

2012

Identification and incorporation of quantitative indicators of ecosystem function into single-species fishery stock assessment models and the associated biological reference points

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IDENTIFICATION AND INCORPORATION OF QUANTITATIVE INDICATORS OF
ECOSYSTEM FUNCTION INTO SINGLE-SPECIES FISHERY STOCK ASSESSMENT
MODELS AND THE ASSOCIATED BIOLOGICAL REFERENCE POINTS

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by
Melissa Monk
B.S., Virginia Tech, 2004
M.S., Virginia Tech, 2007
August 2012

DEDICATION

To my husband Dr. Joshua Monk, for his support during my pursuit of a doctoral degree.

ACKNOWLEDGMENTS

First, I would like to thank my major advisor, Dr. Joseph Powers for all of his valuable insight, support, advice, and for challenging me as a student and scientist over the past four years. I also want to thank Dr. Powers for the opportunities he provided for me to attend conferences, symposiums and meetings and exposing me to the world of fisheries management. I am also grateful for Dr. Powers for answering my unending questions and always keeping his door open. I also owe a great amount of my gratitude to my committee members Dr. Jim Cowan, Dr. Chris D’Elia, Dr. Brian Marx, Dr. Kenny Rose, and my dean’s representative Dr. Fern Galvez. All of my committee members have been a wonderful source of knowledge in fisheries, statistics, and modeling. I want to thank all of my committee members for the time and effort they have given to my dissertation.

I want to thank Dr. Liz Brooks at the National Marine Fisheries Center for being my mentor through the NMFS/ Sea Grant Fellowship program. Thank you Dr. Brooks for encouraging me to learn R and taking the time to host meet for a week at the Northeast Fisheries Science Center. Dr. Brooks also provided valuable insight during the development process of my dissertation and provided feedback on my chapters.

I am especially grateful to Kirsten Simonsen and Dr. Michelle Zapp Sluis for taking me into the field to see real fish, deciding to pursue their “PhDs in Friendship” and for making this process so much more enjoyable. I am also grateful to Lauren Land, Dr. Melissa Baustian and Courtney Saari for making the EnvironMentors program such a huge success.

Finally, I would like to thank my husband, parents, grandparents, and in-laws for all of their love and support throughout my dissertation studies. I could not have done this without them.

This project was funded by the National Marine Fisheries Service / Sea Grant PhD Fellowship for Marine Population Dynamics as well as the Louisiana Department of Wildlife and Fisheries.

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ABSTRACT

The move towards an ecosystem approach to fisheries management requires baseline information on the biotic communities and an understanding of the interactions among species. The two objectives of this study were to describe the demersal fish community (DFC) associated with the northwestern Gulf shrimp trawl fishery, and to utilize a multispecies Lotka-Volterra model to examine possible community level effects of fishing. Community level effects include predator-prey interactions and the responses of fish in the same community to fishing pressure. The summer and fall Southeast Area Monitoring and Assessment Program (SEAMAP) bottomfish trawl surveys were used to identify spatial and temporal indicators in the northwestern Gulf. Cluster analysis and nonmetric multidimensional scaling analysis identified four distinct demersal fish communities (DFCs) from the summer survey data and three distinct spatial DFCs from the fall survey data. Indicator species analysis identified two different dominant communities within each DFC during the summer and fall survey periods. No statistically significant temporal trends were identifiable in the SEAMAP data over the selected time period (1986-2007). However, the community metrics from the DFCs were used to create initial parameters for a multispecies Lotka-Volterra simulation model. The Lotka-Volterra model was developed to study the implications of estimating single-species biological reference points from multispecies data and to determine the effect of fishing on other species in the same community. Three series of simulations were created to explore connectance, rebuilding plans, and multispecies fisheries in the Lotka-Volterra model. Across all simulations, the single-species F_{MSY} rates were estimated between 10-75% of the expected values from the Lotka-Volterra model, indicating that fishing mortality rate buffers are needed to account for predator-

prey interactions. No trends were detected as to the magnitude of the buffer for the species examined across all levels of community connectance. The magnitude of biomass changes in unfished species decreased as community connectance increased. The projected time for a species to rebuild was longer in the multispecies model versus the single-species model in four of five case studies. Indirect effects were important in all simulations and these results indicate a need for ecological buffers when determining single-species fishing mortality rates.

GENERAL INTRODUCTION

Commercial and recreational fisheries are of high economic value in the Gulf of Mexico (Gulf). In 2010, the Gulf produced 582 million metric tons of commercial fishery and 147 million fish were caught in recreational fisheries (National Marine Fisheries Service, 2011). All of the recreationally and commercially harvested species in federal waters are managed by the regional Fishery Management Council and stock assessments are most often conducted for individual species.

In the Gulf, two of the most economically significant fisheries are for red snapper (*Lutjanus campechanus*) and penaeid shrimps (brown, white, and pink). The red snapper and shrimp trawl fisheries are part of different Fishery Management Plans (FMPs) and the stock assessments for each are conducted separately. However, the two fisheries are connected. Juvenile red snapper are caught as bycatch in the shrimp trawl fishery in the northwestern Gulf. Estimates of age-0 and-1 year old red snapper discarded in the shrimp trawl fishery averages 36 million fish per year from 1948-2003 with high variability between years (SEDAR, 2005). The northwestern Gulf shrimp trawl fishery is believed to have contributed to the overfishing status of red snapper, as well as species of small coastal sharks (SEDAR, 2005; Shepherd and Myers, 2005). In addition to red snapper, over 800 additional fish and invertebrate species are discarded as bycatch in the shrimp trawl fishery (Sheridan et al., 1984; Alverson et al., 1994; Watling and Norse, 1998). The majority of bycatch species are not recreationally nor commercially harvested species. Species for which stock assessments are not conducted are often not well studied and the effects of bycatch on their populations are unknown.

In addition to the specific issue of bycatch, overfishing has been shown to drive ecosystem level changes such as trophic cascades (Daskalov, 2002; Folke et al., 2004; Crowder

et al., 2008). Other examples of community level changes caused by fishing include predatory release, reduction in the ecosystem's mean trophic level, a decrease in biodiversity, and shifts in species abundance distributions (National Research Council, 2006; Crowder et al., 2008; De Mutsert et al., 2008). Exploitation of natural resources also alters community structure and ecosystem function (Jackson et al., 2001; SEDAR, 2005). Fish communities off the coast of the northeast United States have exhibited shifts in species abundance in response to exploitation (Fogarty and Murawski, 1998; Garrison and Link, 2000). The Gulf has experienced similarly high exploitation rates that have potentially altered species dynamics and community composition.

One goal of the Magnuson-Stevens Fisheries Conservation and Management Act is the need to manage the effects of ecosystems and community-level responses to fishing pressure (MSRA, 2007). This in turn implies the need to understand the role of fishing on the ecosystem. The ecosystem impact of reducing fishing mortality on targeted species and reducing bycatch must be explored to ensure sustainability of all fish stocks. Multispecies/community or ecosystem models are approaches that have been used to explore changes in community dynamics. Multispecies and ecosystem models have gained traction with the move towards an ecosystem approach to fisheries management (Link, 2010; Pikitch et al., 2012)

The National Oceanic and Atmospheric Administration stated in its 5-year research plan a goal to “produce at least two integrated ecosystem assessments that evaluate the ecological response to various anthropogenic stressors” and... “to improve resource management by advancing our understanding of ecosystems through better simulation and predictive models” (NOAA, 2008). The plan also stressed the need to develop ecosystem indicators and determine the costs and benefits of management decisions that incorporate ecosystem considerations.

The study herein was designed to contribute to those goals. The overall goals of this dissertation were two-fold: 1) to define spatial and temporal changes in the demersal fish community associated with the northwestern Gulf shrimp trawl fishery, and 2) to examine the effects of fishing at the community level through the use of a multispecies Lotka-Volterra simulation model.

Currently, no studies have examined the community gradient along the entire northwestern Gulf shelf. In Chapter 1, the objectives were to utilize the fishery-independent Southeast Area Monitoring and Assessment Program (SEAMAP) bottomfish trawl survey data to identify regional demersal fish communities (DFCs) from a suite of multivariate statistics. The goal was to determine if the northwestern Gulf was a single homogenous DFC or if the area could be delineated into smaller, spatially explicit DFCs. This provides baseline information on the community composition of the demersal fishes and indicator species analysis was applied as a post-hoc analysis to identify species affiliating with particular DFCs.

The communities and indicator species within a specific DFC region can be used as ecosystem indicators for future studies. Ecosystem indicators can then be used to determine ecosystem health and the effects of fishing on all species in the same community. Temporal trends were explored due to the reduction of shrimp effort beginning in 2000 (Figure 1.1) (Nance et al., 2006). The decline in shrimp fishery effort is a result of the economic impact of hurricanes Katrina and Rita, rising fuel prices, and competition from imported shrimp. The reduction in shrimp effort resulted in a decline in bycatch, which could possibly have altered community composition.

To achieve the second goals, I used the ecological indicators identified from the SEAMAP data as input for a multispecies Lotka-Volterra model. However, due to the lack of

significant temporal trends, simulated data were used to initialize the Lotka-Volterra model. Chapters 2-4 explore the community level impacts of fishing and the implications of implementing a single-species fishing mortality rate when predator-prey interactions are known. Chapter 2 objectives focus on the development of the multispecies Lotka-Volterra model with a community of 25% connectance (see Dunne et al., 2002 for a review of connectance). A set of five species were selected to fish based on their connectivity properties, e.g., the species with the highest number of connections. For each of the five species, a single-species fishing mortality rate was estimated from the multispecies Lotka-Volterra time series. The single-species fishing mortality rate producing maximum sustainable yield (F_{MSY}) was compared to the value expected from the multispecies model. A single-species estimated F_{MSY} lower than the expected value indicates that species interactions affect the fished species productivity. The estimated fishing mortality rate of F_{MSY} was then implemented back into the multispecies Lotka-Volterra model to examine the effects of fishing on all other species in the community. In Chapter 2, the five selected species were also overfished to a level of 20% of their virgin biomass. Rebuilding times from projections of single-species and multispecies models were compared.

Chapters 3 and 4 are extensions of the Lotka-Volterra model developed in Chapter 2. The objective of Chapter 3 was to determine if connectance affected the magnitude of fishing mortality rate buffers and rebuilding times for five species with the same characteristics as in Chapter 2. The communities in Chapter 3 were created with connectance values of 35% and 45%. The objective of Chapter 4 was to utilize the community of 25% connectance to explore multispecies fisheries. Two fishing scenarios were implemented in Chapter 4. In the first scenario, five species with no direct connections to one another were simultaneously fished at their estimated single-species F_{MSY} rates. In the second scenario, five species with direct

connections were fished simultaneously at their individual single-species F_{MSY} rates. Each of the selected species was also fished independently to compare a single-species fishery with a multispecies fishery. The impacts on all other species in the same community were also examined for each simulation.

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CHAPTER 1 : SPATIAL AND TEMPORAL PATTERNS IN THE DEMERSAL FISH COMMUNITY ASSOCIATED WITH THE NORTHWESTERN GULF OF MEXICO SHRIMP TRAWL FISHERY

INTRODUCTION

Managing large exploited marine ecosystems in the more holistic approach of ecosystem based fisheries management (EBFM) encompasses a wide array of research needs (Pikitch et al., 2004; Link, 2010). Many factors affect the Gulf of Mexico (Gulf) large marine ecosystem, including fishing pressure, oil and gas exploration, land subsidence, sea level rise, and the outflow of the Mississippi and Atchafalaya Rivers. An understanding of all of these factors come together to make ecosystem management and marine spatial planning possible; ecosystem-based fisheries management is only one part.

Fisheries can alter the physical landscape, alter community assemblages in heavily exploited areas, and change species biodiversity (Bohnsack, 1998; Rice, 2000; National Research Council, 2002; Barnes and Thomas, 2005; Løkkeborg, 2005). Shrimp trawls alter the physical environment of the seafloor and also catch a large biomass and diversity of bycatch species (Churchill, 1989; Watling and Norse, 1998; Duplisea et al., 2002). The Gulf shrimp trawl fishery occurs primarily on the continental shelf in the northwestern Gulf, with the majority of effort in areas of <30 fathoms (Nance et al., 2006). Many of the species caught as bycatch in the Gulf are neither commercially/recreationally harvested nor managed, and have not been monitored as closely as species with high economic value. Few studies, outside of those using fishery-dependent data have examined the biodiversity and community assemblage patterns in the northwestern Gulf. Studies that have been conducted focused on specific areas of the Gulf, the effect of oil and gas platforms on community assemblages, and the effect of trawling on

specific species (Chittenden Jr and McEachran, 1976; Stanley and Wilson, 1997; Wells et al., 2008). Understanding the spatial changes in the ecological communities in heavily exploited systems can be used to monitor the health of the ecosystem (Leslie and McLeod, 2007; Link, 2010; Fogarty and Murawski, 1998).

Fishery Effect on Non-target Species

Interactions among species within an ecosystem are often important aspects in single-species management, but they have not always been considered when developing Fishery Management Plans (FMPs) or in single-species stock assessments. In the Gulf of Mexico two of the most economically significant fisheries are for the red snapper (*Lutjanus campechanus*) and penaeid shrimps (brown, white, and pink). The red snapper and shrimp fisheries are managed within separate FMPs and the stock assessments for each are conducted separately. However, the two fisheries greatly impact one another. The Gulf shrimp trawl fishery catches a large high numbers of non-target bycatch (Sheridan et al. 1984, Alverson et al. 1994, Watling and Norse 1998), and is believed to have contributed to overfishing of some species, including red snapper and species of small coastal sharks (SEDAR 2004, Shepherd and Myers 2005). Estimates of age-0 and-1 year old red snapper discarded in the shrimp trawl fishery averages 36 million fish per year from 1948-2003 with high variability among years (SEDAR 2004). In general, the impact of bycatch on both harvested and non-harvested populations as well as on overall ecosystem function is unknown and difficult to study (Crowder et al. 2008, Walters et al. 2008).

Red snapper in the U.S. Gulf are currently considered to be overfished with overfishing no longer occurring in the western Gulf (Gulf of Mexico Fishery Management Council, 2010) as the stock is recovering. There is a long history of debate regarding the magnitude of age-0 and age-1 juvenile red snapper caught as bycatch in the shrimp trawl fishery (Workman and Foster,

1994; Gallaway and Cole, 1999; Gallaway et al., 1999; Gazey et al., 2008). Juvenile red snapper may have experienced competitive release as a result of historically high levels of bycatch in the shrimp fishery. While the current red snapper assessment focuses on scenarios for shrimp bycatch reduction, the actual effects at an ecosystem level of reducing fishing mortality on age-0 and age-1 fishes is unknown.

One discussion found throughout the red snapper assessment is that of density-dependence and when in the life history of the fish it occurs. The age-0 and age-1 fish can be considered recruited into the fishery during age-0 because of the bycatch in the shrimp trawl fishery. It is also postulated that natural density-dependent processes occur during the pre-recruit stages of life for red snapper (Myers and Cadigan, 1993; Brooks and Powers, 2007; Gallaway et al., 2009; Cowan et al., 2011). The question of timing of density-dependence is important for stock assessment modeling because it affects the estimates of natural mortalities rates, i.e., in the larval and early post-larval stage or during settlement.

In addition to the specific issue of bycatch, overfishing likely causes a multitude of changes in an ecosystem. These ecological changes include predatory release, reduction in the ecosystem's mean trophic level, a decrease in biodiversity, and shifts in species abundance (National Research Council 2006, Crowder et al. 2008). Each of these factors affects the community structure and ecosystem function (SEDAR 2004, Jackson et al. 2001). While many species have been impacted by fishing, their response both to fishing and subsequent regulations has been varied (NEFSC 2008). Additionally, there have been shifts in species abundance distributions indicating ecosystem changes (Fogarty and Murawski 1998, Garrison and Link 2000).

The Magnuson-Stevens Fisheries Conservation and Management Act (MSFCMC) required overfishing to end by 2010. The ecosystem impact of reducing fishing mortality on targeted species and reducing bycatch should be explored to ensure sustainability of all fish stocks. The National Oceanic and Atmospheric Administration most recent 5-year research plan stresses the need to develop ecosystem indicators and determine the costs and benefits of management decisions made on an ecosystem scale. A objective of the National Ocean Policy is for increased use of ecosystem-based management and increased consideration of coastal and marine spatial planning as a management tool (Sievanen et al., 2011).

Marine spatial planning is one vehicle to implement ecosystem-based management (Douvere, 2008; Gilliland and Laffoley, 2008). Spatial planning is a common practice in terrestrial systems, where multiple stakeholders are often involved in the decision making process regarding natural resources, and where environmental considerations must also be accounted for in management plans. Marine spatial planning aims to reduce user group conflict, while sustainably managing natural resources, mitigating environmental impacts, and preserving ecosystem services (Obama, 2010). Marine resources in the United States are managed by a multitude of agencies and over 140 statutes (Crowder and Norse, 2008). There are different statutes and laws in place to independently manage threatened and endangered species, fisheries, marine mammals, and the oil and gas industry. Marine spatial planning can be used to manage the needs of multiple stakeholders. Marine spatial planning is not limited to marine reserves and preserves. It also encompasses, but is not limited to, management practices of rotating or seasonal area closures, gear restrictions, artificial reef habitat, and identification and management of essential fish habitat.

One scientific need for both ecosystem-based management and marine spatial planning is a baseline spatial inventory of the biotic and abiotic communities. The research presented herein utilizes the fishery-independent surveys to identify spatial shifts in the northwestern Gulf demersal fish communities and also to identify seasonal and temporal shifts in the species inhabiting the northwestern Gulf.

This study will also look at correlations between changes in the community structure and changes in the shrimp fishery effort. It is unknown if the recent 70% reduction in shrimp effort (Nance et al., 2006), and assumed reduction in bycatch, has resulted in a change in the community composition.

Gulf of Mexico Shrimp Fishery and Bycatch

The shrimp trawl fishery in the federal waters of the Gulf of Mexico is managed by the Gulf of Mexico Fishery Management Council through the Shrimp Fishery Management Plan (FMP). The four targeted species of shrimp managed under the plan include brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Penaeus setiferus*), pink shrimp (*Penaeus duorarum*), and royal red shrimp (*Hymenopenaeus robustus*). In the western Gulf only brown and white shrimp are heavily harvested.

Amendments have been added to the original shrimp FMP to reduce bycatch, specifically bycatch of juvenile red snapper. Bycatch reduction devices have been required on shrimp trawls since 2002. Amendment 13, added in 2005, established overfishing thresholds for the penaeid shrimp stocks in the Gulf, as well as established methods to report bycatch and a moratorium on commercial shrimp vessel permits. Amendment 14 in 2007 passed as a joint amendment to the Reef Fish FMP created a targeted goal of reducing juvenile red snapper mortality by 74% of the values during 2001-2003. The goal was to again reduce mortality by 67% beginning in 2001,

with to the ultimate reduction goal of 60% by 2032. The recent reduction in shrimp effort in the Gulf may allow these requirements to be met without implementing additional fishing regulations (Figure 1.1).

The shrimp trawl fishery in the Gulf catches a large biomass and diversity of bycatch species (Alverson et al., 1994; Diamond, 2004; Scott-Denton, 2007). The shrimp fishery occurs along the entire continental shelf in the northwestern Gulf, with the majority of effort in areas of <30 fathoms (Nance et al., 2006). The majority of bycatch species are juvenile, and are neither harvested nor regulated species and have not been monitored as closely as species with high economic value (Diamond, 2004). As a result, there is little understanding of how the shrimp fishery affects fishery population rates.

This study aims to provide baseline information on the spatial and temporal dynamics of the demersal fish community associated with the shrimp trawl fishery. The first objective of this study was to characterize the spatial dynamics of the northwestern Gulf demersal fish community. Indicator species were identified for all of the identified spatial regions and also by season. The objective of the temporal component was to determine if the communities showed significant changes over time and if those changes could be correlated with the reduction in shrimp fishing effort. The temporal dynamics of a subset of dominant species were also examined to visually note any potential changes over time.

Little is known about the possible long-term ecological and community assemblage changes caused by bycatch removal. The recent reduction in Gulf shrimp effort adds another level of complexity to the system. The reduction in shrimp effort will act as a natural experiment to observe any reorganization or changes occurring in the demersal fish community assemblage. There is a current effort to study the shrimp effort reduction from the fishery-dependent observer

data (E. Scott-Denton, pers. comm.). Temporal trends in the Gulf ichthyoplankton community assemblages have been partially explained by changing shrimp effort and sea surface temperature, but the leading drivers remain unknown (Muhling et al., 2012).

METHODS

Data sources

The Southeast Area Monitoring and Assessment Program (SEAMAP) database was obtained from the Gulf States Fisheries Commission. SEAMAP is a collaborative program for collecting fisheries-independent data in the southeastern United States. The two yearly surveys utilized in this study are the fall shrimp and bottomfish trawl survey (1986-2007) conducted in June-July, and the summer shrimp and bottomfish trawl survey (1982-2008) conducted in October-November (Eldridge, 1988). The methodologies for both the summer and fall surveys are the same. The bottomfish trawl survey design is a stratified random sample with sampled sites (latitude, longitude) selected randomly within strata of depth, day/night, and shrimp statistical zone (location). The gear is a 12.8-m semi-balloon shrimp trawl with a 2.4-m \times 1-m chain bracketed wood doors and a standard free tickler chain cut 1.07-m shorter than the footrope. Vertical profile data of temperature, salinity, dissolved oxygen (DO), and fluorescence were collected with each tow using conductivity, temperature, depth profiler (CTD).

The depth strata of focus for this study is 10-30 fm, the depths over which the majority of the shrimp fishery effort affecting red snapper is concentrated (Gallaway et al., 2003). The Gulf is divided into shrimp statistical zones for management of the shrimp trawl fishery in federal waters (Figure 1.2). The northern Gulf is bifurcated by the Mississippi River outflow, which includes discharge from waters covering two-thirds of the United States (Gallaway, 1981).

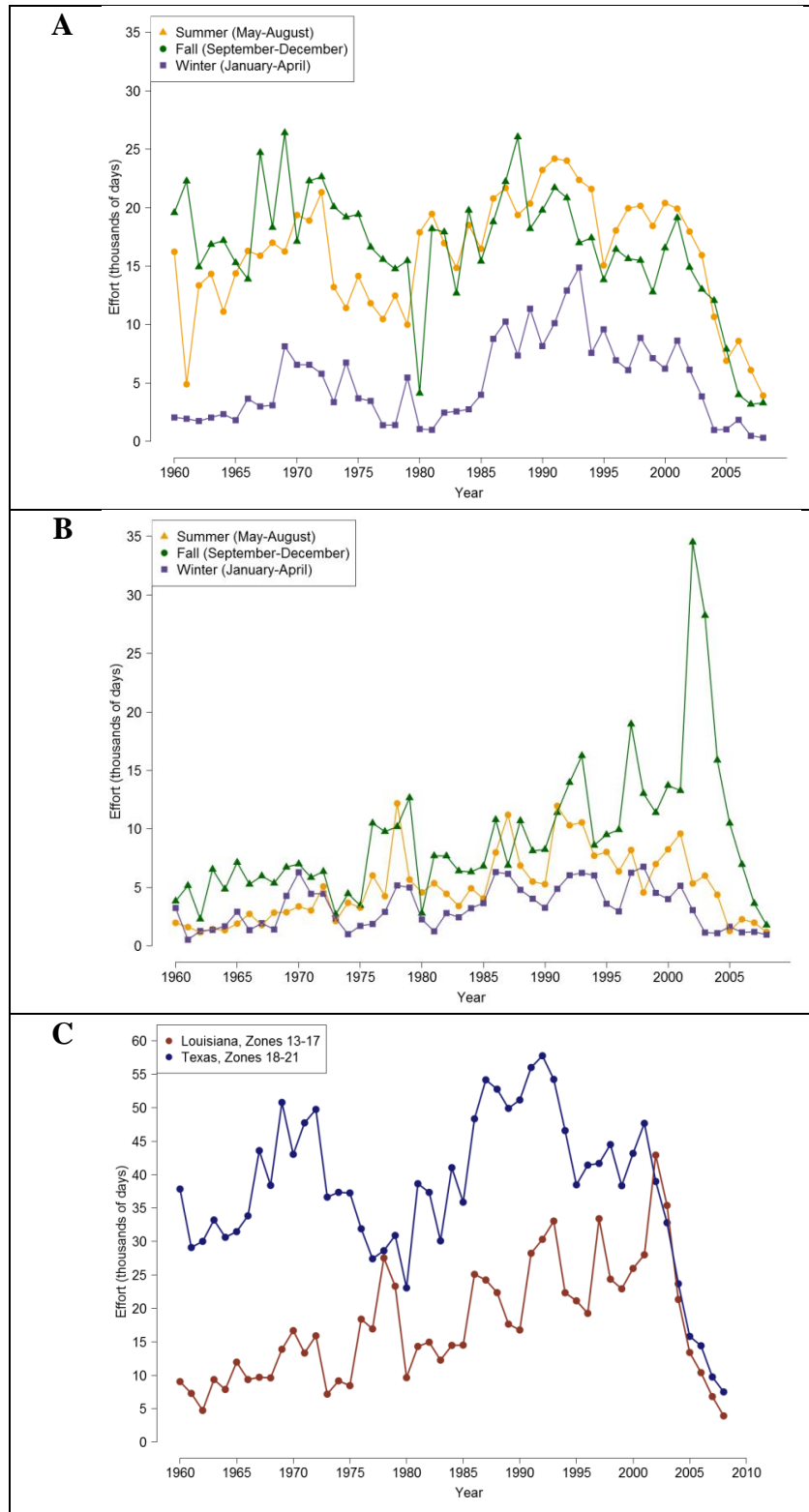


Figure 1.1. Shrimp effort in the northwestern Gulf of Mexico by season for Texas (A), Louisiana (B), and total annual effort by state (C) for the depth range of 10-30 fm. Data courtesy of Jim Nance, NMFS.

The northeastern Gulf (shrimp statistical zones 1-9) is dominated by sandy bottom habitat with only 6% of the annual shrimp catch originating from Florida (Gallaway et al., 2003). Shrimp statistical zones 10-12 are directly to the east of the mouth of the Mississippi River's bird foot delta and represent species from both the northeastern and northwestern Gulf. I chose to examine only the northwestern Gulf. Zones 13-21 were selected as a subset for this study because they represent the area with the highest level of shrimp fishery effort and have been consistently sampled during SEAMAP cruises.

The design of the SEAMAP survey is stratified by shrimp statistical zone; 13-15 ($89^{\circ}00'$ - $92^{\circ}00'$ W long), 16-17 ($92^{\circ}00'$ - $94^{\circ}00'$ W long), 18-19 (west of $94^{\circ}00'$ W long and north of $28^{\circ}00'$ N lat), and 20-21 ($26^{\circ}00'$ - $28^{\circ}00'$ N lat). The stratification of depth in the sample design is sampling at 1 fm intervals from 5-20 fm, 2 fm intervals from 20-22 fm, 3 fm intervals from 22-25 fm, 5 fm intervals from 25-50 fm, and 10 fm intervals from 50-60 fm. Additional details for each cruise can be obtained in the SEAMAP environmental and biological atlases and the individual cruise reports (Johnson, 2008; Rester et al., 2008).

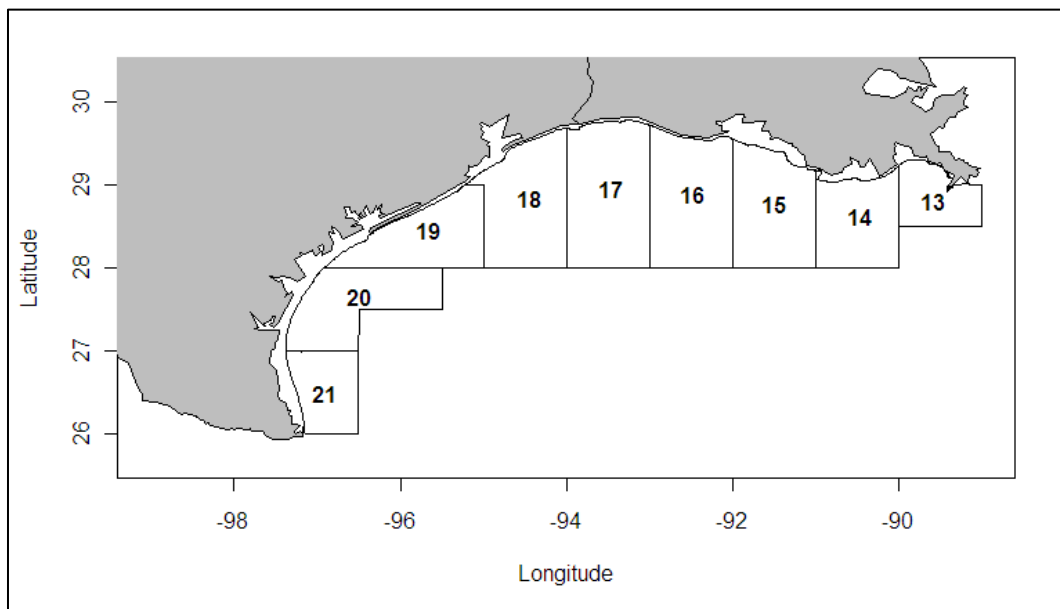


Figure 1.2. Map of the northwestern Gulf of Mexico shrimp statistical zone delineations.

During the survey period there were numerous experimental tows deployed that used sampling gear other than the standard SEAMAP shrimp trawl. Only the non-experimental trawls that were categorized as employing a standard shrimp trawl net with a 12.8-m headrope were included in this analysis. This also excludes some trawl survey data conducted by either Louisiana or Texas that used trawls of a different headrope length or mesh size. The data were also examined for any other biases that could influence statistical analyses. SEAMAP protocol dictates that an individual tow be between 10 and 55 minutes. However, some tows require a longer amount of time to cross the 1 fm depth contour required by the protocol and some tows may represent two individual tows needed to complete the sampling location. Stations with recorded tow times less than ten minutes were discarded. Stations with recorded tow times between 55 and 80 minutes were examined for anomalies and comments to ensure that the data recorded for these tows followed protocol. The maximum tow time was 70 minutes for the summer data and 79 minutes for the fall data. Stations with comments indicating that a particular tow did not perform successfully were also removed from the data, to reduce the potential of sampling bias. These “unsuccessful” tows included reports of mechanical problems, torn nets from hard bottom structures, and incomplete tows. For stations that used paired tows, only one was selected for analysis to keep the samples as balanced as possible.

The final effort for summer trawls used in this analysis (in units of number of tows by year and shrimp statistical zone) can be found in Table A.1 and for fall trawls in Table A.2. A total of 3309 tows were used from the summer survey and 2849 from the fall surveys. There are two missing years of data (1983 and 1986) for the summer survey in Zone 13. The number of tows in a given year/zone combination are variable depending on weather, mechanical problems, vessel crew and gear conditions. For these analyses, all species data were standardized to

number (abundance) of fish caught per hour. Abundance was used for the multivariate analyses (nonmetric multidimensional scaling and cluster analysis) because there was no missing data.

Two additional datasets utilized in this study include information on the bottom habitat type and the location of oil platforms in the northwestern Gulf of Mexico. The bottom habitat data were obtained from the GSMFC and include the dbSEABED database, which is a compilation of bottom habitat studies in the Gulf with approximately 377,000 observations (Buczkowski et al., 2006). For this study, the bottom habitat types were classified as “gravel, sand, mud mix,” “gravel, mud mix,” “gravel, sand mix,” “sand, mud mix,” “sand dominant,” “mud dominant,” “gravel dominant,” and “rock dominant.” For a habitat type to be classified as dominant, the sample or observation had to contain at least 50% of the particular bottom type. Each individual SEAMAP tow was classified as one of these eight bottom habitats based on the nearest habitat observation. Distance between habitat observations and SEAMAP tows were measured using the haversine formula to calculate the great-circle distance. If the closest habitat measurement was more than 10km from any tow, then the tow was classified as having no available habitat assignment. The oil platform data was of interest due to findings from previous studies in the northern Gulf that correlated species abundance and composition to distance from oil platforms (Stanley and Wilson, 1991; Stanley and Wilson, 1996; Stanley and Wilson, 1997). The oil rig dataset was obtained from Minerals Management Services. Each individual SEAMAP tow was assigned a distance from the nearest oil platform. I accounted for dates that platforms were installed, removed or toppled.

Standardized Species Index

The catch was dominated by a few abundant species and many rare species. More than 800 species are represented in the SEAMAP bottomfish trawl surveys. Only samples identified

to the species level were included in the study to eliminate any confounding effects with species possibly appearing twice. Species appearing in less than 3% of all tows were discarded from the data for analyses (Koch, 1987; Mueter and Norcross, 2000). Rare species (observed less than 3% of the time) can mask patterns in ordination and create excess noise in the data (McCune et al., 2002). In addition, gelatinous zooplankton species were removed from the dataset due to inconsistent sampling of these species over time (J. Rester, pers. comm.). The number of species present in a minimum of 3% of all tows was 110 species for the fall survey (Table A.3.) and 112 species for the summer survey (Table A.4). All species used in analyses and their scientific names can be found in Table A.3 and Table A.4.

Either species counts or biomass can be used to calculate the standardized index. The decision to use of species counts or biomass in community analyses is subjective, and has been shown to have only small effects on the outcome of community analyses (Bianchi and Hoesaeter, 1992). Species counts were used in the standardized index for the multivariate analyses because there was no missing count data. Species biomass was used in the standardized index for the temporal analyses because population level changes were of interest. Species count and biomass were both standardized as species presence per hour in each tow. No adjustments were made for differing catchabilities among species

The standardized index of catch per unit effort (CPUE) was calculated separately for each statistical zone. The index used was an extension of the geometric mean that accounts for tows in which a species was not observed (Connors et al., 2002):

$$Index = \left(\prod_{i=1}^n a_i \right)^{\frac{1}{n}} * \frac{n}{T} \quad (1.1)$$

where a_i was the species abundance in tow i per hour, n is the number of tows in which the species was present, and T was the total number of tows contributing to the index, including tows in which the species was not observed. An index was created for each combination of species, zone, season, and year.

Distance measure

A first step in analyzing community data for multivariate analyses was to determine the similarity, or distance between any two samples. The community matrix of the survey index was created in which rows represented shrimp statistical zones and columns represented species. The chord distance (D_{chord}), or Relative Euclidian Distance, was chosen as the distance metric (Legendre and Legendre, 1998; McCune et al., 2002).

$$D_{chord(ih)} = \delta_{ih} = \sqrt{\sum_{i=1}^p \left[\left(\frac{a_{ij}}{\sqrt{\sum_{j=1}^p a_{ij}^2}} \right) - \left(\frac{a_{hj}}{\sqrt{\sum_{j=1}^p a_{hj}^2}} \right) \right]^2} \quad (1.2)$$

In equation 1.2, a_{ih} represented the species dissimilarity between any two shrimp statistical zones i and h , and p was the number of tows in which the species was observed. The chord distance measure was equivalent to normalizing the row (zone) totals so the marginal sum of squares is one and taking the Euclidian distance (Orloci, 1967; McCune et al., 2002). This ensures that no single species dominated the calculation of the dissimilarity matrix. This also gave the sample units (shrimp statistical zones) the same weight, making the differences in effort among those sample units irrelevant.

One post-hoc analysis was conducted using the distance metric. The dissimilarity matrix was partitioned to determine the contribution of each species to the overall dissimilarity between any two pre-defined sampling units i and h (Clarke, 1993). The pre-defined sampling units were

the DFC regions identified in the multivariate analyses. The contribution of a species to the chord distance was:

$$\delta_{ih}(j) = \frac{a_{ij} - a_{hj}}{D_{chord(ih)}} \quad (1.3)$$

Multivariate Analyses

Two multivariate analyses were conducted to characterize regional DFCs in the SEAMAP data: non-metric multidimensional scaling (NMDS) (Shepard, 1962; Kruskal, 1964) and agglomerative hierarchical cluster analysis. Advantages of using NMDS include the preservation of rank order distances from any dissimilarity measure, no assumption of multivariate normal distributions, and the ability to freely rotate the ordination axes (Clarke, 1993). The final coordinates in ordination space were evaluated by fitting a regression through a plot of the original distances from the dissimilarity matrix to the fitted distances in ordination space. The sum of squares from the regression analysis (known as stress) was the goodness-of-fit statistic used for the NMDS (Kruskal, 1964). Stress was used to determine the number of axes that best explained the data. Axes were retained until the decrease in stress obtained by adding an additional axis was reduced by less than five percent.

Hierarchical agglomerative cluster analysis (henceforth cluster analysis) using Ward's minimum variance linkage method was the second statistic used to explore community similarity among shrimp statistical zones (Ward Jr, 1963; Orloci, 1967; Wishart, 1969; McCune et al., 2002). Cophenetic correlation was used as the goodness-of-fit statistics for the cluster analysis (Sokal and Rohlf, 1962). Cophenetic correlation is the correlation between distances in the original dissimilarity matrix and the distances in the dendrogram. The goodness of fit statistic used to assess the dendrogram was the cophenetic correlation coefficient.

NMDS and cluster analysis were first applied to a dissimilarity matrix with each year within a shrimp statistical zone as one row. If clustering among years within a zone was found, data were pooled across years for each zone. The dissimilarity matrix was recalculated using the pooled data and the multivariate statistics were recalculated.

Exploratory analyses resulted in degenerate ordination solutions in PRIMER and PC-ORD (Clarke and Warwick, 2001; McCune and Mefford, 2006). The Vegan package in R was used for all multivariate analyses (Oksanen et al., 2010; R Core Development Team, 2011)

Indicator species analysis

Indicator species analysis provided a method to assign species to the regional DFCs identified in the multivariate analyses based on that species fidelity and occurrence frequency (Dufrene and Legendre, 1997; McCune et al., 2002). The indicator value (IV) for a species, j , is a combination of relative abundance (RA) and relative frequency (RF) in a pre-defined group, k (Eq. 1.4).

$$IV_{kj} = 100 * (RA_{kj} * RF_{kj}) \quad (1.4)$$

The pre-defined groups were the regionally defined DFCs. The IV ranges from 0 to 100, with 100 indicating the species was a perfect indicator of the regional DFC. Statistical significance of the IV was determined from 10,000 Monte Carlo simulations. The dissimilarity matrix in which each year/zone was a row was used for the indicator species analysis.

The NMDS and cluster analysis were programmed in R (R Core Development Team, 2011) utilizing the Vegan community ecology package for the NMDS (Oksanen et al., 2010) and the cluster package for cluster analyses (Maechler et al., 2002). The indicator species analysis was conducted in PC-ORD (McCune and Mefford, 2006).

Temporal Analysis

Temporal trends were explored within the regional DFCs identified from the multivariate analyses. Species biomass was used for the temporal analyses because overall population level changes were of interest. Missing biomass data were inferred by using information from the same species in the same year if possible or from neighboring years in the same regional DFC.

The goal of the temporal analysis was to determine if changes in community composition could be explained by changes in the shrimp fishery effort. Canonical correspondence analysis was also conducted, using shrimp effort as an explanatory variable. Other explanatory variables explored included sea surface temperature and dissolved oxygen. Time lags of one, two, three and five years were also explored.

A subset of species was selected for further investigation of temporal trends. For a given regional DFC and season (summer or fall), the ten species with the highest average biomass that were also present in at least 3/4 of all years were selected. The motivation for selecting species based on presence and biomass was to have a set of species with enough data to detect statistical trends over time. The selection routine was also conducted using abundance to ensure that the species selected as having high biomass were not low in numerical abundance (e.g., sea turtles). A total biomass index was calculated for each DFC, by summing the individual species standardized biomass indices in a given year. Visual observations were made of the changes in biomass of the top ten species and also the total biomass within a DFC.

RESULTS

While some of the shrimp statistical zones for the summer and fall were within the same branches of the analysis, zones within season clustered together (i.e. F17 and S17 are less similar than F17 and F18) (Figure 1.3). This corroborated the decision to analyze the fall and summer

data independently. The cophenetic correlation for the cluster analysis was 0.7834, indicating a good fit between the original distance matrix and the clusters. All further analyses were conducted independently for the summer and fall surveys.

Sediment classification

All selected SEAMAP tows were successfully assigned a sediment type (Figure 1.4). The majority of the northwestern Gulf within 10-30 fm was dominated by a mud substrate. However, a wide range of habitat types were represented in the SEAMAP tows. There was a transition moving west from a mud dominated substrate to a sand dominated substrate along the inner Texas shelf. The continental shelf was also steeper along southern Texas, resulting in 10-30 fm tows with a closer proximity to land. There was a noticeable spatial void of tows in Zone 17 at approximately 29°N. A possible explanation is that the area was exceptionally flat. SEAMAP protocol states tows needed to trawl across a one fathom depth contour. The distance required to meet the protocol would exceed the time limit of 55 minutes for a station tow to cover the contour requirement in this area. There were no statistically significant results using habitat type as an explanatory variable for community assemblage.

