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Modeling Pelagic Feeding in the Gulf of Mexico with Implications for Ecosystem-Based Fisheries Management

by

Rebecca L. Scott

A dissertation submitted in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
with a concentration in Marine Resource Assessment
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DEDICATION

This dissertation is dedicated to two little girls. To the first, my niece: even though we haven’t met yet, I already love you with my whole heart. I can’t wait to show you the wonders of the world and to cheer on all your wildest dreams. To the second, a toddler with a bleach-blonde bowl cut watching Deep Sea Dive in her New Jersy living room: we did it.

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LIST OF ABBREVIATIONS

Abbreviations	**Definitions**
BE	Beta distribution
BEINF	Zero-and-one-inflated beta distribution
BEZI	Zero-inflated beta distribution
DWF	Deepwater fish
DWH	*Deepwater Horizon*
EBFM	Ecosystem-based fisheries management
GOM	Gulf of Mexico
HCR	Harvest control rule
MSE	Management strategy evaluation
YTN	Yellowfin tuna

ABSTRACT

The focus of this dissertation was simulating trophic dynamics in the pelagic Gulf of Mexico (GOM) with an emphasis on ecosystem-based fishery management (EBFM) strategies for large pelagic species. Fisheries management in the United States largely utilizes single-species assessments, although managers are increasingly interested in EBFM approaches to better account for ecosystem effects on stocks such as predator/prey dynamics. Production in the surface layer of the pelagic zone is variable with environmental conditions and prey is often concentrated in patches by hydrodynamic features. Production is also transported vertically via diel vertical migration, during which deep-sea species provide potentially key forage resources for epipelagic predators. Locating prey in the pelagic zone can be a difficult task for visual predators, more so than in inshore habitats. Management of exploited pelagic predators could benefit from more investigation into how trophodynamics affect populations. The objectives of this work were to 1) explore spatial patterns and environmental drivers of pelagic feeding, 2) improve the estimation of pelagic diets in an ecosystem model of the GOM, and 3) evaluate ecosystem-based management strategies for a pelagic fish predator considering bottom-up trophic dynamics. I combined a hydrodynamically informed particle-tracking model with an Atlantis ecosystem model of the GOM to simulate feeding opportunities available to juvenile sea turtles depending on dispersal location. I found that food availability to juveniles was greatest offshore along the West Florida Shelf edge, and that hydrodynamic features including frontal zones facilitated retention in these areas. I then explored different statistical distributions to improve the representation of pelagic feeding dynamics in the GOM Atlantis model. To capture the mechanism of locating patchy prey in the pelagic environment, I applied zero inflated-type beta distributions to diet data that separately model the binomial process of encounter probability and the continuous beta distribution for diet composition. I found the zero-inflated beta model to be an improvement over a traditional beta distribution for fitting offshore predator diets. These improved diet estimates were incorporated into the GOM Atlantis model. Fitted diets showed that large offshore fishes heavily utilized deep-sea prey species, which could result in increased vulnerability to deep water disasters such as oil spills. I then used the GOM Atlantis model to conduct a management strategy evaluation that examined whether it was beneficial to consider the availability of mesopelagic fish prey in control rules for a large pelagic predator. Biomass and catch of the example predator, *Thunnus albacares*, were higher under ecosystem-based harvest control rules than under single-species and constant F management strategies. The benefit of EBFM increased as mesopelagic fish abundance decreased, suggesting that proactive EBFM for large pelagic fishes may be particularly strategic in the case of future deep-sea disturbances. This project demonstrates the utility of statistical and numerical modeling to simulate pelagic trophic dynamics and evaluate potential EBFM approaches.

CHAPTER 1: INTRODUCTION

Federal fisheries management in the United States has been moving toward the goal of an ecosystem-approach to addressing management questions, also referred to as 'ecosystem-based fisheries management (EBFM)' (NOAA 2016, Brodziak and Link 2002). Traditional single-species stock assessments that do not explicitly account for ecosystem effects on managed populations can be uncertain in their predictions (Walters and Martell 2004). EBFM strategies can include a variety of ecosystem considerations, including abiotic drivers of production (Tommasi et al. 2017, PFMC 2023), environmental sources of mortality (SEDAR 2021, Vilas et al. 2023), and population impacts due to predator-prey dynamics (Deroba et al. 2019, Punt et al. 2016). Trophic dynamics can be classified as exhibiting top-down (predation limiting prey populations), bottom-up (prey availability limiting predator populations), or wasp-waist (intermediate trophic levels affecting both predator and prey) control (McQueen et al. 1986, White 1978, Cury et al. 2000). Trophic modeling approaches are often applied to simulate these impacts, such as in ecosystem models like Ecopath with Ecosim, OSMOSE, and Atlantis (Christiansen and Walters 2004, Shin and Cury 2001, Fulton et al. 2011). Ecosystem models are therefore useful tools for investigating EBFM questions that include predator-prey considerations.

The overall focus of this dissertation is modeling feeding in the pelagic zone, specifically investigating how prey availability influences pelagic predator populations (bottom-up control). The pelagic ecosystem is vertically structured by depth and resulting light intensity (Wyatt 1976). In the epipelagic, or 'sunlight', zone (0-200 m depth), primary production is spatiotemporally dynamic and driven by environmental conditions such as temperature and nutrient availability (Steele 1976). Lower trophic level organisms (e.g. phytoplankton, macroalgae, zooplankton) are concentrated in patches by physical oceanographic features such as frontal zones, currents, and eddies (Steele 1976, Zhang and Hu 2021). These frontal zones also influence the distribution and abundance of the larvae of top pelagic predators such as tunas (Cornic and Rooker 2018), and visual predators (e.g. mammals, large fishes) may target these aggregations for the shoals of planktivorous forage fishes that they attract (Suthers et al. 2023).

While prey in the epipelagic zone is spatiotemporally dynamic across the horizontal plane, the pelagic food web also features vertical connectivity across depth layers via diel vertical migration (DVM). Zooplankton, crustaceans, cephalopods, and small fishes from the mesopelagic (200-1000 m depth) and upper bathypelagic (1000 – 4000 m depth) zones vertically migrate into surface waters at night to feed on planktonic prey (Sutton 2013). This daily migration of deep-water species provides an important trophic link between the vertical habitat zones of the open ocean; large pelagic predators that consistently occupy the epipelagic zone feed upon these visiting mesopelagic migrators before they return to the deep at dawn. This massive vertical movement of production is a crucial component of carbon transport and sequestration in the open ocean (Hoagland et al. 2019). However, mesopelagic species are increasingly at risk with deep-sea drilling and mining activities. Many large pelagic predators are of either conservation (e.g. marine mammals, sea turtles, sea birds) or commercial (e.g. tunas, billfishes) importance; the dynamics of prey availability in the pelagic zone and resulting bottom-up impacts on predator populations are therefore important considerations for ecosystem-based management. This study aimed to simulate pelagic food web dynamics in the Gulf of Mexico (GOM) using an Atlantis ecosystem model (Fulton et al. 2011), and to use Atlantis to examine EBFM questions for the management of large pelagic predators considering pelagic predator/prey dynamics.

The GOM Atlantis model was developed by Ainsworth et al (2015) and updated by Perryman et al. (in press). It is an end-to-end ecosystem model, linking low-level processes to higher trophic levels, and includes hydrodynamics, biogeochemical cycling, and fishing effort (Audzijonyte et al. 2017). The GOM Atlantis model contains 91 functional groups (Appendix 3) that are either single-species (e.g. managed species) or aggregated by similar life history traits. Vertebrate groups are age-structured with up to ten age classes. The polygon geometry of the GOM Atlantis model was defined to capture major bathymetric, jurisdictional, and estuarine features (Figure 4.1). Polygons have up to seven depth layers including a sediment layer. The GOM Atlantis model has been used to evaluate EBFM strategies (Masi et al. 2018), test the performance of ecological indicators (Masi et al. 2017), and study the ecosystem impacts of the 2010 *Deepwater Horizon* (DWH) oil spill in the northern GOM (Ainsworth et al. 2018, Dornberger et al. 2020). A more detailed description of Atlantis and the GOM Atlantis model can be found in Chapter 2 of this dissertation.

In Chapter 2, *Modeling transport and feeding of juvenile Kemp's ridley sea turtles on the West Florida shelf* (Scott et al. 2024), I combined an ICHTHYOP particle-tracking model (Lett et al., 2009, Putman et al. 2020) with the GOM Atlantis model to simulate the dispersal of juvenile Kemp's ridley sea turtles (*Lepidochelys kempii*) from nesting beaches in Mexico and onto the West Florida Shelf (WFS). The main goal of this work was to examine how physical oceanographic features effect the transport of pelagic-type juveniles to areas of adequate food availability. Dispersal patterns across the GOM were simulated using ICHTHYOP's physical oceanographic model and the GOM Atlantis model was used to quantify feeding opportunities available to juveniles (i.e. consumption) upon reaching the WFS. I then examined relationships between the spatial patterns of consumption, regional frontal features (Zhang and Hu 2021), and large-scale climatological indices to identify physical drivers and determine implications for feeding success under future climate change. The work for this chapter was funded by a Florida Restore Act Centers of Excellence Program grant awarded to Dr. Cameron Ainsworth.

In Chapter 3, *Inflated-type models for estimating fish diet composition*, I presented an improved statistical method for estimating the diet of pelagic predators in the GOM Atlantis model. Diet estimates for ecosystem models are typically created by simply averaging across stomach content data, which can skew estimates and over-estimate rare feeding events (Masi et al. 2014). The current statistical method for estimating diet in the GOM Atlantis model uses the Dirichlet distribution, a multi-variate version of the beta distribution (Tarnecki et al. 2016). The beta distribution is bound by zero and one and is therefore appropriate for fitting proportional data such as diet composition. However, diet data is inherently zero-inflated as only a few potential prey items are typically found in a given stomach and may also be one-inflated if a stomach contains only one prey item. The classic beta distribution cannot fit true zeroes or ones and may skew diet estimates in an effort to fit to zero- and/or one-inflated data. Zero- and one-inflation may be particularly prevalent in pelagic diets as prey is patchily distributed and opportunistic feeding occurs.

In Chapter 3 I fit both zero-and zero-and-one-inflated beta distributions (Ospina and Ferrari 2010) to GOM diet data, which separately model the binomial process of encounter probability (i.e. zeroes and/or ones) with the continuous beta distribution of how much prey was consumed upon a successful encounter. I analyzed results for a suite of example predators that represented various habitat associations and trophic levels. I assessed model performance using measures of fit and parsimony. I hypothesized that the diet of offshore-pelagic predators would be best estimated by inflated-type models that include the binomial encounter rate process because prey in the pelagic zone is patchily distributed (such as in the frontal features examined in Chapter 2). This work incorporated new stomach content data from GOM sampling efforts including large pelagic fish stomachs from offshore sampling. The results from this work were used to parameterize the GOM Atlantis model for the work performed in Chapter 4. My results showed that offshore-pelagic predators (i.e. tuna species) consumed a large amount of deep-water prey; this strong trophic linkage could indicate increased vulnerability of pelagic predators to environmental disturbances (e.g. oil spills) affecting deep-water species (Morzaria-Luna et al. 2022).

The DWH disaster released over 100 million gallons of crude oil into the meso-and bathypelagic zones of the GOM, resulting in mortality and long-term population declines of deep-water fish species (Sutton et al. 2022, Romero et al. 2018). This has implications for commercially important large pelagic predators that heavily utilize vertically migrating mesopelagic prey (Satoh et al. 2004, Iglesias et al. 2023). Recent sampling efforts in the GOM (Murawski, unpublished data) have found an abundance of mesopelagic fish prey in the stomachs of tuna species (*Thunnus albacares, Thunnus atlanticus*), more so than epipelagic forage fishes. Mesopelagic fishes could offer a reliable source of prey via diel vertical migration that makes epipelagic predators less vulnerable to variable environmental conditions and ephemeral overlaps with epipelagic prey. Given the continued expansion of offshore oil rigs into deeper water, it is important to consider potential population impacts on large pelagic predators if this reliable mesopelagic prey pool were to experience another large-scale mortality event. In Chapter 4, *Considering mesopelagic forage availability in management strategies for pelagic* *predators*, I used the GOM Atlantis model to conduct a management strategy evaluation for an example managed pelagic predator, *Thunnus albacares*. I tested five candidate harvest control rules (HCRs), including one single-species two-point HCR and four ecosystem-based HCRs that reduced fishing mortality on the example predator based on the available biomass of mesopelagic fish prey. I used mesopelagic fish abundance data collected by the DEEPEND Consortium (Sutton et al. *in prep*) to create three different mesopelagic abundance regimes and evaluated the performance of candidate HCRs under each. The overall goal of this chapter was to examine whether considering the availability of mesopelagic fish prey could be beneficial in the EBFM of large pelagic predators.

Overall, this research demonstrates the importance of concentrating frontal features and vertical trophic connections in the pelagic food web, and the potential benefit of considering bottom-up dynamics in EBFM. While I conducted all analyses for this dissertation, each chapter benefited from the guidance of co-authors; the collective ‘we’ is used throughout the dissertation to reflect this and to prepare the work for journal submission. Dr. Cameron Ainsworth, Dr. Nathan Putman, R. Taylor Beyea, and Hallie Repeta were co-authors on Chapter 2. Dr. Cameron Ainsworth was my co-author for Chapter 3. Dr.’s Cameron Ainsworth, Holly Perryman, Tracey Sutton, and Rosanna Milligan were my co-authors for Chapter 4.

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CHAPTER 2: MODELING TRANSPORT AND FEEDING OF JUVENILE KEMP’S RIDLEY SEA TURTLES ON THE WEST FLORIDA SHELF

Note to Reader

This work was published in the journal Ecological Modelling in April of 2024 with co-authors Nathan F Putman, R. Taylor Beyea, Hallie C. Repeta, and Cameron H. Ainsworth. It is included in this dissertation with permission from Elsevier Publishers, which provides a release for authors to include published works in theses or dissertations. Reference, permissions, and access information for this work is provided in Appendix 1. The online supplement for this chapter is provided in this dissertation in Appendix 2.

Abstract

Survivorship during the juvenile oceanic phase likely acts as a bottleneck on the growth of sea turtle populations, and starvation mortality through this period is one potential factor influencing year class strength. We combined a simulation of juvenile Kemp’s ridley (*Lepidochelys kempii)* sea turtle dispersal based on an ocean circulation model with an Atlantis ecosystem model to examine the spatial overlap of young sea turtles with their prey resources. We were particularly interested in whether ocean currents facilitated the movement of juveniles from western Gulf nesting beaches to areas in the eastern Gulf along the West Florida Shelf (WFS) with adequate food availability. We found that strong frontal gradients on the WFS may increase the potential for juveniles to remain offshore in areas of high *per capita* prey availability, allowing for more feeding opportunities during critical early life stages. Additionally, we found that multiple climatological indices are related to Gulf-wide patterns of juvenile dispersal, potentially via effects on the Loop Current. Findings from this study hold implications for continued population viability of protected sea turtle populations in the Gulf of Mexico, as well as other species with early life stages that disperse via ocean currents such as commercially important fishes.

Introduction

Organisms with a dispersive pelagic phase are advected by ocean currents which can have a major effect on prey encounter rates, feeding, and ultimately early life history survivorship. Several ecological hypotheses have been put forward to explain recruitment variability in terms of spatiotemporal overlap with prey resources. Cushing's (1974, 1990) match/mismatch hypothesis posited that the survival of fish larvae is higher in years when hatching coincides with peaks in system production (e.g., the spring plankton bloom). If adults' spawning occurs too early or late, less prey is available to newly hatched larvae during this essential period of growth and development. A temporal match between reproduction and peak availability of prey resources for offspring can be important in determining year class strength. The Aberrant Drift hypothesis suggests that larval survivorship depends on advection of larvae to favorable habitats via wind and ocean currents (Hjort 1914, 1926, Houde 2008). This is particularly critical to species with pelagic larvae that are strongly influenced by currents and can therefore be advected to unfavorable settlement sites such as those with limited refuge from predation or low prey density. Juvenile carrying capacity, defined by feeding opportunities and available habitat, may be more influential on recruitment than the number of eggs produced

(Walters and Martell 2004). These impacts on survival may become more pronounced with time as climate change is expected to increase the frequency of phenological mismatches between predator and prey (Winton et al. 2013, Visser and Gienapp 2019).

As with fishes, transport by currents can have a large effect on feeding rates and early survivorship of sea turtles (Hays et al. 2010; Putman et al. 2010a; Putman et al. 2012a) that may ultimately play a major role in population size (Putman et al. 2010b). Sea turtles from families *Cheloniidae* and *Dermochelyidae* have an oceanic phase which is often referred to as the 'lost years' because historically, so little was known about what happens during this critical period (Shillinger et al. 2012, Mansfield et al. 2014, Putman et al. 2020a). On coastal beaches, most sea turtle hatchlings enter the water and swim offshore to begin an oceanic stage that lasts for at least 1-2 years (Bolten et al. 2003, Carr 1987). One critically endangered sea turtle species, Kemp's ridley (*Lepidochelys kempii*), is primarily found in the Gulf of Mexico (GOM). As hatchlings, Kemp's ridleys emerge from nesting beaches in the Western Gulf and spend several years dispersing widely in the open waters of the Gulf of Mexico and Northwest Atlantic Ocean before recruiting to nearshore habitats, such as along the West Florida Shelf (WFS) (Putman and Mansfield 2015). In these coastal areas, larger juvenile Kemp's ridleys shift from surface-based foraging in floating macroalgal habitats, to benthic foraging (Avens et al. 2020). Once recruited to coastal waters, these sea turtles feed on benthic invertebrates in sand-, rock-, macroalgae, or live-bottom habitats (Schmid et al. 2003), many of which are dependent on the seagrass beds of the WFS for nursery habitat (Ralph et al. 2013). Transport to these coastal foraging areas may therefore be crucial for the survivorship of early life stage Kemp's ridleys. Indeed, a marked leveling off of exponential growth in Kemp's ridley nesting from approximately 2010-2017 was suggested to have been due to limited *per capita* food availability and resulting density-dependent effects on population abundance (Caillouet et al. 2018). Sufficient *per capita* food resources may also play an important role in the ability of Kemp's ridley populations to recover following large-scale mortality events (Kocmoud et al. 2019).

Circulation patterns that influence dispersing juvenile Kemp's ridley in the deep GOM are dominated by the Loop Current and its associated eddies. Circulation over the WFS is additionally influenced by buoyancy fluxes (e.g., those caused by changes in temperature and freshwater inputs) and wind-driven upwelling (Weisberg et al. 2005). Likewise, the distribution and abundances of the juveniles of many commercially and ecologically important species in the GOM are influenced by mesoscale circulation features (Gorecki et al. 2022). For example, high larval numbers of several tuna species have been associated with the presence of convergent zones and eddies (Cornic and Rooker 2018, Cornic et al. 2018), and the dispersal patterns of the highly managed *Panulirus argus* have been related to the location of gyres and the Loop Current (Lara-Hernández et al. 2019). Similarly, survival of the oceanic stage for sea turtles is thought to be dependent on their access to oceanographic fronts which concentrate prey in surface waters (Carr 1987; Polovina et al. 2000). For example, these concentrating features in the GOM may affect the availability of *Sargassum*-dominated surface pelagic drift communities, an important foraging habitat for Kemp's ridleys (Witherington et al. 2012). Thus, circulation patterns on the WFS likely play a key role in determining prey availability for juvenile sea turtles.

Many studies have used ocean circulation models to simulate hatchling sea turtle dispersal (Hays et al. 2010; Shillinger et al. 2012, Putman et al. 2013, Putman et al. 2020a). However, few if any studies have quantified the prey resources available to young sea turtles based on their simulated dispersal patterns (Harrison et al. 2021; Gaspar et al. 2022). Given the protected status of nearly all marine sea turtle species, and that transport to areas of adequate food availability is critical for early life survivorship (Hjort 1914, 1926, Houde 2008), understanding this potential bottleneck of juvenile sea turtle survival in the oceanic ‘lost years’ is crucial to managing populations (DuBois et al. 2021). Sea turtle population dynamics models are highly sensitive to assumptions regarding this juvenile oceanic-stage mortality (Kocmoud et al. 2019); these models could therefore be improved by a better understanding of the physical drivers of early-stage mortality.

