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Developing an ecosystem-based approach to management of the Gulf menhaden fishery

using Ecopath with Ecosim

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Abstract of the Thesis

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The Gulf of Mexico (GoM) is a valuable ecosystem both socially and economically, and fisheries contribute substantially to this value. Gulf menhaden, *Brevoortia patronus*, support the largest fishery in the Gulf (by weight) and provide forage for marine mammals, seabirds and commercially and recreationally important fish species. Understanding the complex interactions among multiple fisheries and myriad unfished species requires tools different from those used in traditional single-species management. Ecopath with Ecosim (EwE) is increasingly being used to construct food web models of aquatic ecosystems and to evaluate fisheries management options within a broader, ecosystem context. An EwE model was developed to examine the impact of the menhaden fishery on both fished and unfished species in the GoM. This model builds on previously published EwE models of the GoM, and is tailored to the range and habitat of Gulf menhaden. Several management scenarios were run for commercially and recreationally important fisheries. Results indicated that recreational fishing levels for some species may be unsustainable, but that recovery is not currently inhibited by a lack of prey. Increased fishing for menhaden to target or limit levels resulted in a decrease in ecosystem maturity and ascendency as well as decreases in predator biomasses including seabirds, sharks, red drum and red snapper. Additionally, a number of different harvest strategies for menhaden and other forage fish were

modeled under both deterministic and stochastic conditions and the results were evaluated in terms of impacts on other fisheries and unfished predator populations. The results of the stochastic simulations indicated that harvesting forage fish groups at 100% F_{MSY} levels using a constant fishing mortality rate is likely to result in population collapse, lower long-term average yields and substantial declines in predator populations. Fishing at 75% F_{MSY} appears to cause much lower declines in predator populations, while producing as high or higher yields than fishing at 100% F_{MSY}. Pressure on both commercial and recreational fisheries will likely continue to increase in the future and menhaden fisheries are no exception. The results of this analysis stress the need for a precautionary, ecosystem-based approach to management of Gulf menhaden in order to maintain ecosystem structure and prevent declines of both fished and unfished predator species.

Dedication Page

This work is dedicated to my parents, Kathy Misak and Rod Geers, for their unwavering love, support, and encouragement throughout this endeavor and always.

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Chapter 1: Introduction to Gulf Menhaden and the Gulf of Mexico Ecosystem

1.) Premise

Gulf menhaden, *Brevoortia patronus*, is a small fish in the clupeid family that inhabits the northern Gulf of Mexico (GoM). Though it is an important species, both economically and ecologically, most humans do not consume menhaden directly; rather, menhaden is ground into fishmeal and used as a protein supplement in poultry, swine, and aquaculture feeds (VanderKooy & Smith 2002). Menhaden oil is also processed into Omega-3 dietary supplements (VanderKooy & Smith 2002). Despite its relative anonymity, Gulf menhaden supports the second largest commercial fishery, by weight, in the United States (Vaughan et al. 2007). Perhaps even more important is the role that menhaden play in the Gulf of Mexico ecosystem, providing a link between the lowest and highest trophic levels by filtering plankton from the water column and providing forage for upper trophic level predators. This intermediate trophic level is critical to marine ecosystems (e.g. Cury et al. 2000) and the loss of dominant filter feeders such as menhaden and other clupeids has been observed to lead to changes in ecosystem structure and functioning (Heymans et al. 2004, Nuttall et al. 2011).

In recent years, scientists and managers have begun to shift from the traditional single-species management approach to a more holistic ecosystem-based approach that takes into account trophic interactions and other ecosystem-level effects (Hall & Mainprize 2004, Pikitch et al. 2004). Several current studies have further demonstrated a pressing need to take an ecosystem-based approach to the management of forage fish given their crucial role in marine ecosystems (e.g. Cury et al. 2011, Smith et al. 2011, Pikitch et al. 2012). Management of menhaden has not yet embraced this view. Although Gulf menhaden is not currently considered overfished (Vaughan et al. 2007), a number of factors point towards the need to re-evaluate the current single-species assessment methodology and management strategy. First, a number of important fishery species rely on menhaden during all or part of their lifecycle including spotted seatrout and red drum (VanderKooy & Smith 2002). Furthermore, many of these dependent species are managed federally through the National Marine Fisheries Service (NMFS) and are not accounted for in current state and inter-state management of menhaden by the Gulf States Marine Fisheries Commission (GSMFC). In addition, management by the GSMFC does not account for the dietary needs of marine mammals and seabirds that also rely on menhaden. Secondly, continued exploitation and degradation of the Gulf of Mexico has placed it in a vulnerable state (Peterson et al. 2011). Recurring hypoxia, the recent Deepwater Horizon oil spill and climate change are likely to impact menhaden directly or indirectly through direct fish kills, availability of and physical changes to habitat and changing abundance and distribution of predators (Thronson & Quigg 2008, Peterson et al. 2011). Third, forage fish fisheries have a history of boom and bust cycles. Heavy fishing pressure, when combined with fluctuations in environmental factors, can lead to rapid collapse and slow recovery (Beverton 1990). Lastly, though recent landings have been steady, there is likely to be an increased demand for fish in the future, both farmed and wild (Pauly et al. 2002, Diana 2009). Aquaculture of carnivorous marine species continues to rise and with it an increased demand for fishmeal (Naylor & Burke 2005). The Gulf menhaden industry may look to expand its catch in the future to meet this growing demand.

2.) The Gulf of Mexico Ecosystem

The Gulf of Mexico is a large, semi-enclosed coastal sea, bordered by the United States, Mexico and Cuba. It encompasses more than 1.5 million km^2, about one third of which is made up of the continental shelf (Heileman & Rabalais 2009). Water circulates clockwise via the Loop Current, which begins in the Yucatan Channel and ends at the Straits of Florida. The Loop Current creates fronts and eddies that are important oceanographic features in the ecology of the Gulf. Fresh water input is also very important in this system, particularly from the Mississippi-Atchafalaya watershed, which contributes about two-thirds of the fresh-water flow into the Gulf (Figure 1.1, Heileman & Rabalais 2009). The GoM has moderately high productivity (Heileman & Rabalais 2009), though conditions range from eutrophic in the coastal estuaries to oligotrophic in open and deep waters. The highest levels of primary productivity occur in the region of the Mississippi River outflow, though this also contributes to large areas of hypoxia in the same region throughout the summer (Heileman & Rabalais 2009).
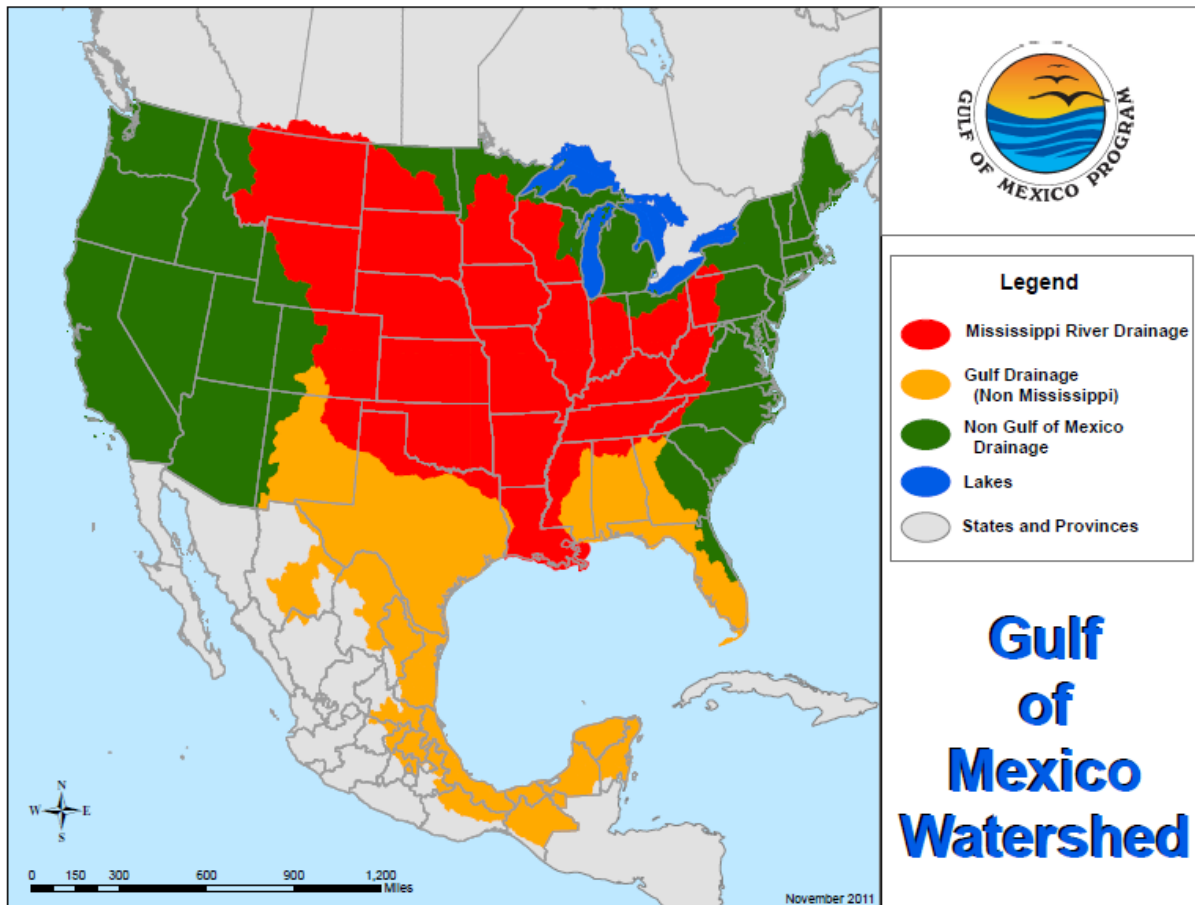
Figure 1.1. Watersheds of the Mississippi River (red) and Gulf of Mexico (red and yellow), including Mexican sources of freshwater. From the US EPA Gulf of Mexico Program: http://www.epa.gov/gmpo/

The hydrologic features of the Gulf have produced a diverse ecosystem that supports a major part of the Gulf coast economy; however, this ecosystem is far from pristine (Peterson et al.

2011). We depend on the Gulf of Mexico for a large portion of our domestic oil and natural gas supply and its waters and ports support one of the world's largest marine transport industries (Giattina & Altsman 1999). Meanwhile, continued nutrient input from the Mississippi River watershed has contributed to one of the world's largest dead zones, an area of hypoxic water, the size of New Jersey off the coasts of Louisiana and Texas (Rabalais & Turner 2001, ENS 2011). Wetlands along the northern coast of the Gulf of Mexico are also being lost at an alarming rate (Birkett & Rapport 1999). Moreover, recent disasters, natural and manmade, such as Hurricane Katrina and the Deepwater Horizon oil spill have further damaged the Gulf coast (Peterson et al. 2011). Compounded with these ongoing impacts is the influence of global climate change, which may serve to accelerate wetland loss, change estuarine salinity regimes, increase river outflow, and increase the frequency and severity of storms (Mulholland et al. 1997). Such exploitation and degradation has left the Gulf of Mexico in a vulnerable condition, making it all the more critical that management approaches be changed to reflect and consider the state of the entire ecosystem.

3.) Biology of Gulf Menhaden

B. patronus is found throughout the northern Gulf of Mexico, from Cape Sable, Florida north and west to Texas and south to Veracruz, Mexico (Lewis & Roithmayr 1981, Ahrenholz 1991, Vaughan et al. 2007). Menhaden inhabit both oceanic and coastal waters during their lifecycle, spawning offshore and returning inshore to develop and feed. Gulf menhaden are intermittent (fractional) spawners and spawning occurs from October through March with peaks in December and January (Lewis & Roithmayr 1980). Although spawning has not been observed directly, observations of larvae and eggs offshore as well as gonadal development of adults, indicates that spawning occurs up to 100 km offshore and from shallow water to water over 100 m in depth (Lewis & Roithmayr 1980, Ahrenholz 1991). Eggs hatch within 2 days (Ahrenholz 1991) and larvae spend a few weeks (estimates range from 3-5 weeks [Reintjes 1970] to 6-10 weeks [Deegan & Thompson 1987]) in the oceanic plankton phase before being carried inshore by currents and tides. Larvae metamorphose into juveniles in northern Gulf coast estuaries where they develop and grow until the following fall when they migrate offshore with the mature adults. Gulf menhaden become sexually mature at age 1, after 2 years of growth (Lewis & Roithmayr 1980). The maximum life span of Gulf menhaden is 5-6 years (Ahrenholz 1991).

Gulf menhaden are omnivorous filter-feeders. Phytoplankton and detritus make up the majority of the diet of juvenile Gulf menhaden with some zooplankton being consumed (Ahrenholz 1991). Diet studies of adult Gulf menhaden, however, have not been conducted. Adult menhaden lack teeth and have a complex system of gill rakers and, as filter-feeders, likely consume both zooplankton and phytoplankton within a particular size fraction (Ahrenholz 1991). There are few studies of menhaden predators; however, menhaden are thought to be important forage for fish, seabirds and marine mammals in the Gulf of Mexico (Ahrenholz 1991, Vaughan et al. 2007).

4.) Gulf of Mexico Fisheries and Multi-species Interactions

Fishing is one of the top four industries along the US Gulf coast, along with oil-related industry, tourism and shipping. Over a third of all marine recreational fishing in the United States occurs within the Gulf of Mexico and nearly 20% of domestic commercial fishery harvests come from the Gulf (Giattina & Altsman 1999). Landings in the US Gulf of Mexico were valued at approximately $800 million USD in 2006 (Sea Around Us Project 2011). Penaeid shrimp (*Farfantepenaeus aztecus, Litopenaeus setiferus, Farfantepenaeus duorarum*) are the most valuable species landed, followed by blue crab (*Callinectes sapidus*), menhaden and oysters (*Crassostrea virginica*). The most valuable finfish are mullets (*Mugil spp.*), groupers (*Epinephelus spp.* and *Mycteroperca spp.*) and red snapper (*Lutjanus campechanus*, Sea Around Us Project 2011). In terms of weight, Gulf menhaden make up over half of the landings in the Gulf of Mexico. Shrimp is the next highest landed group at approximately 100,000 tonnes (t), followed by oysters and blue crab (Sea Around Us Project 2011). Only 4% of the common species in the Gulf of Mexico are assessed by the NMFS, while the majority of common species are unmanaged and unassessed or are managed, but an assessment has not yet been conducted (Webb 2011). Of those that have been assessed, four species (gag grouper *Mycteroperca microlepis*, grey triggerfish *Balistes capriscus*, greater amberjack *Seriola dumerili*, and red snapper) are considered overfished by the Gulf of Mexico Fisheries Management Council (GMFMC). However, alternative analysis by the Sea Around Us Project places Gulf fisheries in a more critical state. The Sea Around Us Project defines a stock as over-exploited if catches are 10 – 50% of peak catches and the year is post-peak. A stock is considered collapsed if catches are less than 10% of peak catches and the year is post-peak. Exploited stocks are those where catches are greater than or equal to 50% of peak catches. Stocks in the rebuilding phase are those where catches are between 10% and 50% of peak catches and the year is after the post-peak minimum. According to this methodology, approximately 60% of the Gulf catches come from overexploited stocks, and 40% from exploited stocks, while only a tiny fraction of the catch comes from stocks that are in the rebuilding phase. Overall, approximately 25% of GoM fisheries stocks are collapsed, 20% are overexploited, 35% are fully exploited and 20% are in the rebuilding phase (Sea Around Us Project 2011). Overexploited groups include large coastal pelagic fishes, sharks, red drum (*Sciaenops ocellatus*), spotted seatrout (*Cynoscion nebulosus*), groupers and red snapper, with the latter considered being in the worst shape (Heileman & Rabalais 2009). Bycatch, particularly of juveniles, is considered a major impediment to the recovery of several finfish stocks (Heileman & Rabalais 2009).

Many of the commercially and recreationally harvested fish species, including king mackerel (*Scomberomorus cavalla*), Spanish mackerel (*Scomberomorus maculates*), dorado (*Coryphaena hippurus*), crevalle jack (*Caranx hippos*), tarpon (*Megalops atlanticus*) and bonito (*Sarda sarda*), rely on the abundant schools of menhaden along the Gulf coast (Franklin 2007, Dailey et al. 2008). Menhaden are also important in the diet of red drum (Boothby & Avault Jr. 1971). Red drum was historically an important commercial and recreational species in the Gulf, but due to overfishing, retention and possession is now prohibited in federal waters (GMFMC 2010). Additionally, recent work (e.g. Hoffmayer & Parsons 2003, Bethea et al. 2004, Bethea et al. 2006, Barry et al. 2008) has shed light on the diets of some coastal shark species. These studies have found that blacktip (*Carcharhinus limbatus*), spinner (*C. brevipinna*), finetooth (*C. isodon*) and Atlantic sharpnose (*Rhizoprionodon terraenovae*) sharks feed heavily on menhaden during all or part of their life cycles. Among marine birds, the brown pelican (*Pelecanus occidentalis*), Louisiana's state bird, is notable for having a diet of over 95% menhaden in some studies (Hingtgen et al. 1985, Franklin 2007).

5.) History and Management of the Gulf Menhaden Fishery

The history of menhaden fishing began on the east coast of the US where Atlantic menhaden (*Brevoortia tyrannus),* a close relative of Gulf menhaden, has been caught in large numbers since the time of the early European settlers. By the late 19th century northern populations of Atlantic menhaden had begun to decline (Smith 1991, Franklin 2007); nevertheless, the industry continued to expand by developing and investing in larger, lighter nets, bigger boats, refrigeration and fish-finding technology (Smith 1991). Catches in the mid-Atlantic boomed after WWII, but they were severely reduced in the 1960s, leading to consolidation and contraction of the industry (Smith 1991). Atlantic menhaden catches increased again slightly in the 1970s, but did not reach previous levels. By the mid-1960s the catch from the Gulf fishery exceeded the Atlantic catch and continues to surpass Atlantic catches today (Smith 1991, NOAA 2012).

The Gulf menhaden fishery got its start in the late 1800s, much later than its Atlantic counterpart. However, prior to World War II, landings in the Gulf were dwarfed by Atlantic landings and were highly variable (Vaughan et al. 2007). Annual landings ranged from 2,000 to 12,000 tonnes between 1918 and 1944 (Smith 1991). After World War II, the Gulf industry rapidly expanded, reaching over 100,000 tonnes by the late 1940s. As in the Atlantic, the Gulf industry greatly benefited from the adoption of new technology, with larger boats and spotter planes increasingly being utilized. From the 1940s through the 1980s, the Gulf industry continued to grow, peaking at close to 1 million tonnes in 1984 (Smith 1991, Vaughan et al. 2007). During its peak years, 11 fish processing plants operated along the Gulf coast, centered on the Mississippi Delta. However, just as the industry reached its peak, one of the largest processing companies acquired one of its major competitors, thereby gaining ownership of over half of the processing facilities (Smith 1991, Vaughan et al. 2007). Since then, the industry has consolidated with one company, Omega Protein, Inc., owning 3 of the 4 active plants on the Gulf coast. Today, approximately 40 purse seine vessels offload their catch at plants in Moss Point, MS and Empire, Abbeville and Cameron, LA (NOAA 2010). The fleet primarily harvests its catch nearshore (within 16 km of the coast), and over 90% of the catch is landed in Louisiana (Vaughan et al. 2007).

Gulf menhaden are currently managed by the GSMFC, an inter-state organization composed of representatives from the five Gulf States: Texas, Louisiana, Mississippi, Alabama and Florida. The current management plan, last updated in 2002, provides only one management measure, a menhaden fishing season open from the 3rd Monday in April through Nov. 1st (VanderKooy & Smith 2002). Individual states have enacted other management measures for their territorial waters. Florida and Alabama have each banned purse-seining for reduction (to fishmeal and fish oil as opposed to direct consumption) in their state waters (VanderKooy & Smith 2002, Vaughan et al. 2007) and recently, Texas has placed a cap on menhaden landings in its waters at 31.5 million pounds (~14,300 mt; Mattei 2008, TPWD 2010). However, little regulation exists in the waters off of Louisiana and Mississippi where the majority of the Gulf menhaden fishery occurs. Landings in recent years have been about 500,000 tonnes and the stock is not currently thought to be overfished (Vaughan et al. 2007).

Nevertheless, Gulf menhaden and the GoM ecosystem may benefit from precautionary management. Forage fish populations and recruitment are particularly susceptible to climate and environmental perturbations (Bakun & Broad 2003, Chavez et al. 2003). Numerous forage

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fisheries in the United States and around the world have crashed, due to a combination of fishing pressures and environmental factors; some have rebounded, while others have not (Alder and Pauly 2006, Pikitch et al. 2012). In Peru, the anchoveta (*Engraulis ringens*) fishery, the largest fishery in the world (Chavez et al. 2003), collapsed to near-zero levels in the early 1970s due to a combination of heavy fishing pressure and a strong El Niño event (Aranda 2009), followed by several years of poor climatic conditions for anchoveta (Chavez et al. 2003). Though the fishery eventually recovered, the collapse left a lasting economic and ecological scar. On the other side of the world, in the northern Benguela Current, off the coast of Namibia, the forage fishery for anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*) also collapsed, but instead of recovering, the ecosystem has shifted a to a different, possibly permanent state (Cury & Shannon 2004). Under this new ecosystem regime, the planktivorous fish have been replaced by jellyfish and the ecosystem appears to be less efficient and less productive than in the past (Cury & Shannon 2004). In the United States we have witnessed similar collapses of forage fisheries on the east and west coasts in the past century. California's sardine industry collapsed between the 1940s and 1960s, due in part to overfishing (Wolf 1992), and current biomass estimates are still well below those from the early 1900s (Baumgartner et al. 1992, Wolf 1992, Hill et al. 2011). The Atlantic menhaden fishery too, declined rapidly in the 1960s and again in the 1990s and its range was greatly contracted (Vaughan et al. 2010). These historic cases can be used as a guide to create a more farsighted and informed plan for menhaden management in the GoM.

6.) EwE Modeling – background, overview of other Gulf models

Ecosystem modeling is becoming an increasingly important tool for answering a wide range of biological, physical and economic questions that were previously difficult to address on such a large scale. Several types of modeling programs now exist, each with their pros and cons (for a review see Fulton 2010). I chose Ecopath with Ecosim (EwE), due to its widespread use (over 5,600 users and 300 publications), user-friendly and freely distributed software, and its focus on fisheries management (www.ecopath.org). Ecopath was first developed by J.J. Polovina in 1984 to estimate the biomass, production and consumption of species or groups of species in marine ecosystems. It was updated in 1992 by V. Christensen and D. Pauly to incorporate analysis of flows between ecosystem elements, following the approach of R. E. Ulanowicz (1986). The time-dynamic portion of the modeling software, Ecosim, that allows for the exploration of fishing policies, was added in 1997 (Walters et al. 1997). EwE models are now used to study a wide variety of aquatic ecosystems, from freshwater to saltwater and estuaries to the open ocean. Several EwE models have been developed for all, or parts of the Gulf of Mexico (see Table 1.1). These have evolved from small-scale Ecopath models to large-scale integrated Ecosim models (e.g. Vidal and Pauly 2004). While some of these models have considered fisheries impacts in the Gulf, none have focused on Gulf menhaden, an important prey item and major fishery in the northern Gulf. This study is an attempt to fill that gap, focusing on the role of menhaden as prey for numerous upper trophic level predators. It also serves as an update, aggregating new sources and data that have been produced since the last EwE models were published.

The objective of this project is to develop a comprehensive ecosystem model for the northern Gulf of Mexico that can be used to evaluate management scenarios for the Gulf menhaden fishery. The goal of the model simulations is to determine how different levels of Gulf menhaden fishing impact predator-prey interactions and fisheries yields. It is hypothesized that increasing

menhaden fishing above current levels will have negative consequences for menhaden predators, particularly long-lived species such as sharks and seabirds. Furthermore, increased menhaden fishing may have negative impacts on yields of commercially and recreationally important fish species in the northern Gulf.

Table 1.1. Ecopath and Ecosim models of the Gulf of Mexico

Name	Author	Ecosystem Type
Tamiahua Lagoon, Mexico	Abarca-Arenas et al. 1993	Estuary
Celestun Lagoon, Mexico	Chavez et al. 1993	Estuary
Mandinga Lagoon, Mexico	De la Cruz-Aguero 1993	Estuary
Southwestern coast, Mexico	Arreguin-Sanchez et al. 1993b	Non-estuarine coast
Campeche Bank, Mexico	Vega-Cendejas et al. 1993	Soft bottom shelf
Yucatan shelf, Mexico	Arreguin-Sanchez et al. 1993a	Soft bottom shelf
Continental Shelf	Browder 1993	Soft bottom shelf
Looe Key, Florida	Venier & Pauly 1997	Coral reef
Terminos Lagoon, Mexico	Manickchand-Heileman et al. 1998a	Estuary
Southwestern shelf, Mexico	Manickchand-Heileman et al. 1998b	Soft bottom shelf
Southern Gulf of Mexico, Mexico	Arreguin-Sanchez & Manickchand-Heileman 1998	Continental shelf
Tampamachoco Lagoon, Mexico	Rosado-Solorzano et al. 1998	Estuary
St. Mark's National Wildlife Refuge, Florida	Christian & Luczkovich 1999	Bay
Celestun Lagoon, Mexico	Vega-Cendejas & Arreguin-Sanchez 2001	Estuary
Weeks Bay, Alabama	Althauser 2003	Estuary
Gulf of Mexico, LME	Vidal & Pauly 2004	All
West Florida Shelf, Florida	Okey et al. 2004	Shelf
Southwestern Gulf of Mexico, Mexico	Arreguin-Sanchez et al. 2004	Soft bottom shelf
Apalachicola Bay, Florida	Carlson 2007	Estuary
Alvarado Lagoon, Mexico	Cruz-Escalona et al. 2007	Estuary
Northern Gulf Coast, US	Walters et al. 2008	Coast
Breton Sound, Louisiana	de Mutsert 2010	Estuary

Chapter 2: Development of an Ecopath with Ecosim Model of the Northern Gulf of Mexico for use in Evaluating Ecosystem Impacts of Fishing

1.) Ecopath Methodology

The original Ecopath model (Polovina 1984) was developed to provide a simple method for generating information about the standing stock and energy flow within an ecosystem that could be used in relatively data-sparse circumstances. Ecopath, as originally conceived, was used to estimate mean annual biomass, production and consumption of major ecosystem elements for a static situation under equilibrium conditions (Polovina 1984). It was also used to derive an estimate of the net primary productivity needed to support the modeled ecosystem (Polovina 1984). Ecopath was later updated (Christensen & Pauly 1992) to include routines for analyzing the energy flows among the Ecopath groups based on the theory of Ulanowicz (1986). Ulanowicz hypothesized that the flow structure within a community is sufficient to describe the behavior of that system (Ulanowicz 1980). He further postulated that this flow structure could be quantified by the concept of ascendency – defined as an index representing both system size and organization – and that systems would develop over time so as to maximize ascendency (Ulanowicz 1980). The updated Ecopath software also provided additional statistics that quantified several of Odum's (1969) indices of ecosystem maturity. Currently, the Ecopath software program is updated and improved on an ongoing basis. Using Ecopath no longer requires the assumption of equilibrium or steady state as first proposed by Polovina (1984). Model parameterization is now based on the assumption of mass balance over the time period modeled, usually a year (Christensen & Walters 2004). This assumption requires that flows into the model are equal to flows out of the model, as well as that flows into and out of each individual group are equal.

There are two master equations in Ecopath, the first describes production (Eq. 1), and the second describes the energy balance of each group (Eq. 2). Ecopath model groups consist of the major biological components of the ecosystem of interest and can be a single species or a group of similar species (e.g. similar habitat, feeding habits, predators, etc.). Groups may also be broken down into two or more age classes to represent trophic differences between juveniles and adults. There are four Ecopath input parameters linked to each Ecopath group: biomass (B), ratio of production to biomass (P/B), the ratio of consumption to biomass (Q/B) and ecotrophic efficiency (EE), the proportion of production that is used within the system. However, via the mass balance approach modeled in the two master equations, the Ecopath software only requires the input of three of the four parameters for each group. In addition, diet information for each group must be input in terms of percent diet composition.

Equation 1: Production = catches + predation mortality + biomass accumulation + net migration + other mortality, which can be reformulated as:

$$B_i \cdot \left(P/B \right)_i \cdot EE_i - \sum_{j=1}^{n} B_j \cdot \left(Q/B \right)_j \cdot DC_{ji} - Y_i - E_i - BA_i = 0 \tag{1}$$

where, for a given group i, B_i is the biomass, $(P/B)_i$ is the production/biomass ratio, EE_i is the ecotrophic efficiency, B_j is the biomass of the predator group j, DC_{ji} is the fraction of prey (i) in the average diet of predator (j), Y_i is the total fishery catch rate, E_i is the net migration rate, and BA_i is the biomass accumulation rate.

The previous equation allows the model to estimate "missing parameters" (i.e. whichever is not entered of B, P/B, Q/B and EE) so as to ensure mass balance between modeled groups, while the following equation ensures energy balance within a group:

Consumption = production + respiration + unassimilated food   (2)

Respiration in Ecopath is estimated as the difference between the consumption term and the production and unassimilated food terms, rather than estimated directly (Christensen & Walters 2004).

2.) Model Construction and Inputs

The area modeled was selected based on the region most relevant to the focal species, Gulf menhaden. Gulf menhaden inhabit the northern Gulf of Mexico, spending the spring and summer in inshore areas and moving up to 80 km offshore in the fall and winter (Roithmayr and Waller 1963, Vaughan et al. 2007). They are most abundant from the Florida panhandle to eastern Texas (Vaughan et al. 2007). Therefore, the model includes the area of the northern Gulf between the coastline and 80 km offshore from Aransas Pass, Texas to Cedar Key, Florida. The total area represented in the model is approximately 145,000 km^2 (Fig. 2.1).
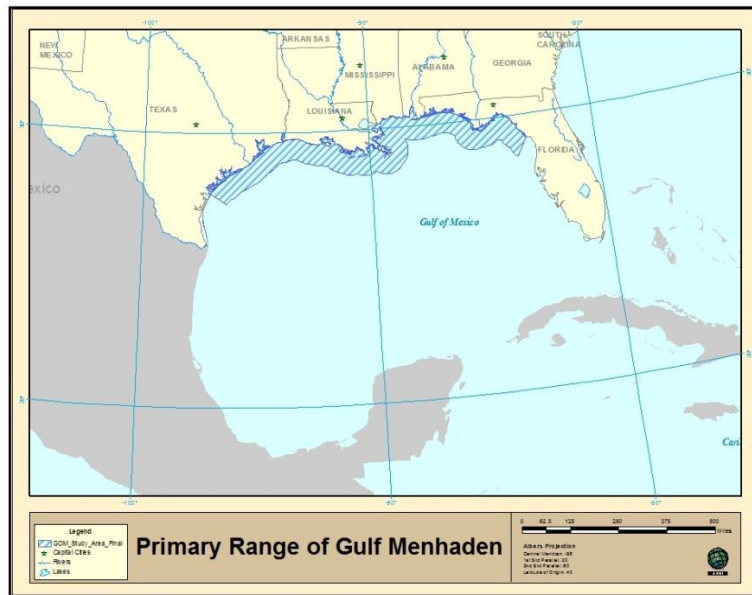
Figure 2.1. Map of the Gulf of Mexico depicting the region modeled (hatched area), which represents the primary habitat of Gulf menhaden. Area estimate and shapefile, courtesy of Andrew Hayslip, Florida Fish and Wildlife Research Institute.