Summer Bottomfish Trawl Survey

The similarity matrix revealed that the community associated with Zone 13 was not similar to any other shrimp zones with only 48% similarity to Zone 14, the closest zone geographically (Table 1.1). Adjacent zones, excluding Zone 13, had similarity values ranging from 65-85%, and exhibited a trend of decreasing similarity of species composition as the distance between a pair of zones increases. There is a general trend that Zones 14-18 all exhibit low similarity with Zone 20.

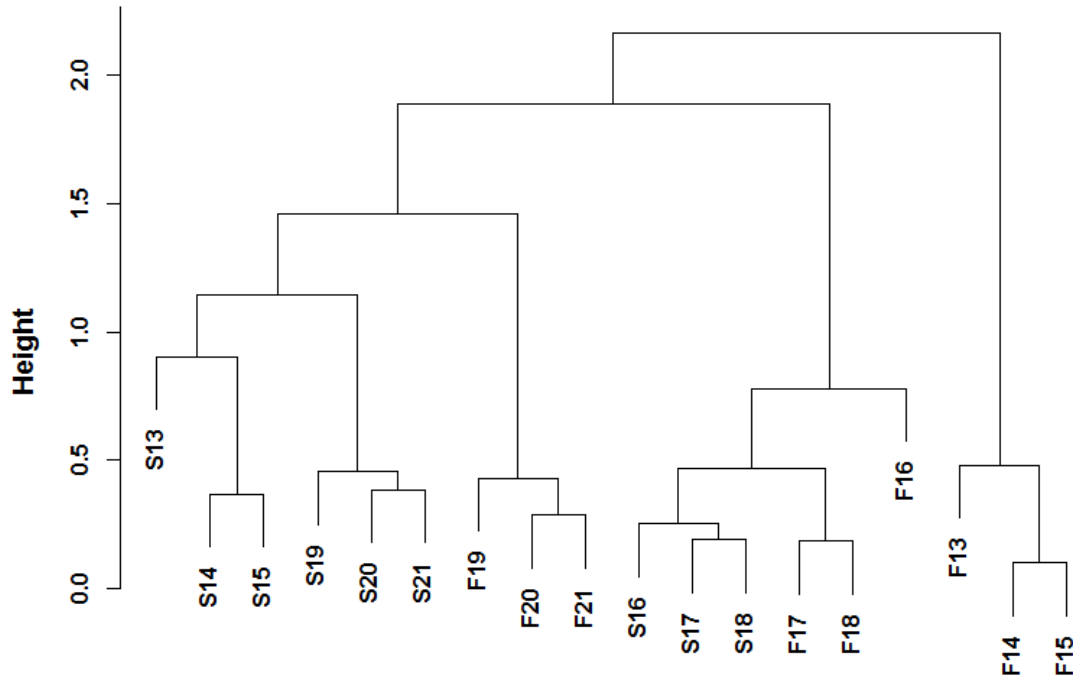


Figure 1.3. Dendrogram for the cluster analysis using one sample per shrimp statistical zone and survey (summer and fall). For zones 13-21, the “S” indicates the summer survey and the “F” indicates the fall survey.

The stress values for the summer data indicated that three axes explain the data. The axes are arbitrary in NMDS and upon visual inspection the separation among shrimp zones was most visible in the first two axes. The NMDS results using a data point for each year and zone combination revealed the temporal heterogeneity in species composition among the zones, especially Zone 13 (Figure 1.5). The NMDS coordinates for Zone 13 indicated a separation from all other zones along the first axis and the yearly variability with the points along the entire second axis. The NMDS analysis with each year as a data point indicated that there was similarity within zone and that the data could be pooled by year (Figure 1.5).

After pooling the data across years, there were four distinct clusters evident from the NMDS; Zone 13, Zones 14-15, Zones 16-18, and Zones 19-21. It does appear that zones 19 and 21 are more similar than zones 20 and 21 along the second axis. The species contributing to the

dissimilarity between zone pairs and also the species contributing to the zone similarities will be discussed later in this chapter.

The cophenetic correlation coefficient in the cluster analysis was 0.780, which is a reasonable value given the variability in the raw data. In the cluster analysis, Zone 13 was again dissimilar from all the other zones and forms its own branch in the dendrogram (Figure 1.7). Zones 14-18 formed a second distinct branch and within that branch Zones 14-15 and Zones 16-18 showed further separation of species composition. Zones 19-21 formed a separate branch, indicating a fourth unique grouping of species composition in the northwestern Gulf. The repeatability of the results between the NMDS and the cluster analysis provides evidence that in the summer months there are four distinct regional DFCs in the northwestern Gulf. These regions represent a gradient of changing species composition starting at the mouth of the Mississippi River and moving westward. The four DFCs will be denoted as Zone 13 DFC, the East DFC (representing Zones 14-15), Mid DFC (representing Zones 16-18) and West DFC (representing Zones 19-21) (Figure 1.8).

Species' contributions to the dissimilarity index between any two DFCs were identified (Table 1.5). Roughback shrimp (*Trachypeneus similus*), longspine porgy (*Stenotomus caprinus*), and Atlantic croaker (*Micropogonias undulates*) all contributed at least 5% of the dissimilarity between the East DFC and the other three DFCs. Roughback shrimp and longspine porgy also contributed at least 5% to the dissimilarity among the Mid DFC and both other regions. Brown shrimp (*Farfantepenaeus aztecus*), longspine porgy, and roughback shrimp contributed to the dissimilarity between the West DFC and all other regions.

The p -values from the correlation of species to the NMDS axes were calculated for each region (Table 1.6). No species could be significantly correlated to the Mid DFC due to the location of zones 14-15 on the first axis. All of the species identified as having a statistically significant correlation with either the Zone 13, Mid or West DFC also had a statistically significant indicator values to the same region (see Indicator Species Analysis). The repeatability of the correlation to the NMDS axes and the statistically significant indicator values indicated that these suites of species could be monitored and used as ecological indicators for each of the identified DFCs.

Fall Groundfish Survey

The similarity matrix calculated from the relative chord distance indicated that adjacent zones contain the most similar species assemblages for the fall survey (Table 1.4). Zone 13 had 70% similarity with Zone 14 and 71% with Zone 15, a much higher value than in the summer trawls. The similarity of species composition between Zones 18 and 19 was the lowest at 42%. Zones 13-18 all had less than 30% similarity with Zones 20 and 21. There was a general trend of decreasing community assemblage similarity as zones became farther apart geographically. The dissimilarity between zones that were farther apart in geographical space indicated a shift in the community assemblages along a longitudinal gradient in the 10-30 fm depth range.

Most years within statistical zones clustered together (Figure 1.9). For visualization purposes, the data were color coded by the results from the NMDS used to define DFCs. This confirmed the motivation to create one index for each zone over all years to explore the spatial changes in community assemblages.

The stress value for the fall survey NMDS ordination without temporal variation indicated that the first two axes explained the data and can be used to examine the spatial shifts

in the fall survey. The NMDS revealed spatial separation in community assemblage among the shrimp statistical zones (Figure 1.10). Axis one described a longitudinal shift in community assemblages from the mouth of the Mississippi River to the Texas/Mexico border. Zone 13 was the only zone that did not fall in numerical order with the other zones, but is still clustered with Zone 14 and 15. The zones clustered into three distinct zoogeographic areas, zones 13-15, zones 16-18, and zones 19-21.

The cophenetic correlation coefficient for the fall survey cluster analysis was 0.912, indicating the dendrogram accurately reflected the data. The cluster analysis from the fall survey revealed the same pattern as the NMDS, identifying three regional clusters. Zones 13, 15, and 19 had a larger height value in the dendrogram and this could indicate that these are the zones in which the transition of the assemblages was occurring as one moved from east to west along the northwestern Gulf (Figure 1.12). The NMDS and cluster analysis both indicated three distinct DFCs from the fall survey, an East DFC (representing Zones 13-15), a Mid DFC (representing Zones 16-18), and West DFC (representing Zones 19-21).

Fewer species contributed at least 5% to the dissimilarity between two DFCs in the fall than in the summer survey (Table 1.5). In all pairs of DFCs, two species contributed to over 50% of the dissimilarity index. Atlantic croaker contributed around 30% to the dissimilarity between all pairs of DFCs. Longspine porgy contributed the most of any species to a dissimilarity, 62% between the East and Mid DFCs. Brown shrimp contributed about 7% to the dissimilarity between the West and both other regions. The fewer number of species contributing indicates a community in the fall that is dominated by fewer species of high abundance.

The separation of the three DFCs along the two NMDS allowed for correlation between species abundance centers with one of the three regions. Axis one of the NMDS ordination separated the East and West DFCs while axis two separates the Mid DFC from the other two regions. Species associating with the East DFC (negative correlation with both axes) were the fringed flounder (*Etropus crossotus*), sand seatrout (*Cynoscion arenarius*) and southern flounder (*Paralichthys lethostigma*). Thirteen species associated with the Mid DFC with weak correlation to the first axis based on the Pearson correlations. The species with high positive correlation of at least 0.9 were the red goatfish (*Mullus auratus*), roundel skate (*Raja texana*), lane snapper (*Lutjanus synagris*), longspine porgy, brown rock shrimp (*Sicyonia brevirostris*), round scad (*Decapterus punctatus*), and planehead filefish (*Monacanthus hispidus*). Species associating with the West DFC are the Gulf of Mexico fringed sole (*Gymnachirus texae*), lesser rock shrimp (*Sicyonia dorsalis*), and the arrow squid (*Loligo pleii*). All of the species with high correlation to a particular axis were also identified in the indicator value analysis as having the same maximum group association (see Indicator Species Analysis Results).

Table 1.1. Percent similarity between each pair of shrimp statistical zones based on chord distances for the summer survey.

Zone	S13	S14	S15	S16	S17	S18	S19	S20
S14	48%							
S15	35%	74%						
S16	15%	56%	71%					
S17	9%	46%	62%	85%				
S18	12%	47%	62%	77%	85%			
S19	30%	59%	71%	60%	57%	65%		
S20	29%	44%	44%	33%	30%	39%	65%	
S21	18%	45%	51%	48%	47%	57%	73%	73%

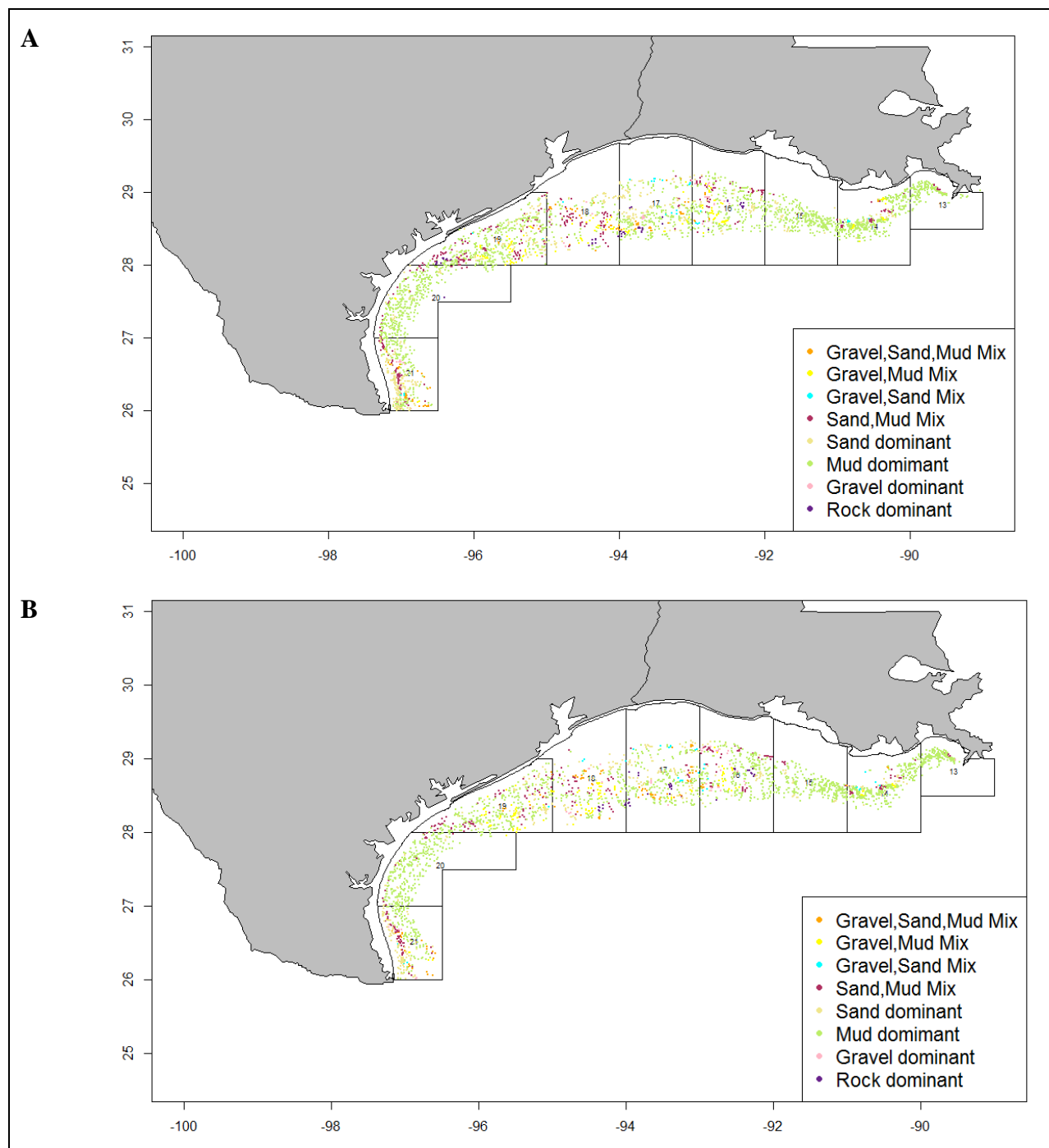


Figure 1.4. Map of the summer (A) and fall (B) within 10-30 fm color coded by the assigned habitat type.

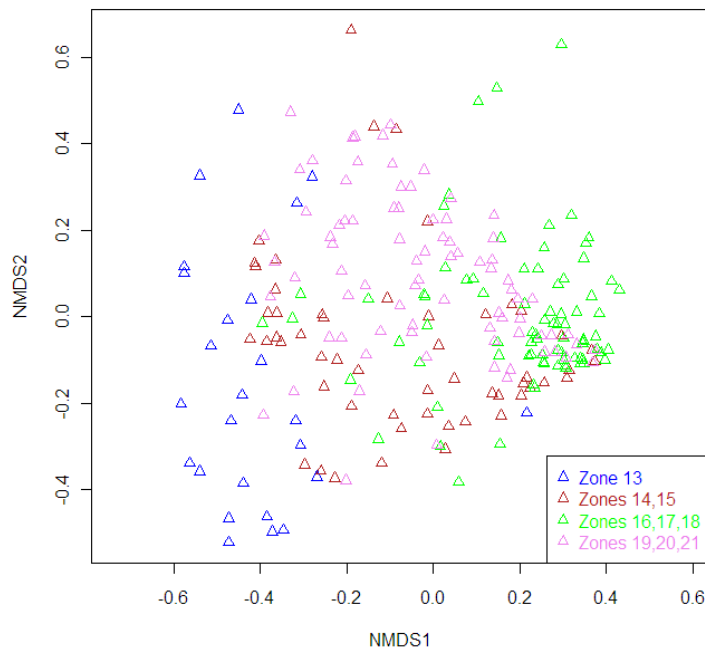


Figure 1.5. Nonmetric multidimensional scaling results to map changes in species composition by shrimp statistical zone in the northwestern Gulf of Mexico. Each point represents one year of data for a particular zone.

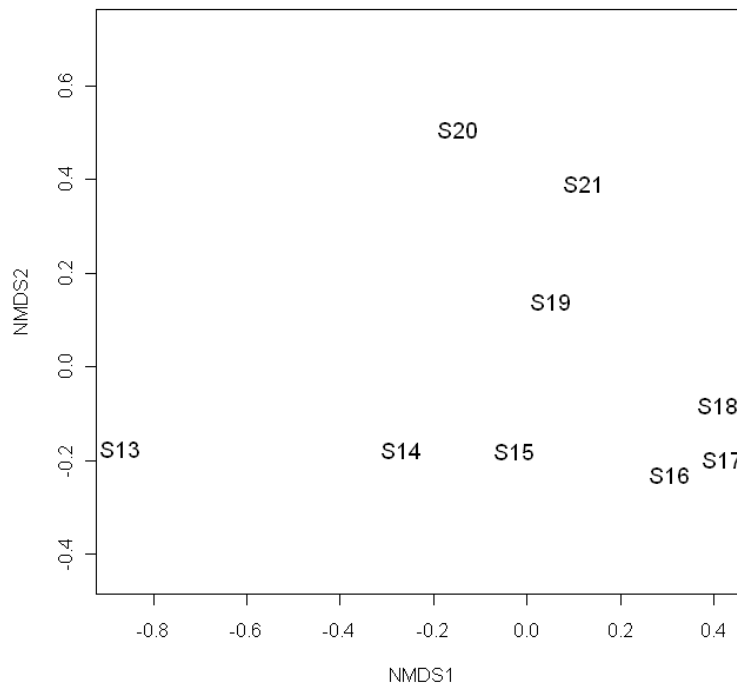


Figure 1.6. Nonmetric multidimensional scaling results for the fall bottomfish trawl survey. The data by year for each shrimp statistical zone were pooled to determine overall community structure among the zones.

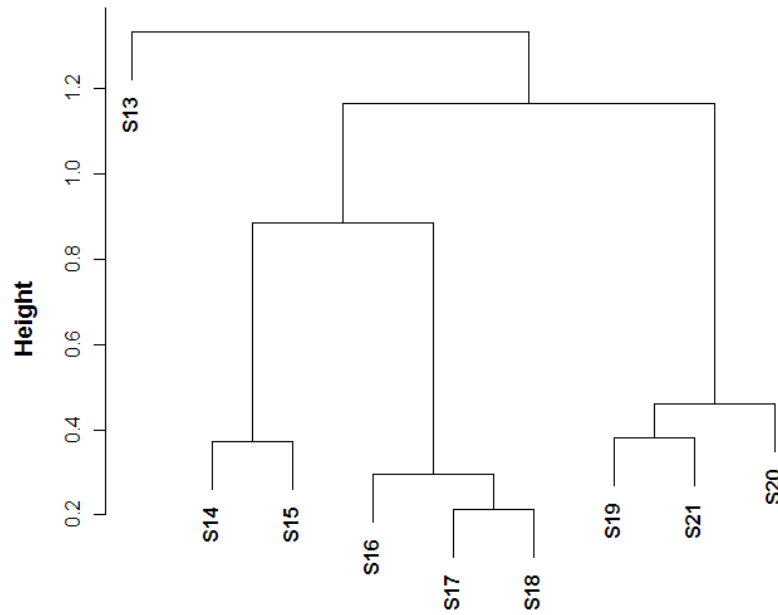


Figure 1.7. Dendrogram from the cluster analysis of shrimp statistical zones from the summer SEAMAP surveys. The height measures the similarity of species composition within a branch. Smaller values indicate greater similarity.

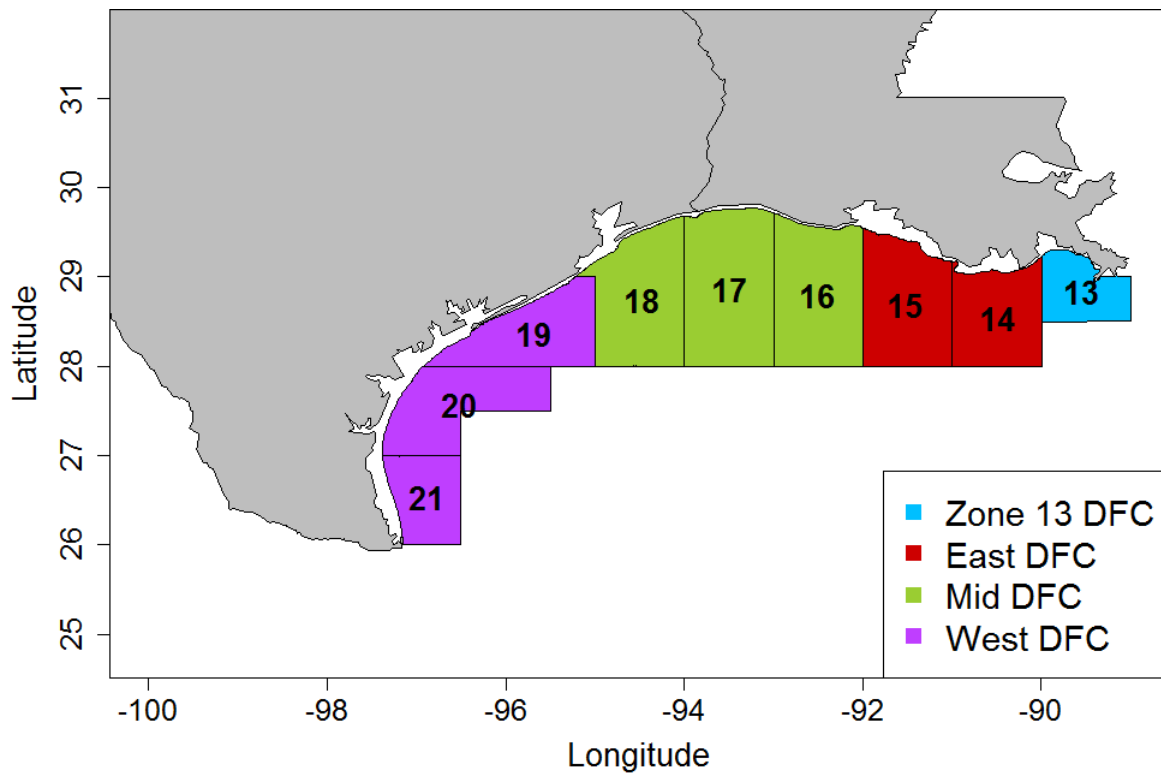


Figure 1.8. Delineation of the summer regional demersal fish communities (DFCs) as determined from the NMDS and cluster analyses.

Table 1.2. Species accounting for the dissimilarity between any two regions up to the 95% cumulative contribution to the total dissimilarity. The maximum group is from the indicator species analysis and is the region with which the species is most prevalent. A value of *NS* indicates a non-significant indicator value for any region.

Species	$\bar{\delta}_k$	$\bar{\delta}_k / \sum \bar{\delta}_k$ %	Maximum Group
East vs. Mid DFCs			
Roughback shrimp	0.159	26.33	Zone 13
Longspine porgy	0.114	18.77	Mid
Bigeye searobin	0.075	12.32	Zone 13
Atlantic croaker	0.060	9.91	East
Brown rock shrimp	0.033	5.47	Mid
Gulf butterfish	0.030	4.88	<i>NS</i>
Mantis shrimp (<i>S. empusa</i>)	0.028	4.63	Zone 13
Brown shrimp	0.017	2.75	West
Lesser blue crab	0.015	2.51	West
Blackear bass	0.008	1.40	East
Iridescent swimming crab	0.008	1.33	East
Rock sea bass	0.008	1.32	Zone 13
Lesser rock shrimp	0.007	1.12	West
Fringed flounder	0.004	0.70	East
Broad-striped anchovy	0.004	0.66	Zone 13
Atlantic cutlassfish	0.004	0.66	Zone 13
Arrow squid	0.004	0.60	West
Atlantic bumper	0.003	0.56	Mid
East vs. West DFCs			
Brown shrimp	0.242	35.956	West
Bigeye searobin	0.077	11.492	Zone 13
Atlantic croaker	0.076	11.307	East
Longspine porgy	0.066	9.776	Mid
Roughback shrimp	0.053	7.910	Zone 13
Arrow squid	0.038	5.640	West
Mantis shrimp (<i>S. empusa</i>)	0.021	3.067	Zone 13
Gulf butterfish	0.018	2.626	<i>NS</i>
Lesser blue crab	0.016	2.396	West
Dwarf goatfish	0.012	1.843	West
Iridescent swimming crab	0.011	1.628	East
Rock sea bass	0.008	1.147	Zone 13
Fringed flounder	0.005	0.703	East

(Table 1.2 continued)

Mid vs. West DFCs			
Brown shrimp	0.315	43.205	West
Longspine porgy	0.215	29.476	Mid
Lesser blue crab	0.044	6.047	West
Roughback shrimp	0.039	5.377	Zone 13
Brown rock shrimp	0.031	4.310	Mid
Arrow squid	0.020	2.776	West
Atlantic croaker	0.014	1.985	East
Dwarf goatfish	0.008	1.037	West
Gulf butterfish	0.007	1.004	NS
Atlantic bumper	0.006	0.763	Mid
Zone 13 vs. All Other DFCs			
Longspine porgy	0.443	41.478	Mid
Roughback shrimp	0.232	21.750	Zone 13
Brown shrimp	0.084	7.834	West
Bigeye searobin	0.082	7.690	Zone 13
Mantis shrimp (<i>S. empusa</i>)	0.069	6.508	Zone 13
Atlantic cutlassfish	0.026	2.449	Zone 13
Arrow squid	0.019	1.745	West
Atlantic croaker	0.014	1.351	East
Lesser blue crab	0.013	1.221	West
Gulf butterfish	0.010	0.915	NS
Blackwing searobin	0.008	0.768	Zone 13
Brown rock shrimp	0.008	0.724	Mid
Sand seatrout	0.008	0.704	Zone 13
Ragged goby	0.007	0.661	Zone 13

Table 1.3. Species ranked by correlation (ρ) with dimension one for Zone 13 and Mid DFC and dimension two for the West DFC of the multidimensional scaling. For dimension one, negative values indicate species with a higher abundance in Zone 13 and positive values indicate species with a higher abundance in the Mid DFC. For dimension two, the positive values indicate species with a higher abundance in the West DFC.

Species	Dimension one ρ	Dimension two ρ
Zone 13		
Bigeyed frogfish	-0.917	-0.116
Roughback shrimp	-0.909	-0.345
<i>S. chy.</i> mantis shrimp	-0.903	-0.073
Bay whiff	-0.837	-0.924
Sq. emp. Mantis shrimp	-0.823	-0.470
Atlantic cutlassfish	-0.820	-0.408
Mid DFC		
Longspine porgy	0.955	0.023
Inshore lizardfish	0.904	-0.001
Ocellated flounder	0.871	-0.338
Atlantic bumper	0.857	-0.144
Planehead filefish	0.839	-0.086
Gray triggerfish	0.814	0.298
West DFC		
Bigeye scad	-0.223	0.942
Arrow squid	0.179	0.912
Lined sea star	0.016	0.907
Two-spined sea star	0.014	0.902
Brown shrimp	-0.217	0.892
Sea pansy	-0.109	0.884
Shortwing searobin	0.141	0.882
Smooth puffer	0.281	0.878
Brazilian lizardfish	0.072	0.826
Longfin inshore squid	-0.027	0.826
Round sardinella	0.079	0.820
Wenchman	0.408	0.817

Table 1.4. Percent similarity between each pair of shrimp statistical zones for the fall survey using the chord distance.

Zone	F13	F14	F15	F16	F17	F18	F19	F20
F14	70%							
F15	71%	93%						
F16	47%	53%	58%					
F17	26%	28%	33%	72%				
F18	19%	19%	24%	61%	87%			
F19	32%	25%	29%	41%	39%	42%		
F20	29%	17%	19%	24%	22%	24%	71%	
F21	23%	13%	16%	23%	24%	28%	73%	80%

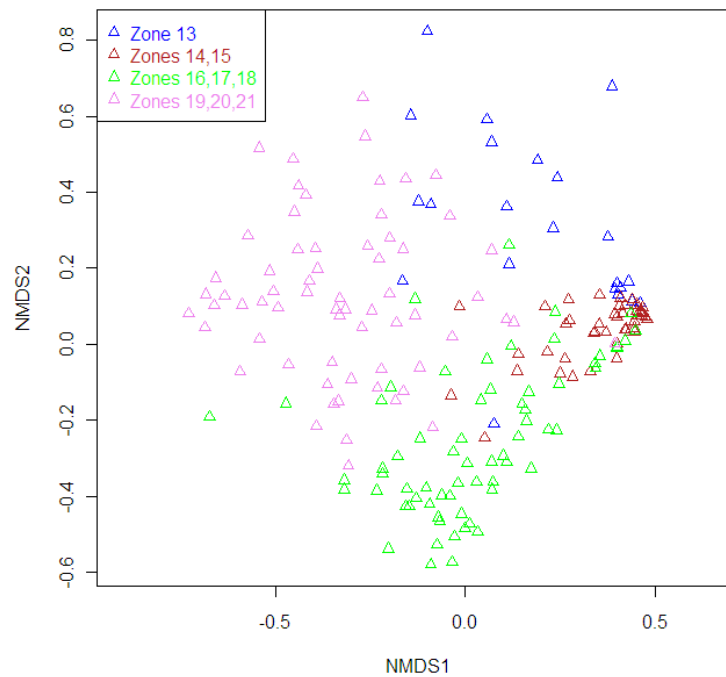


Figure 1.9. Nonmetric multidimensional scaling for mapping changes in species composition by shrimp statistical zone in the northwestern Gulf of Mexico. Each point represents one year of data for a particular zone.

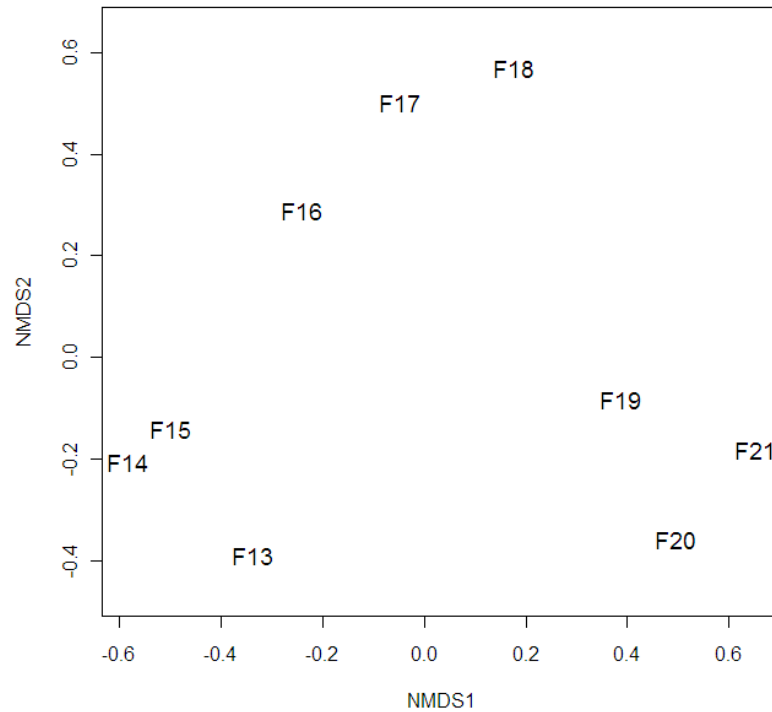


Figure 1.10. Nonmetric multidimensional scaling ordination results for the fall bottomfish trawl survey. The data by year for each shrimp statistical zone were pooled to determine overall community structure among the zones.

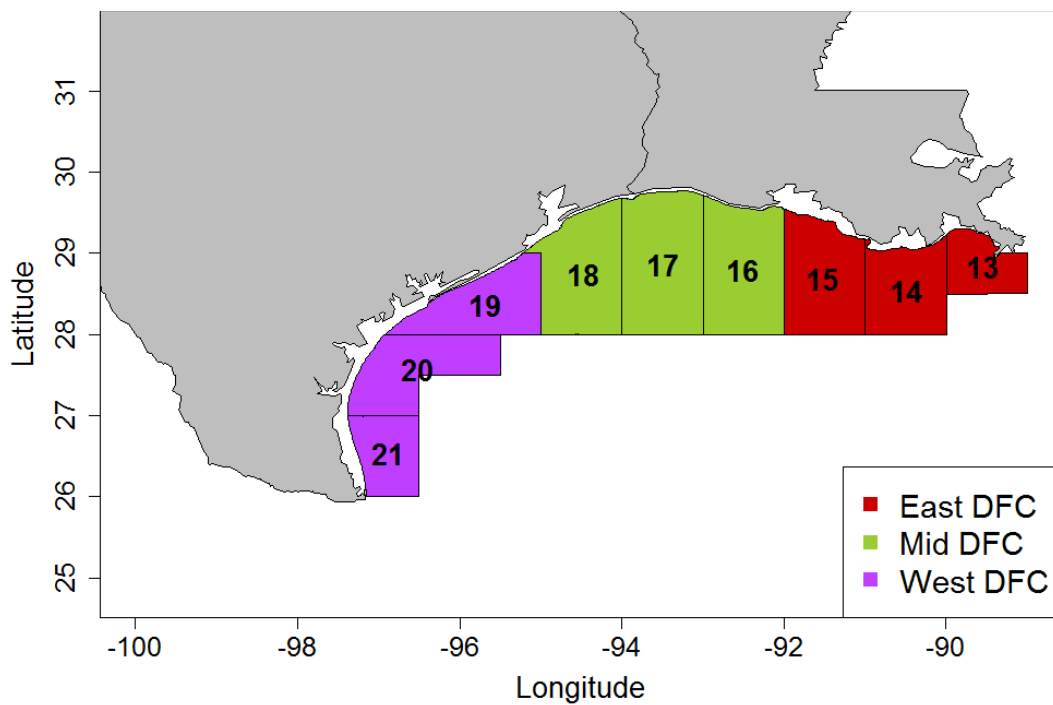


Figure 1.11. Map of the shrimp statistical zones indicating the DFCs from the fall trawls.

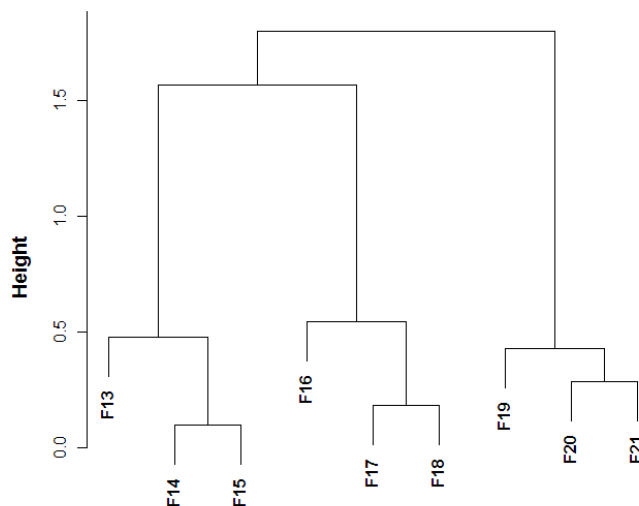


Figure 1.12. Dendrogram from the cluster analysis of shrimp statistical zones from the fall SEAMAP surveys. The height measures the similarity of species composition within a branch. Smaller values indicate greater similarity

Indicator Species Analysis

The indicator species analysis for the fall was conducted with the Zone 13 DFC separated from zones 14-15, so that direct comparisons could be made with the summer survey (Table 1.8). The results from the fall indicator analysis illustrated that there are species affiliating with only Zone 13 that did not have high indicator values for zones 14-15.

The number of indicator species for each region varied as well as the strength of the indicator values by species. For the summer survey, 22 species were identified as indicators for Zone 13 DFC, seven species as affiliating with the East DFC, 28 species identifying with the Mid DFC, and 26 species identifying with the West DFC (Table A.5). For the fall survey, 29 species were identified as indicators for Zone 13 DFC, eight species as affiliating with the East DFC, 29 species identifying with the Mid DFC, and 32 species identifying with the West DFC (Table A.5).

Table 1.5. Species contribution to the average dissimilarity between two DFCs for the fall SEAMAP trawl survey. The species presented are those that cumulatively sum to 95% of the percent contribution. The maximum group association is the result from the indicator species analysis, with *NS* is a non-significant result

Species	$\bar{\delta}_k$	$\bar{\delta}_k / \sum \bar{\delta}_k$ %	Maximum group association
East vs Mid			
Longspine porgy	0.575	61.54	Mid
Atlantic croaker	0.276	29.59	East
Atlantic cutlassfish	0.010	1.04	East
Roughback shrimp	0.009	0.99	<i>NS</i>
Northern white shrimp	0.007	0.77	East
Lesser blue crab	0.007	0.74	East
Atlantic bumper	0.005	0.58	West
Gulf butterfish	0.005	0.58	Mid
East vs West			
Atlantic croaker	0.437	39.88	East
Atlantic bumper	0.332	30.27	West
Brown shrimp	0.079	7.17	West
Shoal flounder	0.043	3.95	West
Roughback shrimp	0.037	3.34	<i>NS</i>
Longspine porgy	0.036	3.28	Mid
Dwarf sand perch	0.032	2.91	West
Northern red snapper	0.013	1.21	West
Lesser blue crab	0.013	1.15	East
Atlantic cutlassfish	0.009	0.79	East
Gulf butterfish	0.008	0.74	Mid
Iridescent swimming crab	0.007	0.68	East
Mid vs West			
Longspine porgy	0.345	34.70	Mid
Atlantic bumper	0.291	29.25	West
Atlantic croaker	0.080	8.05	East
Brown shrimp	0.074	7.47	West
Roughback shrimp	0.053	5.37	<i>NS</i>
Shoal flounder	0.042	4.19	West
Dwarf sand perch	0.025	2.56	West
Lesser blue crab	0.018	1.80	East
Iridescent swimming crab	0.012	1.23	West
Red snapper	0.008	0.83	West

Table 1.6. Species ranked by correlation (ρ) with the axes from the NMDS. For dimension one, negative values indicate species with a higher abundance in the East DFC and positive values indicate species with a higher abundance in the West DFC. For dimension two, the positive values indicate species with a higher abundance in the Mid DFC.

Species	Dimension One ρ	Dimension Two ρ
East DFC		
Fringed flounder	-0.846	-0.500
Sand seatrout	-0.693	-0.536
Southern flounder	-0.783	-0.517
Mid DFC		
Red goatfish	0.976	-0.033
Roundel skate	0.962	0.037
Lane snapper	0.942	0.037
Longspine porgy	0.919	-0.191
Brown rock shrimp	0.919	0.138
Round scad	0.905	0.092
Planehead filefish	0.900	-0.119
Horned searobin	0.865	0.110
Inshore lizardfish	0.855	0.072
Mexican searobin	0.847	0.218
Paper scallop	0.835	0.110
Tomtate grunt	0.829	0.203
Smoothhead scorpionfish	0.805	0.122
West DFC		
Gulf of Mexico fringed sole	0.860	-0.446
Lesser rock shrimp	0.826	-0.456
Arrow squid	0.815	-0.546
Mexican flounder	0.629	-0.501
Southern kingcroaker	0.744	-0.528

The summer and fall surveys shared 17 similar indicator species in Zone 13, three of the same indicator species in the East DFC, 19 of the same species in the Mid DFC, and 14 of the same species in the West DFC. There were also 27 species in the summer and 14 in the fall that had non-significant indicator values. Species with non-significant indicator values either had low indicator values for all regions or had indicator values that were higher for more than one region.

An example of this was the Atlantic spadefish (*Chaetodipterus faber*) from the fall survey, which had an indicator value of 14 for both the East and Mid DFCs.

The top five indicator species for Zone 13 had higher overall indicator values than other regions. For both surveys, indicator species in Zone 13 had low indicator values for the other three regions (Table A.5). For example, in the fall survey, the Atlantic cutlassfish (*Trichiurus lepturus*) had an indicator value of 51 for Zone 13 and the next highest value of four for the East DFC. The Atlantic cutlassfish, Mantis shrimp (*S. empusa*) and sand seatrout (*Cynoscion arenarius*) were in the top five indicator species for both surveys. The relatively high values for the species in Zone 13 indicate that these species can be used with confidence to monitor the community in this region.

The small number of indicator species for the East DFC suggests that this may be a transitional area between Zone 13 and the Mid DFC. This is corroborated by the lower indicator values for species in this region. Atlantic croaker, which was found in high abundance throughout the SEAMAP survey, was a significant indicator species for both the summer and the fall. In the fall survey, Atlantic croaker had a much higher indicator value than in the summer survey (Table 1.8).

The species in the Mid DFC had relatively high indicator values, with the top five species all having indicator values above 25. Four species were found in the top five in both surveys, brown rock shrimp (*Sicyonia brevirostris*), inshore lizardfish (*Synodus foetens*), lane snapper (*Lutjanus synagris*), and longspine porgy. The continuity of the significant indicators in both surveys indicated that these species may not be as transient species in other DFCs. Longspine porgy and inshore lizardfish are the only two species that have indicator values higher than 20 for any other DFC.