Here, we use ICHTHYOP, virtual particle tracking software (Lett et al. 2008), informed by physical oceanographic data, sea turtle hatchling production, and estimated sea turtle mortality rates to simulate the density and distribution of juvenile Kemp’s ridleys as they leave their natal beaches and are transported eastward across the Gulf of Mexico (Putman et al. 2020a). An assumption of these sea turtle movement simulations is that they consider only the role of ocean circulation, not the role of swimming behavior. Tracking studies indicate that young (1–2-year-old) Kemp’s ridleys show directed swimming that influences their movement (Putman and Mansfield 2015). Previous models that have simulated observed or hypothesized swimming behavior have tended to show that ignoring this component of movement results in predicting fewer sea turtles in “favorable” locations and more turtles in “unfavorable” locations (Putman et al. 2012a, 2012b, 2015a, 2015b). However, ocean circulation dynamics remain the dominant driver in spatiotemporal variation in simulated distributions and overall dispersal patterns. More importantly, ICHTHYOP predictions based on ocean circulation alone correspond well to observed spatiotemporal variation in various metrics of juvenile sea turtle recruitment, particularly transport of Kemp’s ridley to the WFS and the eastern U.S. coast (Putman et al. 2020a, 2020b). We therefore use these model outputs as a first-order approximation of Kemp’s ridley distribution that could be combined with a spatially explicit trophic ecosystem model, the

Gulf of Mexico Atlantis model (Ainsworth et al. 2015), to quantify the amount of prey available to young sea turtles once they reach juvenile habitat on the West Florida Shelf. This integrates estimates of diet composition and consumption rates for Kemp's ridleys. We then consider spatiotemporal consumption patterns alongside hydrodynamic datasets to examine whether variations in Gulf circulation patterns may be driving the dispersal of Kemp's ridley recruits to areas of adequate food availability.

Materials and Methods

Modeling juvenile sea turtle abundance and distribution

Putman et al. (2020a) simulated the distribution and density of oceanic-stage Kemp's ridley sea turtles using ICHTHYOP (ver. 2.2.1) particle-tracking software (Lett et al. 2008). Lagrangian particles representing hatchling sea turtles were released from the primary Kemp's ridley nesting sites in the western Gulf of Mexico (Tamaulipas, Mexico; Veracruz, Mexico; and Texas, USA). Throughout the 60 days of peak hatchling emergence, 350 virtual particles were released from each region each day. This number was chosen as a balance of computational efficiency and ensuring transport pathways within the model were adequately sampled; prior modeling work indicates that this number of particles is appropriate (DuBois et al. 2021, Putman et al. 2012b, Putman et al. 2013, Putman and He 2013). Dispersal of hatchlings was then modeled by ICHTHYOP using Global HYCOM daily surface velocities at 0.08° resolution for years 1993-2017 (Chassignet et al. 2009, HYCOM experiments 19.0, 19.1, 90.9, 91.0, 91.1, 91.2). ICHTHYOP uses a Runge-Kutta fourth-order time-stepping method to calculate particle position each half-hour as they are moved through HYCOM surface velocity fields. For Kemp's ridley hatchlings, particles from each cohort were tracked for 2.5 years to capture the entire the oceanic-stage (Putman et al. 2013, 2015a; Avens et al. 2020).

An annual time series of Kemp's ridley hatchling abundance was produced using a combination of hatchling release numbers (for Tamaulipas and Texas) and nest counts that were converted to hatchling abundance using species-specific egg production and clutch survival estimates (for Veracruz) (Putman et al. 2020a). These production estimates were then multiplied by annual survival rates obtained from the literature and used to scale ICHTHYOP transport predictions and to estimate the abundance of each cohort. We used the median annual survival estimate (81.7%) for oceanic-stage juvenile sea turtles obtained from a previous literature review (Putman et al. 2015a). This resulted in monthly, spatially distributed estimates of juvenile Kemp's ridley abundance from 1996 through 2017. The annual predicted abundance of juvenile Kemp's ridleys shows close agreement with spatiotemporal variation in the recruitment of oceanic-stage sea turtles to coastal waters on the WFS and along the eastern U.S. coast, as inferred from strandings, survey, and fisheries dependent bycatch data (Putman et al. 2020a; 2020b, 2023). For this study, we specifically consider the Gulf of Mexico West Florida Shelf extent of the ICHTHYOP model (24.0-30.7°N, $^{-}$80.1-$^{-}$88.0ºW).

Modeling juvenile sea turtle feeding

Atlantis is a spatially explicit whole ecosystem model that is utilized worldwide as a tool for modeling fisheries and ecology (Fulton et al. 2004, 2011). A complete set of process equations is available in Audzijonyte et al. (2017). Atlantis links both high and low-level trophic processes via a suite of sub-models that simulate important ecosystem dynamics such as physical processes (e.g., hydrodynamics, stratification), biochemistry (e.g., nutrient cycling, primary productivity), trophic interactions, habitat dependence, and fisheries production. Species are organized into functional groups aggregated by niche and life history traits, each having corresponding sub-models related to reproduction, movement, consumption, and production. The flow of nitrogen is tracked between functional groups through trophic interactions. Consumption is modeled based on diet composition, gape limitation, spatiotemporal predator-prey co-occurrence, and density-dependent feeding functions. Atlantis uses irregularly shaped polygons to capture biophysical provinces and regulatory areas and to reduce computation time in homogeneous space.

The Gulf of Mexico Atlantis model (‘Atlantis-GOM’) was developed by Ainsworth et al. (2015). The map is composed of 66 polygons, each with up to seven depth layers (Figure 1). There are 91 functional groups in the Atlantis-GOM model including 61 vertebrate (which are age-structured), 19 invertebrate, 6 primary producer, 2 bacteria, and 3 detritus groups. Species of commercial or managerial importance belong to their own functional group (e.g., yellowfin tuna, white shrimp).

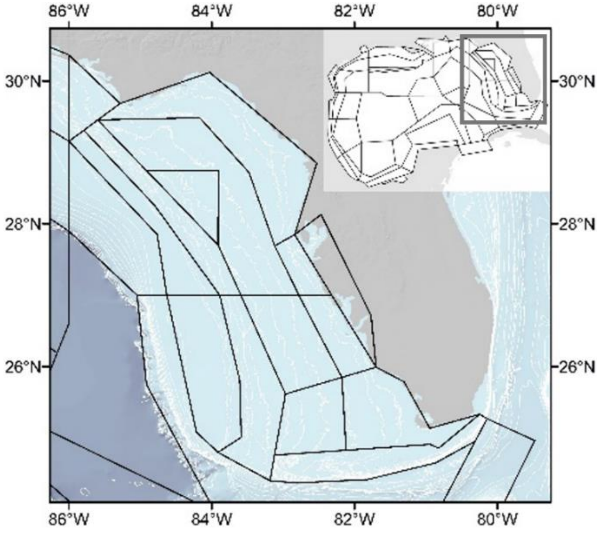

Figure 2.1: The spatial extent and polygon geometry for the West Florida Shelf Extent of the Atlantis ecosystem model for the Gulf of Mexico (Atlantis-GOM) (inset shows entire GOM extent, Ainsworth et al. 2015), light blue shading denotes the continental shelf and slope, darker blue indicates the deep GOM.

We updated the life history parameters of our Kemp's ridley sea turtle group based on a literature review including maximum lifespan, and age at sexual maturity (Avens et al. 2017, Chabot et al. 2021, Chaloupka and Zug 1997, Gallaway et al. 2016, Seney 2008). The updated age structure for Kemp's ridleys can be found in Table A.1. We also updated the model's diet matrix for adult and juvenile Kemp's ridley using published Gulf of Mexico-specific diet studies (Witzell and Schmid 2005, Schmid and Tucker 2018, Servis et al. 2015) (Table A.2). There is a major ontogenetic transition in habitat and diet that occurs in Kemps ridley juveniles after the first few years of life, at which point oceanic phase juveniles feeding in Sargassum surface drift communities begin to move closer inshore and feed more on benthic crustaceans (Schmid and Tucker 2018). The juvenile age classes of the Kemps ridley sea turtle Atlantis functional group (KMP) encompass both the pelagic-feeding and benthic-feeding juvenile stages (the only ontogenetic diet change modeled is the transition from juveniles to adults). The locations of the sea turtles in Atlantis are driven by ICHTHYOP, and feeding rates on benthic versus pelagic prey are partly determined by simulated spatiotemporal predator-prey overlap that is relevant to the effects of ocean currents on dispersal patterns. Where stomach contents included unidentifiable fish prey, we evenly divided the diet proportion of fish among taxa most commonly found in Gulf shrimp trawl discards (e.g., Lutjanidae, Sciaenidae) as previous studies have suggested that Kemp's ridleys opportunistically scavenge from shrimping boats (Harrington et al. 2005).

We used the average Kemp's ridley abundance outputs from Putman et al.'s (2020a) ICHTHYOP model's median annual survival rate scenario to force the numbers of the three juvenile Kemp's ridley age class stanzas in Atlantis-GOM on monthly time steps. Kemp's ridley numbers were updated (forced) in Atlantis using the ICHTHYOP data in each 30-day time step. We used a ray casting method to determine which Atlantis polygon each particle fell into based on their latitude and longitude and numbers were summed for that polygon and timestep. Since the ICTHYOP data refers only to juveniles, the numbers were applied only to the juvenile age classes (Table A.1). The numbers of sea turtles in older age classes were scaled relative to juveniles using equilibrium age structure estimates from Siler's competing risk model as modified by Barlow and Boveng (1991). This mortality model is often used for cetaceans because it combines a constant rate of mortality with an end-of-life mortality. The parameters we used (based on cetaceans) do not include early life stage mortality, but this is appropriate as the first Atlantis age class includes individuals up to 3 years of age and the hatchling phase is implicit. We ran a 22-year Atlantis simulation representing the 1996-2017 extent of ICHTHYOP model outputs, with the consumption of prey biomass by each predator age class reported on a 30-day time step. Note that each Atlantis output reflects only the prey biomass consumed during the last day of the 30-day time step period; each output therefore represents the quantity consumed by juvenile sea turtles in the system over the course of one day.

Consumption by predators in Atlantis-GOM follows a Hollings type 2 functional response. Parameters defining the slope at the origin and the asymptote of the feeding response are functional group-specific and are important tuning parameters used in model calibration. The consumption rate for each group is calculated using a weight-consumption relationship and an assimilation efficiency term (Audzijonyte et al. 2017). The particular prey groups consumed by a given predator are determined by the user-defined diet composition and spatiotemporal overlap. Sea turtle position and density were determined by ICHTHYOP outputs, and prey functional groups move in space dynamically through diffusion and three types of migration (ontogenetic, seasonal, and diel). Primary production is affected spatiotemporally by physical processes including advection and upwelling. For this study, consumption within each model polygon was summed across depth layers.

Hydrodynamic processes

We compiled monthly time series and (when available) spatial data for several hydrodynamic processes associated with surface circulation patterns in the Gulf of Mexico (Table 1). Two such variables were frontal gradient magnitudes (‘FGM’s) calculated from sea surface temperature and color index values taken from MODIS satellites and are representative of the strength of ocean fronts (Zhang and Hu 2021). We also gathered spatiotemporal upwelling data derived from Satellite-Derived Upwelling Indices; in this dataset, negative values indicate downwelling (Zhang and Hu 2021). Finally, we utilized monthly time series data for two climatological indices that have been associated with important Gulf hydrodynamical patterns: the Atlantic Multidecadal Oscillation (AMO) (NOAA 2023a) and North Atlantic Oscillation (NAO) (NOAA 2023b). The AMO is a measure of sea-surface temperature variation that is associated with density-driven changes in wind and current patterns and Mississippi River outflow and has been hypothesized to affect the dispersal patterns of marine taxa with a planktonic stage (Enfield et al. 2001, del Monte-Luna et al. 2015, Nye et al. 2014). The NAO has been shown to vary on the same amplitude and period as patterns in the Gulf of Mexico Loop Current and can change the latitude of the Gulf Stream into which the Loop Current feeds (Lugo-Fernández 2007, Taylor and Stephens 1998, Weisberg and Liu 2017).

Spatial hydrodynamic variables were trimmed to the West Florida Shelf geographic extent of the ICHTHYOP model. We were able to compile consistent monthly data for all hydrodynamic variables beginning in 2003; all analyses presented in this study therefore consider the years 2003-2017.

Statistical analyses

We hypothesized that there is spatiotemporal variation in juvenile Kemp's ridley dispersal, feeding, and food availability, and that these patterns may be related to variations in mesoscale hydrodynamic features as these will influence both the distribution of sea turtles and their prey. To examine patterns in the spatial distribution of young sea turtles, we used the COGravity function in the SDMTools R package (VanDerWal et al. 2014) to calculate the geographic center of mass of juvenile Kemp's ridleys for each monthly time step; the resulting center of mass coordinate is calculated using a weighted average of ICHTHYOP abundance values.

We then calculated spatially explicit total consumption (Q_i) values for each ICHTHYOP grid cell (i) based on consumption in the corresponding Atlantis polygon (Q_{polygon}) (Equation 2.1).

$$Q_i = \left(\frac{Q_{polygon}}{C_{polygon}}\right) \cdot N_i \qquad \text{(Eq. 2.1)}$$

The consumption of prey by the juvenile age classes of Kemp's ridley within each Atlantis polygon was divided evenly amongst all ICHTHYOP model grid cells that fell within it (C_{polygon}). This value was then multiplied by a scaling factor representing the abundance of Kemp's ridley juveniles (N_i) present at grid cell i from ICHTHYOP. The unit of the resulting (Q_i) value is therefore still in tonnes of prey consumed by all juvenile Kemp's ridleys in the WFS model domain. This was repeated for each monthly time step. We then summed across all cells within the model domain to create a non-spatial monthly time series of total consumption Q_I as in Equation 2.2.

$$Q_I = \sum_i Q_i \qquad \text{(Eq. 2.2)}$$

We also calculated a spatially explicit measure of *per capita* consumption within each ICHTHYOP model grid cell (‘pcQi’) to quantify the amount of food available to each individual juvenile Kemp’s ridley (Equation 2.3).

$$pcQ_i = \left(\left(\frac{Q_{polygon}}{C_{polygon}}\right)/N_i\right) * 1e^6 \qquad \text{(Eq. 2.3)}$$

Total juvenile Kemp’s ridley consumption within each Atlantis polygon (Q_{polygon}) was divided evenly amongst all ICHTHYOP model grid cells that fell within it (C_{polygon}). This value was then divided by the abundance of Kemp’s ridley juveniles (N_i) within ICHYTHOP grid cell *i* to determine the amount of prey consumed by each individual in a given cell. Atlantis quantifies prey consumption in tonnes; we converted the units to grams (x $1e^6$) to be more easily interpreted on a *per capita* scale. To create a monthly time series of *per capita* consumption ($pc\text{Q}_\text{I}$), we averaged pcQ*i* values across all model grid cells as in Equation 2.4, where C is the total number of grid cells in the WFS model domain.

$$pcQ_I = \left(\sum_i pcQ_i\right)/C \qquad \text{(Eq. 2.4)}$$

We looked for temporal (seasonal, annual) differences in abundance, overall consumption, and *per capita* consumption using one-way ANOVAs and, if statistically significant, post-hoc Tukey Honest Significant Difference (HSD) tests for multiple comparisons. For seasonal analyses we defined winter as December 1st – February 28/29th, spring as March 1st-

May 31st, summer as June 1st – August 31st, and fall as September 1st – November 30th. To test the hypothesis that dispersal patterns dictate feeding opportunities during critical early life stages we identified periods of high and low *per capita* feeding by dividing our 15 model years into terciles based on mean pcQ_I values. We considered the first and third terciles as 'low pcQ_I' and 'high pcQ_I' groups, respectively. and compared latitude and longitude components of the center of mass of juveniles during these times using two-sample t-tests.

Monthly timeseries of the hydrodynamic variables in Table 1 were compared against the latitudinal and longitudinal center of mass components from ICHTHYOP abundance data using linear regression models to understand circulation and climate drivers behind broad scale movement patterns. We applied a feasible generalized least squares estimation method to account for heteroscedasticity in the data.

Results

Temporal patterns in consumption

One-way ANOVAs revealed statistically significant patterns in juvenile abundance and overall consumption (Q_I) between at least seasons (abundance: F(3, 176) = 8.992, p<0.001; Q_I: F(3, 176) = 3.286, p = 0.022). We found no statistically significant difference in *per capita* consumption (pcQ_I) between seasons (p = 0.158). Seasonal trends for all variables are visualized in Figure 2.

Post-hoc Tukey HSD tests for multiple comparisons found that the abundance of juvenile Kemp's ridleys was not significantly different between winter and spring or summer and fall but differed significantly between spring and fall, spring and summer, and winter and fall (Table 2). Abundance in general was higher in summer and fall months than in spring and winter months.

The only statistically significant difference in total consumption (Q_I) between seasons was found between winter and summer, with summer having higher Q_I ($p = 0.029$).

Table 2.1: Gulf of Mexico hydrodynamic variables considered in statistical analyses.

Variable	Units	Spatial?	Source
Sea surface temperature frontal gradient magnitude (SST-FGM)	ΔSST (°C)/km	Yes	Zhang and Hu 2021
Color index frontal gradient magnitude (CI-FGM)	ΔCI/km	Yes	Zhang and Hu 2021
Upwelling index (UI)	None	Yes	Zhang and Hu 2021, FSU Center for Ocean-Atmospheric Prediction Studies
Atlantic Multidecadal Oscillation index (AMO)	None	No	NOAA Physical Sciences Laboratory
North Atlantic Oscillation index (NAO)	None	No	NOAA Center for Weather and Climate Prediction

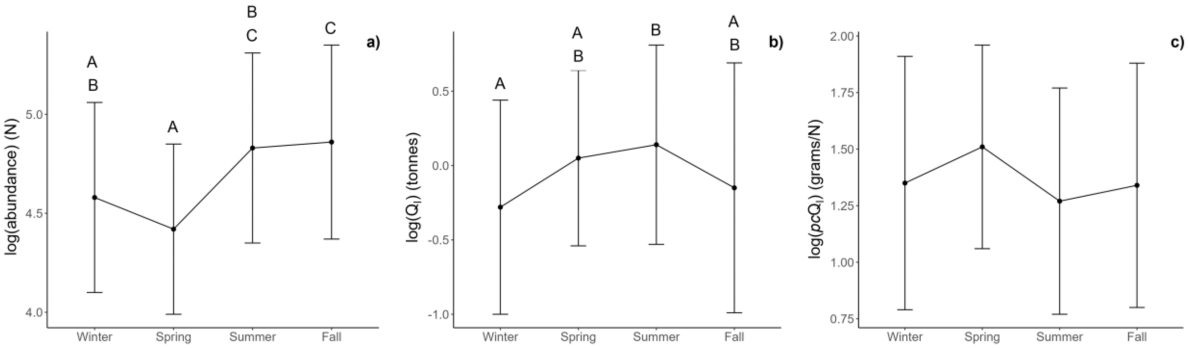

Figure 2.2: System-wide seasonal average values of abundance (a), total prey consumption (Q_I) (b), and *per capita* consumption (*pc*Q_I) (c) of juvenile Kemp's ridleys. Letter groupings represent significant differences ($p < 0.05$) between groups determined via post-hoc Tukey HSD tests; if any letters are shared, groups were not statistically distinct. Error bars are +/- one standard deviation around the mean. Values are shown log transformed.

Table 2.2: Results from post-hoc Tukey tests comparing season pairs for juvenile Kemp's ridley sea turtle abundance and total consumption (Q_I). Bolded values indicate statistical significance at $p < 0.05$.

	log(abundance) (N)			log(Q_I) (tonnes)		
	Diff.	*p*	95% CI	Diff.	*P*	95% CI
Spring-Fall	-0.44	**<0.001**	(-0.70,-0.18)	0.21	0.502	(-0.18,0.60)
Summer-Fall	-0.03	0.991	(-0.28,0.23)	0.29	0.216	(-0.10,0.68)
Winter-Fall	-0.28	**0.029**	(-0.53,-0.02)	-0.13	0.823	(-0.52,0.26)
Summer-Spring	0.41	**<0.001**	(0.15,0.67)	0.08	0.949	(-0.31,0.47)
Winter-Spring	0.16	0.357	(-0.09,0.42)	-0.34	0.111	(-0.73,0.05)
Winter-Summer	-0.25	0.062	(-0.50,0.01)	-0.42	**0.029**	(-0.81,-0.03)

Because we did not identify any seasonal patterns in *per capita* consumption (*pc*Q_I), we further examined annual trends to determine any drivers of variability in food availability (Figure 3). A one-way ANOVA was conducted to compare average *pc*Q_I in the study system between years; abundance values were log-transformed and homogeneity of variance was confirmed using a Shapiro-Wilk test. We found statistically significant differences in *pc*Q_I between years ($F(14, 165) = 3.775$, $p<0.001$); the results from post-hoc Tukey HSD tests can be found in Table A.3.

We divided our 15 model years into terciles based on mean *pc*Q_I values; the five years with the highest average *pc*Q_I in the study system were, in chronological order, 2005, 2007, 2012, 2014, and 2017. The five years with the lowest average *per capita* Q were 2003, 2006, 2008, 2011, and 2013. These years comprised our 'low *pc*Q_I' and 'high *pc*Q_I' groups, respectively.

