



Impacts of deep-water spills on mesopelagic communities and implications for the wider pelagic food web

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ABSTRACT: Mesopelagic fishes link lower trophic levels and higher predators, as well as production at the surface to the deep sea. Mesopelagic fish may be vulnerable to deep entrained oil plumes of the type seen in the 2010 *Deepwater Horizon* spill; even at low concentrations, exposure to polycyclic aromatic hydrocarbons (PAHs) may cause lethal and sublethal effects, such as endocrine disruption, growth inhibition, and genetic damage. A reduction in the abundance of mesopelagic fish could potentially shift predation pressure by large pelagics to epipelagic forage or other species, with potential fisheries consequences. We explored this hypothesis on the West Florida Shelf using an Atlantis model for the Gulf of Mexico. Atlantis is a 3-dimensional, spatially explicit marine and coastal modeling framework that incorporates multiple submodels integrating biophysical, chemical, ecological, and fisheries dynamics. We found that biomass, trophic niche width, and predation mortality exerted by mesopelagic predators showed small but varied responses across different contributions of mesopelagics to predator fish diet under oil impacts. We observed shifts in the diet of pelagic predators with increasing availability of mesopelagic fish prey, suggesting that pelagic fish predator populations are more vulnerable to oil exposure if they are tightly coupled to the mesopelagic food web. These results suggest that when measured at the population level, oil-spill impacts may be harder to detect due to the response of individual fish species.

KEY WORDS: Mesopelagic · Atlantis ecosystem model · Oil spill · Uncertainty · Gulf of Mexico

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1. INTRODUCTION

The *Deepwater Horizon* oil spill released approximately 4 million barrels of oil into the Gulf of Mexico between April and September 2010 (McNutt et al. 2012). Factors such as the size of the spill, the source depth, and the subsurface application of dispersants made this oil spill unlike any before it. These factors conspired to produce a large undersea plume more than 35 km in length at approximately 1100 m depth that persisted for months without substantial biodegradation (Camilli et al. 2010). The mesopelagic ecosystem, the 200–1000 m depth zone of the deep-

pelagic habitat between the sunlit layers and the seafloor, was therefore exposed to high levels of oil contamination, and carbon from the oil spill entered the mesopelagic food web (Sutton et al. 2017). Mesopelagic fish were exposed to acute and chronic sublethal impacts including exposure to polycyclic aromatic hydrocarbons (PAHs) (Pulster et al. 2020). The content of PAHs in the muscle tissues of mesopelagic fishes from the Gulf of Mexico increased 7- to 10-fold following the *Deepwater Horizon* spill; dietary intake and maternal transfer of PAHs were the primary mechanisms for bioaccumulation (Romero et al. 2018). Fish exposure to PAHs can cause lethal and sublethal

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effects, such as endocrine disruption, growth inhibition, and genetic damage, even at low concentrations (Whitehead et al. 2012).

Oil-spill impacts on the mesopelagic biota also have the potential to affect other components of the food web, ecosystem resilience, and the sustainability of pelagic fisheries, as mesopelagic fishes are (numerically and in terms of biomass) the greatest component of bony fishes in the open oceans (Irigoiien et al. 2014, Sutton et al. 2020). The mesopelagic food web plays a vital role in the flow of carbon through marine ecosystems (Olivar et al. 2019), carbon sequestration (Davison et al. 2013), and climate regulation (Hudson et al. 2014). Mesopelagic species are intricately tied into the food webs of both the epipelagic (surface–200 m) and bathypelagic zones (1000–4000 m) (Romero et al. 2018, Sutton et al. 2020). A majority of the dominant mesopelagic fishes are zooplanktivorous (Koslow et al. 2014), such as myctophids feeding primarily on calanoid copepods and euphausiids (Olivar et al. 2019). Myctophids are important prey for deep-sea and epipelagic predators, including key fisheries stocks such as tuna, sharks, and billfish (Potier et al. 2007), as well as squid (Field et al. 2007), seabirds (Thompson et al. 1998), and marine mammals (Pauly et al. 1998). The mesopelagic fish assemblage appears to respond coherently to environmental forcing (Koslow et al. 2014) and can exert strong trophic control within pelagic ecosystems through strong top-down control of zooplankton and bottom-up control as prey for high trophic-level predators (Griffiths et al. 2010). Large-scale observed declines in the abundance of large, high trophic-level pelagic fish such as marlins, sharks, and tunas have been accompanied by increases in mesopelagic fish prey (Polovina et al. 2009).

The mesopelagic fish assemblage in the Gulf of Mexico accounts for ~31 % of the total volume of the Gulf (Fisher et al. 2016), is characterized by high species richness, and exhibits a high degree of niche partitioning in time, space, and diet (Sutton et al. 2017). The large stock of mesopelagic fishes requires a correspondingly large fraction of annual net primary productivity (NPP; via consumption by herbivores) to support its metabolism (Davison et al. 2013). Investigation has confirmed the presence of strong trophic linkages between meso- and epipelagic food webs in the Gulf of Mexico. Small mesopelagic fish like myctophids migrate at night into the epipelagic zone where they ingest zooplankton and migrate to deeper waters during the day in search of predator refuge (Olivar et al. 2019). The presence of high proportions of mesopelagic species in the diets of predator fish indicates feeding in the mesopelagic layer

and extensive dive behavior (Olafsdottir et al. 2016). Large predators like swordfish *Xiphias gladius* and escolar *Lepidocybium flavobrunneum* also migrate from deeper in the mesopelagic to the surface at night to feed. They join other surface predators like wahoo, yellowfin tuna (Scombridae), and lancetfish (Alepisauridae) (Murawski et al. 2018). Mesopelagic fish vertically migrate along with a variety of associated taxa, including siphonophores, cephalopods, copepods, euphausiids, and salps, which may benefit from reduced visual predation (Bianchi et al. 2013). Thus, both small and large denizens of the mesopelagic depths migrate to the surface at night, facilitating exchange of material with the epipelagic food web and at multiple size classes and trophic levels. Looking at the food habits of pelagic predators, we can also infer that reverse diel migration occurs, where surface predators like lancetfish migrate deep in the evenings to feed on non-migrating mesopelagic prey, such as hatchetfish, and remain near the surface during the day to feed on epipelagic prey (S. Murawski pers. comm.). Thus, there are complex, potentially opposing diel vertical migrations that link the epipelagic and mesopelagic food webs.

Ecosystem-based approaches to assessing the consequences of oil spills can help address non-linear and ecosystem-level interactions (Curtin & Pallezo 2010, Dornberger et al. 2020). However, mesopelagic fishes are often minimized or neglected in ecosystem models, largely due to uncertainty of their biomass (which can be as high as 10 billion mt globally; Irigoien et al. 2014) and the lack of detailed information on the contribution of mesopelagic fish to energy transfer and consumption and production across different trophic levels (Varghese et al. 2014). Carbon export by mesopelagic fish is larger than mean zooplankton flux estimates; in the Northeast Pacific it represents as much as 28 % of the total carbon flux and can exceed $20 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Davison et al. 2013). The mesopelagic contribution to the diet of pelagic predators varies spatially and temporally, reflecting oceanographic conditions and the biogeographic distribution of potential prey species (Olafsdottir et al. 2016). The contribution of mesopelagics to the diet of pelagic fish may influence the ecosystem's response to oil spills. Uncertainty in diet composition can have large effects on ecosystem model outputs and may influence damage assessments of oil exposure (Morzaria-Luna et al. 2018).