The West DFC did not have any of the top five species in common between the summer and fall surveys. Brown shrimp, which had a high indicator value in the summer, did have a significant indicator value for the West in the fall. In the fall, brown shrimp had a broader range across the northwestern Gulf (Table A.6). Atlantic bumper had the highest indicator value for the fall survey, but associated with the Mid DFC in the summer. The summer indicator value was significant, but low at a value of 20. Red snapper (*Lutjanus campechanus*) also exhibited an interesting shift in distribution. Red snapper was found in the top five indicator value in the Mid DFC in the summer survey and in the West DFC in the fall survey.

Community assemblage trends

The Pearson correlation coefficient between tow time and species richness was 0.2814, indicating a weak association, using the raw data of one point per tow. However, when the data were pooled over year and zoogeographic area, the pattern of overall species richness follows that of a species-area curve (Figure 1.13) (MacArthur and Wilson, 1967). However, the DFCs with higher species richness did not necessarily have a higher overall biomass of the total catch. The West DFC presents high species richness, yet the total index value for the region was most often the lowest over the time series.

Two other noticeable trends were that for the 1984 summer survey, all of the DFCs had peaks in the total biomass. The fall survey did not begin until 1986 so there was no data for the fall surveys for comparison. In 1996, there were peaks in total biomass in the fall survey for Zone 13 and the East DFC, and both surveys in the Mid DFC. In 2000, all surveys except for Zone 13 and the East DFC in the fall, exhibited a low total biomass index, but species richness did not exhibit the same trend.

Table 1.7. Five species with the highest significant indicator value for each demersal fish community (DFC). The indicator value is in parentheses and a ‘*’ indicates a species is one of the top five in both surveys.

DFC	Summer Survey	Fall Survey
Zone 13	Atlantic cutlassfish (51) Mantis shrimp (<i>S. empusa</i>) (41) Sand seatrout (41) Atlantic brief squid (40) Bigeye searobin (37)	Northern white shrimp (64) Atlantic cutlassfish (52)* Mantis shrimp (<i>S. empusa</i>) (46)* Sand seatrout (42)* Lesser blue crab (42)
East	Iridescent swimming crab (37) Fringed flounder (27) Atlantic croaker (25) Blackear bass (16) Crested cuskeel (9)	Atlantic croaker (53)* Bigeye searobin (34) Spot croaker (30) Rock sea bass (21) Fringed flounder (16)
Mid	Brown rock shrimp (41) Longspine porgy (35) Red snapper (31) Inshore lizardfish (27) Lane snapper (26)	Longspine porgy (50)* Lane snapper (40) Brow rock shrimp (39)* Inshore lizardfish (33)* Gray triggerfish (29)
West	Brown shrimp (58) Dwarf goatfish (53) Lesser blue crab (32) Lesser rock shrimp (28) Brazilian lizardfish (25)	Atlantic bumper (62) Dwarf sand perch (47) Brazilian lizardfish (34) Red snapper (33) Shoal flounder (33)

The species identified as comprising the dominant communities varied by DFC and also by survey season (Table A.7). The only two species that were identified as being part of the dominant community in both surveys for all DFCs were the Atlantic croaker and the brown shrimp. The entire data set used includes 522 species identified to the species level, but not present in any dominant community or the summer trawls. For the fall survey, there were 469 possible species that comprise the “other” category. The species richness for any DFC and year

combination ranged from 14 to 180. The proportion of these species contributing to the “other” category also varied by year and DFC, and was correlated to the total minutes towed.

In all DFCs, the biomass of the “other” species was consistently around 40% of the total biomass during the summer survey. The proportion of biomass contributed by the “other” species was consistently higher in the summer than in the fall, except for the East DFC. For all of the DFCs, the composition of the biomass of the most prevalent species differed between the summer and fall surveys.

The total biomass index for Zone 13 was the highest of all regions in four years, but Zone 13 also had the smallest sample sizes (Figure 1.13). This is in part because a single zone comprises the entire DFC. Zone 13 had lower species richness in both surveys than other regions, which is a function of the smaller area and fewer total minutes towed in Zone 13 versus the other regions.

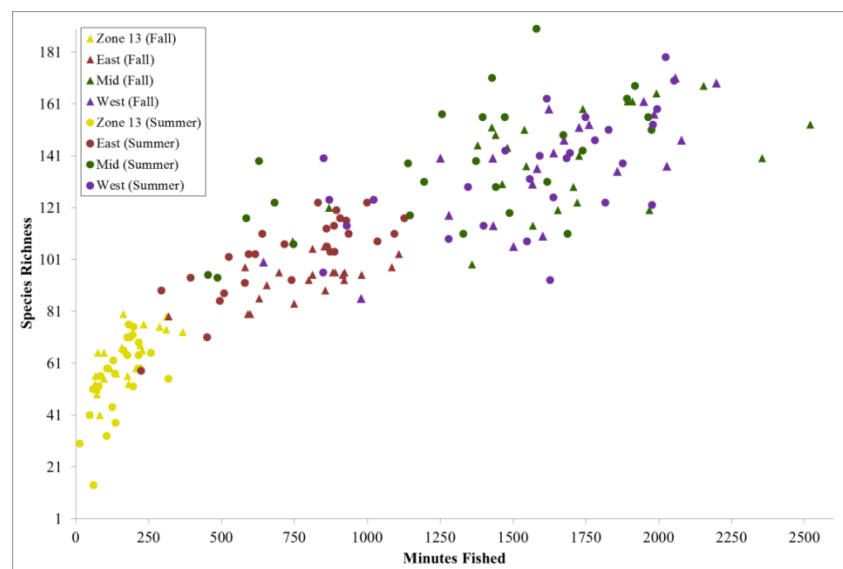


Figure 1.13. Relationship between the total minutes fished in a given year species richness. The data points are color coded by the regional demersal fish community and survey season.

In the summer trawl, the non-dominant species represent a high proportion of the total biomass index and exhibited no discernible temporal pattern in either in species composition or total biomass (Figure 1.14). Looking only at the dominant community in Zone 13), species with a high proportional biomass during the summer trawl such as the lesser blue crab, bigeye searobin, sand seatrout, and brown shrimp, were only a small component of the fall community assemblage. Atlantic croaker dominates the summer community during three years of the summer survey, 2002, 2006 and 2008. The species in the “other” category in the fall was often less than 40% of the standardized biomass. The fall community was largely dominated by the Atlantic croaker throughout the time series, and consistently so in the last three years of available data. The Atlantic croaker was responsible for the high total biomass in 2005 and 2006. Spot croaker appeared to have a decreasing presence over time as Atlantic croaker biomass increased.

The East DFC, which in this case represents Zones 14-15 for both the summer and fall surveys, had a lower total biomass index for the summer tows than in the fall (Figure 1.16). Species richness was consistently higher in the summer than the fall for the entire time series (Figure 1.13). This was also true for the count and biomass of “other” species in the summer trawl survey. The contributed biomass of the non-dominant species in the fall is less than 40% over the entire time series. The dominant community assemblage during the summer shifted over time. In the early years of the survey, there was a more evenly distributed biomass among the top species. Since 2000, the dominance of Atlantic croaker in the summer trawls has increased from being less than 20% of the dominant biomass, to over 60% in the last three years of the summer survey. The prevalence of the longspine porgy has decreased over time, while the Gulf butterfish and brown shrimp remained prevalent until 2006 (Figure 1.13). The total standardized biomass in the fall survey has shown a marked increase in the last five years of the

survey, which are all after the shrimp effort reduction. Atlantic croaker was a dominant portion of the biomass over the entire time series of the fall survey. Spot croaker, silver seatrout, and sand seatrout were also consistently present in the fall survey.

The Mid DFC had the lowest percentage of “other” species of the four regions, with a maximum of 55% of the standardized biomass index in 1983 in the summer (Figure 1.18). The non-dominant species comprised less than 40% of the total biomass index over the entire time series. Since 2000, the biomass index for the summer has, on average, increased, and the fall survey total biomass reached peak years in 2005 and 2007. Atlantic croaker has noticeably increased in dominance in the summer survey and has also increased over the time series in the fall survey (Figure 1.19). Longspine porgy composed a large proportion of the catch and followed the same trend in abundance over the survey period in both the summer and fall surveys. The proportion of the catch for sand seatrout, silver seatrout, and spot croaker remained constant for the fall survey period. Atlantic bumper exhibited a higher presence in the summer survey than the fall, with two peaks in abundance in 1989 and 2000.

The West DFC catch has a consistently low total biomass index compared to the other three regions (Figure 1.20). The three highest years are the first three years of the summer survey (1982-1984), of which there is no data available for the fall survey. There are no visible and consistent temporal trends in the summer data. Brown shrimp compose the highest percent of the biomass index over the entire summer survey period. There is a slight upward trend in the biomass from the fall survey from 2003-2007, but cannot be contributed to any single of the dominant species. However, the percent of catch in the “other” category exhibits a slow decline from 1996 to the end of the fall survey period. Atlantic bumper are not present in the dominant catch for the summer, but do comprise as much as 40% of the catch in the fall survey. Two

squids, the arrow squid and the longfin inshore squid are only present in the dominant community in the summer survey, with the longfin inshore squid exhibiting a consistent presence in the latter years of the survey. The spot croaker and the silver seatrout are only present in the fall community, and the percent contribution to the total biomass declines for both species over time.

DISCUSSION

Both the NMDS and cluster analysis identified an ecological gradient from East to West and regional demersal fish communities in the northwestern Gulf. Three distinct DFCs were identified from the summer SEAMAP data and four DFCs were identified from the fall SEAMAP data. However, many of the dominant species identified in the indicator analysis differed by season within a DFC.

The seasonal change in community assemblages may be explained by the life history characteristics of the species associated with the shrimp trawl. Many of the species are juveniles when captured as bycatch in the shrimp trawl and undergo ontogenetic shifts in abundance over the course of the year. The size distributions (pooled over all years and zones) of eight species with high biomass were examined to explore changes in size distributions (Figure A.1-2). For example, red snapper exhibited a decrease in size from the summer to fall survey. This is likely the result of the young-of-the-year settling onto trawlable, low relief habitat as age-1 fish move to more complex habitat and deeper waters (Patterson, 2007).

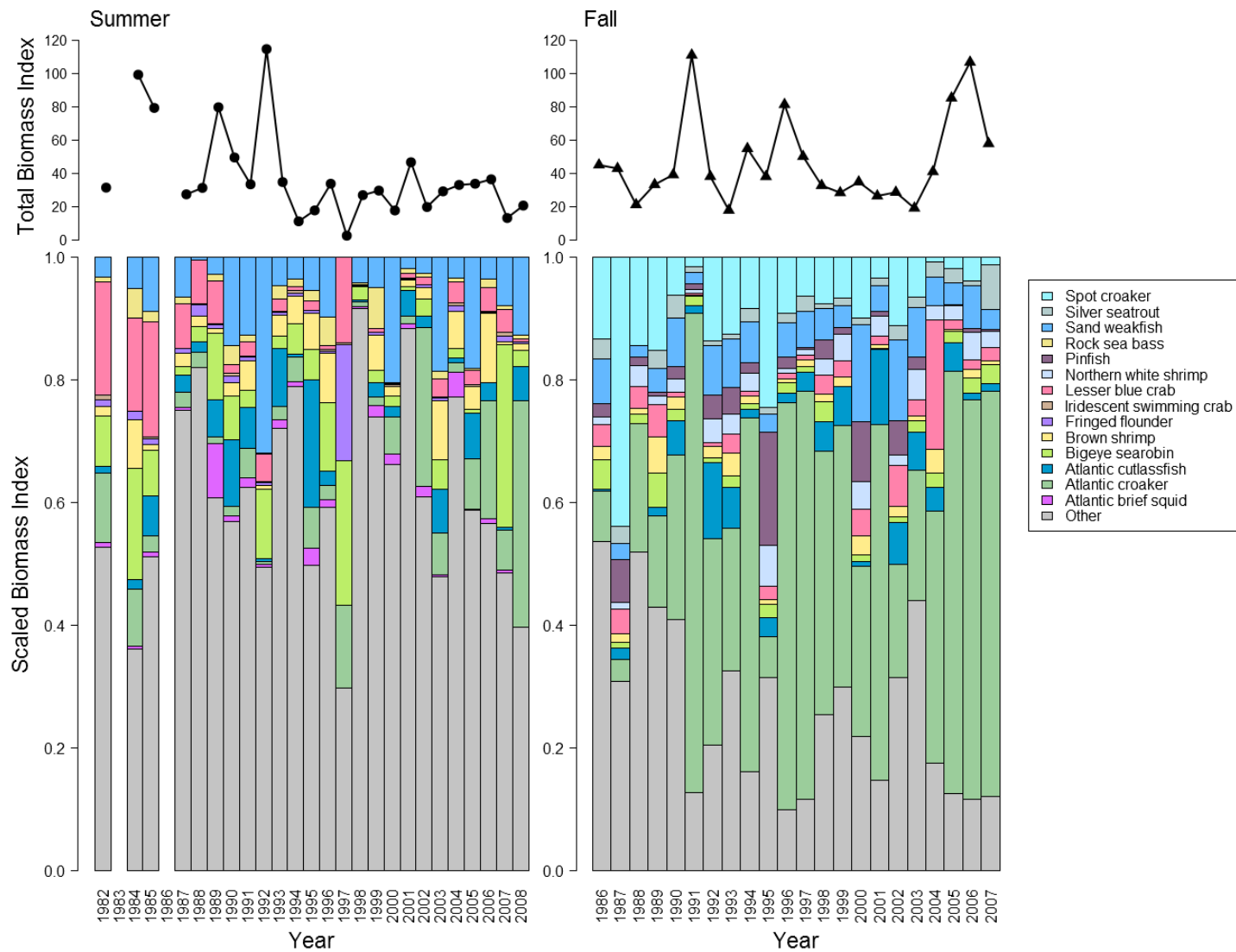


Figure 1.14. Zone 13 plots of the total standardized biomass and the breakdown of the community composition of the ten most dominant species scaled to 1.0. The other category includes all other species identified to the species level.

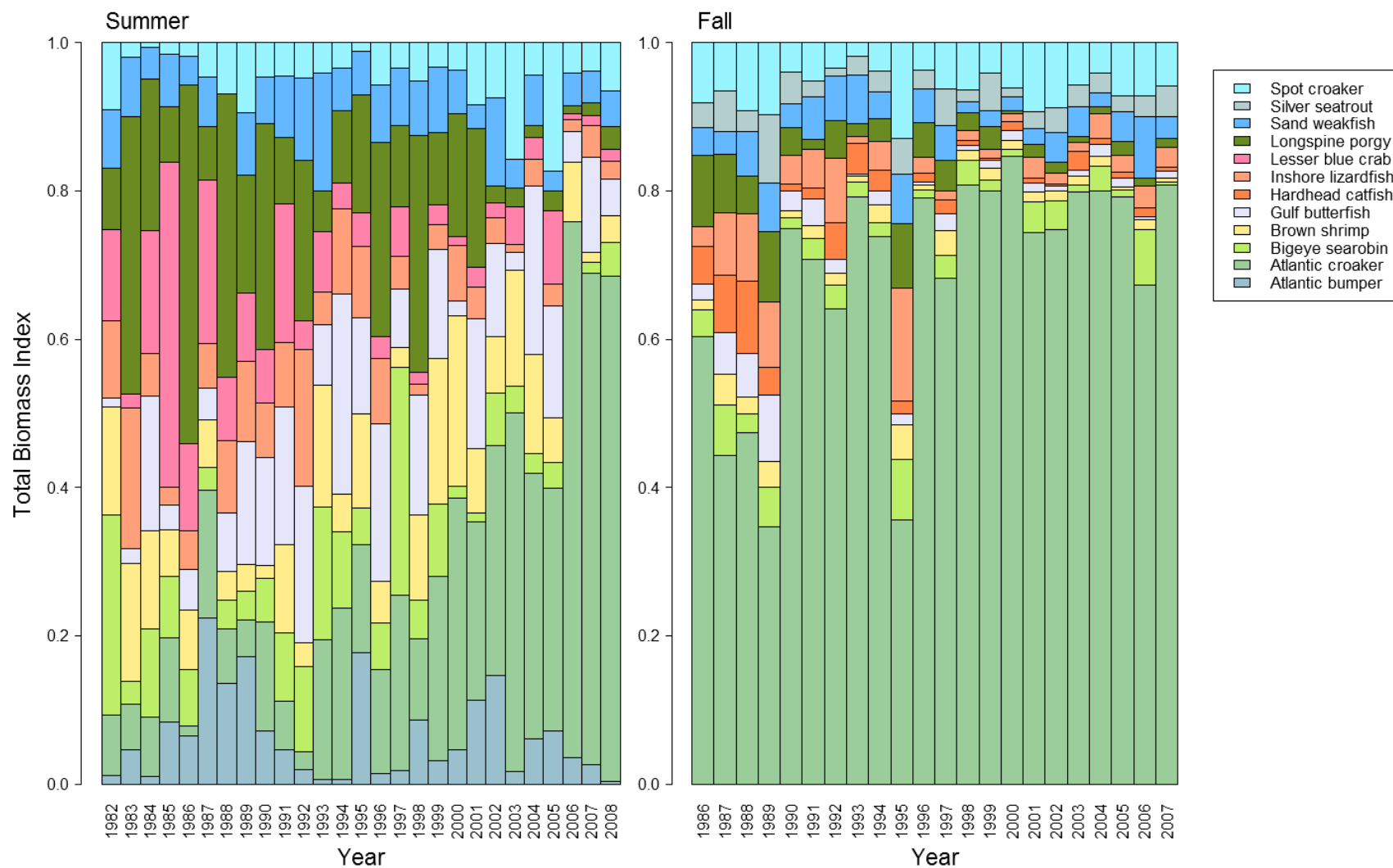


Figure 1.15. Zone 13 plots of the community composition of the ten most dominant species scaled to 1.0.

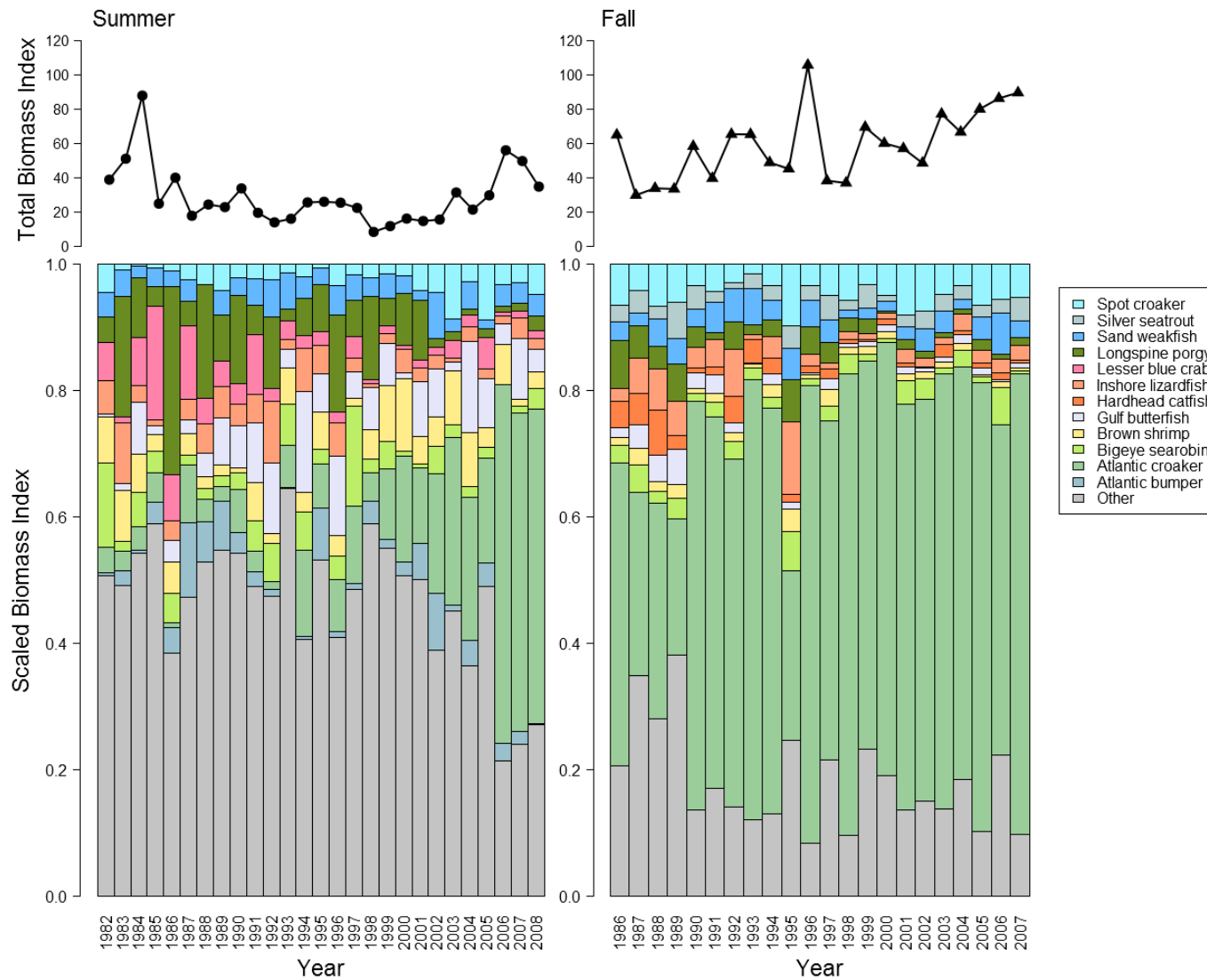


Figure 1.16. East DFC plots of the total standardized biomass and the breakdown of the community composition of the ten most dominant species scaled to 1.0. The other category includes all other species identified to the species level.

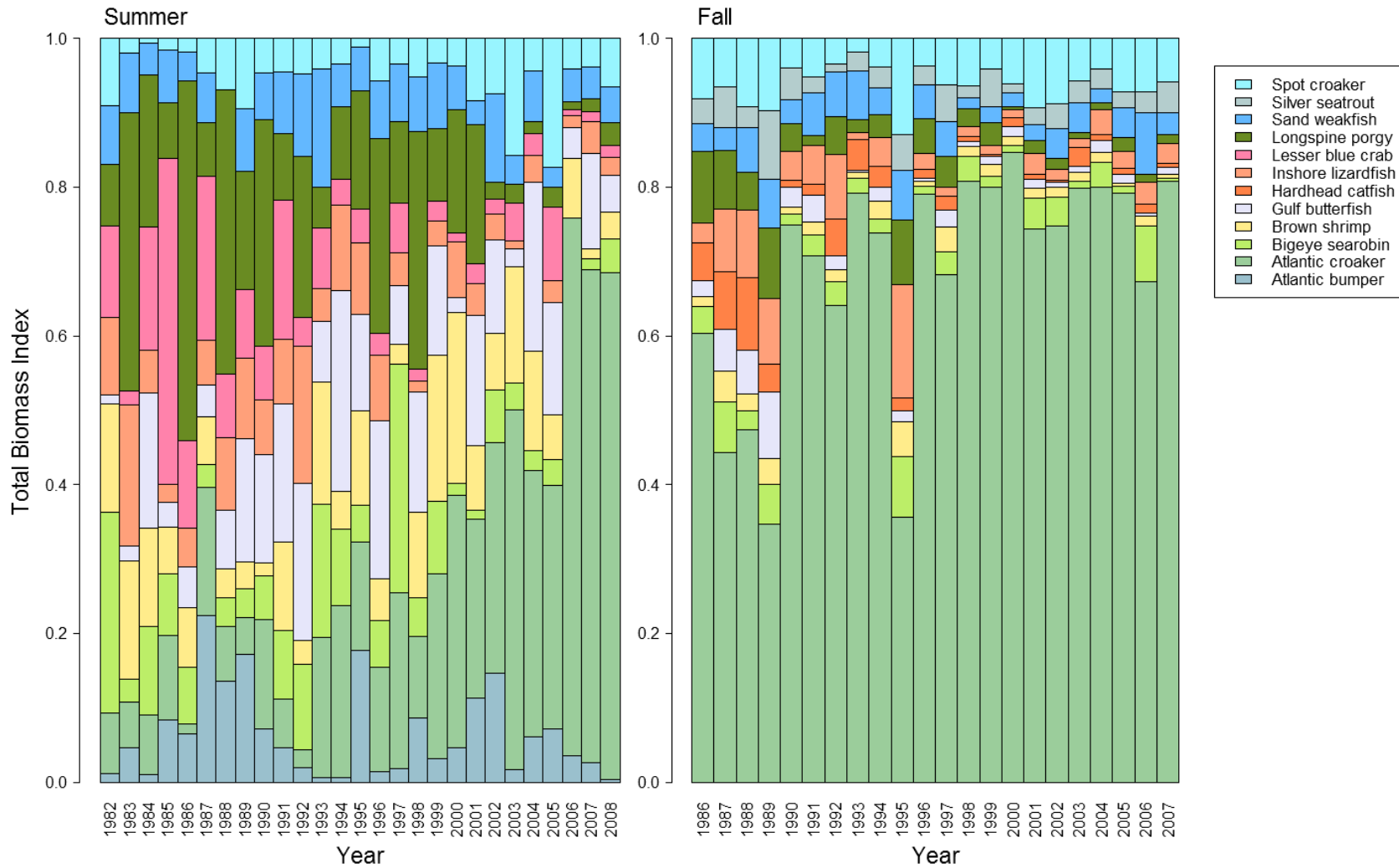


Figure 1.17. East DFC plots of the community composition of the ten most dominant species scaled to 1.0.

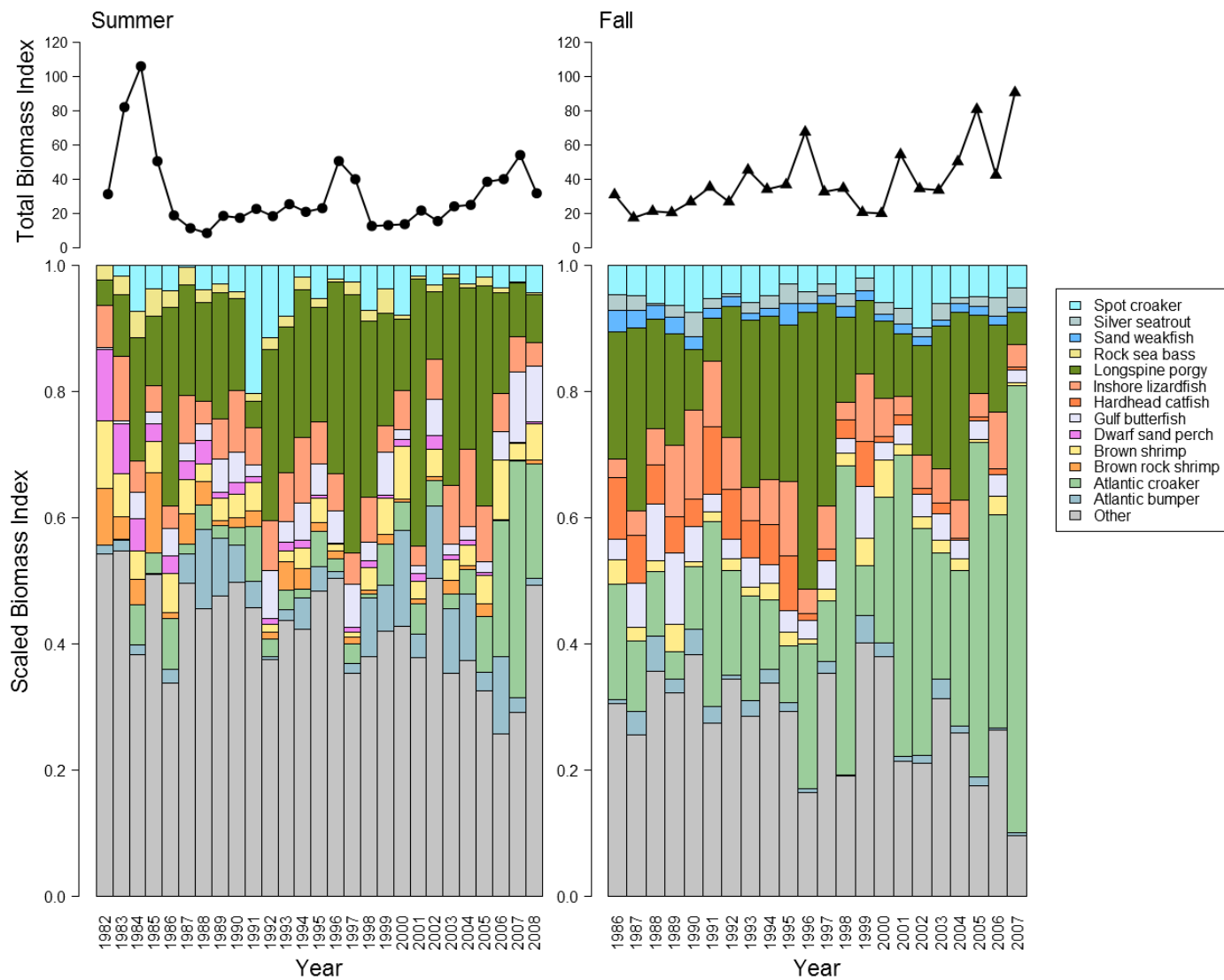


Figure 1.18. Mid DFC plots of the total standardized biomass and the breakdown of the community composition of the ten most dominant species scaled to 1.0. The other category includes all other species identified to the species level.

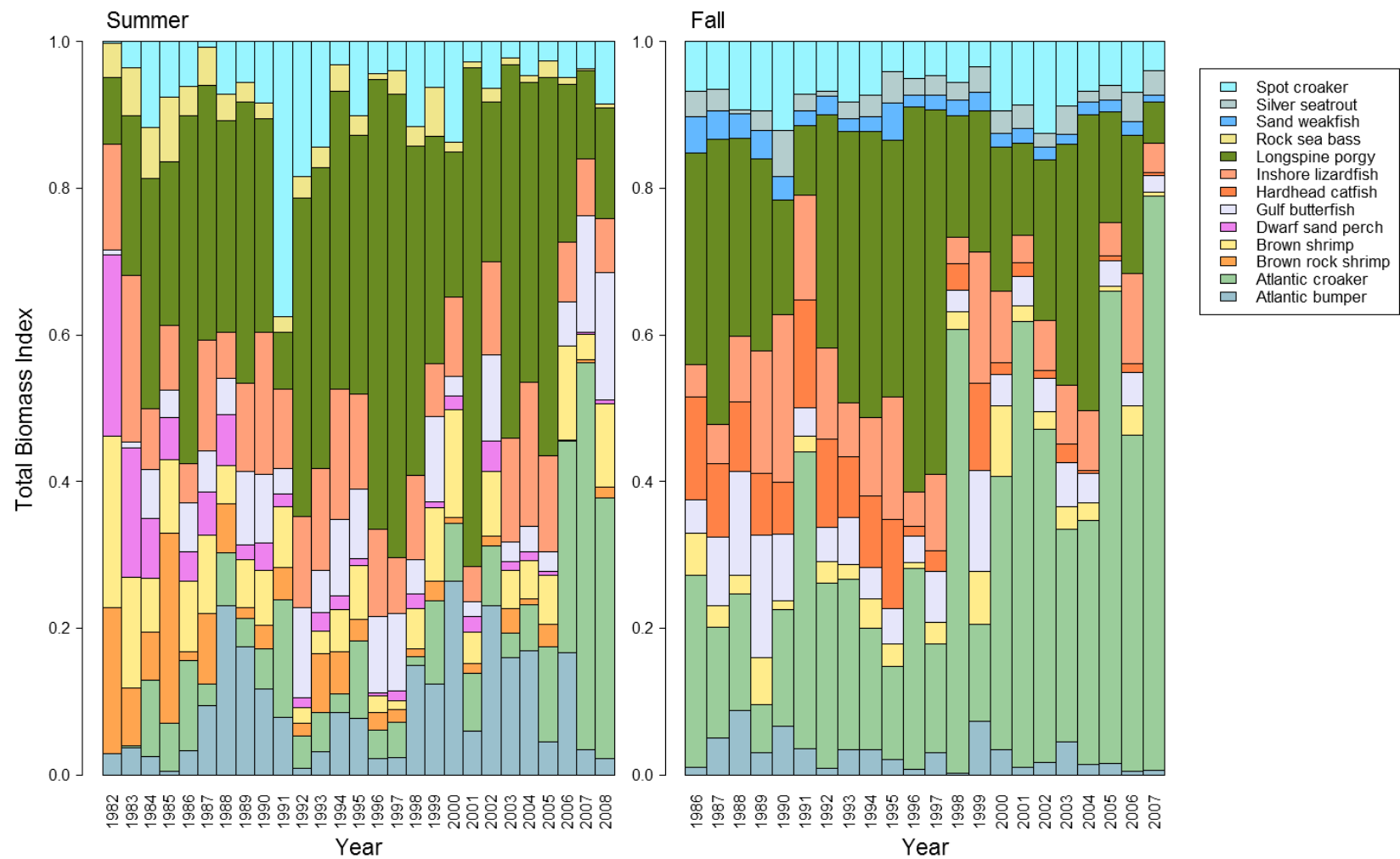


Figure 1.19. Mid DFC plots of the community composition of the ten most dominant species scaled to 1.0.

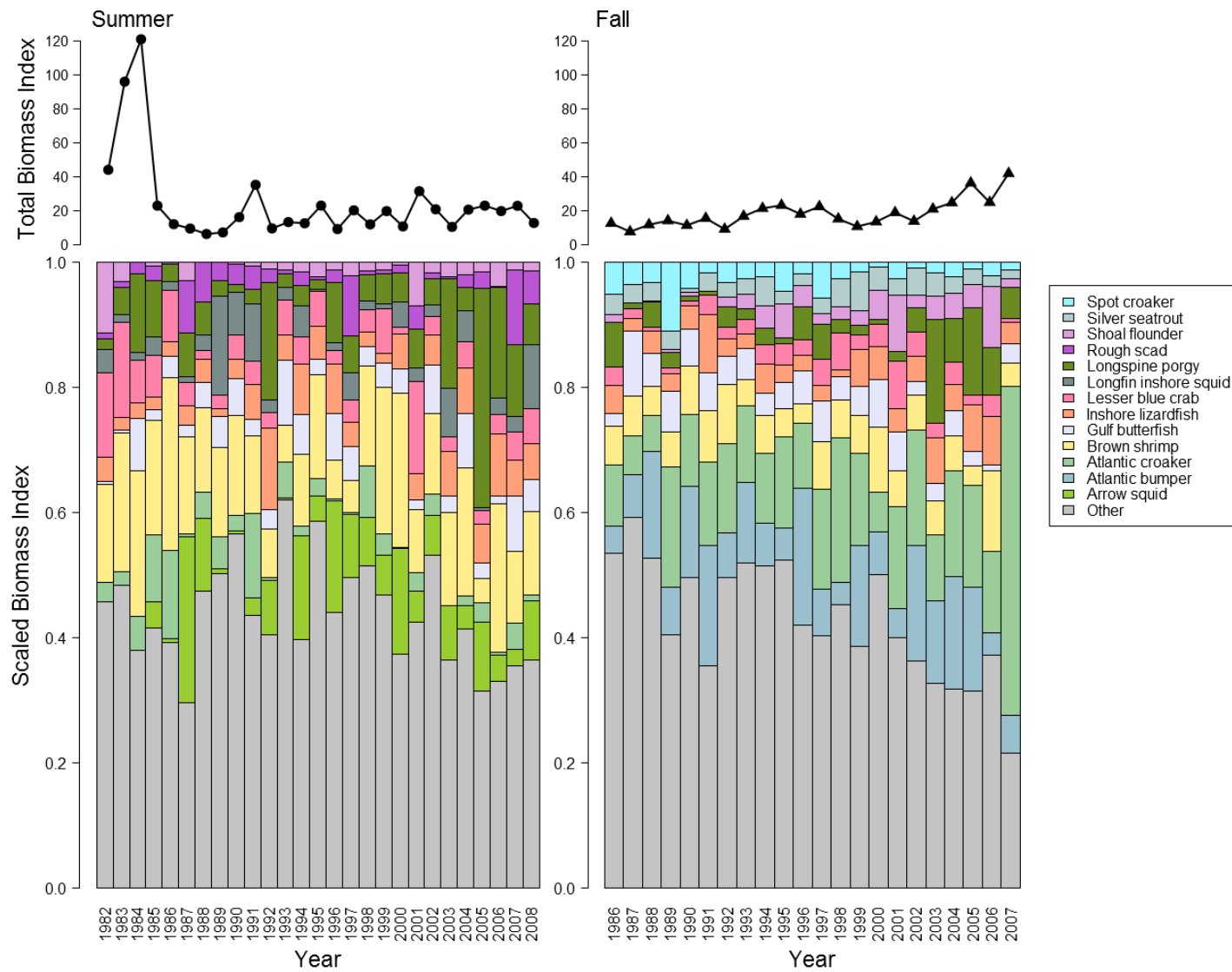


Figure 1.20. West DFC plots of the total standardized biomass and the breakdown of the community composition of the ten most dominant species scaled to 1.0. The other category includes all other species identified to the species level.

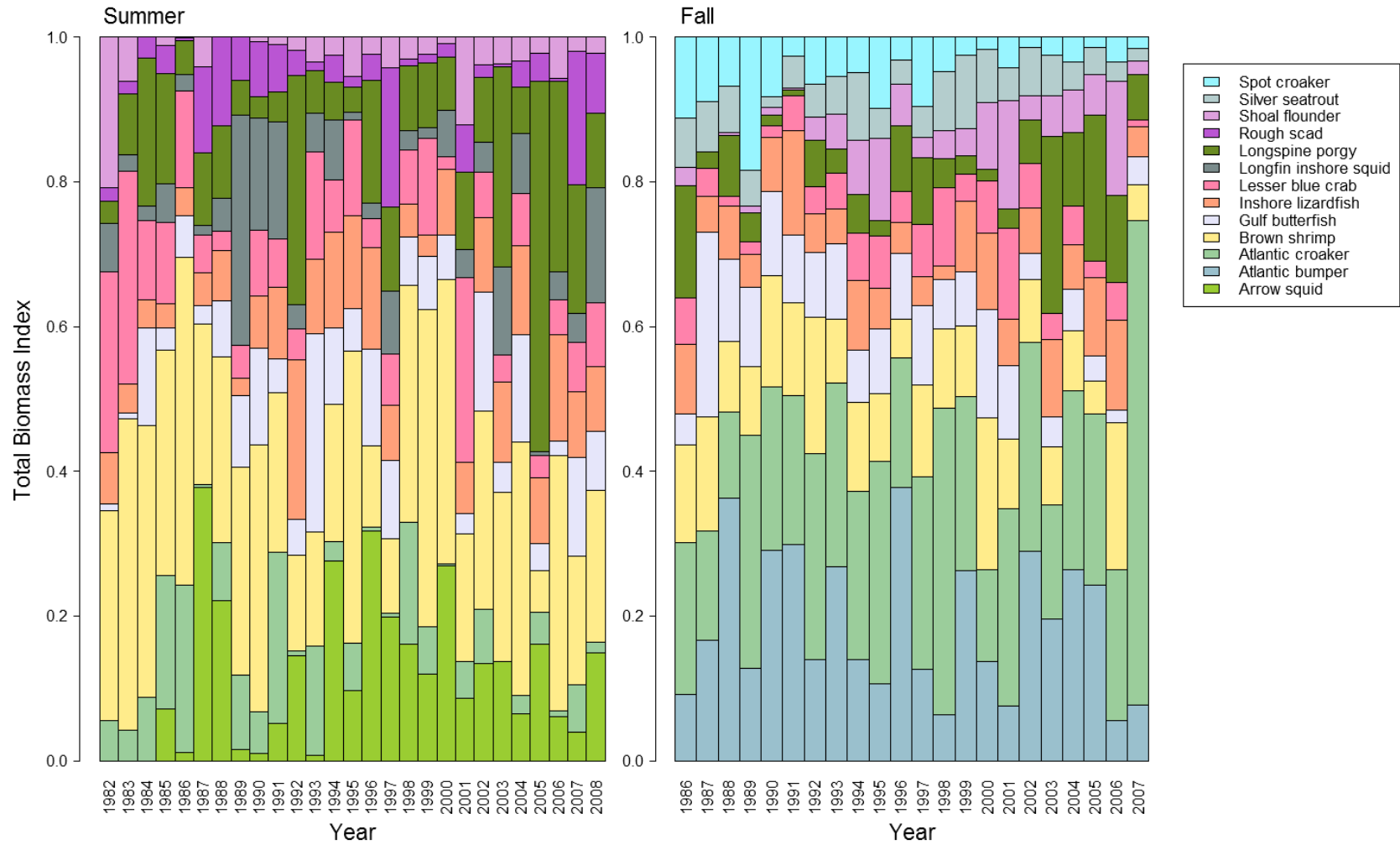


Figure 1.21. West DFC plots of the community composition of the ten most dominant species scaled to 1.0.