The region modeled contains approximately 1100 – 1300 fish species, in addition to many birds, marine mammals, reptiles and countless invertebrates (Felder and Camp, eds. 2009). Incorporating each of these species individually into one model is not feasible, so one of the first

steps in model development is to determine what the model groups will be and which species each group will include. All predators, competitors and prey of Gulf menhaden were included, as it is the focal species of this modeling endeavor. In addition, other major GoM fishery species were included in order to facilitate the examination of interactions among fisheries and the tradeoffs between fisheries and ecosystem health. Three documents provided a jumping off point for creating and specifying the model groups, Gulf of Mexico models developed by Vidal and Pauly (2004) and Walters et al. (2008) and the Regional Management Plan for the Gulf Menhaden Fishery (VanderKooy & Smith 2002). Table 2.1 provides a complete list of the modeled groups and the species they include. Descriptions of the modeled groups and the sources of their input parameters are provided in the following sections.

Table 2.1. Model groups for the northern Gulf of Mexico Ecopath model and species included in each group.

Model #	Group Name	Species Included	Common Names
1	Birds of Prey	*Haliaeetus leucocephalus, Pandion haliaetus*	bald eagle, osprey
2	Loons	*Gavia immer*	common loon
3	Gulls and Terns	*Gelochelidon nilotica, Hydroprogne caspia, Larus argentatus, Leucophaeus atricilla, Larus delawarensis, Larus marinus, Rynchops niger, Sterna forsteri, Sterna hirundo, Sternula antillarum, Thalasseus maximus, Thalasseus sandvicensis*	gull-billed tern, Caspian tern, herring gull, laughing gull, ring-billed gull, great black-backed gull, black skimmer, Forster's tern, common tern, least tern, royal tern, sandwich tern
4	Pelicaniformes	*Fregata magnificens, Pelecanus erythrorhynchos, Pelecanus occidentalis, Phalacrocorax auritus, Morus bassanus*	magnificent frigatebird, white pelican, brown pelican, double-crested cormorant, northern gannet
5	Coastal Dolphins	*Stenella frontalis, Tursiops truncatus*	Atlantic spotted dolphin, common bottlenose dolphin
6	Large Coastal Sharks	*Carcharhinus falciformis, Galeocerdo cuvier, Ginglymostoma cirratum, Sphyrna lewini, Sphyrna mokarran, Sphyrna zygaena, Carcharhinus brevipinna, Carcharhinus leucas, Carcharhinus limbatus, Carcharhinus plumbeus, Negaprion brevirostris*	silky shark, tiger shark, nurse shark, scalloped hammerhead, great hammerhead, smooth hammerhead, spinner shark, bull shark, blacktip shark, sandbar shark, lemon shark
7	Small Coastal Sharks	*Carcharhinus isodon, Rhizoprionodon terraenovae, Sphyrna tiburo, Carcharhinus acronotus*	finetooth shark, Atlantic sharpnose shark, bonnethead, blacknose shark
8	Skates and Rays	*Raja eglanteria, Dasyatis sabina,*	clearnose skate, Atlantic

		Dasyatis say, Dasyatis centroura, Dasyatis americana, Rhinoptera bonasus	stingray, bluntnose stingray, roughtail stingray, southern stingray, cownose ray
9	Coastal Pelagic Piscivores	*Caranx crysos, Caranx hippos, Lutjanus griseus, Pomatomus saltatrix, Rachycentron canadum, Euthynnus alletteratus*	blue runner, crevalle jack, grey snapper, bluefish, cobia, little tunny
10	Tunas	*Thunnus atlanticus, Thunnus albacares*	blackfin tuna, yellowfin tuna
11-12	Juvenile (0-6 months) and Adult (6+ months) Mackerels	*Scomberomorus cavalla, Scomberomorus maculatus*	king mackerel, Atlantic Spanish mackerel
13-14	Juvenile (0-8 months) and Adult (8+ months) Red Drum	*Sciaenops ocellatus*	red drum
15-16	Juvenile (0-18 months) and Adult (18+ months) Spotted Seatrout	*Cynoscion nebulosus*	spotted seatrout (weakfish)
17	Groupers	*Epinephelus spp., Mycteroperca spp.*	groupers
18	Red Snapper	*Lutjanus campechanus*	northern red snapper
19	Ladyfish	*Elops saurus*	ladyfish
20	Spot	*Leiostomus xanthurus*	spot croaker
21	Atlantic Croaker	*Micropogonias undulatus*	Atlantic croaker
22	Butterfish	*Peprilus burti*	Gulf butterfish
23	Black Drum	*Pogonias cromis*	black drum
24	Flounders	*Paralichthys lethostigma, Paralichthys albigutta*	southern flounder, Gulf flounder
25	Gars	*Lepisosteus osseus, Atractosteus spatula*	longnose gar, alligator gar
26	Sea Catfishes	*Ariopsis felis, Bagre marinus*	hardhead sea catfish, gafftopsail sea catfish
27	Mullets	*Mugil cephalus, Mugil curema*	flathead grey mullet, white mullet
28	Other Demersal Fishes	*Cynoscion arenarius, Orthopristis chrysoptera, Bairdiella chrysoura, Diapterus spp., Menticirrhus spp., Haemulon spp., Trachinotus carolinus, Archosargus probatocephalus, Trinectes maculatus, Lutjanus synagris, Opsanus beta, Trichiurus lepturus, Chloroscombrus chrysurus*	sand seatrout (weakfish), pigfish, silver perch, mojarras, kingfish/kingcroakers, grunts, Florida pompano, sheepshead, hogchoker, lane snapper, Gulf toadfish, largehead hairtail, Atlantic bumper

29	Nearshore Omnivores	*Lagodon rhomboides, Chaetodipterus faber, Tetraodontidae spp.*	pinfish, Atlantic spadefish, puffers
30-31	Adult (12+ months) and Juvenile (0-12 months) Menhaden	*Brevoortia patronus*	Gulf menhaden
32	Shads	*Dorosoma petenense, Dorosoma cepedianum*	threadfin shad, American gizzard shad
33	Other Clupeids	*Harengula jaguana, Sardinella aurita, Opisthonema oglinum, Etrumeus teres, Trachurus lathami*	scaled herring, round sardinella, Atlantic thread herring, red-eye round herring, rough scad
34	Anchovies and Other Small Fishes	*Anchoa mitchilli, Anchoa hepsetus, Cyprinodontidae & Poeciliidae, Menidia spp.*	bay anchovy, broad-striped anchovy, killifishes, silversides
35	Squid	*Lolliguncula brevis,Doryteuthis pealeii, Loligo plei*	Western Atlantic brief squid, longfin inshore squid, slender inshore squid
36	Caridean Shrimp	*Caridea* (infraorder)	shrimp
37	Penaeid Shrimp	*Penaeidae*	prawns/penaeid shrimp
38	Stone Crab	*Menippe mercenaria*	Florida stone crab
39	Blue Crab	*Callinectes sapidus*	Atlantic blue crab
40	Benthic Invertebrates		
41	Macrozooplankton		
42	Microzooplankton		
43	Infauna		
44	Algae		
45	Seagrass		
46	Phytoplankton		
47	Detritus		

2.1) Bird Groups

Brown pelicans, common loons, osprey and terns are listed as menhaden predators in the 2002 Gulf Menhaden Regional Management Plan (VanderKooy & Smith 2002) and therefore provided the initial list of birds to include in the model. This initial list was supplemented through a search of Audubon bird guides (www.audubonguides.com). This search identified piscivorous bird species common along the Gulf coast that inhabit saltwater wetlands, coasts and shorelines and resulted in model groups 1 – 4 (Table 2.1).

Biomass. Bird biomasses were derived from Audubon Christmas Bird Count data (http://birds.audubon.org/christmas-bird-count). The historical database was queried for each bird species listed in Table 2.1, using counts 106 – 110 (2005/2006 – 2009/2010). Only counts

made in the states of Texas, Louisiana, Mississippi and Alabama were used. Counts from Florida were excluded to prevent inclusion of birds inhabiting Caribbean or Atlantic coastal areas. The individual year counts from 2006 – 2010 were averaged to arrive at a 5 year average of the number of birds. This number was then corrected and converted to an estimate of biomass. The detection probability and the proportion of habitat sampled was used to derive a correction factor (detection probability * proportion of habitat sampled = correction factor). The detection probability used was 98%. This is the average detection probability among all habitats and species during a 10 minute survey as determined by Forcey and Anderson (2002) in a study examining variation in bird detection probabilities. In order to determine the proportion of habitat sampled, the total sample area was first found, which was equal to the average number of counts in years 2006 – 2010 multiplied by the count circle area (456 km^2), and then divided by the habitat area (145,000 km^2). After determining the corrected count by dividing the average number by the correction factor, the biomass was then estimated by multiplying the corrected number by each species' weight. A list of these weights and their sources can be found in Appendix A. Biomass estimates were then converted to the Ecopath units of mt/km^2/ yr.

Production/Biomass Ratio. 0.1 was used as an estimate of the P/B ratio for all bird groups. This value was used in a model of the West Florida Shelf developed by Okey et al. (2004). This P/B value was based on an estimate of seabird mortality in Florida waters, derived empirically, for a model developed by Acosta et al. (1998).

Consumption/Biomass Ratio. Consumption/biomass ratios were initially calculated based on estimates obtained from the literature of kilograms of food consumed per bird per day. Restani et al. (2000) gave an estimate of 639.8 g eagle^{-1} day^{-1} for bald eagles feeding on salmon in a Montana reservoir. This was then multiplied by the corrected count of eagles from the Audubon Christmas count surveys to arrive at kg day^{-1}. This value was then divided by the biomass of the eagles in the model to arrive at a consumption rate per day, which was multiplied by 365 to arrive at a yearly consumption rate of 48.75. Stalmaster and Gessaman (1982) gave a consumption rate for captive bald eagles feeding on salmon of 92 g fish per kg eagle per day. This was converted to a yearly consumption rate of 33.58 by multiplying by 365. These two yearly consumption rates were then averaged to arrive at an estimated consumption rate for bald eagles of 41.17 year^{-1}. Stickley (1990) looked at the impacts of avian predators on southern aquaculture. He provides a consumption rate for osprey of 0.5 lb/day. This was converted to a yearly consumption rate in kilograms, multiplied by the number of ospreys in the model and divided by the biomass of ospreys in the model, arriving at a consumption rate of 243.3 year^{-1}. Finally, the weighted average of each species' consumption rate was calculated and these were added together to arrive at a consumption rate for the birds of prey group of 147 year^{-1}.

Okey and Mahmoudi, eds. (2002) provide an estimate of common loon daily consumption of 0.147 kg loon^{-1} day^{-1}. This value was converted to a yearly consumption rate of 28.6 using the steps detailed above for eagles and osprey. Okey and Mahmoudi, eds. (2002) also provide an estimate of the daily consumption rate of terns and gulls as well as for the five species of pelicaniformes included in the model. Following the same conversion procedure, a Q/B value of 196 year^{-1} for terns and gulls and 17.7 year^{-1} for pelicaniformes was calculated.

Diet. Four studies were used to characterize the diets of the birds of prey group. Markham & Watts (2008) described the diet of bald eagles in the lower Chesapeake Bay and

McEwan & Hirth (1980) characterized eagle diets in north-central Florida. Osprey diets were described by McLean & Byrd (1991) for the Chesapeake Bay and by Glass & Watts (2009) for the upper and lower estuaries of the lower Chesapeake Bay. Results were reported in percent biomass or percent number (Glass & Watts 2009). Diets from the four studies were averaged to arrive at an overall percent diet composition for the group. Species such as ducks or rodents that are not included in this model were designated as import from outside the system. The final diet composition (after balancing) can be seen in Appendix B.

Due to the lack of comprehensive data on gull and tern diets in the northern Gulf of Mexico, several studies from various regions and including related species were used to develop the diet composition for this model group. Data from each of these studies were averaged to arrive at an overall diet composition for the group. The same method was used to develop the diet composition of the pelicaniformes model group, using sources that incorporated a number of different regions. The sources of the diet composition data for the gulls and terns and pelicaniformes model groups are listed in Table 2.2 and final diet compositions used in the model are found in Appendix B.

Table 2.2. Sources used for the diet compositions of the gulls and terns and pelicaniformes model groups, including the region where the studies were conducted.

Species	Region	Source
Gulls & Terns		
Larus adouinii	Southwest Mediterranean	Pedrocchi et al. 1996
Rynchops niger	Louisiana	Arthur 1921
Rynchops niger	Argentina	Mariano et al. 2007
Sterna fuscata & Anous stolidus	Florida	Hensley & Hensley 1995
Larus atricilla	Virginia	Knoff et al. 2001
Gull-billed tern	Virginia	Erwin et al. 1998
Gull-billed tern	Eastern Spain	Dies et al. 2005
Caspian tern	Washington	Thompson et al. 2002
Caspian tern	Columbia River estuary	Lyons et al. 2005
Royal tern	Virginia	Aygen & Emslie 2006
Common tern	Southern Brazil	Bugoni & Vooren 2004
Pelicaniformes		
Brown pelican	South Carolina, Florida, Louisiana, Texas	Hingtgen et al. 1985
Brown pelican	US	USFWS 2008
Phalacrocorax auritus	Texas	Withers & Brooks 2004
Phalacrocorax auritus	Texas	Campo et al. 1993
Phalacrocorax carbo	Greece	Liordos & Goutner 2007
Phalacrocorax olivaceous	Texas	King 1989
Morus bassanus	North Sea	Hamer et al. 2000

Information pertaining to the diet of the common loon along the Gulf coast was not found. Therefore data from Gingras & Paszkowski (2006), who studied the diets of common loons in Canadian Lakes, was used to estimate the proportion of fish and other items in the diet. Qualitative information from the field guide *Birds of North America* (McIntyre & Barr 1997) was used to determine which species in the model might be considered prey for loons. This led to

an estimate of diet composition of the common loon as 26% shads, 40% anchovies and other small fish, and 34% infauna.

2.2) Marine Mammals

The Gulf Menhaden Regional Management Plan (VanderKooy & Smith 2002) identifies marine mammals as predators of menhaden. Several species of marine mammals are common in the GoM, however, only the bottlenose dolphin and the Atlantic spotted dolphin are common in the nearshore areas of the northern GoM (Mullin & Hansen 1991, Vidal 2000), making them the most likely mammalian predators of Gulf menhaden and other fish in this region.

Okey and Mahmoudi, eds. (2002) provide individual biomass estimates for the marine mammal species included in their model of the West Florida Shelf. Their estimates for bottlenose dolphin and Atlantic spotted dolphin were combined to arrive at a biomass estimate of 0.031 mt/km^2/ year. Initial estimates of P/B and Q/B were also taken from the West Florida Shelf model (Okey et al. 2004).

Diet composition for dolphins as well as many of the fish groups in the model was determined by the following process. Access was granted to a pre-existing Microsoft Access Database (Chagaris, unpublished) that included dietary information from numerous sources for many of the species in the model. This database was then updated using both current and historic literature sources on diet composition not already included in the database. This database allows the user to input each literature source, including listing the prey items quantitatively or qualitatively, the region, habitat and time the study was conducted, and information about the predator such as size, sex, etc. Once the database was fully updated following a comprehensive search of the primary literature, diet sources for each model group were combined to arrive at an overall diet composition for the group. Sources were weighted based on the type of information they provided (i.e. percent weight or percent volume had the highest weight while qualitative descriptions had the lowest weight) as well as the region or species studied (i.e. the exact species studied in the northern GoM received the highest weight, while a similar species studied in a different region received the lowest weight). Sources used to arrive at the diet composition for the coastal dolphins group are listed in Table 2.5.

2.3) Sharks, Skates and Rays

Sharks are common predators in the Gulf and sharks, in general, are considered predators of Gulf menhaden (VanderKooy & Smith 2002). Shark species included in this model are those listed in the large coastal shark group and small coastal shark group, excluding prohibited species, in the Fishery Management Plan for Atlantic Tuna, Swordfish and Sharks (NMFS 1999). These groups include all of the shark species common in the coastal waters of the GoM. In addition, using these groups already delineated by the NMFS made gathering input data such as biomass, fishing mortality rates and catches feasible.

A comprehensive list of skates and rays of the GoM was compiled from *Fishes of the Gulf of Mexico: Texas, Louisiana, and Adjacent Waters* (Hoese & Moore, eds. 1998). This list was then pared down to include only those species that were considered common and for which information on diet and other parameters was available.

The biomasses for the large and small coastal shark groups were calculated based on catch and fishing mortality data, where Biomass = Catch/F. Catch data for large and small coastal sharks were downloaded from NOAA's Fisheries Statistics Division (http://www.st.nmfs.noaa.gov/st1/index.html); average values from 2005 – 2009 were used. Catches included commercial and recreational landings as well as estimates of recreational discards. The estimated F value used was 0.01 for large coastal sharks and 0.05 for small coastal sharks. A biomass estimate for the skates and rays group was taken from Walters et al. (2008).

Initial estimates of P/B and Q/B for the large coastal sharks group were taken from the Walters et al. (2008) model of the Gulf of Mexico, while estimates for the small coastal sharks group were taken from Carlson's (2007) model of shark trophic dynamics in Florida. Estimates provided in Walters et al. (2008) were used as initial input parameters for the skates and rays group. Diets for all three groups were compiled following the methodology described above for coastal dolphins and diet sources can be found in Table 2.5.

2.4) Fish Groups

The fish species included in the model were identified based on their relationship to Gulf menhaden (as predators or competitors) or on their importance to GoM fisheries. Several methods were used to identify the important fish species in the Gulf. Data on recreational and commercial landings and value of GoM species were downloaded from NOAA's Fisheries Statistics Division in order to identify those groups that were important fisheries species. A number of literature sources were also reviewed (e.g. Dagg et al. 1991, Hoese & Moore eds., 1998, VanderKooy & Smith 2002, Lewis et al. 2007, Walters et al. 2008) in order to identify the major predators of Gulf menhaden, as well as other common prey species in the estuaries and coastal waters of the Gulf. Species whose common habitat was distinct from that of Gulf menhaden (e.g. reef, deep continental shelf, fresh water) were excluded from the model. Finally, this list was reviewed and refined with the help of experts from the Florida Fish and Wildlife Research Institute.

Several fish species were classified into groups representing similar size, dietary habits and habitat preferences. This was a necessary step to maintain a relatively simple, workable model, while still representing all of the important species in this environment. Species that were important to fisheries and for which substantial data were available were left as individuals in order to accurately represent their roles in later Ecosim analyses. Additionally, certain species groups were divided into juvenile and adult categories to better represent trophic differences between life stages. The final model groups and species included are listed in Table 2.1.

Biomass estimates for fish groups were derived in one of three ways. For some groups/species, catch and fishing mortality data were used to calculate biomass. Catch and F estimates used to derive these biomass estimates are listed in Table 2.3. In some cases, fishery-independent survey data were used to estimate biomass. Lewis et al. (2007) conducted trawl surveys along the northern Gulf coast during the summers of 1992 – 1994 and reported the percent relative abundance of species caught. Since actual biomass was not reported, the biomass of Gulf menhaden from the recent stock assessment was used as a conversion factor as it was deemed to be the most accurate biomass estimate in the model. Percent relative abundance values from Lewis et al. (2007) and the derived biomasses are given in Table 2.4. For all other

species, biomass estimates were taken from Brown et al. (1991) who estimated biomasses for a number of Gulf of Mexico fish species or from Walters et al. (2008) model of the Gulf of Mexico. Maximum, minimum, and initial estimates of input parameters for all groups can be found in Appendix C-1.

Table 2.3. Biomass estimates derived using Catch/F, including F values used and their sources.

Species	F	Source	Catch (t/km^2/yr)	Biomass (t/km^2)
Coastal Pelagic Piscivores	0.31 (Average of all species in group)	Brown et al. 1991, Williams 2001	0.006	0.019
Tunas	0.325 (Average of Yellowfin and Blackfin)	Brown et al. 1991	0.0086	0.026
Black Drum	0.4	Brown et al. 1991	0.022	0.055
Gars	0.3	Estimate	0.002	0.0065
Sheepshead	0.165	Blanchet 2010	0.012	0.07
Lane Snapper	0.147	Johnson et al. 1995	0.00013	0.0009

Table 2.4. Biomasses derived from relative abundance data in Lewis et al. (2007).

Species/Group	% Relative Abundance	Biomass (t/km^2)
*Gulf menhaden	10.4	7.2
Gulf flounder	0.3	0.208
Southern flounder	0.3	0.208
Hogchoker	0.6	0.415
Gulf toadfish	0.1	0.069
Atlantic cutlassfish	0.2	0.138
Atlantic spadefish	0.5	0.346
Puffers	0.5	0.346
Gizzard shad	0.2	0.138
Threadfin shad	2.4	1.66
Striped anchovy	0.8	0.554

*Used as the reference value.

Production/biomass ratios in Ecopath are equivalent to total mortality (Z) estimates, which can often be found in the literature (Allen 1971). As such, estimates of total mortality from the literature or stock assessments were used as the P/B input for several species. In some cases, an estimate of natural mortality, either calculated or from the literature, was added to an estimated fishing mortality to attain a total mortality rate. As with biomass, some P/B values were taken from other Gulf of Mexico models. In the case of shads, for which no estimate of P/B was found, the P/B value for Gulf menhaden, a similar species, was substituted. For multi-species groups, a simple average of the P/B estimates for each species was used to estimate the P/B for the group. Initial estimates and their sources, along with maximum and minimum P/B estimates are found in Appendices C-1 and C-2.

Consumption/biomass ratios can be calculated from physical characteristics of the species (maximum weight, aspect ratio, etc.) and physical characteristics of the environment (temperature, salinity; Palomares & Pauly 1998). The website Fishbase (Froese and Pauly, eds. 2012), hosted by the University of British Columbia, provides estimates of Q/B for several

species in the model. All that is required is the water temperature (25° C was used in this case), an estimate of the aspect ratio and the type of consumer (e.g. detritivore, herbivore, omnivore, carnivore). For those species not available from Fishbase, estimates provided in other models (e.g. Walters et al. 2008, Chagaris, unpublished) were used or were calculated following Pauly (1989).

　　　As with the dolphins and sharks groups, literature diet sources were compiled in an Access Database and then aggregated for each species group using the method previously outlined. Sources of diet composition data are listed in Table 2.5.

Table 2.5. Sources used in constructing diet compositions for model groups.

Group	Diet Sources
Coastal Dolphins	Gunter 1942, Barros & Wells 1998, Pauly et al. 1998, Bowen 2009, Berens et al. 2010
Large Coastal Sharks	Snelson et al. 1984, Schmidt 1986, Cortes & Gruber 1990, Wetherbee et al. 1990, Stillwell & Kohler 1993, Hueter & Manire 1994, de Silva et al. 2001, Barry 2002, Huepel & Hueter 2002, Hoffmayer & Parsons 2003, Bethea et al. 2004, Ellis & Musick 2007, Barry et al. 2008, Wrast 2008, Cabrera-Chavez et al. 2010
Small Coastal Sharks	Hueter & Manire 1994, Cortes et al. 1996, Gelshleichter et al. 1999, Barry 2002, Hoffmayer & Parsons 2003, Bethea et al. 2004, Bethea et al. 2006, Bethea et al. 2007, Wrast 2008
Skates & Rays	Hess 1961, Struhsaker 1969, Smith & Merriner 1985, Bowman et al. 2000, Link & Almeida 2000, Bethea et al. 2006, Collins et al. 2007, Ebert & Bizzarro 2007, Navia et . 2007, Wrast 2008
Coastal Pelagic Piscivores	Knapp 1950, Knapp 1951, Odum & Heald 1972, Naughton & Saloman 1984, Saloman & Naughton 1984, Manooch et al. 1985, Harrigan et al. 1989, Franks et al. 1996, Meyer & Franks 1996, Buckel et al. 1999, Franks & VanderKooy 2000, Arendt et al. 2001, Keenan & Benfield 2003, Gartland et al. 2006, Guevara et al. 2007, Wrast 2008, Sley et al. 2009
Tunas	Manooch & Mason 1983
Adult & Juvenile Mackerels	Knapp 1950, Naughton & Saloman 1981, Saloman & Naughton 1983a, Saloman & Naughton 1983b, Godcharles & Murphy 1986, Finucane et al. 1990, Pelaez-Rodriguez et al. 2005
Adult & Juvenile Red Drum	Knapp 1950, Simmons & Breuer 1962, Boothby & Avault 1971, Bass & Avault 1975, Overstreet & Heard 1978, Scharf & Schlicht 2000
Adult & Juvenile Spotted Seatrout	Knapp 1950, Klima & Tabb 1959, Seagle 1969, Overstreet & Heard 1982, Rutherford et al. 1982, Minello et al. 1989, Peebles & Hopkins 1993, Russell 2005, Wrast 2008
Groupers	Randall 1967, Naughton & Saloman 1985, Matheson et al. 1986, Bullock & Smith 1991, Brule & Canache 1993, Weaver 1996, Lindberg et al. 2002, Koenig & Coleman 2009
Red Snapper	Futch & Bruger 1976, Szedlmeyer & Lee 2004, McCawley et al. 2006
Ladyfish	Knapp 1950, Harrington & Harrington 1960, Randall 1967,

	Rickards 1968, Odum 1971, Odum & Heald 1972, Sekavec 1974, Vega-Cendejas & Hernandez 2002, Jud et al. 2011
Spot	Weaver & Holloway 1974, Kobylinksi & Sheridan 1979, Sheridan 1979, Alexander 1983, Sheridan & Trimm 1983, Minello et al. 1989, Peebles & Hopkins 1993, Wrast 2008
Atlantic Croaker	Reid et al. 1956, Darnell 1961, Hansen 1969, Weaver & Holloway 1974, Overstreet & Heard 1978, Sheridan 1979, Sheridan & Trimm 1983, Minello et al. 1989, Darnell 1991
Butterfish	Darnell 1991
Black Drum	Breuer 1962, Overstreet & Heard 1982, Peters & McMichael 1990, Simmons & Wrast 2008
Flounders	Knapp 1950, Powell & Schwartz 1979, Overstreet & Heard 1982, Minello et al. 1989, Peebles & Hopkins 1993
Gars	Lambou 1961, Goodyear 1967, McGrath 2010
Sea Catfishes	Knapp 1950, Odum & Heald 1972, Sheriden & Trimm 1983, Yanez-Arencibia & Lara-Dominguez 1988, Vega-Cendejas et al. 1994, Kobelkowsky & Castillo-Rivera 1995, Motta et al. 1995, Rudershausen & Locascio 2001, Wrast 2008
Other Demersal Fishes	Reid 1954, Rodriguez-Pino 1962, Randall 1967, Odum 1971, Odum & Heald 1972, Carr & Adams 1973, Moffett et al. 1979, Sheridan 1979, Mericas 1981, Overstreet & Heard 1982, Sheridan & Trimm 1983, Chavance et al. 1984, Minello et al. 1989, Darnell 1991, Peebles & Hopkins 1993, Schmidt 1993, Cendejas et al. 1994, Ley et al. 1994, Vega-Cendejas et al. 1994, Vega- Motta et al. 1995, Aguirre-Leon & Diaz-Ruiz 2000, Bowman et al. 2000, Franks & VanderKooy 2000, Wheeler et al. 2002, Peleaz-Rodriguez et al. 2005, Aguirre-Leon & Diaz-Ruiz 2006, Castillo-Rivera et al. 2007, Wrast 2008
Nearshore Omnivores	Reid 1954, Randall 1967, Hansen 1969, Carr & Adams 1973, Alexander 1983, Stoner & Livingston 1984, Tipton & Bell 1988, Minello et al. 1989, Hayse 1990, Schmidt 1993, Vega-Cendejas et al. 1994, Motta et al. 1995, Russell 2005, Canto-Maza & Vega-Cendejas 2008
Adult & Juvenile Menhaden	Weaver & Holloway 1974, Govoni et al. 1983, Deegan et al. 1990, Castillo-Rivera et al. 1996
Shads	Haskell 1959, Creed 1985, Maitland & Lyle 2005
Other Clupeids	Odum 1971, Odum & Heald 1972, Carr & Adams 1973, Darnell 1991, Chen et al. 1992, Vega-Cendejas et al. 1994, Motta et al. 1995, Vega-Cendejas et al. 1997, Tsikliras et al. 2005
Anchovies and other small fish	Martin 1970, Odum 1971, Odum & Heald 1972, Bennett 1973, Carr & Adams 1973, Weaver & Holloway 1974, Sheridan 1978, Alexander 1983, Perschbacher & Strawn 1986, Minello et al. 1989, Rozas & LaSalle 1990, Darnell 1991, Peebles & Hopkins 1993, Ley et al. 1994, Motta et al. 1995
Squid	Bowman et al. 2000
Caridean Shrimp	Odum 1971

Penaeid Shrimp	Odum 1971, Kennedy et al. 1977, Schmidt 1993
Stone Crab	Wilber & Hernkind 1986
Blue Crab	Laughlin 1982, Hsueh et al. 1992, Schmidt 1993
Benthic Invertebrates	Dingle & Caldwell 1978, Botton & Ropes 1989, Coulon & Jangoux 1993, Cox et al. 1997, Moncreiff et al. 2001

2.5) Invertebrate Groups

Biomass for all invertebrate groups was estimated by Ecopath using assumed ecotrophic efficiencies, with the exception of squid and infauna, for which biomass estimates from Okey et al. (2004) and Walters et al. (2008) were used, respectively. Ecotrophic efficiency was estimated based on values in Okey et al. (2004), Walters et al. (2008) and Nuttall et al. (2011). P/B and Q/B values for invertebrate groups were taken from Walters et al. (2008), with the exception of squid, whose estimate was taken from Okey et al. (2004). The same procedure was followed as for fish and other groups to arrive at diet compositions for the invertebrate groups and the sources used are listed in Table 2.5. The exceptions were macrozooplankton, microzooplankton and infauna for which diet data were based on estimates provided in Walters et al. (2008).

2.6) Primary Producers and Detritus

All biomass and production estimates for these groups were taken from Walters et al. (2008).

2.7) Fisheries

Fisheries landings data were downloaded from NOAA Fisheries Statistics Division's databases of commercial and recreational landings (http://www.st.nmfs.noaa.gov/st1/index.html). The Annual Commercial Landings database was queried for "all species individually" and "all gear individually" from 1950 – 2009 for the Gulf of Mexico, separated by state. Data from Florida were eliminated to prevent inclusion of catches from the southern Gulf or Atlantic coasts. Gear types were grouped into 13 categories: cast net, crab trap, dredge, fish trawl, gillnet/trammel net, hand/spear/diving, haul seine, hook and line, longline, purse seine, shrimp trawl, troll, and other gear. These groupings provided sufficient resolution to analyze the impact of fishing by different gear types, but also allowed grouping of some smaller gear categories to make the model less cumbersome. The database reports landings in tonnes, so these numbers were divided by the modeled area of 145,000 km^2 to convert to the Ecopath units of mt/km^2. The five-year average of landings from 2005 – 2009 were used as the base landings for the Ecopath model.