Here, we applied an ecosystem modeling approach to test the hypothesis that the mesopelagic contribution to the diet of pelagic species mediates the response of pelagics to the effects of oil spills in the Gulf of Mexico. In this region, the risk of oil spills

remains high, and petroleum exploration in ever-deeper water ensures that subsurface spills are a new environmental threat to the mesopelagic biome. It is important to better understand the factors that influence the responses of pelagic fauna to these anthropogenic impacts. We focused on the West Florida Shelf because many of the diet data in the ecosystem model framework used here were collected as part of a West Florida Shelf sampling program conducted by the Florida Wildlife Commission Fish and Wildlife Research Institute (Masi et al. 2014, Tarnecki et al. 2016).

2. MATERIALS AND METHODS

We used an ecosystem model to explore how uncertainty in the contribution of mesopelagics to pelagic fish diet influences the guild-wide response of pelagic species to oil spill effects.

2.1. Atlantis modeling framework

We used the marine and coastal modeling framework Atlantis, which is spatially explicit and incorporates multiple submodels that integrate biophysical, chemical, ecological, and fisheries dynamics in a 3-dimensional domain. It uses a computationally efficient irregular polygon structure to represent important climatic, biophysical, or jurisdictional features (Fulton et al. 2011). Atlantis is a deterministic simulation model, such that for a given parameter set and model specification, model outputs are identical (McGregor et al. 2019). Atlantis is parametrized for a specific marine system using data for that system; it simulates the food web and fisheries and is designed to produce realistic simulations of ecosystem dynamics and allow exploration of ecosystem responses under different ecological, management, or impact scenarios (Nilsen 2018). The model has been applied successfully to support strategic decision making for marine resource management worldwide; Atlantis model usage and parameterization are described in (Audzijonyte et al. 2019), the Atlantis Wiki (<https://research.csiro.au/atlantis/home/links/>), and recently published Atlantis applications (Dornberger et al. 2020, Ortega-Ortiz et al. 2020). We used code version 6177 of Atlantis2.

Briefly, Atlantis is coupled to a hydrodynamic model to provide current, temperature, and salinity forcing, which then influence nutrient cycling, primary production, and organism physiology and distribution.

Species are represented as functional groups aggregated by niche and life history; the model tracks the flow of nitrogen across functional groups (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m681p037_supp.pdf). The groups in the model can have a detailed age structure or be modeled as biomass pools. The biological processes represented include consumption, production, respiration, reproduction, and movement. Atlantis represents movement of functional groups as prescribed horizontal and vertical movements, active density-dependent movement towards food concentrations, forced seasonal or multi-year migrations within or outside the model domain, or as vertical movement simulating diel activity patterns.

The Atlantis-GOM model represents the Gulf of Mexico ecosystem and has been used to understand the food web impacts of the *Deepwater Horizon* oil spill (Ainsworth et al. 2018, Berenshtein et al. 2020, Dornberger et al. 2020), to evaluate the effectiveness of fishery closures and marine protected area networks (Perryman 2017, Drexler 2018), and to assess the performance of harvest control rules (Masi et al. 2017, 2018). The model features, parameters, and sources are described in detail in Ainsworth et al. (2015). The Atlantis-GOM is initialized for 1 Jan 2010. Polygon geometry includes 66 polygons (Fig. 1) that follow circulation, bioregions, and management divisions in the Gulf of Mexico. In each model polygon, there are up to 6 water column layers and one sediment layer. The model simulates food web dynamics between 91 functional groups (Table S1): reef fish (11 groups), demersal fish (12), pelagic fish (15), forage fish (4), elasmobranchs (6), shrimps (4), seabirds (2),

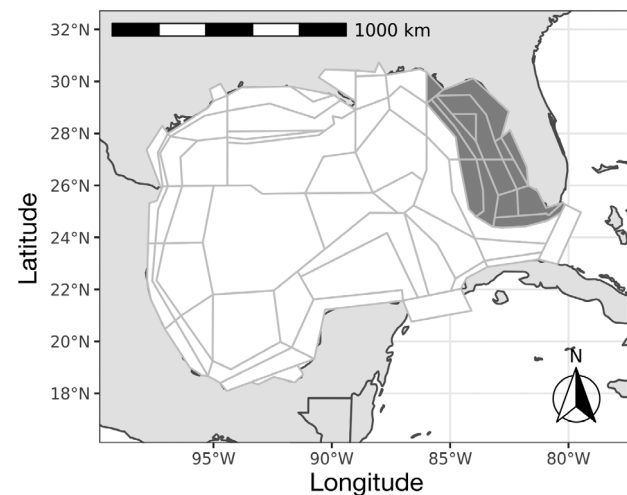


Fig. 1. Extent and polygon configuration of the Atlantis ecosystem model for the Gulf of Mexico (Atlantis-GOM). Shaded area: West Florida Shelf

mammals (4), sea turtles (3), commercial benthos (3), structural species (4), macrobenthos (3), filter feeders (3), primary producers (8), pelagic invertebrates (4), and nutrient cyclers (bacteria and 3 detritus groups). Important species including managed species and species of conservation interest are assigned to a dedicated functional group, while other species that share habitat, diets, or niches are aggregated. Functional group biomass (Table S2) was allocated across the Atlantis domain following predictions of abundance-based models that considered environmental conditions (Drexler & Ainsworth 2013). Nutrient flux and passive oceanic transport in Atlantis-GOM are driven by the American Seas model (AMSEAS), based on the Navy Coastal Ocean Model (NCOM) (Martin 2000). One year of hydrodynamic data (currents, salt, and temperature flux) (1 Jan–31 Dec 2014) is looped continuously, capturing realistic seasonal variability in the Gulf of Mexico but not interannual variability.

Atlantis-GOM models predation as a Holling Type II predator–prey functional response that is scaled using prey 'availability' parameters. The availability reflects predator total consumption potential and diet preference for both adult and juvenile ontogenetic stages that can consume both juvenile and

adult prey. The realized diet varies dynamically based on a gape limitation sub-model, on predator and prey abundances, temporal and spatial co-occurrence, feeding rates, and habitat refugia (for habitat-dependent species) (Audzijonyte et al. 2019). The availability matrix in the Atlantis-GOM was developed using probabilistic analysis of gut contents (Masi et al. 2014, Tarnecki et al. 2016). The multiple trophic links between predators and mesopelagic fish represented in the availability matrix at model initialization are illustrated in Fig. 2.

2.2. Scenarios

We simulated oil-spill impacts on mesopelagic fish as growth and mortality forcing functions. We used the approach developed by Ainsworth et al. (2018), who applied fish mortality and (sub-lethal) fish growth modifiers to simulate impacts from the *Deepwater Horizon* oil spill using the Atlantis-GOM. Briefly, modifiers were derived from dose–response models developed based on organismal response to PAHs in exposure studies and field sampling of the *Deepwater Horizon* oil spill and elsewhere (Dornberger et al.