Spatial patterns in consumption

Spatial distribution of juvenile (i.e., sexually immature) sea turtle total consumption (Q_I) and per capita consumption (*pc*Q_I) are shown in Figure 4. In winter months, when both

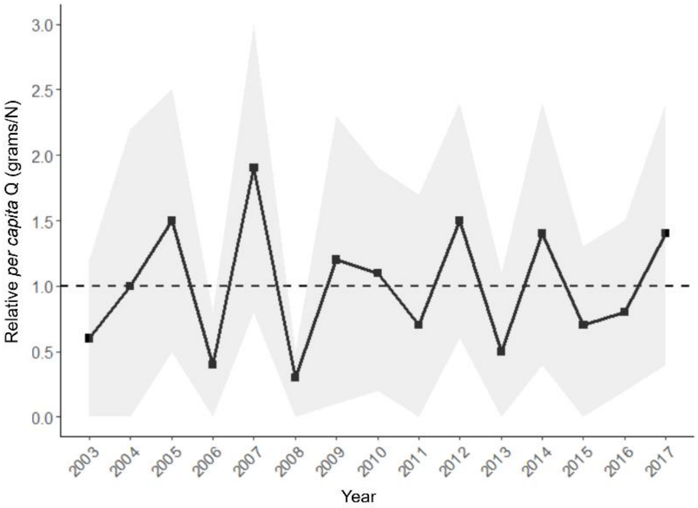

Figure 2.3: Average *per capita* consumption (*pc*Q_I) by juvenile Kemp's ridleys relative to the average of all time steps combined (dashed line). The black line represents yearly averages, with values averaged across all 30-day timesteps within in a given year. The shaded gray area represents +/- one standard deviation around the mean.

abundance and total consumption are significantly lower relative to other seasons, the juveniles that are present converge in the northern Gulf along the coasts of Alabama and the panhandle of Florida; Q_I is therefore also concentrated in this area. During the summer, when both abundance and Q_I are significantly higher relative to other seasons, feeding and abundance are additionally concentrated inshore along the southwest coast of Florida (including the Tampa Bay and Charlotte Harbor regions). Spatial patterns in *pc*Q_I do not appear to vary much between seasons, which is not surprising given the insignificant one-way ANOVA results.

There was a significant difference in the east-west distribution (i.e., longitude) of juvenile Kemp's ridleys between years of low *per capita* Q (M = -84.9, SD = 1.3) and high *per capita* Q (M = -85.6, SD = 0.9); t(105) = 3.444, p = <0.001 (Table 3). Specifically, the center of modeled mass of juvenile Kemp's ridleys was further west (i.e., offshore) in years with high *pc*Q_I. This was visually supported by the spatial pattern of *pc*Q_I in Figure 4. Because the abundance values used to calculate the center of gravity values were significantly different in the summer and fall from the winter and spring (Table 2), we also divided the *pc*Q_I data seasonally in this way within high/low groups to determine if any annual spatial relationships were being temporally driven. The results of both seasonal two-sample t-tests were statistically significant at $p < 0.05$, suggesting that the relationship between juvenile distribution and *per capita* consumption is consistent year-round and that there is no seasonal component (Table 3). There was not a significant relationship between *per capita* consumption and the north-south distribution of juvenile Kemp's ridleys for any grouping.

Hydrodynamic relationships

Results from linear regressions of hydrodynamics variables against abundance center of mass are shown in Table 4. Many hydrodynamic variables were significantly related to the horizontal component of juvenile Kemp's ridley distribution (east–west center of mass). Note that a negative slope in a significant relationship with center of mass longitude or latitude indicates a more western (or offshore) or southern distribution, respectively, with higher values of a given predictor variable. Our results suggest that movement of juveniles inshore towards the west coast of Florida is more likely during years with high AMO and low NAO indices. The center of mass of sea turtles was further offshore on the WFS when ocean fronts (FGMs) were stronger. The vertical (north–south center of mass) distribution of sea turtles was significantly related to patterns in the upwelling and NAO indices. Higher NAO index values, which follow patterns in the Loop Current, were associated with a more northern distribution of juveniles. In contrast, results suggested that higher upwelling may be associated with more southward advection.

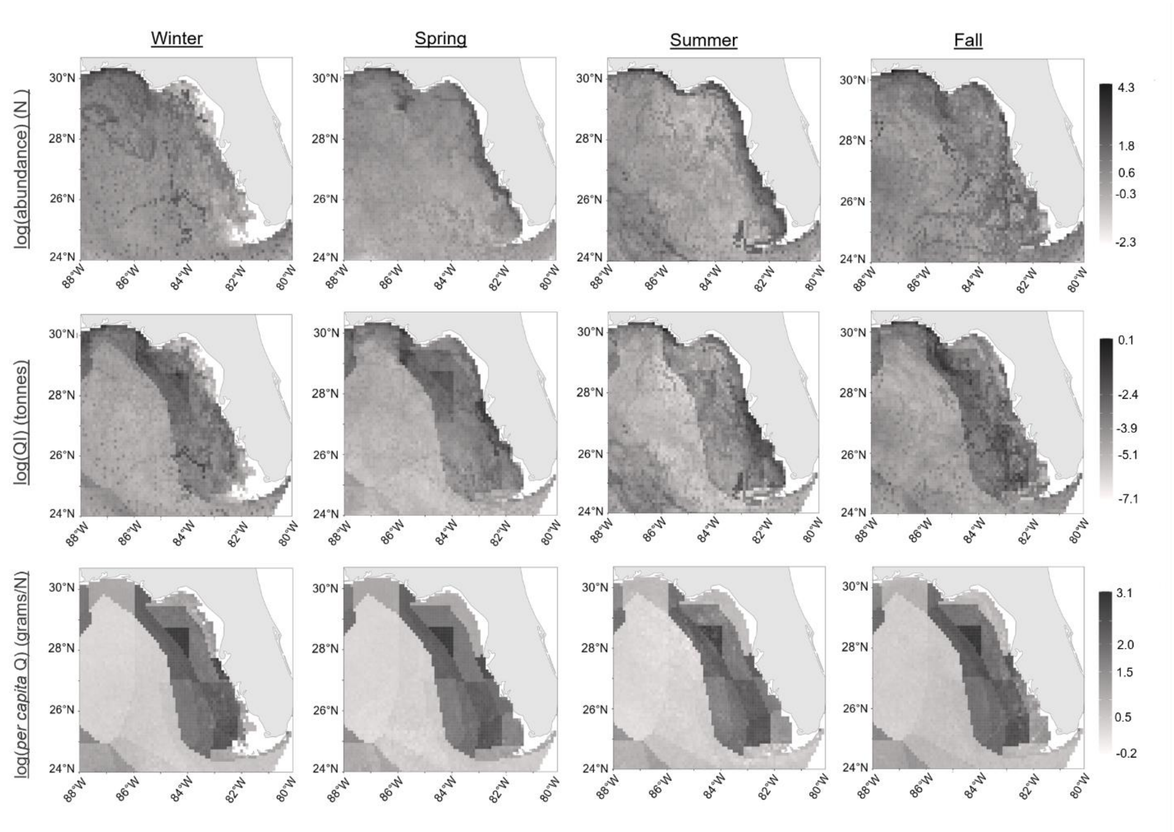

Figure 2.4: Seasonal average maps of juvenile Kemp's ridley sea turtle abundance (Atlantis age groups age 0 -3, Table A.1), total prey consumption (Q_I), and *per capita* consumption (pcQ_I). Seasonal averages encompass the years 2003-2017. Values are shown log-transformed. Maps have a 0.08° spatial resolution.

Table 2.3: Results from two-sample t-tests assuming unequal variances comparing juvenile Kemp's ridley sea turtle abundance center of mass values between years of low and high *per capita* consumption (pcQ_I). p-values are two-tailed, t-tests assumed unequal variances, bolded values indicate significance at $p < 0.05$.

	pcQ_I grouping	All months (n = 60)				Winter and Spring only (n = 30)				Summer and Fall only (n = 30)			
		Mean	SD	T	*p*	Mean	SD	t	*p*	Mean	SD	t	*p*
Center of Mass (N-S)	Low	28.5	1.1	-1.273 (df = 109)	0.206	28.5	1.1	-0.416 (df = 54)	0.679	28.4	1.1	-1.398 (df = 53)	0.168
	High	28.7	0.8			28.6	0.9			28.8	0.8		
Center of Mass (E-W)	Low	-84.9	1.3	3.444 (df = 105)	**<0.001**	-85.0	1.3	2.359 (df = 53)	**0.022**	-84.9	1.3	2.473 (df = 50)	**0.017**
	High	-85.6	0.9			-85.6	0.9			-85.6	0.9		

Table 2.4: Results of linear regressions conducted on monthly time series of hydrodynamic predictor variables and the center of mass of juvenile Kemp's ridleys from 2003 to 2017. Regression models used a feasible generalized least squares estimation method. Bolded values highlight significant results at $p < 0.05$. Negative slope values indicate a more western or southern distribution of juvenile sea turtles with increasing predictor values.

	Center of Mass (E-W)				Center of Mass (N-S)			
	slope	F	R^2	p	slope	F	R^2	p
CI-FGM	-22063.68	7.39	0.04	**0.007**	518.04	0.01	0.00	0.943
SST-FGM	-40.24	6.37	0.04	**0.012**	-16.62	1.42	0.01	0.236
Upwelling index	0.99	0.15	0.00	0.695	-6.60	9.67	0.05	**0.002**
NAO index	-0.22	8.90	0.05	**0.003**	0.14	4.55	0.03	**0.034**
AMO index	1.90	12.08	0.07	**0.001**	-0.58	1.42	0.01	0.235

Discussion

We identified seasonal patterns in both the abundance and overall consumption of prey by juvenile Kemp's ridleys in the WFS region of the GOM. In winter months, both the number of juveniles and the amount of prey consumed in the system was significantly lower than in other seasons. Conversely, juvenile abundance and total consumption was significantly higher in summer months. Because abundance and consumption followed similar seasonal patterns, there was no significant difference in *per capita* consumption between seasons. Ectothermic organisms such as sea turtles would be expected to have a lessened metabolic rate (and therefore consumption) in winter months, but this effect was not reflected in our model outputs.

In the summer when there is high abundance and overall consumption, juvenile Kemp's ridleys are concentrated in inshore areas including areas of high seagrass density (Gorecki et al. 2022) and large estuaries such as Tampa Bay and Charlotte Harbor. While these inshore habitats are rich with benthic invertebrate prey (Ralph et al. 2013, Darnell and Dutton 2015), the arrival of high numbers of juvenile Kemp's ridleys will result in increased competition and less available food for each individual sea turtle. This was reflected in our results, which found a more inshore distribution (center of mass) of juvenile Kemp's ridleys in years with the lowest average *per capita* consumption rates. Spatial patterns showed areas of high *per capita* consumption over the deep shelf (Figure 4). We hypothesize that this may be reflective of areas of high offshore production such as convergence zones, which we discuss more below. The success of these young sea turtles may therefore depend on whether oceanic conditions favor being retained offshore over the WFS where there is higher *per capita* prey availability during critical periods of growth. We found no seasonality to the relationship between the spatial distribution of juveniles and *per capita* consumption, although existing literature suggests that juvenile Kemp's ridleys migrate somewhat southward in the Gulf of Mexico during winter months (Schmid and Witzell 2006, Coleman et al. 2017).

A significant relationship was identified only between *per capita* consumption and the horizontal component of juvenile distribution. Therefore, we focus on the effect of circulation on east-west advection and retention in good foraging habitat for this discussion. The timeseries of FGM and upwelling index variables used in these analyses were created using only data from the WFS model domain, so results should be considered on this spatial extent. However, NAO and AMO indices were not spatially resolved, so patterns may reflect processes happening on a more Gulf-wide scale. In the WFS region, we found that the strength of ocean frontal features, such as those indicated by SST gradients, were positively associated with a more westward (i.e., offshore) distribution of juvenile sea turtles. Because *per capita* consumption was higher offshore over the shelf, these fronts could be facilitating the retention of juveniles in areas of high food availability (e.g., sargassum and sargassum-associated species). Satellite mapping in the Gulf of Mexico shows agreement between the location of frontal features and aggregation of *Sargassum* mats (Zhang and Hu 2021). On the WFS, both SST and CI fronts were significantly correlated to coastal upwelling indices in southern regions but not in the north; this suggests that local environmental dynamics may be driving front features in this area (Zhang and Hu 2021, Weisberg and He 2003). Riverine discharge does not appear to be a local driver of SST and CI frontal strength on the WFS; discharge from the Apalachicola River was not found to be correlated with frontal strength on the northern WFS, and there are no major river systems that drain onto the southern WFS (Zhang and Hu 2021).

The NAO index, which may serve as a proxy for the strength of the Loop Current (Lugo-Fernández 2007, Taylor and Stephens 1998, Weisberg and Liu 2017), was positively associated with a more western distribution of juvenile Kemp's ridleys in the model domain. Periods of high Loop Current strength may retain juveniles in offshore areas with high feeding rates. On a global scale, the NAO index has been increasing at a rate inconsistent with natural variability in response to increasing greenhouse gases and sea surface temperatures (Gillett et al. 2003). On the regional WFS scale, the NAO index has been observed to vary on the same amplitude as the Loop Current (Lugo-Fernández 2007, Taylor and Stephens 1998, Weisberg and Liu 2017), but, conversely to the NAO, the Loop Current is expected to decrease in magnitude with warming sea surface temperatures (Liu et al. 2012). Climate change implications for the correlations found here between the east-west distribution of juvenile sea turtles and the NAO climatological index are therefore difficult to predict on the WFS spatial scale of this study. If increasing sea surface temperatures result in a future weakening of the Loop Current, this may result in more inshore (eastern) transport of juvenile Kemp's ridley sea turtles to where feeding opportunities are lower.

We found that the AMO climatological index was related to the horizontal dispersal of juvenile sea turtles, but in the opposite direction of the relationship with NAO. Sea turtles were more eastward/inshore during times of high AMO values. The AMO index is adjusted for anthropogenic warming (Enfield et al. 2001) and fluctuates naturally between warm and cold periods. Warm AMO periods, the current AMO state since 1995, are associated with lower Mississippi River output (Enfield et al. 2001). This lessened output of freshwater may be impacting density-driven circulation patterns. Interestingly, AMO has been negatively correlated with important prey species (e.g., *Callinectes sapidus*) for Kemp's ridley in the Gulf of Mexico (Nye et al. 2014, Sanchez-Rubio et al. 2011). Correlations between the AMO and other sea turtle species suggest relationships may be complex. The abundance of hawksbill sea turtles (*Eretmochelys imbricata*) in the southern GOM shows negative associations with the AMO (del Monte-Luna et al. 2012). High AMO periods positively impact juvenile loggerhead sea turtle (*Caretta caretta*) recruitment in the North Atlantic as higher SSTs release physiological temperature restraints on hatchlings (Bostrom et al. 2010, Van Houtan and Halley 2011); however, juveniles experience less low-temperature stress in a subtropical system such as the Gulf (Arendt et al. 2022). When the AMO cycles back to a cool phase, cooler sea surface temperatures and increased Mississippi River outflow will change density-driven circulation patterns, particularly in the northern Gulf. At the WFS spatial extent, the positive correlation found here between the AMO index and a more eastward/inshore distribution of juvenile Kemp's ridleys suggests that young sea turtles may be more westward/offshore during cool AMO phases.

Patterns identified in this study may shift over time as the local hydrodynamics that drive juvenile Kemp's ridley feeding rates are affected by climate change (Arendt et al. 2022). Frontal gradients over the WFS that contribute to the retention of juvenile sea turtles offshore in the winter may weaken in magnitude with rising sea surface temperatures. A warmer climate is predicted to reduce the strength, transport, and northern penetration of the Loop Current into the GOM (Liu et al. 2012). On the WFS, these new circulation patterns may result in less time retained offshore in areas of high *per capita* feeding opportunities and a higher risk of juvenile starvation mortality. Because the modeling conducted in the present study assumed passive transport, these potential early life history bottlenecks should be considered as mainly relevant to the early oceanic stage of the Kemp's ridley lifecycle and are less relevant to the older, actively swimming juvenile stages. The consequences of these changing patterns may also extend to other species with passive pelagic transport, such as the larvae of commercially important fish species. Several *Thunnus* species have been found to concentrate in high densities on the edges of frontal features in the Gulf of Mexico where productivity is high, and mesoscale features associated with the Loop Current may serve to partition nursery habitat between tuna species (Cornic et al. 2018). For example, the highest densities of blackfin (*Thunnus atlanticus*) and yellowfin tuna (*Thunnus albacares*) larvae in the northern Gulf occurred in years of high northward Loop Current penetration (Cornic et al. 2018). Weaker frontal features and lessened Loop Current penetration due to climate change may therefore have population-level effects on many Gulf of Mexico species.

In addition to being a potential area of high juvenile Kemp's ridley abundance and resource competition, the approximate area from Tampa Bay to south of Charlotte Harbor is also the most vulnerable area to harmful algal blooms (HABs) (Weisberg et al. 2019). Red tide caused by the toxic dinoflagellate *Karenia brevis* is detrimental to many GOM species. While we did not simulate HAB events in this study, spatial overlap with red tide blooms could lead to mortality in juvenile sea turtles either directly or indirectly through reduction in prey species or consumption of contaminated prey (Foley et al. 2019, Gravinese et al. 2019, Perrault et al. 2014). The spatial extent of red tide blooms is influenced by similar hydrodynamic patterns that disperse hatchling Kemp's ridleys (Weisberg et al. 2019), and the extent of juvenile dispersal into areas of high red tide concentration may therefore vary year-to-year depending on these mesoscale circulation features. Offshore retention on the WFS by frontal features and the Loop Current may further benefit juvenile sea turtles by keeping them out of areas where the food web has been highly impacted by HABs. Additionally, recreational fishing bycatch provides another potential source of mortality to juvenile Kemp's ridley sea turtles when they reach inshore areas (Reimer et al. 2023).

Another potentially important mechanism that we did not directly address in this study given the limits of our modeling framework was the presence and probable benefit of *Sargassum* mats. Previous work has indicated that oceanic stage (age class 0, Table A.1) Kemp's ridleys utilize *Sargassum* for shelter and foraging (Witherington et al. 2012). Hydrodynamic patterns likely play a role in these feeding associations as well, as small juvenile sea turtles have been found to utilize mesoscale circulation features that concentrate *Sargassum* and associated prey items (Gaube et al. 2017). There is extensive ongoing work to map the distribution and transport of *Sargassum* in the Gulf of Mexico via satellite (e.g. Zhang et al. 2024). Gulf-wide patterns of *Sargassum* distribution are heavily driven by the Loop Current and resulting eddies, and locally on the West Florida Shelf *Sargassum* mats align with the ocean frontal features used as predictor variables in this study (Zhang et al. 2024, Zhang and Hu 2021). Atlantis does not have the fine spatial resolution to model individual macroalgae aggregations; however, *Sargassum* distribution could be simulated via ICHTHYOP and assessed for overlap with juvenile Kemp's ridleys in a future study (Putman et al. 2018, Putman et al. 2020c). The concentrating features that we examined here combined with the spatial patterns of *per capita* consumption suggest that offshore feeding opportunities such as *Sargassum* mats may be important for growth during early life history stages of Kemp's ridley sea turtles. Any disruptions to these concentrating features, such as the potential climate-induced changes discussed above, may have negative implications for Kemp's ridley conservation by increasing the potential for early life stage mortality. These results have further implications for the resilience of Kemp's ridley populations as sufficient *per capita* feeding is an important component of successful population recovery following large-scale mortality events such as HABs or oil spills (Kocmoud et al. 2019).

Conclusions

The relationships described here between annual oceanic circulation patterns and feeding opportunities for immature Kemp's ridleys provide insight on the continued viability of protected sea turtle populations in the Gulf of Mexico. Specifically, the positive association between the strength of hydrodynamic circulation components and the retention of juveniles in favorable feeding areas offshore may be of interest in conservation and management decisions. Weakening of these regional circulation features in future climate change scenarios could have a negative impact on the feeding success and survival of juvenile Kemp's ridleys. Given that this study used passive ICHTHYOP particles to simulate juvenile sea turtles, our findings may also be applicable to other species with pelagic early life histories that have been shown to utilize mesoscale concentrating features for foraging purposes such as large pelagic fishes (Cornic and Rooker 2018, Cornic et al. 2018). The patterns that we have identified in this paper regarding the relationship of offshore feeding opportunities, mesoscale circulation patterns, and potential climate change implications could therefore also be relevant for fisheries stock recruitment and management.