For the recreational data, there are two ways of downloading the landings from the Recreational Fisheries Statistics database, either as a "Snapshot" or as a "Time Series." These two different queries result in slightly different values for landings of some of the species or species groups, so both sets of data were downloaded and the greater value was used, assuming that since, if anything, catches are underreported, it was more accurate to use the larger value of

landings. For both queries, an annual output was obtained in numbers and weight of fish from 1981 – 2011 for Gulf of Mexico landings by state and by gear type and for A and B1 catches only. A and B1 harvest refer to observed and reported harvest, respectively. Fishes were then categorized into model groups or were identified as "non-model" species and excluded. As with the commercial landings, catches from Florida were also excluded. An average value of landings from 2006 – 2010 was used. Recreational fishing methods were divided into "private" and "charter" categories to distinguish between recreational fishing by the tourism industry and private recreational fishing.

B2 harvest data were also downloaded from the recreational landings database, following the same procedure outlined above; these data represent fish "released alive." Fish released alive often suffer some post-release mortality (Muoneke & Childress 1994), so this was calculated to arrive at a value for bycatch in the recreational fishery. B2 data are only available in terms of numbers of fish, so the first step was to convert these numbers to weight. An average weight/fish was calculated using the A and B1 data, which is reported in both numbers and weight. This average weight was multiplied by the average numbers released from 2006 – 2010 to arrive at a total weight released. This was then multiplied by an estimate of the discard mortality rate to arrive at an estimate of the biomass of dead discards in the recreational fishery. A list of the discard mortality rates applied and their sources are listed in Table 2.6.

Table 2.6. Discard mortality rates used to estimate dead discards from the recreational fishery.

Group	Discard Mortality Estimate	Source
Adult Mackerels	0.2 (value for King mackerel)	SEDAR 2009a
Red Drum	0.08 (value from South Atlantic)	SEDAR 2009b
Spotted seatrout	0.12 (average of treble and single hook mortality)	Duffy 1999, AMRD 2007
Atlantic croaker	0.1 (value from South Atlantic)	ASMFC 2010
Black Drum	0.08	Used value from red drum
Coastal Pelagic Piscivores	0.2	Used value from mackerels
Flounders	0.1	NEFSC 2010
Groupers	0.14 (average for black, red, gag and goliath groupers)	Turner et al. 2001, SEFSC 2002, SEDAR 2010, SEDAR 2011
Mullets	0.04 (for grey mullet hook and line fishery in Australia)	Broadhurst et al. 2011
Nearshore Omnivores	0.1	Used value from Atlantic croaker
Other Demersals	0.1	Used value from Atlantic croaker
Red Snapper	0.21	SEDAR 2005
Saltwater catfish	0.1	Used value from Atlantic croaker
Small Coastal Sharks	0.1	Heuter & Manire 1994
Spot	0.1	Used value from Atlantic croaker
Tunas	0.2	Used value from mackerels

3.) Balancing process

An Ecopath model must be "balanced" before it can be used to analyze an ecosystem. That is, fluxes of energy into the model must be equal to energy fluxes out of the model, and the same

goes for each individual group. Following equation 2, the total energy demand on a group cannot exceed the production of that group. This balance is described by the Ecopath parameter known as ecotrophic efficiency (EE). Ecotrophic efficiency is essentially the proportion of production that is used within the system, that is, it is consumed by predators or fisheries or is exported (Okey and Mahmoudi, eds. 2002, Christensen et al. 2008). An ecotrophic efficiency of greater than 1 for a group means that more energy is consumed or exported than is produced, an impossible situation that results in an unbalanced model. An unbalanced model requires the user to vary the initial input values until parameters are found that result in a balanced model.

The initial inputs used in this model resulted in the majority of groups being unbalanced. The balancing approach taken was to begin with the groups with the highest EE values, or the ones most out of balance. The input parameters for these groups and their sources were examined to determine where the most uncertainty lay. For a number of the groups, closer examination of the diet composition data revealed instances of predation or consumption that appeared highly unintuitive. In cases where diet compositions seemed uncertain, the individual studies were reviewed and the estimates revised based on information from the most in-depth studies and those most applicable to the northern Gulf region. For many groups, several long-term and wide-ranging diet studies were available, while stock assessments estimating biomass or abundance had not been conducted. Initially, biomass estimates for several groups were based on parameters in Walters et al. (2008) model of the Gulf of Mexico; however, using these estimates resulted in high EE values for many groups, generally as a result of an overestimation of their predators' biomasses. Biomass values were therefore compared to estimates from other models and adjusted to fall within the range of values seen in these other models (see Appendix C-1 for ranges of input parameters). Production and consumption estimates were generally considered reliable and remained unaltered for most groups. The primary exception is that consumption rates for some of the upper trophic level groups (e.g. seabirds and dolphins) appeared to be too high and these were adjusted down based on the advice of scientists at the Florida Fish and Wildlife Research Institute.

Once most groups had EEs close to or less than one, a PREBAL analysis was used to guide the alteration of input parameters (Link 2010). Link (2010) describes a set of diagnostic tools that can be used to evaluate the input parameters in an Ecopath model and assess which values most likely need to be changed. Diagnostics such as comparison of biomass or vital rates (P/B, Q/B, R/B) across trophic level were used to determine which groups and input values to focus the balancing effort on. These parameters were then adjusted within the range specified by other sources (Appendix C-1). A list of the parameters of the balanced model can be found in Table 2.7.

Table 2.7. Parameters of the balanced Ecopath model. Values in bold were estimated by Ecopath.

	Group name	Trophic level	Biomass (t/km²)	P/B (year⁻¹)	Q/B (year⁻¹)	EE
1	Birds of Prey	4.0	5.150E-05	0.100	60.000	**0.000**
2	Loons	3.6	9.880E-05	0.100	28.634	**0.475**
3	Gulls and Terns	3.9	1.473E-03	0.100	50.000	**0.087**
4	Pelicaniformes	3.7	7.468E-03	0.100	17.737	**0.006**
5	Coastal Dolphins	4.0	3.064E-02	0.099	15.000	**0.106**
6	Large Coastal Sharks	4.0	8.443E-02	0.300	3.200	**0.033**

7	Small Coastal Sharks	4.0	7.576E-02	0.510	4.700	**0.315**
8	Skates and Rays	3.4	2.380E-01	0.380	4.000	**0.154**
9	Coastal Pelagic Piscivores	3.8	1.000E-01	0.614	5.433	**0.934**
10	Tunas	4.1	2.444E-02	0.900	13.000	**0.587**
11	0-6 Mackerels	3.9	2.100E-04	4.000	32.683	**1.000**
12	6+ Mackerels	4.0	6.000E-02	0.700	5.400	**0.992**
13	0-8 Red Drum	3.1	1.262E-03	3.447	24.965	**0.193**
14	8+ Red Drum	3.5	1.800E-01	0.600	4.800	**0.677**
15	0-18 Spotted Seatrout	3.5	3.694E-02	1.416	12.940	**0.086**
16	18+ Spotted Seatrout	3.5	3.100E-01	0.700	5.100	**0.733**
17	Groupers	3.7	2.890E-01	0.469	2.800	**0.574**
18	Red Snapper	3.7	4.000E-01	0.700	5.240	**0.130**
19	Ladyfish	3.5	9.880E-02	0.880	4.304	**0.668**
20	Spot	2.9	8.000E-01	1.100	6.900	**0.217**
21	Atlantic Croaker	3.0	6.000E-01	1.500	10.000	**0.194**
22	Butterfish	3.1	**2.003E-01**	2.000	10.400	0.300
23	Black Drum	3.1	5.000E-01	0.578	3.654	**0.319**
24	Flounders	3.5	4.140E-01	0.775	4.516	**0.328**
25	Gars	3.8	4.000E-02	0.562	3.471	**0.456**
26	Sea Catfishes	3.3	5.000E-01	0.800	7.600	**0.225**
27	Mullets	2.0	6.900E-01	0.978	10.021	**0.665**
28	Other Demersals	3.2	2.200E+00	1.065	7.700	**0.986**
29	Nearshore Omnivores	2.8	1.440E+00	0.996	8.600	**0.946**
30	Adult Menhaden	2.6	7.240E+00	1.900	8.100	**0.432**
31	Juvenile Menhaden	2.6	1.851E+00	2.300	19.617	**0.411**
32	Shads	3.0	1.793E+00	1.900	11.800	**0.425**
33	Other Clupeids	3.0	5.448E+00	1.533	11.381	**0.429**
34	Anchovies etc.	2.8	3.032E+00	2.443	13.475	**0.880**
35	Squid	3.7	2.670E-01	4.000	**17.643**	0.990
36	Caridean Shrimp	2.2	**3.243E+00**	2.400	18.000	0.800
37	Penaeid Shrimp	2.5	**2.254E+00**	2.400	19.200	0.990
38	Stone Crab	2.5	**1.029E+00**	2.000	7.000	0.950
39	Blue Crab	2.6	**9.832E-01**	2.400	8.500	0.950
40	Benthic Invertebrates	2.1	**2.499E+01**	4.500	22.000	0.800
41	Macrozooplankton	2.1	**6.434E+00**	22.000	67.000	0.500
42	Microzooplankton	2.0	**6.460E+00**	36.000	89.000	0.500
43	Infauna	2.0	2.000E+01	2.000	10.000	**0.229**
44	Algae	1.0	2.978E+01	25.000	0.000	**0.134**
45	Seagrass	1.0	1.756E+02	9.014	0.000	**0.001**
46	Phytoplankton	1.0	2.500E+01	182.130	0.000	**0.261**
47	Detritus	1.0	1.000E+02			**0.083**

4.) Ecopath Tools/Output Analysis

Once the model has been balanced, Ecopath can be used for a number of different purposes. First and foremost, a balanced Ecopath model is required to run the time-dynamic simulation Ecosim, which will be discussed in detail later. The quality of the individual inputs and the overall model quality can be assessed through the Ecopath pedigree index. Each individual input parameter is categorized according to its source (e.g. estimated, taken from another model, derived from high- vs. low-precision sampling) and these categories are converted to a value. Ecopath then calculates the overall "pedigree" of the model based on these values. A low pedigree index is indicative of primarily using guesstimates and parameters from other models, while a high pedigree index is associated with use of high precision studies of the specific species within the ecosystem being modeled. The Ecopath modeling software also contains a built-in routine for network analysis following the theory of Ulanowicz (1986), which allows the user to characterize a system and compare it to other systems. The network analysis also produces several metrics that can be combined to estimate the level of ecosystem maturity (Odum 1969). The indices estimated and used for analysis are described below.

4.1) Ecosystem Properties

Ecosystem properties were calculated to give a general idea of the overall structure of the northern GoM ecosystem. These include total system production and total system consumption, net primary production and total system throughput. Net primary production represents the activity of lower trophic levels, while the activity of upper trophic levels is represented by the total respiration (Nuttall et al. 2011). Total system throughput represents the size of the ecosystem in terms of the summation of flows from total consumption, respiration, export and flows to detritus. Estimates of the total catch, as well as the mean trophic level of the catch and the gross efficiency (represented by the ratio of total catches to net primary production) were calculated to give an idea of the characteristics of the fishery. In addition, an estimate of the primary production required to sustain catches (PPR) was estimated; a detailed description of how it is calculated in Ecopath can be found in the EwE User Guide (Christensen et al. 2008). The trophic transfer efficiency, representing the average energy transferred between trophic levels, was also estimated.

The characteristics of individual groups and their interactions are also important to consider. Ecopath estimates the fractional trophic level of each group, which can be used to examine the role of species/groups in the ecosystem. The interactions among groups within the model are presented via the mixed trophic impact calculations. The mixed trophic impact estimates the impact that a change in biomass of one group will have on the biomass of the other groups in the model.

4.2) Ecosystem Maturity

Indices of ecosystem maturity were calculated for the northern Gulf of Mexico model. Odum (1969) first presented the concept of ecosystem maturity, describing the evolution of an ecosystem from new to fully evolved, in which a system was stable and achieved maximum biomass and/or diversity (Christensen 1995). Christensen (1995) described Odum's attributes of ecosystem development that can be quantified using the Ecopath software. These attributes are grouped into six categories: community energetics, community structure, life history, nutrient cycling, selection pressure, and overall homeostasis. Several metrics are used to describe community energetics. The primary productivity to respiration ratio is expected to approach one as a system matures; in immature systems primary production is expected to exceed respiration, while respiration may exceed primary production in systems with excessive organic pollution (Christensen 1995). The primary production to biomass (excluding detritus) ratio is also a measure of maturity. Immature systems are expected to have a lower biomass and therefore the highest Pp/B ratios. Two measures are used to quantify the biomass supported per unit energy flow. These are the ratio of biomass to total system throughput and the ratio of biomass to the sum of primary production and system respiration; both measures are expected to increase as a system matures (Christensen 1995). The net system production, closely related to the Pp/R ratio, is the difference between primary production and respiration and is expected to decrease as a system matures. Food web structure is measured by connectance and the system omnivory index. Connectance represents the ratio of the number of actual links to the number of possible links (Gardner and Ashby 1970, Christensen 1995). The omnivory index is the variance of the trophic levels of a consumer's prey (Christensen & Pauly 1992) and the system omnivory index simply represents the average omnivory index of all consumers (Christensen 1995).

Community structure is a difficult concept to quantify. Total system biomass, excluding detritus, is one metric that can be used and is assumed to increase as a system matures. Species diversity is also expected to increase as a system matures, but is difficult to measure when several species are grouped together to form the model groups. Christensen (1995) proposed flow diversity as a measure to use instead, which can be quantified by the statistical entropy (H) for all groups in the system. Life history attributes are also difficult to measure due to the grouping of species, but can be quantified indirectly by the ratio of biomass to total system production, which is a proxy for organism size.

Odum (1969) described nutrient recycling as one aspect of ecosystem maturity with mature systems displaying a higher degree of recycling than immature systems. Finn (1980) developed an index with which to measure energy cycling within an ecosystem. The Finn's cycling index is the proportion of total throughput that is recycled (Christensen 1995). A similar measure, the predatory cycling index (Christensen & Pauly 1992) is also used to measure energy cycling, but excludes cycling through detritus. Path length, also developed by Finn (1980), is another descriptor of flows in the ecosystem and is expected to be highest for mature systems. It is calculated as the ratio of total system throughput to the sum of total export and total respiration.

Selection pressure, as described by Odum (1969), is mainly related to growth and production. As systems mature, dominance of faster growing, r-selected species is replaced by dominance of slower growing, k-selected species. Both growth and production are related to the overall P/B ratio for the system. Species growth can also be described by the residence time of energy in the system, which is estimated as the ratio of total biomass to the sum of total respiration and total exports.

Mature ecosystems have a large and diverse organic structure and maintain a high level of stability (Odum 1969). This stability or homeostasis can be quantified in a number of ways. Nutrient conservation is considered to be an important factor in stability and is measured by the overhead on exports. Total system overhead is considered a direct measure of maturity as is the total ascendency relative to capacity. Overhead on internal flows can also be used as a measure of stability (Christensen 1995). The Schrödinger ratio, described by Odum as the ratio of total respiration to system biomass, is also a direct measure of stability and increases as a system matures. The last measure of ecosystem maturity used is the information content of flows, calculated as part of ascendency, and also increases as an ecosystem matures.

Ulanowicz (1986) developed a measure termed ascendency, which is related to Odum's attributes of ecosystem maturity. Ulanowicz proposed the ascendency measure as an index that could capture both the attributes of ecosystem size and flow organization (Ulanowicz 1980). Trends that lead to increased maturity also contribute to higher network ascendency, so this metric estimated by Ecopath can also be used as an overall measure of ecosystem maturity. Developmental capacity is related to ascendency in that it measures the scope for further ecosystem development (Kay et al. 1989, Frisk et al. 2011).

5.) Ecosim Methodology

Ecosim inherits its initial parameters from the balanced Ecopath model and produces dynamic estimates of biomass and catch rates over time. These biomass dynamics are expressed through a series of coupled differential equations of the form:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \tag{3}$$

where dB_i/dt is the growth rate in terms of biomass (B_i) over time for group i, g_i is the net growth efficiency (i.e. production/consumption ratio), and the two summations represent consumption rates. Q_{ji} is the total consumption by group i, while Q_{ij} is the predation by all predators on group i. I_i is the immigration rate, MO_i is the "other" natural mortality rate (unrelated to predation), F_i is the fishing mortality rate and e_i is the emigration rate (Christensen et al. 2008).

Predator-prey interactions are an important component of Ecosim dynamics. The availability of prey to predators and the ability of predator populations to grow in relation to their prey base greatly influence the biomass dynamics of the model. Consumption rate calculations are based on the foraging arena concept (Walters & Juanes 1993), where the biomass of prey groups is divided into invulnerable and vulnerable components, following equation 4:

$$Q_{ij}(B_i, B_j) = \frac{a_{ij}v_{ij}B_iB_j}{(2v_{ij}+a_{ij}B_j)} \tag{4}$$

where a_{ij} is the effective search rate for prey i by predator j, v_{ij} is the vulnerability parameter, which expresses the rate that prey move between vulnerable and invulnerable states, B_i is the prey biomass, and B_j is the predator biomass (Christensen et al. 2008). The vulnerability

parameter is what determines top down (predator control) vs. bottom up (prey control) control. Low vulnerabilities values (close to 1) lead to bottom up control and an increase in predator biomass will not cause a substantial increase in predation mortality on its prey. Conversely, high vulnerabilities (approaching 100 or more) lead to top down control, where increases in predator biomass are directly proportional to increases in predation mortality (Christensen et al. 2008).

Although Ecosim is capable of running simulations forward from the model start year without any input aside from the initial Ecopath parameters, it is helpful to check the model's predictions by comparing them to known time series of abundance, catch, or total mortality rates. This step is critical in developing a model for policy analysis. Time series fitting requires adjusting the model's parameters in order to reasonably recreate observed historical trends and is important for improving the credibility the model.

6.) Ecosim Inputs

6.1) Collection of Time-series Data

Time series inputs can be either reference data or forcing data. Forcing data are generally instantaneous fishing mortality rates (F) by model group or fishing effort by gear type and are used to drive the model. Biomass, total mortality and catches can also be forced. Reference data are those time series that one attempts to recreate with the model; these, generally, are relative biomass, total mortality and catches. Biomass and F time series were generally found in single-species stock assessments, while catch data were downloaded from NOAA Fisheries Statistics Division's database of commercial and recreational catches (see section 2.7). Commercial catch data extend back to 1950, while recreational catch and discard data are only available from 1981 forward. A list of time series used and their sources can be found in Table 2.8.

Forcing data must be present for all years modeled. Due to the variety of sources used and the fact that recreational data, in particular, did not extend back as far as commercial data, some of the time series needed to be extrapolated in order to cover the entire time period from 1950 – 2009. For series that ended prior to 2009, the series was extended forward using a constant value from the last available year. For those series that began after 1950, various methods were used to back-calculate the historic values. It was assumed that catch and effort data were not zero either before the time series began or after the time series ended due to the fact that there were commercial catches during the entire modeled period. In Ecopath, effort is standardized, with a value of one being given to the effort in the first year for which data are available. In order to extrapolate effort backwards, a linear decrease was used from the first year data were available to 1950, ending with ½ the effort from the first year (0.5). This method was used for recreational effort (charter and private), purse seine effort and shrimp trawl effort. For fishing mortality series, the same method was used, linearly decreasing F to ½ the value from the first year of data. This was done for large coastal shark F, small coastal shark F and blue crab F. For red drum F, a constant value, the average from the years for which data were available, was used for all previous years. Recreational catches were also extrapolated backwards to 1950 to match the records from the commercial data. The average recreational catch and average recreational bycatch from 1981 – 2011 were taken and added to the commercial catches in the years 1950 – 1980 to arrive at a complete commercial and recreational catch record from 1950 – 2009.

Table 2.8. Time series used during model validation. Group numbers correspond to the model groups listed in Table 2.1, or in the case of effort data, the fleet number. Series type is the Ecopath code representing the type of time series used: 0 = relative biomass, 3 = effort data by gear type (forcing), 4 = fishing mortality by group (forcing), 6 = catches, -6 = forced catches.

Series Name	Group Number	Series Type	Years Covered	Source
Recreational Effort (Charter)	15	3	1981 – 2011	NOAA Fisheries Statistics Division (FSD)
Recreational Effort (Private)	15	3	1981 – 2011	NMFS FSD
Purse Seine Effort (Menhaden)	11	3	1964 – 2004	Vaughan et al. 2007
Shrimp Trawl Effort	12	3	1984 – 2010	Hart, personal communication
Large Coastal Shark F	6	4	1972 – 2004	SEDAR 2006
Small Coastal Shark F	7	4	1972 – 2005	SEDAR 2007
Red Drum F (Ages 1+)	14	4	1979 – 1996	Porch 2000
Gulf Menhaden F	30	4	1948 – 2010	Mahmoudi, personal communication
Red Snapper F	18	4	1872 – 2008	Linton, personal communication
Blue Crab F (Louisiana)	39	4	1968 – 2008	West et al. 2011
Adult Mackerel Catch	12	6	1950 – 2009	NOAA FSD
Atlantic Croaker Catch	21	-6	1950 – 2009	NOAA FSD
Black Drum Catch	23	6	1950 – 2009	NOAA FSD
Coastal Pelagics Catch	9	6	1950 – 2009	NOAA FSD
Groupers Catch	17	6	1950 – 2009	NOAA FSD
Mullets Catch	27	-6	1950 – 2009	NOAA FSD
Other Demersals Catch	28	6	1950 – 2009	NOAA FSD
Red Drum Catch	14	6	1950 – 2009	NOAA FSD
Red Snapper Catch	18	6	1950 – 2009	NOAA FSD
Marine Catfish Catch	26	6	1950 – 2009	NOAA FSD
Spot Catch	20	6	1950 – 2009	NOAA FSD
Spotted Seatrout Catch	16	6	1950 – 2009	NOAA FSD
Benthic Invertebrates Catch	40	6	1950 – 2009	NOAA FSD
Blue Crab Catch	39	6	1950 – 2009	NOAA FSD
Menhaden Catch	30	6	1950 – 2009	NOAA FSD
Penaeid Shrimp Catch	37	6	1950 – 2009	NOAA FSD
Squid Catch	35	-6	1950 – 2009	NOAA FSD

Adult Mackerels Relative Abundance	12	0	1983 – 2009	SEAMAP 2011
Butterfish Relative Abundance	22	0	1983 – 2009	SEAMAP 2011
Red Snapper Relative Abundance	18	0	1983 – 2009	SEAMAP 2011
Marine Catfish Relative Abundance	26	0	1983 – 2009	SEAMAP 2011
Squid Relative Abundance	35	0	1983 – 2009	SEAMAP 2011
Small Coastal Sharks Relative Abundance	7	0	1972 – 2005	SEDAR 2007
Blue Crab Relative Abundance (LA)	39	0	1968 – 2009	West et al. 2011
Menhaden Egg Abundance	30	0	1948 – 2009	Mahmoudi, personal communication
Red Drum Relative Abundance	14	0	1979 – 1997	Porch 2000
Penaeid Shrimp CPUE	37	0	1984 – 2009	Hart, personal communication
Large Coastal Shark Relative Abundance	6	0	1972 – 2004	SEDAR 2006
Striped Mullet Abundance (LA)	27	0	1996 – 2010	Blanchet 2010
Spotted Seatrout Abundance (TX Fall Gill Net)	16	0	1975 – 2009	Martinez-Andrade, personal communication
Black Drum Abundance (TX Fall Gill Net)	23	0	1975 – 2009	Martinez-Andrade, personal communication
Southern Flounder Abundance (TX Fall Gill Net)	24	0	1975 – 2009	Martinez-Andrade, personal communication
Atlantic Croaker Abundance (TX Fall Gill Net)	21	0	1975 – 2009	Martinez-Andrade, personal communication
Spot Abundance (TX Bag Seine)	20	0	1977 – 2009	Martinez-Andrade, personal communication

6.2) Fitting Time Series

Initial time-series inputs to Ecosim do not usually result in ideal fits between the model and the data, and generally some adjustments are needed in order for the model to reasonably recreate the reference time series. Ecosim produces a statistical measure of goodness of fit to the time series data, represented by a weighted sum of squared deviations (Christensen et al. 2008)

that can be used to guide the fitting procedure. The EwE User Guide (Christensen et al. 2008) also provides a list of suggestions for correcting discrepancies between modeled trends and time series: 1) eliminate bad trend data, 2) examine forcing data for incompleteness or inaccuracies, 3) change vulnerability parameters, 4) examine P/B values in Ecopath and change if necessary, 5) look for changes in system productivity that may affect trends in biomass for upper trophic level groups, 6) look for trophic mediation effects, where changes in consumption or mortality may be caused by indirect effects. Several of these methods were utilized, along with, in some cases, changing biomass values in Ecopath in order to adjust catch levels. Catches were also forced for some species for which no fishing mortality or effort data were available.

The fitting procedure was begun by identifying those model groups with the highest sum of squares value and then each group was corrected individually. For each group, the trend data applied to that group was examined to determine if it was appropriate to use, following step one from the EwE User Guide. Biomass series were eliminated if they were deemed not accurately representative of the group in question. For example, SEAMAP groundfish surveys likely do not accurately capture small pelagics such as bay anchovy. Additionally, as mentioned above, rather than removing certain catch series that were not reproduced by the model, these catches were forced. Secondly, vulnerability values for each group examined were manually adjusted. In some cases, input parameters in the base Ecopath model were also adjusted. This was the case for groups where the model significantly overestimated catches. In these cases, reducing the biomass of the group slightly often resulted in a better fit to the catch time series. The vulnerability search tool in Ecosim was also used to refine the vulnerability parameters that had been manually adjusted. The tool searches for vulnerability parameters that give better fits to the time series data (Christensen et al. 2008). However, after running several scenarios forward in time, it was realized that many vulnerability parameters were set to extreme levels during the vulnerability search. These were adjusted back towards the default value of two to prevent the extreme changes in biomass that arose during some simulations. Therefore, a balance was struck between adjusting parameters to provide a better fit and maintaining parameters within the bounds of reality.

7.) Ecosim Model Runs – Policy/management scenarios

Once the fitting procedure was completed and a satisfactory fit to the time-series data was found, different fishery management strategies and policy scenarios were tested. The impact of recreational fishing on the ecosystem was examined by halving and doubling recreational fishing mortality rates from their 2009 levels for all recreationally caught species (i.e. "Half Rec" and "Double Rec"). The impact of fishing on potentially vulnerable fish groups (e.g. red drum, red snapper and groupers) was further examined by shutting down these fisheries entirely (i.e. "Species Recovery") and observing their recovery under continued fishing of their prey groups (e.g. menhaden and shrimp). Conversely, fisheries for menhaden and penaeid shrimp were shut down (i.e. "No Menhaden F" and "No Shrimp Effort") to examine the impact of prey abundance on important predator groups. Scenarios were also developed that fished menhaden at the target ($F_{targ} = 0.94$) and limit ($F_{lim} = 1.46$) levels proposed in the 2007 stock assessment (Vaughan et al. 2007). Other forage fish groups in the model (e.g. shads, other clupeids and anchovies etc.) are currently fished at very low levels (< 0.005), but scenarios were developed to examine the impact of new forage fish fisheries on predators, should they arise in the future. The first

involved fishing the three "new" forage fish groups at an F of 0.3, similar to the level of the current menhaden fishery, while menhaden continued to be fished at present levels (i.e. "New FF Fisheries"). The second scenario fished all four forage fish groups (including menhaden) at their single species F_{MSY} levels (i.e. "FF at F_{MSY}"). A description of how F_{MSY} was calculated for these species is given below. The final set of scenarios involved increasing and decreasing fishing mortality rates for all currently fished groups (i.e. "Increase All" and "Decrease All"). Fishing rates were increased by 5% per year for 25 to simulate a situation in which fishing continues without further regulation. A scenario was also run in which all fisheries decreased by 5% per year for 25 years. All Ecosim simulations were run through 2109, 100 years after the end of current time series.

The second set of test runs followed the methods outlined in Pikitch et al. (2012). The management strategy evaluation tool with an additional module (Pikitch et al. 2012) was used to test the impact of different fishery management strategies for forage fish (e.g. constant F, constant yield, step functions, and hockey-stick control functions) over many different levels of fishing. These runs were conducted using both a deterministic and a stochastic method. The deterministic constant F scenario tested fishing mortality rates from 0 to 3 in increments of 0.05 on each forage fish group individually. The results of this scenario allowed for the calculation of F_{MSY}, MSY, B_{MSY} and the unfished biomass (B_0) for each forage fish group. The deterministic constant yield strategy tested yields from $0 - 5$ mt/km^2/yr at intervals of 0.5 mt/km^2/yr. The stochastic scenarios included a constant F strategy, two step functions, and two hockey stick functions, each with a coefficient of variation of 30%. For the constant F strategy, fishing mortality rates were set to 50%, 75% and 100% F_{MSY} (based on the F_{MSY} calculated from the deterministic constant F run); each scenario was run 100 times for 50 years each. For the step functions and hockey stick functions, minimum biomass limits were set at 20% and 40% of the target fish's unfished biomass (B_0 calculated above). The step functions fished at a constant fishing mortality rate (e.g. 50%, 75% or 100% F_{MSY}) until the biomass limit was reached (e.g. 20% B_0 or 40% B_0), at which point fishing stopped altogether. For the hockey stick functions, fishing rates were initiated at 50%, 75% or 100% of F_{MSY}, but then declined linearly as the target population declined until the biomass threshold was reached, at which pointed fishing stopped. The step functions and hockey stick functions were also run 100 times for 50 years each.

8.) Ecopath Model Outputs

The final Ecopath model contains 47 functional groups as follows: 4 seabird groups, 1 marine mammal group, 3 elasmobranch groups, 26 bony fish groups, 9 invertebrate groups, 3 primary producer groups and 1 detritus group. The parameters of the final model are listed in Table 2.7. The flow diagram in Figure 2.2 shows the energy flows between groups as well as the trophic level of each group. The colored nodes correspond to the biomass of each group and are also scaled relative to the biomass. The trophic level of consumers varied from 2 (infauna) to 4.1 (tunas).