The separation of Zone 13 from all other zones was more pronounced in the summer months. The summer SEAMAP bottomfish trawl survey is conducted from mid-June to the end of July, which is the peak timing for the annual hypoxia event in the northwestern Gulf, which creates an hypoxic area known as the “dead zone” (Rabalais et al., 1994; Rabalais et al., 2002). Hypoxia is defined as bottom-water oxygen levels $\leq 2\text{mg l}^{-1}$ and appears on the Louisiana/Texas continental shelf from May-September. Hypoxia was detected in the summer SEAMAP groundfish trawls (Figure 1.22). In this study, no significant trends were detected between changes in community assemblage and decreasing oxygen levels.

Craig (2012) conducted an independent study to determine the effect of hypoxia on the spatial distribution of demersal fish and brown shrimp. He found that Atlantic bumper and sand seatrout exhibit markedly low DO thresholds (between 1.06 and 1.16mg l⁻¹). This may explain the lack of significant results in this study. Craig (2012) also found Atlantic croaker and Atlantic cutlassfish (both species associating with Zone 13) to have DO thresholds below 2.0mg l⁻¹. The SEAMAP environmental data are only collected at one point during the trawl, which may also bias the results if the trawl passes through ephemeral patches of hypoxic waters. Mobile species are able to migrate both vertically and horizontally to avoid hypoxic areas, compounding the ability to detect changes in avoidance from trawl data.

The DFCs identified cross the survey boundaries in the sampling design, suggesting that while the survey is designed using the shrimp statistical zones, this may not be the most ecologically meaningful design. The species assemblages defined within the DFCs can be used as ecological indicators to monitor changes such as habitat or fishing pressure. Although Zone 13 grouped with Zones 14-15 in the fall surveys, I recommend that it be monitored and remain as a separate DFC. Many species had significant indicator value for Zone 13 when it was separated

from the East DFC in the fall. This indicates that Zone 13 may be a transitional area. Many of the same species has significant indicator values for Zone 13 in the summer and fall surveys, e.g. Atlantic cutlassfish and Mantis shrimp (*S. empusa*). Zone 13 experiences unique environmental factors and is heavily influenced by its proximity to the mouth of the Mississippi River. Direct comparisons between the summer and fall surveys from Zone 13 incorporating additional environmental data (e.g. Mississippi River outflow, nutrient loading, upwelling/downwelling events) could explain some of the temporal variability.

The SEAMAP groundfish survey is the only long-term fisheries independent survey available in the northwestern Gulf for monitoring demersal fish community dynamics. The sampling protocol has been consistent over time and this study now provides a database that has been managed and inspected for errors. Each of the SEAMAP surveys (summer and fall) represents a snapshot of the demersal community during approximately a two-month period of the year. The SEAMAP survey provides valuable information regarding the species captured as bycatch in the survey and has been used as an index of abundance in stock assessments. The SEAMAP survey data, combined with data from state surveys and the shrimp fishery observer data can provide a wealth of information on the health and status of the demersal fish communities.

It may prove difficult to disentangle the changes in species biomass from the natural variability in juvenile population sizes. The history of heavy exploitation by the shrimp fishery may have also disrupted the natural community assemblage, which makes it more difficult to detect trends relating one to a single driving force such as shrimp effort (Hughes, 1994). This is true for red snapper, which receives much of the management attention of the bycatch species.

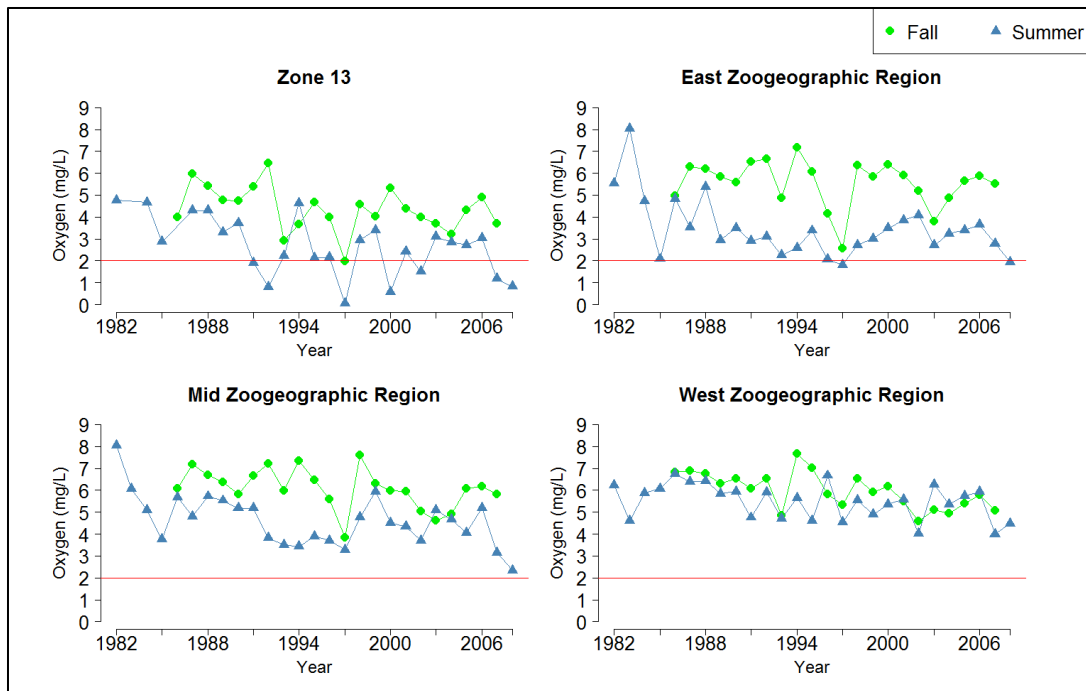


Figure 1.22. Annual averages of the bottom oxygen from the SEAMAP bottomfish trawl survey. Zone 13 was separated from the East DFC for the fall in this plot. The red horizontal line at 2mg/L is the oxygen concentration below which the water is hypoxic.

However, red snapper does not appear in the dominant community in any of the DFCs (Table A.7). Species that appear in more than 3% of all summer and fall survey trawls and have management plans are: Spanish mackerel (*Scomberomorus maculatus*), red snapper, lane snapper, wenchman (*Pristipomoides aquilonaris*), gray triggerfish (*Balistes capriscus*), dwarf sand perch (*Diplectrum bivittatum*), and sea pansy (*Renilla mulleri*) (part of the Coral and Coral Reef FMP). Those species only appearing in the summer survey are king mackerel (*Scomberomorus cavalla*) and cobia (*Rachycentron canadum*), while anchor tilefish is present in only the fall survey. Of the fishfish species with FMPs, no formal stock assessments have been conducted for the wenchman, dwarf sand perch, and anchor tilefish (*Caulolatilus intermedius*). However, Magnuson-Steven Reauthorization Act requires Annual Catch Limits to be set for all species with an FMP. Without a stock assessment or formal study, the effect of shrimp trawl bycatch on

individual populations will remain unknown. Stock assessment models could be conducted for any of these species, utilizing both the fishery-dependent observer data and with the fishery-independent SEAMAP bottomfish trawl survey.

The importance of defining the spatial and temporal community dynamics of a system has become apparent as we move towards an ecosystem-based management approach (Mangel and Levin, 2005). The regional and seasonal communities identified in this study can be used in marine spatial planning, and incorporated in ecological models. The standardized indices of abundance/biomass can be used as input into existing stock assessment models for managed species or to develop baseline assessments for unmanaged species. Walters et al. (2008) developed an Ecopath model for the Gulf, that was primarily focused on the dynamics of the northeastern Gulf. The extensions of Ecopath to Ecosim and Ecospace allow the temporal and regional dynamics identified in this study to be incorporated in an existing model (Polovina, 1984; Walters et al., 1997; Walters et al., 2000)

The results of this study indicate that the northwestern Gulf demersal fish community associated with the shrimp fishery is not spatially homogeneous. There is an ecological gradient from East to West along the shelf and the dominant species within the community assemblages change seasonally. This provides baseline information on the species abundances and distributions that can be incorporated into ecosystem models and be used to monitor the health of the ecosystem. The baseline data can also be used to monitor future changes in community assemblages result of the shrimp effort reduction or any other physical and environmental drivers. The non-significant correlations between the community assemblages and shrimp effort are not a negative result. The time scale of the data may not be long enough to detect ecological trends. Visual observations suggest that the East and Mid DFCs (both summer and fall) have

increased in total biomass since 2005. Atlantic croaker in the East and Mid DFCs should be investigated further to determine if the population is in fact increasing. The standardized CPUE indices generated for all species from the temporal analysis can also be used for future analyses and stock assessments.

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CHAPTER 2 : UTILIZATION OF A MULTISPECIES LOTKA-VOLTERRA MODEL TO EXPLORE BIOLOGICAL REFERENCE POINTS FROM A SINGLE-SPECIES SURPLUS PRODUCTION MODEL

INTRODUCTION

Ecosystem-based fisheries management (EBFM) has drawn much attention in fisheries research and management since the 1999 National Marine Fisheries Service (NMFS) report to Congress (NMFS, 1999). That report outlines EBFM principles and recommendations for NMFS and the Regional Fishery Management Councils (Councils). More recently, the National Oceanic and Atmospheric Administration stated a goal in its 5-year research plan “to improve resource management by advancing our understanding of ecosystems through better simulation and predictive models” (NOAA, 2008). The research plan also stressed the need to develop ecosystem indicators and determine the costs and benefits of management decisions incorporating ecosystem considerations.

Two recurring themes found in both of these documents are: the need to develop conceptual and quantitative food web models, determine community and ecosystem level effects of fishing. Conceptual models can provide an insight on the functioning of an ecosystem (or part of an ecosystem) and the interactions among species, leading to an understanding of how fishery management practices affect species other than the targeted or fished species. Conceptual models and simulation studies may elucidate many of the questions surrounding EBFM and help to understand the possible effects fishery management decisions have on the ecosystem.

There is no universal definition of EBFM and it will be difficult to create a list of requirements and goals to govern every ecosystem. A number of approaches to EBFM have been explored through models and monitoring programs (Cowan et al., 2012). Ecosystem indicators are also being investigated to help gauge the state or health of an ecosystem (Rice,

2000; Fulton et al., 2005; Jennings, 2005; Link, 2005). It is unlikely that any one indicator will provide a holistic picture of the ecosystem, but more likely that a suite of ecosystem indicators can prove useful in determining the current state of a system (Link, 2005; Powers and Monk, 2010). Possible ecosystem indicators include species diversity, habitat characteristics, fishery bycatch, size-based indicators, and changes in trends in biomass and CPUE (Link, 2010; Hilborn, 2011).

A number of models that include a wide range of complexity have been employed to explore the multispecies and ecosystem level interactions and indicators. Plagányi (2007) provides a thorough review and comparison of currently used community and ecosystem models. A multispecies Lotka-Volterra (L-V) predator-prey model was chosen for this study to examine possible community level effects of fishing.

A multitude of theoretical literature has been published addressing solutions to an N -species Lotka-Volterra model, however few studies have used the Lotka-Volterra method in simulation exercises to explore ecological perturbations (Case, 1990; Gamble and Link, 2009). Models utilizing the L-V equations have been The Multi-Species Production Model (MS-PROD) is one of the more recent community models utilizing L-V-based equations to model predator-prey, and competition interactions (Gamble and Link, 2009). MS-PROD aggregates species into functional groups and uses a Leslie-Gower to model within and between species group competition. The single-species Schaefer model used to model production in MS-PROD is essentially a modified Lotka-Volterra system. MS-PROD was applied to the Northeast United States Large Marine Ecosystem to examine the effect of fishing on other species in the system at various harvest levels. The authors were not attempting to provide precise predictive feedback for management scenarios, but to provide a plausible range of predictions given the current

knowledge of how the ecosystem functions. The L-V model in this study is designed to serve a similar purpose.

The L-V model was chosen because it has been well studied in the theoretical literature and the linear interactions are mathematically tractable (May, 1972; Lawlor, 1979). L-V models assume species interactions are linearly dependent on the interacting species densities and at a given rate of change (Lotka, 1925; Volterra, 1926). A Type I functional response (Holling, 1959) is maintained in this study so that direct comparisons can be made with the Schaefer single-species surplus production model. While this may be an overly simplistic model for the real world, modeling of any kind requires simplification and/or compromises (Yodzis and Innes, 1992).

Food webs and species interactions are at the core of community dynamics. The L-V model allowed me to explore the effects of fishing on the food web and predator-prey interactions. Predation mortality is recognized as an important driver of natural mortality, but it is not often considered as a driving force in fishery stock assessment (Christensen, 1996; Bax, 1998). Of specific interest were the biomass changes resulting from indirect links among species. Several studies indicate that changes in biomass resulting from indirect pathways are just as important as direct predator-prey interactions (Menge, 1995; Wootton, 2002; Montoya et al., 2009). The L-V model allowed me to track the biomass time series of all species within the system and to elucidate the effects of fishing on all species within the same community.

The large marine ecosystems (LMEs) are at spatial and temporal scales too large to be tractable for the purposes of this study (Steele, 1985; Mann and Lazier, 2006). The term community is used in this study to represent the theoretical group of 100 species modeled. One hundred species were chosen because the analysis in Chapter 2 revealed that approximately a

hundred species account for 95% of the biomass within the Gulf demersal fish community. The intention was not to model all species in the Gulf ecosystem, nor to incorporate physical and environmental drivers within the system. I aimed create and examine the ecological characteristics of a “Gulf-like” community in response to fishing.

The objectives of Chapter 2 are four-fold. The first objective is to describe the multispecies L-V model and the parameters used to initialize the system at equilibrium. The model was developed using the characteristics of the community described in Chapter 1 and also conditions described in the literature. Five species, selected based on their link characteristics, were chosen to fulfill the objectives 2-4. The second objective is to use the multispecies data in a single-species stock production model to estimate the fishing mortality rate producing maximum sustainable yield, F_{MSY} . The single-species estimated F_{MSY} will be compared to the expected value from the L-V model. A single-species value lower than expected indicates that species interactions affect species productivity and a buffer should be considered when determining fishing mortality rates. The third objective is to fish the selected species at the single-species estimated F_{MSY} . The biomass time series for the fished species will be explored, as well as the effects of fishing on all other species in the community. The third objective is to overfish a species and examine rebuilding timeframes from both single-species and multispecies projections. The fourth objective is to overfish the selected species to a level of 20% of its virgin biomass and the rebuild the species. The time required for a species to rebuild to a level of B_{MSY} will be compared from single-species and multispecies projections.

METHODS

Community Connectance

The structure and complexity of the food web is at the core of the L-V model. There are multiple accepted methods for calculating food-web connectance, defined as the percent of non-zero links in the interaction matrix of α_{ij} 's. Gardner and Ashby (1970) first defined connectance as $C = L/S(S-1)$, which scaled the value from 0 to 1. I followed the methods of Link (2002b) and that used only the half matrix did not incorporate the self-interaction links (diagonal elements). Thus, connectance (C) was defined as:

$$C = \frac{L'}{S(S-1)/2} \quad (2.15)$$

where S was the number of species in the community and L' was the number of links per species without self-interactions.

Multispecies Lotka-Volterra model

Lotka (1925) and Volterra (1926) independently developed a system of equations modeling predator-prey interactions have been widely used in ecology. The L-V system of ordinary differential equations and can be extended to an N -dimensional state to model multi-species interactions (Chesson, 2000; Wilson et al., 2003; Gamble and Link, 2009; Powers and Brooks, 2011). The L-V model for N species is:

$$\frac{dB_i}{dt} = B_i(t) \left[r_i + \sum_{j=1}^N \alpha_{ij} B_j(t) \right] \quad i=1,2,\dots,N \text{ species} \quad (2.2)$$

The alpha parameters in equation 2.2 became an $N \times N$ matrix where N is the number of species in the system. Any element of the interaction matrix, α_{ij} , was interpreted as the per capita effect species j has on species i , which can also be interpreted as coefficients of predation, prey,

competition, or symbiosis depending on the sign of the coefficient. A definition of the parameters used in the L-V model in this chapter can be found in Table 2.1. Time- and species-dependent fishing mortality was incorporated by modifying the r_{LV} values:

$$\frac{dB_i(t)}{dt} = B_i(t) \left[r_{LV} - F_i(t) + \sum_{i=1, j=1}^N \alpha_{ij} B_i(t) \right] \quad (2.3)$$

Table 2.1. Variables and commonly used biological reference points

Parameter	Definition / Theoretical Basis
Lotka-Volterra Model Parameters	
$B_i(t)$	Biomass of species i at time t $i = 1, 2, \dots, N$ species
$B(t)$	Summed biomass across all species
$r_i = r_{LV}$	Intrinsic production rate of species i
$F_i(t)$	Fishing mortality rate of species i at time t
α_{ij}	Interaction rate between species i and j
α_{ii}	Self-interaction parameter on the diagonal of interaction matrix (intra-species density-dependence)
B_0	Equilibrium biomass or the biomass at year 0 in the Lotka-Volterra simulations when no fishing is occurring
Reference points based on production models (e.g., ASPIC)	
q	Catchability
K	Carrying capacity
F_{MSY}	Fishing mortality (F) for maximum sustainable yield
B_{MSY}	Biomass (B) for maximum sustainable yield
MSY	Maximum sustainable yield
Parameters specific to this study	
r_{LV}	Intrinsic production rate of species i , as defined in the Lotka-Volterra model
r_{ASPIC}	Intrinsic production rate of species i , as estimated from ASPIC as $2 * F_{MSY}$

Initial parameter values

The L-V model was initialized with 100 species. The following sections describe the methods for setting up the model. The interactions between pairs of species were defined and initialized, as well as initial intrinsic rates of increase, r_{LV} , and biomass.

Initial intrinsic rate of increase and biomass

Marine fish and invertebrate species cover the entire spectrum of life history characteristics, resulting in a large variation of natural mortality estimates. A compilation of 843 natural mortality estimates for Atlantic Ocean fish species had a median of 0.4yr^{-1} and interquartile range of $[0.26\text{yr}^{-1}, 0.89\text{yr}^{-1}]$ (Froese and Pauly, 2000). There was high variance among these estimates, which can be expected given the life history differences among the 843 species. These data represented the entire Atlantic Ocean from the FishBase database; data by region, e.g. Gulf of Mexico, were not readily available.

One rule of thumb in fisheries stock assessment is that $F = M$ (e.g. fishing mortality rate is equal to the natural mortality rate) (Alverson and Pereyra, 1969). If this is followed through algebraically:

$$MSY = \frac{rK}{4} \quad B_{MSY} = \frac{K}{2}, \quad (2.4)$$

where MSY is maximum sustainable yield, K is carrying capacity, and B_{MSY} is the biomass at which the population achieves maximum sustainable yield. This implies that

$$F_{MSY} = \frac{r}{2} \text{ and if } F = M \text{ then } r = 2F \text{ or } 2M.$$

where F_{MSY} is the fishing mortality rate producing maximum sustainable yield. A complete derivation can be found in Haddon (2001) .

I selected the values of r_{LV} from a lognormal distribution with mean 0.6 and standard deviation of 0.4. This right-skewed distribution provided r values ranging from 0.2 to 1.4, which

was in line with the current natural mortality literature and spans a range of life history strategies. The r values and initial biomass were assigned to a species independent of one another. The relationship between r and initial biomass is illustrated in Figure 2.3.

The initial biomass was distributed lognormally, with a mean of 100 and standard deviation of 1.0. The mean of 100 was chosen as the baseline biomass; however, true biomasses could be considered to be any scalar of these values, e.g., 100 could represent 100 million pounds or 100 thousand pounds. The standard deviation also allowed the system to be initialized with a desired lognormal distribution of the relative biomass, with the most abundant species having a biomass approximately ten times larger than the mean (Figure 2.2).

Species links

The algorithm for generating the interaction matrix and links among the 100 species in the community was based on the methods of network growth of Barabási and Albert (1999) and utilized for fisheries in Powers and Brooks (2011). Positive interactions (inward links) represented a positive per-capita growth rate from prey and negative interactions (outward links) represented a negative per-capita growth rate. If no interaction was defined between a pair of species the α_{ij} remained zero and those two species were said to have no direct link. The methods for determining the prey links for species $i = 1, 2, 3, \dots, N$ were as follows:

1. Assign species $i = 1$ with no interactions (all $\alpha_{ij}=0$)
2. Add species $i+1$.
3. If $i+1 < Links$, then $p = i$; else $p = Links$ where p is number of prey randomly chosen.
4. Randomly select p species from the pool of j species, where $j=1, 2, 3, \dots, N$ and $i \neq j$
5. Assign a $+1$ to the α_{ij} in the interaction matrix for each of the p species in step 4.
6. Repeat steps 2-5 until $i = N-1$

The methods for assigning the predator links were as follows:

1. Assign species $i = 1$ with no interactions (all $\alpha_{ij}=0$)
2. Add species $i+1$.
3. If $i+1 < Links$, then $p = i$; else $p = Links$ where p is number of predator randomly chosen.
4. Randomly select p species from the pool of j species, where $j=1, 2, 3, \dots, N$, $i \neq j$, and $\alpha_{ij}=0$, for each of the p species in step 4.
5. Assign a -1 to α_{ij} in the interaction matrix
6. Repeat steps 2-5 until $i = N-1$

The parameter *Links* was predefined by the user and was chosen to create a community with a desired connectance (see *Community Connectance*). The magnitude of the interaction rates was not determined in this step. For each non-zero α_{ij} , a dummy value of the opposite sign was assigned to each α_{ji} in the interaction matrix. The α_{ji} values were assigned based on the principal that if species i was preyed upon by species j , the population of species j experienced positive growth from this interaction. A series of simulation trials were run to find combinations of the *Links* parameter for the prey and predator assignments values that produced desired levels of connectance of 25%. The final values were six for prey *Link* and nine for predator *Links*.

The system of equations was parameterized such that all 100 species were in equilibrium in at the start of the simulations, $\frac{dB}{dt} = 0$ for each species. To achieve this, the right-hand side of the L-V equation was set to equal zero:

$$\frac{dB_i}{dt} = B_i \left[r_{LV} + \sum_{j=1}^N \alpha_{ij} B_j \right] = 0 \quad (2.5)$$

The bracketed part of equation 2.5 was partitioned into positive and negative effects and set equal to one another. The alpha matrix was separated into the positive and negative α_{ij} parameters:

$$r_{LV} + \sum_{j=1}^N +\alpha_{ij}B_j = \sum_{j=1}^N -\alpha_{ij}B_j \quad j=1,2,\dots,N \text{ species} \quad (2.6)$$

All of the self-interactions (α_{ii}) were assigned to the negative side of the equation. Each species' growth (r_{LV}) was partitioned into two parts: an inherent intrinsic rate of increase (\hat{r}_i) and the positive interactions (g_i). The positive side of the equation was partitioned with 10% of r_{LV} to \hat{r}_i :

$$r_{LV} = \hat{r}_i + g_i \quad (2.7)$$

$$\text{where } \hat{r}_i = .10 * r_{LV} \quad \text{and} \quad g_i = \sum_{i=1}^N \alpha_{ij} * B_j \quad \text{for all } \alpha_{ij} > 0 \quad (2.8)$$

The sum of the negative interactions in the matrix, including the self-interactions on the diagonal was set equal to $-r_{LV}$. The diagonal of the alpha matrix (self-interactions) were calculated as:

$$-\alpha_{ii} = \frac{0.15 * r_{LV}}{B_i} \quad (2.9)$$

and 15% of the $-r_{LV}$ contributed to the self-interaction. The remaining portion of the $-r_{LV}$, denoted as m_i , was partitioned to the off-diagonal negative interactions.

$$m_i = -d_i + \alpha_{ii} \quad (2.10)$$

$$\text{where} \quad d_i = \sum_{i \neq j}^n -\alpha_{ij} * B_j \quad \text{for all } \alpha_{ij} < 0; i \neq j \quad (2.11)$$

The interaction strengths were assigned such that the distribution was skewed towards weaker predator-prey interactions (Paine, 1980; Paine, 1992; Raffaelli and Hall, 1996; Berlow, 1999; Emmerson and Yearsley, 2004; Wootton, 1997).

To calculate interaction strength, first, the number of α_{ij} interactions for each species i was counted. For each of species i 's interactions, an alpha scalar value, w_i , determined the percent of g_i (for positive interactions) or m_i (for negative interactions) assigned to each link. The w_i 's were drawn from a lognormal uniform distribution, $U \left[\ln \left(\frac{1/n}{3} \right), \ln \left(\frac{1}{n} * 2 \right) \right]$, where n was the number of interactions for species i . The lognormal distribution allowed me to scale the parameters to the number of interactions and create a right-skewed distribution of interaction strengths.

Alpha scalar values were drawn for $n-1$ interactions, with the last value equal to $(1 - \sum_{i=1}^{n-1} w_i)$. If the summation of the values exceeded 1.0 before reaching $n-1$ values, the drawing of all w_i 's was reinitialized. The α_{ij} interactions strengths were then calculated as:

$$\alpha_{ij} = g_i * w_i / B_j \quad \text{For all } \alpha_{ij} > 0 \quad (2.12)$$

$$\alpha_{ij} = -d_i * w_i / B_j \quad \text{For all } \alpha_{ij} < 0; i \neq j \quad (2.13)$$

Lotka-Volterra simulations

The final equation used in the L-V simulations was:

$$\frac{dB_i}{dt} = \left[\hat{r}_i - F_i + \sum_{j=1}^N \alpha_{ij} B_j \right] * B_i \quad (2.14)$$

The simulations were run for 300 years with 6000 time steps, resulting in 20 time steps for each calendar year in the simulation. The number of time steps chosen provided a large enough value to produce stable results from the Runge-Kutta solver. The fishing mortality rates were updated at the beginning of each year in the simulation.

The code to solve the differential equations and run simulations were written in R (R Core Development Team, 2011) , utilizing the deSolve package (Soetaert et al., 2010). The deSolve package in R solves ordinary differential equations including fixed and adaptive time-step explicit Runge-Kutta solvers. All post-simulation statistics and graphics were also created in R.

Surplus-Production Model

Time series from the multispecies L-V model were used as input to A Stock-Production model Incorporating Covariates (ASPIC) (Prager, 1994; Prager et al., 1996; Prager, 2011). ASPIC is a single-species model that uses maximum-likelihood estimation to generate estimates of biological reference points, e.g., B_{MSY} and F_{MSY} .

Five species were selected for fishing, with two fishing scenarios applied to each species. Only one species was fished in each of the fishing. The five species chosen for fishing were:

1. The species with the most links (Species A)
2. The species with fewest links (Species B)
3. A species with few predators, and a large number of prey (relative to other species in the system) (Species C)
4. A species with large number of predators, and a few number of prey (relative to other species in the system) (Species D)
5. A randomly selected species (Species E)

To determine the input time series for ASPIC, an initial fishing regime was implemented in the L-V model for each species. Each species was fished at a rate of $r_{LV}/10$ in year 25, and fishing was increased until the stock was depressed to 20% of its virgin biomass at the midpoint

of the simulation (year 150). Fishing mortality was then relaxed over a period of 125 years so that a “one way trip” was not used as input into ASPIC.

To create an index of the catch and effort for input into ASPIC, lognormal error was applied to the time series of catch and effort from the L-V model. The series of catch was calculated as the average of catches from the beginning and the end of the year:

$$C_t = \frac{(B_t * F_t) + (B_{t+1} * F_t)}{2} \quad (2.16)$$

Catch could not be estimated using Equation 6b in Prager (1994) due to the lack of traditional single-species r and K values in the L-V model. Effort was calculated as fishing mortality rate divided by a constant catchability (q) of 0.005. The error for the catch was lognormally distributed with a mean of 0 and standard deviation of 0.3. The standard deviation of the catch was determined by examining stock assessments for species with similar life history characteristics to the five species selected (Table 2.2).

Other input values for ASPIC were initial guesses for K (carrying capacity), MSY , B_1/K (ratio of the biomass at the beginning of the first year to the carrying capacity), and an estimate of q_i , the catchability coefficient (Prager, 2011). Additional values required to assist in the optimization process are search constraints for the maximum estimated fishing mortality rate F , and lower and upper bounds for estimates of MSY and K . The logistic (Schaefer) model was fit to the simulated data, where the fit was conditioned on fishing effort for all runs in this study. Assumptions of the Schaefer model included: a constant catchability (q), no species interactions, no environmental variability, and that catch and effort are measured accurately (Schaefer, 1954;

Schaefer, 1957). The 80% confidence intervals for B_{MSY} , F_{MSY} , MSY , K and q were estimated from 1,000 bootstrap trials in ASPIC (Prager, 1994).

Runs in ASPIC that estimated MSY close to the bound of K , indicating there was not enough information in the biomass index and the catch to estimate parameters, were rerun with q fixed at 0.005.

Model projections

The ASPIC-estimated F_{MSY} was used in the two different fishing scenarios for each of the five species. In Fishing Scenario 1, the selected species was fished up to a rate of the ASPIC estimated F_{MSY} , and that fishing mortality rate was held constant for the remainder of the simulation. In Fishing Scenario 2, the selected species was fished up to a level of $1.5 * F_{MSY}$ to simulate overfishing, and then rebuilt using a fishing mortality rate of $0.5 * F_{MSY}$. In both fishing scenarios, the only species fished was the species of interest, i.e. species A-E. All of the other 99 species were not fished.

Three different models were used to project Fishing Scenario 1 and Fishing Scenario 2. The time series of applied fishing mortality rate was the same for each model. Model 1 was a projection of the L-V model initialized at the equilibrium biomass. Models 2 and 3 projected only the species of interest and ignored the other 99 species. Model 2 was a single-species surplus production model projection (Prager, 1994) that used the ASPIC-estimated intrinsic population growth rate, r_{ASPIC} (following that $r = 2 * F_{MSY}$) and ASPIC-estimated carrying capacity, K . Model 3 was a single-species projection that used the L-V intrinsic population growth rate, r_{LV} , and the L-V model initial biomass, B_0 , as the carrying capacity, K . The single-species projections were based off of equations 4a and 6a from Prager (1994).

RESULTS

Community Attributes

The community had a connectance of 25.39% (2514/10000 links realized). The median number of total links per species was 24 and the distributions of inward and outward links (prey and predator) per species are illustrated in Figure 2.1. The total number of links per species did not follow any specified distribution. The distribution of alpha interactions for each species was skewed, so that species had only a few strong direct links and a larger number of weaker direct links. The final distributions of the initial r_{LV} value and initial biomass can be found in Figure 2.2 and Figure 2.3.

Estimated biological reference points

All parameters were estimated for each species A-E (Table B.1). However, q was fixed for species C and E. If catchability was not fixed for species C and E, ASPIC did not converge and estimated MSY near K , which was biologically impossible. The estimated intrinsic rate of increase from ASPIC (r_{ASPIC}) were all lower than the expected intrinsic rate of increase (r_{LV}) (Table 2.5) ASPIC estimated the intrinsic rate for Species A (species with the most number of links) at only 34% of the true rate from L-V. The ASPIC estimate of the intrinsic rate for Species B (species with the fewest total links) was only 36%. The ASPIC estimate of the intrinsic rate for Species D (species with many predators, few prey) was 75% of the intrinsic growth rate from the L-V model. The ASPIC estimate of the intrinsic rate for Species D (species with few predators, many prey) was 40% of the true rate from L-V model. The ASPIC estimate of the intrinsic rate for Species E (randomly selected species) was only 55% of the true rate from the L-V model. The fact that all of the estimates of r_{ASPIC} were less than the values of r_{LV}

indicates that species interactions, specifically predator-prey interactions, affect the species' productivity.

Table 2.2. Characteristics of the species chosen for fishing and the standard deviation added to the true catch for ASPIC. Inward links are equivalent to positive α_{ij} values in the interaction matrix, and are the prey of the species in the first column. Outward links are equivalent to negative α_{ij} values (excluding the α_{ii} self-interaction) in the interaction matrix, and are the predators of the species in the first column.

Species	Inward Links	Outward Links	Total Links	r_{LV}	B_0	Catch s.d.
Species with the most total links: #11 (A)	20	23	43	0.547	103.22	0.25
Species with the fewest total links: #79 (B)	4	9	13	0.592	50.90	0.35
Species with many predators, few prey: #49 (C)	8	14	22	1.009	56.25	0.50
Species with few predators, many prey: #10 (D)	32	5	37	0.596	698.86	0.20
Randomly selected species: #29 (E)	21	11	32	0.738	301.81	0.20

Fishing Scenario 1 (Fish species of interest at F_{MSY})

Species A (most connected species)

The stock was sustainable when fished at the ASPIC-estimated F_{MSY} and few unfished species in the system were affected. The productivity of species A did not change throughout the simulation, meaning its r_{LV} value was not affected by species interactions (Table 2.5). Only 9% of all other species exhibited a change in biomass as a result of fishing Species A (Figure 2.4). Of the possible direct links, 13% of the predators of Species A exhibited an increase in biomass. Models 1 and 2 resulted in the same equilibrium biomass in year 300 of the simulation, which was at B_{MSY} . However, the multispecies model captured the species interactions that resulted in Model 1 projecting the species biomass below B_{MSY} for approximately 100 years (Figure 2.4). Model 3 predicted an equilibrium biomass at more than twice the biomass of Models 1 and 2, and a corresponding higher yield.

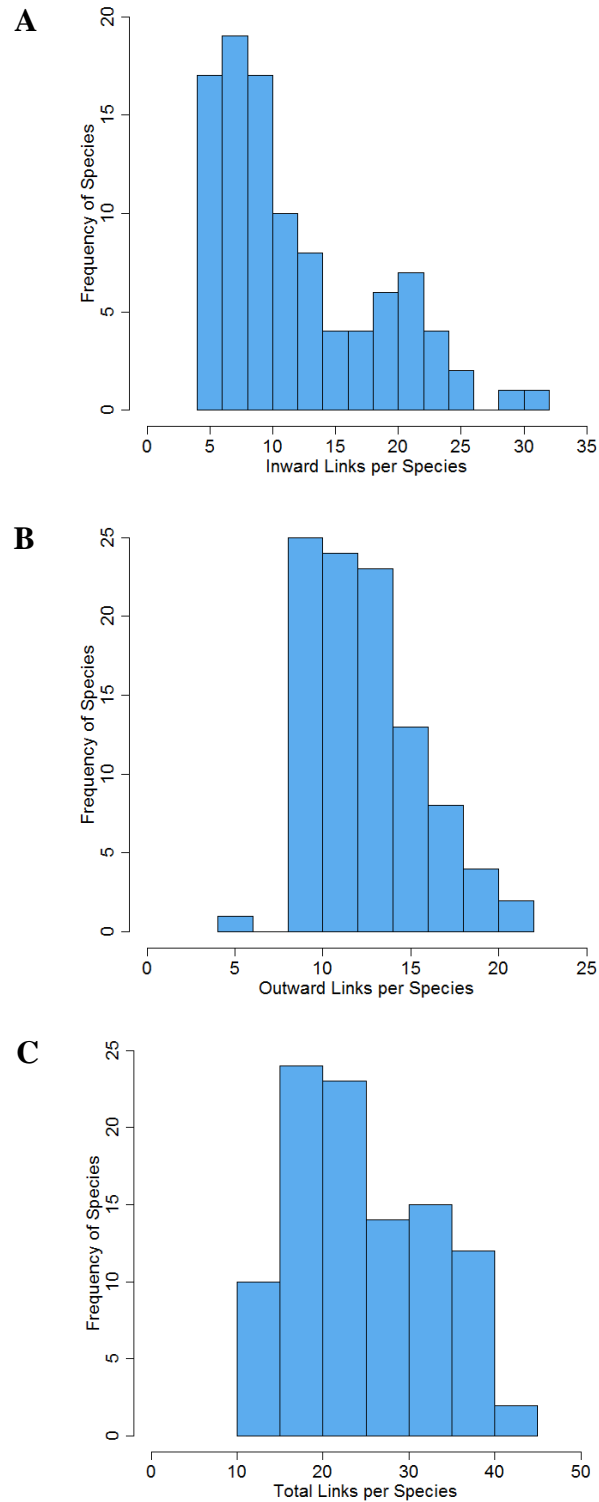


Figure 2.1. The number of inward links per species is the number of prey items of a species (A) and the outward links is the number of predators per species (B). The distribution of total number of links per species for the ecosystem with 100 species and 25% connectance (C).

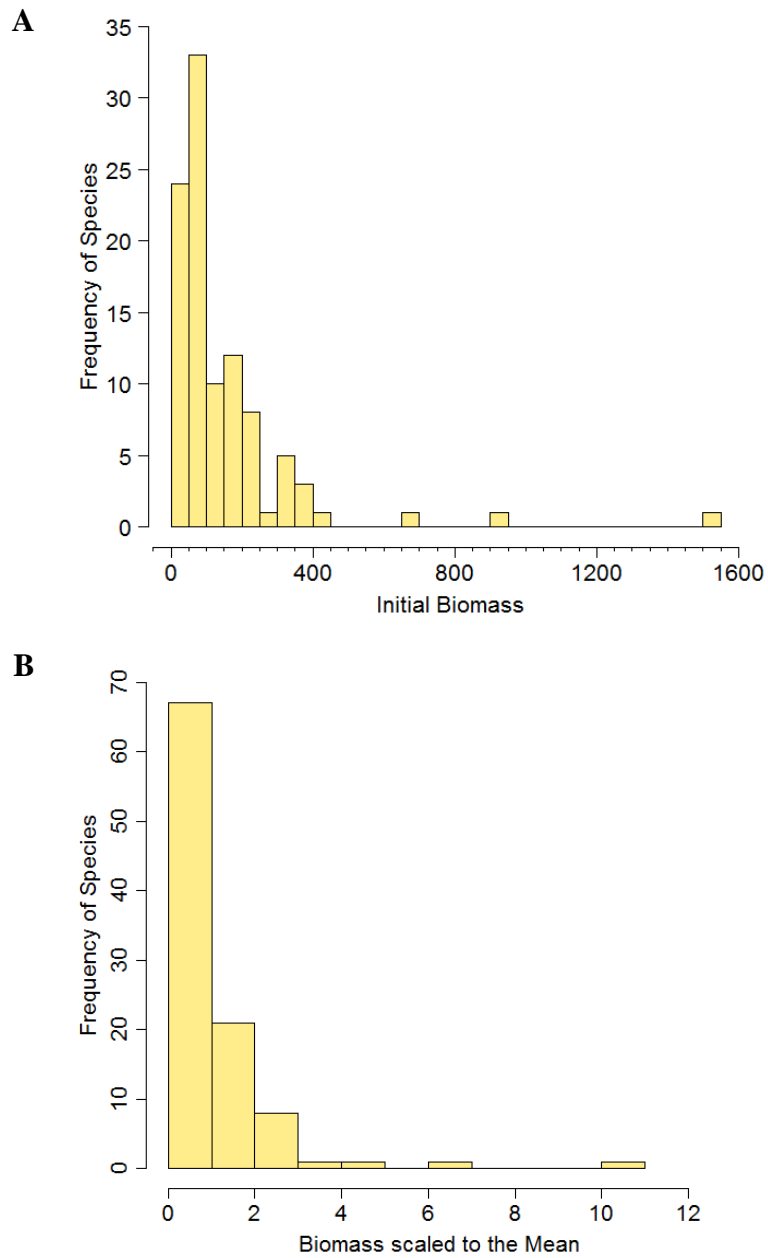


Figure 2.2. The initial time zero biomass for all species (A) and the biomass scaled to the ecosystem mean biomass (B). The median biomass was 100, a unit-less measurement.