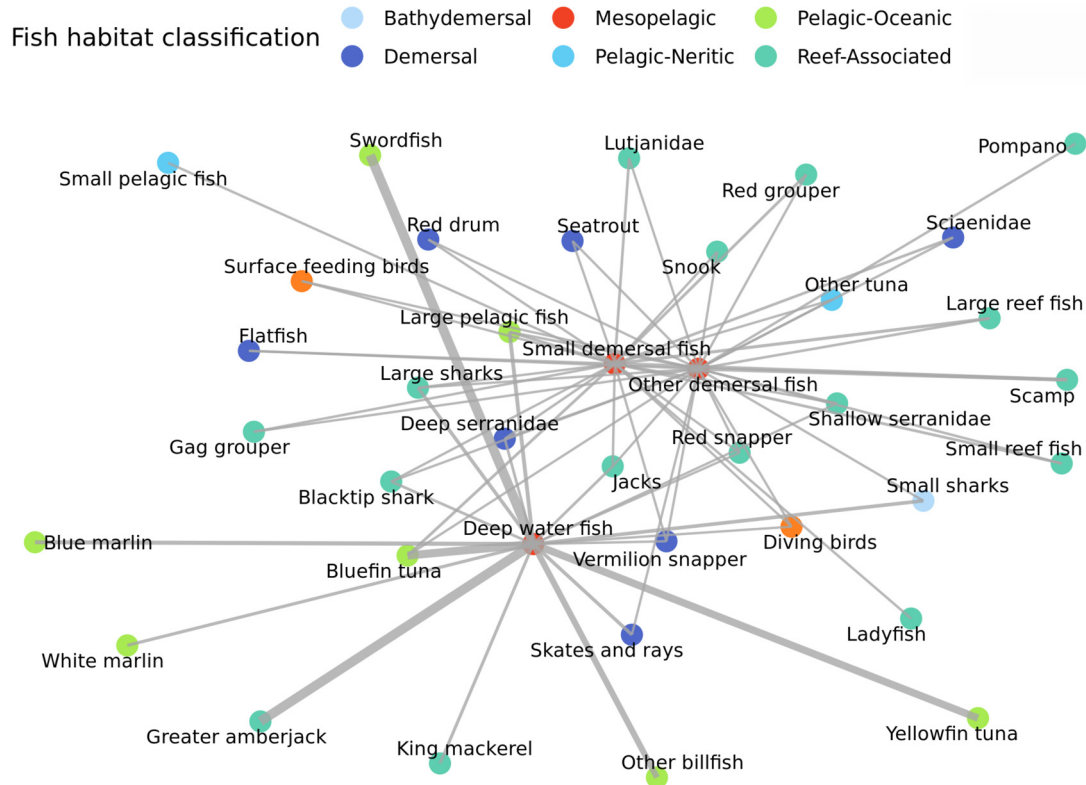


Fig. 2. Food web illustrating species that feed on mesopelagic groups in the Atlantis-GOM. Line width is proportional to availability values, which reflect predator total consumption potential and diet preference aggregated across adult and juvenile stages. Colors indicate habitat classification

2016). Both the fish mortality and growth modifiers were scaled to reflect the proportion of an affected group's diet that comes from benthic prey, as a proxy for how intimately a functional group is associated with oil-contaminated sediments, as the *Deepwater Horizon* oil spill had high rates of benthic deposition and impacts on benthic species. We used the growth and mortality modifiers from the worst-case PAH scenario, which serves as an upper bound for potential impacts. This scenario (K1000 β 363, as defined in Ainsworth et al. 2018) assumes a 1000 \times concentration factor between water column and sediment oil and a dose–response threshold for mortality effects of 363 ppb. Further details are in Ainsworth et al. (2018). We applied the worst-case oil exposure scenario developed by Ainsworth et al. (2018) in order to be consistent with previous work (Dornberger et al. 2020) and because it produces an unambiguous qualitative result from Atlantis. Thus, we encourage the reader to consider the qualitative rather than quantitative response.

We tested a scenario that applied the mortality and growth forcings only to mesopelagic functional groups: deep-water fish, small demersal fish, and other demersal fish. The majority of the species in these functional groups are categorized as mesopelagic in Ross et al. (2010) and McClain-Counts et al. (2017). The functional group composition in Atlantis-GOM is described in Ainsworth et al. (2015). Two groups, small pelagic fish and Spanish mackerel, include benthopelagic and bathypelagic species that show up in surveys of mesopelagic fish but are intended to represent epipelagic species. The scenario applied a 100 d ‘spin up’ period before introducing growth and mortality forcing functions in Atlantis-GOM to allow for transient dynamics to stabilize in the model. Forced changes to mortality and growth were applied for 167 d, followed by a 20 d oil depuration period that represents 99% clearance via gill elimination, metabolic transformation, fecal egestion, growth dilution, and elimination via egg deposition and sperm ejection (Ainsworth et al. 2018). Scenario outputs were compared to an Atlantis-GOM simulation that included no oil impacts. Hereafter, we refer to this experimental growth/mortality forcing scenario as the ‘oil-spill impacts’ scenario.

2.2.1. Uncertainty in mesopelagic contribution to predator diet

We explored the effect of uncertainty in the mesopelagic contribution to the diet of their adult and juvenile predator fish by testing a range of standardized availability values. Mesopelagic groups (deep-water

fish, small demersal fish, and other demersal fish) are potentially preyed upon by 38 fish groups (Fig. S1); these linkages are indicated in the availability matrix. We replaced these existing predator–prey interactions for both juveniles and adults with standardized values, a logarithmic series of 32 values between 0.00001 and 0.85. We then ran Atlantis-GOM forward 15 yr simulations (2010–2025) under the oil-spill impacts scenario and the no-oil scenario, in 12 h time steps. We employed virtual machines running on the Microsoft Azure cloud computing platform (Standard F16 series, 16 cores, 32 GB memory) using Ubuntu 16.04. Docker containers with all the dependencies to run Atlantis are available at <https://hub.docker.com/repository/docker/hmorzaria/atlantisdockerbatch>. The R code used to generate the simulations, analyze data, and generate figures is freely available in GitHub (<https://github.com/hmorzaria/gommesopelagic>). The R packages used in data retrieval, analysis, and visualization are in Table S3.

2.2.2. Analysis of Atlantis-GOM outputs

We focused on the impacts on pelagic and reef-associated fish functional groups in terms of biomass, catch, predation mortality, economic benefit, and system-wide ecological indicators. We report results relative to the no-oil scenario. We present results averaged over the last 3 yr of the 15 yr simulation to integrate over any interannual variability. We present results separately for Atlantis model polygons within the West Florida Shelf and for the whole model extent. For ease of presentation, we report the scenario results for functional groups aggregated by fish habitat guild (Table S1), where habitat guild is defined as a group of fish that use similar habitat (Jowett & Richardson 1995). Fish habitats were obtained for each of the species that compose each functional group (see Table A.2. in Ainsworth et al. 2015). Functional groups were assigned the most frequent habitat classification amongst the species that compose that group.

Predation mortality is the realized mortality of each prey group by each predator, scaled from 0–1. We also characterized trophic niche width, to better understand the response of biomass and predation mortality. Niche width was estimated from the antilogarithm of the Shannon index H (Hill 1973). This index gives more weight to the rare resources used by a species and is calculated as:

$$H = -\sum_i^n \pi_i \times \ln(\pi_i) \quad (1)$$

where π_i is the proportion of the realized predation mortality for a specific prey (i) at the end of the simulation, given the total number of species (n). H was standardized on a 0–1 scale using the evenness measure, J' (Krebs 1998) as:

$$J' = \frac{H}{\text{Max } H} \quad (2)$$

We assessed the impact of scenarios on ecosystem indicators that might reflect system-wide changes in ecosystem structure, considered as part of the Integrated Ecosystem Assessment (IEA) program to assist implementation of ecosystem-based fisheries management in the Gulf of Mexico (<https://www.integratedecosystemassessment.noaa.gov/>). The IEA program uses ecological indicators that are measurable, robust to observation, and process uncertainty to detect variability in ecosystem structure and function as related to management objectives (Levin et al. 2009). We used the indicators that Masi et al. (2017) previously identified for the Gulf of Mexico that account for large-scale changes in ecosystem structure (i.e. reef fish catch, pelagic to demersal ratio, piscivore to planktivore ratio), and those indicators robust to error (i.e. red snapper biomass, shrimp biomass, forage fish biomass, elasmobranch biomass).