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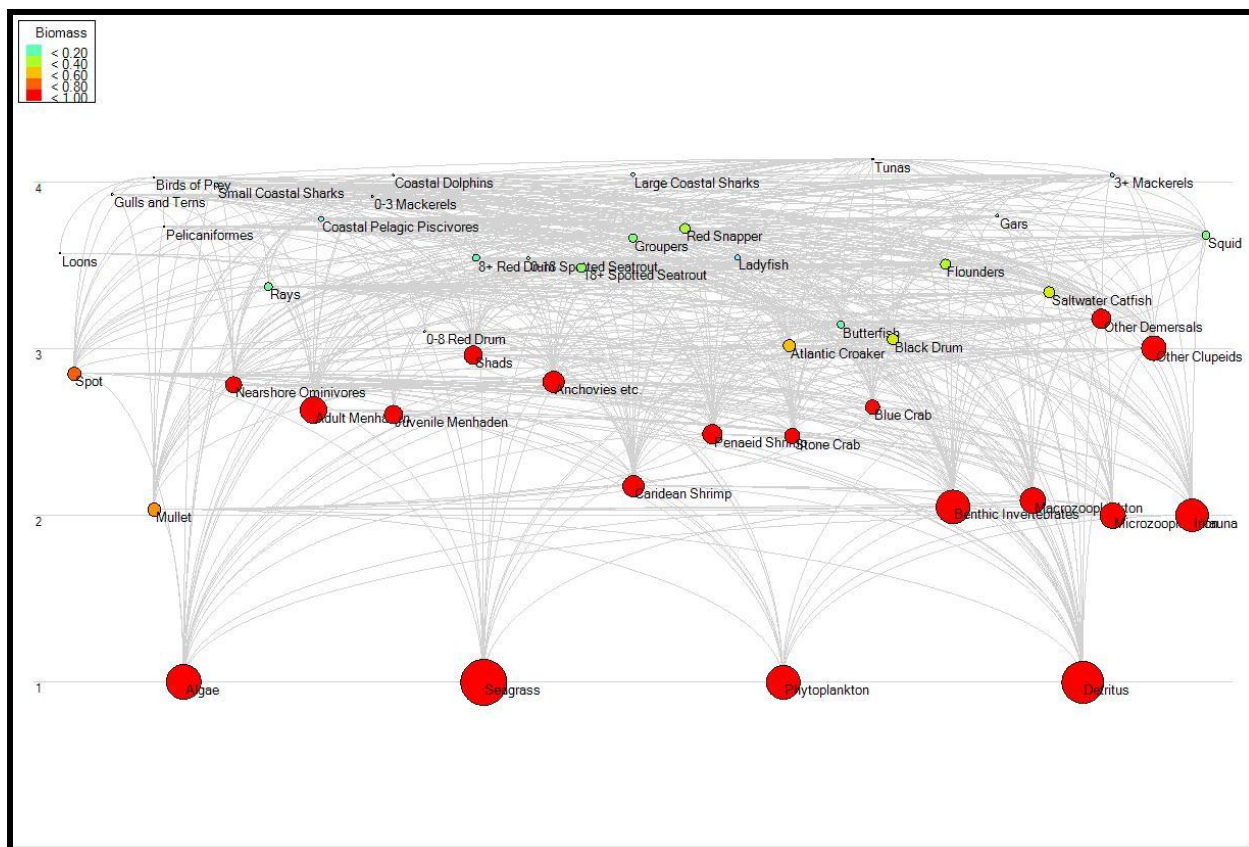
Figure 2.2. Flow diagram of the northern Gulf of Mexico ecosystem model. Horizontal lines refer to trophic levels, while the colored nodes refer to the biomass of the group and are scaled by relative biomass.

Structural properties of the ecosystem, estimated by Ecopath, are listed in Table 2.9. Total system production was 7,472 t/km^2/yr. Primary production was 6,881 t/km^2/yr and respiration was 806 t/km^2/yr, resulting in a primary production to respiration ratio (Pp:R) of 8.5. The primary production to biomass ratio was 21.2. The high value of these ratios indicates that the northern Gulf of Mexico ecosystem is in a developmental stage. The primary production required for catch was approximately 2% of the total primary productivity. The mean trophic level of the catch was 2.64. This is due to menhaden and shrimp, the top two species targeted by fisheries in the region, having low trophic levels of 2.6 and 2.5, respectively. The mean trophic transfer efficiency was 11.4%.

Table 2.9. Summary statistics of the northern Gulf of Mexico model.

Metric	
Sum of all consumption	2164.0 t/km^2/yr
Sum of all exports	6074.7 t/km^2/yr
Sum of all respiratory flows	806.1 t/km^2/yr
Sum of all flows into detritus	6623.0 t/km^2/yr
Total system throughput	15667.7 t/km^2/yr
Sum of all production	7472.0 t/km^2/yr

Mean trophic level of the catch	2.6
Gross efficiency (catch/net p.p.)	0.000585
Total net primary production	6880.7 t/km^2/yr
Total primary production/total respiration	8.5
Net system production	6074.6 t/km^2/yr
Total primary production/total biomass	21.2
Total biomass/total throughput	0.02
Total biomass (excluding detritus)	324.7 t/km^2/yr
Total catches	4.02 t/km^2/yr
Connectance Index	0.30
System Omnivory Index	0.19
Ecopath pedigree index	0.33

9.) Ecosim Fitting to Data

The Ecosim model was fit to observed biomass data for adult mackerels, butterfish, red snapper, sea catfishes, squid, small coastal sharks, blue crab, adult menhaden, adult red drum, penaeid shrimp, large coastal sharks, striped mullet, adult spotted seatrout, black drum, flounders, Atlantic croaker, and spot (Figure 2.3). The model was also fit to catch time series for adult mackerel, black drum, coastal pelagics, groupers, other demersals, adult red drum, red snapper, sea catfishes, adult spotted seatrout, benthic invertebrates, adult menhaden and penaeid shrimp (Figure 2.4). The overall log sum of squares for these 28 fits to the base model was 151. The model was able to approximately recreate the observed values and trends in biomass for red snapper, adult red drum, blue crab, adult menhaden, and penaeid shrimp (Figure 2.3). To a lesser extent, the model captured the biomass trends of small coastal sharks, adult mackerels, squid, adult spotted seatrout, Atlantic croaker and spot (Figure 2.3). The model did not capture the decline in flounder biomass, the high sea catfishes biomass in the 1980s, the decline in butterfish biomass in the 1980s, the increase in black drum biomass, or the decline in mullet biomass in the early 1990s (Figure 2.3). The model also predicts an increase in large coastal shark biomass, whereas the observed data point to a leveling off of biomass at low levels (Figure 2.3). The model did a decent job of recreating catch time series for adult mackerels, coastal pelagics, spotted seatrout, sea catfishes, other demersal fishes, black drum, blue crab, adult menhaden, and penaeid shrimp, although the model tended to overestimate catches of coastal pelagics and blue crab (Figure 2.4). The model was unable to mimic the fluctuation in groupers or benthic invertebrate catches over time (Figure 2.4). The model mostly replicated the trend in red drum catches, though it overestimated the catch in the beginning and middle of the time series and underestimated the catch towards the end (Figure 2.4). Red snapper catches were well modeled with the exception of the 1970s, during which the model showed an increasing trend while the observed data showed a decreasing trend (Figure 2.4).
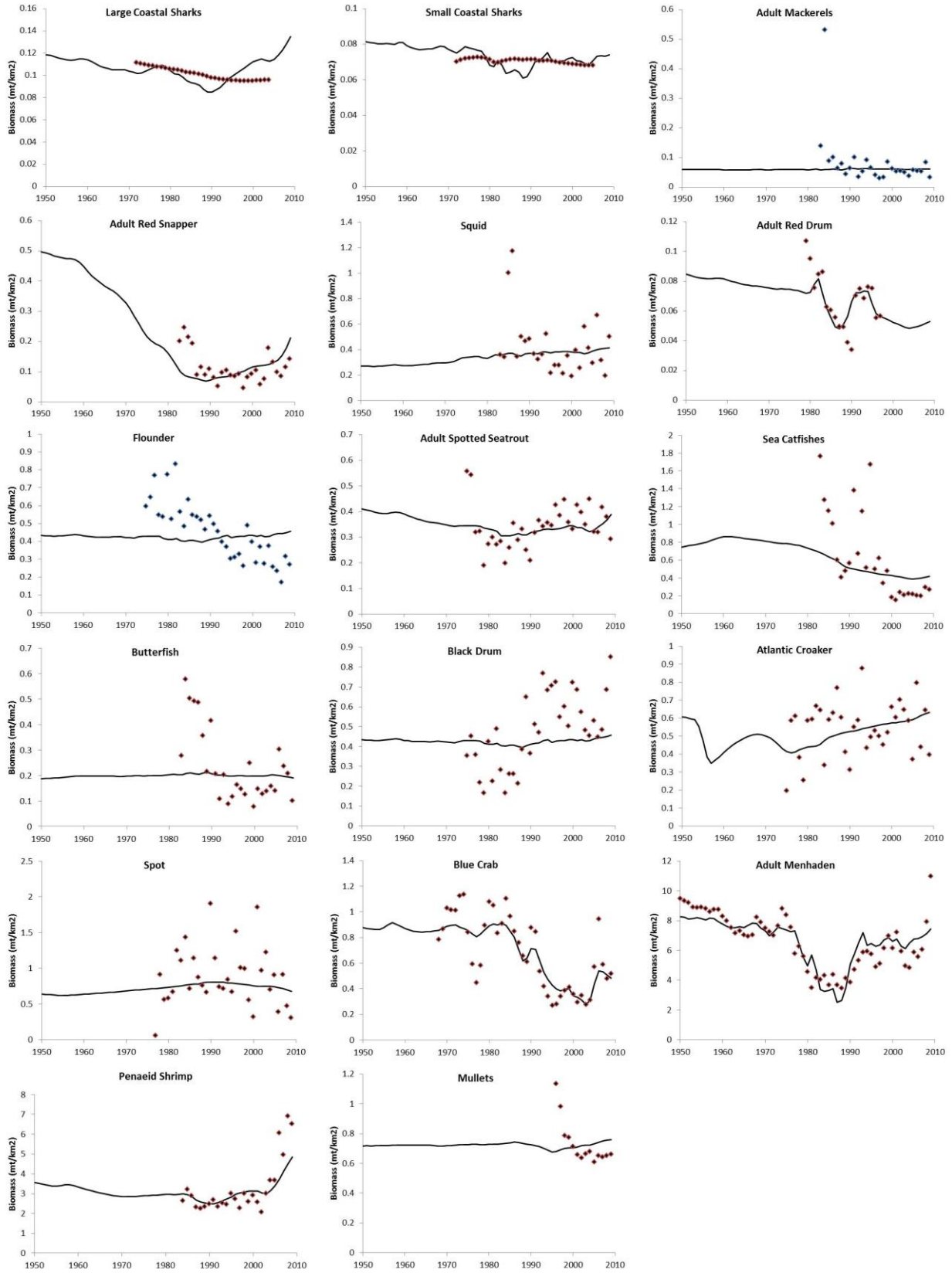
Figure 2.3. Observed (dots) and predicted (solid lines) biomass for the northern Gulf of Mexico Ecosim model.

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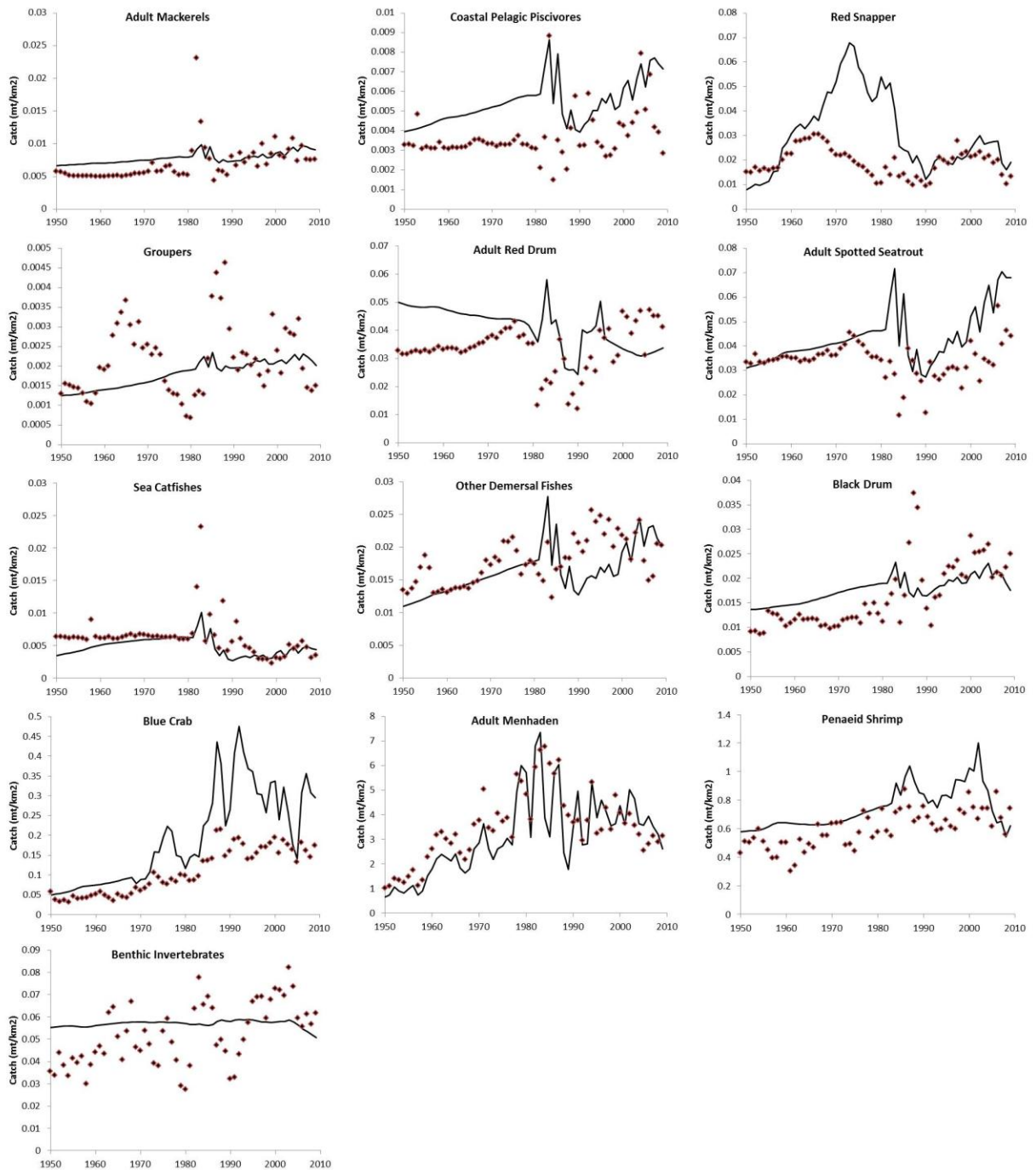
Figure 2.4. Observed (dots) and predicted (solid lines) catches for the northern Gulf of Mexico Ecosim model.

10.)   Results of Deterministic Ecosim Scenarios

Several different fishery management scenarios were tested to determine the impact of alternative fishery policies on important recreational and commercial species, top predators, major forage fish consumers and species of concern. Standard ecosystem metrics and indices of

maturity were compared among the simulations (Figure 2.5 and Table 2.10). Substantial increases in catches and corresponding decreases in overall system biomass occurred when menhaden were fished at higher than present levels (e.g. F_{targ} and F_{lim}), when all fisheries were increased by 5% per year and when all forage fish groups (menhaden, anchovies, other clupeids, shads) were fished at F_{MSY} levels (Figure 2.5). Slight increases in overall system biomass occurred when menhaden fishing was eliminated and when all fisheries were decreased by 5% per year; these simulations also resulted in substantial decreases in overall catches (Figure 2.5). The trophic level of the catch generally increased when low trophic level species were not fished (e.g. "No Shrimp Effort," "No Menhaden F") and decreased when catches of higher trophic level species were reduced (e.g. "Species Recovery", "Half Rec"; Figure 2.5). The trophic level of the catch also increased when new fisheries for forage fish species were introduced (Figure 2.5). Shad, other clupeids, and anchovies all have a higher trophic level than the other major fishery species (menhaden and shrimp), hence the increase in mean trophic level. Kempton's Q index represents the diversity of upper trophic level species. Upper trophic level diversity decreased when menhaden were fished at higher levels, as well as when all fisheries were increased and when recreational fishing levels were doubled (Figure 2.5).
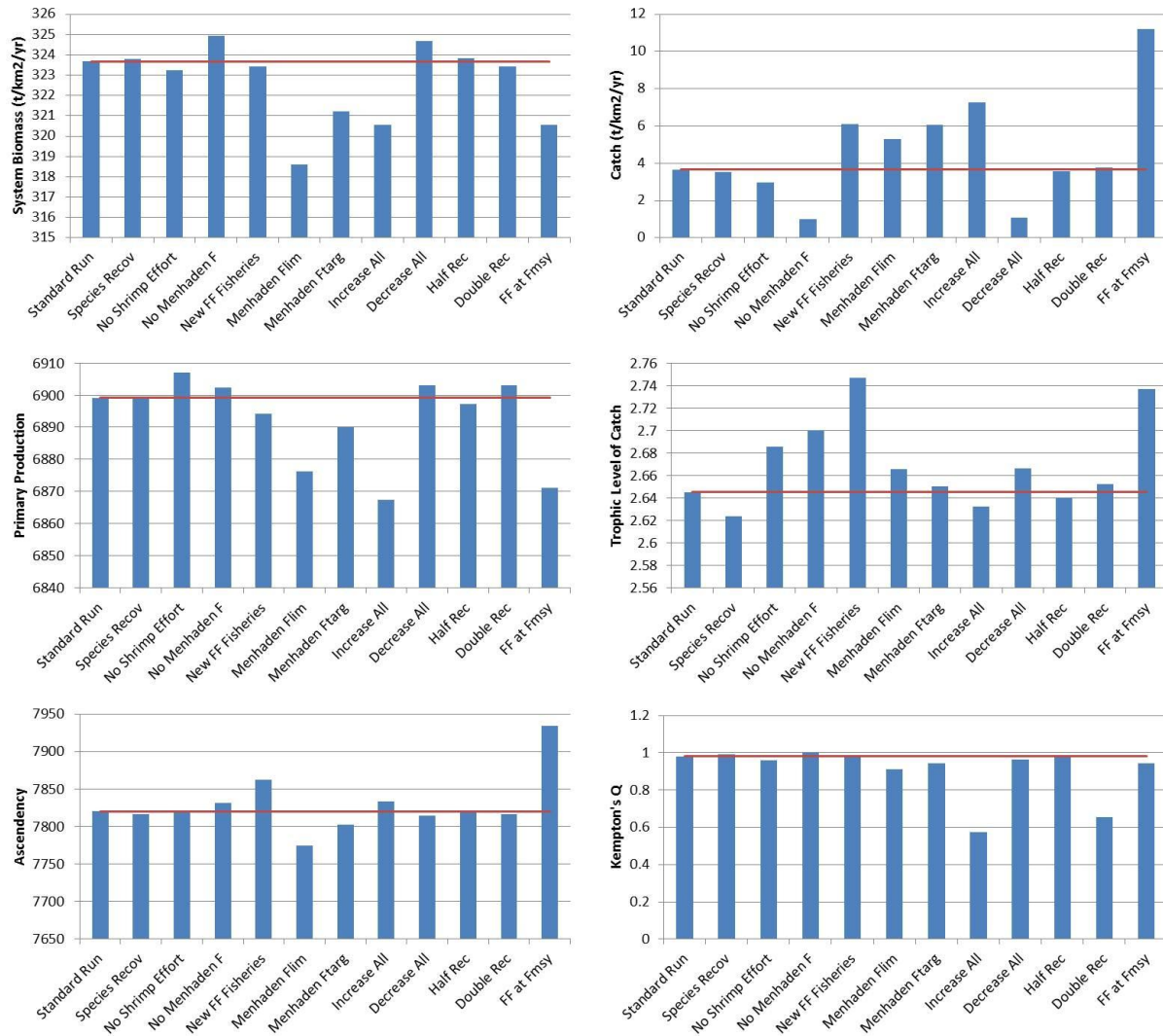
Figure 2.5. Comparison of ecosystem metrics among different Ecosim runs. Metrics were calculated for 2109, the last year of the simulation. The solid red line is the reference level from the standard run.

Network analysis in Ecosim allowed for further comparison among Ecosim runs. Seven indices of maturity (Odum 1971) were used to develop a maturity index following Christensen (1995). An additional metric, Finn's Cycling Index, was also added. The overall trends in maturity, relative to the standard run, for each of the Ecosim scenarios are presented in Table 2.10. Four runs resulted in an increase in ecosystem maturity, and therefore stability, based on these indices: species recovery, no menhaden F, decreasing all fisheries and halving recreational fishing rates. The remaining runs (no shrimp effort, new forage fish fisheries, forage fish fisheries at F_{MSY}, increasing menhaden fishing to F_{targ} and F_{lim}, increasing all fisheries, and doubling recreational fishing rates) all resulted in a decrease in system maturity. Not all indices used for the maturity index, in particular path length and dominance of detritus, fit with the overall trend (Table 2.10).

Scenarios were also compared using Ulanowicz's (1986) metric of ecosystem growth and development, ascendency (Figure 2.5). Six runs showed an increase in ascendency: no shrimp effort, no menhaden F, new forage fish fishing (at both low and high levels), increasing all

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fisheries, and halving recreational fishing rates (Figure 2.5). The other five runs showed a decrease in ascendency: species recovery, increasing menhaden fishing to F_{targ} and F_{lim}, decreasing all fisheries and doubling recreational fishing rates (Figure 2.5).

Table 2.10. Trends in select maturity indices. The column labeled "trend with maturity" shows the expected trend in the index as maturity increases. Arrows represent an increase or decrease in maturity from the standard run.

Index	Trend with Maturity	Species Recovery	No Shrimp Effort	No Menhaden F	Menhaden Flim	Menhaden Ftarg	Increase All	Decrease All	Half Rec	Double Rec	New FF Fisheries	FF at Fmsy
Diversity (Capacity/Throughput)	+	↓	↓	↑	↓	↓	↓	↑	↓	↓	↑	↓
Biomass/Throughput	+	↑	↓	↑	↓	↓	↓	↑	↑	↓	↓	↓
Finn's Cycling Index	+	↑	↓	↑	↓	↓	↑	↑	↑	↓	↓	↓
Mean Path length	+	↑	↑	↓	↑	↑	↓	↑	↓	↑	↓	↓
Residence Time	+	↑	↑	↑	↓	↓	↓	↑	↓	↑	↓	↓
Biomass/Production	+	↑	↓	↑	↓	↓	↓	↑	↑	↓	↓	↓
Dominance of Detritus	+	↓	↓	↑	↑	↑	↑	↓	↑	↓	↑	↑
Primary Production/Biomass	-	↑	↓	↑	↓	↓	↓	↑	↑	↓	↓	↓
Overall Trend in Maturity		↑	↓	↑	↓	↓	↓	↑	↑	↓	↓	↓

All scenarios were run through 2109, 100 years after the end of the current time series. Figure 2.6 shows the percent change in biomass of species groups from 2009 to 2109 under the standard run, in which all fishing mortality rates were maintained at their current (2009) levels. Most groups showed little change relative to their 2009 biomass (Figure 2.6). Red snapper, however, showed a nearly 200% increase in biomass under continued fishing at current levels (Figure 2.6). Tunas, groupers, black drum, spot and blue crab displayed decreasing trends in biomass of 25% or more, while sea catfishes and penaeid shrimp displayed increasing trends of the same magnitude (Figure 2.6).
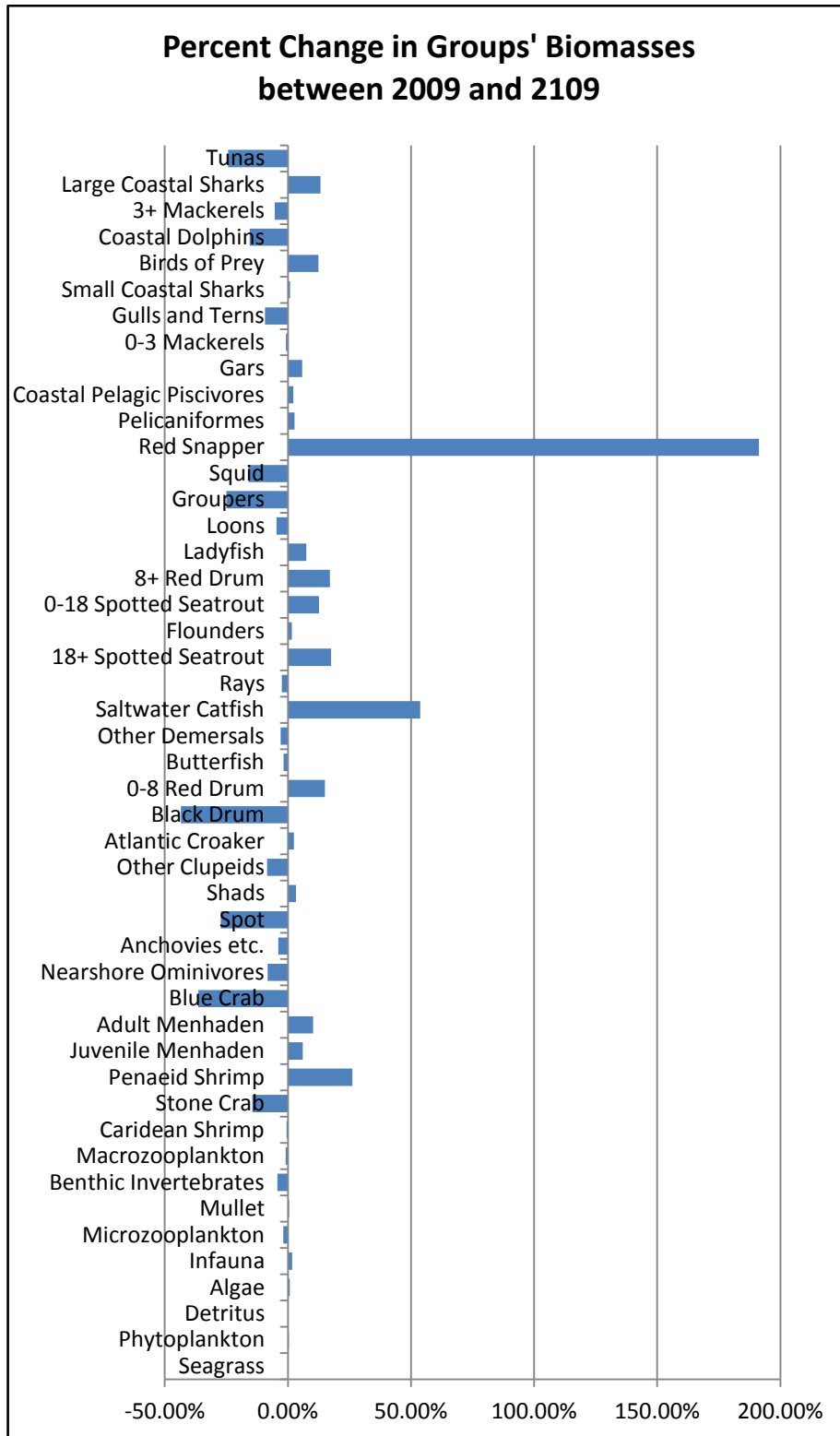
Figure 2.6. Percent change in groups' biomasses between 2009 and 2109 using the standard run. Groups are arranged by trophic level, with the highest trophic level at the top of the figure.

The impact on important recreational fishery species of halving and doubling recreational fishing rates (from the value in 2009) was examined. The top 5 recreationally caught groups in

this model of the GoM are adult spotted seatrout, adult red drum, other demersals, black drum and red snapper. Some of these species and species groups (red drum, red snapper, spotted seatrout, groupers) are regulated federally or by state due to concerns of overfishing. Doubling recreational fishing mortality rates resulted in a decrease in the biomass from the standard run of all of these important recreational species (red bars, Figure 2.7). Halving recreational fishing mortality rates, predictably, had the opposite effect on these groups. Red drum, in particular, was greatly affected by changes in recreational fishing mortality, showing a nearly 150% increase in biomass when fishing rates were cut in half and a 100% decrease in biomass when fishing rates were doubled (Figure 2.7). The change in red snapper biomass from the baseline scenario was minimal because red snapper biomass already increased greatly by the end of the standard run.
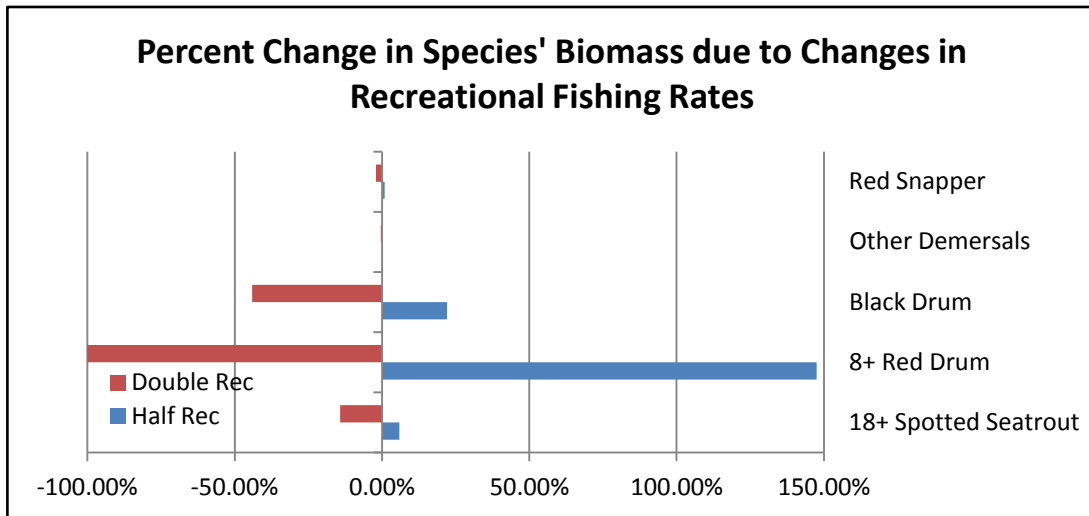
Figure 2.7. Percent change in groups' biomass relative to the standard run due to a doubling (red bars) or a halving (blue bars) of recreational fishing mortality rates.

A simulation was also run, following Walters et al. (2008), in which fisheries for red drum, red snapper and groupers were shut down after 2009, while other groups' fishing levels remained constant. Red drum showed a large increase in biomass from the baseline scenario when directed fishing ceased (Figure 2.8), indicating that continued fishing of menhaden, shrimp and other prey groups at current fishing levels would not impact red drum recovery. Red snapper also showed an increase from baseline, but groupers showed a slight decrease when fishing was halted (Figure 2.8). When menhaden fishing was increased to F_{targ} and F_{lim} levels, recovery of red drum and red snapper was somewhat less, though red drum still showed a nearly 250% percent increase from baseline levels.
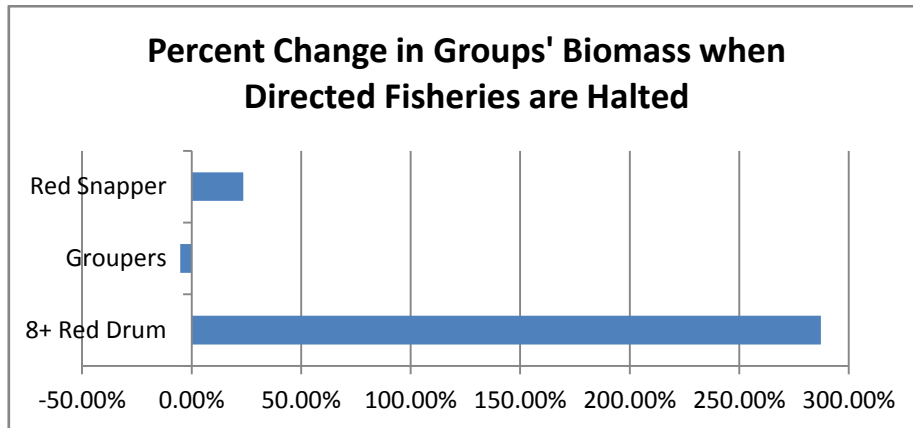
Figure 2.8. Percent change in red snapper, groupers, and adult red drum biomasses from the base run when fisheries for these species are halted.