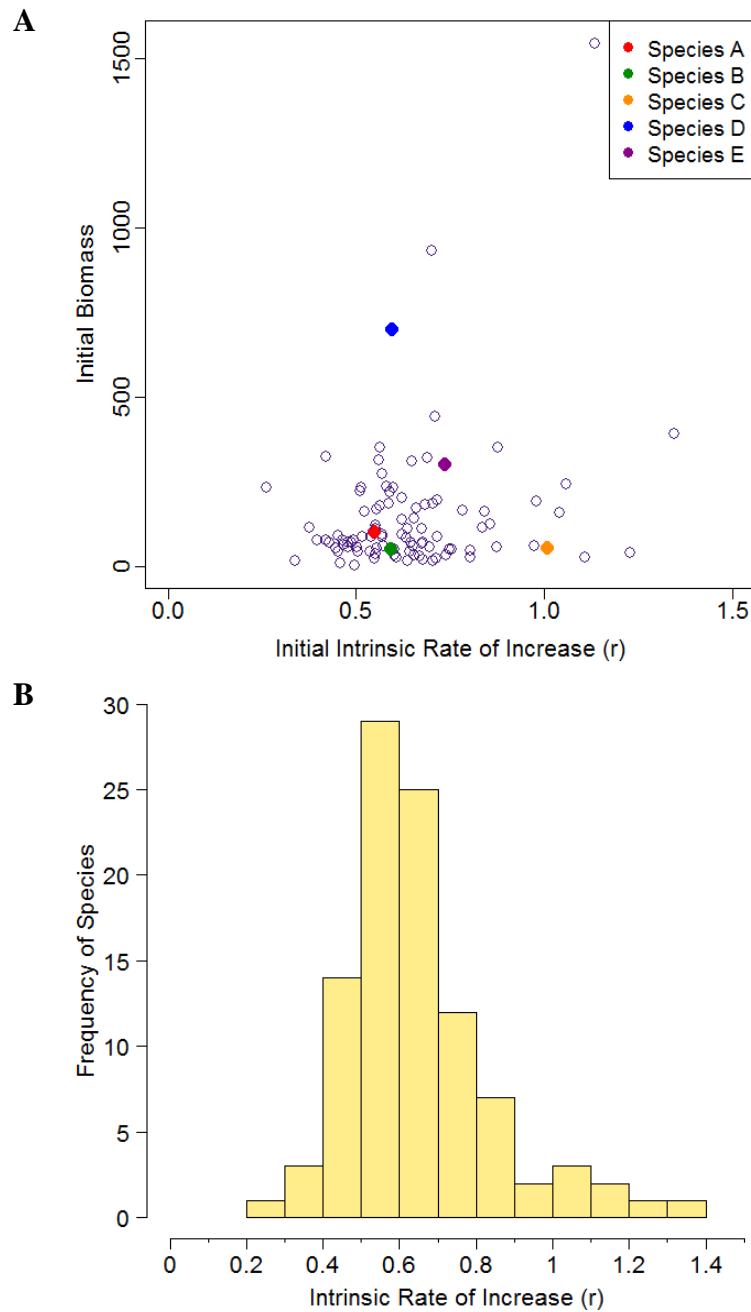


Figure 2.3. Scatter plot showing the relationship between the r value and initial biomass for each species in the system (A). The colored points represent the species selected for fishing. A frequency histogram of the initial intrinsic rate of increase (r) of each species in the system (B).

Table 2.3. Biological reference points estimated from ASPIC when the particular species fished is the only species in the ecosystem undergoing fishing. ASPIC does not provide a direct estimate of r , but r can be approximated in the logistic model as $2 \cdot F_{MSY}$.

Species	MSY	B_{MSY}	q	K	F_{MSY}	r_{ASPIC}
A	3.767	40.430	0.006	80.850	0.093	0.186
B	3.686	34.220	0.004	68.440	0.108	0.215
C	9.957	26.270	fixed at 0.005	52.530	0.379	0.758
D	37.200	305.500	0.005	611.000	0.122	0.244
E	33.670	164.000	fixed at 0.005	327.900	0.205	0.411

Table 2.4. Comparison of species' intrinsic production rates used in the L-V model and those estimated with ASPIC. The values from the L-V model are denoted with the L-V subscript, and all other parameters were estimated in ASPIC. In theory, F_{MSY}/r would equal 0.5, as is estimated from the logistic curve. However, the last column is the ratio of F_{MSY} from ASPIC to the r_{LV} from the L-V model.

Species	F_{MSY}	r_{ASPIC}	r_{LV}	r_{ASPIC}/r_{LV}	F_{MSY}/r_{LV}
A	0.093	0.186	0.547	0.341	0.170
B	0.108	0.215	0.592	0.364	0.182
C	0.379	0.758	1.009	0.751	0.376
D	0.122	0.244	0.596	0.408	0.204
E	0.205	0.411	0.738	0.557	0.278

Species B (least connected species)

Fishing species B at the ASPIC-estimated F_{MSY} did not affect the biomass of any other species in the community (Figure 2.5). Model 1 projected the biomass of Species B to remain lower than B_{MSY} once F_{MSY} was reached, indicating species interactions may affect the productivity of the stock (Figure 2.5). Model 2 projected the stock to equilibrate at B_{MSY} , and Model 3 predicted an equilibrium biomass and yield higher than the other two models.

Species C (species with high predator:prey ratio)

Fishing species C affected the most other species in the community (18%) (Figure 2.6). There were also three species that increased and one that decreased in biomass by 50-75% as a result of fishing Species C.

The projections of Model 1 and Model 2 are very similar. The biomass of Species C fell below B_{MSY} in Model 1 before reaching an equilibrium biomass (Figure 2.6). The projections of biomass and yield from Model 3 are higher than the other two models.

Species D (species with high prey:predator ratio)

Species D exhibited a marked increase (9%) in productivity during the projection of Model 1 (Table 2.5). This suggested that when Species D was fished, indirect effects increased prey availability for Species D. The projection of the L-V model for Species D exhibited a similar pattern as Species A. In Model 1, the stock reached B_{MSY} by the end of the projection. However, species interactions prevented Species D from reaching B_{MSY} during the first 100 years of fishing at F_{MSY} . Sixteen percent of all other species in the community exhibited a change in biomass when Species D was fished. However, no species exhibited a change in biomass greater than 50% (Figure 2.7).

Species E (randomly selected species)

Species E exhibited the highest increase in productivity in the projection of Model 1 (36%) (Table 2.6). Fishing Species D also resulted in the most number of unfished species exhibiting a change biomass (60%). Nineteen other species in the community increased in biomass by 25-50% and sixteen species decreased by 25-50% (Figure 2.8). Thirteen species increased in biomass and four species decreased in biomass by 50-75%. An additional seven species increased in biomass by more than 75% due to fishing Species E.

Species E was the only species to exhibit dampened oscillatory behavior when fished at F_{MSY} , and remained below B_{MSY} in the terminal year (Figure 2.8). The projection of biomass and yield from Model 2 resulted in the species' biomass at B_{MSY} . As with all of the other species, the projected biomass from Model 3 was higher than the other two models.

Table 2.5. Comparison of the intrinsic rate of increase in the terminal year and the biomass of the fished species during overfishing and at the end Fishing Scenario 1. The r -values for Models 2 and 3 do not change during the simulation.

		$r_{yr=0}$	$r_{yr=300}$	B_0	B_{300}
<i>Species A</i>					
	Model 1	0.547	0.547	103.22	40.08
	Model 2	0.186	0.186	103.22	40.43
	Model 3	0.547	0.547	103.22	85.68
<i>Species B</i>					
	Model 1	0.592	0.606	50.90	30.69
	Model 2	0.215	0.215	50.90	34.22
	Model 3	0.592	0.592	50.90	41.64
<i>Species C</i>					
	Model 1	1.009	1.227	56.25	26.26
	Model 2	0.758	0.758	56.25	26.267
	Model 3	1.009	1.009	56.25	35.12
<i>Species D</i>					
	Model 1	0.596	0.652	698.86	298.78
	Model 2	0.244	0.244	698.86	305.50
	Model 3	0.596	0.596	698.86	556.04
<i>Species E</i>					
	Model 1	0.738	1.004	301.81	148.98
	Model 2	0.411	0.411	301.81	163.95
	Model 3	0.738	0.738	301.81	217.81

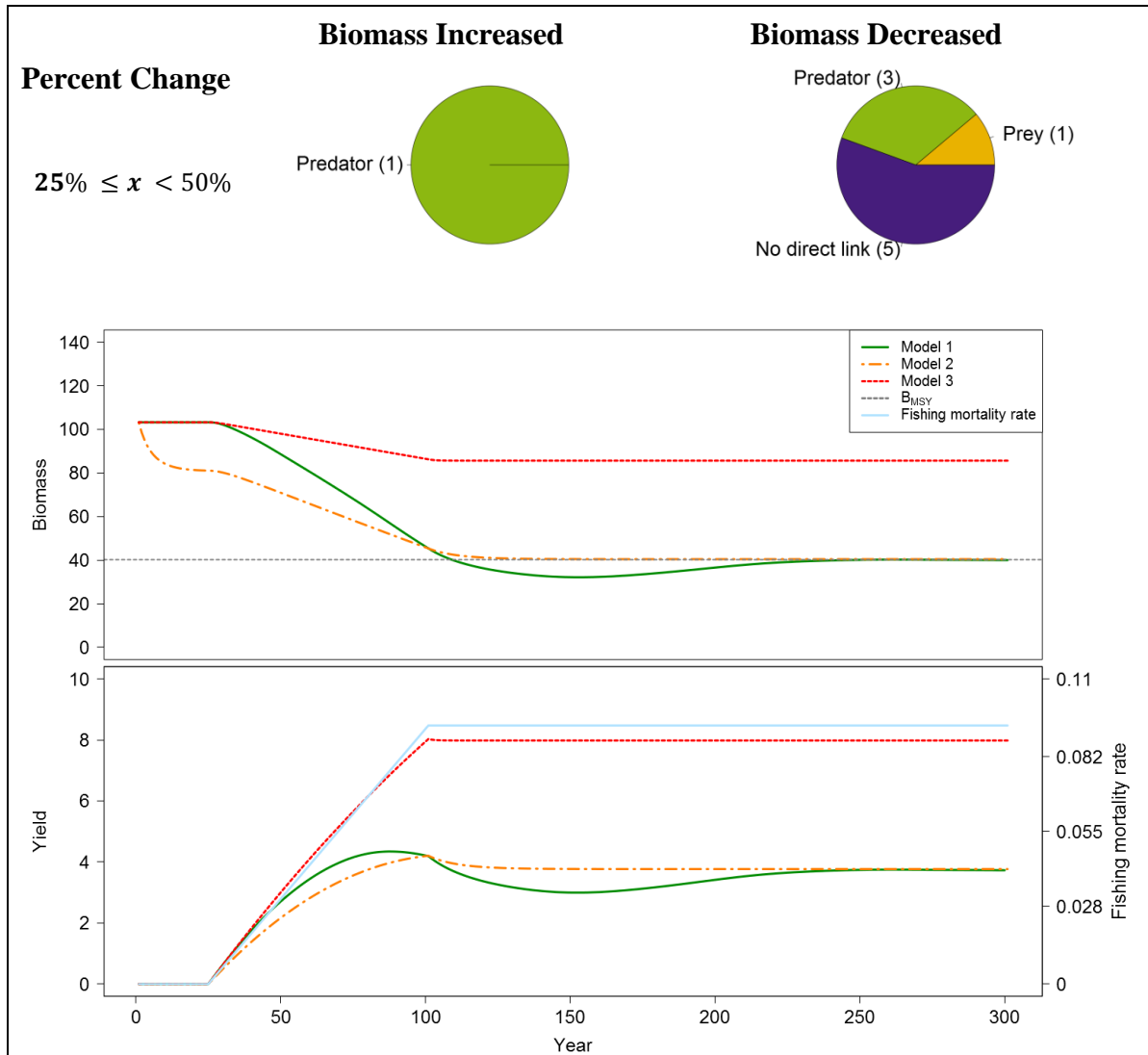


Figure 2.4. Model results for Species A when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A, the prey of Species A, and species with no direct link to Species A. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

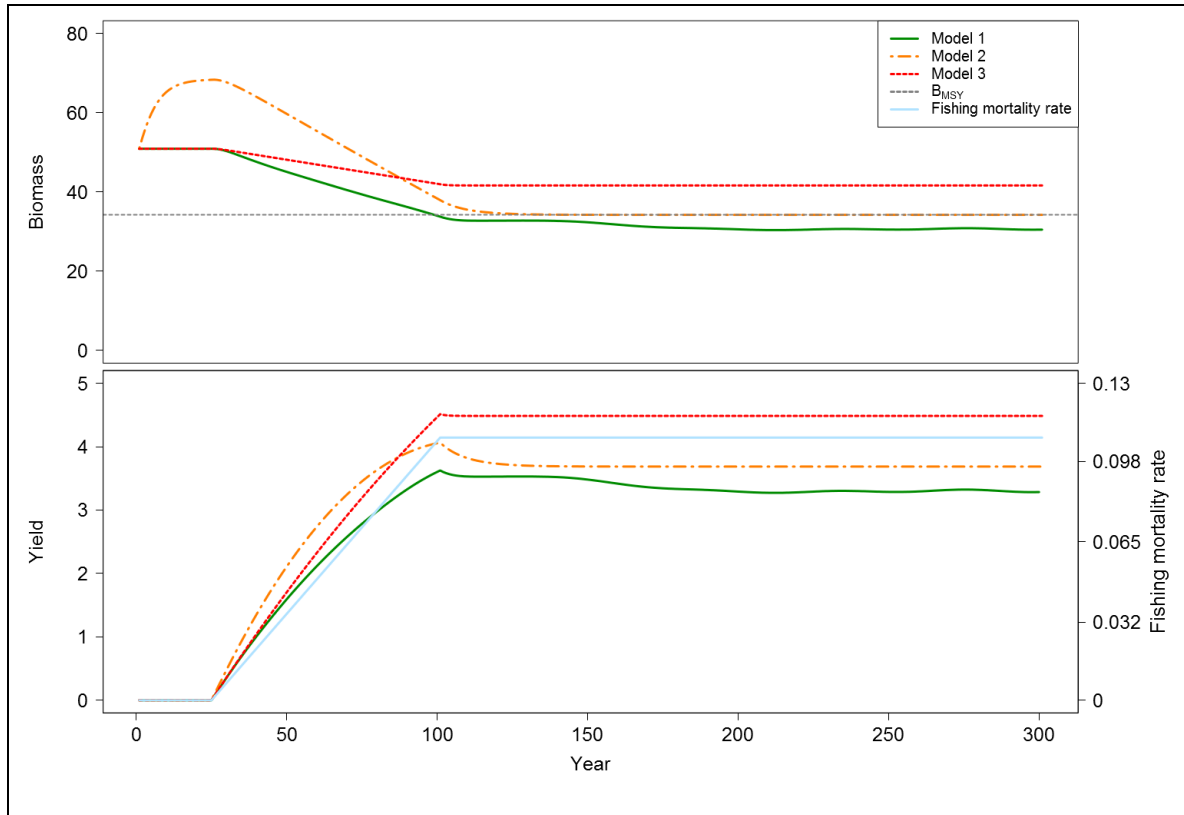


Figure 2.5. Model results for Species B when fished at F_{MSY} . No unfished species changed in biomass by $\geq 25\%$. The time series of biomass and yield are represented for all three models using the same fishing regime. Model1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

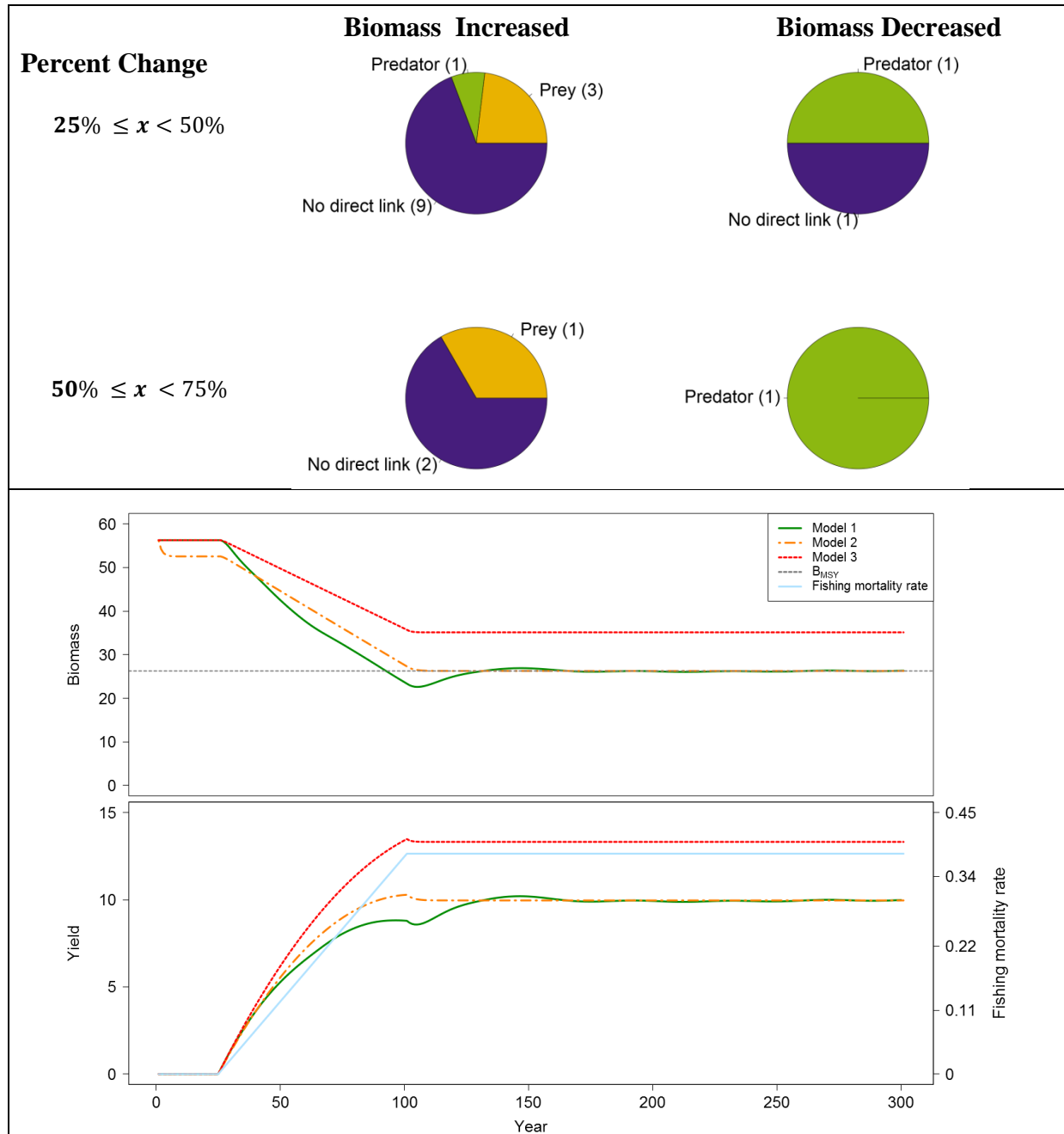


Figure 2.6. Model results for Species C when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C, the prey of Species C, and species with no direct link to Species C. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

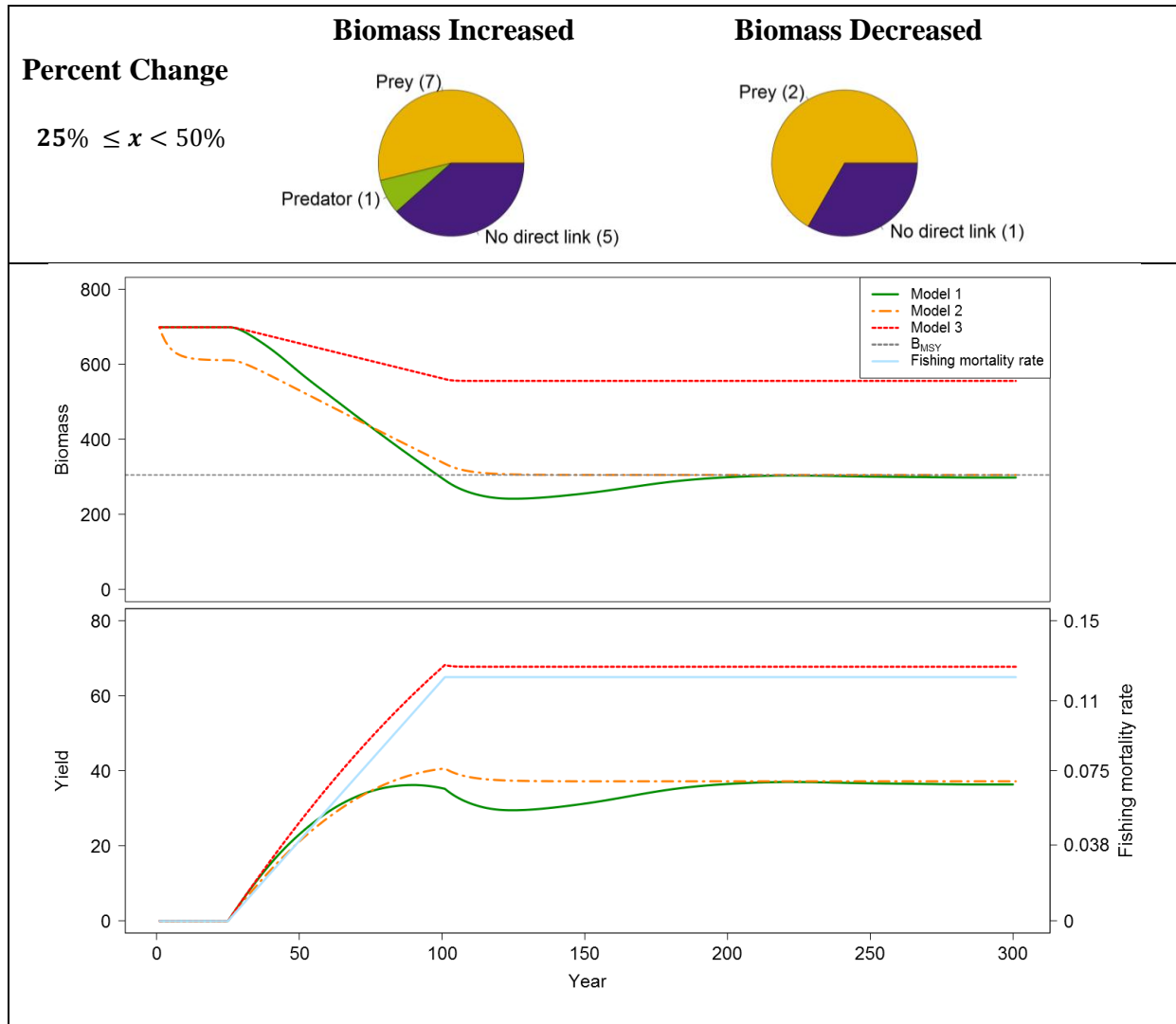


Figure 2.7. Model results for Species D when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D, the prey of Species D, and species with no direct link to Species D. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

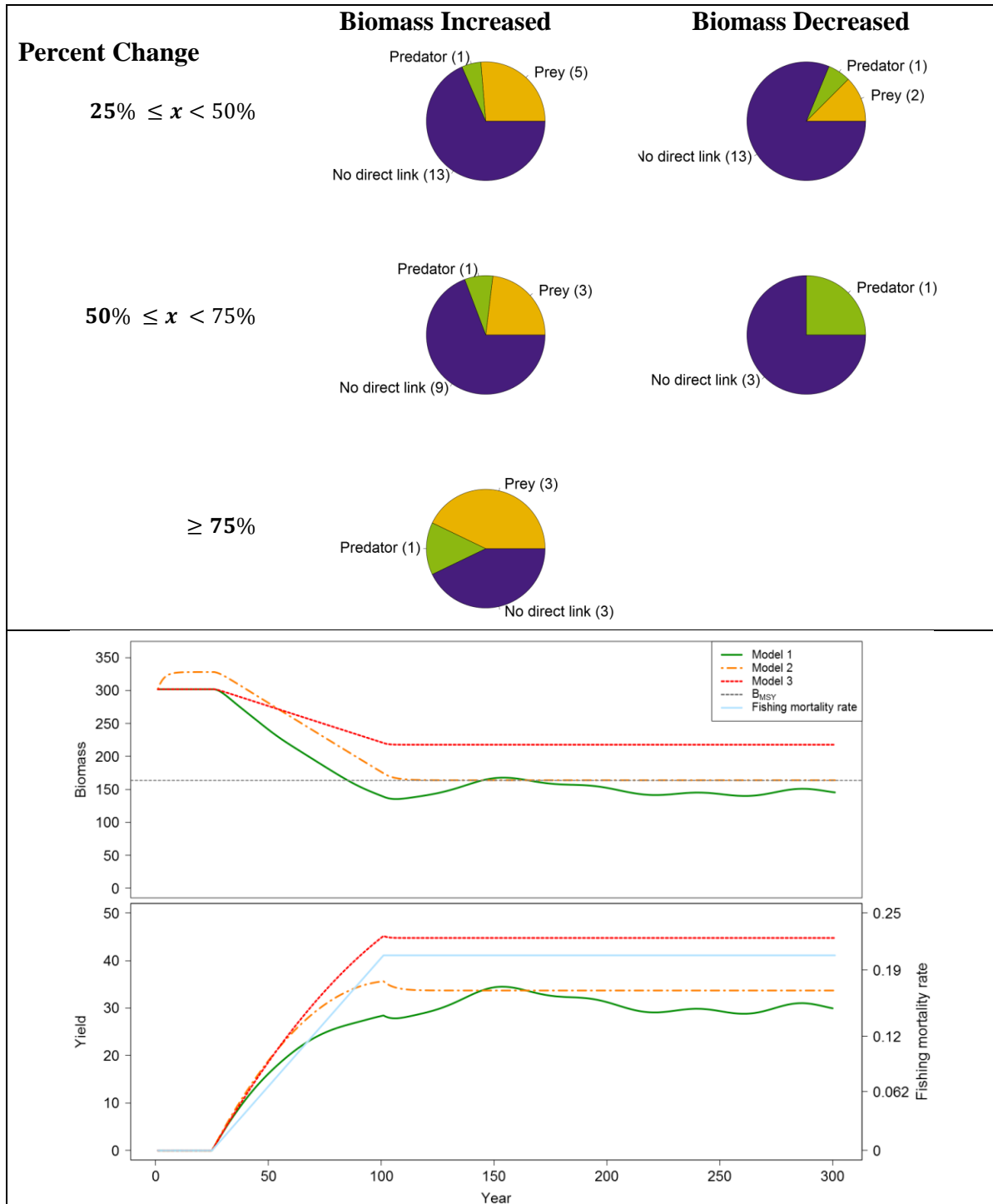


Figure 2.8. Model results for Species E when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E, the prey of Species E, and species with no direct link to Species E. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

Fishing Scenario 2 (Overfish and rebuild species)

Species A (most connected species)

Model 1 projected species A to take longer to recover than the single-species model, Model 2, 23 versus nine years respectively (Table 2.6). Model 1 also projected a higher terminal biomass than Model 2, indicating that species interactions positively affect the productivity and biomass of Species A (Figure 2.9). During the period of overfishing, twice as many unfished species exhibited a change in biomass than in Fishing Scenario 1 (Figure 2.9). However, all unfished species in the community returned to near equilibrium biomasses when Species A was recovered.

Species B (least connected species)

Species B was the only species projected to rebuild in a shorter time period (five years) in Model 1 than Model 2 (eight years) (Table 2.6). The impacts of species interactions were evident in the oscillatory nature of the biomass in Model 1. Model 1 did project a biomass higher than B_{MSY} once the stock was rebuilt. This was also the only simulation in which the equilibrium biomass for Model 2 was higher than the projected biomass from Model 3 (Figure 2.10). Two species increased in biomass while overfishing was occurring, but returned to equilibrium levels once Species B was rebuilt (Figure 2.10).

Species C (species with high predator:prey ratio)

During the peak of overfishing, Species C was at 14.5% of its virgin biomass (Table 2.6). Model 1 projected Species C to rebuild within four years of stopping overfishing and Model 2 projected that it would only take two years (Table 2.6). Model 1 captured the species interactions that predicted an increase in biomass to 60 after overfishing stopped and an eventual equilibrium biomass at around 40, close to that of Model 2's projection (Figure 2.11). Species C had a high intrinsic rate of increase that allowed the species to quickly increase in biomass, once

released from fishing pressure. This was the only simulation in which Model 3 predicted a species would be overfished. During the period of overfishing, a total of 40 species exhibited a change in biomass, compared to the 18 species from Fishing Scenario 1 (Figure 2.11). In year 300, after Species C was rebuilt, four species still exhibited a change in biomass by 25-50%.

Species D (species with high prey:predator ratio)

Model 1 projected that Species D would be rebuilt fifteen years after overfishing stopped and Model 2 projected Species D would be rebuilt in eight years (Table 2.6). The equilibrium biomass in year 300 for Models 1 and 2 were both near 490 and produce similar yield (Figure 2.12). The terminal year biomass was higher in the multispecies model (Model 1) than in the single-species Model 2. During the period of overfishing, twenty-six unfished species exhibited a change in biomass, but all returned to equilibrium levels once over fishing had stopped (Figure 2.12).

Species E (randomly selected species)

Species E exhibited the most oscillatory behavior in the multispecies projection once overfishing was stopped. This illustrated the need to understand species interactions. Both Models 1 and 2 projected the stock to be rebuilt five years after overfishing stopped.

During the period of overfishing, 60 species exhibited a change in biomass (Figure 2.13). The fourteen species exhibiting a change in biomass $>75\%$ all increased in biomass, and seven had no direct link to Species E. IN the terminal year of the simulation, 24 species still exhibited a change in biomass $\geq 25\%$.

Table 2.6. Comparison of the intrinsic rate of increase in the terminal year and the biomass of the fished species during overfishing and at the end of Fishing Scenario 2. The r values for Models 2 and 3 do no change during the simulation. The NA values indicate the population was never below the B_{MSY} threshold.

	$r_{yr=300}$	$B_{yr=151}$	B_{300}	Years until $B_t / B_{MSY} > 1$
<i>Species A</i>				
Model 1	0.547	12.03	73.39	23
Model 2	0.186	22.37	60.42	9
Model 3	0.547	76.84	94.42	NA
<i>Species B</i>				
Model 1	0.597	23.18	41.24	5
Model 2	0.215	18.50	51.33	8
Model 3	0.592	37.01	46.27	NA
<i>Species C</i>				
Model 1	1.123	8.25	41.54	4
Model 2	0.758	13.14	39.39	2
Model 3	1.009	24.54	45.68	1
<i>Species D</i>				
Model 1	0.630	81.63	491.98	15
Model 2	0.244	162.33	458.25	8
Model 3	0.596	484.62	627.40	NA
<i>Species E</i>				
Model 1	0.864	64.62	229.36	5
Model 2	0.411	83.24	245.95	5
Model 3	0.738	175.81	259.81	NA

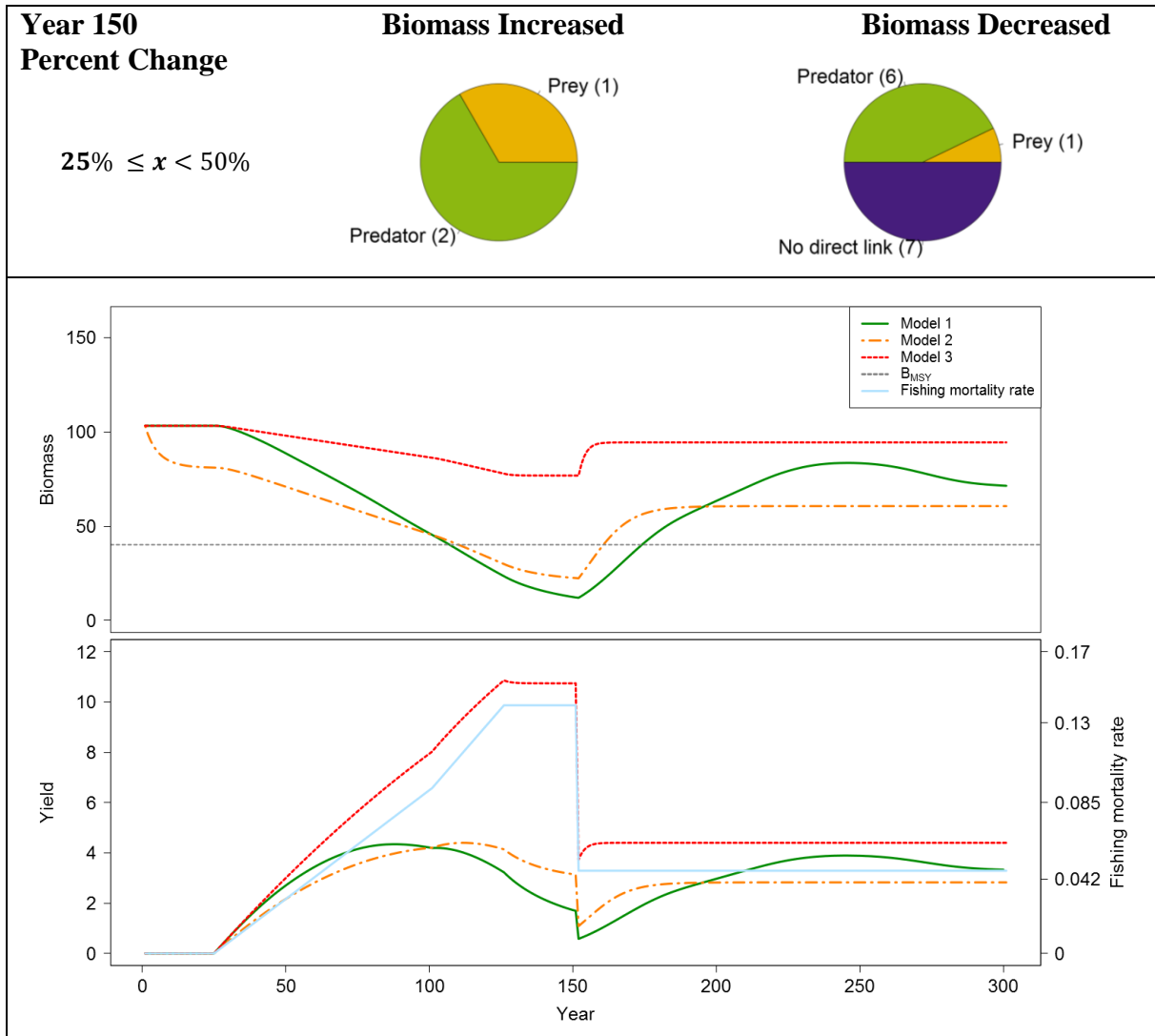


Figure 2.9. Model results for Species A when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A, the prey of Species A, and species with no direct link to Species A. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

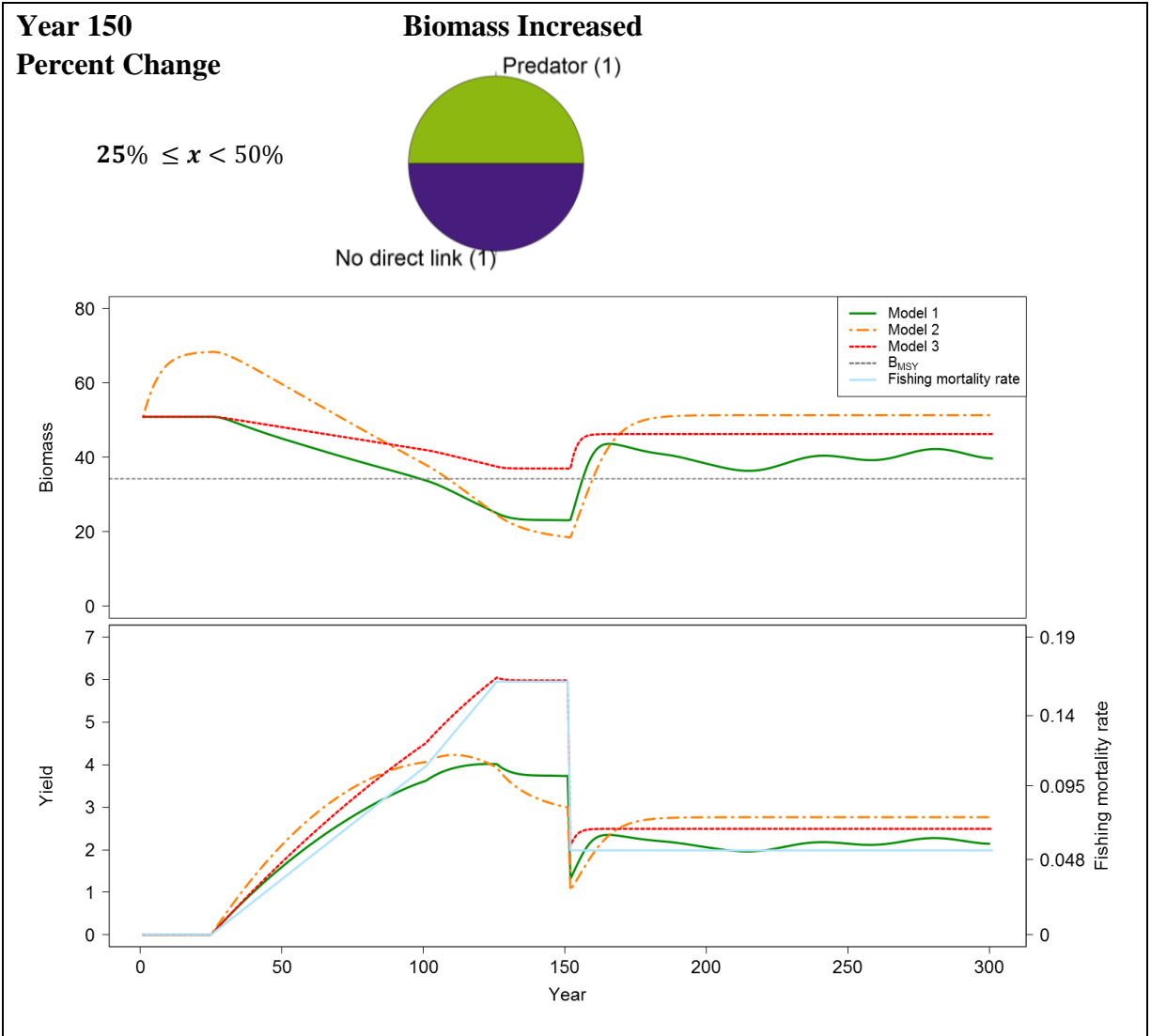


Figure 2.10. Model results for Species B when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species B, the prey of Species B, and species with no direct link to Species B. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

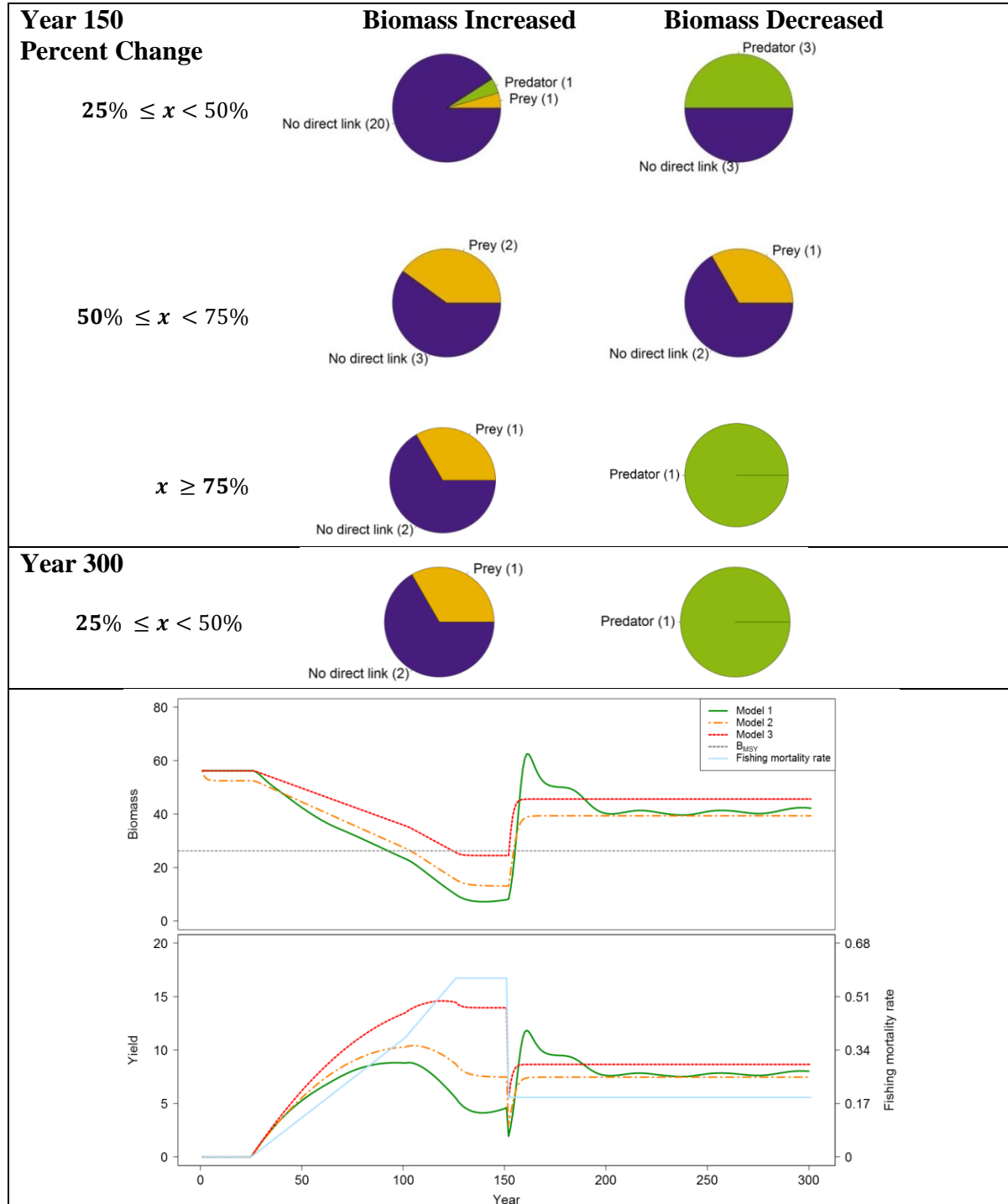


Figure 2.11. Model results for Species C when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C, the prey of Species C, and species with no direct link to Species C. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