Economic benefit was calculated as the average profit per fishing fleet for the last 5 yr of the simulation. We defined profit as the sum of the profits (P) derived from the harvest of all functional groups (i) caught by the fleet:

$$P = -\sum_i GB_i [1 - C] \quad (3)$$

where GB is gross benefit (i.e. value of catch) for year t and C is cost rate for fishing. The value of the catch is dollars t^{-1} by functional group (Table S4) and was estimated from annual commercial landing statistics obtained from NOAA fisheries (NOAA Fisheries Office of Science and Technology, commercial landings query; <https://foss.nmfs.noaa.gov/>) as the average of 2015–2018 data. Cost was set as 0.655, based on 2016 cost data for yellowtail snapper (64%) and Gulf gag grouper (67%) (Stevens 2018).

3. RESULTS

3.1. Changes in biomass

As expected, the biomass of mesopelagic prey groups, deep water fish, and other demersal fish decreased as their relative contribution to the diet of

predators increased (Fig. S2), while the third mesopelagic prey group, small demersal fish, showed a variable, non-linear response indicative of trophic effects. The biomass of pelagic and reef-associated mesopelagic predators also showed non-linear changes as the relative importance of mesopelagic fish to predator diets increased (Fig. 3). All of the pelagic oceanic groups and many of the pelagic neritic groups showed a monotonic decrease in biomass as mesopelagic prey availability increased. This implies that these large pelagic predator populations are more vulnerable to oil exposure if they are tightly coupled to the mesopelagic food web. Other billfish experienced the largest change: a 6% decrease in biomass between the lowest and largest availability value. Forage fish groups like small pelagic fish and small reef-associated fish showed a monotonically increasing biomass, indicating that they benefit from predation release as predators are forced to target mesopelagic prey. Biomass of all other functional groups showed non-monotonic responses. Many groups like jacks, large sharks, pompano, and scamp showed an inverted dome response, with biomass lowest under mid-range availability values. We suggest the increase under high prey availability values may be due to an increased abundance of some prey items. This may suggest that a combination of the previous effects, trophic coupling and predation release, are at work. These same patterns on functional group biomass were observed when analyzing the complete Atlantis model extent (Fig. S3). Other pelagic and reef-associated groups that do not directly consume mesopelagic fish, such as Spanish sardines, bioeroding fish, and filter-feeding sharks also showed a response in their biomass ratio (Figs. S4 & S5) as a result of trophic effects.

3.2. Predation mortality and trophic niche width

Predation mortality exerted by pelagic and reef-associated mesopelagic predators on their prey varied across different contributions of mesopelagics to the diet (Fig. 4). For large pelagic predators, including jacks, large sharks, swordfish, and other billfish, increasing mesopelagic availability resulted in a straightforward response of an increase in mesopelagic predation above availability 0.4. Other groups such as the many reef-associated groups are not heavily dependent on mesopelagic prey and did not show a significant change in diet despite the presence of diet linkages (Fig. S1). They even occasionally showed a small decrease in mesopelagic preda-

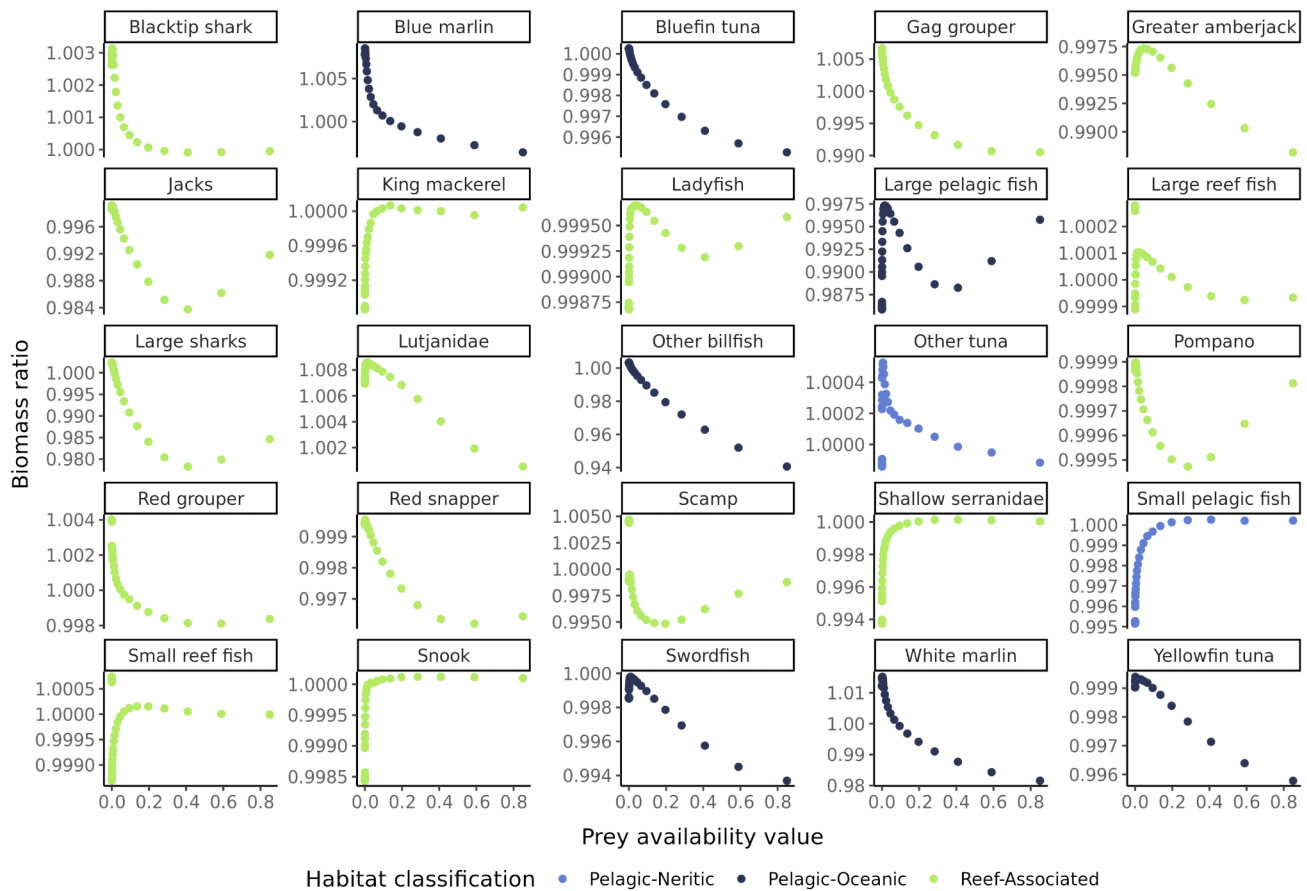


Fig. 3. Biomass ratio (oil:no oil) for pelagic and reef-associated mesopelagic predators, representing the difference in biomass between the oil-effects and no-oil scenarios across prey availability values. Values show the end state of a simulation. Simulations towards high availability values assume strong coupling between predators and the mesopelagic food web. Data for the West Florida Shelf

tion as other non-mesopelagic prey became more available. Other species such as blue marlin, bluefin tuna, and greater amberjack did not significantly access mesopelagic prey until availability values increased to 0.6 and above. Realized predation in Atlantis varies through time and space based on prey movement, abundance, and gape limitation (Kaplan et al. 2010). These patterns in predation mortality were also observed in the no-oil scenario (Fig. S6) and for other mesopelagic fish predators (Figs. S7 & S8), demonstrating the patterns are largely driven by variability in availability values rather than oil effects.