The role of Gulf menhaden in the northern GoM ecosystem was examined via the mixed trophic impact calculation in Ecopath as well as through multiple Ecosim scenarios. The mixed trophic impact (MTI) of adult Gulf menhaden on other model groups is shown in Figure 2.9. Ecopath calculates the MTI to show the impact that a slight increase in biomass of one group (in this case adult menhaden) will have on other groups in the model. Important menhaden predators[1] showed a positive impact from an increase in menhaden biomass, as did the purse seine fishery (Figure 2.9), which principally targets menhaden. Adult menhaden showed a negative impact on themselves due to increased within-group competition (Christensen et al. 2008).

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[1] Important menhaden predators are designated here as those groups having a diet of 10% or more menhaden and include: birds of prey, pelicaniformes, large coastal sharks, small coastal sharks, gars, red snapper, ladyfish, adult red drum, adult spotted seatrout, juvenile mackerels, and squid.
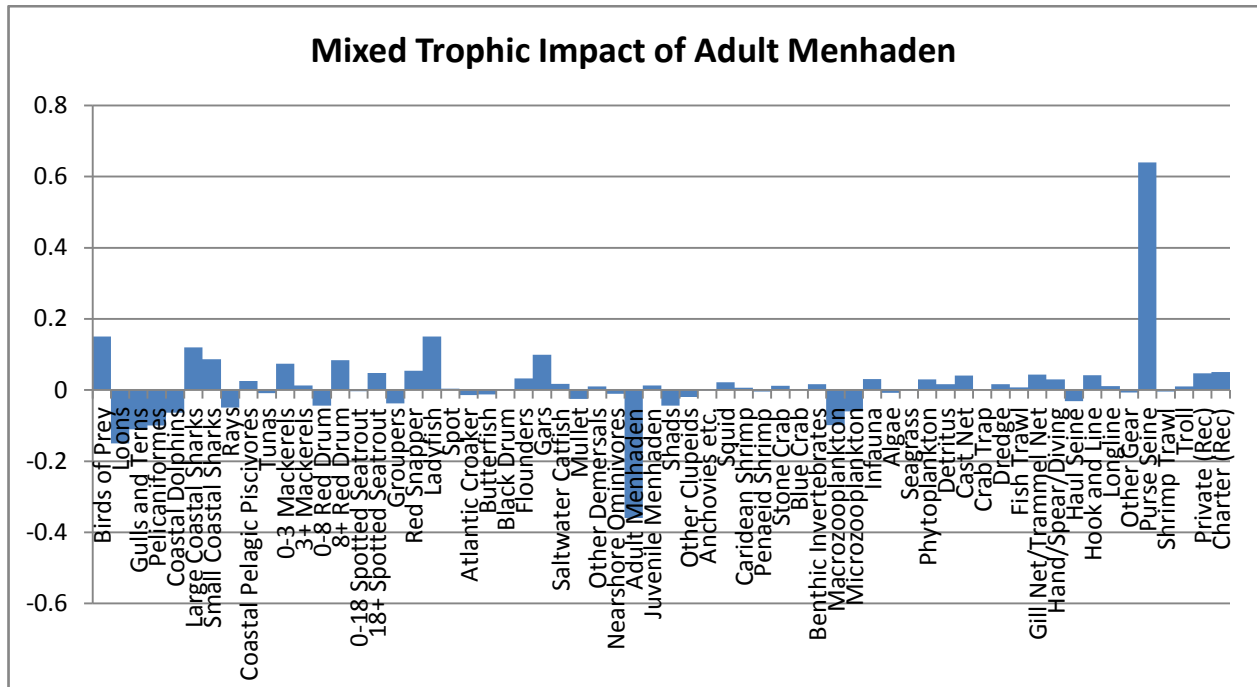
Figure 2.9. Mixed trophic impact plot of adult Gulf menhaden, showing the impact that a small increase in menhaden biomass has on other ecosystem groups. Impacts are relative, but comparable among groups.

Menhaden fishing mortality levels were adjusted to examine the impact of the fishery on menhaden predators as well as on recreational and commercial catches of other species. Results were compared to the standard run, which maintained all fisheries at their 2009 levels (F = 0.35 for menhaden). Elimination of the menhaden fishery generally had a positive impact on predators whose diet was composed of 10% or more menhaden (blue bars, Figure 2.10b). Increases in predators' biomass from the standard run ranged from 3 − 20%. Two menhaden predators, squid and adult spotted seatrout showed a decline in biomass from a reduction in the menhaden fishery. When menhaden fishing mortality was increased from the baseline value of F = 0.35 to the fishing mortality target level of 0.94, menhaden predators in general, showed a decrease in biomass (red bars, Figure 2.10b). When fishing mortality was increased to the F limit level of F = 1.46, a decline of 30% or more was seen in some predators (green bars, Figure 2.10b).

In terms of commercial and recreational fisheries, menhaden fishing mortality rates had varying impacts. When menhaden were fished at F_{targ}, their direct catches increased by about 90% from baseline (red bars, Figure 10a); however, when they were fished at F_{lim}, catches only increased by about 60%. Black drum, red drum, red snapper, other demersals, and benthic invertebrates all showed an increase in recreational or commercial catches (or both) due to elimination of the menhaden fishery and a corresponding decrease in catches when menhaden were fished at the F target and F limit levels (Figure 2.10 c & d). Black drum showed a greater than 50% decline in both commercial and recreational catches when menhaden were fished at the F limit level (Figure 2.10 c & d). Spotted seatrout, blue crab and penaeid shrimp all showed a decrease in catches when menhaden fishing was eliminated and an increase in catches when menhaden fishing increased (Figure 2.10 c & d).
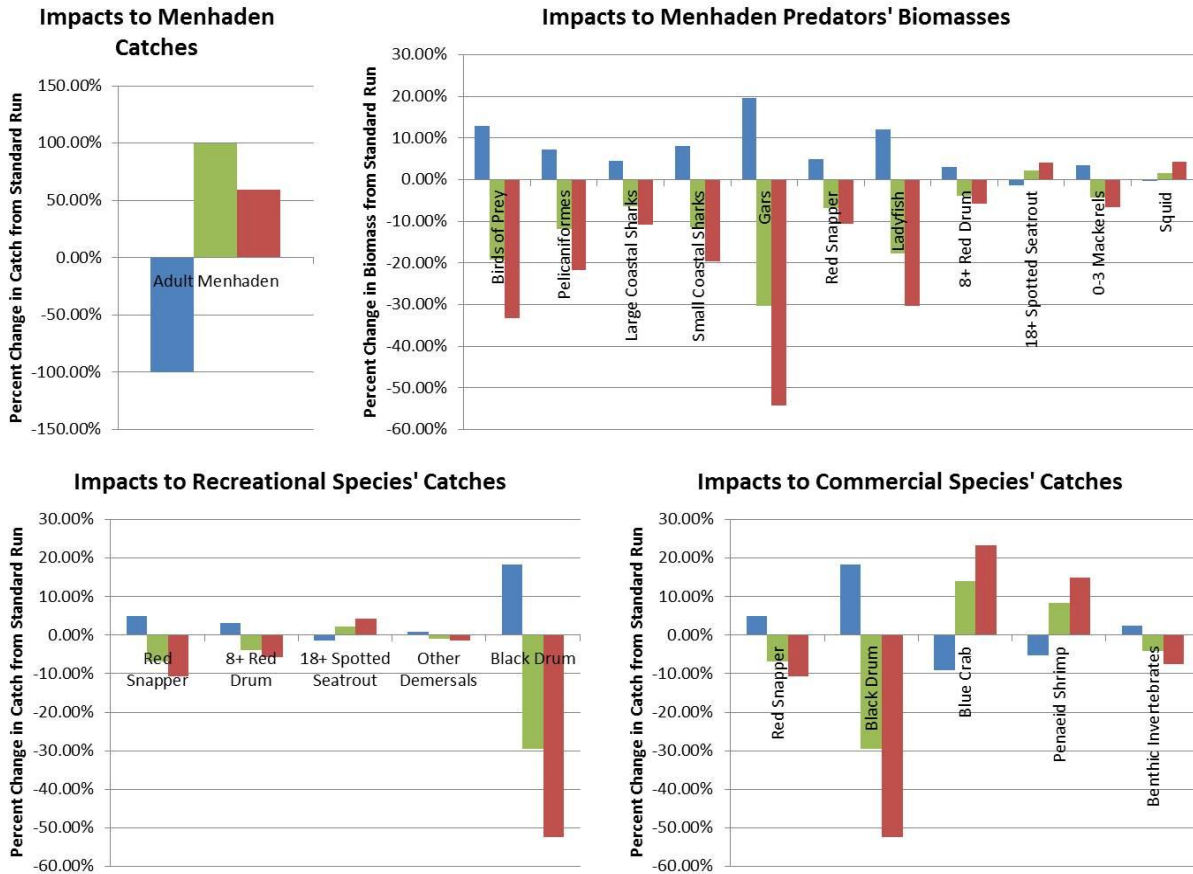
Figure 2.10. Ecosystem impacts under different levels of menhaden fishing: Blue, F = 0; Green, F = 0.94 (F_{targ}); Red, F = 1.46 (F_{lim}). a.) percent change in menhaden catches b.) percent change in predator biomasses c.) percent change in recreational catches d.) percent change in commercial catches.

The impact that the opening of new forage fish fisheries would have on the northern Gulf of Mexico ecosystem was also examined. Implementing new forage fish fisheries, whether at a low level of F = 0.3 or at a higher F_{MSY} level, generally resulted in a decrease in biomass of forage fish predators[2] (Figure 11a). However, several predators demonstrated a counterintuitive response. Juvenile spotted seatrout, adult red drum and large coastal sharks all showed an increase in biomass following the implementation of new forage fish fisheries (blue bars, Figure 11a). Gars, red snapper and small coastal sharks all showed an increase in biomass at low levels of forage fish fishing, but showed a decrease in biomass when forage fish fishing was raised to F_{MSY} levels (Figure 11a). Commercial and recreational fisheries show varied responses to forage fish fishing. Adult spotted seatrout and red drum catches (recreational) appeared to benefit from the advent of new forage fish fisheries at both low and high levels (Figure 2.11b). Black drum and red snapper showed a slight increase in recreational catches at low levels of forage fish fishing, while black drum catches declined under higher levels of forage fish catch (Figure 2.11b). Recreational catches of other demersals showed little change under either scenario

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[2] Forage fish predators examined were those consuming 25% or more of the combined forage fish groups and include: birds of prey, gulls and terns, pelicaniformes, loons, large coastal sharks, small coastal sharks, adult mackerels, gars, coastal pelagics, red snapper, ladyfish, adult red drum, juvenile mackerels, juvenile spotted seatrout, and squid.

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(Figure 2.11b). Menhaden and penaeid shrimp catches appeared to benefit under the implementation of fisheries for anchovies, other clupeids and shads (new forage fish fisheries, Figure 2.11c). Both groups also showed a substantial increase when all forage fish groups were fished at their F_{MSY} levels (Figure 2.11c). Blue crab and black drum fisheries suffered when all forage fish groups were fished at their F_{MSY} levels (Figure 2.11c).
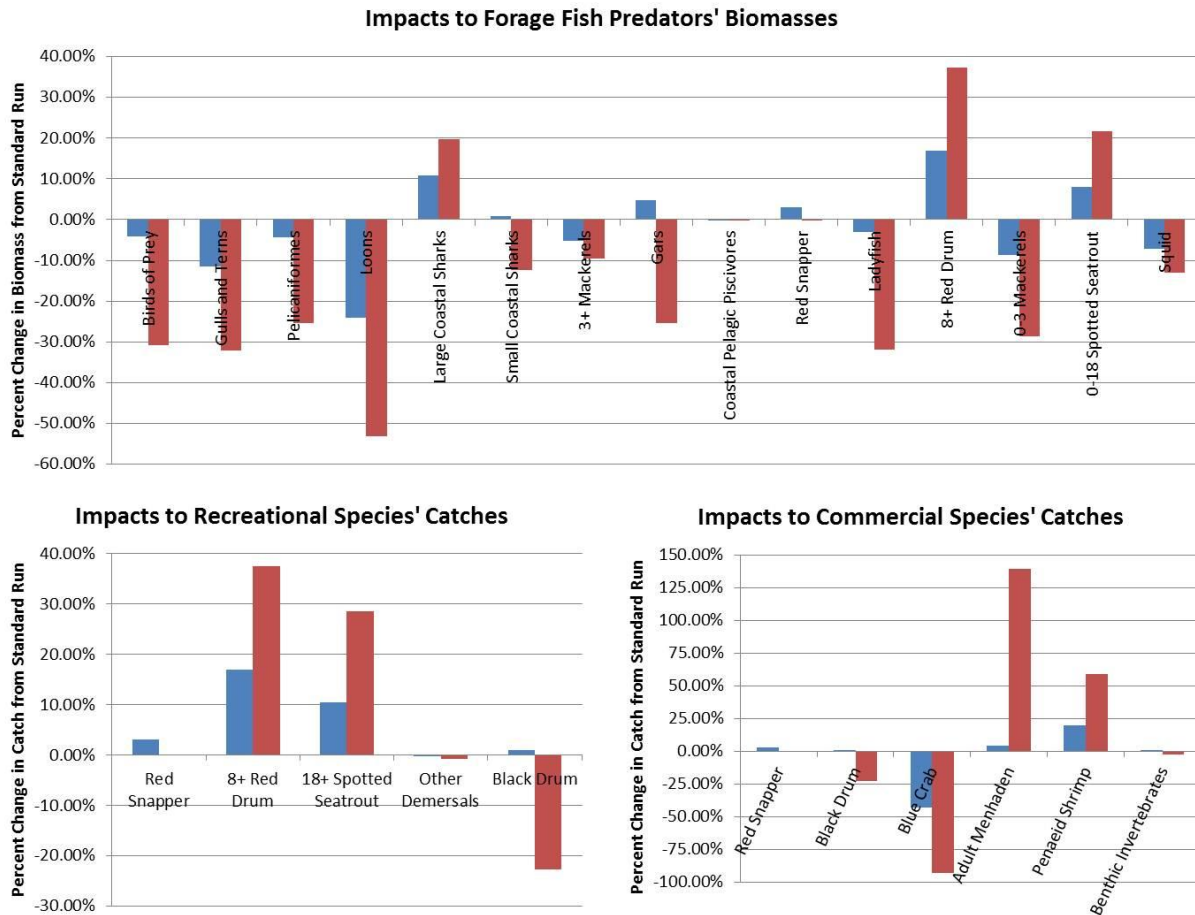
Figure 2.11. Ecosystem impacts due to different levels of forage fish fishing: Blue: anchovies, other clupeids, and shads fished at F = 0.3, all other groups fished at base level; Red: all forage fish groups (menhaden, anchovies, other clupeids, shads) fished at their F_{MSY} levels. a.) percent change in forage fish predators' biomasses, b.) percent change in recreational catches, c.) percent change in commercial catches.

11.) *Management Strategy Evaluation – Deterministic Results*

The management strategy evaluation batch module tool in Ecosim was used to evaluate the impact of a range of fishing mortality rates for forage fish groups on other model groups. Under deterministic constant fishing mortality rules, the biomass of all forage fish groups (menhaden, anchovies, shads, other clupeids) declined as fishing mortality rates increased (Figure 2.12). However, menhaden showed the slowest decline and was able to sustain the highest fishing level, while the other clupeids group declined the fastest and could only sustain a much lower fishing level (Figure 2.12). Biological benchmarks and reference points were calculated for these four forage fish groups (Table 2.11) using the deterministic constant fishing mortality scenarios.

Menhaden F_{MSY} was estimated at 1.05, while F_{MSY} for the other groups ranged from 0.55 to 0.7. The ratio of B_{MSY} to B_0 averaged 55% for all groups.
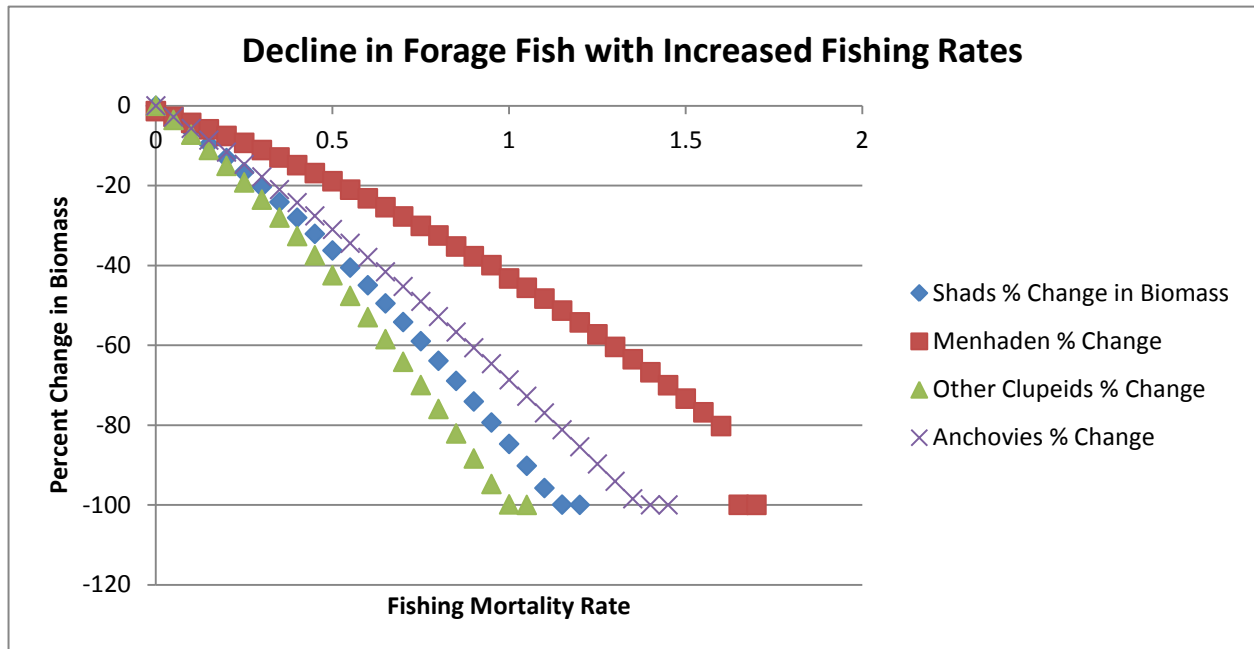
Figure 2.12. Percent decline in forage fish groups' biomass associated with different fishing mortality rates under deterministic conditions.

Table 2.11. Reference points derived for different forage fish groups using constant F rates under deterministic conditions.

Benchmark	Menhaden	Anchovies	Clupeids	Shads
MSY	5.02	1.16	1.57	0.59
B_{MSY}	4.72	1.66	2.85	0.99
F_{MSY}	1.05	0.7	0.55	0.6
B_0	8.32	3.03	5.45	1.79
$B_{MSY}:B_0$	0.57	0.55	0.52	0.55

The impact of forage fish fishing on other model groups varied according to which forage fish group was fished and in general, these impacts were exaggerated at higher fishing levels (Figure 2.13). Percent change in groups' biomasses is relative to their biomass when no forage fish fishing was occurring. In this model, seabirds, marine mammals, and (non-forage fish) teleosts responded negatively to fishing for menhaden, anchovies and shads at all fishing levels (Figure 2.13). Seabirds reacted more strongly to changes in menhaden and anchovy fishing, while marine mammals reacted more strongly to changes in anchovy and shad fishing and teleosts only showed a strong response to changes in menhaden fishing (Figure 2.13). All three predator groups showed a positive impact when other clupeids were fished (Figure 2.13). Elasmobranchs only decreased when menhaden were fished and showed a positive reaction when other forage fish groups were fished (Figure 2.13). Non-target forage fish generally showed an increase in biomass, except for a small negative reaction to low levels of anchovy fishing (Figure 2.13). Other animals in the model (benthic and planktonic invertebrates) demonstrated a positive

impact from menhaden, anchovy and other clupeid fishing, but a slight negative impact from shad fishing (Figure 2.13).
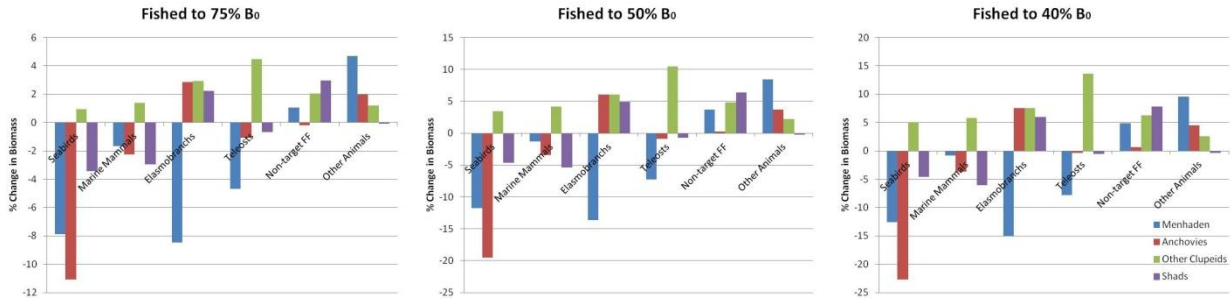
Figure 2.13. Average impacts to ecosystem groups (aggregated functionally) as a result of different levels of target forage fish fishing. Blue bars refer to fishing of menhaden, red bars to fishing of anchovies, green bars to fishing of other clupeids, and purple bars to fishing of shads.

When the response of forage fish predators was evaluated independent of other model groups, the impact of forage fishing became clearer, as one would expect. In general, there was a negative linear response between the percent of the target forage fish in a predator's diet and the decline in that predator's biomass (Figure 2.14). This relationship became more negative as forage fish fishing levels increased.

Response of Predators to Changes in Forage Fish Abundance
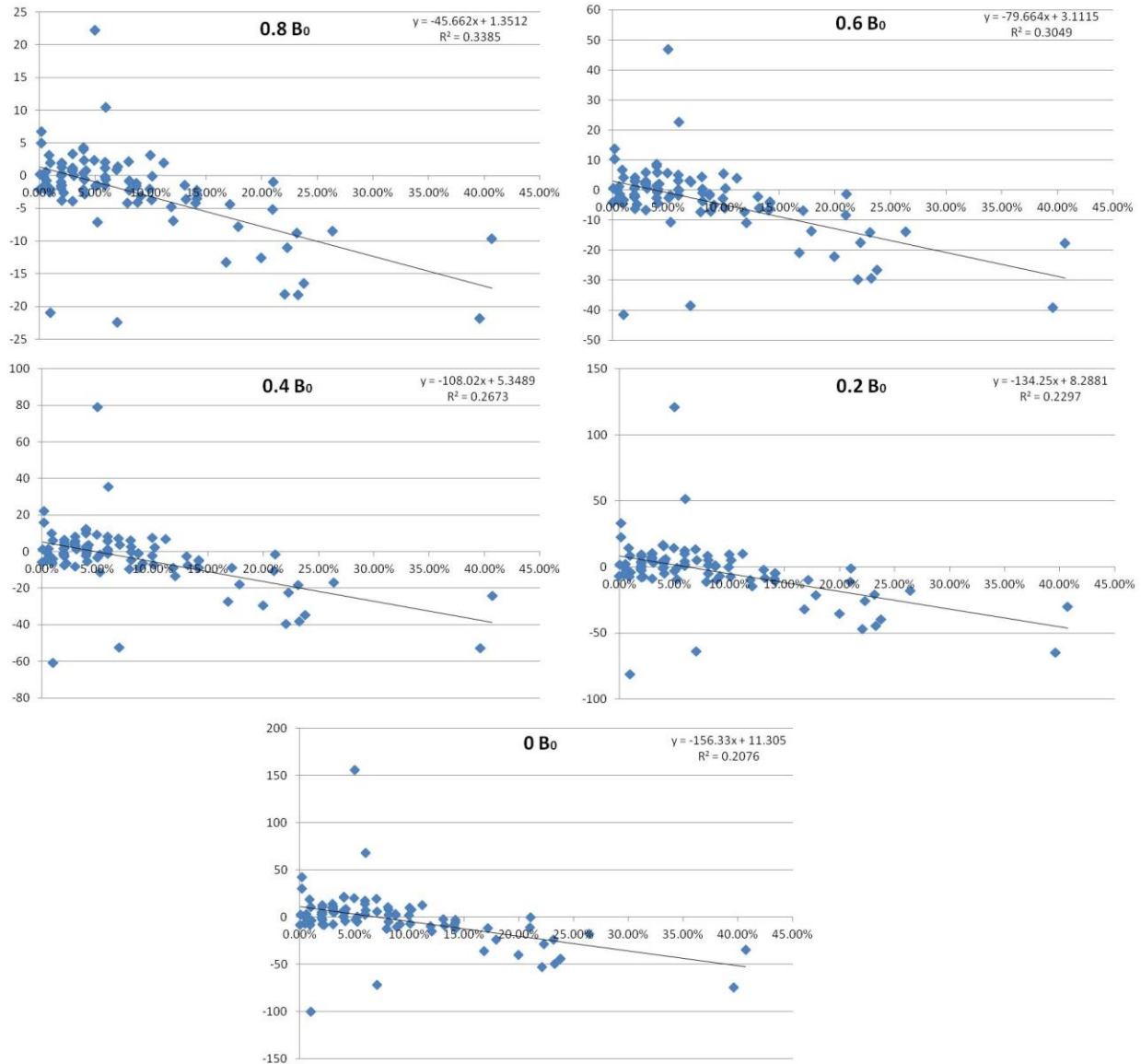
Figure 2.14. Predator response to forage fish fishing. Horizontal axis measures the percent of the target forage fish in the predator's diet and the vertical axis measures the percent change in the predator's biomass relative to the biomass when no forage fish fishing occurred. Each graph shows different levels of forage fish fishing (e.g. $0.8B_0$, $0.6B_0$, etc.)

The impact of a constant yield strategy was also evaluated for menhaden. A constant yield similar to current catch levels of approximately 3.0 $mt/km^2/yr$ did not result in collapse of the menhaden fishery. A decline was seen, however, in some menhaden predators, relative to their biomass when no menhaden fishing was occurring (Figure 2.15). Using a constant yield strategy that approximated MSY (derived from the constant F strategy outlined above) did result in a collapse of the menhaden fishery. The results further indicated that the menhaden fishery could be sustainable under a constant yield strategy up to a yield of approximately 4.5 $mt/km^2/yr$.
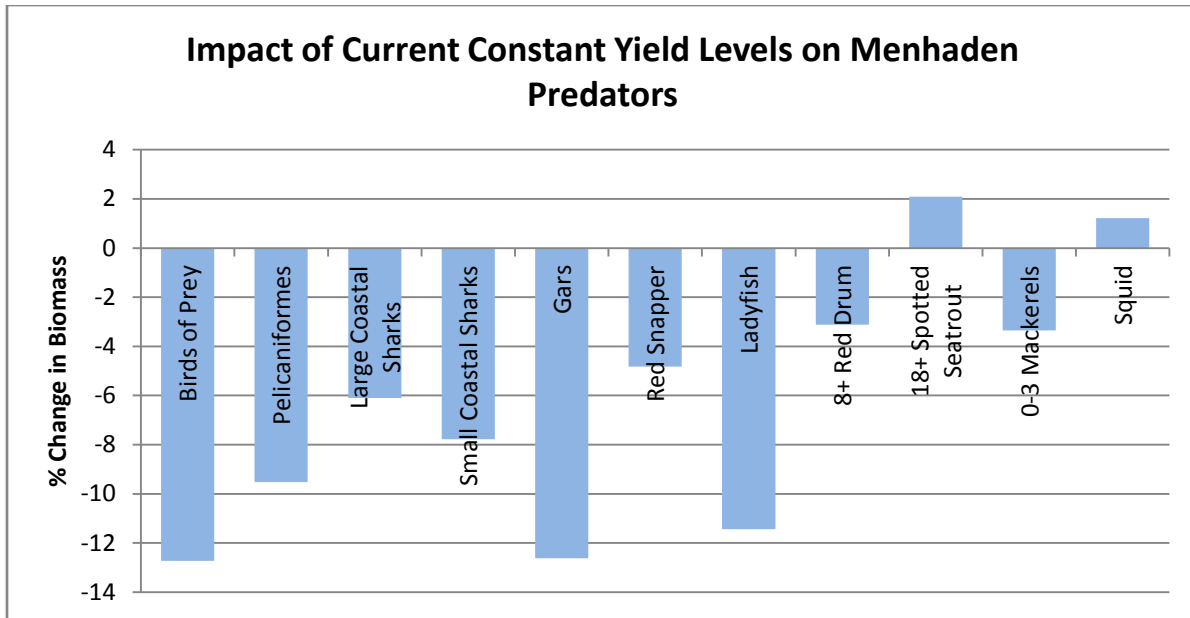
Figure 2.15. Percent change in menhaden predators' biomasses (relative to their biomass when no menhaden fishing was occurring) resulting from a constant yield harvest strategy equivalent to current fishing levels.

12.)   Management Strategy Evaluation – Stochastic Results

Harvest control rules, incorporating stochasticity were tested on all four forage fish groups in the model. Each harvest control rule (constant fishing mortality, 20% minimum biomass limit step function, 40% minimum biomass limit step function, 20% minimum biomass limit hockey stick function, 40% minimum biomass limit hockey stick function) was tested at 50% F_{MSY}, 75% F_{MSY}, and 100% F_{MSY}. The minimum biomass limits and MSY benchmarks were derived from the deterministic constant fishing mortality results reported in Table 2.11. Fishing at 50% of F_{MSY} resulted in higher relative biomass (79 – 96% of the unfished biomass) for all forage fish groups and across all harvest control rules (Figure 2.16a). In contrast, only 65 – 87% of the unfished forage fish biomass remained at the 75% F_{MSY} level (Figure 2.16b). At the 100% F_{MSY} level, the constant F strategy resulted in collapse for two groups, anchovies and menhaden, and very low median biomasses relative to unfished levels for the other two groups (Figure 2.16c). Even the most conservative strategy, the 40% B_{lim} hockey stick rule, resulted in a reduction of forage fish biomasses to between 65% and 80% of B_0 when fished at 100% F_{MSY} (Figure 2.16c). Across all fishing levels, the hockey stick control rules consistently resulted in a higher median biomass for all forage fish groups (Figure 2.17). The constant F strategy performed approximately the same as the step functions at the 50% and 75% F_{MSY} levels (Figure 2.16), but resulted in much lower median forage fish biomass at the 100% F_{MSY} level (Figures 2.16 & 2.17).