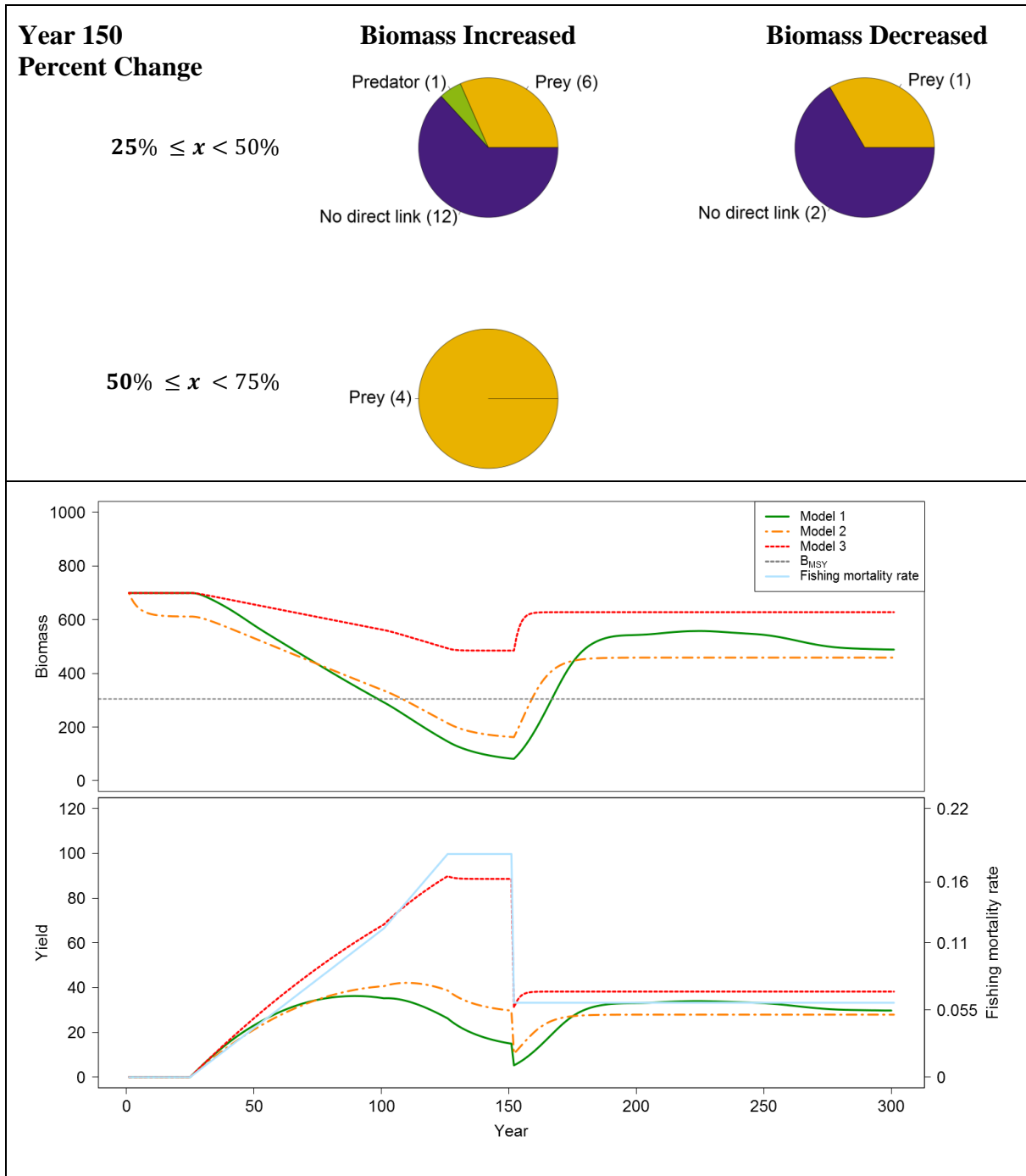


Figure 2.12. Model results for Species D when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D, the prey of Species D, and species with no direct link to Species D. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

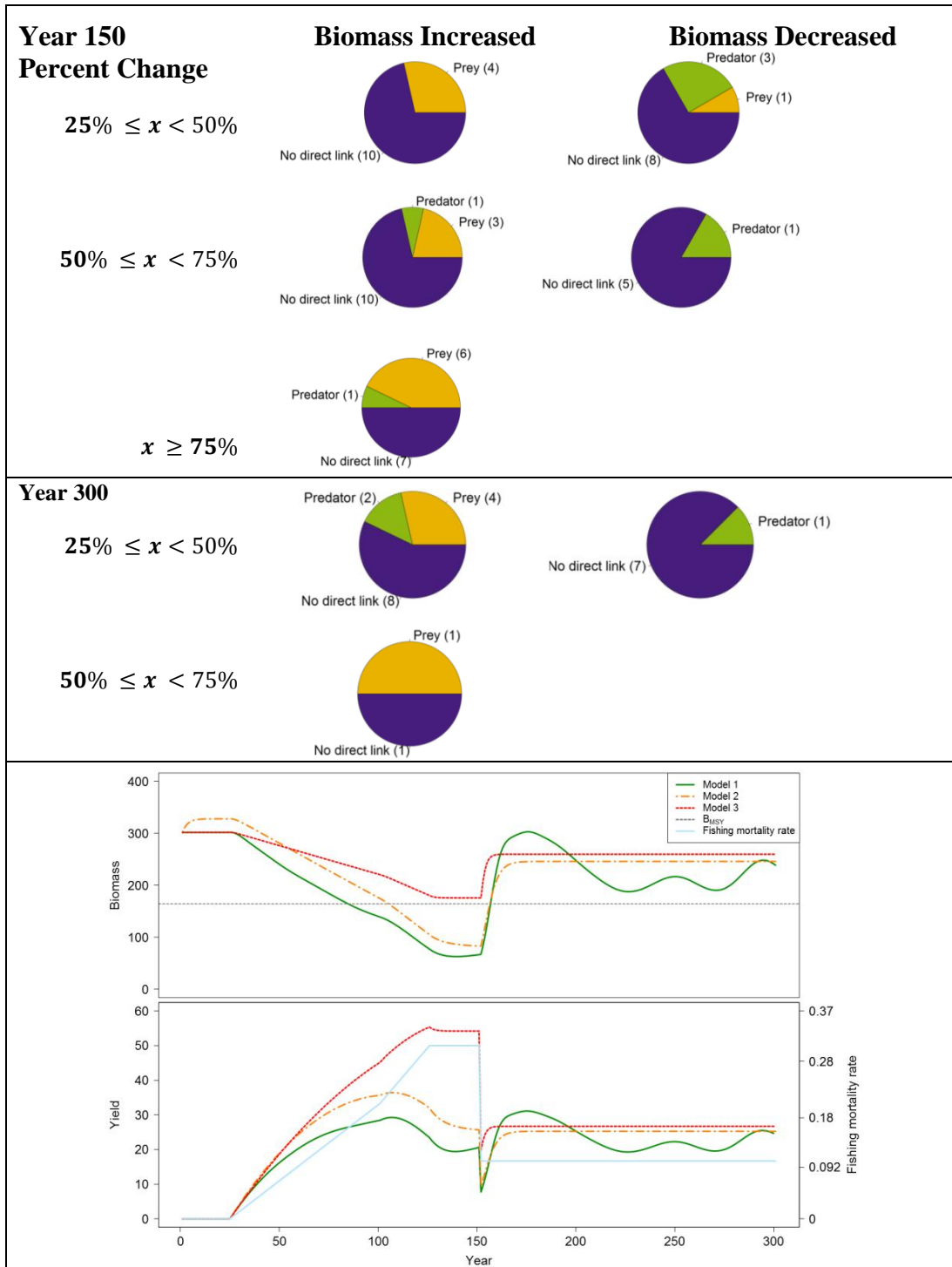


Figure 2.13. Model results for Species E when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E, the prey of Species E, and species with no direct link to Species E. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the L-V model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

DISCUSSION

Parameter estimates and Fishing Scenario 1

The ASPIC-estimated biological reference points for all species examined were 35-75% lower than what is theoretically expected from the logistic Schaeffer model. This indicates that species interactions are important in determining species productivity and should be accounted for when determining fishing mortality rates. The estimate of r_{ASPIC} for Species C was the closest to r_{LV} , but still only 75% of the true value. While Species C had a high predator:prey ratio, it is likely that the high intrinsic rate of increase allowed the species to be fished at a higher rate even when species interactions had occurred. The estimated r_{ASPIC} for Species E (randomly selected species) was 56% of r_{LV} , and may have been higher than other estimates because of the higher growth rate, initial biomass, and the relatively low number of number of predators. As a note, none of the fished populations were sustainable when fished at the theoretical F_{MSY} rates. All of these lower than expected estimates of F_{MSY} and r_{ASPIC} values indicate that the ecological interactions do in fact decrease single-species production. Several recent studies and management plans have recommended that traditional single-species models are not conservative enough when estimating F_{MSY} and other biological reference points (Abrams and Ginzburg, 2000; ICES, 2007; Field et al., 2010; Tyrrell et al., 2011; Cury et al., 2011).

This study also illustrated the extent to which other species in the same ecosystem are affected by fishing, even when a single species is fished at F_{MSY} . Both direct and indirect effects were evident in this study from the number of unfished species exhibiting changes in biomass. As might be expected, Species B, with the fewest direct connections did not affect the biomass of any other species in the community. Species A, which had the most connections, resulted in 9% other species exhibiting a change in biomass. The large number of total links of Species A

dampened the effect Species A had on any one individual species. The impact of indirect links was evidenced in the results for Species E. In the case of Species E, 41 unfished species with no direct link to Species E exhibited a change in biomass. Three of these species even increased in biomass by $\geq 75\%$ when Species E was fished. These results, while only from a simulation model, confirm the theory that indirect effects play an important role in fished communities (Menge, 1995; Pinnegar et al., 2005; Roberts and Stone, 2004).

The three models used in the projections were selected to illustrate a spectrum of possible outcomes. Model 1 was the multispecies L-V model and accounted for all species interactions. This model was a representation of a community in which all interaction strengths and species parameters were known. Model 2 was selected to examine the projections if the multispecies parameters were used as input in the single-species model. The intrinsic rate of increase and initial biomass were drawn from the L-V model for Model 2. The r value in Model 3 was the single-species intrinsic rate of increase, and did not account for any knowledge of species interactions. The parameters used in Model 3 are the most commonly used in the real world because the effects of interactions, especially indirect effects, are difficult to measure (Tyrrell et al., 2011; Wootton, 2002; Novak et al., 2011).

The three models did not predict the results I expected in all cases. In three cases (Species A, C, and D) the multispecies model projected a higher equilibrium biomass than did the single-species Model 2. This again stresses the need to understand the species interactions and how they can inform stock assessment and the biological reference points used for management (Gaichas et al., 2010; Hollowed et al., 2011; Gamble and Link, 2009).

Fishing Scenario 2

The immediate and drastic decrease in fishing mortality rate used to rebuild species in this study would not be feasible in the real world, but presents a best case scenario. The time required for rebuilding to B_{MSY} was not always longer in multispecies model. Model 1 projected that Species B would be rebuilt within five years after overfishing was halted, while Model 2 projected eight years. This may not be a large difference, but it does indicate that there is a possibility for species interactions to enhance the ability for a stock to rebuild or not. The terminal year biomass was also higher Species A, C, and E in the multispecies model than Model 2. The higher biomass is a direct effect of species interactions.

Lotka-Volterra Multispecies and Surplus-Production Models

The multispecies L-V model illustrated the importance of accounting for species interactions when determining fishing mortality rates. The multispecies L-V model was created based on what was learned about the Gulf's demersal fish community in Chapter 2. Species in the L-V model were not given nor related to specific species. However, the characteristics of the demersal fish community were incorporated. The demersal fish community described in Chapter 2 indicated that approximately 100 species account for 95% of the community biomass. The lognormal biomass distribution used in the L-V model was informed by the distribution of species biomass in Chapter 2. In most of the demersal fish communities defined in Chapter 2, ten dominant species accounted for half of the total community biomass. The other 90% of the biomass was comprised of hundreds of other species.

The single-species definition of r (the intrinsic rate of increase) does not translate directly to a multispecies L-V model. In a two species L-V model, the r -value represents a species' maximum growth rate in the absence of predators. However, in the multispecies L-V model,

prey are present that contribute to a positive growth rate. In the single-species model, all positive rates are collapsed into the single parameter, r . Values chosen for the original intrinsic rates of increase are based on traditional single-species growth rates, but partitioned among other interacting species from which that growth is acquired. This is a quasi-bioenergetics approach to parameterizing the L-V model, with the assumption that species growth and mortality are direct results of consumption and predation.

While data required to create an interactions matrix and to quantify the interaction strengths are often not available, considerable research effort is now being expended to characterize food webs through models such as Ecopath with Ecosim (Polovina, 1984; Walters et al., 1997; Christensen and Walters, 2004). Continued simulation work and the incorporation of real-world data will hopefully result in the emergence of patterns that can be generalized and applied to real-world ecosystems.

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The multispecies L-V model created for this study can be used for a multitude of other simulation exercises. I only explored the effects of fishing five pre-selected species, but this same exercise might be done for all 100 species. The multispecies L-V model can also be used to make comparisons with other multispecies models, e.g., Ecopath/Ecosim, MS-PROD or AGG-

PROD. Comparison of projections among these models would provide interesting insight into species interactions and the variability among biological reference points estimated from each.

Other methods to generate the interaction matrix could also be explored, such as using preferential predator and prey selection (Powers and Brooks, 2011). There are also other models available for creating the network connections, such as the ‘niche’ model that builds the interaction matrix by assigning species to a ‘trophic niche,’ which results in a series of rules about which species can prey upon another (Williams and Martinez, 2000; Dunne et al., 2004; Williams and Martinez, 2008). In addition to modeling Holling’s Type II or Type III functional responses (Holling, 1959), it may also be possible to incorporate a foraging arena functional response into the interaction matrix (Walters and Juanes, 1993; Walters et al., 1997)

Network analyses could also be used to visualize the interaction matrix and attempt to assign trophic levels or ecosystem roles to each of the species. This would allow the species in the model to be compared to species in ecosystems that have been well studied. Data from the Northeast U.S. large marine ecosystem are also available and could be used to create the topology of and parameterize the interaction matrix (Link, 2002a; Gamble and Link, 2009; Gamble and Link, 2012). The diet matrix data from the Northeast U.S. ecosystem provides a starting point for creating the interaction matrix, but still presents challenges in estimating interaction strengths between species.

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CHAPTER 3 : EFFECT OF CONNECTANCE ON BIOLOGICAL REFERENCE POINTS FROM MULTISPECIES AND SINGLE SPECIES MODELS

INTRODUCTION

Community ecology theory plays an important role in the development of an ecosystem approach to fisheries management. Community ecology encompasses research to understand the biological connections and interactions among species within the same ecosystem (Pielou, 1974; Bender et al., 1984). Quantitative food web and multispecies models can be used to investigate dynamic species interactions and the impact of changes, or perturbations, to a community (May, 2006; Pascual and Dunne, 2006; Williams and Martinez, 2008).

One component of community theory debated in the literature is the paradigm of complexity versus stability (Pimm, 1984; Hannah et al.; Gatto, 2009; Pinnegar et al., 2005; Polis and Strong, 1996; Sole and Montoya, 2001; McCann, 2000). In the 1950s, several studies published empirical evidence from field studies showing that ecosystems with higher complexity were more stable (Elton, 1958; MacArthur, 1955; Odum, 1953). This theory was challenged by May (1973), who used randomly created community matrices to argue that increasing community complexity (e.g. number of species, connectivity, number of functional groups, etc.) would lead to decreased stability, or that the community would not return to an equilibrium point after a perturbation. McCann (2000) presents a review of the complexity-stability paradigm, concluding that the most recent studies indicated increased diversity leads to increased ecosystem stability. However, the driver of stability is not purely a complexity or diversity debate. One commonly cited driver of the paradigm is functional redundancy, when the process rates of an ecosystem do not change when one species goes extinct or is removed. The process rates do not change because another species' population that serves the same ecological function assumes the role of the removed species. Although MacArthur (1955) first proposed the theory

that increased ecosystem connectance (number of links among species) drives stability, he did not consider predator-prey interactions (Armstrong, 1982).

One metric of community complexity is connectance, the percent of realized links in the interaction matrix ((Martinez, 1991; Martinez, 1992). A review of marine system connectance estimates revealed that current estimates are underestimates due to the large sampling requirements and diet analysis required to define all links (Raffaelli, 2000; Goldwasser and Roughgarden, 1997; Martinez et al., 1999; Link, 2002). Connectance values for marine systems reported in the literature are also markedly higher than in terrestrial and freshwater system (Dunne et al., 2004; Link, 2002). The higher values of connectance in marine ecosystems is attributed to species being omnivorous and generalists, whereas in terrestrial or freshwater systems species may have fewer direct links to prey or predator species (Cohen, 1994; Link, 2002; Bengtsson, 1994). Empirical studies have estimated directed connectance (L/S^2) for marine systems from 10% to 48% (Link, 2002; Yodzis, 1998; Opitz, 1996) (Figure 3.1).

Figure 3.1. Food web properties from published studies on marine systems. Taxa = number of taxa from the original food web, S = number of species, C = connectance (L/S^2), and L/S = links per species.

Ecosystem	Taxa	S	C	L/S	Source
Benguela	29	29	0.24	7.0	Yodzis (1998)
Caribbean Reef, small	50	50	0.22	11.1	Opitz (1996)
Northeast US Shelf	81	79	0.22	17.8	Link (2002)
Caribbean Reef, large	249	245	0.05	13.8	Opitz (1996)

The goal of Chapter 3 is to gain a better understanding the role of complexity when estimating biological reference points. I created two communities of 35% and 45% connectance to compare to the community of 25% connectance described in Chapter 2. The two new

communities of 35% and 45% connectance are created independently of one another. The results for the two new communities of 35% and 45% connectance are compared to the results from Chapter 2.

METHODS

The methods for the creation of the Lotka-Volterra model were the same as those in Chapter 2. Each community had 100 species. The communities with 35% and 45% connectance were created by altering the prey and predator *Links* parameters (see Chapter 2). For the community of 35% connectance, the predator *Links* was 14 and the prey *Links* was nine. For the community of 45% connectance, the predator *Links* was 19 and prey *Links* was sixteen. The distribution of links for each of the communities of 35% and 45% connectance can be found in Figure 3.2 and Figure 3.3, respectively.

Five species were selected for fishing:

1. The species with the most links (Species A)
2. The species with fewest links (Species B)
3. A species with few predators, and a large number of prey (relative to other species in the system) (Species C)
4. A species with large number of predators, and a few number of prey (relative to other species in the system) (Species D)
5. Randomly selected species (Species E)

These were the same species characteristics used to select species in Chapter 2. The vector of initial r values and initial biomass values remained the same as in Chapter 2. The motivation was assign species with similar characteristics the same initial conditions.

The randomly selected species were selected independently among all the communities. Species A-E were identified among communities with a subscript representing the community connectance, i.e., A_{25} represented species A from the community with 25% connectance. The species were also assigned the same standard deviation applied to the catch for input into ASPIC as in Chapter 2.

The same two fishing scenarios outlined in Chapter 2 were applied to each of the five species in the communities of 35% and 45% connectance. The fishing scenarios were 1) fish the selected species at the ASPIC-estimated F_{MSY} , and 2) overfish the selected species and implement a rebuilding plan by reducing fishing to $0.5 * F_{MSY}$.

Both fishing scenarios were projected for 300 years using the same three models as in Chapter 2. Model 1 was a projection of the Lotka-Volterra model, which was initialized at the equilibrium biomass for all species. Models 2 and Model 3 were projection of a single-species surplus production model for only the species of interest, i.e., all species interactions were ignored. The species' initial biomass in Model 2 was the ASPIC-estimated carrying capacity, K and the intrinsic rate of increase was r_{ASPIC} . Model 3 used the Lotka-Volterra equilibrium biomass as a proxy for K , and the r_{LV} as the intrinsic rate of increase.

RESULTS

Estimated biological reference points

Parameters were estimated for all species A_{35} - E_{35} and A_{45} - E_{45} . However, q was fixed at the true value of 0.005 for species B_{35} , C_{45} , D_{45} , and E_{45} (Table C.1). There were not identifiable trends in any of the parameters correlated with increasing community connectance.

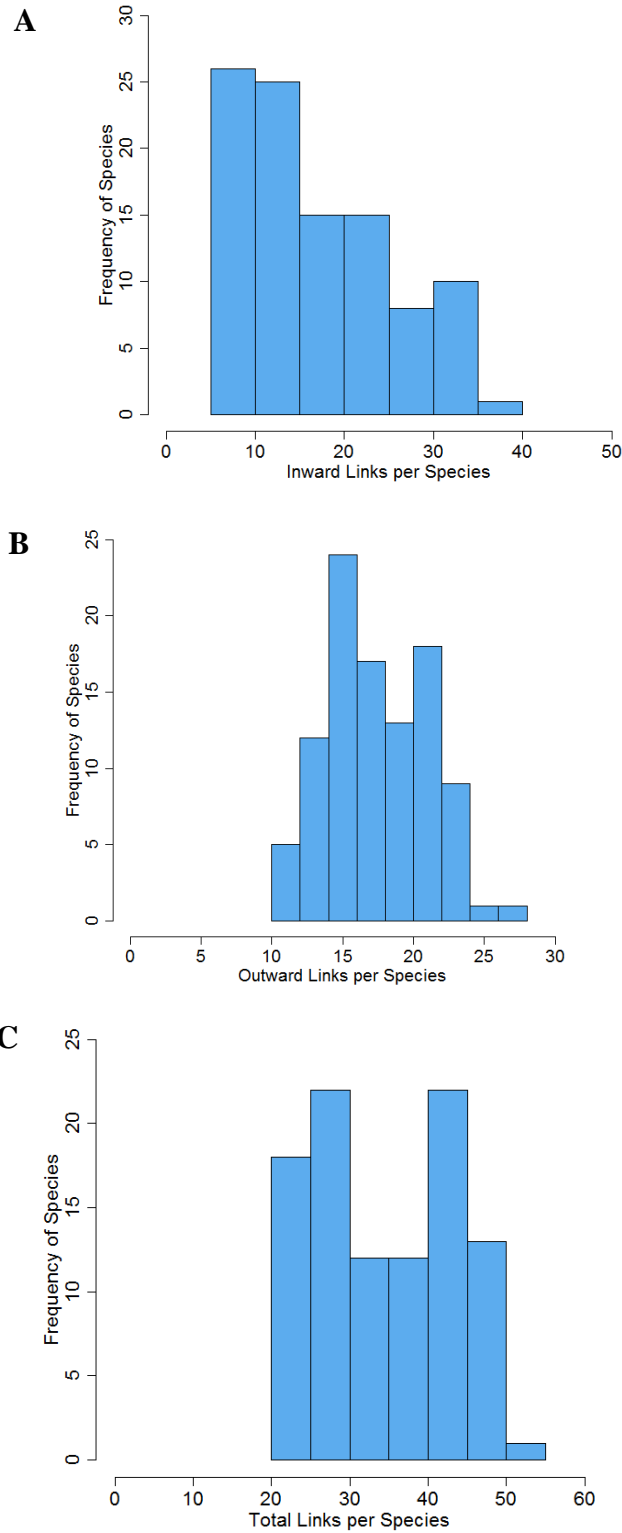


Figure 3.2. The number of inward links per species is the number of prey items of a species (A) and the outward links is the number of predators per species (B). The distribution of total number of links per species for the ecosystem with 100 species and 35% connectance (C).

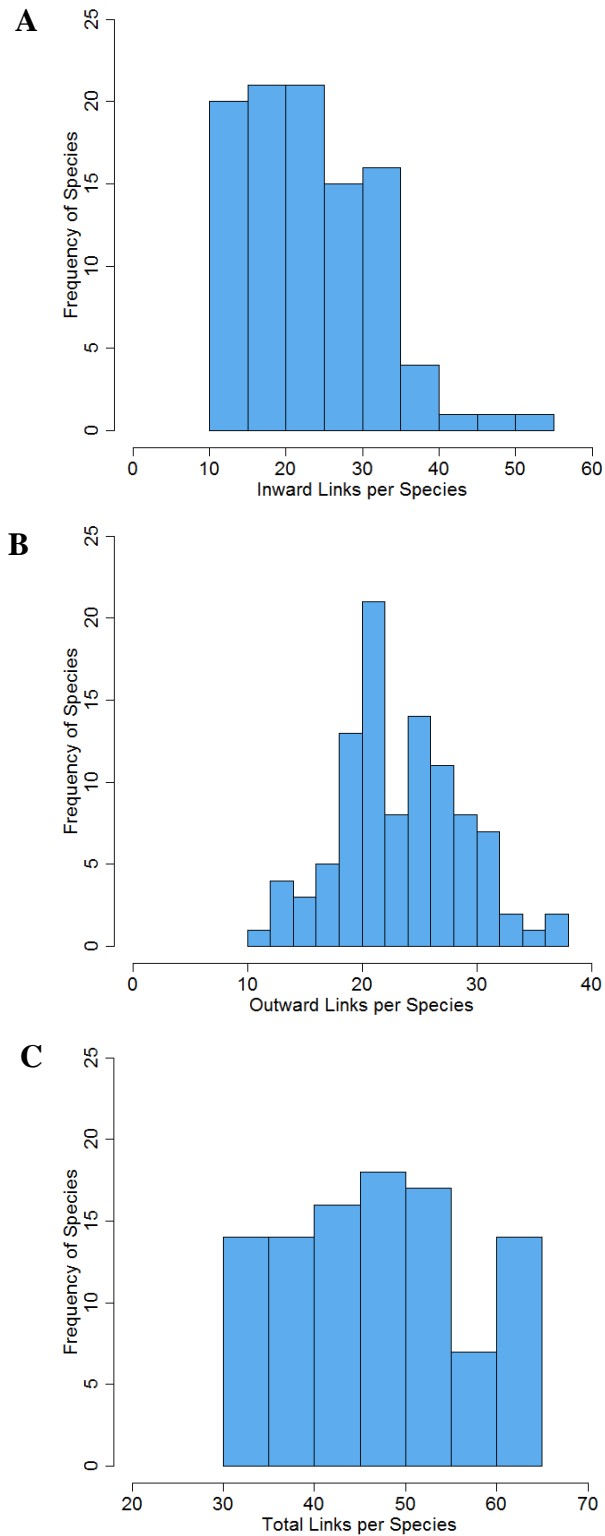


Figure 3.3. The number of inward links per species is the number of prey items of a species (A) and the outward links is the number of predators per species (B). The distribution of total number of links per species for the ecosystem with 100 species and 45% connectance (C).

Table 3.1. Characteristics of the species chosen for fishing for the community of 35% connectance. Inward links are equivalent to positive α_{ij} values in the interaction matrix, and are the prey of the species in the first column. Outward links are equivalent to negative α_{ij} values (excluding the α_{ii} self-interaction) in the interaction matrix, and are the predators of the species in the first column.

Species	Inward Links	Outward Links	Total Links	r_{LV}	B_0
Species with the most total links: #19 (A_{35})	31	23	53	0.547	103.22
Species with the fewest total links: #96 (B_{35})	6	15	21	0.592	50.90
Species with many predators, few prey: #25 (C_{35})	16	28	44	1.009	56.25
Species with few predators, many prey: #11 (D_{35})	36	12	48	0.596	698.86
Randomly selected species: #77 (E_{35})	13	16	29	0.738	301.81

Table 3.2. Characteristics of the species chosen for fishing for the community of 45% connectance. Inward links are equivalent to positive α_{ij} values in the interaction matrix, and are the prey of the species in the first column. Outward links are equivalent to negative α_{ij} values (excluding the α_{ii} self-interaction) in the interaction matrix, and are the predators of the species in the first column.

Species	Inward Links	Outward Links	Total Links	r_{LV}	B_0
Species with the most total links: #25 (A_{45})	32	33	65	0.547	103.22
Species with the fewest total links: #94 (B_{45})	10	20	30	0.592	50.90
Species with many predators, few prey: #65 (C_{45})	13	28	41	1.009	56.25
Species with few predators, many prey: #20 (D_{45})	54	11	65	0.596	698.86
Randomly selected species: #13 (E_{45})	36	13	49	0.738	301.81

The estimates of K from ASPIC, exhibited a wide range of values within a species. Carrying capacity was estimated at 81 for Species A₂₅ and 166 for A₃₅, which affects the estimation of biological reference points from the logistic model. Fixing q did not appear to produce more accurate results (an estimate of r_{ASPIC} closer to r_{LV}) within or among species.

The estimates of r_{ASPIC} were lower than r_{LV} for all species, across all communities (Table 3.3). The estimated r_{ASPIC} was only 10% of the r_{LV} value for species, the lowest of all estimates. Species C had the widest range of r_{ASPIC} estimates, ranging from 24-78% of r_{LV} . Two estimates of r_{ASPIC} for Species E₂₅ and E₃₅ were among the highest, even though the estimates of K for these two simulations were not the closest among the three communities. This indicated that species interactions may be driving the productivity of Species E. The results among communities suggest that species productivity could be between 10-75% of the traditional single-species estimates, when species interactions are accounted for.

Fishing Scenario 1 (Fish species of interest at F_{MSY})

Species A

The multispecies projections of Species A were different among the three communities (Figure 3.4, Figure 3.9). In the community of 25% connectance Species A was projected to equilibrate at B_{MSY} , but was projected to remain below B_{MSY} in the other two communities. In the terminal year of the simulation, the biomass was still declining in the community of 45% connectance. The estimated B_{MSY} for A₃₅ was double the estimate for Species A₂₅ (which maintained a biomass at B_{MSY}). This suggests that species interactions prohibit Species A₃₅ from being sustainably fished at even the F_{MSY} . Model 2 and 3 projected biomass estimates were higher than Model 1 in the projections of A₃₅ and A₄₅.

Table 3.3. ASPIC estimated biological reference points for the selected species from the three communities of 25%, 25%, and 45% connectance. The last column is the percent of the *r-value* from the Lotka-Volterra model that was estimated by ASPIC. The ‘*’ denotes species for which *q* was fixed in the ASPIC runs.

Species	MSY	B_{MSY}	K	F_{MSY}	$\frac{r_{ASPIC}}{r_{LV}}\%$
Species with the most total links					
A₂₅	3.77	40.43	81	0.093	34%
A₃₅	2.22	83.19	166	0.027	10%
A₄₅	4.99	52.08	104	0.096	35%
Species with the fewest total links					
B₂₅	3.69	34.22	68	0.108	36%
*B₃₅	2.39	17.71	35	0.135	46%
B₄₅	2.94	38.29	77	0.077	26%
Species with many predators, few prey					
*C₂₅	9.96	26.27	53	0.379	75%
C₃₅	4.05	33.08	66	0.123	24%
*C₄₅	3.07	21.49	43	0.143	28%
Species with many prey, few predators					
*D₂₅	37.20	305.50	611	0.122	41%
D₃₅	34.34	256.70	513	0.134	45%
D₄₅	34.24	343.00	686	0.100	33%
Randomly selected species					
*E₂₅	33.67	164.00	328	0.205	56%
E₃₅	23.39	107.90	216	0.217	59%
*E₄₅	20.76	147.30	295	0.141	38%

Fishing Species A₃₅ and A₄₅ affected very few other species in the community. This was the same result as in the projection of Species A₂₅. In the case of A₃₅, one predator decreased in biomass by 50-75%. Other than this one species, no species exhibited a change in biomass $\geq 50\%$ in any of the projections.

Species B

Model 1 projected a continually declining biomass for Species B₃₅ after fishing began in year 50 of the simulation (Figure 3.5). The initial decline at the start of fishing indicated that this species may be intolerant of any fishing pressure, due to strong predator-prey interactions.

Species B₄₅ remained below B_{MSY} in the Model 1 projection, but exhibited a stable population biomass at the end of the projection. Model 2 projected the population biomass at B_{MSY} for both Species B₃₅ and B₄₅. Model 3 projected the population to remain at a biomass well above B_{MSY} in all three communities.

Species B₃₅ appeared to have strong species interactions (Table 3.4). There were an additional 44 species that had a change in biomass of $\geq 25\%$, 33 of which were predators of species B₃₅. Of these, two species were considered depleted, with a biomass decline of $\geq 75\%$. As in Species B₂₅, the species interactions were not as strong in Species B₄₅. Only six species were affected by a change in biomass between 25-50% when species B₄₅ was fished at F_{MSY} .

Species C

Species C remained at a level of B_{MSY} in all simulations of Species C from Models 1 and 2 (Figure 3.6, Figure 3.11). The stability of Species C, suggest that species interactions did not drive the dynamics of Specie C. Model 3 projected little change in the species biomass after fishing began, due to the high intrinsic rate of increase.

Across all projections of Species C, few species with direct links to Species C exhibited a change in biomass Table 3.4). If any species did exhibit a change in biomass, it was less than 50% for Species C₃₅ and C₄₅.

Species D

The estimated B_{MSY} and MSY for all of the communities were relatively close (Table 2.3). Model 1 for Species D_{35} and D_{45} predicted an equilibrium biomass just under the B_{MSY} threshold (Figure 3.6, Figure 3.11). The projections of Model 2 were higher for Species D_{35} and D_{45} , which was not true for Species D_{25} . In all three communities, Model 3 projected the highest equilibrium biomass.

The effect of fishing on other species in the community varied among the three communities. When Species D_{35} was fished, a total of 43 other species in the community exhibited a change in biomass. Of these, three species (none of which had a direct link to Species D_{35}) increased in biomass by $\geq 75\%$. An additional ten species increased in biomass between 25-75% and 30 species decreased in biomass by 25-75%. Only thirteen species were affected by a change in biomass between 25-50% when species D_{45} was fished, all of which increased in biomass.

Species E

Species E presented the most interesting results across all three communities. Species E had the least continuity across communities because it was randomly selected. Model 1 projected an initial decrease in biomass to a level of 50% of B_{MSY} for Species E_{35} . However, at the constant fishing rate of F_{MSY} , the population increased to an equilibrium biomass near B_{MSY} (Figure 3.8). This dynamic was not predicted in the other two models when species interactions were ignored. Model 2 projected the species biomass at B_{MSY} and Model 3 projected equilibrium well above B_{MSY} . The effects of species interactions were not as prominent when Species E_{45} was fished. Model 1 projected a stable equilibrium biomass for Species E_{45} slightly below B_{MSY} .

When Species E₃₅ was fished, six species increased and one decreased in biomass by $\geq 75\%$. An additional 33 species increased in biomass by 25-75%, 24 of which had no direct link to species E₃₅. When Species E₄₅ was fished, only two species were affected by less than a 50% change in biomass

Fishing Scenario 2 (Overfish and rebuild species of interest)

The plots for overfishing for the species A₃₅-E₃₅ and A₄₅-E₄₅ can be found in Appendix C. Model 3 projected the population biomass was never below the estimated B_{MSY}, for all species across all communities, except C₂₅. Species C₂₅'s high intrinsic rate of increase allowed the population rebuild quickly. There were three projections in which the multispecies model projected a shorter rebuilding time than Model 2 (Species B₂₅, B₄₅, C₃₅). Even though Model 1 projected species B₄₅ reaching a biomass above B_{MSY} earlier than Model 2, the project of Model 1 declines to a level below B_{MSY} before settling at an equilibrium biomass in year 180 (Figure. C.7).

Species interactions played a role in the recovery of species, allowing some species to rebuild to a higher biomass than predicted in the single-species model or prevented species from rebuilding within a reasonable timeframe. Species A₃₅, which was below the level of B_{MSY} when fished at F_{MSY} did not recover from overfishing within the time frame of the simulation, even though the fishing mortality rate was reduced to a level of .5*F_{SMY}. Species B₃₅, which had a continual decline when fished at F_{MSY}, required 68 years to recover in Model 1. Species E₃₅ is predicted to recover after 22 years in projections from Model 1. This was the only species that exhibited a dynamics of increasing to a level higher than the equilibrium level attained in year 300. The biomass in year 300 for species D₃₅, E₃₅, C₄₅ was higher in Model 1 than in Model 2,

indicating that species interactions affected the dynamics of these species and increased the biomass to a level higher than a model without species interactions predicted.