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CHAPTER 3: INFLATED-TYPE MODELS FOR ESTIMATING FISH DIET COMPOSITION

Introduction

Ecosystem models are increasingly popular tools for evaluating dynamics in marine environments and populations and are often used to answer questions related to living resource management. To simulate complex system dynamics, ecosystem models contain multiple subroutines modeling hydrodynamics, biogeochemistry, and ecology. Trophic information for all modeled species is required in the form of a square diet matrix (i.e., one proportional value for each predator-prey interaction). Trophic dynamic modeling is routine with use of models like Ecopath with Ecosim, Atlantis, ERSEM, OSMOSE and many others (Christensen and Walters 2004, Fulton et al. 2011, Shin and Cury 2001, Baretta et al. 1995). The transition towards probabilistic ecosystem modeling approaches has been advanced by improved methodology to overcome computational limits (Morzaria-Luna et al. 2022, Allen et al. 2007) and statistical techniques are only now being developed that can properly characterize error around a wide variety of trophic ecologies.

A common problem in analyzing diet data is that it is zero-inflated by nature. In a diet matrix of many prey items, the most frequently observed diet proportion is often zero. This is because any given stomach likely contains a non-zero quantity for only a few of the many potential prey species. Stomach content data may be zero-inflated in predators for whom prey is patchy or feeding events are rare. Additionally, diet data can become one-inflated if a stomach often contains only one prey species. One-inflation may be more common in specialist predators.

Both zero- and one-inflation make using simple data averages to estimate diet composition problematic as they can result in under- or overestimation of diet, respectively. Taking a simple average conflates the underlying processes of prey encounter (a binomial outcome) and capture success (a continuous outcome). This source of error is made worse when diet information for either predator or prey is aggregated into functional groups as is often done in trophic modeling.

The Gulf of Mexico (GOM) food web has been described statistically using the Dirichlet distribution (Tarnecki et al. 2018, Morzaria-Luna et al. 2018, 2022), which is the multivariate generalization of the beta distribution. It is defined on the interval (0, 1) so it is appropriate for fitting proportional diet data. In building a diet matrix for ecosystem models, a statistical approach is better than averaging predator stomach contents because it preserves error information useful in probabilistic modeling (Morzaria-Luna et al. 2022). However, this method again combines the encounter and capture processes, which may be inappropriate for some interactions. Inflated-type models could yield more accurate estimates of diet composition from zero- or one-inflated stomach content data with a more consistent representation of error across different predator feeding ecologies. In this study, we use zero- and zero-and-one-inflated beta distributions that employ a discrete-continuous approach to separately model occurrences of zeroes and ones (Ospina and Ferrari 2010). Through these inflated-type models we can separately model the binomial probability of prey encounter and the continuous quantity of prey consumed during a successful feeding event.

Productivity and resulting prey aggregations are often patchy in open ocean systems and availability can be highly coupled with environmental fluctuations (e.g., Steele 1976, Gomez et al. 2019). There is particularly high potential for zero- and one-inflated data in the diets of large pelagic predators that use a bout feeding strategy to target large aggregations of forage species, such as vertically migrating mesopelagic organisms (Sutton 2013, Murawski et al. 2014, Iglesias et al. 2023). This may also be generally true in wasp-waist food webs, such as in major upwelling systems (Cury et al. 2000) where predators target a small number of species. Effectively estimating diet and simulating trophic linkages in ecosystem models is important for capturing system connectivity (Grilli et al. 2016) and quantifying ecosystem impacts following environmental disturbances. For example, following the 2010 *Deepwater Horizon* oil spill in the GOM, the deep oil plume resulted in a large biomass loss of deep-sea species and accumulation of oil toxins in many meso- and bathypelagic species (Murawski et al. 2014, Romero et al. 2018, Sutton et al. 2022). In Atlantis simulations where oil-related mortality forcing functions were applied to mesopelagic prey groups, the contribution of mesopelagic prey to a pelagic predator's diet was important in determining the predator's response to the deep oil spill (Morzaria-Luna et al. 2018, 2022). By better characterizing pelagic food web connections we improve our ability to model cascading ecosystem effects following a deep-water disturbance.

Through this work we will create an improved diet matrix for the Atlantis ecosystem model of the GOM (Ainsworth et al. 2015, 2018, Perryman et al. *in press*). We specifically aim to improve the representation of pelagic trophic connectivity by testing whether an inflated-type statistical model is better suited to simulate bout feeding. We incorporated new data from recent sampling and fit inputs to both non-inflated and inflated-type models to find the best-fitting distribution. Once the models were fit, we were particularly interested in 1) differences in diet estimates between non-inflated and inflated-type models, and 2) whether the best-fitting model varied across predator species by particular life history traits such as trophic level or habitat association. We hypothesized that pelagic predator diets would be better represented by inflated-type models as prey is patchy and predators utilize a bout feeding strategy.

Methods

Diet data preparation

We compiled diet data from multiple surveys conducted in US Gulf of Mexico waters, including the Fisheries Independent Monitoring survey through the Florida Fish and Wildlife Conservation Commission and the Gulf of Mexico Species Interaction database through Texas A&M University. Because most of these sources were inshore- or shelf-focused, we also included stomach content data from offshore pelagic predators provided by Murawski, S. (unpublished data). Collectively, these sources added 6,492 new stomachs to the diet dataset used to create the existing diet matrix for the GOM Atlantis model (Tarnecki et al. 2016). All stomach contents were converted into volumetric units (mm^3) and normalized to proportions so that each stomach's contents summed to one. We then coded predator and prey species into GOM Atlantis model functional groups (Appendix 3) for future diet matrix creation. More information regarding the informing and parameterization of the GOM Atlantis model can be found in Ainsworth et al. (2015) and Perryman et al. (*in press*).

Distribution fitting

To find the best model for estimating diet composition from datasets that may be zero- or zero-and-one inflated, we fit our proportional diet dataset to three different forms of a beta distribution (Table 3.1). We first fit data to a non-inflated, two-parameter beta distribution (BE). This is a special case of the Dirichlet distribution currently used to create the GOM Atlantis model diet matrix (Ainsworth et al. 2010). The density function for the BE distribution can be defined as

$$f(y;\mu,\phi) = \frac{\Gamma(\phi)}{\Gamma(\mu\phi)\Gamma((1-\mu)\phi)} y^{\mu\phi-1}(1-y)^{(1-\mu)\phi-1} \quad \text{for } 0 < y < 1 \qquad \text{(Eq. 3.1)}$$

where $\Gamma(\cdot)$ is the gamma function. The parameter ϕ plays the role of a precision parameter in the sense that, for fixed μ, the larger the value of ϕ, the smaller the variance of y. Different values of the parameters generate different shapes of the beta density (Ospina and Ferrari 2010). The mean of the beta distribution is calculated as

$$E(y) = \mu \qquad \text{(Eq. 3.2)}$$

Because the interval of the BE density function does not include true zero, we next employed a mixed continuous-discrete distribution that combines the beta distribution with a degenerate discrete distribution to represent occurrences of zero. In other words, we are combining the beta distribution of our proportional diet data with the probability of that prey item being patchy (i.e., having a value of 0). This is referred to as the zero-inflated beta distribution ('BEZI') and is outlined further in Ospira and Ferrari (2010). The corresponding probability density function for the mixed model combining the beta distribution with the degenerate distribution would therefore be

$$\text{bezi}(y;\alpha,\mu,\phi) = \begin{cases} \alpha, & \text{if } y = 0, \\ (1-\alpha)f(y;\mu,\phi), & \text{if } y \in (0,1), \end{cases} \qquad \text{(Eq. 3.3)}$$

where $f(y{:}\ \mu, \phi)$ is the beta density (1) and α represents an added third-parameter; the probability of observing a zero for a given prey item in a predator stomach, or the probability mass at y=0. The mean of the BEZI distribution is calculated as

$$E(y) = \frac{\mu}{(1+\alpha)} \qquad \text{(Eq. 3.4)}$$

Finally, we included a four-parameter model with the ability to fit ‘one’ values, such as in the case of a stomach that only contained one prey item. This is referred to as the zero-and-one-inflated beta distribution (‘BEINF’) (Ospina and Ferrari 2010), and has the density function

$$\text{beinf}(y;\alpha,\gamma,\mu,\phi) = \begin{cases} \alpha(1-\gamma), & \text{if } y = 0, \\ \alpha\gamma, & \text{if } y = 1, \\ (1-\alpha)f(y;\mu,\phi), & \text{if } y \in (0,1), \end{cases} \qquad \text{(Eq. 3.5)}$$

where $f\,(y{:}\ \mu, \phi)$ is the beta density (1), α represents the probability of observing a zero for a given prey item in a predator stomach, or the probability mass at y=0, and $\alpha\gamma$ represents the probability of observing a one for a given prey item in a predator stomach, or the probability mass at y=1. The mean of the BEINF distribution is calculated as

$$E(y) = \frac{\gamma+\mu}{(1+\alpha+\gamma)} \qquad \text{(Eq. 3.6)}$$

Table 3.1: Candidate statistical distribution models fit to our diet dataset. Names and acronyms are adopted from Ospina and Ferrari (2010). Column k represents the number of parameters in each model.

Model	Code	k	Parameters
Beta	BE	2	μ,σ
Zero-inflated beta	BEZI	3	μ,σ,α
Zero-and-one-inflated beta	BEINF	4	μ,σ,α,γ

Model selection

The input diet dataset was fit to all three candidate models using the gamlss() and gamlss.dist() packages in R statistical software (Rigby and Stastinopoulos 2005, Ospina 2006). We used model outputs to calculate the residual sums-of-squares (SS) for each fitted predator-prey interaction, with a lower sum of squared residuals (SS) value indicating a better model fit. In addition, we calculated Akaike Information Criterion (AIC) values for each fitted model as a measure of model parsimony, with lower AIC values indicating a more parsimonious model. Because AIC values include a penalty for the number of model parameters, they allowed us to examine whether the added 3rd and 4th parameters of the BEZI and BEINF models, respectively, improved fit significantly enough to warrant their use.

Matrix creation and food web analysis

We calculated the distribution means of each model (Equations 3.2, 3.4, 3.6) to determine the final diet composition estimate of each predator-prey interaction. We also calculated 95% confidence intervals for distribution means using bootstrapped samples of our input data. We then examined quantitative differences in diet composition values between models for predator-prey interactions to determine how estimates varied across inflated- vs non-inflated-type models. We were particularly interested in examining diet estimates across models for different trophic levels and life histories, as we hypothesized that certain life histories and habitats may lead to more zero- or zero-and-one-inflated input data (e.g., patchy prey in the pelagic environment). To visualize any potential patterns, we chose example 'high trophic level' and 'low trophic level' predators for four different marine life histories: demersal, reef-associated, pelagic-inshore, and pelagic-offshore (Table 3.2). Trophic levels and habitat associations were determined using

FishBase (Froese and Pauly 2024), and all chosen example species were teleost fish with most belonging to their own GOM Atlantis model functional group. Because offshore sampling surveys are limited in the Gulf, we did not have sufficient sample sizes to present results from any low trophic level ‘pelagic-offshore’ species, and so the two high trophic level species with the largest number of stomachs are presented. Additionally, we examined how diet evenness changed when diets were represented by non-inflated vs inflated-type models by calculating Shannon’s evenness (E) for fitted diets (e.g., in Jones 2004).

Table 3.2: Selected predator species highlighted in results, chosen to represent multiple trophic levels and habitat associations. Trophic levels were taken from FishBase (Froese and Pauly 2024).

Predator species	**Trophic Level (TL)**	**Stomachs (n)**
Demersal		
Red drum (*Sciaenops ocellatus*)	3.74	4,320
Striped mullet (*Mugil cephalus*)	2.48	241
Reef-associated		
Gray snapper (*Lutjanus griseus*)	4.23	5,626
White grunt (*Haemulon plumierii*)	3.59	1,367
Pelagic-inshore		
Spanish mackerel (*Scomberomorus maculatus*)	4.53	223
Spanish sardine (*Sardinella aurita*)	3.4	337
Pelagic-offshore		
Blackfin tuna (*Thunnus atlanticus*)	4.35	54
Yellowfin tuna (*Thunnus albacares*)	4.41	30

Results

Based on goodness-of-fit metrics, the zero-inflated BEZI distribution was the best-fitting and most parsimonious model for the highest contributing prey item to every predator’s diet, but model fit varied across predator-prey interactions for the next highest contributing prey groups (Table 3.3). The BEZI distribution fit best for two to three of the top three prey items for lower-trophic level predator diets, whereas it was only the best fit for the highest contributing prey item in higher-trophic level species' diets. The exceptions to this were the pelagic-offshore predators and mullet, for which all three top prey items were best represented by the zero-inflated model. An example of a pelagic-offshore predator/prey interaction that was better fit by the BEZI distribution is shown in Figure 3.1. There was no apparent difference in the best-fitting model selected between trophic levels. The AIC values for all interactions agreed with sums-of-squares, suggesting that the additional third parameter modeling the occurrences of zero values significantly improved model fit in those cases. The zero-and-one-inflated (BEINF) distribution was never chosen as the best-fitting model based on either sums-of-squares or AIC values, suggesting there was no benefit to the added fourth parameter. Therefore, only BE and BEZI results are presented from this point forward.

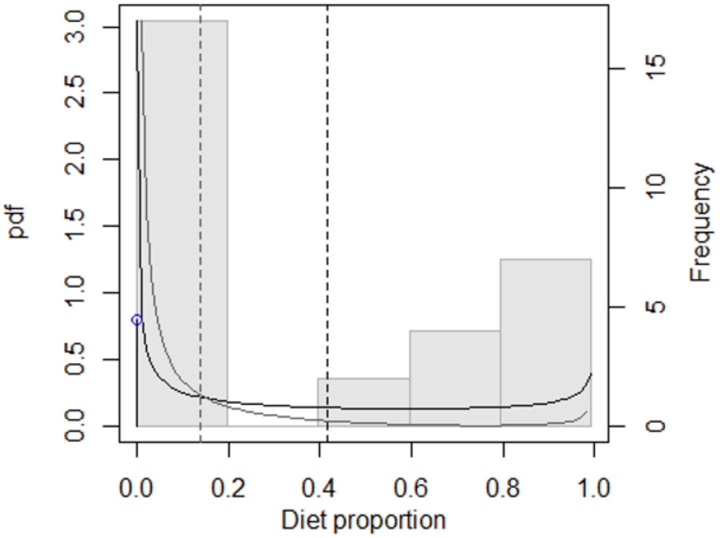

Figure 3.1: The diet interaction of predator *Thunnus albacares* consuming functional group Deepwater Fish fit to a beta, BE (solid gray line), and zero-inflated beta, BEZI (solid black line), distribution. The dashed gray and black lines indicate the fitted μ parameters for the BE and BEZI distributions, respectively. A histogram of the raw diet data is shown underneath in light gray. The vertical solid black line at y=0 represents the α parameter fit by the BEZI.

Table 3.3: Goodness-of-fit criteria and measure of parsimony for each fitted model. The top three prey items of each example predator species are shown.

Trophic interaction		**Sum-of-squared (SS) residuals**			**Akaike Information Criterion (AIC)**		
Predator (habitat)	Prey	BE	BEZI	BEINF	BE	BEZI	BEINF
Sciaenops ocellatus (Demersal)	Crabs and lobsters	3162.1	**3027.1**	4328.3	10917.7	**10731.2**	12278.0
	Other demersal fishes	**2911.8**	3487.7	4273.6	**10561.5**	11343.1	12223.0
	Infaunal meiobenthos	**2697.2**	3606.1	4243.8	**10230.8**	11487.3	12192.7
Mugil cephalus (Demersal)	Detritus	199.2	**120.0**	287.8	644.0	**523.8**	736.7
	Infaunal meiobenthos	190.3	**151.3**	259.4	633.0	**579.8**	711.7
	Protists	187.3	**149.9**	259.8	629.2	**577.5**	712.0
Lutjanus griseus (Reef-associated)	Other Shrimp	4631.8	**3282.9**	5615.3	14877.9	**12943.4**	15965.2
	Other demersal fishes	**3822.5**	4297.6	5676.3	**13797.5**	14458.5	16025.9
	Crabs and lobsters	**3659.1**	4613.5	5622.1	**13551.7**	14857.6	15972.0
Haemulon plumierii (Reef-associated)	Infaunal meiobenthos	1112.7	**819.4**	1420.4	3604.0	**3187.7**	3941.8
	Shrimps	1042.5	**878.1**	1305.0	3515.0	**3282.3**	3825.9
	Crabs and lobsters	**857.0**	1137.7	1343.0	**3247.1**	3636.4	3865.2
Scomberomorus maculatus (Pelagic-inshore)	Other demersal fishes	188.9	**130.3**	224.7	601.8	**521.1**	644.6
	Small pelagic fishes	**153.1**	173.1	232.7	**555.0**	584.3	652.3
	Infaunal meiobenthos	**127.1**	220.6	217.1	**513.5**	638.4	636.9
Sardinella aurita (Pelagic-inshore)	Small zooplankton	286.1	**177.6**	345.9	907.2	**748.5**	975.1
	Infaunal meiobenthos	255.5	**245.7**	285.0	869.0	**857.8**	909.9
	Large zooplankton	**209.3**	278.0	362.2	**801.8**	899.5	990.7
Thunnus atlanticus (Pelagic-offshore)	Deep water fishes	43.6	**30.9**	56.0	147.7	**131.2**	165.2
	Other demersal fishes	42.2	**28.9**	57.4	145.9	**127.4**	166.6
	Squid	39.2	**32.8**	53.7	141.9	**134.3**	163.0
Thunnus albacares (Pelagic-offshore)	Squid	29.4	**24.3**	24.5	90.5	**86.9**	89.1
	Deep water fishes	26.5	**15.2**	25.3	87.4	**72.8**	90.1
	Small pelagic fishes	18.9	**14.0**	40.5	77.3	**70.3**	104.1

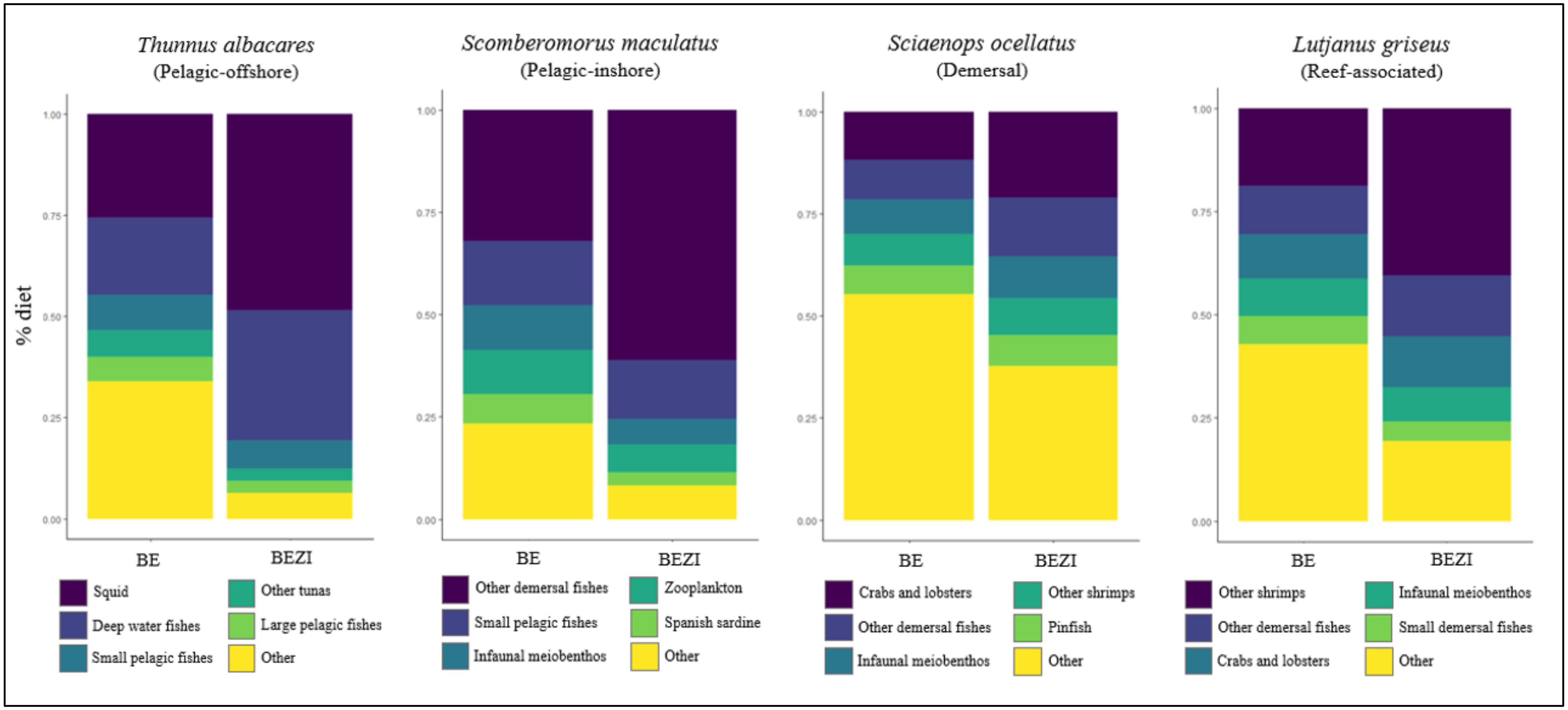

Figure 3.2: Contribution of all prey items to the diets of example predators for each habitat-type based on different fitted distributions. The yellow 'other' category represents the sum of all other prey items not otherwise specified.