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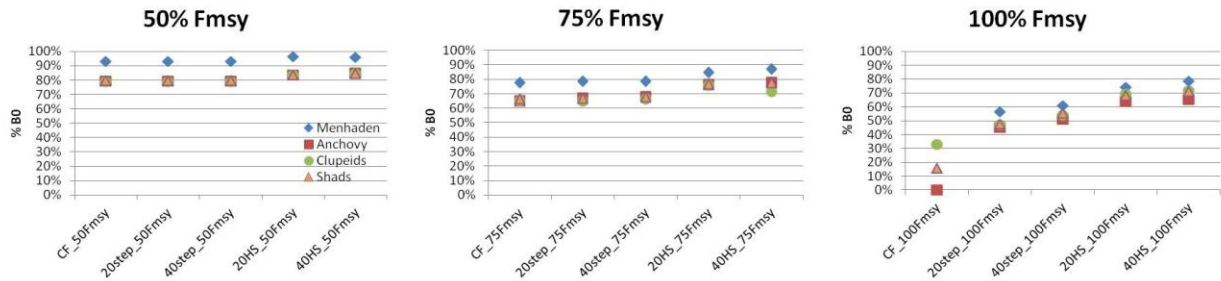
Figure 2.16. Median forage fish biomass (median at year 50 of 100 simulations) as a percentage of the unfished biomass for each harvest control rule at each F_{MSY} level. Blue diamonds – menhaden, red squares – anchovies, green circles – other clupeids, orange triangles – shads.
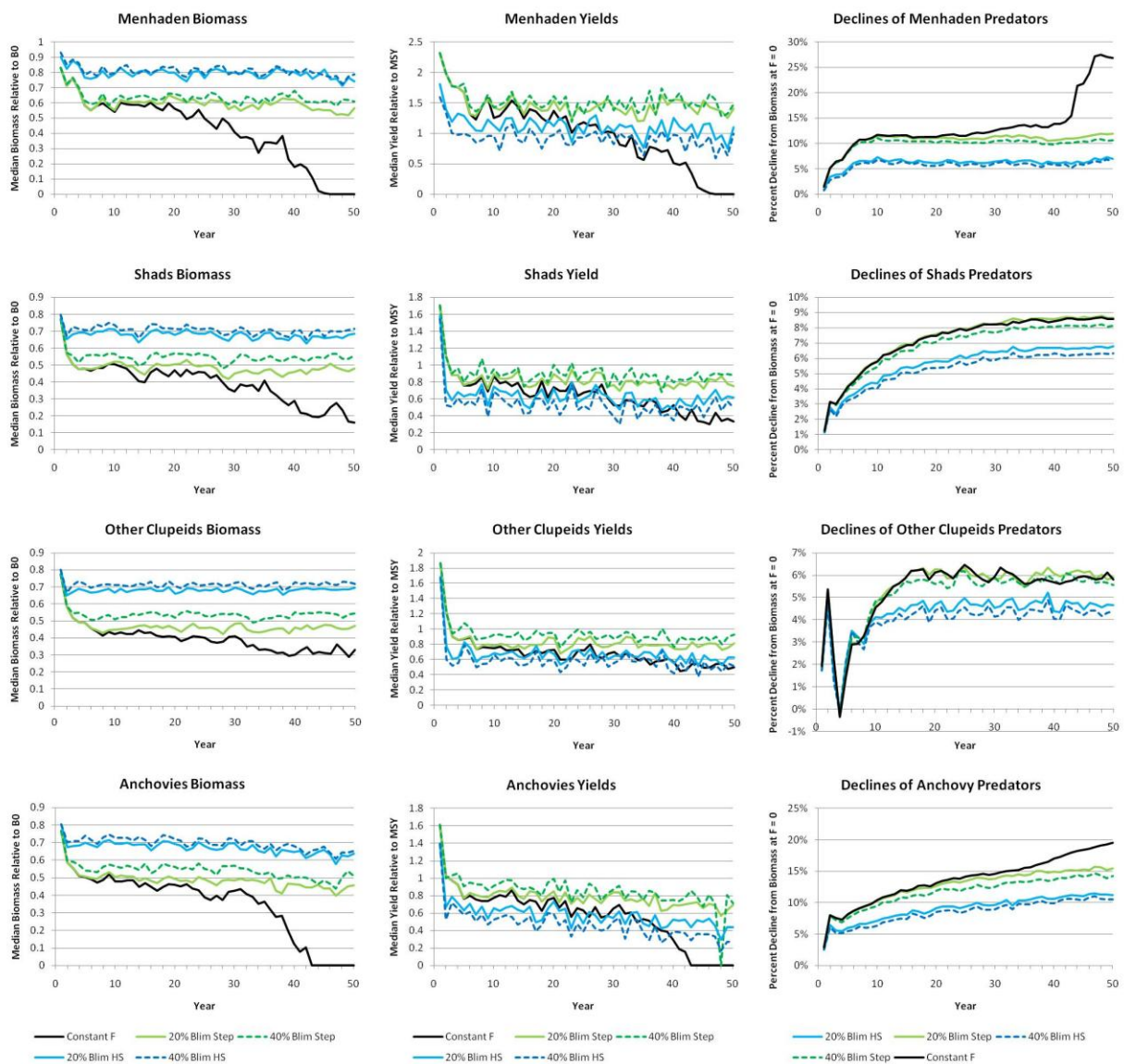
Figure 2.17. Time series of biomass, yields and predator declines for each forage fish group. Harvest strategies are all shown at 100% F_{MSY} levels.

In looking at how these same harvest control rules impacted forage fish yields, increased fishing mortality generally resulted in increased yield, though this was not always the case (Figure 2.18). Fishing at the 75% F_{MSY} level consistently resulted in higher yields across all harvest strategies when compared to fishing at the 50% F_{MSY} level (Figure 2.18). Fishing at 100% F_{MSY} resulted in similar or lower yields than fishing at 75% F_{MSY}, depending on the harvest control rule used (Figure 2.18). Using the constant F strategy at 100% F_{MSY} resulted in lower yields than fishing at either 75% or 50% F_{MSY} due to fishery collapses at the 100% F_{MSY} level (Figures 2.17 & 2.18). At 100% F_{MSY}, the step functions consistently resulted in higher yields than either the constant F or hockey stick functions (Figure 2.17) and did not result in fisheries collapse.
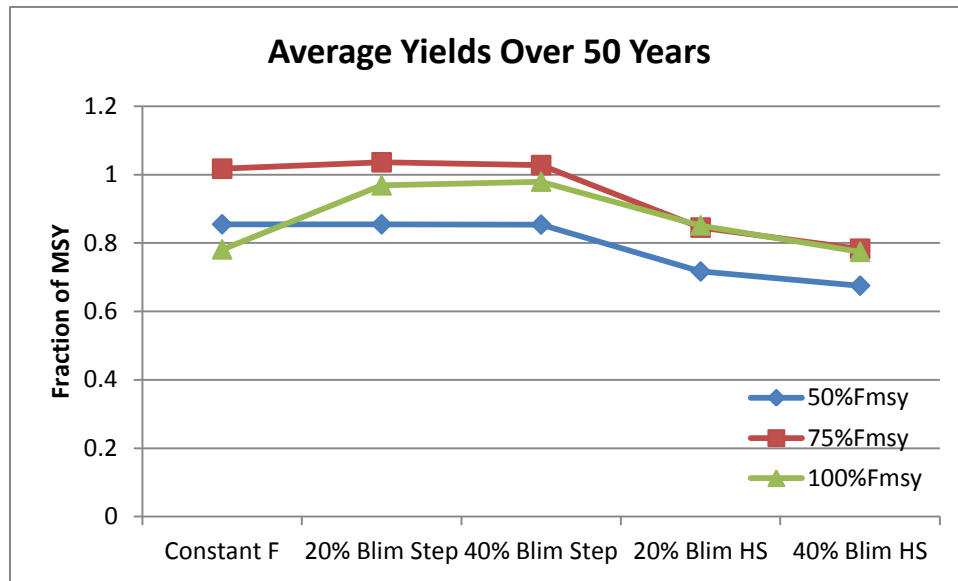
Figure 2.18. Average forage fish yields over 50 years and 100 simulations and across all forage fish groups. Yields are represented as a fraction of MSY.

Although yields were generally higher at the 75% and 100% F_{MSY} levels, the risk of collapse of the forage fish groups at these levels was also greater (Figure 2.19). At the 50% F_{MSY} level, no forage fish group collapsed in any of the 100 simulations for any of the harvest strategies (Figure 2.19). At the 75% F_{MSY} level, there was a low (i.e. < 20%), but non-zero chance of collapse for all harvest strategies (Figure 2.19). At the 100% F_{MSY} level there was a much greater chance of collapse for all forage fish groups and all harvest strategies (Figure 2.19). The constant F strategy resulted in a 50 – 75% chance of collapse depending on the species, while the less risky, hockey stick strategies resulted in a 20 – 50% chance of collapse at the 100% F_{MSY} level (Figure 2.19).
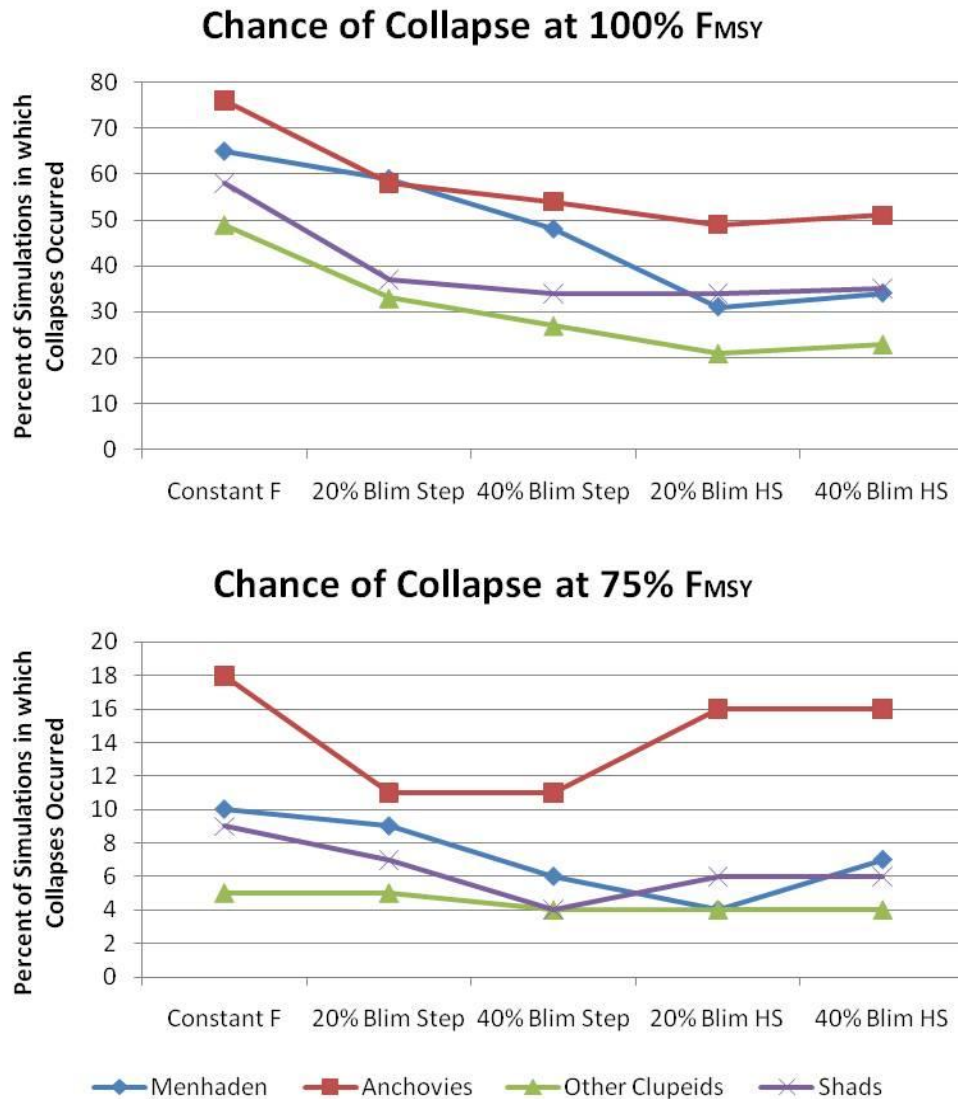
Figure 2.19. Percent of simulations in which forage fish groups collapsed (fell below 10% of the estimated unfished biomass) at a.) 100% F_{MSY} and b.) 75% F_{MSY}.

The response of forage fish predators to different forage fish harvest strategies was also examined. Forage fish predators were again defined as those species consuming 10% or more of the target forage fish. Median predator declines over 100 simulations, averaged for all predator groups and across all four forage fish groups, were closely correlated to the fishing level used (Figure 2.20). The 100% F_{MSY} level resulted in greater predator declines for all harvest strategies than the lower fishing levels (Figure 2.20). The constant F and step functions generally resulted in the same level of predator declines, while the hockey stick functions consistently resulted in lower levels of decline (Figures 2.17 & 2.20). Using the constant F strategy at the 100% F_{MSY} level was particularly risky for predators, resulting in a median 15% decline in predator biomass, as opposed to a 10% decline when using the step function rules or a 7% decline with the hockey stick rules (Figure 2.20). There was also greater disparity with regard to predator decline between the constant F strategy and the step functions when forage fish groups collapsed (e.g. menhaden and anchovies) than when they didn't (e.g. shads and clupeids, Figure 2.17).

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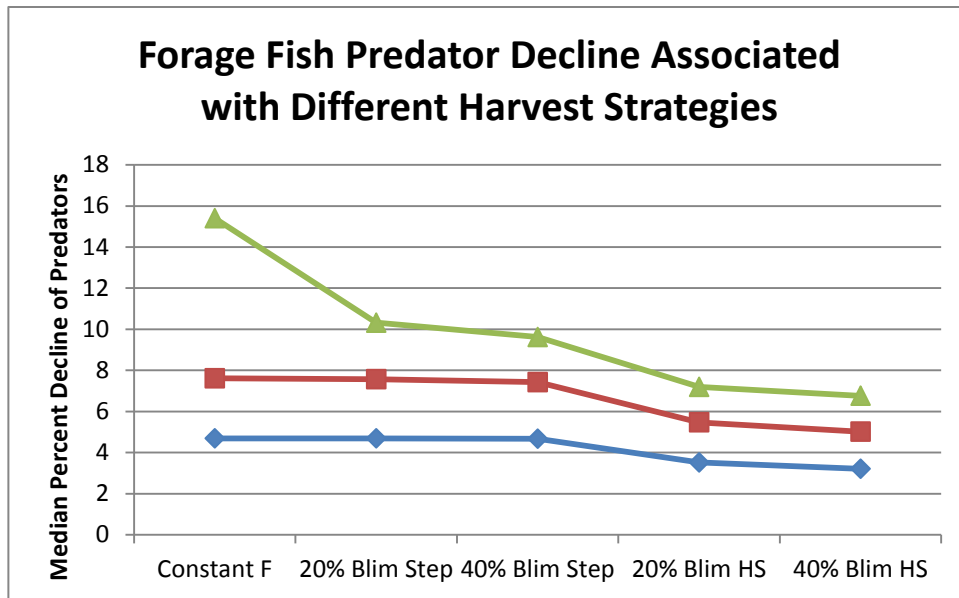
Figure 2.20. Median decline of forage fish predators (those consuming 10% or more of the target forage fish) across 100 simulations, averaged for all four forage fish groups. Green triangles – 100% F_{MSY}, red squares – 75% F_{MSY}, blue diamonds – 50% F_{MSY}.

In order to shed more light on specific predator responses, the decline of each forage fish's predators was examined at the 100% F_{MSY} level (Figure 2.21). The magnitude of response varied by the forage fish species, with menhaden and anchovy predators displaying the greatest impacts. Ladyfish and gars were most impacted by fishing for menhaden, particularly under the constant F strategy (Figure 2.21). Red snapper, small coastal sharks, birds of prey and juvenile mackerels were also heavily impacted under this strategy (Figure 2.21). For anchovies and shads, seabird groups appeared to be the most impacted (Figure 2.21). Due to the high impact of forage fish fishing on seabird populations that is evident from Figure 2.21 as well as from recent studies (e.g. Cury et al. 2011, Pikitch et al. 2012), the response of seabirds was further elucidated (Figure 2.22). Seabird groups consume 3 of the 4 forage fish groups in this model: menhaden, shads and anchovies. For both menhaden and anchovies, the constant F strategy resulted in an approximately 15% greater decline in seabirds than the hockey stick strategies at 100% F_{MSY} (Figure 2.22). For shads, the difference was less, but still apparent.

Percent Decline in Forage Fish Predators at 100% F_{MSY}
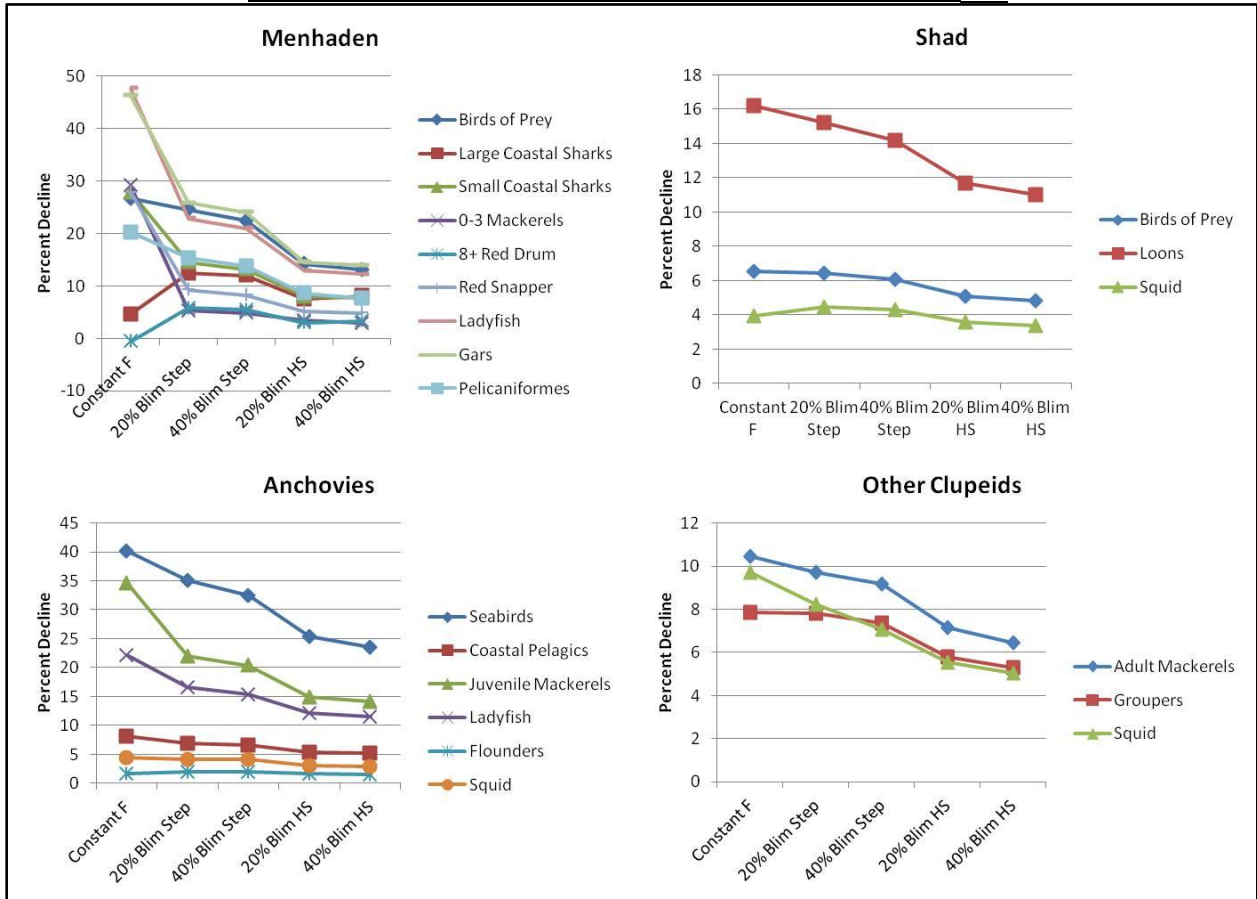
Figure 2.21. Decline of forage fish predators using different harvest strategies at the 100% F_{MSY} level. For anchovies, the seabirds were grouped to improve clarity and include, loons and gulls and terns. For menhaden, those predators showing an increase in biomass when menhaden are fished at 100% F_{MSY} are not shown.

Decline of Seabirds Associated with Fishing Forage Fish Groups at 100% F~MSY~
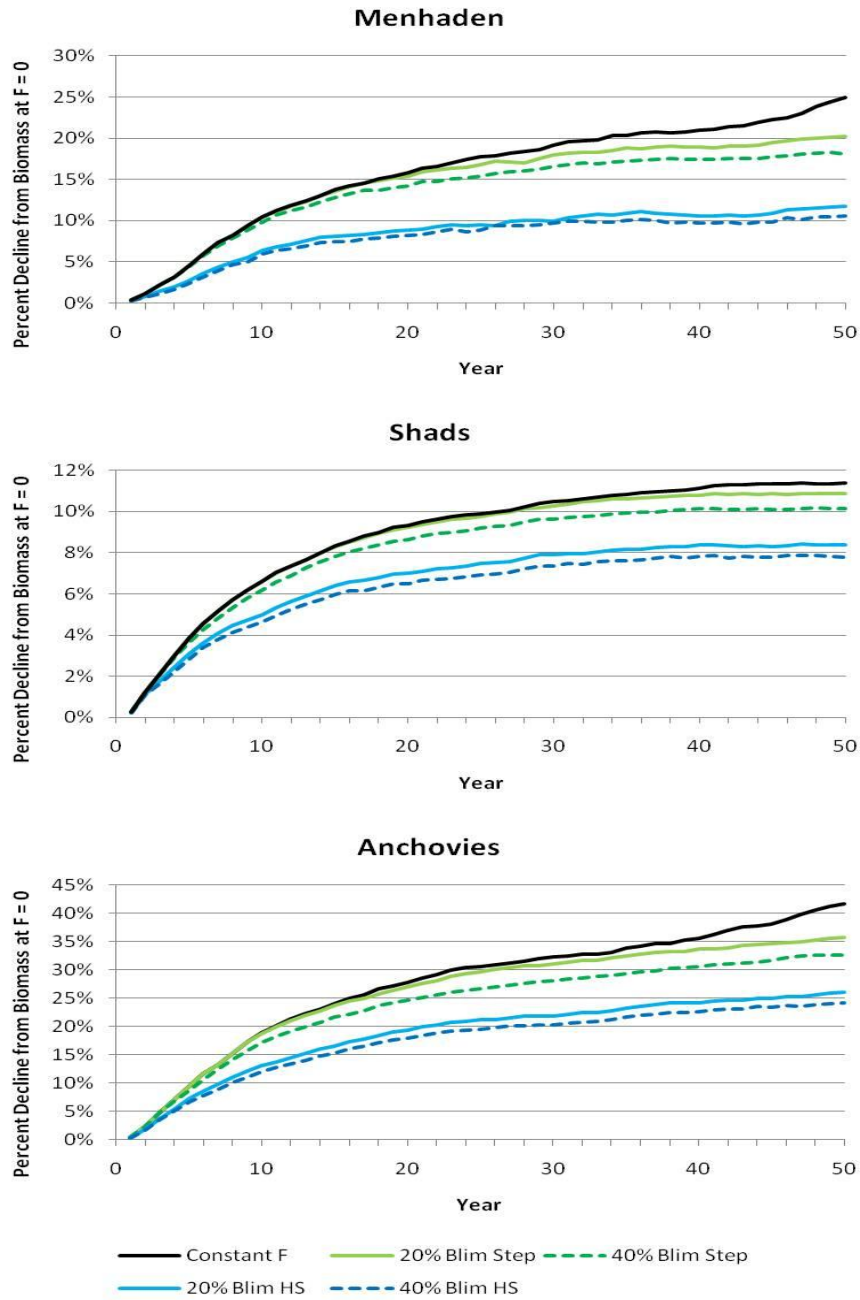
Figure 2.22. Percent decline of seabirds when different forage fish groups are fished. Seabird groups consuming menhaden are birds of prey and pelicaniformes, those consuming shads are birds of prey and loons, and those consuming anchovies are loons and gulls and terns.

Chapter 3: Discussion

1.) Comparison of Ecosystem Structure with other Gulf of Mexico Models

    Several ecosystem indicators are included in EwE to facilitate comparison within and across Ecopath models (Christensen & Walters 2004). Many of these indices are related to the concept of ecosystem maturity (Odum 1971) and can be used to assess how an ecosystem reacts to disturbance. Pristine or undisturbed ecosystems are assumed to be mature, while both natural and manmade disturbances cause the maturity of a system to decrease (Odum 1971, Christensen 1995, Christensen & Walters 2004). The results of the network analysis indicated that the northern Gulf of Mexico is in an immature state with high levels of primary productivity, comparatively few flow pathways and little build-up of age structure. Odum (1971) suggested that in immature systems, primary production would greatly exceed respiration. The Pp/R ratio of this model is 8.5, outside of the common range (0.8 – 3.2) described by Christensen and Pauly (1993). However, it is similar to the value found by de Mutsert (2010) for Breton Sound, Louisiana and within the range estimated by other Gulf of Mexico models, 0.75 (Yucatan Shelf, Mexico, Arreguin-Sanchez et al. 1993) – 15.9 (Celestun Lagoon, Mexico, Vega-Cendejas & Arreguin-Sanchez 2001). The P:B ratio is also fairly high, indicative of a developing system, but again falls within the range of other GoM models, 6.21 (Celestun Lagoon, Chavez et al. 1993) – 64 (Celestun Lagoon, Vega-Cendejas & Arreguin-Sanchez 2001). The overall biomass of the system (324 t/km^2/yr) is close to the estimate of 304 t/km^2/yr found by Vidal (2000) for the entire GoM. Finn's Cycling Index (FCI) represents the proportion of throughput that is recycled within a system; mature systems generally have a higher FCI value. This model has an FCI of 1.99%, which is relatively low compared to other ecosystems. However, Christensen (1995) found that FCI was not always a good indicator of maturity, and did not use it in comparisons among ecosystems. The path length, though, was found to be a good descriptor of flows and cycling and is defined as the total throughput over the sum of total exports and total respiration (Finn 1980, Christensen 1995). Reefs, shelves and upwelling areas tend to have shorter path lengths, while estuaries tend to have longer path lengths (Christensen & Pauly 1993). The model value of 2.28 is towards the middle of the range of other ecosystems, which can be expected given its coastal nature. The average transfer efficiency in this system is 11.4%, similar to the often assumed value of 10% for marine systems (Christensen & Pauly 1993, Lindeman 1942). It was noted that the mean trophic level of the catch (2.64) was relatively low compared to other heavily fished ecosystems (Pauly et al. 1998). This is due to the two largest fisheries, menhaden and shrimp, having low trophic levels. The relatively high biomass of these low trophic level groups in the catch is not, however, a result of "fishing down the food web" as is the case in numerous other ecosystems (Pauly et al. 1998), but is rather a function of target preferences by the fishery. In fact, the trophic level of the catch in the Gulf of Mexico has actually risen slightly since the 1950s (de Mutsert et al. 2008), which appears to be due to an increase in catches of upper trophic level species, rather than to a decline in shrimp or menhaden.

    2.) Comparison of Maturity Indices among Ecosim Scenarios

Odum's (1971) indices of ecosystem maturity were also used to compare Ecosim scenarios within the present model. Odum suggested that ecosystems develop through a series of predictable structural changes, arriving at a fully developed or mature ecosystem in which biomass is maximized and energy utilization is optimized (Odum 1971, Christensen 1995). Scenarios were also compared using Ulanowicz's (1986) metric of ecosystem growth and development, ascendency. Ascendency incorporates growth through system throughput (the sum of flows through all groups) and development through I, the average mutual information. I represents the organization of the system and gives the probability that a flow passes through a given group. Both organization and flows are expected to increase as a system develops, hence an increase in ascendency represents an increase in development. However, Christensen (1995) found an inverse relationship between Odum's attributes of maturity and ascendency. Christensen therefore suggests that Odum's indices of maturity are more closely correlated with stability rather than with growth and development.

Here Christensen's (1995) maturity ranking, based on 7 of Odum's indices of maturity, was used to compare the different Ecosim scenarios. Finn's Cycling Index was also added to the maturity index for use in comparison. Christensen excluded FCI from his index due to its reliance on model parameterization. However, since the present scenarios were based on the same Ecopath model, FCI was deemed appropriate for comparison. Not all indices used for the maturity index, in particular path length and dominance of detritus, followed the overall trend. However, Christensen (1995) demonstrated that these two indices are not as well correlated with the overall trend in maturity as the other indices (i.e. primary production/biomass, biomass/throughput, biomass/production, residence time and diversity). Four runs resulted in an increase in ecosystem maturity, and therefore stability: species recovery, no menhaden F, decreasing all fisheries and halving recreational fishing rates. These results are unsurprising, given that fishing is expected to decrease system maturity (Christensen & Pauly 1998, Christensen & Walters 2004). Although the overall trends for these four scenarios indicated an increase in maturity, as mentioned above, certain indices did not follow the general pattern. The species recovery scenario resulted in a decrease in diversity and dominance of detritus, the opposite of what would be expected as maturity increases. In Ecopath, species diversity is represented by flow diversity. The large increases in red drum populations under the species recovery scenario could actually lead to a decrease in the diversity of flows if a greater proportion of flows were channeled through the red drum group. This could similarly lead to a reduction in the proportion of flows from detritus if red drum were primarily consuming herbivores. Decreasing all fisheries also lead to a decrease in detritivory dominance, likely for similar reasons, that is, an increase in herbivorous species as well as in the piscivores that eat them. Halving recreational effort also lead to a decrease in diversity of flows; similar to the species recovery scenario; halving recreational effort caused a large increase in red drum, which may have channeled flows through this model group. Eliminating menhaden fishing resulted in a decrease in path length, or the average number of groups an inflow or outflow passes through. While path length is expected to increase with maturity, the decrease in path length here makes sense as an increase in menhaden would potentially eliminate less efficient pathways of energy transfer.

The remaining runs (no shrimp effort, new forage fish fisheries, forage fish fisheries at F_{MSY}, increasing menhaden fishing to F_{targ} and F_{lim}, increasing all fisheries, and doubling recreational fishery rates) all resulted in a decrease in system maturity. Notably all scenarios that increased fishing caused a decrease in maturity, a trend previously noticed in other studies (e.g. Christen

1995, Christensen & Pauly 1998, Christensen & Walters 2004). Again, however, not all indices followed the general trend. In particular, all scenarios that increased forage fish fishing increased the dominance of detritus, contrary to what would be expected with a decrease in maturity. This is likely because these scenarios caused an increase in penaeid shrimp biomass. Half of the penaeid shrimp diet is composed of detritus compared to $5 - 20\%$ for forage fish groups, resulting in greater flow from detritus when forage fish groups are reduced. As with a reduction in menhaden fishing, path length did not follow the general trend when menhaden fisheries were increased. Again, this is likely due to their critical role at the middle of the food web. When menhaden biomass decreases, flows must pass though a greater number of groups to reach the same end. Interestingly, elimination of the penaeid shrimp fishery resulted in a decrease in maturity. The trends in the maturity indices for this scenario are not intuitive and are likely a result of the many complex interactions affected by changes in lower trophic levels. The lack of a clear explanation for these trends may also highlight the lack of resolution in the invertebrate and other low trophic level groups in this model.