The trophic niche width, measured using the antilogarithm of H , showed in most cases the opposite pattern of the biomass ratio. For example, for blue marlin and bluefin tuna, trophic niche width increased with availability values (Fig. 5), which represent the contribution of mesopelagics to predator diet, while the biomass ratio decreased. An increase

in trophic niche width indicates that a greater range of species are accessed and that species remain as generalists despite the increased availability of mesopelagic groups. Increasing the contribution of mesopelagics to the diet of species such as swordfish, red grouper, snook, and jacks resulted in these species targeting fewer prey, and their trophic niche widths decreased. Similar patterns were observed in the no-oil scenario (Fig. S9).

3.3. Changes in catch

The catch ratio of commercial species in the West Florida Shelf (Fig. 6), across different availability values, of the oil-spill scenario relative to the no-oil scenario generally decreased with increasing availability of mesopelagics to the diet of their predators, reflecting the effects on biomass. There was a 20 and 25% decrease respectively in the pelagic longline

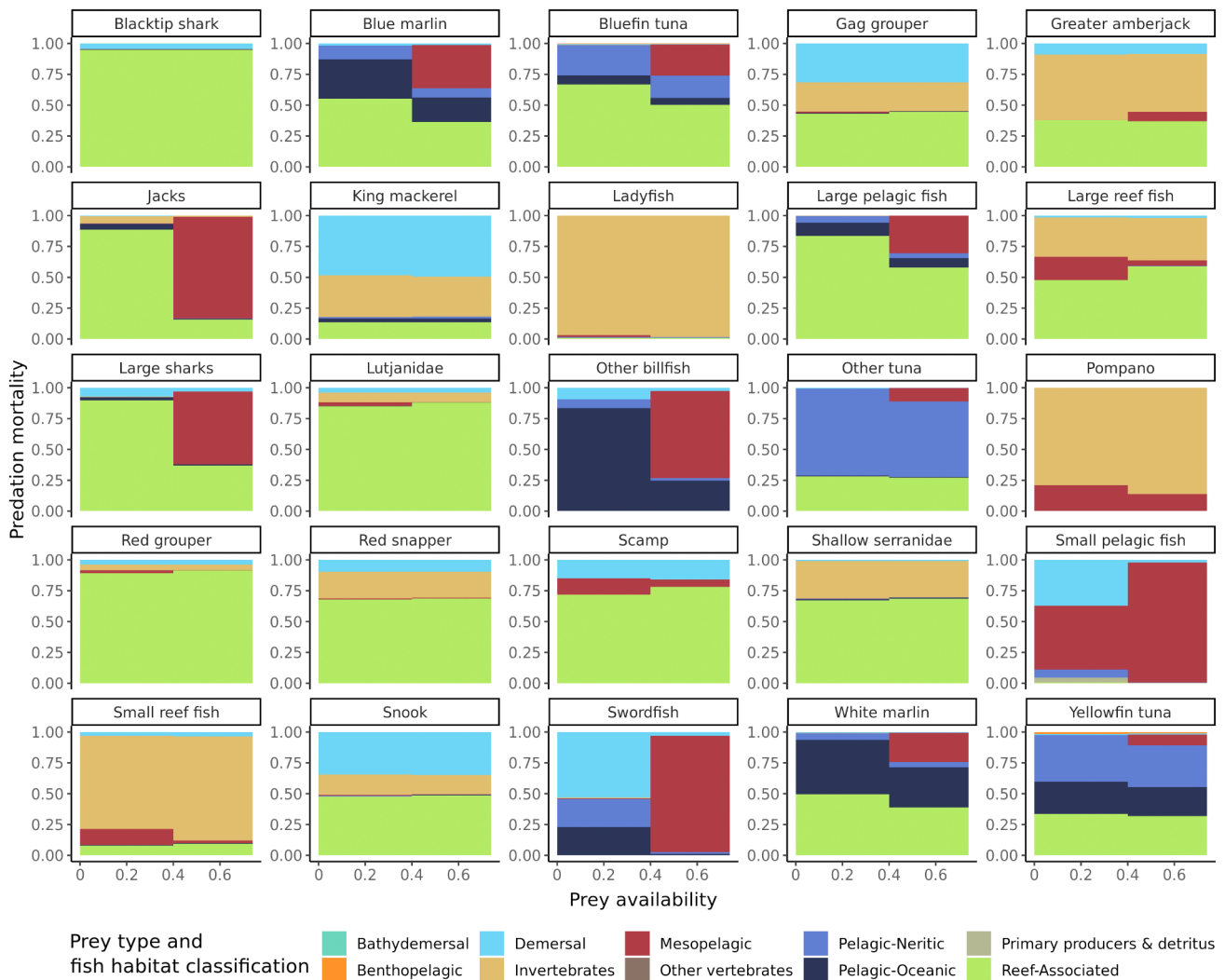


Fig. 4. Distribution of predation pressure exerted by pelagic and reef-associated mesopelagic predators on prey types, across different availability values in the oil-effects scenario. Values show the end state of a simulation. Simulations with high availability values assume strong coupling between predators and the mesopelagic food web. Results for the whole model extent

and sport fishery catch with increasing availability of mesopelagics. Average profit showed a complex response, with some mesopelagic groups experiencing up to a 60% decrease in profit as the contribution of mesopelagics to the diet increased (Fig. 7). The rest of the fish groups showed small changes in profit (<3%). Similar patterns were observed across the complete model extent (Fig. S10).

3.4. Ecosystem indicators

Ecosystem indicators showed minimal change between the mesopelagic forcing and the no-oil scenario (Figs. 8 & S11), but showed a non-linear response across availability values, reflecting the

trophic effects in biomass and catch. The piscivorous to planktonic ratio showed the most complex non-linear response, with an initial decrease and then increase for availability values higher than 0.2. Elasmobranch and red snapper biomass showed an inverted dome response, reef fish catch decreased, and the remaining indicators experienced a monotonic increase across availability values.

4. DISCUSSION

We explored how uncertainty in the contribution of mesopelagics to pelagic fish diet influences the guild-wide response of pelagic species to oil-spill effects in the Gulf of Mexico, with a focus on the