Distribution means (as defined in Equations 3.2, 3.4, and 3.6) were considered as the fitted diet composition estimates for each modeled predator/prey interaction. Diet composition values calculated by the BEZI distribution were higher than those from the non-inflated BE distribution for all predators' top contributing prey items (Table 3.4). Bootstrapped confidence interval ranges did not overlap for any example predator between distributions. However, as prey items became less important (i.e., contributed less) to predator diets, this pattern begins to break down. For the second-most utilized prey item, BE and BEZI distribution means were similar for reef-associated and pelagic-inshore species and some confidence intervals begin to overlap. For the third-most utilized prey item by each predator, zero-inflated diet estimates were less than estimates from the BE distribution for a few predators (e.g., pelagic-inshore species), and most confidence interval ranges overlapped (Table 3.4).

When fitted diet estimates are compared between the BE and BEZI distributions, the non-inflated BE distribution underestimates the highest contributing prey item when compared to BEZI estimates (Figure 3.2). In contrast, the BE can overestimate rarer prey items as compared to the fitted BEZI. Mid-range contributing prey items had similar contribution estimates across the two models. These findings were reflected in the Shannon's E for fitted diets (Table 3.5); a diet with a Shannon's E of 1 would represent a diet equally composed of all potential prey items. For all example predators, diet compositions fitted by the BE distribution had more dietary evenness than those fit with the zero-inflated model.

Table 3.4: Distribution means (% diet contribution) for selected predators and their three most consumed prey items; 95% confidence intervals are provided in parentheses. Bolded values indicate best-fitting model.

Trophic interaction		**% of diet** *(95% CI)*	
Predator (habitat)	Prey	BE	BEZI
Sciaenops ocellatus (Demersal)	Crabs and lobsters	11.6 *(10.1 - 13.9)*	20.3 *(18.4 - 22.6)*
	Other demersal fishes	8.9 *(7.0 - 10.2)*	13.9 *(13.7 - 19.2)*
	Infaunal meiobenthos	8.4 *(6.4 - 11.5)*	10.3 *(9.4 - 12.6)*
Mugil cephalus (Demersal)	Infaunal meiobenthos	21.4 *(19.0 - 22.9)*	26.0 *(24.6 - 28.8)*
	Detritus	20.2 *(18.8 - 22.6)*	25.3 *(23.5 - 29.9)*
	Protists	16.7 *(15.3 - 17.1)*	23.2 *(23.0 - 26.8)*
Lutjanus griseus (Reef-associated)	Other Shrimp	18.8 *(17.7 - 19.7)*	39.3 *(36.0 - 41.0)*
	Other demersal fishes	11.1 *(9.1 - 12.2)*	14.2 *(11.7 - 16.6)*
	Crabs and lobsters	10.8 *(8.7 - 11.5)*	12.0 *(9.8 - 14.1)*
Haemulon plumierii (Reef-associated)	Infaunal meiobenthos	20.2 *(20.2 - 23.0)*	37.1 *(36.7 - 44.6)*
	Other Shrimp	19.6 *(17.8 - 22.4)*	25.4 *(21.8 - 26.1)*
	Crabs and lobsters	11.2 *(5.7 - 11.2)*	10.5 *(9.3 - 12.6)*
Scomberomorus maculatus (Pelagic-inshore)	Other demersal fishes	32.0 *(30.4 - 33.7)*	59.1 *(57.3 - 63.6)*
	Small pelagic fishes	15.4 *(13.9 - 17.6)*	15.1 *(14.0 - 18.2)*
	Infaunal meiobenthos	10.9 *(8.5 - 13.3)*	6.2 *(5.8 - 8.6)*
Sardinella aurita (Pelagic-inshore)	Small zooplankton	26.0 *(24.2 - 27.0)*	45.7 *(42.8 - 46.8)*
	Infaunal meiobenthos	20.7 *(19.3 - 21.6)*	20.9 *(19.0 - 22.8)*
	Large zooplankton	12.0 *(10.5 - 13.4)*	8.7 *(7.2 - 11.0)*
Thunnus atlanticus (Pelagic-offshore)	Deep water fishes	14.3 *(12.7 - 15.4)*	32.4 *(29.3 - 34.4)*
	Other demersal fishes	13.2 *(11.9 - 14.1)*	24.4 *(22.5 - 27.8)*
	Squid	11.8 *(8.7 - 12.8)*	15.2 *(11.8 - 15.6)*
Thunnus albacares (Pelagic-offshore)	Squid	25.5 *(25.0 - 29.4)*	49.0 *(48.4 - 51.7)*
	Deep water fishes	16.2 *(13.6 - 18.7)*	28.4 *(25.8 - 32.8)*
	Small pelagic fishes	8.7 *(5.8 - 8.9)*	7.2 *(6.5 - 8.6)*

Table 3.5: Dietary evenness (Shannon's E) for example predator diet composition as fit by non-inflated beta (BE) and zero-inflated beta (BEZI) distributions.

Predator species	**Shannon's E**	
	BE	BEZI
Demersal		
Red drum (*Sciaenops ocellatus*)	0.93	0.71
Striped mullet (*Mugil cephalus*)	0.93	0.69
Reef-associated		
Gray snapper (*Lutjanus griseus*)	0.91	0.56
White grunt (*Haemulon plumierii*)	0.92	0.59
Pelagic-inshore		
Spanish mackerel (*Scomberomorus maculatus*)	0.86	0.42
Spanish sardine (*Sardinella aurita*)	0.93	0.62
Pelagic-offshore		
Blackfin tuna (*Thunnus atlanticus*)	0.88	0.67
Yellowfin tuna (*Thunnus albacares*)	0.85	0.53

Discussion

Zero-inflated beta distributions (BEZI) were the best-fitting model for estimating marine predator diets, particularly for top prey items. For subsequently ranked prey items, the added third parameter of the BEZI model no longer improved model fit enough to pass measures of parsimony for demersal, reef-associated, and pelagic-inshore predators. The trophic interactions between pelagic-offshore predators and their top three prey items were best represented by zero-inflated distributions. This discrepancy may reflect the more homogenous nature of potential prey species in inshore habitats versus the heterogenous distribution (patchiness) of prey in the open ocean. Low trophic-level productivity in the open ocean, specifically in the epipelagic zone, is highly dependent on environmental factors such as sea surface temperature, salinity, and nutrient inputs, which can be tied to large-scale climatic drivers (e.g., riverine input, ENSO cycles) (Steele 1976, Lorenzen 1976, Gomez et al. 2019). Ocean physics such as eddies and frontal features concentrate this productivity in ephemeral patches that provide essential grazing opportunities for zooplankton, juvenile organisms, and planktivorous forage fishes (Suthers et al. 2023, Belkin et al. 2014, Zhang and Hu 2021, Scott et al. 2024). The spatiotemporal inconsistency of these prey aggregations may result in more zero-inflation in pelagic-offshore predator diets, as evidenced by this study.

The zero-and-one-inflated model (BEINF) did not improve model fit enough to warrant inclusion of an additional fourth parameter in any predator-prey interaction. This was surprising for pelagic-offshore predators who are likely to bout feed on one taxa in a prey patch, but this may be explained by their most-utilized prey group. Pelagic predators, such as the tuna species considered here, heavily utilize the mesopelagic prey that vertically migrate into surface waters each night (Iglesias et al. 2023, Young et al. 2015, Olson et al. 2014). This vertically migrating biomass is composed of numerous mesopelagic fish, cephalopod, and crustacean taxa (Sutton 2013). The pelagic-offshore species highlighted in this study (e.g., *Thunnus albacares*) are non-selective (Young et al. 2015) and opportunistically consume multiple mesopelagic species, potentially preventing a one-inflated diet.

Predators in wasp-waist ecosystems, such as major upwelling zones, may also exhibit zero- and/or one-inflated data as productivity is environmentally stochastic and predators exploit a few key forage species (Cury et al. 2000). Inflated-type models such as the ones presented in this paper could be beneficial for characterizing diets in these systems. Additionally, inflated-type models may be useful for characterizing diets of specialist consumers. We found the diet of the inshore detritivore *Mugil cephalus* to be zero-inflated, which is likely representative of a specialist feeding mechanism. The top three prey items *of M. cephalus*, which all represent sediment feeding, contributed similarly to overall diet make-up and accounted for approximately

75% of the fitted diet composition. All other potential prey items were therefore rare, resulting in zero-inflation.

When diet data was fit to the BEZI model, the resulting estimates of diet composition showed the top 1-2 prey items for each predator contributing more to the diet, middle prey items contributing about the same amount, and rarer prey items contributing less. The BEZI distribution therefore seems to place more importance or reliance on a predator's most common prey items, and less importance on rarely utilized prey items compared to the non-inflated model. In other words, non-inflated models may over-estimate rare prey items and under-estimate key food groups. We found this to be true based on the Shannon's evenness (E) of fitted diet compositions; diet dependence was more evenly distributed amongst potential prey items when fit to non-inflated distributions versus the BEZI. Given that the current diet matrix in the GOM Atlantis model was created using a form of the non-inflated beta distribution, updating our model using the diet estimates from fitted zero-inflated models will result in less 'balanced' diets of predator groups. The methodology presented here is also an important advancement over taking a simple average of stomach data, which conflates the underlying processes of prey encounter (a binomial outcome) and capture success (a continuous outcome). Independently modeling encounter success as the probability of a binomial outcome is not only applicable to feeding in the patchy pelagic zone (e.g. Sims et al. 2006) but has also been used to model mate-finding (e.g. Gilroy and Lockwood 2012).

This increased dependence on top prey groups may leave predators more vulnerable to environmental disturbances affecting key food groups. For example, the tuna species examined in this paper showed an increased utilization of deep-water prey species when their diets were fit to zero-inflated models (Figures 3.1 & 3.2). This is particularly of interest as deep water spills (i.e., *Deepwater Horizon*) have previously resulted in mortality and physiological impairment of meso- and bathypelagic species (Lewis and Ricker 2020). Studies using the current version of the GOM Atlantis model have demonstrated a loss in these pelagic predators following simulated mortality of mesopelagic prey (Morzaria-Luna et al. 2022), an effect that will likely be exacerbated by the diet estimates produced by this study. Additionally, inshore predators such as red drum showed an increased dependence on prey items negatively affected by harmful algal bloom (HAB) events, the frequency of which is increasing with climate change impacts (Walsh et al. 2006). As oil exploration moves into deeper waters and climate change effects become more pronounced, environmental disturbances may become more common. Improving ecosystem model parameterization to more effectively predict predator population effects following environmental disturbances is therefore increasingly essential. As many GOM species are targets of commercial fisheries, this has important implications for fisheries management on both the state and federal levels.

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CHAPTER 4: CONSIDERING MESOPELAGIC FORAGE AVAILABILITY IN MANAGEMENT STRATEGIES FOR PELAGIC PREDATORS

Introduction

Ecosystem-based fisheries management strategies

In recent decades, a growing understanding of marine ecosystems has led to a call for the development and implementation of fisheries management policies that consider ecosystem influences on target species ('ecosystem-based fisheries management', EBFM). The managing body of federal United States (US) fisheries stocks has committed to moving towards an EBFM approach (NOAA 2016), and the concept has gained traction among both decision-makers and stakeholders (Biedron and Knuth, 2016). Marshall et al. (2019) found that about one quarter of US stock assessments included some form of ecosystem consideration, most often in the form in a modifier on assessment inputs (e.g., a mortality modifier on Gag grouper in the Gulf of Mexico to account for red tide impacts; SEDAR 2021, Vilas et al. 2023). However, ecosystem considerations are more likely to be applied in already overfished stocks (Marshall et al. 2019), and most fisheries management rules in the US are set using a single-species framework.

All 507 federally-managed US fish stocks under federal jurisdiction utilize some form of harvest control rule (HCR) to determine catch limits (Free et al. 2022). HCRs can take many different forms, including constant catch, constant escapement, constant instantaneous fishing mortality (F), or threshold HCRs. Threshold HCRs use pre-determined guidelines to scale back or stop fishing mortality on a target species when its biomass drops below pre-determined biological reference points (e.g., US Congress 2004, PFMC 2020). This approach provides a more adaptive management strategy compared to reactive adjustments made following stock assessments, and threshold HCRs have been found to outperform other HCR types in preventing overfishing, reducing rebuilding times, and maintaining high yields in high uncertainty scenarios (Kritzer et al. 2019, Wiedenmann et al. 2017). In the US, threshold HCRs are mostly commonly used in the management Mid-Atlantic stocks (e.g. MAFMC 2016), but there is a push for more regional fisheries councils to move towards the use of threshold HCRs given their robustness to uncertainty and improved performance under climate change scenarios (Wilberg et al. 2011, Wiedenmann et al. 2017, NRC 2014).

Additionally, recent work has called for harvest control rules to move from the traditional single-species structure towards an ecosystem-based approach, and for the use of management strategy evaluations (MSEs) to compare the performance of multiple candidate HCRs (Free et al. 2022). An MSE is an iterative modeling framework used to simulate and test the performance of candidate management strategies, such as HCRs (Sainsbury et al. 2000). The design of HCRs has been identified as a potential avenue for incorporating ecosystem information in fisheries management (Punt et al. 2014). One successful case study of this is the control rule for Pacific sardine, in which the harvest fraction is adjusted based on water temperature (Tommasi et al. 2017, PFMC 2023). Another example is the Atlantic herring management plan (NEMFC 2021), for which an MSE was conducted to examine the performance and tradeoff of several HCRs. The final harvest rule selected by the NEFMC management council was a threshold HCR that managed the Atlantic herring stock to ensure that it remained high enough to support key predators (e.g., bluefin tuna) (Deroba et al. 2019, Feeney et al. 2019). A similar hypothetical harvest control rule was developed for the Pacific sardine fishery that considers retaining enough sardines in the system to provide an adequate forage base for predators, although this has not yet been adopted into management (Punt et al. 2016).

Predation effects such as these play crucial roles in marine population dynamics yet are only included in 1% of US stock assessments and are disproportionately more likely to be considered in regions that have access to a well-established stomach contents laboratory and robust diet datasets (Marshall et al. 2019). The examples described above consider the top-down impact of predation mortality on population size, but it is also important to consider bottom-up impacts on a harvested predator population. Kaplan et al. (2020) conducted a pseudo-MSE that accounted for bottom-up trophic impacts by adjusting fishing mortality on targeted predator species based on the availability of their main forage prey (zooplankton), finding that these ecosystem-based threshold rules resulted in widespread ecosystem effects. In these limited cases where food-web connections have been assessed in relation to management questions, only epipelagic forage species have been considered. However, in the pelagic ecosystem, mesopelagic forage resources may play a more important mid-tropic level role in food web dynamics.

The ecosystem role of mesopelagic fishes

Mesopelagic fishes (e.g., families Myctophidae, Gempylidae, Gonostomatidae) are a numerically dominant component of the open ocean pelagic fauna worldwide. One genus in particular, *Cyclothone*, is considered to be the most abundant vertebrate on earth (Ahlstrom et al. 1984). Mesopelagic fishes reside at depths of 200-1000m during daylight hours, but most undergo diel vertical migration into surface waters each night to follow their planktonic prey (e.g., Anderson and Sardou 1992, Frost and McCrone 1979, Hopkins et al. 1996). This massive vertical movement of biomass plays a significant role in carbon transport and biogeochemical cycling in the open ocean (Hoagland et al. 2019). This vertical connectivity results in strong trophic linkages between deep sea species and large pelagic predators. Mesopelagic fishes have been determined to be important prey items for highly migratory finfishes and marine mammals across the World Ocean (Satoh et al. 2004, Iglesias et al. 2023, Duffy et al. 2017, Pusineri et al. 2008). Mesopelagic fishes may even be underestimated in the diets of large pelagic fishes, as many stomachs used for diet analysis are taken from fish caught during the day in sportfishing tournaments or from commercial fishing trips. Mesopelagic fishes from the previous night's feeding, which are higher in fat and lower in protein than epipelagic forage fishes, may already be digested (Yancey et al. 1992, Salvanes and Kristoffereson 2001).

Mesopelagic fishes play an important forage role in pelagic ecosystems that exhibit wasp-waist dynamics. They can occupy a central place in the food web connecting lower and higher trophic levels (Griffiths et al. 2013, Woodstock et al. 2021). Furthermore, it's possible that mesopelagic fishes provide a more stable forage base than epipelagic fishes. The availability of epipelagic forage fishes (e.g., menhaden, sardine) is spatiotemporally dynamic; abundances are heavily tied to climate factors (e.g., Buchheister et al. 2016, Tommasi et al. 2017, Adams et al. 2018). In contrast, the distribution of Myctophidae, one of the most abundant mesopelagic fishes, is spatially homogenous despite fluctuations in environmental conditions (Milligan and Sutton 2020). Given the globally large quantity of high-fat and low-protein, but readily accessible, mesopelagic prey in apex predator diets, it may be that predators are utilizing mesopelagic forage to sustain themselves when more energetically rewarding epipelagic forage is unavailable (Rooney et al. 2006). Mesopelagic fishes may therefore be useful indicators for representing bottom-up drivers of secondary productivity in the pelagic system. The ecosystem role provided by deep sea fishes has historically been under-considered; the intrinsic value of the deep-sea ecosystem is traditionally a tough sell to stakeholders (Smith et al. 2020, Jamieson et al. 2020) and vertical water column connectivity of the pelagic food-web has been understudied (Sutton et al. 2021).

However, the deepwater pool of forage fish and invertebrates is unlikely to remain consistently available under future climate change and increasing anthropogenic exploitation of deep ocean resources. With rising ocean temperatures due to large-scale climate change, there is an expected poleward range shift of many Myctophidae species (Freer et al. 2019). Although too bony and oily for human consumption, there has been talk of a potential fishery on deep sea fishes for use in fish meal to feed livestock to help meet growing global protein demands (St. John et al. 2016). Furthermore, the risk of future deep-water disturbances is high as oil extraction moves increasingly deeper and more of the seafloor is claimed for mining contracts (Smith et al. 2020, Sutton et al. 2020).

The Gulf of Mexico

One of the most extreme examples of a deep-water disturbance came in 2010 with the *Deepwater Horizon* (DWH) disaster, which injected over 100 million gallons of crude oil into the deep Gulf of Mexico (GOM) in the largest accidental marine oil spill in history. The GOM is one of the most highly biodiverse mesopelagic ecosystems in the world, with 97% of its water mass below the 200m isobath (Sutton et al. 2022). Following the DWH spill there was an abundance of funding and research efforts to attempt to evaluate environmental impacts. The task of analyzing impacts on deepwater communities was challenging given the lack of pre-spill deep-water studies. Since 2011, the mesopelagic biomass of the northern GOM has been quantified through sampling efforts by the Deep Pelagic Nekton Dynamics of the Gulf of Mexico

(DEEPEND) Consortium and now the GOM represents one of the most extensively studied deep-sea systems in the world (Sutton et al. 2022). The harshest DWH impacts on GOM mesopelagic fishes were delayed. High levels of oil toxins (e.g., polycyclic aromatic hydrocarbons, 'PAHs') were still detected in guts and eggs five years after the DWH spill suggesting bioaccumulation and maternal transfer, and numbers remain depleted likely due to repeated recruitment failure (Romero et al. 2018, Sutton et al. 2022). Mesopelagic fishes in the GOM are thus highly vulnerable and exhibit low resilience to deep-water oil spills due to prolonged exposure to oil, long-term toxicity effects, consumption of contaminated prey, and low fecundity (Sutton et al. 2022).