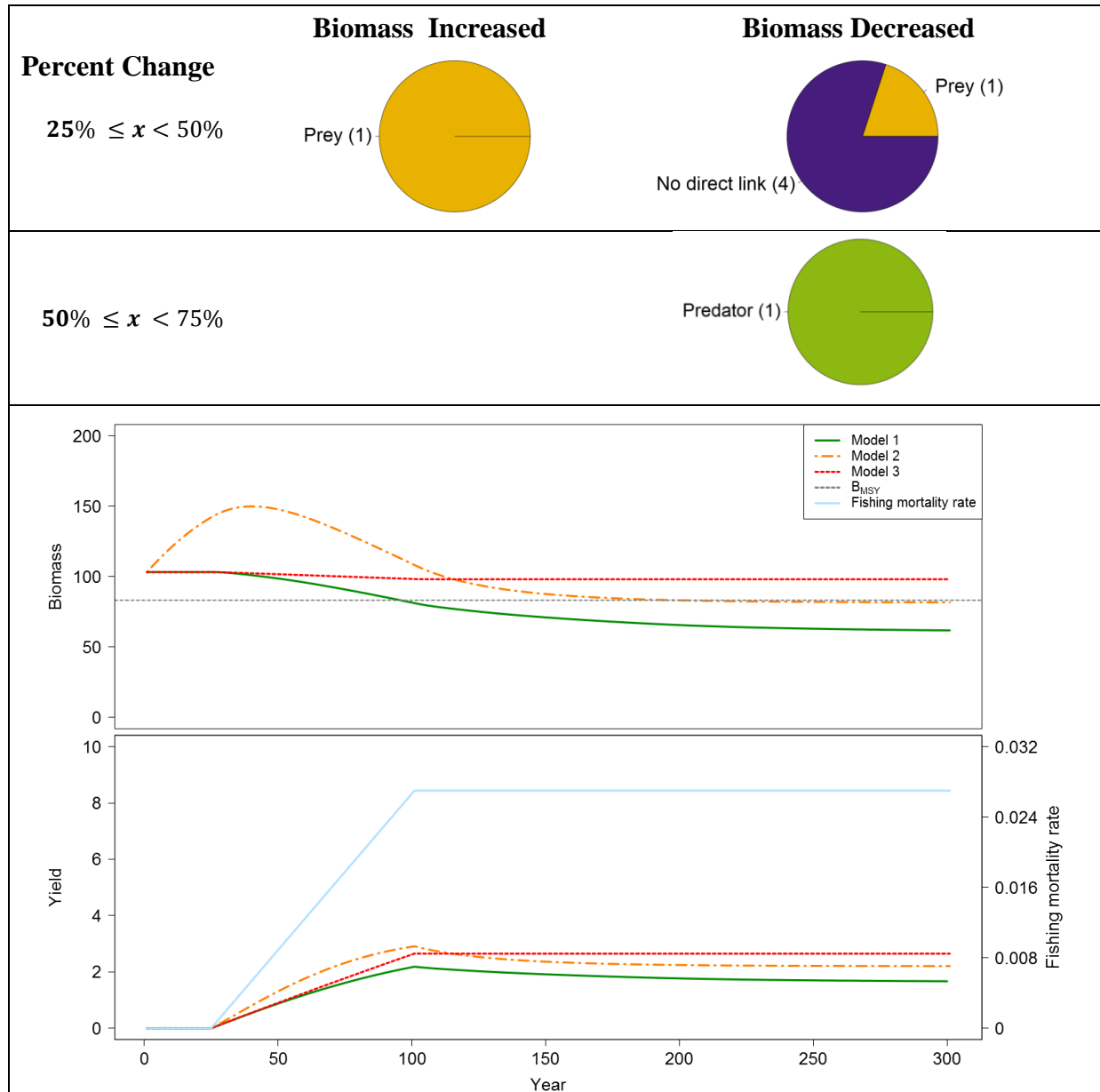


Figure 3.4. Model results for Species A_{35} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A, the prey of Species A, and species with no direct link to Species A. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

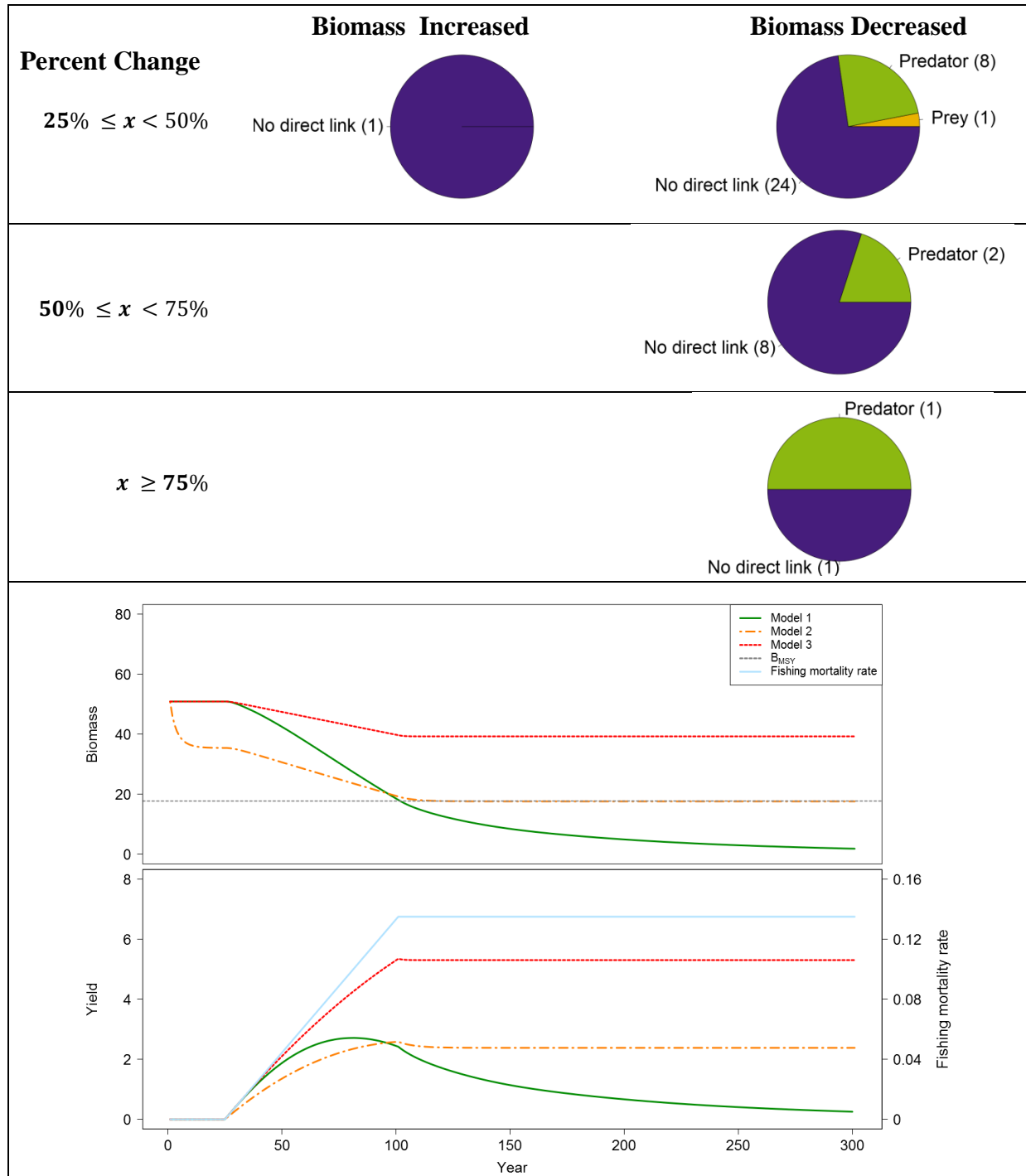


Figure 3.5. Model results for Species B_{35} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species B, the prey of Species B, and species with no direct link to Species B. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

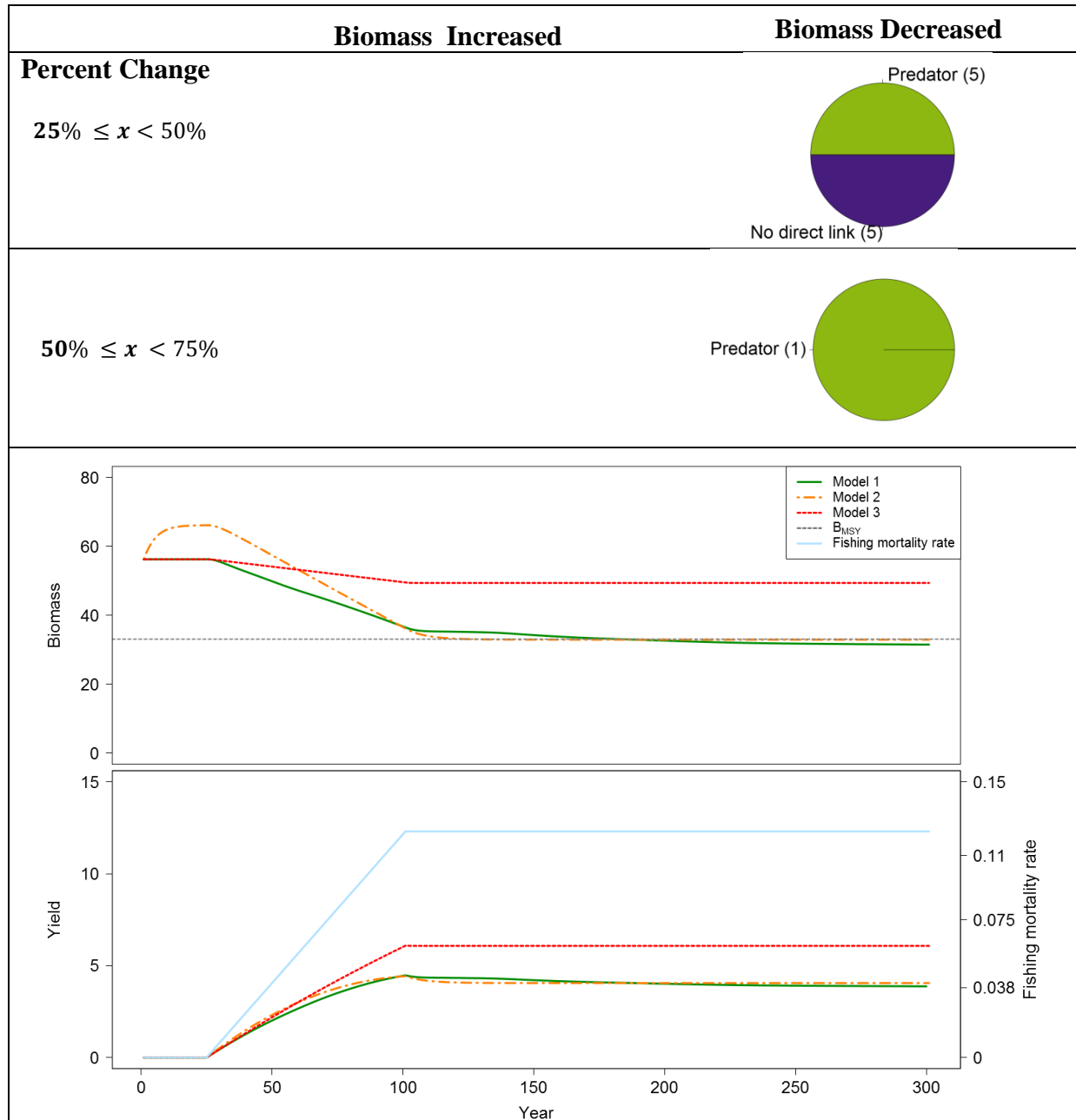


Figure 3.6. Model results for Species C_{35} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C, the prey of Species C, and species with no direct link to Species C. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

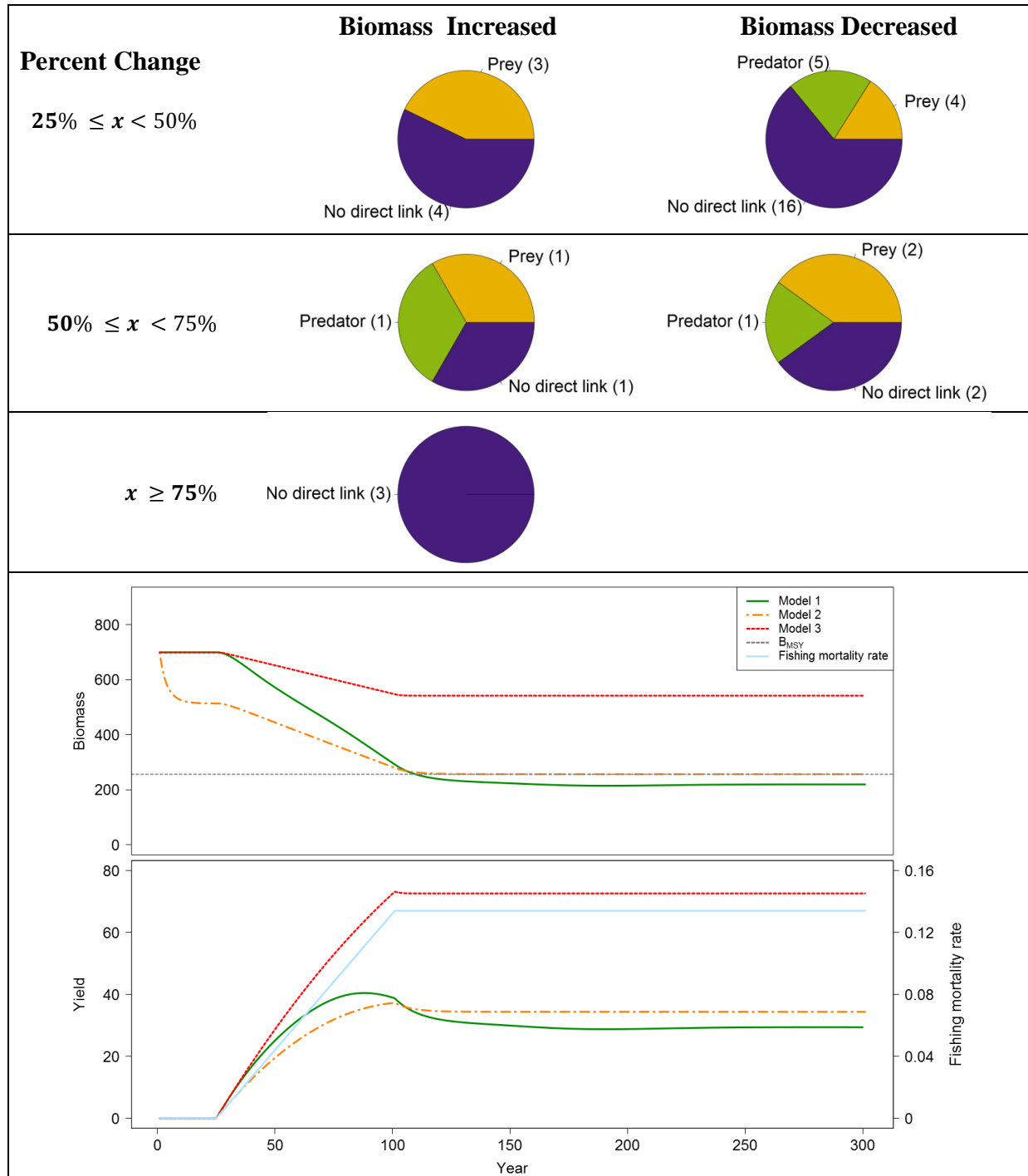


Figure 3.7. Model results for Species D_{35} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D, the prey of Species D, and species with no direct link to Species D. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

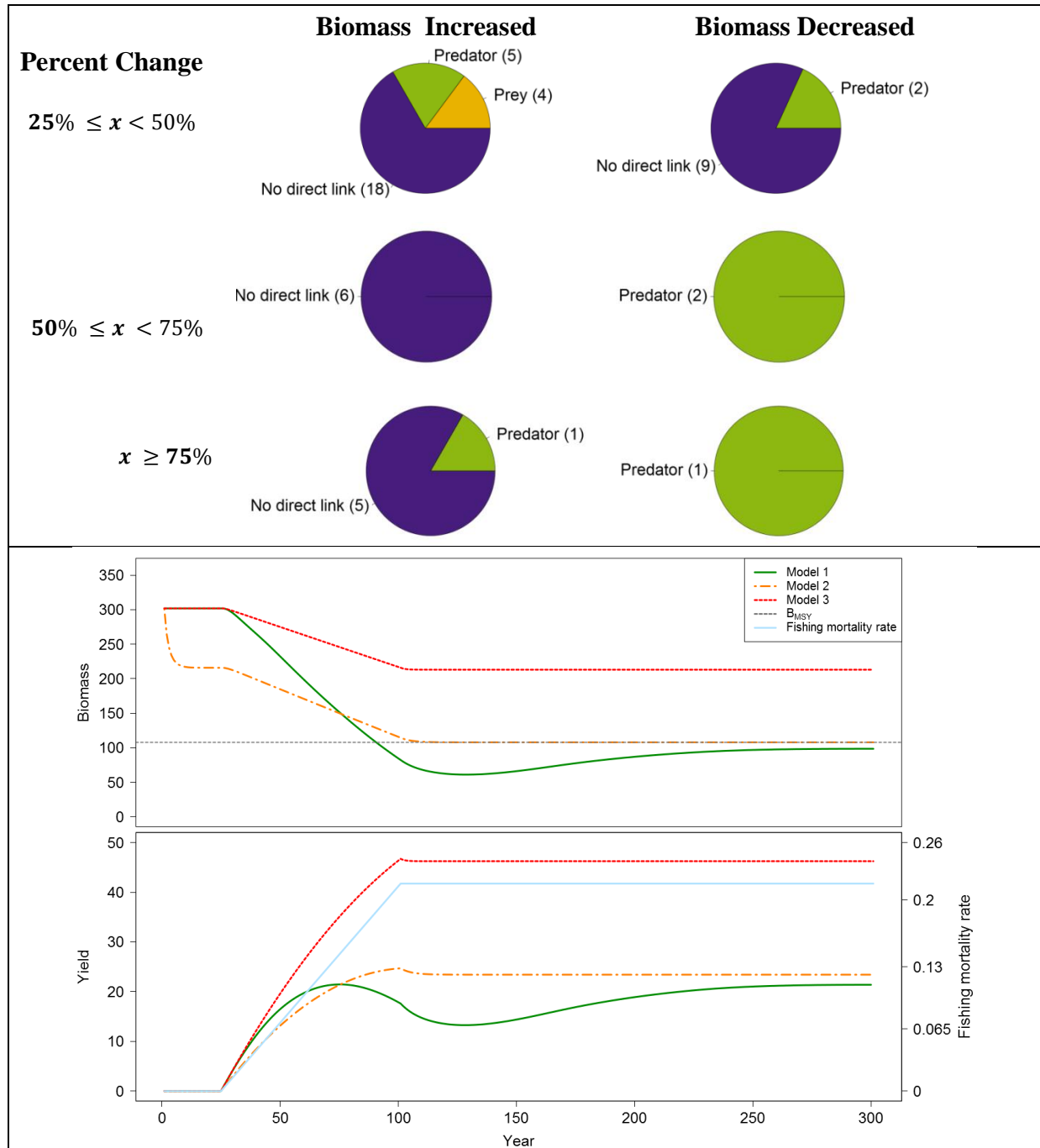


Figure 3.8. Model results for Species E_{35} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E, the prey of Species E, and species with no direct link to Species E. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

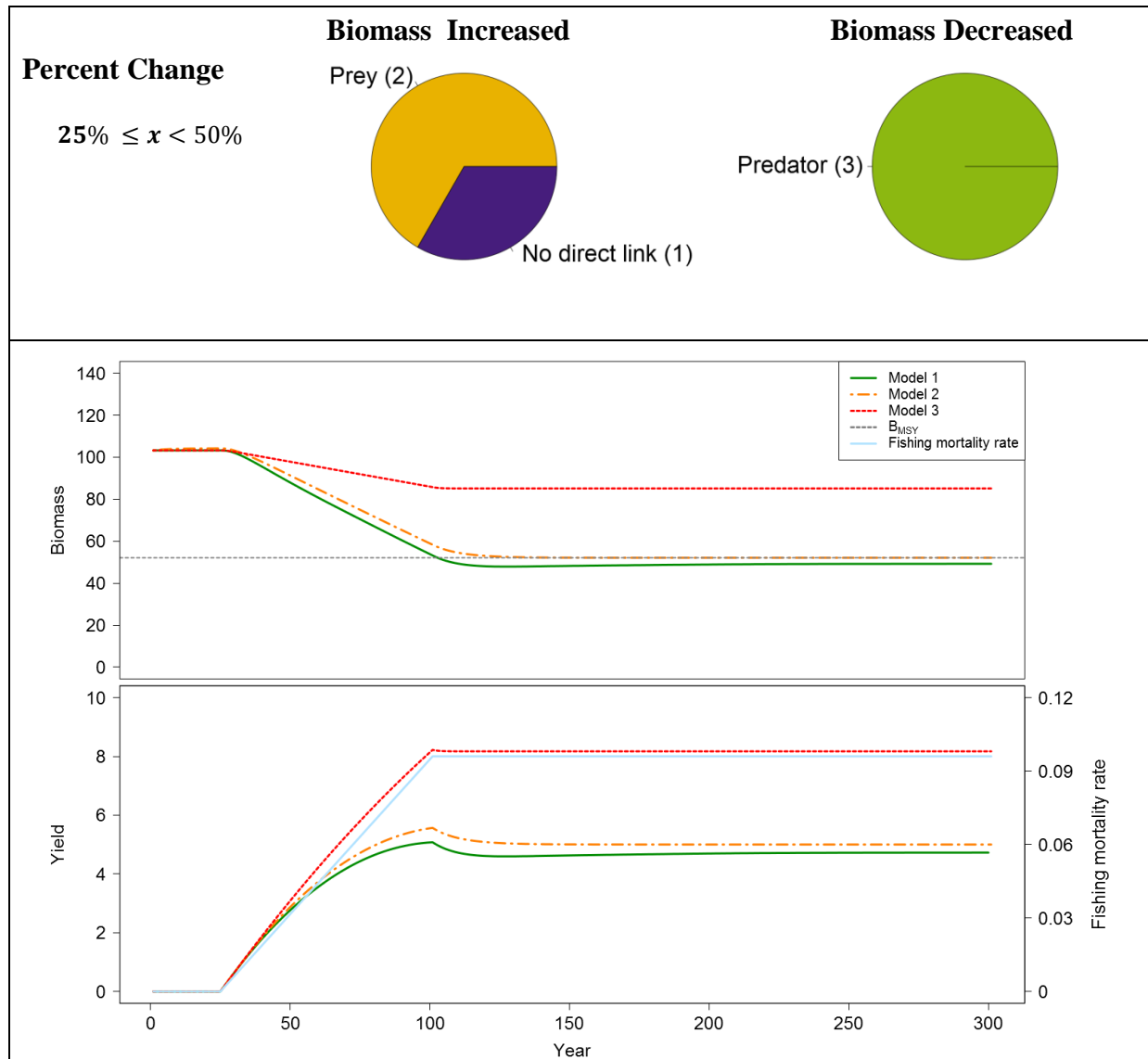


Figure 3.9. Model results for Species A_{45} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A, the prey of Species A, and species with no direct link to Species A. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

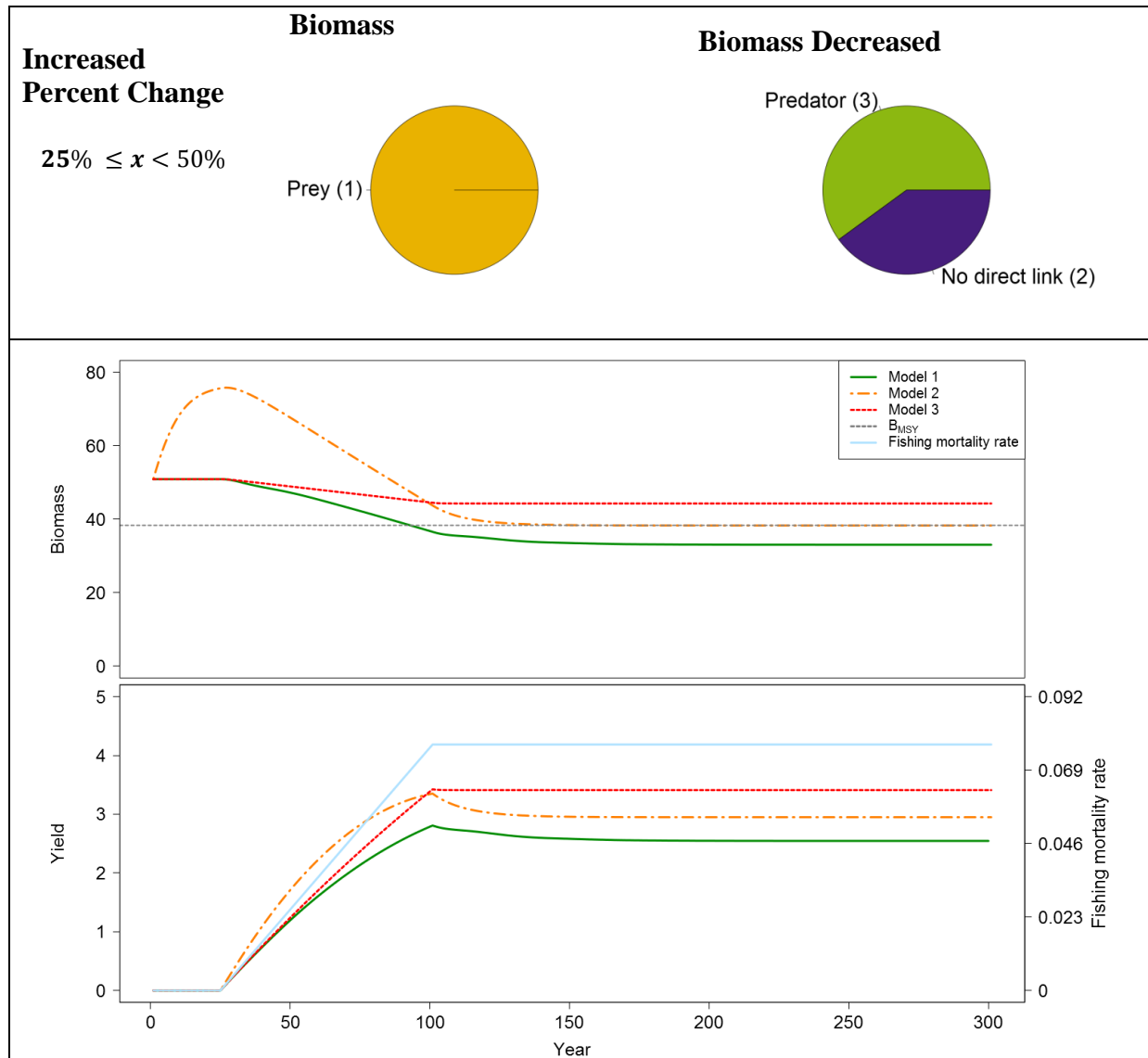


Figure 3.10. Model results for Species B_{45} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species B_{45} , the prey of Species B_{45} , and species with no direct link to Species B_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

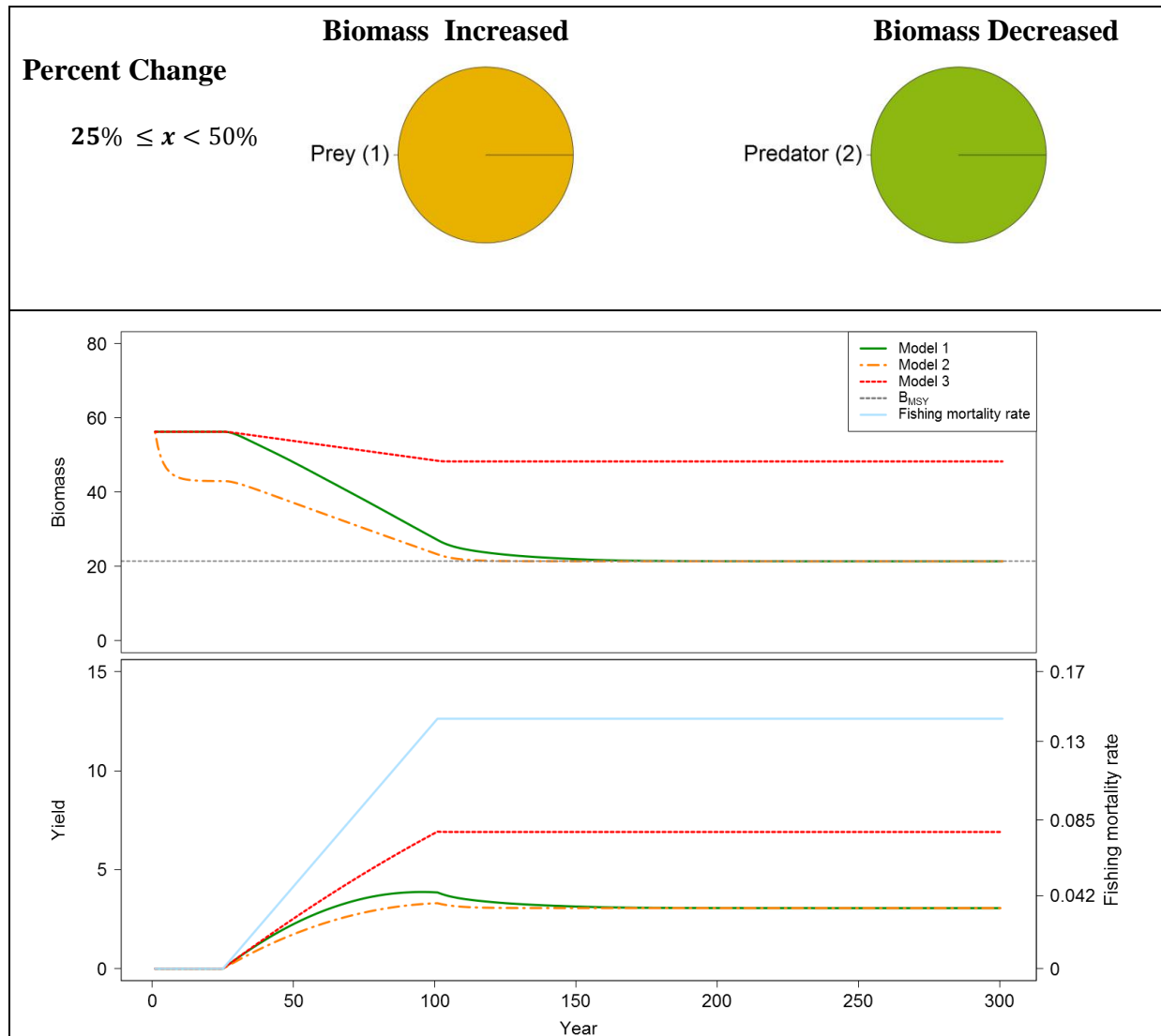


Figure 3.11. Model results for Species C_{45} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C_{45} , the prey of Species C_{45} , and species with no direct link to Species C_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

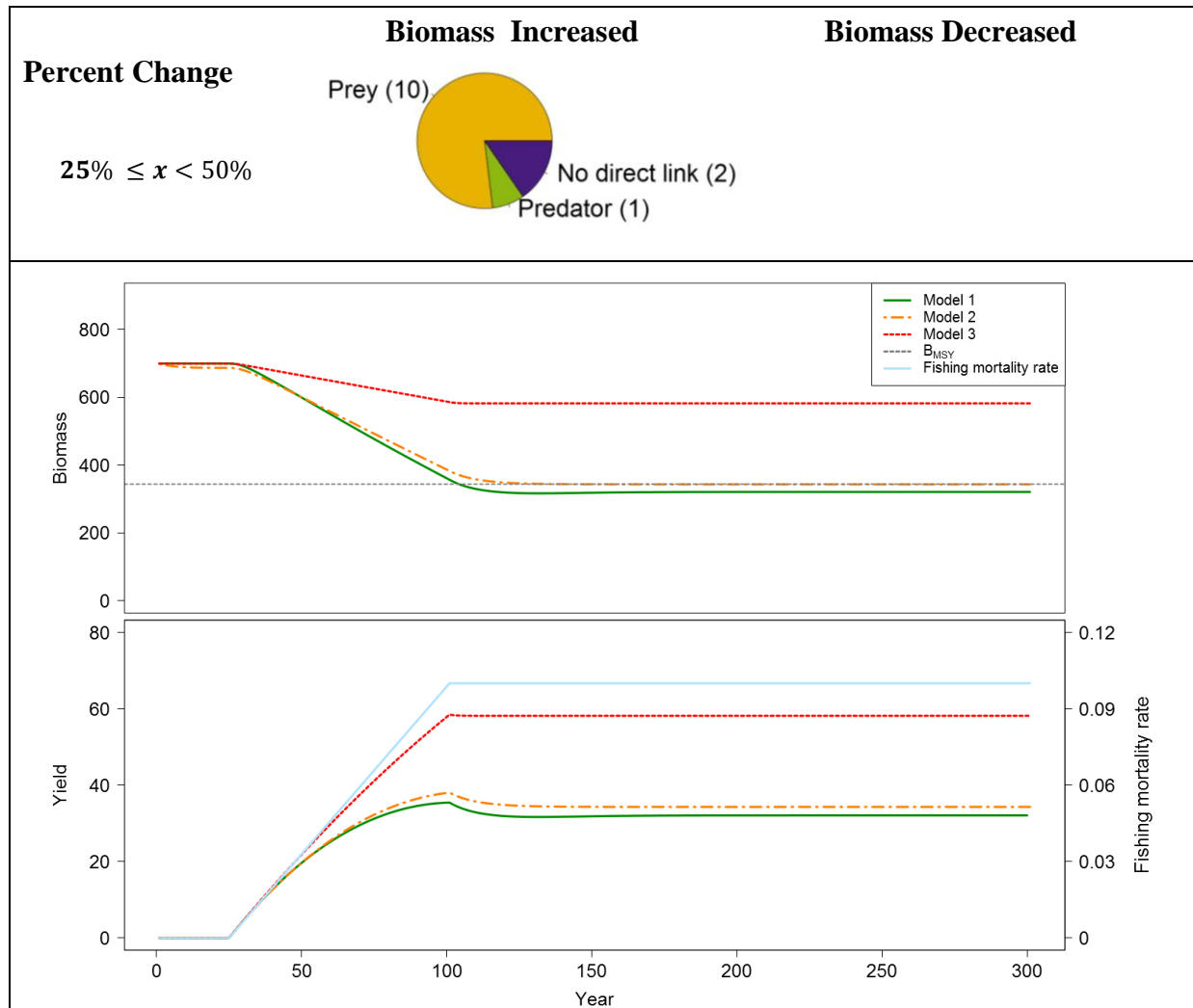


Figure 3.12. Model results for Species D_{45} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D_{45} , the prey of Species D_{45} , and species with no direct link to Species D_v . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

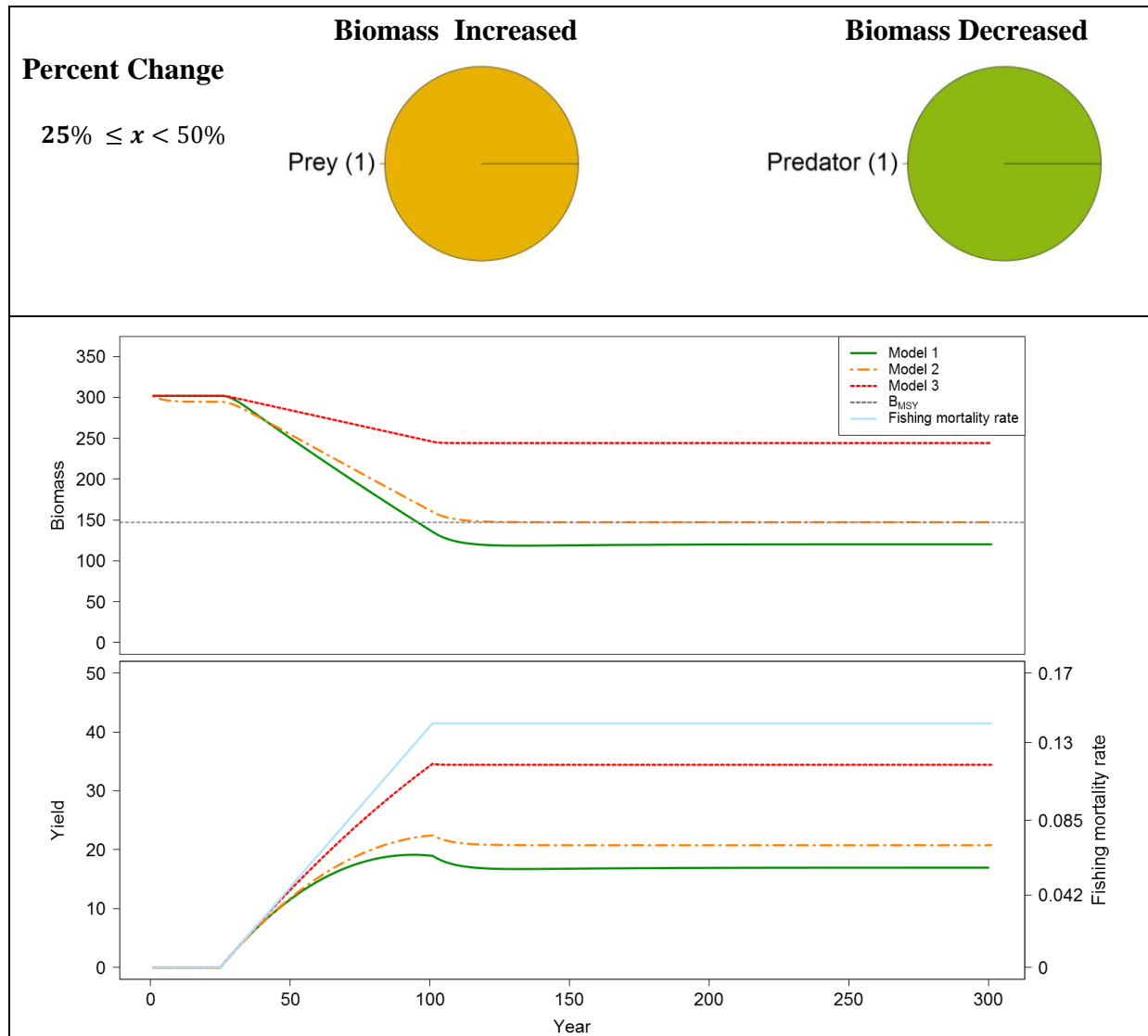


Figure 3.13. Model results for Species E_{45} when fished at F_{MSY} . Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E_{45} , the prey of Species E_{45} , and species with no direct link to Species E_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

Table 3.4. Fraction of unfished species with a change in biomass $\geq 25\%$ from year zero to year 300 of the Lotka-Volterra simulation when the species of interest was fished at F_{MSY} . The percent change is specific to the number of links for each species.

Species	Outward links (predators)	Inward links (prey)	No direct link	Total species
Species with the most total links				
A₂₅	3/23	1/20	5/56	9/99
A₃₅	1/23	1/31	4/46	6/99
A₄₅	3/33	2/32	1/34	6/99
Species with the fewest total links				
B₂₅	0/9	0/4	0/86	0/99
B₃₅	11/15	1/6	34/78	46/99
B₄₅	3/20	1/10	1/69	5/99
Species with many predators, few prey				
C₂₅	2/14	4/8	12/77	18/99
C₃₅	6/28	0/16	5/55	11/99
C₄₅	2/28	3/13	2/58	7/99
Species with many prey, few predators				
D₂₅	1/5	9/32	6/62	16/99
D₃₅	7/12	10/36	26/51	43/99
D₄₅	1/11	10/54	2/34	13/99
Randomly selected species				
E₂₅	5/11	13/21	41/67	59/99
E₃₅	11/16	4/13	38/70	53/99
E₄₅	1/13	1/36	0/50	2/99

Table 3.5. Comparison of the number of years to rebuild to B_{MSY} once over fishing was stopped in Fishing Scenario 2. The subscript represent the community connectance and NA indicates the species biomass was never below B_{MSY} and never overfished.

Species	Model 1	Model 2	Model 3
Species with the most total links			
A₂₅	23	9	NA
A₃₅	>150	20	NA
A₄₅	11	9	NA
Species with the fewest total links			
B₂₅	5	8	NA
B₃₅	68	7	NA
B₄₅	7	10	NA
Species with many predators, few prey			
C₂₅	4	2	1
C₃₅	3	8	NA
C₄₅	9	7	NA
Species with many prey, few predators			
D₂₅	15	8	NA
D₃₅	16	7	NA
D₄₅	12	9	NA
Randomly selected species			
E₂₅	5	5	NA
E₃₅	22	5	NA
E₄₅	13	7	NA

DISCUSSION

The simulations in this study demonstrate the importance of understanding and quantifying connectance within an ecosystem. The outcomes from the simulation across connectance levels were variable at the individual species level, but the impact on non-target species was reduced for the system of 45% connectance. The single-species biological reference

points, when compared to the Lotka-Volterra values, were variable among species and community connectance. The estimated F_{MSY} values from ASPIC varied among species with the same characteristics of connectance (e.g. most connected, least connected) among the three communities of 25%, 35%, and 45% connectance. Thus, accounting for species interaction regardless of the community connectance level, is important for understanding the direct and indirect impacts of fishing. I also illustrated the importance of accounting for indirect effects, which in some cases had a higher impact on individual unfished species and community dynamics than species with directed links.

The results from my use of multispecies time series in a single-species stock assessment model stress the importance of accounting for the ecological interactions among species. All of the simulations in this study, across community complexity, suggest that buffers are needed when determining fishing mortality rates. Fishing mortality rates estimated from single-species growth rates alone, may not be sustainable and may result in population level changes in non-target species. A recent review found that natural mortality from traditional stocks assessments was consistently underestimated when compared to studies that estimated natural mortality more explicitly, through the use of an ecosystem or multispecies model (Tyrrell et al., 2011). In this study, the estimate of r_{ASPIC} ranged from only 10% of the r_{LV} value for species A35, species with the most number of links, to 59% of r_{LV} for species E35, the randomly selected species. Among the fifteen species studied the average $r_{ASPIC} : r_{LV}$ ratio was 0.4, which suggests that community dynamics do decrease the estimation of biological reference points. Even when fishing at these lower fishing mortality rates, unfished species were observed to increase or decrease in biomass by $\geq 75\%$. It is evident that fishing, even at sustainable levels, will require trade-offs among species. Future sensitivity simulations of projecting the Lotka-Volterra model with fishing

mortality rates higher and lower than the ASPIC-estimated F_{MSY} will elucidate the trade-offs between harvesting a species and community level effects.

The direct and indirect effects of species in the same community were especially evident in the increase of species changing in biomass during the period of overfishing in Scenario 2. Increasing community connectance had the strongest effect on the magnitude of community effects. No unfished species in any of the scenarios of a system with 45% connectance increased or decreased in biomass by $\geq 50\%$. In general, very few unfished species were affected by fishing the target species at a community connectance of 45%. This may suggest that the increased omnivory and generalist behavior of marine species buffers the community-level effects of fishing.

The Fishing Scenario 2 of overfishing and then rebuilding species also illustrated the importance of incorporating species interactions into management decisions. In one case (Species A₃₅), the species did not recover to B_{MSY} within the projection time frame. In three other cases, the multispecies model projected a shorter time to recovery than the single-species model. The shorter time to recovery was a direct effect of species interactions.

The approach for rebuilding used in these simulations was a “best case scenario.” I used the fishing mortality rate to $.5 * F_{MSY}$ as the fishing mortality rate to rebuild species from an overfished state. This rate was chosen to demonstrate the effects on recovery trajectories of the unfished species and the species interactions. While instantaneously reducing fishing mortality rates to the level of $.5 * F_{MSY}$ would not be socially nor economically feasible in most situations, this scenario defines a “best case” scenario of a recovery timeframe. It is also important to note that the time frame of the projections in this study, 300 years, is longer than any available

fisheries or ecological data series. However, it allowed us to observe the long-term effects of fishing on the community dynamics.