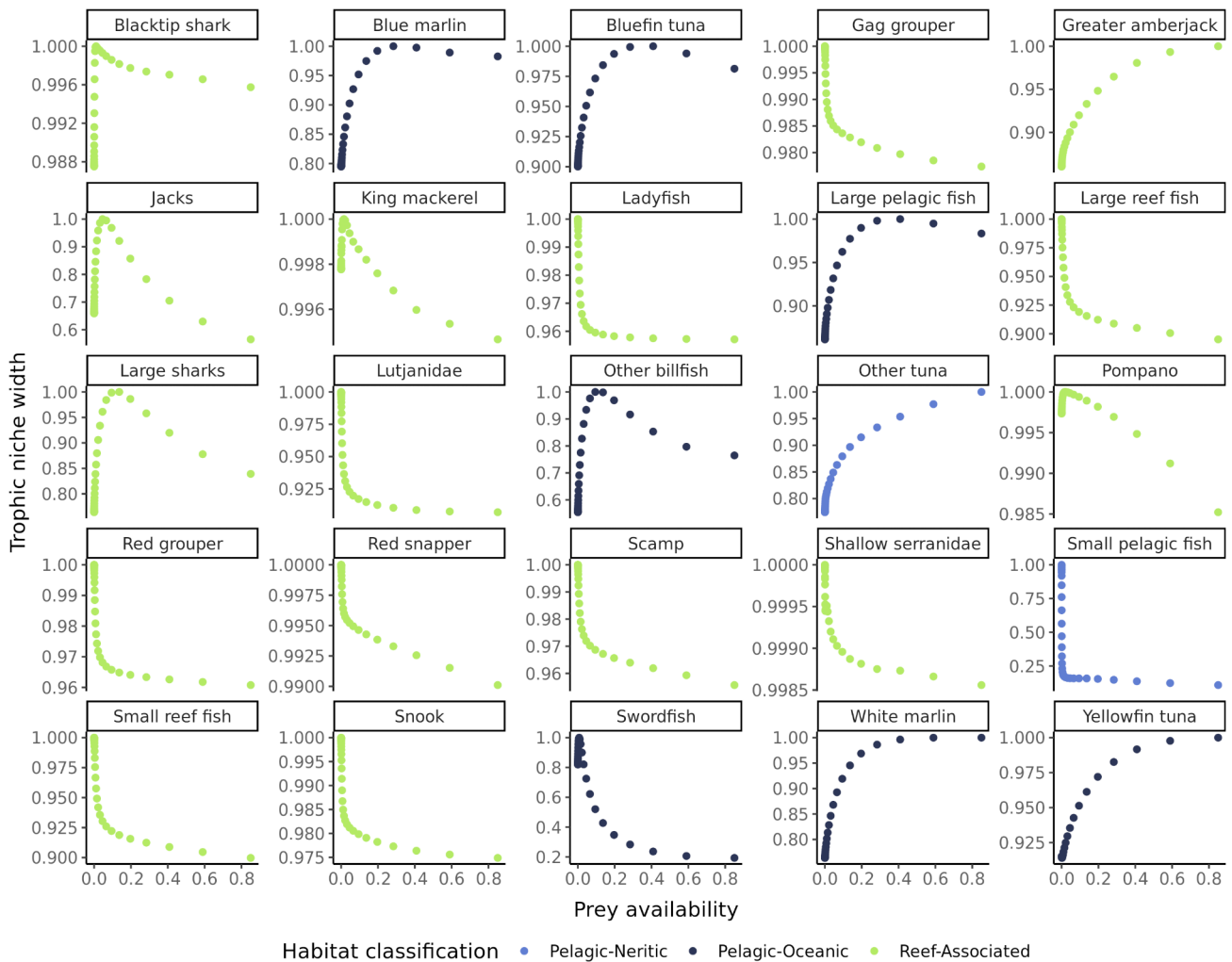


Fig. 5. Trophic niche width for pelagic and reef-associated mesopelagic predators, calculated as the antilogarithm of the Shannon index using predation mortality across prey. An increase in trophic niche width indicates a greater range of species are accessed. Values show the end state of a simulation. Simulations with high availability values assume strong coupling between predators and the mesopelagic food web

West Florida Shelf, because a large proportion of the diet data that informed the Atlantis-GOM came from that area of the Gulf. Our research is significant because the Gulf of Mexico has one of the most diverse mesopelagic ichthyofaunal communities with a high degree of niche partitioning in time, space, and diet preference (Fisher et al. 2016). Mesopelagics in the Gulf of Mexico have higher abundance, richness, and biomass than in adjacent regions because of the influence of tropical waters, winter cooling, and the Mississippi River (Sutton et al. 2017). In the Gulf, pelagic fish take deep-water excursions to meso- and bathypelagic depths for foraging or reproduction, representing a link and transfer of nutrients across depth layers (Howey et al. 2016). The *Deepwater Horizon* oil spill in the Gulf of Mexico

led to a surface oil layer, dispersed microdroplets throughout the water column, and sub-surface plumes that resulted in direct mortality of marine wildlife (Quintana-Rizzo et al. 2015). The oil also led to sub-lethal effects that may affect abundance, recruitment, habitat use, growth, longevity, and reproductive capacity and lead to long-term, population-level impacts (Whitehead et al. 2012, Romero et al. 2018, Pulster et al. 2020); for example, there was likely a loss of early recruits of many epipelagic predators that spawn in the open Gulf (Incardona et al. 2014).

We simulated oil-spill impacts on mesopelagic fish as growth and mortality forcing functions (Dornberger et al. 2016, Ainsworth et al. 2018). The oil-spill scenario used here had previously predicted that the *Deepwater Horizon* oil spill caused changes

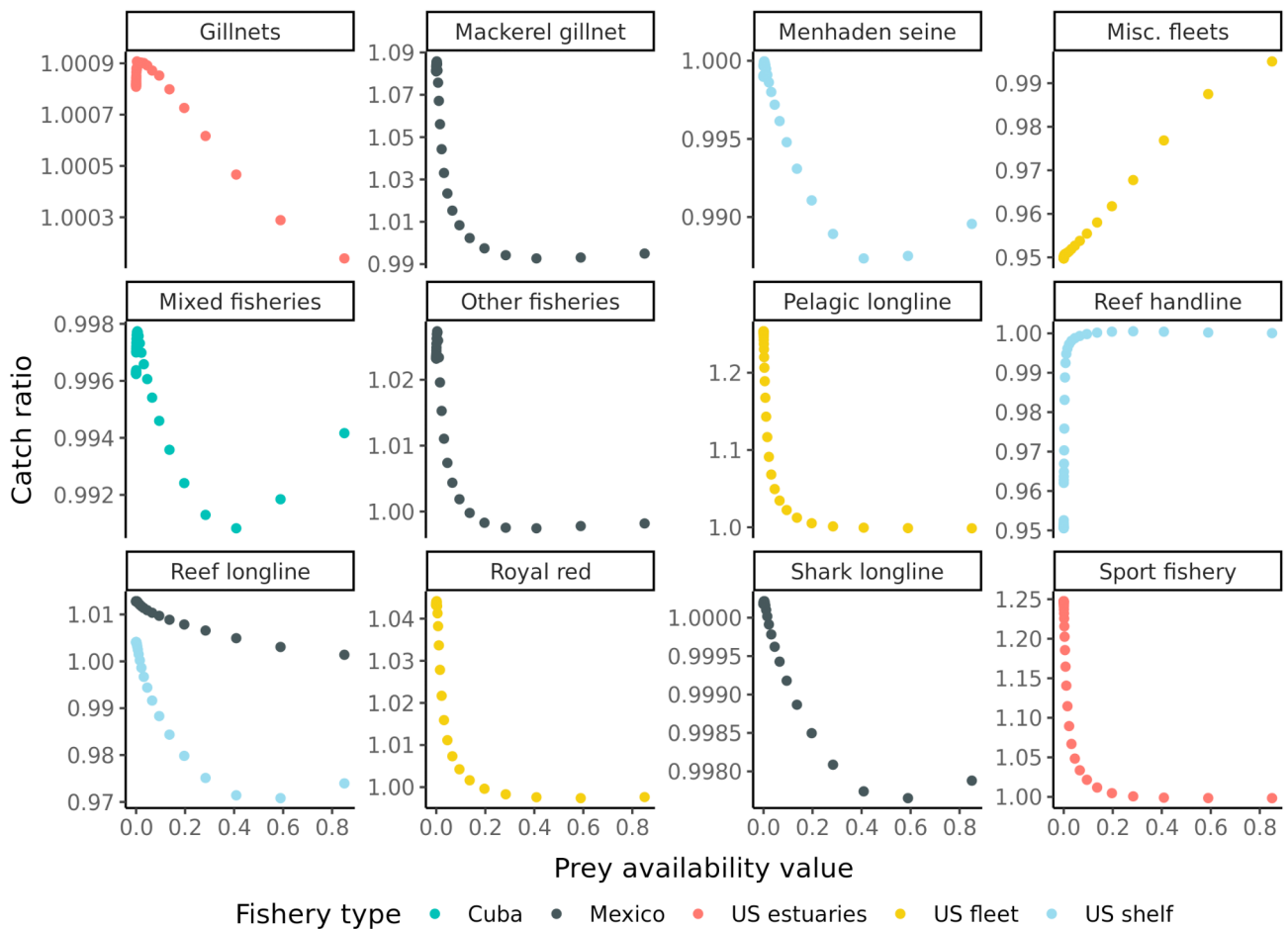


Fig. 6. Catch ratio (oil:no oil) for fishing fleets, representing the difference in fisheries catch between the oil-effects and no-oil scenarios, across prey availability values. Values show the end state of a simulation. Simulations with high availability values assume strong coupling between predators and the mesopelagic food web. Data for the whole model domain