There are limited diet studies of large pelagic fishes specific to the GOM, but those that exist paint an interesting story of how mesopelagic fishes are utilized as prey. In the 1980s, Manooch and Mason (1983) conducted a diet study of yellowfin (*Thunnus albacares*) and blackfin (*Thunnus atlanticus*) that found only epipelagic prey (e.g., sargassum-associated fishes) in stomachs. Following the DWH oil spill, Murawski (unpublished data) conducted targeted longline and hook-and-line sampling for large pelagic fishes in the northern GOM and found mesopelagic fishes in the stomachs of yellowfin tuna, blackfin tuna, swordfish (*Xiphias gladius*), great barracuda (*Sphyraena barracuda*), and wahoo (*Acanthocybium solandri*). Mesopelagic fishes have also been found in the stomachs of bluefin tuna (*Thunnus thynnus*) and swordfish (*Xiphias gladius*) in the GOM and Florida Straits, respectively (Butler et al. 2015, Heemsoth 2009). Stomach contents from Murawski (unpublished data) showed a greater prevalence of mesopelagic fish prey in the stomachs of predators captured around oil rigs at night. This suggests that while deep-water oil rigs are sites of potential disasters, they may also be creating new feeding opportunities via structure and artificial light. In the GOM, research suggests that oil rigs may be functioning as fish aggregating devices for highly migratory species (Snodgrass et al. 2020) and there is evidence of intentional directed movement of yellowfin tuna between oil rigs (Price et al. 2022). These offshore oil rigs may be providing feeding opportunities for large pelagic predators where vertically migrating mesopelagic species are attracted to artificial light; these feeding events may be more dependable than the availability of epipelagic prey in the open-ocean GOM (Adams et al. 2018). However, given the susceptibility of mesopelagic fishes to deep-water oil spills, large pelagic predators become more vulnerable to the impacts of deep-water disturbances with increased utilization of mesopelagic prey (Morzaria-Luna et al. 2022). Given these strong food-web connections and the many risks to deepwater species including mesopelagic fish, it is important for managers to consider the population impacts on exploited pelagic predators if the availability of reliable mesopelagic forage fishes were to decrease.

Project purpose

We used an Atlantis ecosystem model of the Gulf of Mexico to conduct a management strategy evaluation (MSE) on a variety of threshold HCRs for an example large pelagic predator (yellowfin tuna, *Thunnus albacares*), including some that reduce fishing mortality on the target species depending on the availability of mesopelagic fish prey. The use of ecosystem models as operating models in MSEs has been recommended for informing ecosystem-based management in the Gulf of Mexico (Grüss et al. 2017). Atlantis has previously been used to conduct MSEs with ecosystem considerations. Masi et al. (2018) applied blanket HCRs to the entire managed GOM reef fish complex and Kaplan et al. (2020) evaluated threshold HCRs that account for bottom-up trophic effects. We took inspiration from the forage-based HCRs applied by Kaplan et al. (2020), and our objective with this work was to provide a proof-of-concept study that examined whether considering the availability of mesopelagic prey could be beneficial for the management of large pelagic fishes.

Methods

The Gulf of Mexico Atlantis ecosystem model

The Atlantis ecosystem modeling framework is a three-dimensional ‘end-to-end’ simulation model that represents detrital processes up through apex predators and human exploitation (Audzijonyte 2017a). Species in Atlantis are incorporated into functional groups, which can be fully age-structured and have unique suites of sub-routines (e.g. growth, reproduction, movement) to represent their ecology. Other biological dynamics simulated by the model include habitat affinities, space competition, and feeding. Atlantis models also incorporate physical and biogeochemical processes to capture environmental and nutrient dynamics and include an effort prediction routine for simulating fisheries behavior. A built-in policy simulation routine allows the user to implement and assess the ecosystem impacts of desired management policies, such as total allowable catch (TAC) and HCRs (Audzijonyte 2017b).

The Gulf of Mexico (GOM) Atlantis model was created by Ainsworth et al. (2015) and updated by Perryman et al. (in press). It includes 91 functional groups (Appendix 3). Functional groups are either single-species (if of managerial importance) or aggregated into a group with similar life history traits (e.g. ‘small reef fish’). The polygon geometry of the GOM Atlantis model was designed to capture biogeography, bathymetry, important estuarine areas, and jurisdictional boundaries (Figure 4.1).

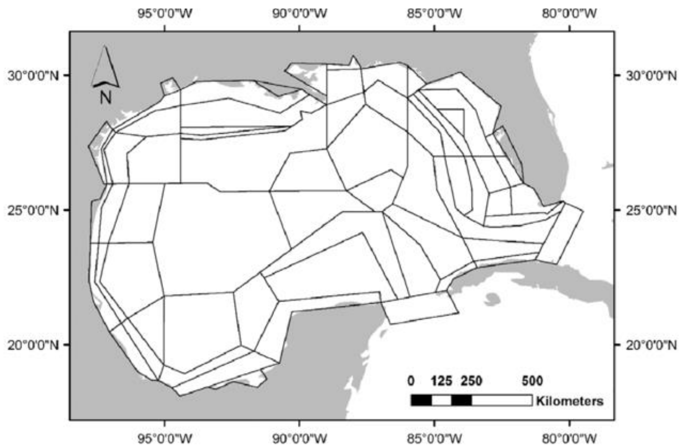

Figure 4.1: Polygon geometry of the GOM Atlantis model (Source: Ainsworth et al. 2015)

We used yellowfin tuna (*Thunnus albacares*, 'YTN') as an example predator to simulate feeding effects of large pelagic predators that utilize both epipelagic and mesopelagic fish prey (e.g., Iglesias et al. 2023). Mesopelagic fishes in GOM Atlantis are represented by the deepwater fish ('DWF') group (Appendix 3). For this study, we compiled the most up-to-date available diet information for YTN (and other large pelagic predators) from the Florida Fish and Wildlife Conservation Commission's (FWC) Fisheries Independent Monitoring (FIM) group (K. Thompson, FWC-FIM, pers. comm.), the Gulf of Mexico Species Interaction (GoMexSI) database (Simons et al., 2013; http://gomexsi.tamucc.edu), and stomach contents from ongoing offshore sampling efforts Murawski (unpublished data). We also conducted a literature review of large pelagic diet studies from the Gulf of Mexico and the southern portion of the US Atlantic coast (Davies and Bortone et al. 1976, Satoh et al. 2004, Rudershausen et al. 2010, Butler et al. 2015, Manooch and Mason 1983, Heemsoth 2009, Matthews et al. 1977). Diet data from these sources were fitted to a zero-inflated beta distribution to create a matrix of diet availabilities for input to the GOM Atlantis model (Scott, unpublished manuscript). See Audzijonyte et al. (2017a) for a description of availabilities in Atlantis. The parameterized diet composition for adult and juvenile yellowfin tuna in the GOM Atlantis model is visualized in Figure 4.2.

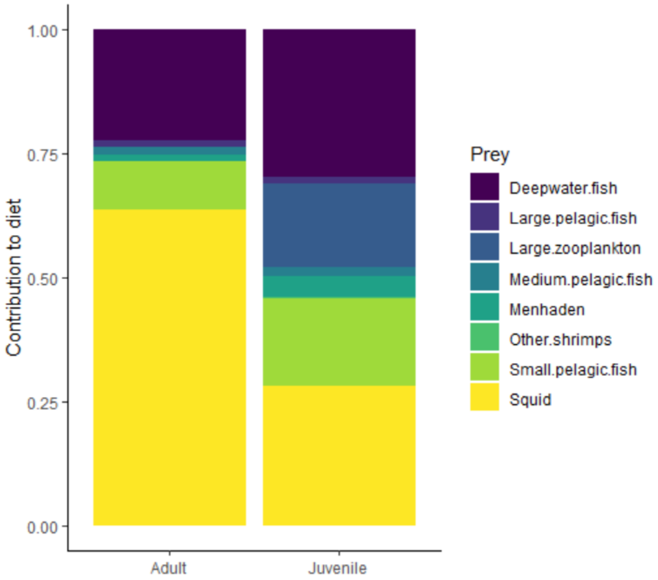

Figure 4.2: Normalized prey availabilities for yellowfin tuna (YTN) in the GOM Atlantis model

Simulating mesopelagic fish abundance

Following the 2010 DWH oil spill in the Gulf of Mexico, the Deep Pelagic Nekton Dynamics of the Gulf of Mexico (DEEPEND) Consortium (https://restore.deependconsortium.org/) conducted consistent water column sampling of the mesopelagic community in the northern Gulf using a Multiple Opening and Closing Net (MOCNESS), resulting in a timeseries of mesopelagic fish abundance (n fish per m^3 sampled). For this study, we considered the combined abundance of all captured mesopelagic fish taxa. For consistency, we only used abundance data from surveys conducted at night, as this is when most mesopelagic fishes are active and migrating, so night-time samples are more likely to be representative of the true abundance of mesopelagic fishes. There were seasonal differences in mesopelagic fish abundance throughout the timeseries as determined by a two-sample t-test ($t(62) = -3.66, p < 0.001$), and so we chose retain only summer data as summer sampling events had both the highest mean abundance and variance; by only using summer values we avoided underestimating the variance. We then scaled all data points that so the mean = 1, and each data point functioned as a scalar relative to the mean value.

We divided the abundance data into two sets based on abundance trends (Figure 4.3), with one set (2011 sampling events, n = 33) representing a former, higher mesopelagic abundance regime, and one (2015-2021 sampling events, n = 31) representing the presumed current, lower abundance levels. These levels may represent the long-term population decline following the DWH oil spill due to maternal toxin transfer and resulting recruitment failure in mesopelagic fish species (Romero et al. 2018, Sutton et al. 2022), but causation cannot be proven given the lack of pre-spill data. We henceforth refer to abundances from 2011 sampling events as 'pre-decline' and abundances from 2015-2021 sampling events as 'post-decline'.

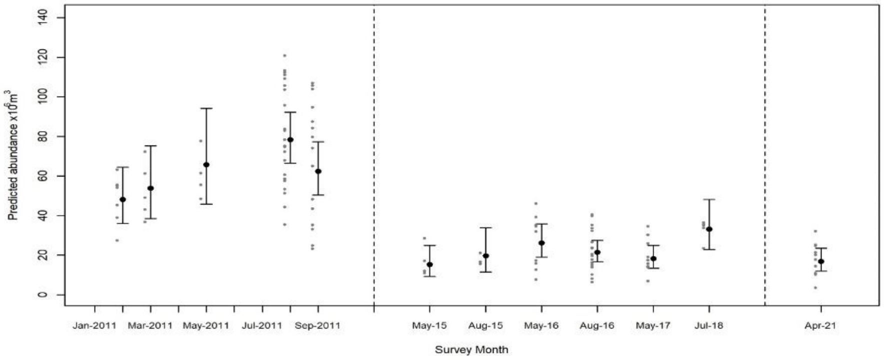

Figure 4.3: Mesopelagic fish abundance as determined by MOCNESS trawl sampling conducted by the DEEPEND Consortium (https://restore.deependconsortium.org/). Sampling efforts were funded by the NOAA National Resource Damage Assessment program (2011), the Gulf of Mexico Research Initiative (2015-2018), and the NOAA RESTORE program (2021+). Values are shown as the predicted number of individuals captured per 10^6m3 of water sampled and represent all captured mesopelagic fish taxa. Values from 2011 sampling events were used to create the 'pre-decline' mesopelagic regime forcing files for Gulf of Mexico Atlantis model simulations, and values from 2015+ sampling events were used to create the 'post-decline' regime forcing files. (Source: Sutton et al. in prep)

We then created a third hypothetical 'future decline' fish abundance dataset by dividing the 'post-decline' mesopelagic abundances by the difference in the means (35%) between the ‘pre-decline’ (mean = 0.00844 n m^{-3}) and the ‘post-decline’ datasets (mean = 0.00295 n m^{-3}). Those pseudodata represent a potential future deep-water disturbance where mesopelagic fish populations are reduced even further, such as in the case of another deepwater oil spill or the creation of a mesopelagic fishery (St. John et al. 2016). We then bootstrapped the three abundance vectors with replacement to create three (‘pre-decline’, ‘post-decline’, ‘future decline’) timeseries with daily values for 50 years that had similar means and variances to the original DEEPEND sampling data. Capturing true variability in mesopelagic fish abundance is important to ensure that applied HCRs turn on and off at a realistic frequency. We confirmed via F-tests and a Welch 2-sample test that the variance and mean were not significantly different between bootstrapped vectors and the original data. We used these three timeseries to create forcing files for the GOM Atlantis model, one for each mesopelagic fish abundance regime, that forced the abundance of mesopelagic fish daily for 50 years. This was accomplished by taking the initial value for numbers of our deepwater fish (DWF) group in the model and multiplying it by each timeseries vector to create three timeseries forcing files. The same process was applied to all age classes of the DWF group.

Management strategy simulations in Atlantis

For each of the three mesopelagic abundance regimes (‘pre-decline’, ‘post-decline’, ‘future decline’), we ran a 50-year model simulation with fishing mortality (F) on our yellowfin tuna group (YTN) held constant at FMSY (no adaptive management) (Table 4.1). We determined FMSY for YTN to be approximately 0.38 by creating an equilibrium catch curve by varying F on YTN and keeping F for all other groups in the model constant. We compared the ‘post-decline’ and ‘future decline’ scenarios as relative to outputs from the ‘pre-decline’ scenario. We examined yellowfin tuna population impacts at multiple levels of mesopelagic forage (group DWF) availability under no adaptive management.

Table 4.1: A list of simulated management strategies. All simulations were conducted for each mesopelagic abundance regime (‘pre-decline’, ‘post-decline’, ‘future decline’), for a total of 18 Atlantis simulations. All simulations were run for 50 years.

Simulated management strategies

1. Constant fishing at FMSY for yellowfin tuna (no adaptive management)
2. Single-species threshold harvest control rule for yellowfin tuna
3. Threshold harvest control rule that decreases F on yellowfin tuna by 33% when mesopelagic forage is low (<75% of B_0)
4. Threshold harvest control rule that decreases F on yellowfin tuna by 50% when mesopelagic forage is low (<75% of B_0)
5. Threshold harvest control rule that decreases F on yellowfin tuna by 33% when mesopelagic forage is low (<50% of B_0)
6. Threshold harvest control rule that decreases F on yellowfin tuna by 50% when mesopelagic forage is low (<50% of B_0)

We then ran a two-point single-species threshold harvest control rules (HCR) for each mesopelagic abundance regime with yellowfin tuna biomass thresholds defined by B_0; we set Btarget to 50% of B_0 and Blim to 25% of B_0 (Figure 4.4). We considered B_0 as the starting biomass in the model.

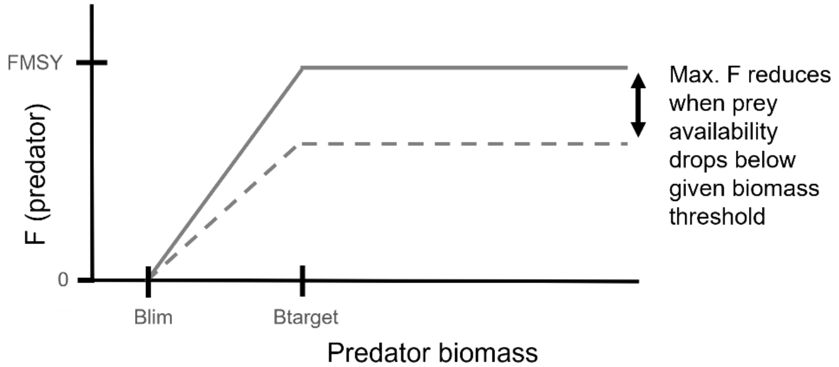

Figure 4.4: An example conceptual diagram of a two-point single-species threshold HCR (solid line) versus an ecosystem-based threshold HCR (dashed line)

Finally, we tested multiple configurations of ecosystem-based HCRs (Figure 4.4) that reduced the fishing mortality on YTN based on the biomass of the deepwater fish (DWF) group. We tested two different DWF biomass thresholds ($B/B_0 = 50\%$ and $B/B_0 = 75\%$) and two different YTN F scalars when DWF biomass drops below defined thresholds (F decrease of 33% and F decrease of 50%), for a total of 4 candidate ecosystem-based HCR management strategies (Table 4.1). Each candidate management rule was applied throughout all 50 years of the Atlantis simulation. To assess the performance of each candidate management strategy under the varying mesopelagic abundance regimes, we present changes in catch and biomass relative to the FMSY scenario. We also calculated the coefficient of variation (CV) of YTN catch under each management rule, following the example of other MSEs (e.g. Tommasi et al. 2017, Wiedenmann et al. 2017). In this study, the CV of catch is largely determined by how often HCRs are triggered by biomass thresholds (i.e. how often F is reduced due to a management rule). They should therefore be interpreted not as a measure of population stability but as a reflection of how often effort is restricted.

Results

Mesopelagic fish abundance

Over the 50 years of Atlantis model simulations, the biomass of the deepwater fish (DWF) group was below the 75% B/B_0 threshold in 20 years and below the 50% B/B_0 threshold in two years under the ‘post-decline’ mesopelagic fish abundance regime. Under the ‘future decline’ mesopelagic fish abundance regime, DWF biomass was below the 75% B/B_0 threshold in three years and below the 50% B/B_0 threshold in 47 years (Figure 4.5).

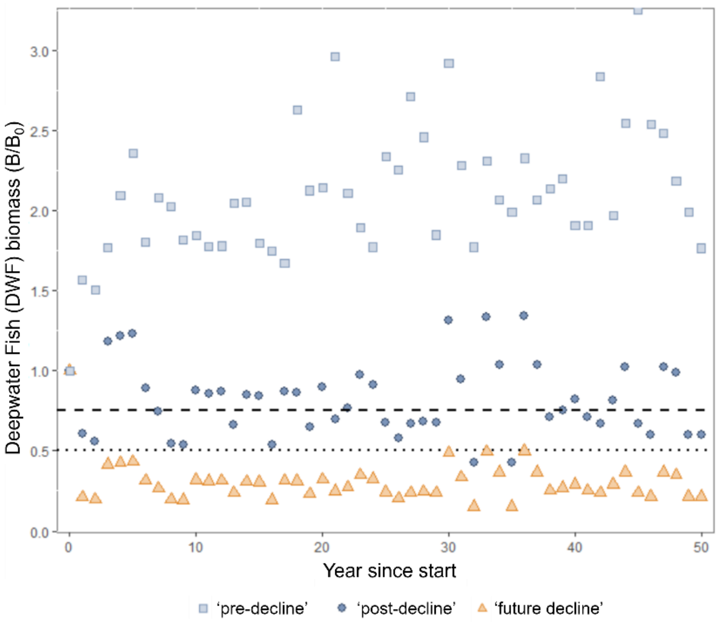

Figure 4.5: Biomass of the deepwater fish (DWF) group over a 50-year Atlantis simulation. Values are shown as relative to the model's starting biomass (B_0) for the group for the three simulated mesopelagic fish abundance regimes. The dashed and dotted lines represent the 75% and 50% B/B_0 thresholds (respectively) utilized in the simulated ecosystem-based harvest control rules.

Under the 'post-decline' mesopelagic abundance scenario, YTN biomass decreased to a minimum of 40% of what biomass was under 'pre-decline' but increased back up to 75% by the end of the 50-year model simulation (Figure 4.6). Under the 'future decline' scenario, yellowfin tuna biomass decreased to a minimum of 22% of what biomass was under 'pre-decline' mesopelagic fish biomass but increased back up to 60%.

Performance of harvest control rules (HCRs)

Target species biomass

No threshold harvest control rules were activated under the 'pre-decline' mesopelagic abundance scenario as the biomasses of both the DWF and YTN groups were too high to trigger the parameterized biomass thresholds (see Figure 4.5, Figure 4.7). Results hereafter are

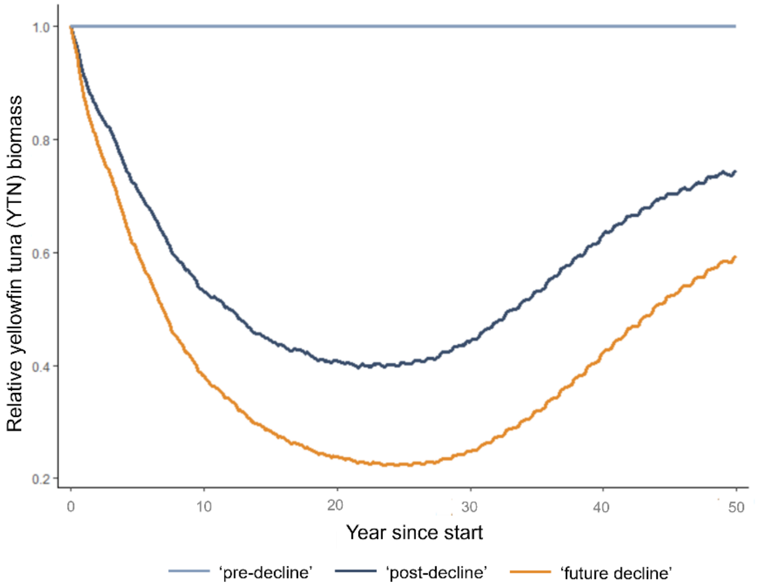

Figure 4.6: Yellowfin tuna biomass under constant FMSY management throughout 50-year Atlantis simulations. Results are shown as relative to yellowfin tuna biomass under 'pre-decline' mesopelagic fish abundance.

therefore only presented for the 'post-decline' and 'future decline' mesopelagic abundance scenarios. For both scenarios, YTN biomass was consistently higher under adaptive management than under constant fishing pressure at FMSY. Under the 'post-decline' mesopelagic fish abundance regime, YTN biomass was highest under management by the ecosystem-based threshold HCRs that reduced YTN F when DWF biomass fell below a 75% B/B_0 threshold (Figure 4.8). Specifically, the total YTN biomass produced by the system over 50 years resulted from the control rule that reduced YTN F by 50% when DWF biomass was below 75% B/B_0 (Table 4.2). For both the 'post-decline' and 'future decline' scenarios, the YTN biomass relative to the constant FMSY scenario peaked throughout years 15-30 of the model run (Figure 4.8). Biomass differences between candidate management strategies began to level out at the end of the 50-year simulations. By the last ten years of the model simulation, YTN biomass under the single-species HCR and the ecosystem-based HCRs using a 50% B/B_0 DWF threshold leveled out to a similar biomass as under constant FMSY management, whereas ecosystem-based HCRs using a 75% B/B_0 DWF threshold remained consistently higher (Figure 4.8).