Changes in ascendency were also evaluated as an alternative index of ecosystem state. Six runs showed an increase in ascendency: no shrimp effort, no menhaden F, new forage fish fishing, increase all fisheries, halving recreational fishing rates, and fishing forage fish at F_{MSY}. The other five runs showed a decrease in ascendency: species recovery, increasing menhaden fishing to F_{targ} and F_{lim}, decreasing all fisheries and doubling recreational effort. The relationship between ascendency and Odum's indices of maturity is not straightforward. Typically, ascendency and Odum's maturity indices are thought to be positively correlated (Christensen 1995). However, in a review of ecosystem goal functions, Christensen (1995) found these two indices to be inversely related. Christensen hypothesized that maturity may be more closely related to ecosystem stability, while ascendency represents growth and development. This explanation may help to address the different trends in ascendency and maturity for the various scenarios seen in this study. Implementing new forage fish fisheries and fishing all forage fish at their F_{MSY} levels resulted in a decrease in maturity but an increase in ascendency. Forage fish play a dominant role in the middle of the food web, transferring energy from primary producers to upper trophic levels. Scenarios that remove biomass of forage fish may actually cause an increase in the diversity of flows through the ecosystem, which could explain the increase in ascendency. Furthermore, depleting several lower trophic level species is likely highly destabilizing for the system, causing changes in the diet composition of predators and changing the ecosystem in potentially unpredictable ways. Several runs did result in a positive correlation between ascendency and maturity, in particular those related to Gulf menhaden. Eliminating menhaden fishing resulted in an increase in maturity and ascendency, while increasing menhaden fishing to F_{lim} or F_{targ} levels resulted in a decrease in both maturity and ascendency. These results point to both the stabilizing role of menhaden in the ecosystem as well as it being an important component of promoting ecosystem growth and maintaining ecosystem organization. Maturity and ascendency are also correlated for scenarios related to recreational fishing effort. Doubling recreational fishing rates resulted in a decrease in maturity and ascendency. This is as expected since the majority of recreationally caught species are in the upper trophic levels and the removal of predators is considered destabilizing (Christensen 1996).

3.) Fisheries Management in the Gulf of Mexico

3.1) Impact of Changes in Recreational Fishing Rates on Important Recreational Fishery Species

Red drum displayed the greatest response to changes in recreational fishing rates. The catch of red drum is prohibited for commercial purposes in the northern Gulf, but recreational catches are allowed. The model estimated the current recreational instantaneous fishing mortality rate for adult red drum to be approximately 0.53. Doubling this fishing mortality rate caused a 100% decline in adult biomass, while halving this rate caused an almost 150% increase in biomass (from the standard run). This suggests that red drum are quite sensitive to changes in fishing pressure and that regulation of the recreational fishing sector is key to their sustainability. In contrast, the other important recreational fishery species had much lower (i.e. ≤ 0.15) fishing mortality rates and therefore did not respond as dramatically to changes in recreational fishing pressure.

Fisheries for red drum, red snapper and groupers are already highly regulated due to historic overfishing or current concerns of overfishing. In order to facilitate full recovery, these species could become even more restricted in the future. These groups are also dependent on menhaden and shrimp, which are heavily fished commercially. The red snapper, grouper and red drum fisheries were shut down to examine their recovery under continued menhaden and shrimp fishing. Red drum showed an almost 300% increase in biomass from the standard run. As with the previous scenario, this indicates that red drum are highly sensitive to fishing pressure and their recovery would not be restricted by a lack of prey. Red snapper also showed an increase in biomass, though not as extreme as red drum. Red snapper was historically overfished in the Gulf and is now regulated under a federal Individual Fishing Quota system (IFQ). It therefore appears that red snapper is not subject to the same fishing pressure as red drum and is not as affected by changes in fishing pressure. Groupers actually declined when fishing was stopped. This result is somewhat puzzling, but likely arises from three factors. First, the fishing mortality rate for groupers in the model is very low, around 0.006, so halting fishing may not have a large impact on the population dynamics. Secondly, grouper biomass declined in the base run from 2009 to 2109; increased predation mortality rates on groupers due to the recovery of red snapper may have exacerbated this decline. Third, groupers may suffer from greater competition due to the massive increase in biomass of red drum and the increase in red snapper. These results are in line with Walters et al. (2008) who found that stock recovery rates for red drum and red snapper under continued menhaden and shrimp fishing were similar to those predicted by single species models. However, Walters et al. also predicted stock recovery for the grouper complex. The current model was not developed to focus on reef habitats important in groupers' life history and therefore may not accurately capture the dynamics of this species complex.

These results, in conjunction with the maturity analysis discussed above, suggest that current recreational fishing rates may be unsustainable. This appears to be particularly true for red drum, whose numbers increased dramatically when recreational fishing rates were cut in half. This scenario and the scenario where red drum fisheries are halted altogether also resulted in an increase in system maturity. Although red drum harvest is prohibited commercially in the GoM, as well as recreationally in federal waters, large numbers are still landed by recreational fisherman in state waters. While bag and size limits do exist, there is no limit to the number of licenses or days fished. In order to prevent overfishing of red drum and other recreationally caught species in the Gulf, catches in the recreational fishery will need to be addressed.

3.2) Impact of Changes in Menhaden Fishing Rates on Predators and Fisheries

Menhaden predators (those with diets of 10% menhaden or more) generally show a 3% – 20% increase in biomass when menhaden fishing was reduced to zero from current levels. Two predators, adult spotted seatrout and squid actually show a slight decrease in biomass (-1.3% and -0.35%, respectively). This is likely due to the fact that these two species groups consume a wide variety of lower trophic level prey, including other forage fish species and shrimp. These other low trophic level groups tend to decline when menhaden biomass increases due to competition for resources. In contrast, increasing menhaden fishing levels to F_{targ} and F_{lim} generally resulted in a decrease in predator biomass of 4 – 30% and 6 – 54%, respectively. Birds of prey, pelicaniformes, small coastal sharks, gars and ladyfish showed the greatest negative effects. Again, spotted seatrout and squid show the opposite trend, increasing slightly in biomass at higher menhaden fishing levels. This is most likely a result of an increase in other prey sources as menhaden biomass declines.

When menhaden fishing was halted, red drum and red snapper populations increased by 5% or less from the base run. In terms of recovery of these vulnerable groups, it appears that halting direct catches is more effective than halting fisheries for their prey, given current menhaden harvest levels. Continued menhaden fishing at current rates does not appear to impact the recovery of these species. However, an increase in menhaden fishing to target or limit levels without a subsequent decrease in fishing mortality for red drum and red snapper may cause a 4 – 11% decline in these two species.

Changes in recreational catches reflected the changes in biomass outlined above for those species that consume menhaden (e.g. red snapper, red drum and spotted seatrout). Black drum catches appeared to be greatly affected by changes in menhaden fishing pressure, even though this species does not consume menhaden. This can be explained by two factors, the first, is that black drum consume over 70% benthic invertebrates, which increased with a reduction in menhaden fishing. The second is that black drum experienced decreased predation mortality when menhaden biomass increased. Therefore an increase in their prey and a reduction in predation mortality allowed black drum and therefore their catches to increase substantially when menhaden fishing was halted. In terms of commercial catches, black drum and red snapper catches tended to increase when menhaden fishing stopped, as occurred in the recreational fishery. Benthic invertebrates, which included mollusks and some crustaceans such as crawfish, were also positively impacted by a reduction in the menhaden fishery. The reason for the increase in benthic invertebrate biomass, and therefore catches, is unclear. The model showed a decrease in predation mortality by penaeid shrimp on benthic invertebrates when menhaden fishing dropped to zero, due to a decrease in penaeid shrimp biomass. However, the benthic invertebrates group is not well resolved in this model and includes large species such as crayfish as well as much smaller invertebrates. Therefore, the impact on invertebrate catches should be viewed with caution. On the other hand, both penaeid shrimp and blue crab catches increased when menhaden fishing levels increased. Again, the reason for this is unclear. The diet data for these groups are not of great quality, nor is the model well resolved for benthic or invertebrate groups; therefore, it is difficult to determine what is driving their dynamics. Developing a model with greater resolution of these groups would be beneficial to understanding the mechanism for these responses and their implications for commercial and recreational fisheries in the Gulf.

Current fishing mortality rates for menhaden are quite low (e.g. 0.35 in 2009) and have historically been much higher. The 2007 Menhaden Stock Assessment (Vaughan et al. 2007) gives an F target level of 0.94. When fished at this level, menhaden catches increased nearly 100% from the base run. However, when menhaden were fished at the F_{lim} level, which provides a proxy for F_{MSY}, catches increased by just over 50% from the base run. This indicates that the F_{lim} level is higher than F_{MSY} in this model and that from a multi-species perspective F_{MSY} may be closer to the F_{targ} level.

As discussed above, increasing menhaden fishing mortality rates resulted in a decline in system maturity as well as ascendency. This, in conjunction with the decline in several upper trophic level groups (e.g. seabirds, sharks, red drum, red snapper) under increased menhaden fishing, highlights the need for a precautionary and conservative approach when managing Gulf menhaden. However, the goal of management must be clearly defined, as not all groups will be negatively impacted by increased menhaden fishing. In particular, blue crab, penaeid shrimp and spotted seatrout populations may increase. These increases will have to be weighed against decreases in other groups.

3.3) Impacts of Forage Fish Fishing on Predators and Fisheries

Forage fish are important ecologically and economically around the world. Continued pressure on forage fish appears to be inevitable due to growth in the aquaculture, livestock, and pharmaceutical industries as well as increasing demand for fish for direct human consumption (Naylor et al. 2000). Even if demand for aquaculture doesn't increase and only continues at its present rate, demand for fish oil and fish meal will soon outstrip supply (Naylor and Burke 2005). It is therefore important to consider the impact that new forage fish fisheries might have on ecosystem predators and other fisheries in the Gulf of Mexico. Forage fish, other than menhaden, are currently being fished at very low levels (< 0.005), so the first scenario examined the impact of increasing shad, other clupeids and anchovies fishing mortality rates to 0.3, a level similar to that of the current F for Gulf menhaden. The majority of forage fish predators all declined in biomass under this scenario; however, large and small coastal sharks, gars, red snapper, red drum, and juvenile spotted seatrout all increased in biomass. This was due to the fact that, for these predators, the slight decrease in anchovies, other clupeids and shads was offset by an increase in other species' biomasses such as menhaden or penaeid shrimp. The second scenario caused all forage fish groups to be fished at F_{MSY} levels. This meant a doubling or tripling of the fishing mortality rate used in the previous scenario. In this case, all but three predator groups declined. In particular, seabirds were greatly impacted, with declines ranging from 25% (pelicaniformes) to over 50% (loons). Of the predator groups that increased under the previous scenario, only three continued to show an increase in abundance, while the rest declined. Small coastal sharks, gars and red snapper, were no longer able to sufficiently supplement their diet with menhaden or other prey, causing them to decline. Large coastal sharks, red drum and juvenile spotted seatrout continued to show an increase in abundance. This was primarily due to the fact that these groups were able to supplement their diet with penaeid shrimp, which increased dramatically under heavy forage fish fishing.

Changes to commercial and recreational catches reflected the changes in abundance outlined above. Red drum and spotted seatrout catches increased at both low and high levels of forage

fish fishing, while red snapper and black drum catches increased only when new forage fish fisheries occurred at low levels. When all forage fish were fished at their F_{MSY} levels, black drum declined substantially. The reasons for this are unclear, but the decline was likely the result of complex trophic interactions that exacerbated the decline that was already occurring. In terms of commercial catches, blue crab declined under both scenarios while penaeid shrimp increased. As described above, for changes in menhaden fishing, penaeid shrimp likely increased in abundance due to decreased predation by forage and other fishes as well as from release from competition by other forage fishes. Blue crab showed a decrease in abundance that may have been related to an increase in predation mortality by sea catfishes as well as a decrease in abundance of benthic invertebrates for prey. Menhaden catches increased dramatically when fished at F_{MSY}, partly due to an increase in F levels and partly due to an increase in biomass from reduced competition from other forage fish groups.

4.) Use of the Management Strategy Evaluation Tool to Examine Management Strategies

4.1) Impacts of Using a Deterministic Constant Fishing Mortality Rate for Forage Fish Fishing

The model was used to estimate fishing mortality rates at maximum sustainable yield (MSY) for each forage fish group. For menhaden, F_{MSY} was found to be 1.05. This is within the range of F_{targ} and F_{lim} estimated in the 2007 Menhaden Stock Assessment (Vaughan et al. 2007). The impact to other model groups of fishing individual forage fish at levels relative to F_{MSY} was examined. In general, fishing for forage fish had a negative impact on predator groups (e.g. seabirds, marine mammals, non-forage fish). However, fishing for other clupeids actually resulted in an increase in these groups. This is because these groups eat relatively few other clupeids compared to menhaden, anchovies and shads and when other clupeids were fished, it resulted in an increase in the other three forage fish groups. Elasmobranchs (including the large and small coastal sharks groups and skates and rays) only decreased under menhaden fishing. These groups rely heavily on menhaden and less so on other forage fish species, therefore when other forage fish groups were fished, the resultant increase in menhaden was able to more than compensate for the loss of other forage fish in their diet. In general, non-target forage fish groups showed an increase in biomass due to fishing of other forage fish groups. Predator response to forage fish fishing was linearly related to the percent of forage fish in their diets, with those predators with higher forage fish dependence showing greater declines. Declines increased as forage fish fishing increased. These patterns were observed and described in Pikitch et al. (2012) and in Pikitch et al. (in prep). These authors used an analysis of 10 Ecosim models to quantify this negative linear relationship between predator diet dependency and predator decline.

Smith et al. (2011) found that under deterministic scenarios, maintaining forage fish populations at almost twice their current levels lead to considerable reductions in impacts to dependent predators. The authors found that his could only be achieved by a substantial reduction in fishing mortality rates, to less than half F_{MSY} levels. In the current model, impacts to other species groups were greatly reduced when forage fish abundance was maintained at much higher levels, similar to the results reported by Smith et al. However, this only required fishing at 55% - 67% percent of F_{MSY}, depending on the species.

The impact of using a constant yield strategy for menhaden was also examined. Though unregulated, menhaden catches have remained relatively constant for the past 20 years. Therefore, the impact of the current fishery on menhaden predators was estimated by examining a constant yield strategy at current harvest levels. Birds of prey declined by 13% relative to levels when there was no menhaden fishing, while pelicaniformes declined by 10%. Gars and ladyfish also showed a greater than 10% decline in biomass. The large and small coastal sharks groups declined by 6% and 8%, respectively and red drum and red snapper declined by 3-5%. Several of the coastal shark species in the model are listed as near threatened by the IUCN Red List and both the scalloped hammerhead and great hammerhead are listed as endangered. In addition, red drum and red snapper are currently, or have historically been overfished and federal regulations are in place to rebuild their populations. It appears that current levels of menhaden fishing may be negatively impacting these vulnerable groups.

4.2) Impacts of Different Forage Fish Harvest Strategies that Incorporate Stochasticity

Marine ecosystems are in a constant state of flux and forage fish in particular are quite sensitive to changes in climatic conditions and environmental perturbations (Schwartzlose et al. 1999, Chavez et al. 2003, Alheit et al. 2009). Management that does not take this variability into account may result in fishing mortality or yield targets that are too high for the current environmental conditions. Variability was therefore incorporated into several harvest strategies in order to examine the impact on predator abundance and forage fish yields. Pikitch et al. (2012) found that using a hockey stick control rule consistently led to higher forage fish biomasses at all fishing levels and that increased fishing mortality resulted in lower forage fish biomass for all harvest strategies. In turn, hockey stick control rules led to lower yields (Pikitch et al. 2012). The results of the present analysis are consistent with these findings. In general, lower fishing mortality rates also lead to lower yields. However, Pikitch et al. (2012) found that fishing at 75% F_{MSY} as opposed to 100% F_{MSY} led to higher yields under a constant F strategy due to a greater chance of forage fish collapse at the higher fishing level. The current findings are similar; though they showed that fishing at 75% F_{MSY} as opposed to 100% F_{MSY} resulted in similar or higher yields for all strategies. Fishing at 100% F_{MSY} resulted in lower yields than fishing at 50% F_{MSY} under the constant F strategy. These results were consistent for all four forage fish groups modeled.

The lower yields at the 100% F_{MSY} level were a result of a greater chance of collapse of the target forage fish at this high F value. Small, short-lived species with high growth rates have historically been thought to be less vulnerable to overfishing due to these life-history traits (Reynolds et al. 2005, Roberts 2007). Recently, however, Pinsky et al. (2011) demonstrated that these species are just as vulnerable to collapse when fished above their life history – appropriate benchmarks as longer-lived, slower growing species. Pikitch et al. (2012) found that at 100% F_{MSY} there was a greater chance of collapse under all harvest strategies, but that only at the 100% F_{MSY} level was there a substantial difference in chance of collapse among the harvest strategies. In the current model, none of the forage fish groups collapsed in any of the 100 simulations at the 50% F_{MSY} level. Currently, all forage fish groups in the model are being fished well below the 50% F_{MSY} level, so the chance of collapse under the current fishing policy is minimal. At the 75% F_{MSY} level there was a $4 - 20\%$ chance of collapse, with other clupeids showing the lowest levels of collapse and anchovies the highest levels of collapse. The relationship between harvest

strategy and chance of collapse varied among the forage fish groups at the 75% F_{MSY} level. For other clupeids, the constant F strategy and the 20% Blim step function were slightly riskier than the other approaches. For shads, the lowest chance of collapse occurred under the 40% Blim step function, while for menhaden the 20% Blim hockey stick function performed best. For anchovies, both step functions resulted in fewer collapses than either the constant F or hockey stick strategies. At 100% F_{MSY}, anchovies again showed the greatest chance of collapse, while other clupeids showed the least. However, the chance of collapse was much greater for all groups, ranging from nearly 50% to almost 80% using the constant F strategy. At the 100% F_{MSY} level there was a clear trend for all groups, with the constant F strategy being the most risky and the hockey stick strategies being the least risky.

Forage fish predators consistently showed a greater decline at higher F levels and a slightly greater decline under the constant F and step strategies than under the hockey stick strategies. This is consistent with the results of Pikitch et al. (2012). At the 100% F_{MSY} level, the constant F strategy was much worse for predators of forage fish groups that collapsed than the step functions. For forage fish groups that did not collapse, the constant F and step functions caused approximately the same level of predator decline.

The decline of predators was also examined in greater detail at the 100% F_{MSY} level for each forage fish group, to highlight differences and similarities among predators' reactions. Across all forage fish groups, the hockey stick harvest strategies performed better at minimizing predator declines than the constant F or step functions, especially for the most vulnerable predator groups. The constant F strategy for menhaden resulted in a nearly 50% decline of gars and ladyfish and a 15 – 25% decline in other groups (seabirds, recreational fishes and sharks). In contrast, the other strategies resulted in only a 4% to 24% decline in predator biomasses. Under anchovy fishing at 100% F_{MSY}, seabirds (e.g. loons and gulls and terns) showed the greatest declines (up to 40% under the constant F strategy), followed by juvenile mackerels and ladyfish. The remaining predator groups declined by less than 10% under all other harvest strategies. When shad were fished at 100% F_{MSY}, seabird groups also showed the greatest decline, with loons declining by 11-16% and birds of prey declining by 5-7%, depending on the harvest strategy used. Other clupeid predators declined less than other forage fish predator groups, with only an 8-10% decline under the constant F strategy at 100% F_{MSY}. Seabirds are known to be important predators of forage fish in many parts of the world, yet are often overlooked in ecosystem models due to lack of data or a fisheries-centric focus. However, Pikitch et al. (2012) have demonstrated that seabird populations tend to be more sensitive to changes in the abundance of forage fish populations than other predators, and it is therefore particularly important that ecosystem models take their role into account. In addition, Cury et al. (2011) found that seabirds experience reduced and more variable productivity when their prey abundance falls below a certain threshold, which was found to be approximately one-third of the maximum prey biomass observed over the long term. In the current model, seabirds only consume 3 of the 4 forage fish groups. However, for these groups, seabirds also showed large declines relative to other predators.

The results of testing different harvest control rules for forage fish while incorporating stochasticity indicated that fishing forage fish at 75% F_{MSY} is likely the best option in terms of trade-offs between yields and predator declines. Yields tended to be higher at this level than at the 100% F_{MSY} level and median predator decline was less than 10% for all harvest strategies. Furthermore, at this level, no individual predator declined to a level that would cause it to meet IUCN "vulnerable" criteria (i.e. > 50% decline). At the 100% F_{MSY} level, the hockey stick

functions were the least risky option in terms of the chance of forage fish collapse and predator declines. The constant F strategy at 100% F_{MSY} consistently performed the worst, resulting in lower yields, lower forage fish biomass and greater predator declines than all other strategies at this level. These results further indicate that not incorporating stochasticity into assessments and benchmark estimates could result in overfishing and possibly collapse of the target stock over the long term, not to mention substantial declines in predator populations.

5.) Gulf Menhaden Fisheries Management

The Gulf menhaden fishery experienced rapid growth from the early 1950s through the mid-1980s. Catches peaked in 1984 at nearly 1 million mt. Fishing mortality rates exceeded F_{targ} (according to current estimates of F_{targ} and F_{lim}) levels in eight out of ten years and exceeded F_{lim} levels in four out of ten years from 1979 – 1988 (inclusive). However, corporate consolidation drove a decline in effort beginning in the mid-1980s and since that time effort has continued to drop, while catches have remained steady, averaging between 400,000 and 600,000 mt. In more recent years, assessments have shown a stable effort since 2000 and a decline in fishing mortality rates. In 2011, catches exceeded 600,000 mt for the first time since 1999, following a record low year in 2010 in which large areas were closed to the menhaden fishery due to the Deepwater Horizon oil spill.

Increasing efforts and in turn, fishing mortality rates, would require a significant investment from the Gulf menhaden industry. However, history has shown that developing this industry to much higher levels of capacity is not outside the range of possibility. Indeed, with increased demand for fish oil and fish meal, new companies may look to exploit the fisheries resources of the Gulf. The results of this study indicated that increasing fishing levels to F_{targ} or F_{lim} as they were in the 1980s could have substantial negative impacts on menhaden predator populations as well as on catches of some recreational and commercial fishery species. Furthermore, results that incorporated stochasticity indicated that fishing menhaden at a constant F level of 100% F_{MSY} could result in lower long-term average yields, due to increased chance of population collapse as well as declines in sharks, seabirds, recreational fishery species and other menhaden-dependent predators. Accounting for variability in management is very important due to variability in environmental conditions that may impact menhaden and other forage fish stocks. Though current yields and fishing mortality rates are well below MSY benchmarks, precautionary management could benefit menhaden predators as well as the fishery in the long term. Preemptive management measures could prevent overcapitalization of the industry and therefore minimize losses during periods of poor catches. Fishing below F_{MSY} would provide a buffer against environmental variability and using a harvest strategy with strict lower biomass limits could prevent declines in predator populations.

6.) Addressing Issues of Uncertainty in Input Parameters and Model Limitations

An attempt has been made to construct a comprehensive model of the northern Gulf of Mexico ecosystem, focusing on Gulf menhaden and its role in both fisheries and the ecosystem. Substantial uncertainty exists around each individual input parameter; however, a good-faith effort was made to use the most up-to-date and accurate data available. Due to the wide variety

of sources used for the input parameters as well as the inherent difficulty in accurately measuring such inputs as biomass and diet composition, initial model inputs generally result in an unbalanced model (Okey & Mahmoudi, eds. 2002). In order to prevent unrealistic estimates, boundaries were placed on the input parameters during the balancing process, based on a range of values obtained from the literature. The balancing process also highlighted some unrealistic inputs in the diet composition of certain groups. This was likely the result of combining several different studies and attempting to categorize the results of studies into the discrete model groups.

The uncertainty in input parameters stresses the need for further research. In particular, there is a paucity of information on the diets of large shark species and coastal bird groups in the northern Gulf region. Although diet composition is often considered the most uncertain of the input parameters (Okey & Mahmoudi, eds. 2002), biomass was an equally, if not more difficult parameter to estimate for many species. This is because few of the common species in the Gulf of Mexico are assessed (Webb 2011), even though fishery-independent sampling takes place at both the state and federal levels. For many groups, catch and F values were used to determine biomass, likely producing an underestimate of the true biomass. Biomass estimates for non-fish groups were also highly uncertain, especially for such diverse groups as benthic invertebrates and macrozooplankton. An assumed ecotrophic efficiency was used to calculate biomass in these cases. However, this calculation is highly dependent on the dietary inputs and may not provide an accurate representation of the true biomass in the system.

The Ecopath Pedigree Index is a tool that has been introduced to Ecosim (Pauly et al. 2000) in order to quantify model quality and facilitate comparison among models. The pedigree of this model, 0.33, is fairly low, indicating that the majority of data were derived from other models or calculated based on empirical relationships, rather than based on high-precision sampling. Unfortunately pedigree indices are not available for other Gulf of Mexico models, so it is difficult to compare the quality of the present model to others that have been constructed in this region. What is evident is that estimates based on local, high-precision sampling are difficult to come by in the northern Gulf. Diet and catch data are fairly well known and for the most part came from quantitative regional studies and national statistics, respectively, while consumption and production rates have not been studied for the majority of species and so empirical relationships were used to derive some model values. Biomass estimates were generally the most uncertain of the input parameters for this model, due to the lack of Gulf-wide assessments for the majority of common species (Webb 2011). Given more time, one could perhaps use fishery-independent data collected by the states to conduct single species stock assessments for the groups lacking biomass estimates.

Uncertainty also arises during the process of fitting the Ecosim model to observed time series. Several different sets of parameter adjustments can be made to arrive at a similar quality of fit to the data. In this model, time series fitting attempted to minimize the sum of squares, while incorporating all the time series of catch and biomass for major model groups. At the same time, an attempt was made to not deviate from the initial input parameters of the Ecopath model and to maintain the vulnerability parameters within reasonable bounds. Changing vulnerability parameters can have a large impact on how the model fits to observed time series, but can also cause the model to behave in unpredictable ways. For example, after running several scenarios forward in time, it was realized that many vulnerability parameters were set to extreme levels during the initial fitting effort and were adjusted back towards the default value of two to prevent the extreme changes in biomass that arose during some simulations. Therefore, a balance was

struck between adjusting parameters to provide a better fit and maintaining parameters within the bounds of reality. For some species, time series of historical fishing rates were not available and therefore the model was unable to accurately reproduce the catch series. In these cases, catches were forced in order to better represent the impact of fishing on these groups. While several groups did not fit particularly well to time series of biomass or effort, some of the most important groups did have good fits. This is likely due to the fact that these important commercial and recreational species are subject to frequent and direct assessment. For other groups, abundance surveys may be conducted in an ad-hoc fashion or by using gear that does not directly target the species modeled. Penaeid shrimp and menhaden are both examples of frequently assessed species; these groups fit well to time series of both abundance and catches. Another important commercial species, blue crab, fit well to abundance data and was able to generally recreate trends in catch data. Red drum and red snapper, which are important predators in the model as well as important to the recreational fishery, were fit well to time series of abundance and were able to reasonably recreate trends in catches. Other important recreational fishery species (e.g. black drum, spotted seatrout and other demersals) were also able to recreate general trends in catches, despite variability in observed data.

7.) *Future Work*

This project has helped to provide a greater understanding of the role of Gulf menhaden in the northern Gulf of Mexico ecosystem as well as the impact of the Gulf menhaden fishery on other species in the ecosystem. It also provides a platform for future work that may address some of the many yet unanswered questions. An Ecospace model could be developed from the current Ecopath model in order to address questions related to spatial dynamics of the menhaden fishery and menhaden predators. This could be an important tool for looking at issues of pollution as it relates to the fishery. For instance, Ecospace could be used to examine the impact of the large hypoxic zone off the shores of Louisiana. The hypoxic zone could cause menhaden and its predators to concentrate along the edges in non-hypoxic waters, perhaps making them an easier target for fisheries. This model could also be used as a pre-oil spill model and could be used to compare with a post-spill model. Ecospace could also be used in this capacity to track the movement of the spill as well as fishery closures.

This model could also be supplemented with socio-economic data to examine the impact of the menhaden fishery, not only on predators, but also on livelihoods and profits. Pikitch & Rountos et al. (2012) found that globally, the supportive value of forage fish (that is, the value that they contribute as prey to other commercially caught species) is greater than the direct value of the forage fish catch. It would be interesting to know if this holds true in the GoM, where menhaden and other low trophic-level species are the most valuable to commercial fisheries. In addition, recreational fisheries are also important economically in the Gulf due to the draw of tourism. Though difficult to quantify, one could examine the trade-off between jobs in the menhaden fishery and jobs in the recreational fishery that are dependent on menhaden as prey for recreational fish species.

Finally, the development of this model has highlighted the need for greater and continued study of the species in the northern Gulf of Mexico. In particular, diet data is lacking for many of the top predators in the system including large shark species and seabirds. Several of these large sharks are considered near threatened, while some are already endangered. A greater

understanding of their dietary requirements would help managers protect these species. As has been pointed out previously, accurate biomass estimates are difficult to come by for the majority of the model species/groups. All of the states along the Gulf Coast conduct fishery-independent surveys, but few provide regular and comprehensive stock assessments for common species. Federal fishery-independent surveys are also conducted along the entire Gulf coast, but the data have not been used to generate indices of abundance. Putting this data to good use by generating state by state and coast-wide estimates of biomass and indices of abundance would a huge boon to scientists and managers and would greatly benefit the development of future ecosystem models.

8.) *Conclusion*

Although fishing is a major industry along the Gulf coast, fishing mortality rates for menhaden and other forage fish are currently quite low – less than 0.5 for menhaden and less than 0.01 for shads, other clupeids and anchovies. Nevertheless, we are likely to see an increase in fishing pressure for these species due to increased demand for fish (and forage fish in particular) in the future. The results of this study indicated that increasing fishing mortality rates for menhaden to the target or limit levels estimated by the 2007 stock assessment, would cause declines in several species that prey upon menhaden. Substantial declines (of 20 % or more) were predicted for some shark and bird groups. Smaller, but still potentially important declines were seen for some recreationally caught fish species. Both red snapper and red drum fishing is highly regulated due to concerns of overfishing and any decrease in their population due to fishing for their prey, may impede their recovery. Similar impacts to predator species were observed when other forage fish groups were fished at F_{MSY} levels. Furthermore, strategies that increased fishing for menhaden and other forage fish consistently resulted in a decrease in system maturity, accordant with a decline in stability and resilience of the system. It is important to note, however, that not all forage fish predators reacted in the same way to changes in prey abundance. Managers will need to set clearly defined goals for both target and non-target species and evaluate trade-offs in production of each group. The use of whole-ecosystem models such as that used in this study will be indispensable in assessing these trade-offs and in managing these species within an ecosystem context.

It will also be important for managers to account for environmental variability and other uncertainties when managing forage and other fish populations. In this study analyses were performed to examine the impact of different harvest strategies and different fishing mortality rates, while incorporating stochasticity, on forage fish and their predators. Results indicated that fishing for menhaden using a constant fishing mortality rate of 100% F_{MSY} would result in collapse of the menhaden stock and lower long-term average yields over a 50 year time period, when compared to fishing at 50 or 100% F_{MSY} using this same strategy. Such declines in the menhaden population could also lead to substantial declines in predator populations. When using the constant F harvest strategy, fishing at 75% F_{MSY} appeared to be more precautionary and lead to higher yields. However, from an ecosystem perspective, managers may want to use even more conservative approaches. Fishing at 50% F_{MSY} – as recommended by Pikitch et al. 2012 – did not result in collapse of any of the target forage fish stocks and minimized predator declines across all harvest strategies. If a higher fishing level is sought, using a hockey-stick harvest strategy with a minimum biomass threshold of 40% B_0 appeared to minimize predator declines. Again,

these results were consistent across all forage fish groups in the model. In sum, fishing mortality rates will need to be much lower than currently indicated by single-species assessments and management practices in order to ensure a robust menhaden fishery in the future and to maintain the integrity of the Gulf of Mexico ecosystem.

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Appendices

Appendix A. Estimates of bird weights used to estimate biomass and their sources.