in biomass, age structure, and distribution in a variety of fish guilds (Ainsworth et al. 2018). Here, we explored the implications of uncertainty in the mesopelagic contribution to the diet of their predator fish by varying diet availability values, which reflect total consumption potential and diet preference. We found variable responses in the biomass and trophic niche of mesopelagic predators and in the catch by fishing fleets in model simulations. These variable responses may stem from variability in recruitment, spawning, and life history, which may buffer oil impacts due to a portfolio effect, where stability in aggregate community properties results from statistical averaging of the fluctuations in species' properties (Lhomme & Winkel 2002). Our results exemplify how the effects of oil spills, when measured at the aggregate community level, may be harder to detect because of varied responses of individual fish species. This suggests there could be a minimum useful level of taxonomic or niche resolution required for

multispecies modeling of pelagic ecosystems, resulting from the intricate niche partitioning that comes with having a spectrum of movement behaviors exhibited by both predator and prey. Even in cases where our knowledge of such animal behaviors is limited, and there are many examples, Atlantis at least represents spatial partitioning implicitly through the diet matrix. That implicit separation is also characteristic of non-spatial and 2-D trophic modeling, represented by link variability (Yeakel et al. 2012). Additionally, stomach content data ensures a minimum level of realism.

Nevertheless, the functional group structure in Atlantis is sufficient to reveal some important dynamics. In our experiment, we increased availability of mesopelagic prey to a host of predators, but only the predators with the greatest spatial and temporal overlap with the mesopelagic prey base were able to fully capitalize upon increased availability. We therefore see uneven increases among predators and

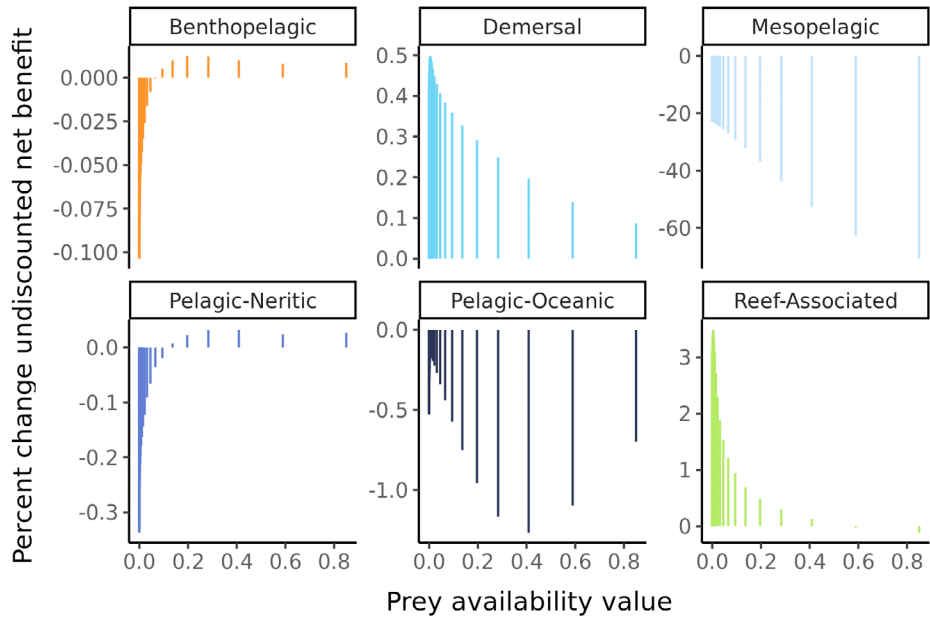


Fig. 7. Percent change in profit from fisheries target groups, representing the difference between the oil-effects relative to no-oil scenarios, across prey availability values. Data for the West Florida Shelf

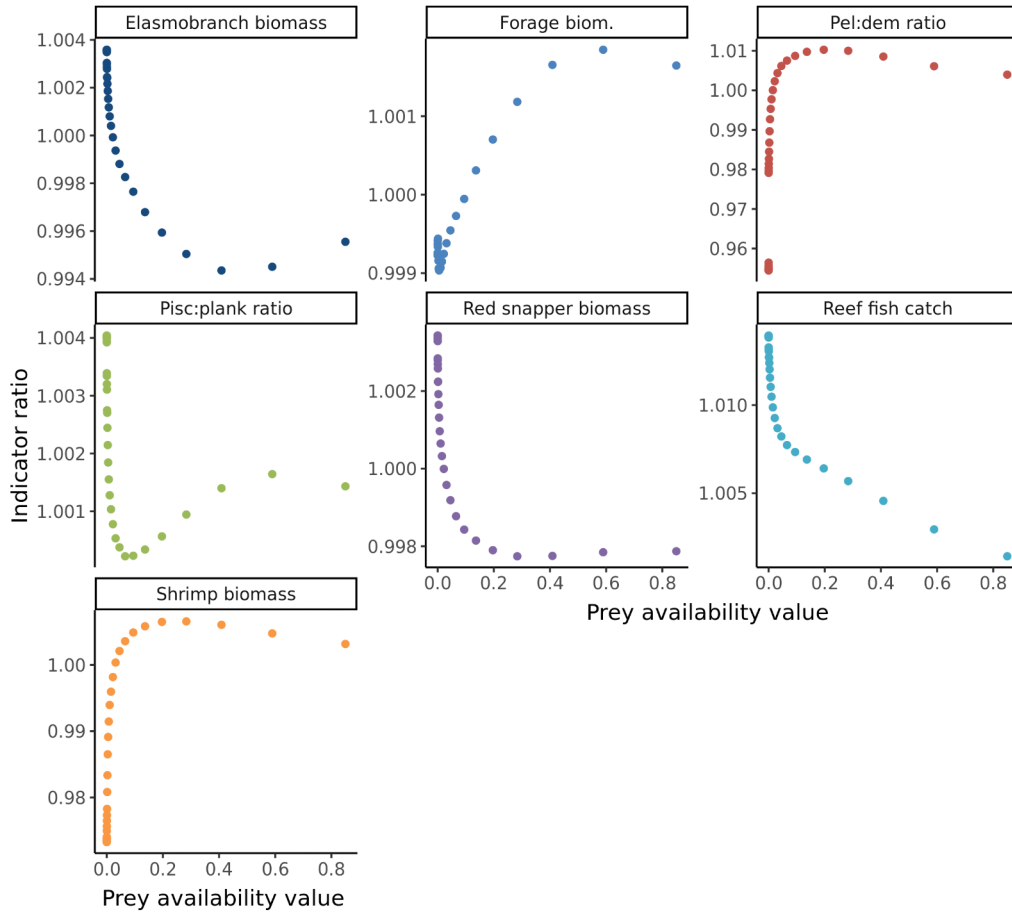


Fig. 8. Normalized ecosystem indicator ratios across different availability values, representing the difference in indicators between the oil-effects and no-oil scenarios, across prey availability values. Data for the West Florida shelf

across space under our experimental conditions, with jacks, large sharks, billfish, and swordfish achieving the greatest effective increase in predation mortality on mesopelagic prey (see increasing red area left to right in Fig. 4). Restricting our focus to these groups offers a learning opportunity since confounding trophic effects are minimized. For the 2 pelagic groups billfish and swordfish, our work reveals an unappreciated hazard of deep-water oil spills. Here, strong trophic connections to the mesopelagic are likely a liability because deep-water ecosystems are at risk from subsurface plumes. This is evident from the decreasing biomass and decreasing profitability of their fisheries as mesopelagic prey are increased in their diets. A similar dynamic can be seen in several other large pelagic predators (blue marlin, white marlin, and bluefin tuna). A different dynamic is demonstrated in reef-associated groups, jacks and large sharks. These reef-associated predators differ from the previous examples of large pelagic predators because they have prey available in other biomes, particularly reef-associated forage fish; evidence of this can be seen in the predation mortality and trophic diversity data. Their portfolio of prey occupy different areas and habitats and perhaps offer protection from the moderate trophic impacts of the oil spill.