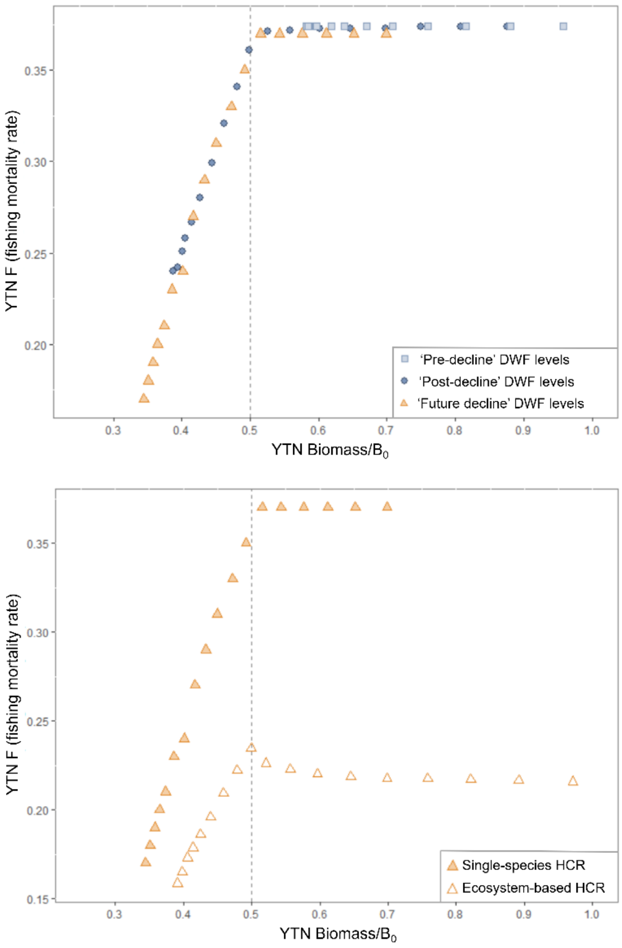

Figure 4.7: F versus biomass under single-species two-point HCRs for each mesopelagic fish abundance regime (**top panel**) and a comparison of F versus biomass between a single-species HCR and an ecosystem-based HCR under the 'future disturbance' mesopelagic fish abundance regime (**bottom panel**). For this example, results are shown for the ecosystem-based HCR that decreased F on YTN by 33% when mesopelagic fish biomass fell below a 50% B/B_0 threshold (Rule 5 in Table 4.1).

Under the 'future decline' mesopelagic fish abundance regime, YTN biomass was consistently higher under the ecosystem-based HCRs that reduced F on YTN by 50% when mesopelagic fish biomass fell below defined B/B_0 thresholds (Figure 4.8). By the last ten years of the model simulation, there was little difference in YTN biomass under control rules using the same reduction in YTN F but different DWF biomass thresholds (75% vs. 50% B/B0); this is because DWF biomass under this abundance regime only rose above the 50% B/B0 threshold in 3 out of 50 years (Figure 4.5). Similarly to the results from the ‘post-decline’ mesopelagic abundance scenario, the increase in YTN biomass relative to the constant FMSY scenario peaked throughout years 15-30 of the model simulation. As the model approached the end of the 50 year simulation, YTN biomass under the traditional threshold HCR approached biomass values under constant FMSY management, but ecosystem-based HCR management strategies maintained an increase in YTN biomass of at least 150% over the constant FMSY scenario (Figure 4.8). The overall benefit of adaptive management strategies (when defined by YTN biomass) was greater under the ‘future decline’ mesopelagic fish abundance regime than under the ‘post-decline’ abundance regime (e.g., a 125% versus 33% increase in total biomass, respectively) (Tables 4.2 & 4.3).

Target species catch

In general, YTN catch decreased in the first 10-15 years under adaptive management strategies as the control rules reduced F in response to various biomass thresholds (Figure 4.8). This reduction in fishing mortality resulted in increased biomass in the system and catch generally peaked in years 15 through 30 in response. Under the ‘post-decline’ mesopelagic fish abundance regime, YTN catch under ecosystem-based HCRs using a 50% B/B_0 DWF threshold was the same as under traditional threshold HCR management until DWF biomass dropped below the 50% B/B_0 threshold in year 32 (Figure 4.5). Catch under ecosystem-based HCRs using a 75% B/B_0 DWF threshold was variable through time as the HCRs were triggered (Figure 4.9), but showed an overall higher catch through time than under other management strategies (Table 4.2). The management strategies that produced the highest total YTN catch over 50 years were ecosystem-based HCRs with the 75% B/B_0 DWF threshold; the strategies that produced the highest average YTN catch over the last ten years were ecosystem-based HCRs with the 50% B/B_0 DWF threshold (Table 4.2). This difference is likely because DWF biomass didn't fall below 50% of B_0 until year 32 in the 'post-decline' scenario (Figure 4.5). The coefficient of variation (CV) of YTN catch under the 'post-decline' mesopelagic abundance regime was the lowest under the single-species threshold HCR, although CV values were similar across all management strategies (Table 4.2).

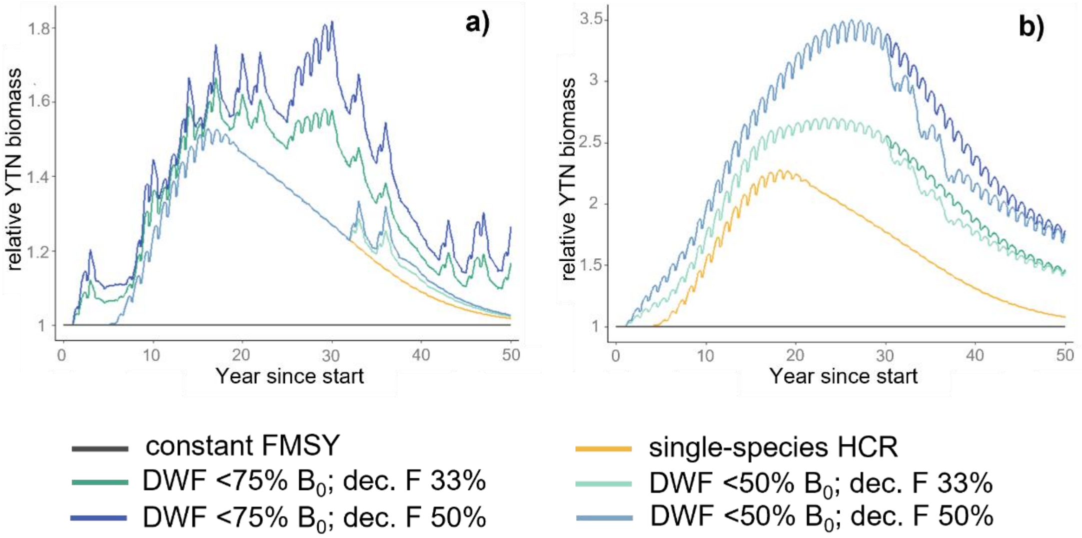

Figure 4.8: Relative yellowfin tuna ('YTN') biomass over a 50-year Atlantis simulation under the 'post-decline' mesopelagic fish abundance regime (a) and the 'future decline' mesopelagic fish abundance regime (b). Values are shown as relative to the constant FMSY management scenario.

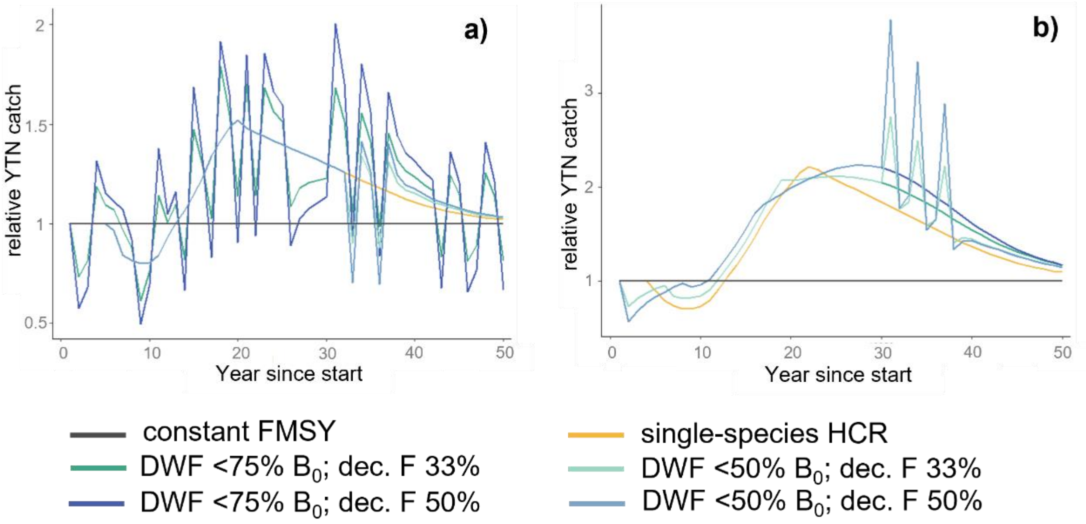

Figure 4.9: Relative yellowfin tuna ('YTN') catch over a 50-year Atlantis simulation under the 'post-decline' mesopelagic fish abundance regime (a) and the 'future decline' mesopelagic fish abundance regime (b). Values are shown as relative to the constant FMSY management scenario.

Under the 'future decline' mesopelagic fish abundance regime, YTN catch under ecosystem-based HCR was higher than under a single-species HCR. Catch spiked under the control rule that used a 50% B/B_0 DWF biomass threshold in the three years when DWF biomass was >50% B_0 (Figures 4.5 and 4.9). Catch was overall highest under ecosystem-based HCR management strategies that used a 75% B/B_0 DWF threshold, although the increase in catch relative to constant FMSY management was similar to that under ecosystem-based HCR management strategies using a 75% B/B_0 DWF threshold. Total catch of YTN over time was 46.5% higher than under constant FMSY management for the best-performing candidate management strategy (decreasing YTN F by 50% when DWF <75% of B_0), and the average YTN catch over the last ten years of the model simulation was 32.1% higher (Table 4.3). Similarly to results from the 'post-decline' mesopelagic fish abundance regime, the CV of YTN catch over 50 years was similar across simulated management strategies. The CV of catch was lower for all control rules than for constant fishing at FMSY under the 'future decline' mesopelagic abundance regime (Table 4.3). The benefit of adaptive management (when defined by YTN catch) was greater under the 'future decline' mesopelagic fish abundance regime than under the 'post-decline' abundance regime (e.g. up to a 46.5% versus 16.4% increase in total catch, respectively) (Tables 4.2 & 4.3).

Table 4.2: Performance metrics of interest for yellowfin tuna (YTN) for all simulated management strategies under the 'post-decline' mesopelagic fish abundance regime. Biomass and catch values are shown as relative to the constant FMSY management scenario.

			F(YTN) dec. by 33%		**F(YTN) dec. by 50%**	
Performance metric	**constant FMSY**	**single-species HCR**	meso. forage $\leq 50\%\ B_0$	meso. forage $\leq 75\%\ B_0$	meso. forage $\leq 50\%\ B_0$	meso. forage $\leq 75\%\ B_0$
Total biomass (50 yrs)	-	+12.9%	+14.6%	+25.2%	+15.6%	+33.4%
Average biomass (last 10 years)	-	+4.3%	+5.8%	+14.3%	+6.6%	+20.5%
Total catch (50 yrs)	-	+11.4%	+12.0%	+14.6%	+12.4%	+16.4%
Average catch (last 10 years)	-	+5.0%	+6.7%	+4.5%	+7.7%	+3.7%
CV catch (50 years)	0.806	0.755	0.770	0.777	0.782	0.820

Table 4.3: Performance metrics of interest for yellowfin tuna ('YTN') for all simulated management strategies under the 'future decline' mesopelagic fish abundance regime. Biomass and catch values are shown as relative to the constant FMSY management scenario.

			F(YTN) dec. by 33%		**F(YTN) dec. by 50%**	
Performance metric	**constant FMSY**	**single-species HCR**	meso. forage $\leq 50\%\ B_0$	meso. forage $\leq 75\%\ B_0$	meso. forage $\leq 50\%\ B_0$	meso. forage $\leq 75\%\ B_0$
Total biomass (50 yrs)	-	+34.5%	+76.1%	+81.5%	+113.6%	+125.3%
Average biomass (last 10 years)	-	+16.4%	+56.8%	+61.3%	+90.3%	+99.4%
Total catch (50 yrs)	-	+30.7%	+40.7%	+42.1%	+45.4%	+46.5%
Average catch (last 10 years)	-	+18.5%	+25.7%	+29.8%	+25.1%	+32.1%
CV catch (50 years)	0.859	0.768	0.777	0.788	0.786	0.785

Discussion

The Atlantis ecosystem model simulations we conducted showed evidence of strong trophic connectivity between large pelagic predators (YTN) and mesopelagic fish prey; YTN biomass decreased markedly in scenarios with lessened mesopelagic fish abundance. These patterns are consistent with other ecosystem and food-web modeling studies in the Gulf of Mexico (Woodstock et al. 2021, Calhoun-Grosch et al. 2024). We tested four different configurations of ecosystem-based threshold HCRs which included two different mesopelagic fish biomass threshold limits and two different fishing mortality scalars on YTN when mesopelagic thresholds were triggered. HCRs that decreased YTN F by 50% yielded higher average YTN biomass in the last ten years of the model run than those that decreased YTN F by 33%. The total catch over time was higher under HCRs that reduced fishing pressure by 50% due to the increased biomass in the system from reduced fishing early in the simulation, suggesting long-term benefits to more conservative EBFM strategies. Average catch over the last ten years and catch CVs were comparable between F reduction strategies.

In a system with the current mesopelagic fish abundance (‘post-decline’), average YTN biomass over the last ten years of the model simulation saw its highest increase (21%) under the most restrictive candidate management strategy (decreasing F by 50% when mesopelagic biomass is <75% B_0). However, average catch over the last ten years was highest under less restrictive strategies that did not activate control rules until mesopelagic biomass was <50% B_0, suggesting a tradeoff between biomass and catch. Under the scenario representing a further dampening of mesopelagic fish populations (‘future decline’), the case for ecosystem-based management becomes stronger. Ecosystem-based management strategies provided up to a 125% and 47% increase in total YTN biomass and catch over time, respectively, in the case of a hypothetical future deep-water disturbance. This management strategy had lower catch variability than under no adaptive management (Table 4.3). The most restrictive control rule (decreasing F by 50% when mesopelagic biomass is <75% B_0) had the highest YTN biomass and catch, suggesting that there are less tradeoffs in management decisions under this scenario. These combined results imply that it may be particularly beneficial to apply ecosystem-based approaches to predator management when key forage resources are considerably reduced.

In Kaplan et al.'s (2020) work, ecosystem-based harvest control rules produced higher catch CVs than a constant FMSY strategy because their zooplankton forage base was so temporally variable that control rules were consistently being triggered and turned off. This combined with our findings suggest that the CV of catch under a given HCR is highly dependent on the user-defined forage biomass thresholds; the highest catch CVs in the current study were produced from an HCR that was activated by forage biomass thresholds in 40-60% of simulation years (DWF <75% B/B_0; 'post-decline' mesopelagic regime, Table 4.2). In simulations where threshold HCRs were either rarely or consistently triggered (e.g., DWF <50% B/B_0; 'post-decline' mesopelagic regime, DWF <75% B/B_0; 'future decline' mesopelagic regime, respectively), catch CV was lower than under constant FMSY management (Tables 4.2 & 4.3). Future MSE studies examining ecosystem-based harvest control rules should use careful consideration when defining biomass threshold limits.

Although we performed a comprehensive data and literature review to parameterize the diet matrix of our Atlantis model for this work, few Gulf of Mexico-specific diet studies for large pelagic predators exist. We are assuming that the trophic interactions simulated by our model are reflective of true yellowfin tuna diet in the GOM, although many highly migratory species diet studies are limited in seasonality and are fisheries-dependent. Because GOM diet studies are few and far between we also considered YTN diet studies from the southern Atlantic coast of the US, which may have a different pelagic food-web structure than the GOM (particularly if GOM YTN are heavily utilizing deep oil rigs for feeding (Snodgrass et al. 2020, Price et al. 2022). Another assumption that we made in that study is that the mesopelagic fish abundance trends gleaned from DEEPEND Consortium sampling are representation of GOM-wide abundance; this may or may not be the case as GOM Loop Current waters contain 2-4 times less mesopelagic biomass than surrounding waters (Sutton et al. 2021).

This work highlighted the importance of mesopelagic forage fish to large pelagic predator populations and suggests that considering the availability of mesopelagic prey may be beneficial in developing predator management strategies. Recent sampling efforts and a literature review suggest that mesopelagic fishes may be more important to yellowfin tuna diets than epipelagic forage species, and this may be particularly true in the GOM due to opportunistic feeding events on oil rigs (Murawski, unpublished data, Snodgrass et al. 2020, Price et al. 2022). If so, mesopelagic fish abundance may be a good candidate regionally-specific ecosystem indicator for the GOM, such as those being considered for potential ecosystem-based management of highly migratory species (ICCAT 2023).

Observant readers may have noticed that the largest contributor to yellowfin tuna diet in the GOM is pelagic squids, which also play a crucial role in the vertical connectivity of the open-ocean GOM food web with 95% of GOM cephalopods occurring at the meso/bathypelagic interface (Sutton et al. 2021). However, the methodology applied in the current work requires a time series of prey abundance and such a time series is not currently available in the GOM. Future work quantifying and characterizing GOM pelagic cephalopod trends would be useful for large pelagic predator management questions.

Ecosystem-based fisheries management of pelagic resources will be particularly important going forward for a multitude of reasons, including increasing variability of epipelagic production due to climate change (Free et al. 2019, Bryndum-Buchholz et al. 2019) and continued exploitation of the still under-studied deep sea. Future deep-water oil spills in the Gulf of Mexico (and elsewhere) are more than just a hypothetical. With the majority of US oil production coming from 'ultra-deep' wells, future deep spills are likely (Muehlenbachs et al. 2013, Murawski et al. 2019, Sutton et al. 2021). While this study used yellowfin tuna as an example pelagic predator, findings may be of interest to other commercially important offshore predators that heavily utilize the mesopelagic prey pool (e.g., swordfish). We do not intend for these results to be taken as specific management recommendations, but to provide a proof-of-concept of the utility of ecosystem models for investing EBFM questions using indicators representing bottom-up drivers of secondary productivity. There is no existing case of outputs from an ecosystem model being explicitly used for management advice, but they can be used as tools to provide guidance in single-species stock assessments (e.g., Howell et al. 2021, Vilas et al. 2023) and have been identified as a tool for conducting MSEs (Grüss et al. 2017). The current federal management of Gulf of Mexico stocks primarily utilizes constant F harvest control rules, but the Gulf of Mexico Fishery Management Council has discussed a move towards threshold-type HCRs for data rich stocks (Cass-Calay & Porch 2019); studies such as this one that perform MSEs to examine trade-offs between multiple candidate threshold HCRs could be beneficial. Additionally, Free et al. (2022) suggested that future MSEs considering various threshold HCRs may be useful for highly migratory stocks as NOAA is considering amendments to the Highly Migratory Species management plan (NOAA 2020). We hope that the methodology presented here can inspire others to explore the use of ecosystem models for testing management strategies that consider predator/prey dynamics, both in pelagic systems and others.

This study provided novel work as it used an ecosystem model as the operating model in a management strategy evaluation that considered mesopelagic forage availability in candidate harvest control rules. Model outputs showed a substantial decrease the biomass of a large pelagic predator when mesopelagic forage fish populations decline, reflecting the strong vertical trophic linkages and bottom-up control in the pelagic food web. We found that adaptive management (all candidate control rules) consistently yielded higher YTN biomass and catch than a constant FMSY strategy, which was not surprising given results from similar work (Kaplan et al. 2020). In general, ecosystem-based harvest control rules out-performed traditional, single-species threshold HCRs, and the benefit (i.e. increased YTN biomass, catch) that ecosystem-based control rules provided over other management strategies increased as mesopelagic forage availability decreased. There were few tradeoffs even under restrictive management strategies in the case of another significant decrease in mesopelagic fish abundance. Our findings indicate that it may be useful for managers to consider ecosystem approaches to pelagic predator management given that threats to the deep-ocean and deep-ocean prey resources are only increasing.