Species	Weight	Description	Source
Bald eagle, *Haliaeetus leucocephalus*	4.79 kg	Avg. male and female, Alaska, Text	Buehler, David A. 2000. Bald Eagle (Haliaeetus leucocephalus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/506
Osprey, *Pandion haliaetus*	1.65kg	Avg. male and female over breeding season, Fig. 5	Poole, Alan F., Rob O. Bierregaard and Mark S. Martell. 2002. Osprey (Pandion haliaetus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/683
Common loon, *Gavia immer*	5.32 kg	Avg. male and female, Maine, Table 2	Evers, David C., James D. Paruk, Judith W. Mcintyre and Jack F. Barr. 2010. Common Loon (Gavia immer), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/313
Magnificent frigatebird, *Fregata magnificens*	1.36 kg	Avg. male and female, Baja California, Table 1	Diamond, Antony W. and Elizabeth A. Schreiber. 2002. Magnificent Frigatebird (Fregata magnificens), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/601
American white pelican, *Pelecanus erythrorhynchos*	7.2 kg	Avg. of range in text	Knopf, Fritz L. and Roger M. Evans. 2004. American White Pelican (Pelecanus erythrorhynchos), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/057
Brown Pelican, *Pelecanus occidentalis*	3.06kg	Avg. male and female, Florida, Text	Shields, Mark. 2002. Brown Pelican (Pelecanus occidentalis), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/609
Double-crested	2.33 kg	Avg. male and	Hatch, Jeremy J. and D. V. Weseloh. 1999.

cormorant, *Phalacrocorax auritus*		female, Mississippi, Text	Double-crested Cormorant (Phalacrocorax auritus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/441
Northern gannet, *Morus bassanus*	3.0 kg	Avg. male and female adults, Bass Rock, Text	Mowbray, Thomas B. 2002. Northern Gannet (Morus bassanus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/693
Gull-billed tern, *Gelochelidon nilotica*	0.17 kg	Mean, Texas, Table 2	Molina, K. C., J. F. Parnell and R. M. Erwin. 2009. Gull-billed Tern (Gelochelidon nilotica), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/140
Caspian tern, *Hydroprogne caspia*	0.66 kg	Avg. male and female, Texas, App. 1	Cuthbert, Francesca J. and Linda R. Wires. 1999. Caspian Tern (Hydroprogne caspia), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/403
Herring gull, *Larus argentatus*	0.21 kg	Avg. male and female, Mass, App. 2	Pierotti, R. J. and T. P. Good. 1994. Herring Gull (Larus argentatus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/124
Laughing gull, *Larus atricilla*	0.31 kg	Avg. male and female, Florida, App. 1	Burger, Joanna. 1996. Laughing Gull (Leucophaeus atricilla), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/225
Ring-billed gull, *Larus delawarensis*	0.51 kg	Avg. male and female, Canada, App. 3	Ryder, John P. 1993. Ring-billed Gull (Larus delawarensis), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/033
Great black-backed gull,	1.62 kg	Avg. male and female,	Good, Thomas P. 1998. Great Black-backed Gull (Larus marinus), The Birds of North

Larus marinus		Monomoy Mass, App. 3	America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/330
Black skimmer, *Rynchops niger*	0.32 kg	Avg. male and female, Argentina	Mariano-Jelicich et al. 2007
Forster's tern, *Sterna forsteri*	0.16 kg	Mean, Oklahoma, Text	Mcnicholl, Martin K., Peter E. Lowther and John A. Hall. 2001. Forster's Tern (Sterna forsteri), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/595
Common tern, *Sterna hirundo*	0.10 kg	Mean, Trinidad, Text	Nisbet, Ian C. 2002. Common Tern (Sterna hirundo), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/618
Least tern, *Sternula antillarum*	0.044 kg	Mean, Texas, Text	Thompson, Bruce C., Jerome A. Jackson, Joannna Burger, Laura A. Hill, Eileen M. Kirsch and Jonathan L. Atwood. 1997. Least Tern (Sternula antillarum), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/290
Royal Tern, *Thalasseus maximus*	0.40 kg	Avg. males and females, boreal, Text	Buckley, P. A. and Francine G. Buckley. 2002. Royal Tern (Thalasseus maximus), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/700
Sandwich tern, *Thalasseus sandvicensis*	0.20 kg	Mean, Texas, App. 2	Shealer, David. 1999. Sandwich Tern (Thalasseus sandvicensis), The Birds of North America Online (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: http://bna.birds.cornell.edu/bna/species/405

Appendix B. Diet matrix of the balanced model. Diets are expressed in percent. Predators are listed in the columns and prey are listed in rows.

	Prey \ Predator	1	2	3	4	5	6	7	8	9
1	Birds of Prey									
2	Loons	0.15								
3	Gulls and Terns	0.39								
4	Pelicaniformes	0.15								
5	Coastal Dolphins							0.09		
6	Large Coastal Sharks									
7	Small Coastal Sharks					0.06		2.03		0.16
8	Rays					0.06		3.04	0.00	0.21
9	Coastal Pelagic Piscivores	2.02		10.99	1.98	0.87	2.02	3.04		1.01
10	Tunas						0.20	0.10		0.62
11	0-3 Mackerels									0.04
12	3+ Mackerels			1.00	2.97	0.48	2.02	2.03		0.77
13	0-8 Red Drum									0.04
14	8+ Red Drum			2.00	0.49	0.71		1.01	0.48	0.85
15	0-18 Spotted Seatrout									0.04
16	18+ Spotted Seatrout	6.07		2.99	0.49	8.00		1.01	0.71	0.92
17	Groupers			0.42			2.02	1.01	0.48	0.81
18	Red Snapper							1.01	0.48	0.69
19	Ladyfish					3.00		1.01	0.48	0.72
20	Spot	2.02		0.46	1.98	13.00		1.01	0.70	1.02
21	Atlantic Croaker	6.07		2.00	1.98	0.48		4.05	1.99	1.02
22	Butterfish	0.17		0.01		0.48		1.01	0.48	2.03
23	Black Drum			1.00	0.49	0.64		1.01	0.48	0.85
24	Flounders	2.02		0.09				2.03	0.93	0.98
25	Gars				0.25			1.01		0.67
26	Saltwater Catfish			0.05	1.98			3.04	0.48	1.02
27	Mullet			2.00	25.71	2.00		2.03	0.48	1.02
28	Other Demersals	34.39		18.99	16.81	29.99	24.18	17.20	8.95	7.12
29	Nearshore Ominivores	2.02		2.99	10.90	22.99		3.04	0.93	2.03
30	Adult Menhaden	23.30		3.99	7.92	2.00	23.18	22.30	0.48	5.09
31	Juvenile Menhaden				8.91					0.87
32	Shads	10.10	26.41	5.98	2.97	0.95		2.03	0.48	2.03
33	Other Clupeids	4.05		6.97	5.94	3.00	2.02	2.03		10.20
34	Anchovies etc.		39.62	19.99	7.92	0.95		5.06	2.98	13.23
35	Squid			0.29		6.00	21.18	4.05	0.09	5.09
36	Caridean Shrimp			0.42		0.87		0.91	23.89	3.05
37	Penaeid Shrimp			0.43		0.87	21.18	1.01	4.97	9.16
38	Stone Crab					0.87		0.29	0.93	3.05
39	Blue Crab			2.00		0.87		7.09	6.96	8.14
40	Benthic Invertebrates			10.99		0.87		3.04	32.79	12.22
41	Macrozooplankton			3.99	0.31					2.03
42	Microzooplankton							0.13		0.50
43	Infauna		33.96					0.10	7.95	0.18
44	Algae							0.12	0.07	0.14
45	Seagrass							0.87		0.16
46	Phytoplankton									
47	Detritus							0.14	0.41	0.18
48	Import	7.08					2.02			

	Predators												
Prey	10	11	12	13	14	15	16	17	18	19	20	21	22
1													
2													
3	0.00												
4													
5													
6													
7													
8								0.20					
9	2.04		2.10					0.17					
10								0.01					
11	0.19												
12	2.04		1.01					0.01					
13	0.19												
14	1.03	1.99	2.10					0.00					
15	0.19	0.39				0.76							
16	1.03		2.10					0.00		2.98			
17	1.03		2.10					0.23	2.19				
18	1.03		2.10										
19	1.03		2.10										
20	1.03	0.71	2.10				1.00	0.00					
21	1.03	0.87	3.15		0.53		2.01						
22	3.08		2.10										
23	1.03	0.15	2.10					0.00					
24			2.10		0.95		0.02	0.01	0.76				
25			0.22										
26	1.03		2.10		0.44								
27	1.03	2.98	2.10		6.05		7.03	0.22		0.66			
28	5.13	16.91	14.75		9.08	14.09	4.01	27.18	5.33	2.98	0.65	3.99	
29	3.08	1.99	3.15		1.01	4.02	11.01	16.09	4.37		0.31	2.00	
30	2.05	11.91	5.24		17.19		10.01	0.09	12.07	23.80			
31	2.05					3.02							
32	2.05	5.96	3.15		3.03	4.02	4.01	0.02	0.20	4.96			
33	4.11	9.96	21.01					14.09	8.75	5.96			
34	1.03	40.72	4.20	1.00	7.06	21.08	8.05	0.44	8.75	17.90	2.01	3.99	4.03
35	45.22	4.97	6.29		0.26		0.16	1.01	14.22				
36	0.04		2.10	6.97	10.09	16.08	12.01	4.02	5.47	11.90	2.01	5.99	16.18
37	0.78	0.37	3.15	4.98	13.09	14.09	22.11	2.01	10.99	1.99	0.79	4.99	5.02
38	0.01		2.10		4.04		3.01	1.01	0.84	1.99	2.01	3.99	2.02
39	0.38		2.10		16.19		5.03	1.01	3.29	1.99	2.01	3.99	2.02
40	1.03	0.13	3.15	34.89	9.08	14.09	6.03	32.18	17.46	11.90	27.07	19.99	36.36
41	0.06			48.79		7.01			4.37	10.90	16.08	5.99	16.18
42	9.25			2.99		1.01			0.30		0.71		
43			0.00		1.01		2.01	0.02	0.65		23.07	27.88	18.18
44	0.51			0.09	0.25	0.12	0.47				2.01	0.23	
45	0.00				0.00		1.00				0.10		
46				0.01							0.11		
47	5.13			0.28	0.64	0.62	1.00			0.09	21.07	16.99	
48													

Prey	Predators												
	23	24	25	26	27	28	29	30	31	32	33	34	35
1													
2													
3													
4													
5													
6													
7													
8													
9						0.00							
10													
11													
12													
13													
14		0.03											
15													
16		0.42	0.13			0.17							
17													
18													
19						0.12							
20		1.01	7.74			0.33							
21		1.01	7.74			0.28							
22			0.13			0.48							
23		0.10				0.24							
24		0.73	0.96			0.20							
25													
26		0.47	8.85			0.16							
27		5.06	3.32			0.57							
28		9.03	7.74	5.02		2.02	0.35				0.35		
29	2.10	12.01	2.21	2.01		0.67	0.19						3.05
30		9.13	22.10	7.02		2.02						2.00	11.20
31										8.09			
32			2.21	3.01		0.66						0.88	14.20
33			0.20	5.02		3.03				8.09			14.20
34	5.26	13.11	8.85	6.01		4.04	0.61			8.09	1.99	1.00	14.20
35		0.42				0.94	0.00						6.09
36	2.10	7.10	0.24	6.01	0.06	7.06	5.00			2.02	1.00	2.00	11.20
37	1.04	11.11	0.64	10.10	0.06	3.03	2.00			2.02	0.89	0.90	11.20
38	0.71	2.03	0.24	10.10	0.11	2.02	0.62				0.64	0.20	0.31
39	0.85	1.01	25.48	10.10	0.11	1.01	0.67				0.64	0.20	0.31
40	73.77	24.41	1.11	20.09	0.11	35.29	41.97			7.08	36.81	30.99	0.76
41	2.10	0.28	0.08	0.19	1.99	8.07	11.99	22.22	17.65	24.21	21.91	18.00	13.20
42	0.39	0.00		0.85	0.93	3.03	3.00	38.89	41.18	13.11	27.91	15.00	
43	5.26	1.01		5.02		20.20	5.00				0.86	2.00	0.10
44	0.09			0.03	56.79	0.79	3.00				1.99	9.00	
45	2.10			0.43		0.53	3.00				0.45	0.32	
46					9.96		0.63	33.34	35.30	6.07	0.60	0.52	
47	4.21	0.52		9.02	29.89	3.03	21.98	5.55	5.88	21.21	3.98	17.00	
48													

	Predators							
Prey	36	37	38	39	40	41	42	43
1								
2								
3								
4								
5								
6								
7								
8								
9								
10								
11								
12								
13								
14								
15								
16								
17								
18								
19								
20								
21								
22								
23								
24								
25								
26								
27								
28								
29								
30								
31								
32								
33								
34								
35								
36								
37				0.09				
38			0.20	0.50				
39			0.30	0.09				
40	12.00	32.00	44.20	57.63	1.00			
41	0.10	7.00		2.98	3.00			
42	5.00	7.00			1.00	9.10	0.10	
43								
44	21.00	0.99			13.00		1.00	
45					0.10			
46					27.00	54.50	98.90	
47	61.90	53.01	55.30	38.72	54.90	36.40		100
48								

Appendix C-1. Initial, maximum, and minimum parameter estimates used during model balancing.

Group	Biomass			P/B			Q/B		
	Initial	Max	Min	Initial	Max	Min	Initial	Max	Min
Birds of Prey	5.15E-05	5.15E-05	5.15E-05	0.10	0.10	0.10	147.00	147.00	147.00
Loons	9.88E-05	9.88E-05	9.88E-05	0.10	0.10	0.10	28.63	28.63	28.63
Gulls and Terns	1.47E-03	3.00E-03	1.00E-03	0.10	5.40	0.10	196.00	196.00	80.00
Pelecaniformes	0.01	0.01	0.01	0.10	0.10	0.10	17.74	17.74	17.74
Coastal Dolphins	0.03	0.07	0.02	0.10	0.92	0.01	40.40	41.07	16.44
Large coastal sharks	0.08	12.00	0.03	0.08	0.94	0.08	1.00	9.70	1.00
Small coastal sharks	0.08	0.53	2.05E-03	0.51	1.03	0.40	7.20	7.90	4.48
Skates and Rays	4.00	4.00	0.01	0.30	0.92	0.20	1.00	10.80	1.00
Coastal Pelagic Piscivores	0.02	1.44	0.02	0.61	0.70	0.42	5.43	10.23	2.00
Tunas	0.03	0.14	0.01	2.11	2.11	0.51	12.87	15.46	6.30
Juvenile mackerels	Ecopath	0.13	3.68E-05	Ecopath	4.00	0.77	Ecopath	73.00	9.00
Adult mackerels	0.25	1.12	0.03	0.70	1.28	0.38	5.40	26.17	5.40
Red Drum (0-8)	Ecopath	0.01	n/a	Ecopath	n/a	2.75	Ecopath	n/a	12.70
Red Drum (8-36+)	2.16	2.16	0.01	0.60	0.86	0.35	1.89	6.30	1.86
Spotted seatrout (0-18)	Ecopath	n/a	0.03	Ecopath	3.70	n/a	Ecopath	13.59	n/a
Spotted seatrout (18+)	0.22	1.88	0.01	0.70	0.83	0.45	1.60	6.80	1.60
Groupers	0.55	2.08	0.01	0.47	0.50	0.40	6.00	6.00	2.30
Red Snapper	0.75	0.91	0.01	0.70	0.87	0.30	8.00	16.78	4.30
Ladyfish	0.10	0.10	2.00E-03	1.72	1.72	0.88	6.00	9.13	4.90
Spot	0.80	0.80	1.49E-04	1.10	1.47	0.08	12.00	20.10	6.90
Croaker	0.60	0.60	0.01	1.50	5.05	0.35	10.00	22.26	5.41
Butterfish	1.22	2.50	4.30E-05	2.00	2.00	0.80	10.40	10.40	8.00
Black Drum	0.06	0.27	2.00E-03	0.58	0.58	0.35	3.65	6.36	3.65
Flounders	0.41	0.90	3.00E-03	0.77	1.86	0.30	4.52	9.46	4.52
Gars	0.01	0.04	0.01	0.56	0.56	0.19	3.47	3.47	1.49
Sea Catfishes	0.15	4.98	0.01	0.80	1.24	0.29	7.60	10.14	5.60
Mullets	0.69	3.36	0.01	0.98	1.22	0.19	10.02	15.44	4.50
Other Demersal Fishes	3.74	6.83	0.12	1.07	1.58	0.64	9.06	13.08	6.52
Nearshore Omnivores	1.44	1.44	0.59	1.00	1.77	0.39	8.60	22.80	5.20

Adult menhaden	6.00	17.24	0.02	1.90	6.96	0.95	6.00	29.70	6.00
Juvenile menhaden	Ecopath	n/a	1.53	Ecopath	2.30	n/a	Ecopath	n/a	14.50
Shads	1.79	1.79	1.79	1.90	1.90	1.90	11.80	11.80	11.80
Other Clupeids	5.45	11.08	0.77	1.53	4.31	0.80	11.38	13.70	11.70
Anchovies, Etc.	3.03	3.03	0.07	2.44	7.64	0.60	13.48	19.70	8.80
Squid	1.10	1.10	0.11	3.00	3.00	1.70	35.00	36.50	11.70
Caridean Shrimp	4.26	4.26	4.26	2.40	2.40	2.40	18.00	18.00	18.00
Penaid shrimp	1.00	6.90	0.29	2.40	7.60	1.81	19.20	37.90	15.60
Stone Crab	0.17	0.17	0.03	2.00	2.00	1.69	7.00	8.50	7.00
Blue Crab	0.20	1.04	0.04	2.40	2.40	0.60	8.50	9.10	2.70
Benthic Invertebrates	31.79	44.60	3.22	4.50	10.00	4.00	22.00	50.00	22.00
Macrozooplankton	10.73	40.00	0.32	22.00	65.00	5.00	67.00	165.00	60.00
Microzoolplankton	7.64	7.64	7.64	36.00	36.00	36.00	89.00	89.00	89.00
Infauna	20.00	37.40	5.20	2.00	7.88	2.00	10.00	27.36	10.00
Algae	29.78	31.78	29.78	25.00	25.00	5.76			
Seagrass	175.62	175.62	13.50	9.01	514.00	9.01			
Phytoplankton	25.00	45.50	1.16	182.00	444.00	45.50			
Detritus	100.00	3400.00	1.90						

Appendix C-2. Sources used for initial, maximum, and minimum parameter estimates.

Group	Biomass		
	Initial	Max	Min
Birds of Prey	Audubon Bird Count Data	Audubon Bird Count Data	Audubon Bird Count Data
Loons	Audubon Bird Count Data	Audubon Bird Count Data	Audubon Bird Count Data
Gulls and Terns	Audubon Bird Count Data	Vidal Hernandez 2000	Okey et al. 2004
Pelecaniformes	Audubon Bird Count Data	Audubon Bird Count Data	Audubon Bird Count Data
Coastal Dolphins	Okey & Mahmoudi 2002	Cruz-Escalona et al. 2007	Browder 1993
Large coastal sharks	Catch/F	Walters et al. 2008	Arreguin-Sanchez et al. 1993b
Small coastal sharks	Catch/F	SEDAR 2007	Okey & Mahmoudi 2002
Skates and Rays	Walters et al. 2008	Walters et al. 2008	Carlson 2007
Coastal Pelagic Piscivores	Catch/F	Manickchand-Heileman et al. 1998a	Catch/F
Tunas	Catch/F	Brown et al. 1991	Okey & Mahmoudi 2002
Juvenile mackerels	Ecopath Estimate	Okey et al. 2004	Walters et al. 2008
Adult mackerels	Walters et al. 2008	Arreguin-Sanchez et al. 1993a	Catch/F
Red Drum (0-8)	Ecopath Estimate	Walters et al. 2008	n/a
Red Drum (8-36+)	Walters et al. 2008	Walters et al. 2008	Okey & Mahmoudi 2002
Spotted seatrout (0-18)	Ecopath Estimate	n/a	Walters et al. 2008
Spotted seatrout (18+)	Walters et al. 2008	de Mutsert 2010	Okey & Mahmoudi 2002
Groupers	Walters et al. 2008	Venier 1997	Catch/F
Red Snapper	Walters et al. 2008	Arreguin-Sanchez et al. 1993a	Okey & Mahmoudi 2002
Ladyfish	Walters et al. 2008	Walters et al. 2008	Okey & Mahmoudi 2002
Spot	Walters et al. 2008	Walters et al. 2008	Catch/F
Croaker	Walters et al. 2008	Walters et al. 2008	Catch/F
Butterfish	Brown et al. 1991	Okey & Mahmoudi 2002	Catch/F
Black Drum	Catch/F	de Mutsert 2010	Okey & Mahmoudi 2002
Flounders	Lewis et al. 2007	Manickchand-Heileman et al. 1998a	Catch/F
Gars	Catch/F	de Mutsert 2010	Catch/F
Sea Catfishes	Walters et al. 2008	Cruz-Escalona et al. 2007	Catch/F
Mullets	Brown et al. 1991	Walters et al. 2008	Althauser 2003
Other Demersal Fishes	See Text	Cruz-Escalona et al. 2007	Catch/F
Nearshore Omnivores	See Text	Equal to Initial Estimate	Okey & Mahmoudi 2002
Adult menhaden	Walters et al. 2008	Brown et al. 1991	de Mutsert 2010
Juvenile menhaden	Ecopath Estimate	n/a	Walters et al. 2008
Shads	Lewis et al. 2007	Lewis et al. 2007	Lewis et al. 2007

Other Clupeids	Brown et al. 1991	Walters et al. 2008	De la Cruz-Aguero 1993
Anchovies, Etc.	See Text	Equal to Initial Estimate	Althauser 2003
Squid	Okey et al. 2004	Okey et al. 2004	Manickchand-Heileman et al. 1998b
Caridean Shrimp	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Penaid shrimp	Walters et al. 2008	Althauser 2003	De la Cruz Aguero 1993
Stone Crab	Walters et al. 2008	Walters et al. 2008	Okey & Mahmoudi 2002
Blue Crab	Walters et al. 2008	Althuaser 2003	Okey & Mahmoudi 2002
Benthic Invertebrates	Walters et al. 2008	Carlson 2007	de Mutsert 2010
Macrozooplankton	Walters et al. 2008	Venier 1997	Althauser 2003
Microzoolplankton	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Infauna	Walters et al. 2008	Manickchand-Heileman et al. 1998a	Cruz-Escalona et al. 2007
Algae	Walters et al. 2008	Althuaser 2003	Walters et al. 2008
Seagrass	Walters et al. 2008	Walters et al. 2008	Carlson 2007
Phytoplankton	Walters et al. 2008	Manickchand-Heileman et al. 1998a	Manickchand-Heileman et al. 1998a
Detritus	Walters et al. 2008	Venier 1997	Arreguin-Sanchez 1993a

Group	P/B		
	Initial	Max	Min
Birds of Prey	Okey et al. 2004	Okey et al. 2004	Okey et al. 2004
Loons	Okey et al. 2004	Okey et al. 2004	Okey et al. 2004
Gulls and Terns	Okey et al. 2004	Vidal 2000	Okey et al. 2004
Pelecaniformes	Okey et al. 2004	Okey et al. 2004	Okey et al. 2004
Coastal Dolphins	Okey et al. 2004	Althauser 2003	Cruz-Escalona et al. 2007
Large coastal sharks	Walters et al. 2008	Manickchand-Heileman et al. 1998a	Walters et al. 2008
Small coastal sharks	Carlson et al. 2007	Okey & Mahmoudi 2002	Chagaris 2011, unpublished
Skates and Rays	Walters et al. 2008	Cruz-Escalona et al. 2007	De la Cruz-Aguero 1993
Coastal Pelagic Piscivores	See Text	Chagaris 2011, unpublished	Arreguin-Sanchez et al. 1993b
Tunas	Browder 1993	Browder 1993	Vidal Hernandez 2000
Juvenile mackerels	Ecopath Estimate	Walters et al. 2008	Okey et al. 2004
Adult mackerels	Walters et al. 2008	Manickchand-Heileman et al. 1998a	Okey et al. 2004
Red Drum (0-8)	Ecopath Estimate	n/a	Walters et al. 2008
Red Drum (8-36+)	Walters et al. 2008	Chagaris 2011, unpublished	Okey & Mahmoudi 2002
Spotted seatrout (0-18)	Ecopath Estimate	Walters et al. 2008	n/a
Spotted seatrout (18+)	Walters et al. 2008	Chagaris 2011, unpublished	Carlson 2007
Groupers	Walters et al. 2008	Arreguin-Sanchez et al. 1993b	SEFSC 2002
Red Snapper	Walters et al. 2008	Chagaris 2011, unpublished	Cruz-Aguero 1993
Ladyfish	Walters et al. 2008	Walters et al. 2008	Chagaris 2011, unpublished
Spot	Walters et al. 2008	Chagaris 2011, unpublished	Althauser 2003
Croaker	Walters et al. 2008	Althauser 2003	Okey & Mahmoudi 2002
Butterfish	Gledhill 1991	Gledhilll 1991	Chagaris 2011, unpublished
Black Drum	Chagaris 2011, unpublished	Chagaris 2011, unpublished	Okey & Mahmoudi 2002
Flounders	Chagaris 2011, unpublished	Cruz-Escalona et al. 2007	Okey & Mahmoudi 2002
Gars	Sum of M + F	Sum of M + F	de Mutsert 2010
Sea Catfishes	Walters et al. 2008	Cruz-Escalona et al. 2007	Chavez et al. 1993
Mullets	Walters et al. 2008	Cruz-Escalona et al. 2007	Althauser 2003
Other Demersal Fishes	See Text	Vega-Cendejas et al. 1993	Arreguin-Sanchez et al. 1993b
Nearshore Omnivores	See Text	Okey & Mahmoudi 2002	Manickchand-Heileman et al. 1998a
Adult menhaden	Walters et al. 2008	Althauser 2003	Okey & Mahmoudi 2002
Juvenile menhaden	Ecopath	Walters et al. 2008	n/a
Shads	Same as menhaden	n/a	n/a
Other Clupeids	See Text	Manickchand-Heileman et al. 1998a	De la Cruz-Aguero 1993
Anchovies, Etc.	Walters et al. 2008	Althauser 2003	Okey & Mahmoudi 2002

Squid	Okey et al. 2004	Okey et al. 2004	Manickchand-Heileman et al. 1998a
Caridean Shrimp	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Penaid shrimp	Walters et al. 2008	Abarca-Arenas & Valero-Pacheco 1993	Althauser 2003
Stone Crab	Walters et al. 2008	Walters et al. 2008	Okey & Mahmoudi 2002
Blue Crab	Walters et al. 2008	Walters et al. 2008	Althauser 2003
Benthic Invertebrates	Walters et al. 2008	Chavez et al. 1993	Abarca-Arenas & Valero-Pacheco 1993
Macrozooplankton	Walters et al. 2008	Venier 1997	Abarca-Arenas & Valero-Pacheco 1993
Microzoolplankton	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Infauna	Walters et al. 2008	Cruz-Escalona et al. 2007	Walters et al. 2008
Algae	Walters et al. 2008	Walters et al. 2008	Althauser 2003
Seagrass	Walters et al. 2008	Carlson 2007	Walters et al. 2008
Phytoplankton	Walters et al. 2008	Althauser 2003	Arreguin-Sanchez et al. 1993
Detritus			

	Q/B		
Group	Initial	Max	Min
Birds of Prey	See Text	Equal to Initial	Equal to Initial
Loons	See Text	Equal to Initial	Equal to Initial
Gulls and Terns	See Text	Equal to Initial	Okey et al. 2004
Pelecaniformes	See Text	Equal to Initial	Equal to Initial
Coastal Dolphins	Okey et al. 2004	Browder 1993	Althauser 2003
Large coastal sharks	Walters et al. 2008	Arreguin-Sanchez et al. 1993b	Walters et al. 2008
Small coastal sharks	Carlson 2007	Carlson 2007	Okey & Mahmoudi 2002
Skates and Rays	Walters et al. 2008	De la Cruz-Aguero 1993	Walters et al. 2008
Coastal Pelagic Piscivores	Fishbase	Okey et al. 2004	Walters et al. 2008
Tunas	Fishbase	Browder 1993	Chagaris 2011, unpublished
Juvenile mackerels	Ecopath Estimate	Walters et al. 2008	Okey et al. 2004
Adult mackerels	Fishbase	Browder 1993	Fishbase
Red Drum (0-8)	Ecopath Estimate	n/a	Walters et al. 2008
Red Drum (8-36+)	Walters et al. 2008	Carlson 2007	de Mutsert 2010
Spotted seatrout (0-18)	Ecopath Estimate	Walters et al. 2008	n/a
Spotted seatrout (18+)	Walters et al. 2008	Arreguin-Sanchez et al. 1993b	de Mutsert 2010
Groupers	Walters et al. 2008	Walters et al. 2008	Venier 1997
Red Snapper	Walters et al. 2008	Okey & Mahmoudi 2002	Arreguin-Sanchez et al. 1993b
Ladyfish	Walters et al. 2008	Okey & Mahmoudi 2002	Fishbase
Spot	Walters et al. 2008	Althauser 2003	Chagaris 2011, unpublished
Croaker	Walters et al. 2008	Althauser 2003	Okey & Mahmoudi 2002
Butterfish	Fishbase	Fishbase	Okey & Mahmoudi 2002
Black Drum	Chagaris 2011, unpublished	de Mutsert 2010	Chagaris 2011, unpublished
Flounders	Chagaris 2011, unpublished	Okey & Mahmoudi 2002	Chagaris 2011, unpublished
Gars	Pauly 1989 Equation	Pauly 1989 Equation	de Mutsert 2010
Sea Catfishes	Walters et al. 2008	Carlson 2007	Fishbase
Mullets	Walters et al. 2008	Fishbase	Abarca-Arenas & Valero-Pacheco 1993
Other Demersal Fishes	Fishbase	Vega-Cendejas et al. 1993	Chagaris 2011, unpublished
Nearshore Omnivores	Fishbase	Okey & Mahmoudi 2002	Arreguin-Sanchez et al. 1993b
Adult menhaden	Walters et al. 2008	Althauser 2003	Walters et al. 2008
Juvenile menhaden	Ecopath Estimate	n/a	Walters et al. 2008
Shads	Fishbase	Fishbase	Fishbase
Other Clupeids	Multiple Sources	Manickchand-Heileman et al. 1998	Cruz Aguero 1993

Anchovies, Etc.	Multiple Sources	Arreguin-Sanchez et al. 1993a	Abarca-Arenas & Valero-Pacheco 1993
Squid	Okey et al. 2004	Manickchand-Heileman et al. 1998	Venier 1997
Caridean Shrimp	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Penaid shrimp	Walters et al. 2008	Manickchand-Heileman et al. 1998	Althauser 2003
Stone Crab	Walters et al. 2008	Okey et al. 2004	Walters et al. 2008
Blue Crab	Walters et al. 2008	Chavez et al. 1993	Althauser 2003
Benthic Invertebrates	Walters et al. 2008	Chavez et al. 1993	Walters et al. 2008
Macrozooplankton	Walters et al. 2008	Venier 1997	Abarca-Arenas & Valero-Pacheco 1993
Microzoolplankton	Walters et al. 2008	Walters et al. 2008	Walters et al. 2008
Infauna	Walters et al. 2008	Cruz-Escalona et al. 2007	Walters et al. 2008
Algae			
Seagrass			
Phytoplankton			
Detritus			