We modeled shifts in the diet of pelagic predators with increasing availability of mesopelagic fish. Dietary shifts resulting from oil-spill impacts reflect shifting prey availability (Velando et al. 2005). Our findings are consistent with the analysis of Quintana-Rizzo et al. (2015), who determined that mesopelagic fish predators exhibited trophic shifts following the *Deepwater Horizon* spill, as evidenced by changes in $\delta^{15}\text{N}$ isotopes up one trophic level, and may reflect changes in the abundance of common prey items. Tarnecki & Patterson (2015) also found significant diet shifts post-spill in red snapper, a common reef fish in the Gulf. Plankton disappeared from the red snapper diet and the contribution of benthic and demersal fish prey increased. The Atlantis ecosystem model used here also predicted these nonlinear ecosystem responses. In our model simulations, the other pelagic and reef-associated groups that do not directly consume mesopelagic fish also showed a response in their biomass as a result of indirect trophic effects cascading through the food web. Forage fish biomass increased with higher mesopelagic availability, suggesting they benefited from predation release. Upper trophic level predators in particular can reflect alterations in food web trophodynamics due to oil-spill pollution (Moreno et al. 2013).

We found a small decrease in the catch of commercial species with increasing availability of mesopelagics to the diet of their predators. Fishery production in the Gulf of Mexico is ~ 1 million mt yr^{-1} and includes a variety of invertebrate and finfish coastal and marine species (Gracia et al. 2020). Following the *Deepwater Horizon* and *Ixtoc-1* spills in the Gulf, there was no collapse or long-term effects on fishery productivity. Economic impacts from oil spills usually arise from the imposition of a moratorium on harvesting activities within the affected area, rather than from any direct biological impacts to fishery stocks (Collins et al. 2003). Our results contrast with modeling of impacts of the *Deepwater Horizon* oil spill using an Ecopath–Ecosim ecosystem model by Rohal et al. (2020) who found a 13% decline in stone crab fisheries but estimated gains of up to 11% in 4 other groups. Long-term economic impacts on fisheries from an oil spill will vary depending on the characteristics of the fishery (i.e. target species, location), the timing and extent of the oil spill, markets, management regime, and fisher's ability to respond (Pascoe 2018). It is also important to consider that oil impacts will interact with the impacts of fishing on reproductive potential, fish body size and condition, the resilience of fishery species, food web structure, and ecosystem function (Short et al. 2021).

A limitation of our study was that our approach of simulating oil-spill impacts on mesopelagic fish as forced changes to growth and mortality does not consider other types of effects oil spills can have on mesopelagic species. For example, following the *Deepwater Horizon* spill there was a reduction in primary production and carbon export to the deep sea (Prouty et al. 2016). Our study also did not consider the effects of chemical dispersants, which are used to break down oil into small droplets; dispersants might be more toxic to some marine organisms than previously thought, while the small oil droplets created by dispersant use in combination with oil are often more toxic to marine organisms than oil alone (Buskey et al. 2016).

Future updates to the Atlantis-GOM model will be made to improve modeling oil-spill effects including simulating connectivity between the deep Gulf and large pelagic predators through improved diet estimates and spatiotemporal predator–prey co-occurrence. Work in progress will create a new availability matrix using a mixed distribution model approach to estimate diet proportions, which will solve problems in the previous diet analyses of Masi et al. (2014) and Tarnecki et al. (2016) related to zero inflation, where diet proportions are heavily skewed by an excessive

proportion of zero values. Trawl data (e.g. MOCNESS) will be incorporated to better inform the biomass distribution of mesopelagic groups through each Atlantis depth layer during day- and nighttime hours (T. T. Sutton et al. unpubl. data), and pop-up satellite archival tagging data will be used to provide similar information for large pelagic groups (NOAA NMFS Highly Migratory Species Division). We expect these model improvements to more effectively capture cascading effects on the populations of large pelagic species following a disruption of the mesopelagic prey pool.

Mesopelagic species might be continuously exposed to oil pollution for long periods following a spill because deep-sea communities can serve as repositories for hydrocarbons (Romero et al. 2017). Oil-derived carbon may enter fish through ingestion of contaminated prey or accidental ingestion into the gut (Quintana-Rizzo et al. 2015). Gulf studies have found PAH concentrations in the gut tissues and eggs of mesopelagic species within the range known to cause early mortality, embryonic abnormalities, and sublethal impacts 5 yr following the *Deepwater Horizon* spill, even after PAHs were undetectable in the water column (Romero et al. 2018). Even low concentrations of oil-contaminated waters can result in sublethal exposures causing changes in genome expression and tissue morphology and physiological and reproductive impairment (Whitehead et al. 2012). Mesopelagic fish might be exposed to oil and dispersants following an oil spill through vertical sinking of sargassum, which may also serve as a significant labile carbon source for microbial communities that can consume dispersed oil and dead plant material (Powers et al. 2013). The deep-sea benthos, which depend on the flux of organic materials from surface waters for food, are also vulnerable to oil spills that form deep-water plumes of oil and gas and lead to the deposition of oil onto the seafloor (Fisher et al. 2016).

As oil exploration in the Gulf of Mexico moves into deeper water, the entrainment of leaked oil into the deep sea is likely to become more frequent over time (Sutton et al. 2020). In the Gulf, most oil production now comes from wells at depths of 1500 m or greater (Murawski et al. 2020), so the mesopelagic may be the ecosystem component most affected by oil spills in the deep sea. Mesopelagic fish may be a long-term sink for oil and, although recovery may be fairly rapid in the water column, impacts to the ecosystem via the food web might affect multiple species and trophic levels (Romero et al. 2018). However, over time, marine systems can lose their adaptability and the system's state is likely to cross a tipping point,

leading to a regime shift (Park et al. 2016). Our results suggest that pelagic fish predator populations are more vulnerable to deep-sea oil contamination if they are tightly coupled to the mesopelagic food web. This implies and requires not only that mesopelagic prey can make a significant contribution to the diet of these large pelagic predators relative to other prey sources, but also that mesopelagic prey are vulnerable to deep-water oil plumes of the type that occurred with the *Deepwater Horizon* oil spill. Although this is not a settled question, there is sufficient evidence from the *Deepwater Horizon* oil spill that at least the mesopelagic biome was impacted.

Acknowledgements. This article is a result of research funded by the Gulf of Mexico Research Initiative to the Center for Integrated Modeling and Analysis of Gulf Ecosystems (C-IMAGE) (GRI2011-I-072). Microsoft Azure cloud computing resources were provided by a Microsoft Azure Research Award to H.N.M.L. The sponsors had no input into the study design, the collection, analysis and interpretation of data, the writing of the article, or in the decision to submit the article for publication.

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