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CHAPTER 5: CONCLUSIONS

In this dissertation I applied both statistical and numerical modeling techniques to characterize pelagic feeding in the Gulf Mexico. I combined a hydrodynamically-driven particle tracking model (Lett et al. 2008, Putman et al. 2020) with an Atlantis ecosystem model of the Gulf of Mexico (GOM) (Ainsworth et al. 2015) to quantify feeding by juvenile sea turtles as they were dispersed onto the West Florida Shelf (WFS). I then presented an improved statistical method for estimating the diets of pelagic predators in the GOM Atlantis model, the zero-inflated beta distribution (Ospina and Ferrari 2010). Finally, I used the GOM Atlantis model to conduct a management strategy evaluation for an example large pelagic predator using harvest control rules (HCRs) which included a consideration of prey abundance. This research overall highlighted the utility of ecosystem models such as Atlantis for simulating pelagic food webs and investigating ecosystem-based fisheries management (EBFM) questions.

In Chapter 2, *Modeling transport and feeding of juvenile Kemp's ridley sea turtles on the West Florida shelf* (Scott et al. 2024; Ecological Modelling 490 (2024) 110659), I found that feeding opportunities for juvenile Kemp's ridley (*Lepidochelys kempii*) sea turtles were greatest offshore towards to the WFS edge, and that the retention of juveniles in these areas was facilitated by oceanographic frontal features. Large-scale climatic indices, such as the North Atlantic Oscillation (NAO), may also be related. These findings are intuitive given that prey items of oceanic-stage sea turtles are often concentrated by frontal features such as the ones analyzed here (e.g. zooplankton, sargassum communities) (Witherington et al. 2012, Zhang and Hu 2021, Zhang et al. 2024). My work suggests that it may be beneficial for juveniles to be retained offshore for a period in these concentrated prey patches before moving to inshore habitats on the WFS. While this work used an ICHYTHOP model where particles represented juvenile sea turtles (Putman et al. 2020), these findings are also applicable to other species with a planktonic-type juvenile stage such as the larvae of commercially important fishes (e.g., Cornic and Rooker 2018).

The importance of locating offshore prey patches was reflected in the characteristics of pelagic predator diets that I estimated in Chapter 3, *Inflated-type models for estimating fish diet composition*. I found that the zero-inflated beta (BEZI) distribution (Ospina and Ferrari 2010) was the best-fitting model for estimating pelagic predator/prey interactions, moreso than in inshore habitats (e.g. reef systems). This likely reflects the patchy nature of pelagic prey resources and suggests a benefit from the additional BEZI model parameter describing the binomial process of encounter success. My results suggest that the BEZI method is a statistical improvement over the current Dirichlet model for estimating diets in the GOM Atlantis model (Tarnecki et al. 2016), particularly for pelagic predators. For offshore-pelagic predators, the regular beta distribution (BE) underestimated top prey items and overestimated rare prey items. Estimation of Shannon's evenness demonstrated a more even diet composition when fit to the BE versus the BEZI, which may not represent true trophic dynamics. Future trophic modeling work, particularly of pelagic food webs, should consider the use of the BEZI distribution for estimating diets. The prey groups most consumed by pelagic-offshore predators were deep-water-associated (squids, deep-water fishes), and diet estimates for these prey items increased under the best-fitting BEZI model. Heavy utilization of deep-water prey resources could cause large pelagic fishes to be increasingly vulnerable to environmental disasters such as deep-water oil spills, which was previously demonstrated by GOM Atlantis model (Morzaria-Luna et al. 2022).

I explored the implications of this vertical trophic linkage and its potential importance for EBFM in Chapter 4, *Considering mesopelagic forage availability in management strategies for pelagic predators.* In this chapter I found that the biomass of an example large pelagic predator, yellowfin tuna (*Thunnus albacares*), decreased markedly in Atlantis model scenarios that simulated declines in mesopelagic fish abundance. I applied a suite of candidate harvest control rules (HCRs) and found that adaptive management strategies consistently outperformed a constant fishing at FMSY strategy in regard to the amount of yellowfin tuna (YTN) biomass retained in the system. Catch of yellowfin tuna under HCRs was lower than under constant FMSY in the first ten or so years, but then increased above constant FMSY for the remainder of the fifty-year simulation. This suggests that there may be tradeoffs in management strategies in the short-term under HCRs, but that adaptive management improves both predator biomass and catch in the long-term. Ecosystem-based HCRs that reduced fishing pressure on YTN when mesopelagic fish abundance was below pre-defined biomass thresholds yielded higher YTN biomass and catch over time than a single-species two-point HCR. The most conservative ecosystem-based HCR produced both the highest YTN biomass and catch over fifty years, suggesting that catch benefits in the long-term from the conserved biomass in the system.

This research presented a case for EBFM strategies that consider bottom-up food web dynamics. I found that the benefit of the ecosystem-based HCRs was greatest when mesopelagic prey availability was the lowest, suggesting that EBFM is particularly strategic when prey resources are scarce. The lowest mesopelagic fish abundance regime that I modeled was intended to simulate a future mortality event of deep-water species, such as another deep-water oil spill (Sutton et al. in prep, Romero et al. 2018). My results showed that implementing EBFM strategies can help conserve pelagic predator populations following an environmental disturbance that harms lower trophic levels. These findings are timely given that anthropogenic exploitation of deep-water resources (e.g. oil drilling, seafloor mining, fishing) is increasing (Smith et al. 2020, Sutton et al. 2020, St. John et al. 2016) and future deep-water disasters like the 2010 *Deepwater Horizon* oil spill are likely (Muehlenbachs et al. 2013, Murawski et al. 2019).

Another potential stressor on pelagic trophic dynamics is a warming climate. In Chapter 2 I highlighted the role of concentrating oceanographic features in providing pelagic feeding opportunities. Patterns in these features, such as currents and frontal zones, are expected to be altered by future climate change. Climate change is expected to weaken the Loop Current, the key driver of circulation in the deep GOM, along with its eddies (Liu et al. 2012). Another key hydrodynamic component of the GOM is freshwater output from the Mississippi River, which is a major driver of surface production in the open Gulf and is at its highest under El Niño conditions (Gomez et al. 2019). The variability of ENSO events is expected to increase under a warming climate (Cai et al. 2021) which will in turn increase the variability in epipelagic forage fishes in the northern GOM (Gomez et al. 2019, Adams et al. 2018). As these hydrodynamic features in the GOM change over time it will be important to consider how the pelagic food web will be affected. Ecosystem models such as Atlantis will continue to be useful tools for simulating these dynamics and potential food web implications. Future trophic modeling of the pelagic Gulf of Mexico could benefit from more fine-scale simulation of areas of concentrated feeding, such as convergence zones that amass sargassum communities (Zhang et al. 2024) or offshore oil rigs that may act as large fish aggregating devices (Snodgrass et al. 2020).

Findings from this research suggest that there is benefit in the further exploration of including predator-prey interactions in management strategies. In general, ecosystem considerations are more likely to be included in US fisheries management when populations are already at an overfished status (Marshall et al. 2019). This work suggests that it is beneficial to proactively manage predator stocks using an ecosystem approach when prey populations are low. Some US management policies have included top-down considerations by selecting HCRs for forage species that ensure there is an adequate forage base left in the system to sustain predators of conservation importance (Deroba et al. 2019). My results demonstrate the value of including bottom-up considerations in predator management strategies, which has only recently begun to be explored using modeling approaches (Kaplan et al. 2020). In Chapter 4 I used yellowfin tuna as an example pelagic predator, which is a highly migratory species that moves between international jurisdictions. United States regulations for this species in the Atlantic and GOM are set by the National Marine Fisheries Service (NMFS) which utilizes management guidance provided by the International Commission for the Conservation of Atlantis Tunas (ICCAT). Highly migratory tunas are currently managed using traditional single-species stock assessments (NOAA 2006, ICCAT 2019), but there has been movement in the last few years towards the investigation of ecosystem considerations (ICCAT 2023). This dissertation provides an example of how ecosystem modeling approaches can be applied to simulate pelagic food web dynamics and advance research efforts towards ecosystem-based approaches in the management strategies of large pelagic predators.

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APPENDIX 1: ACCESS AND PERMISSIONS FOR CHAPTER 2: MODELING TRANSPORT AND FEEDING OF JUVENILE KEMP'S RIDLEY SEA TURTLES ON THE WEST FLORIDA SHELF

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APPENDIX 2: ONLINE SUPPLEMENTARY MATERIAL ASSOCIATED WITH CHAPTER 2: MODELING TRANSPORT AND FEEDING OF JUVENILE KEMP'S RIDLEY SEA TURTLES ON THE WEST FLORIDA SHELF

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Table A.1: Age structure of the Kemp’s ridley group in the Atlantis Gulf of Mexico model. Final values were determined via literature review (Avens et al. 2017, Chabot et al. 2021, Chaloupka and Zug 1997, Gallaway et al. 2016, Seney 2008).

Atlantis-GOM age class	Atlantis-GOM age group	Age range (years)	Size range (cm CCL)	Life history notes
0 (recruits)	Juvenile	0-3	0-29.5	Oceanic
1	Juvenile	4-7	29.6-44.0	Benthic immature
2	Juvenile	8-11	44.1-62.0	Benthic immature
3	Adult	12-15	62.1-65.8	Sexual maturity
4	Adult	16-19	65.9-66.2	Adult
5	Adult	20-23	66.2+	Adult
6	Adult	24-27	66.2+	Adult
7	Adult	28-31	66.2+	Adult
8	Adult	32-35	66.2+	Adult
9	Adult	36+	66.2+	Adult

Table A.2: Proportional diet composition of the juvenile and adult age classes of the Kemp's ridley group in the Atlantis Gulf of Mexico model. Values are sorted high-low for the juvenile age class. Final values were determined via literature review (Witzell and Schmid 2005, Schmid and Tucker 2018, Servis et al. 2015). Species of commercial importance are placed in their own functional group in the Gulf of Mexico Atlantis model (Atlantis-GOM).

Atlantis-GOM prey group	Kemp's ridley age class	
	Juvenile	Adult
Crabs and lobsters	0.512	0.523
Sessile filter feeders	0.130	0.114
Stone crab	0.073	0.097
Bivalves	0.070	0.024
Macroalgae	0.051	0.051
Carnivorous macrobenthos	0.039	0.035
Blue crab	0.035	0.110
Lutjanidae	0.022	0.004
Large reef fish	0.022	0.004
Sciaenidae	0.022	0.004
Other shrimp	0.017	0.000
Sponges	0.006	0.010
Oysters	0.001	0.011
Flatfish	0.000	0.003
Echinoderms	0.000	0.011

Table A.3: Results from post-hoc Tukey tests comparing annual values for juvenile Kemp's ridley *per capita* consumption (*pc*Q_I). Values were log-transformed before analysis and n = 12 months for each group. Bolded values indicate statistical significance at $p < 0.05$.

		pcQ_I (tonnes/N)	
	Diff.	*p*	95% CI
2004-2003	0.18	1.000	(-0.48,0.84)
2005-2003	0.47	0.485	(-0.19,1.13)
2005-2004	0.29	0.972	(-0.37,0.95)
2006-2003	-0.04	1.000	(-0.70,0.62)
2006-2004	-0.22	0.998	(-0.88,0.44)
2006-2005	-0.51	0.340	(-1.17,0.15)
2007-2003	0.65	0.057	(-0.01,1.31)
2007-2004	0.47	0.467	(-0.19,1.13)
2007-2005	0.18	1.000	(-0.48,0.84)
2007-2006	0.69	**0.030**	(0.03,1.35)
2008-2003	-0.24	0.995	(-0.90,0.41)
2008-2004	-0.42	0.663	(-1.08,0.24)
2008-2005	-0.71	**0.021**	(-1.37,-0.05)
2008-2006	-0.20	0.999	(-0.86,0.46)
2008-2007	-0.89	**0.001**	(-1.55,-0.24)
2009-2003	0.37	0.843	(-0.29,1.02)
2009-2004	0.19	1.000	(-0.47,0.85)
2009-2005	-0.10	1.000	(-0.76,0.56)
2009-2006	0.41	0.715	(-0.25,1.06)
2009-2007	-0.28	0.977	(-0.94,0.37)
2009-2008	0.61	0.103	(-0.05,1.27)
2010-2003	0.27	0.983	(-0.38,0.93)
2010-2004	0.10	1.000	(-0.56,0.75)
2010-2005	-0.19	1.000	(-0.85,0.46)
2010-2006	0.31	0.946	(-0.34,0.97)
2010-2007	-0.38	0.813	(-1.03,0.28)
2010-2008	0.52	0.313	(-0.14,1.17)
2010-2009	-0.09	1.000	(-0.75,0.57)
2011-2003	-0.01	1.000	(-0.67,0.64)
2011-2004	-0.19	1.000	(-0.85,0.47)
2011-2005	-0.48	0.433	(-1.14,0.18)
2011-2006	0.03	1.000	(-0.63,0.68)
2011-2007	-0.66	**0.046**	(-1.32,-0.01)
2011-2008	0.23	0.997	(-0.423,0.89)
2011-2009	-0.38	0.803	(-1.03,0.28)
2011-2010	-0.29	0.974	(-0.94,0.37)
2012-2003	0.59	0.138	(-0.07,1.25)
2012-2004	0.41	0.703	(-0.25,1.07)
2012-2005	0.12	1.000	(-0.54,0.78)

2012-2006	0.63	0.079	(-0.03,1.29)
2012-2007	-0.06	1.000	(-0.72,0.60)
2012-2008	0.83	**0.002**	(0.17,1.49)
2012-2009	0.22	0.998	(-0.44,0.88)
2012-2010	0.31	0.946	(-0.34,0.97)
2012-2011	0.60	0.114	(-0.06,1.26)
2013-2003	-0.04	1.000	(-0.69,0.62)
2013-2004	-0.21	0.999	(-0.87,0.44)
2013-2005	-0.50	0.353	(-1.16,0.15)
2013-2006	0.00	1.000	(-0.65,0.66)
2013-2007	-0.69	**0.032**	(-1.34,-0.03)
2013-2008	0.21	0.999	(-0.45,0.86)
2013-2009	-0.40	0.729	(-1.06,0.26)
2013-2010	-0.31	0.952	(-0.96,0.35)
2013-2011	-0.02	1.000	(-0.68,0.64)
2013-2012	-0.62	0.083	(-1.28,0.03)
2014-2003	0.45	0.552	(-0.21,1.10)
2014-2004	0.27	0.984	(-0.39,0.93)
2014-2005	-0.02	1.000	(-0.68,0.64)
2014-2006	0.49	0.400	(-0.17,1.15)
2014-2007	-0.20	0.999	(-0.86,0.46)
2014-2008	0.69	**0.028**	(0.04,1.35)
2014-2009	0.08	1.000	(-0.57,0.74)
2014-2010	0.18	1.000	(-0.48,0.83)
2014-2011	0.46	0.498	(-0.19,1.12)
2014-2012	-0.14	1.000	(-0.80,0.52)
2014-2013	0.49	0.414	(-0.17,1.14)
2015-2003	0.06	1.000	(-0.59,0.72)
2015-2004	-0.11	1.000	(-0.77,0.54)
2015-2005	-0.40	0.726	(-1.06,0.25)
2015-2006	0.11	1.000	(-0.55,0.76)
2015-2007	-0.59	0.141	(-1.24,0.07)
2015-2008	0.31	0.955	(-0.35,0.97)
2015-2009	-0.30	0.961	(-0.96,0.36)
2015-2010	-0.21	0.999	(-0.87,0.45)
2015-2011	0.08	1.000	(-0.58,0.74)
2015-2012	-0.52	0.292	(-1.18,0.13)
2015-2013	0.10	1.000	(-0.56,0.76)
2015-2014	-0.39	0.785	(-1.04,0.27)
2016-2003	0.25	0.992	(-0.41,0.91)
2016-2004	0.08	1.000	(-0.58,0.73)
2016-2005	-0.22	0.998	(-0.87,0.44)
2016-2006	0.29	0.969	(-0.36,0.95)
2016-2007	-0.40	0.746	(-1.06,0.26)

2016-2008	0.50	0.382	(-0.16,1.15)
2016-2009	-0.11	1.000	(-0.77,0.54)
2016-2010	-0.02	1.000	(-0.68,0.64)
2016-2011	0.27	0.987	(-0.39,0.92)
2016-2012	-0.34	0.913	(-0.99,0.32)
2016-2013	0.29	0.973	(-0.37,0.95)
2016-2014	-0.20	0.999	(-0.86,0.46)
2016-2015	0.19	1.000	(-0.47,0.85)
2017-2003	0.39	0.774	(-0.27,1.05)
2017-2004	0.21	0.999	(-0.45,0.87)
2017-2005	-0.08	1.000	(-0.74,0.58)
2017-2006	0.43	0.629	(-0.23,1.09)
2017-2007	-0.26	0.989	(-0.92,0.40)
2017-2008	0.63	0.074	(-0.03,1.29)
2017-2009	0.02	1.000	(-0.63,0.68)
2017-2010	0.12	1.000	(-0.54,0.77)
2017-2011	0.40	0.726	(-0.25,1.06)
2017-2012	-0.20	0.999	(-0.86,0.46)
2017-2013	0.43	0.645	(-0.23,1.08)
2017-2014	-0.06	1.000	(-0.72,0.60)
2017-2015	0.33	0.930	(-0.33,0.98)
2017-2016	0.14	1.000	(-0.52,0.79)

APPENDIX 3: FUNCTIONAL GROUPS IN THE GULF OF MEXICO ATLANTIS MODEL

Category	Functional Group	Code	Category	Functional Group	Code
Reef fish	Gag grouper	GAG		Small sharks	SMS
	Red grouper	RGR		Skates and rays	RAY
	Scamp	SCM	Shrimp	Brown shrimp	BSH
	Shallow serranidae	SSR		White shrimp	WSH
	Deep serranidae	DSR		Pink shrimp	PSH
	Red snapper	RSN		Other shrimp	OSH
	Vermilion snapper	VSN	Seabirds	Diving birds	DBR
	Lutjanidae	LUT		Surface feeding birds	SBR
	Bioeroding fish	BIO	Mammals	Manatee	MAN
	Large reef fish	LRF		Mysticeti	MYS
	Small reef fish	SRF		Dolphins and porpoises	DOL
Demersal fish	Black drum	BDR		Deep diving odontocetae	DDO
	Red drum	RDR	Turtles	Loggerhead	LOG
	Seatrout	SEA		Kemps ridley	KMP
	Sciaenidae	SCI		Other turtles	TUR
	Ladyfish	LDY	Macrobenthos	Blue crab	BCR
	Mullets	MUL		Stone crab	SCR
	Pompano	POM		Crabs and lobsters	LOB
	Sheepshead	SHP		Carnivorous macrobenthos	CMB
	Snook	SNK		Infaunal meiobenthos	INF
	Flatfish	FLT		Herbivorous echinoderms	ECH
	Other demersal fish	ODF	Filter feeders	Oysters	OYS
	Small demersal fish	SDF		Bivalves	BIV
Pelagic fish	Yellowfin tuna	YTN		Sessile filter feeders	SES
	Bluefin tuna	BTN	Structural species	Stony corals	COR
	Little tunny	LTN		Crustose coralline algae	CCA
	Other tuna	OTN		Octocorals	OCT
	Swordfish	SWD		Sponges	SPG
	White marlin	WMR	Primary producers	Epiphytes	EPI
	Blue marlin	BMR		Sea grass	GRS
	Other billfish	BIL		Macroalgae	ALG
	Greater amberjack	AMB		Microphytobenthos	MPB
	Jacks	JCK		Large phytoplankton	LPP
	King mackerel	KMK		Small phytoplankton	SPP
	Spanish mackerel	SMK		Toxic dinoflagellates	DIN
	Spanish sardine	SAR		Protists	PRO

	Large pelagic fish	LPL	Pelagic invertebrates	Jellyfish	JEL
	Deep water fish	DWF		Squid	SQU
Forage	Menhaden	MEN		Large zooplankton	LZP
	Pinfish	PIN		Small zooplankton	SZP
	Medium pelagic fish	MPL	Nutrient cycle	Bacteria	PB
	Small pelagic fish	SPL		Sediment bacteria	BB
Elasmobranchs	Blacktip shark	TIP		Carrion detritus	DC
	Benthic feeding sharks	BEN		Labile detritus	DL
	Large sharks	LGS		Refractory detritus	DR
	Filter feeding sharks	FIL			