	9.52E−65
Step-wise	1.581918425	3	−466.14	19.42	6.07E−05
Hockey-stick	1.258172445	3	−485.56	0	1

they are able to metabolize and excrete toxins that are at low concentrations in the environmental, up until a certain saturation concentration when there begins to be an increasing health impact. Within this analysis, exponential models are the least representative of growth and mortality effects on fishes, which suggests that low levels of exposure do not induce a rapidly increasing organismal response. The models are limited based on the available data used to run the analyses, and could be improved upon with the addition of more data. As these data continue to become available from research being done related to the Deepwater Horizon oil spill, this relationship will continue to be tested and validated. This will also improve our certainty in parameter estimates, and allow for the possible separation of different lifestyles of fishes (e.g. benthic, pelagic, reef).

We recognize that the combination of different exposure mediums with different bioavailabilities is not ideal, and that this effect could also be minimized as more data become available and each exposure medium can be assessed separately. Currently available data sources are not robust enough to analyze these mediums separately to ascertain significant results. Within the growth analysis, more data pertaining to juvenile or young adult growth effects of water or sediment based exposure would be beneficial. For the lesion analysis, additional data is needed on histopathology of the liver or gills for all mediums. A limitation of our analysis of this data was the required use of estimated oil exposure values (Paris et al., 2012) for one study's samples (Murawski et al., 2014), as opposed to direct in-situ measurements. The mobility of wild caught fishes makes these estimates susceptible to error in our exposure approximations, and assumes the fish caught were only exposed to oil in the water column (and not in their food or with contact with the sediment). Some of the species sampled included demersal and benthic lifestyles, which could be missing a large portion of their exposure through these mediums. However, while demonstrating the surprising lack of comparable data these initial analyses also indicate that fish appear to tolerate various low levels of oil exposure before responding to contamination in both growth and mortality, suggesting a generalized response to exposure.

Understanding the relationship between oil exposure and health impacts on fishes is critical to both understanding the impacts of oil on the environment and responding accordingly (Incardona et al., 2011a; Tjeerdema et al., 2013). Determining which lifestyles increase the impact on an organism will also help to highlight the more sensitive aspects of an ecosystem to oil spills. There is a need for sampling non-benthic species, and even benthic species with different behavioral patterns, to have a more robust understanding of impacts throughout the system. The lack of available data defining lifestyle-specific sub-lethal impacts is evident; however, as oil spills occur and funding is made available, researchers are actively working to fill in these gaps. Baseline data to determine the normal state of a system prior to an oil spill is also vital to understanding if and how the system has changed in response to an oil spill.

We considered creating a dose-response relationship between oil exposure and adult fecundity, however there exists a more direct route of estimating larval effects and survivorship. Larval mortality and sub-lethal impacts are well documented even at low concentrations of PAH exposure (Moore and Dwyer, 1974; Rice et al., 1984; Carls et al., 1999; Heintz et al., 1999; Incardona et al., 2012, 2015; Sørhus et al.,

2015). A combination of the results of this paper's estimates on the impacts on growth and mortality with future recruitment impact estimates will be used to model the spill event and run long-term simulations in both an entire GOM Atlantis model (Ainsworth et al., 2015) and an Atlantis model of the northeastern GOM (Gosnell unpublished data). We can compare the projections of Atlantis against data such as before/after reef fish community surveys discussed in Patterson et al. (2014) for validation.

## 5. Conclusions

The results of this paper rely heavily on literature published data sets of laboratory exposure studies with various exposure means. We recognize that ongoing and future studies yet to be published regarding toxicity of oil will greatly improve our ability to simulate the relative impacts of oil spills once these results have been made available. Specifically, field studies documenting impacts on fish health, growth, and reproduction coupled with in situ oil measurements would be ideal. Additional data across all exposure mediums would allow for these data to be analyzed separately, to confirm that the hockey-stick relationship is supported for each individual mode of exposure. Of the studies examining biomarkers of exposure or liver enzyme activity in organisms, a coupled data set involving growth or toxicity impacts on overall health would strengthen the assumption that sampled organisms were both exposed to PAHs and had health impacts from the exposure. A broader species base would be required to test the applicability of a hockey-stick response to different lifestyles of fishes. Large data sets encompassing numerous species of various ecological lifestyles with direct exposure values would allow for this distinction of impact by lifestyle, as it appears the more frequently documented impacted benthic species may be the most heavily impacted in contaminated sediments (Harshbarger and Clark, 1990). In addition, adding in other stressors to the benthos may be vital in capturing the cumulative impact, as there has been shown to be an oxygen depletion in the benthic layer due to increased marine oil snow sedimentation and flocculent accumulation following oil spills (Hastings et al., 2014).

The selection of the hockey-stick model of juvenile and adult organismal response to petrogenic PAH exposure has implications beyond this case study scenario. This allows for an approximation of population-level effects given oil concentrations using ecosystem simulations for future scenarios. It also provides a tool to focus mitigation and research efforts in future spills, highlighting at which concentrations the risk of population-level response is high. This framework can be applied in many simulation scenarios globally, and updated by fitting the hockey-stick model with appropriate site-specific data as needed.

Beyond creating a roadmap for toxicant exposure response on fish health and growth, this project is also the first step towards modeling sub-lethal oil spill impacts on fishes using Atlantis ecosystem modeling (Fulton 2001; Fulton et al. 2004a,b, 2005, 2007). For simulation purposes in Atlantis, the fitted hockey-stick and exponential equations provide an initial starting point using the new routines. Future modifications of these routines will feature an uptake-depuration model similar to Baussant et al. (2001). This will allow for organismal uptake of oil products and time-dependent excretion or detoxification in lieu of an instantaneous equilibration with the ambient concentration.

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