There are important implications from this study that can be utilized as we move towards ecosystem-based fisheries management. One of the most significant observations from these simulations is that life history characteristics alone cannot predict single-species dynamics. The five species chosen were assigned the same initial parameters of r_{LV} and biomass among all three communities, but produced varying results. While there was no singular and evident trend observed as connectance increased, it does appear that the magnitude by which unfished species are affected decreases as connectance increases. Additional simulations of higher and lower levels of connectance may further elucidate this pattern.

An important note about the three different communities is that they were created independently. The species with the most number of connections is not the same species in any of the three communities, nor is the species necessarily linked to the same species in all three communities. Any of the selected species may have different trophic levels and different trophic functions in each of the three systems. This is one caveat of the network structure to keep in mind when comparing the results among the three communities. Each of the three communities is one permutation of an infinite number of possibilities for each system.

There are several model modifications and sensitivity analyses that can be conducted using the multispecies Lotka-Volterra model, and several published methods available to parameterize the species interaction matrix. The species interactions were assigned randomly in all three of the communities created in Chapter 2 and Chapter 3. However, predator-prey interactions can also be assigned preferentially to selected species (Barabási and Albert, 1999). Another model developed to parameterize species interaction matrix is the niche model

(Williams and Martinez, 2000; Williams and Martinez, 2008; Dunne et al., 2004). The niche model allows one to pre-define the trophic role of a species in the ecosystem. This would remove the confounding factor of not knowing each species trophic role in the different communities. Species could also be assigned life history characteristics based on their trophic role or place in the ecosystem, i.e. K-selected top predators versus forage fish. The species in our Lotka-Volterra model were ambiguous and were not assigned trophic levels or roles. However, through network mapping and further analyses, trophic roles could be assigned to species in this particular system.

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CHAPTER 4 : SINGLE-SPECIES BIOLOGICAL REFERENCES POINT IN A MULTISPECIES FISHERY

INTRODUCTION

Current fisheries management in the U.S. focuses on single species, with very few management plans incorporating ecosystem considerations (Link, 2002b; 2008). However, single-species management actions can potentially affect production of other species in the same ecosystem and alter food web dynamics (Pikitch et al., 2004; Link et al., 2011). An ecosystem approach to fisheries management implies that sustainability of other species in the same ecosystem should be accounted for in management considerations. While single-species stock assessment will likely continue to be the preferred analytical tool, management and regulations for commercially and recreationally valuable species will need to address ecosystem issues..

A wide variety of tools are currently available to model communities and explore the community-level effects of fishing. Examples of ecosystem models include Ecopath with Ecosim (Polovina, 1984; Pauly et al., 2000; Christensen and Walters, 2004), Multispecies Virtual Population Analysis (MSVPA) (Helgason and Gislason, 1979; Pope, 1979), and Atlantis (Fulton et al., 2004a; Fulton et al., 2004b; Fulton et al., 2011). These three models have been used to inform management decisions and explore ecosystem effects of fishing. The complexity of each model is determined by the decisions of the developer, and is often limited by available data. When data are not available or the goal is to explore the possible outcomes of harvest scenarios, simulation models are powerful tools. Two such models, MS-PROD and AGG-PROD, have been used to explore the effects of fishing and climate change on the northeast Atlantic large marine ecosystem (Gamble and Link, 2009; Gamble and Link, 2012). The basis for both of these models is a multispecies Lotka-Volterra model, which is mathematically tractable and well-studied. The objectives of the models developed by Gamble and Link (2009; *in press*) were

not to determine management policy, but to explore the possible outcomes of a suite of management decisions and the effect of climate on those fisheries. In this study, I utilize the Lotka-Volterra model described in Chapter 2 to explore the effects of fishing multiple species at their estimated single-species estimated fishing mortality rate.

The goal of this study is to examine the effects of implementing the single-species fishing mortality rates in a multispecies fishery. The response of the fished species as well as the community level effects between the single-species fisheries and the multispecies fisheries will be compared. Two multispecies scenarios will be explored: 1) fish five species that have no direct links to one another, and 2) fish five species that have direct links among them.

METHODS

The methods for the creation of the Lotka-Volterra model were the same as those in Chapter 2. I utilized the interaction matrix from the community of 25% connectance that was developed in Chapter 2. The vector of the initial intrinsic rate of increase r_{LV} and initial biomass were also the same. Therefore, all species from the community in Chapter 2 had the same characteristics in this part of the study.

Selection of species

Two different multispecies fishing scenarios were explored. In the first scenario, five species with no direct connections to one another were fished simultaneously at their single-species estimated F_{MSY} rates. In the second scenario, five species that were all directly connected were fished simultaneously at their single-species estimated F_{MSY} rates. To select five unconnected species, one species was first randomly selected from the 100 species in the community. All species with direct connections to the selected species were eliminated and a second species was randomly chosen from the remaining species. This process was repeated

until five unconnected species had been selected. The five species selected were, by chance, none of the species selected for fishing in Chapter 2.

To select five directly connected species, one species was first randomly selected from the 100 species in the community. All species with no direct connection to the selected species were eliminated and a second species was randomly chosen from the remaining species. This process was repeated until five connected species had been selected. The five species selected from this process not any of the species selected in Chapter 2 for fishing

Once the species were selected, the same methods described in Chapter 2 were applied to estimate the single-species biological reference points for the ten new species. Each of the ten species was fished at the single-species estimated F_{MSY} in ten separate projection of the Lotka-Volterra model. These results are not explicitly presented in this chapter, but will be compared to the multispecies projections.

In each of the two scenarios the five species were fished simultaneously. The species were also fished in individual simulations to draw comparisons between a single-species and multispecies fishery.

RESULTS

Unconnected species scenario

ASPIC estimated the biological reference points from the maximum likelihood estimator for all five species. The estimates of r_{ASPIC} for all five species was below the Lotka-Volterra defined r -value, ranging from 33-62% (Table 4.2). The number of unfished species affected by fishing each of the five species individually ranged from 13 (Species #22, #83) to 37 (Species #8) (Table 4.3).

Table 4.1. Characteristics of the unconnected species chosen for fishing and the standard deviation added to the true catch for ASPIC. Inward links are equivalent to positive α_{ij} values in the interaction matrix, and are the prey of the species in the first column. Outward links are equivalent to negative α_{ij} values (excluding the α_{ii} self-interaction) in the interaction matrix, and are the predators of the species in the first column. Species are listed by their numeric identifier in the community.

Species	Inward Links	Outward Links	Total Links	r_{LV}	B_0	Catch <i>s.d.</i>
#8	29	11	40	0.411	185.69	0.25
#22	13	19	32	0.563	28.70	0.30
#39	11	13	24	0.393	353.75	0.20
#74	7	14	21	0.341	70.48	0.30
#83	7	10	17	0.456	61.96	0.25

Table 4.2. Biological reference points estimated from ASPIC when the particular species fished is the only species in the ecosystem undergoing fishing. ASPIC does not provide a direct estimate of r , but r can be approximated in the logistic model as $2 \cdot F_{MSY}$.

Species	MSY	B_{MSY}	q	K	F_{MSY}	r_{ASPIC}	r_{ASPIC}/r_{LV}	F_{MSY}/r_{LV}
#8	8.98	96.87	0.005	193.70	0.093	0.186	0.451	0.226
#22	1.41	12.41	0.005*	24.82	0.114	0.229	0.406	0.203
#39	12.40	190.70	0.005	381.40	0.065	0.130	0.331	0.165
#74	3.82	36.22	0.005*	72.43	0.106	0.211	0.619	0.310
#83	3.64	32.56	0.005*	65.12	0.112	0.224	0.491	0.245

Table 4.3. Fraction of unfished species with a change in biomass $\geq 25\%$ from year zero to year 300 of the Lotka-Volterra simulation when the species of interest was fished at F_{MSY} . The percent change is specific to the number of links for each species. The species of interest is the only species fished in these results.

Species	Inward Links (prey)	Outward links (predators)	No direct link	Total
#8	13/29	5/11	19/59	37/99
#22	2/13	4/19	7/67	13/99
#39	3/11	3/13	23/75	29/99
#74	2/7	1/14	11/78	14/99
#83	3/7	2/10	8/82	13/99

The results from the multispecies fishing scenario produced more dynamic behaviors than when the five targeted species were fished independently (Figure 4.1). The terminal year biomass of three species (Species #22, #39, #74) was higher in the multispecies model than when the species were fished independently. The two other species exhibited a decline in terminal year biomass when fished in the multispecies fishery versus independently (Table 4.4).

The dynamics of all other species in the system also exhibited oscillations, and possibly, chaotic population changes (Figure 4.2). The species with the highest initial biomasses exhibited either exponential increases or decreases in the last 50 years of the projection. The average biomass of the community did not however, change greatly over time (Figure 4.2). The total biomass of the multispecies community at the end of the simulation was higher than the community biomass from the individual species projections (Figure 4.3). This reflected the impact of the species interactions when fishing multiple species simultaneously. However, while there was an increase in total biomass, the increase is was only 5% above the initial total biomass of the community.

The number of unfished species affected by fishing in the multispecies fishery was greater than in any of the individual fishing projections. A total of 67 unfished species changed in biomass by $\geq 25\%$, of which 18 had no direct link to any of the fished species. Of the 67 species that had a change in biomass, 22 did not change in biomass in any of the single-species fishing scenarios. Fifteen of the 33 species that did not change in biomass also did not change in biomass in any of the single-species projections.

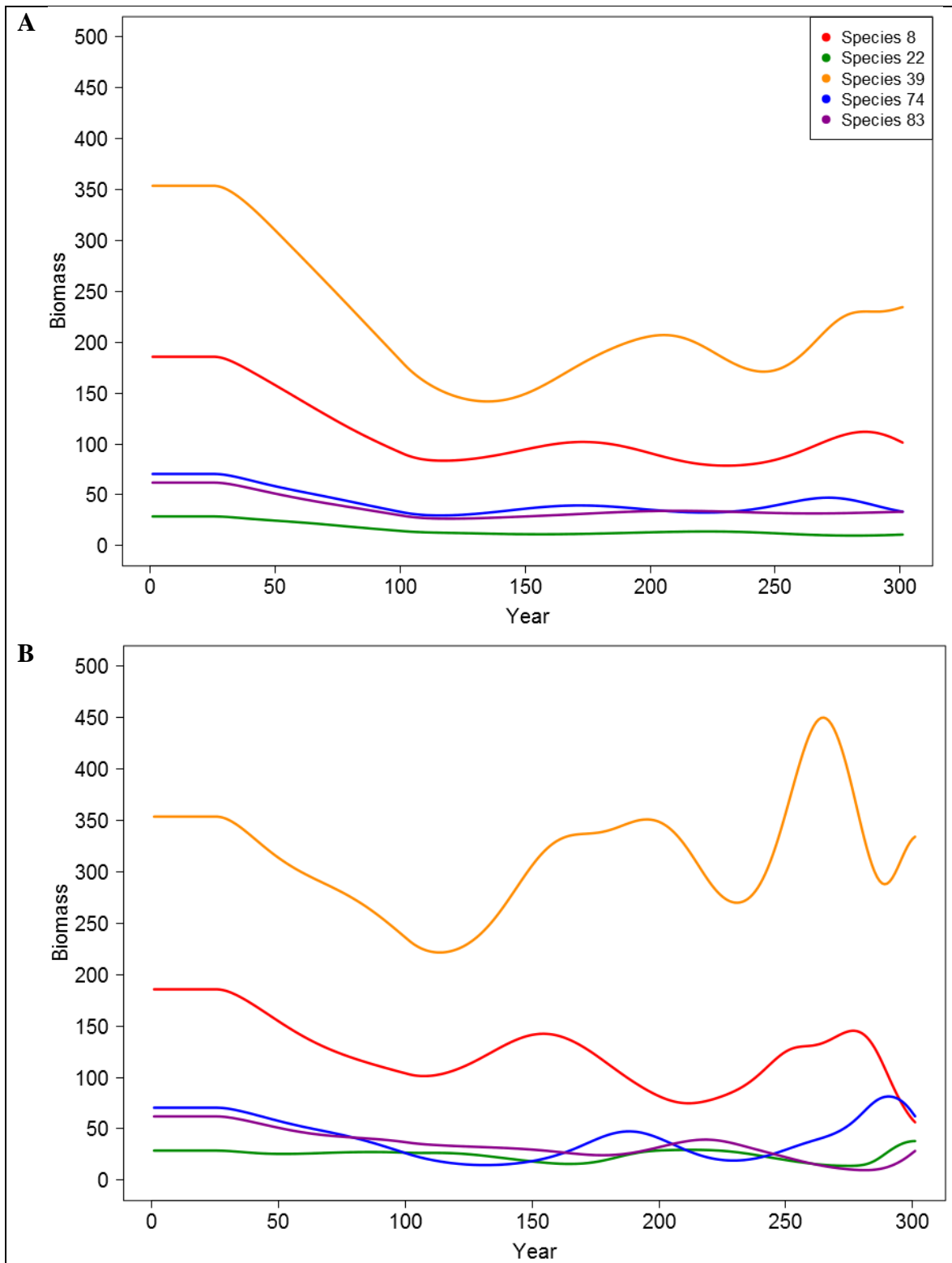


Figure 4.1. Biomass projections from the Lotka-Volterra model of the five species selected for fishing, when the species are fished in separate projections (A) and fished simultaneously in a multispecies fishery (B).

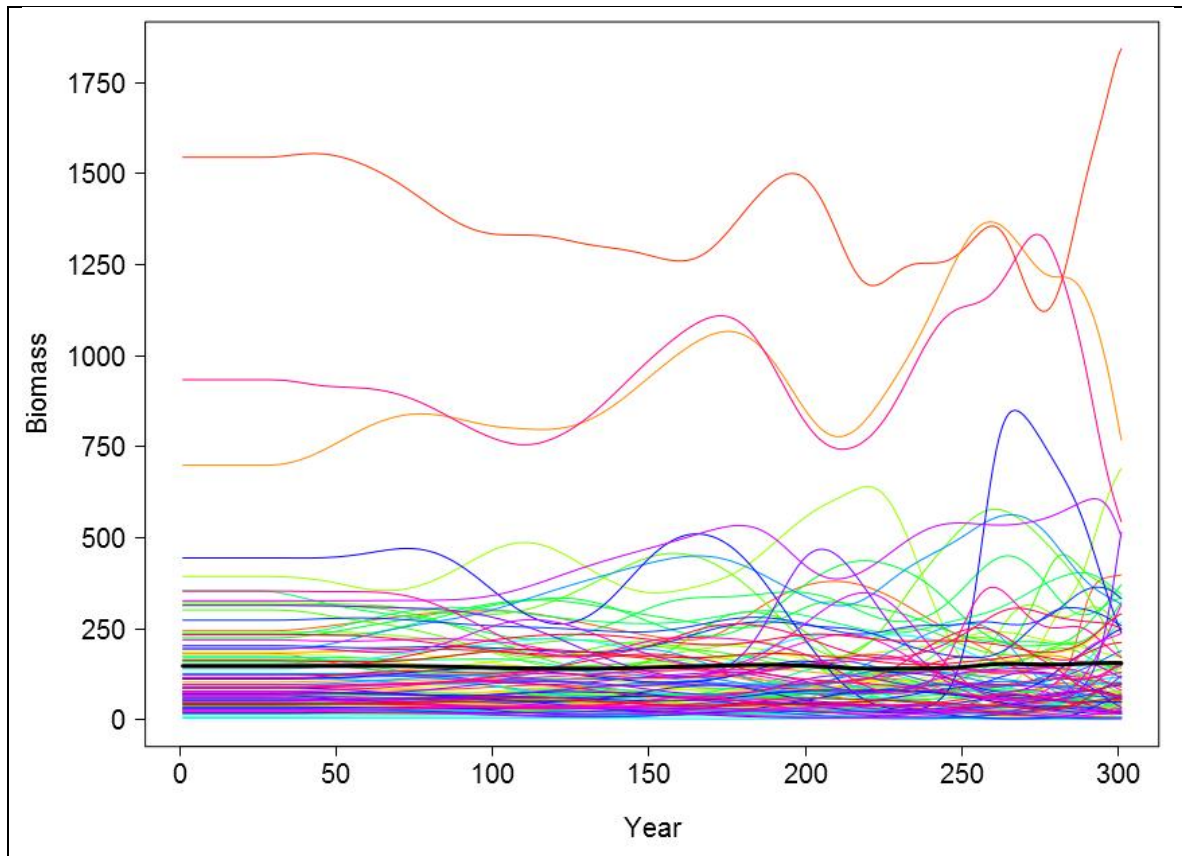


Figure 4.2. Biomass projection for all 100 species when the five unconnected species are fished simultaneously at the estimated single-species F_{MSY} . The bold line is the average community biomass.

Table 4.4. Comparison of the biomass at the beginning and end of the projection when species were fished in individual projections versus simultaneously in a multispecies fishery.

Species	B_0	Individual B_{300}	Multispecies B_{300}
#8	185.69	101.36	56.27
#22	28.70	10.90	37.98
#39	353.75	234.49	334.26
#74	70.48	33.42	62.07
#83	61.96	33.32	28.38

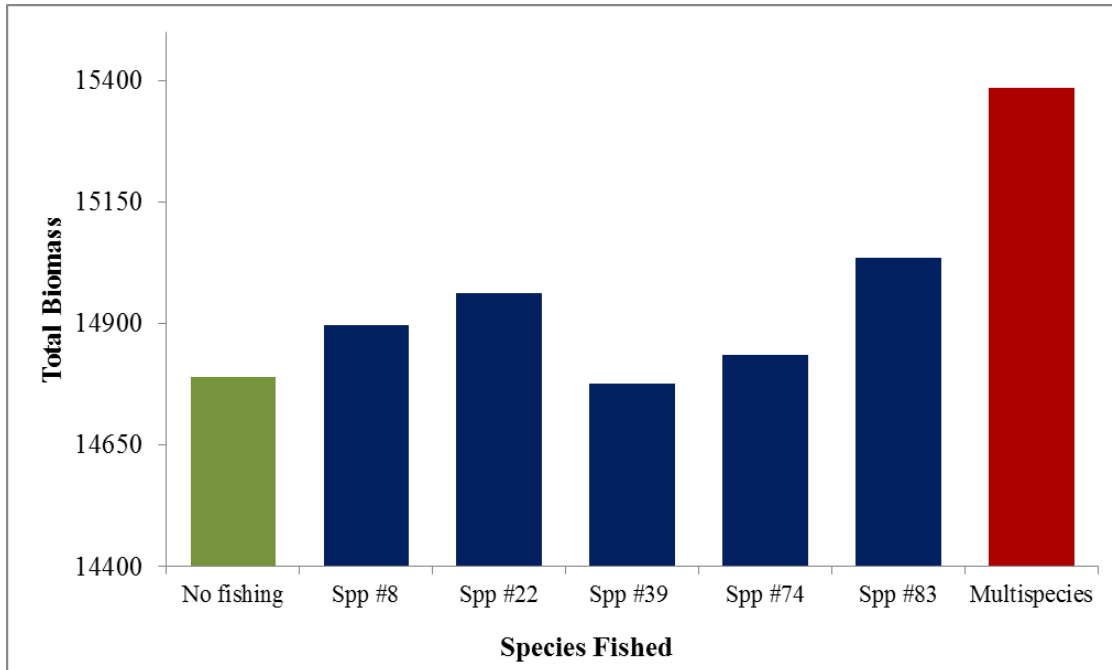


Figure 4.3. Total community biomass at the end of the projection, for projections with no fishing, fishing each species independently, and fishing all five species in a multispecies fishery. The scenario with no fishing also represents the initial biomass for all other projections.

Table 4.5. The number of species with a change in biomass by $\geq 25\%$ separated by the number of species changing in biomass in the single species projections versus the multispecies projection. The species in parentheses are those with no direction connection to any of the five fished species.

Number of single species runs with biomass change	Change in multispecies projection	No change in multispecies projection
0	22	15
1	21	8
2	15	7
3	8	3
4	1	0
5	0	0
Total	67 (18)	33 (8)

Connected species

All five the species chosen for this scenario had direct predator-prey links to one another (Table 4.7). The intrinsic rate of increase for all of the species chosen ranged from 0.6 to 0.98, with total links ranging from 25 to 41 (Table 4.6) For all five species, the estimated r_{ASPIC} was

below 50% of the Lotka-Volterra defined r -values (Table 4.8). For species #38 r_{ASPIC} was estimated at 18% of r_{LV} , which was the lowest of all five species. Species #35 had the highest estimated fraction of r_{LV} at 44%. These low estimates of r_{ASPIC} resulted in low fishing mortality rates.

The fraction of species with direct links affected by fishing ranged from 8 to 49 when the species were fished independently (Table 4.9). In all species, the number of indirectly linked species exhibiting a change in biomass was greater than the directly linked species.

Table 4.6. Characteristics of the unconnected species chosen for fishing and the standard deviation added to the true catch for ASPIC. Inward links are equivalent to positive α_{ij} values in the interaction matrix, and are the prey of the species in the first column. Outward links are equivalent to negative α_{ij} values (excluding the α_{ii} self-interaction) in the interaction matrix, and are the predators of the species in the first column. Species are listed by their numeric identifier in the community.

Species	Inward Links	Outward Links	Total Links	r_{LV}	B_0	Catch <i>s.d.</i>
3	24	14	38	0.974	62.463	0.50
17	22	19	41	0.705	185.803	0.20
18	20	12	32	0.606	28.124	0.35
35	13	12	25	0.636	16.500	0.40
38	13	13	26	0.598	235.510	0.25

Table 4.7. Interaction matrix for the five connected species. The '+' sign indicates an inward link, and a '-' sign indicates an outward link.

	3	17	18	35	38
3	-	+	-	-	-
17	-	-	+	+	+
18	+	-	-	+	-
35	+	-	-	-	+
38	+	-	+	-	-

Table 4.8. Biological reference points estimated from ASPIC when the particular species fished is the only species in the ecosystem undergoing fishing. ASPIC does not provide a direct estimate of r , but r can be approximated in the logistic model as $2 \cdot F_{MSY}$.

Species	MSY	B_{MSY}	q	K	F_{MSY}	r_{ASPIC}	r_{ASPIC}/r_{LV}	F_{MSY}/r_{LV}
3	5.678	31.450	0.005*	62.900	0.181	0.361	0.371	0.185
17	7.334	82.090	0.005*	164.200	0.089	0.179	0.254	0.127
18	0.981	12.570	0.005*	25.150	0.078	0.156	0.257	0.129
35	1.034	7.370	0.005*	14.740	0.140	0.280	0.441	0.220
38	7.819	144.100	0.005*	288.200	0.054	0.109	0.181	0.091

Table 4.9. Fraction of unfished species with a change in biomass $\geq 25\%$ from year zero to year 300 of the Lotka-Volterra simulation when the species of interest was fished at F_{MSY} . The percent change is specific to the number of links for each species.

Species	Inward Links (prey)	Outward links (predators)	No direct link	Total
3	9/29	7/11	30/59	46/99
17	7/13	7/19	17/67	31/99
18	3/11	1/13	4/75	8/99
35	6/7	6/14	37/78	49/99
38	2/7	3/10	23/82	28/99

The projections of all five species in the multispecies projection resulted in a change in terminal year biomass. The biomass projections were less stable for all species than when the species were fished indecently (Figure 4.4). Three species (Species # 3, #18, #38) had a terminal year biomass higher in the multispecies fishery than when fished independently. Species #38 had a terminal year biomass of almost twice that of the single-species model, demonstrating that specie interactions can increase species productivity (Table 4.10). Species #3 also had a marked increase in biomass at the end of the multispecies simulation, benefiting from

the community interactions that have changed when more species are fished (Table 4.10; Figure 4.4).

The average species biomass of the system did not fluctuate over the time series. The only noticeable change in average biomass was a result of the two species with the highest initial biomass peaking around year 175. The resulting final biomass of all of the single-species simulations was similar to that of the simulation with no fishing, which is also the initial community biomass for all of the projections. The total community biomass from the multispecies projection was 12% lower than the initial biomass.

A total of 55 species changed in biomass in the multispecies projections, and 14 of these species had no direct connection to the five fished species. Of the 55 species that had changed in biomass, eight did not change in biomass in any of the single-species fishing scenarios. Twelve of the 45 species that did not change in biomass also did not change in biomass in any of the single-species projections.

DISCUSSION

The multispecies Lotka-Volterra model simulates the direct and indirect species interactions and elucidates the impact of fishing on the community. The species responses to fishing in a multispecies community (either increasing or decreasing biomass) are in line with the current literature. Gaichas et al. (2010) revealed that species trophic level partially explained the expected species response to fishing. Species at high trophic levels that experience little predation mortality will have dynamics similar to those from a single-species assessment projection. However, for species at mid-trophic levels that experience higher rates of predation mortality, the dynamics are not always predictable. The simulations results in this study clearly indicate that a multispecies fishery can actually increase a fished species biomass. The

multispecies fishery of five species also increased the number of unfished species exhibiting a change in biomass. A higher percent (67% versus 55%) of species changed in biomass in the unconnected multispecies fishing scenario. This change in productivity is likely a combination of direct and indirect effects and further solidifies the need to understand the interaction matrix and the strength of the interactions among species.

The fished species that increased in biomass in the multispecies fishing scenarios could in theory be fished at a higher fishing mortality rates than estimated from the single-species model. The conditions necessary to accomplish this without affecting additional species in the community will have to be explored further.

The community total biomass remained stable over both time series when five species were fished. However, all five species were fished a quasi-multispecies fishing mortality rate that incorporated a buffer for species interactions. If the species had been fished a theoretical fishing mortality rate of $0.5 * r_{LV}$ the majority of the single-species simulations would have resulted in species extinction.

The estimation of biological reference points from Chapter 4 also provides an additional ten species to compare with Chapter 2. Biological reference points were estimated for a total of 15 species from the community of 25% connectance and none had an estimated r_{ASPIC} greater than 76% of the r_{LV} value. There are no visible trends indicating a correlations between r_{ASPIC} with r_{LV} , initial biomass, or the number of connections. However, this is likely an artifact of the interaction matrix construction among communities. The average percent of r_{LV} estimated from the single species model was 36%, which is below one study's current recommendation to reduce fishing mortality rates by one-third (Cury et al., 2011).

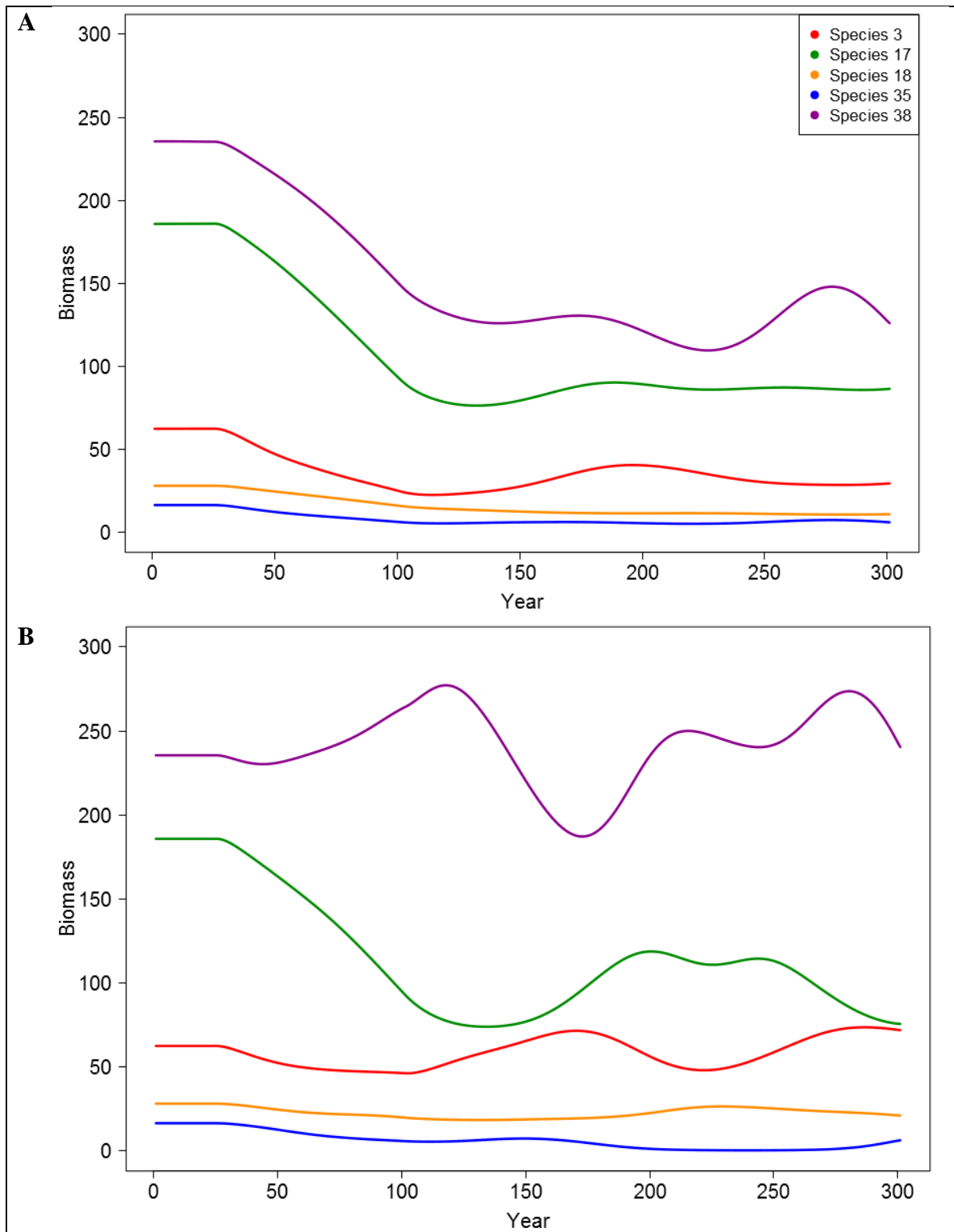


Figure 4.4. Biomass projections from the Lotka-Volterra model of the five species selected for fishing, when the species are fished in separate projections (top) and fished simultaneously in a multispecies fishery (bottom).

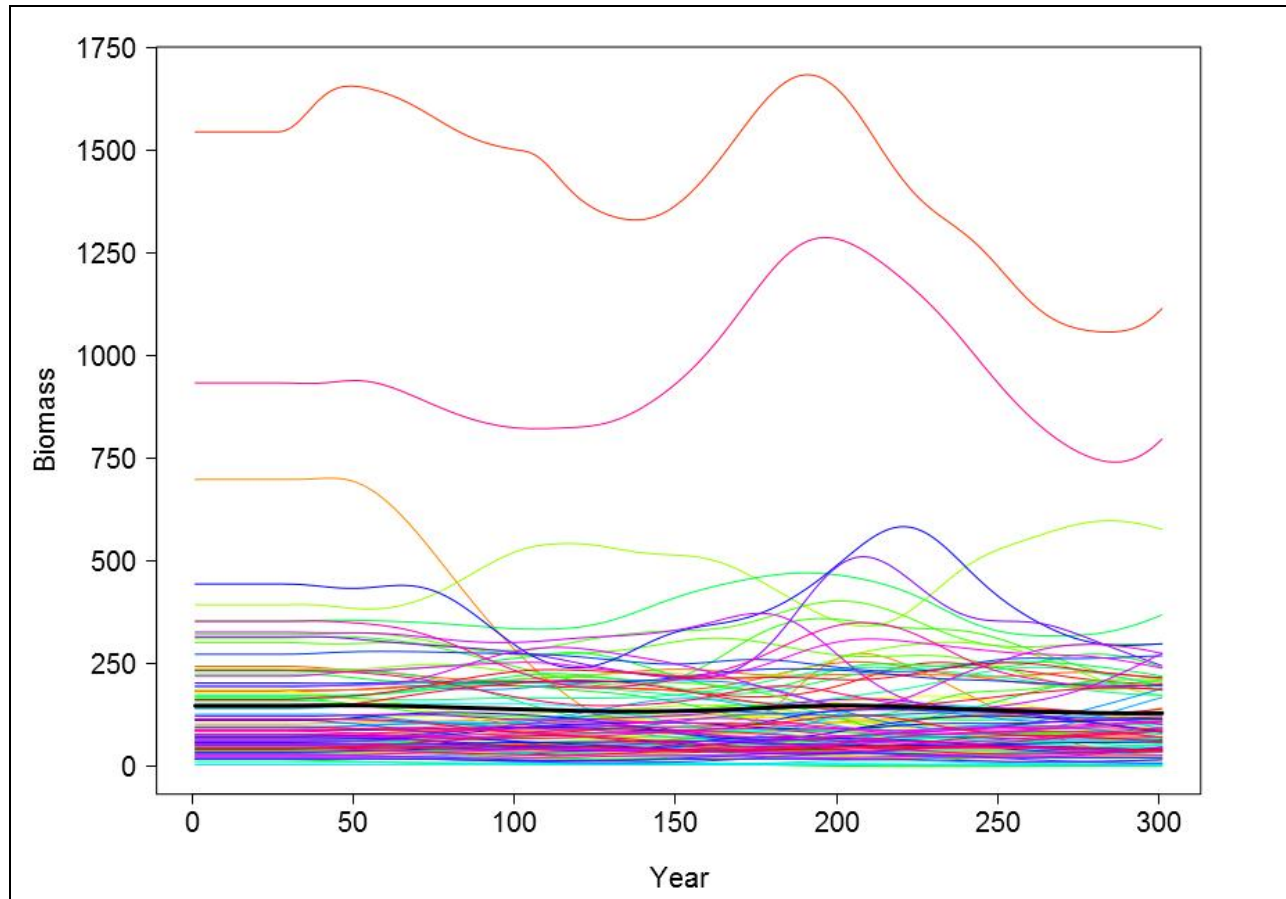


Figure 4.5. Biomass projection for all 100 species when the five connected species were fished simultaneously at the estimated single-species F_{MSY} . The bold line is the average community biomass.

Table 4.10. Comparison of the biomass at the beginning and end of the projection when species were fished in individual projections versus simultaneously in a multispecies fishery.

Species	B_0	Individual B_{300}	Multispecies B_{300}
3	62.46	28.89	73.03
17	185.80	86.10	80.93
18	28.12	10.86	22.27
35	16.50	7.05	3.41
39	353.75	140.43	263.77

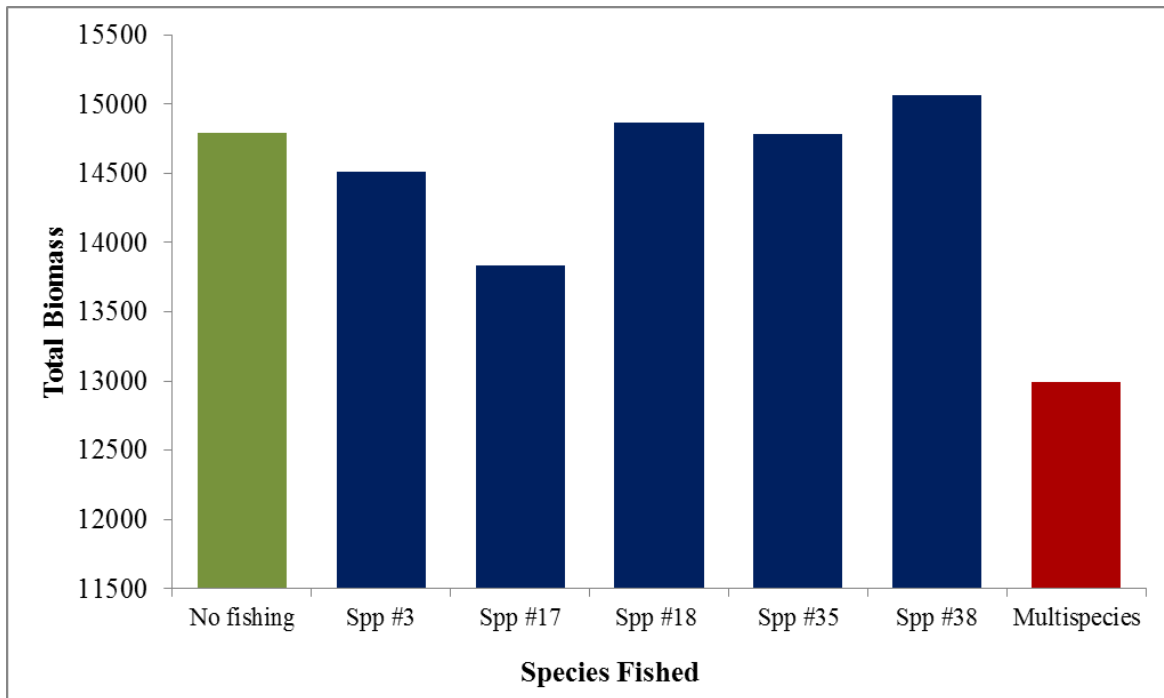


Figure 4.6. Total community biomass at the end of the projection, for projections with no fishing, fishing each species independently, and fishing all five species in a multispecies fishery. The scenario with no fishing also represents the initial biomass for all other projections.

Table 4.11. The number of species with a change in biomass by $\geq 25\%$ separated by the number of species changing in biomass in the single species projections versus the multispecies projection. The species in parentheses are those with no direction connection to any of the five fished species.

Number of single species runs with biomass change	Change in multispecies projection	No change in multispecies projection
0	8	12
1	16	7
2	12	14
3	16	9
4	3	3
5	0	0
Total	55 (14)	45 (6)

Cury et al. (2011) found in a survey of seabird-fish predator-prey interactions that one-third of forage fish maximum biomass should be designated to support seabird populations. A recent examination of forage fish management policies recommended a reduction in catch rates

of forage fish by half in some ecosystems (Pikitch et al., 2012), which will not only have economic implications but also has the potential to affect community dynamics.

As with any model, the assumptions made in this multispecies Lotka-Volterra model affect the results. The results should be interpreted with an understanding of the effect of the assumptions. One assumption made in this Lotka-Volterra model was to model a Hollings Type I functional response. Density-dependence was incorporated for each species as a portion of the intrinsic rate of increase. Modeling Type I functional response maintains the shape of the logistic model for direct comparison with the Schaefer stock production model. Altering the shape of the logistic model, i.e. functional response, would need to be accounted for in the stock production models as well. This is possible in ASPIC through the use of the shape parameter in a Pella-Tomlinson production model (Prager, 2011). Species were not assigned trophic levels or niches in the multispecies Lotka-Volterra community. The species chosen for fishing in these simulations may not reflect species with the same characteristics as those most commonly fished for recreation or commercial harvest. Assigning trophic levels or trophic roles to the species would allow one to simulate a community of specific interest, or simulate conditions such as fishing down the food web.

The multispecies Lotka-Volterra model is a powerful simulation tool to explore the possible community effects of fishing harvest scenarios. Lawlor (1979) stressed the utility of the L-V model for “examining the logical consequences of even the simplest assumptions about community structure and function.” Several current studies have continued to use modified L-V models to study ecosystem dynamics (Link, 2002a; Wilson and Lundberg, 2004; Tokita, 2006; Gamble and Link, 2009). Extensions of L-V models can be used to evaluate tradeoffs among harvest strategies, rebuilding plans, and make decisions regarding ecosystem based fisheries

management. This is also a useful tool to analyze the effects of interaction rates and the strength of interaction rates on species responses to fishing.

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GENERAL SUMMARY AND CONCLUSIONS

The two main objectives of this study were to identify the spatial and temporal demersal fish communities (DFCs) in the northwestern Gulf of Mexico (Gulf), and to explore the community level effects of fishing using a multispecies Lotka-Volterra model. The delineation of the northwestern Gulf into DFCs was successful through a suite of multivariate analyses. While none of the DFCs exhibited statistically significant temporal trends, the indices of abundance are value for future investigations. The suite of simulations from the multispecies Lotka-Volterra model demonstrated the importance of incorporating ecological considerations when harvesting and managing single-species.

In Chapter 1, the fishery-independent summer and fall SEAMAP bottomfish trawl survey data were utilized to define the spatial heterogeneity in the northwestern Gulf. Two multivariate statistics (cluster analysis and nonmetric multidimensional scaling) identified four demersal fish communities (DFCs) in the northwestern Gulf. Zone 13, the shrimp statistical zone nearest the Mississippi, separated spatially during the summer survey. Zone 13 was also considered a distinct region in the fall data for comparisons. Indicator species analysis identified species affiliating with each of the DFCs and revealed a shift in community assemblages between survey seasons. Temporal analyses of the SEAMAP data did not show any statistically significant trends within any of the DFCs. However, the indices of abundance calculated for each species can be updated as more survey data become available and incorporate into future community models.

In Chapter 2, a multispecies Lotka-Volterra model was developed to explore the effects of fishing a single species in the community on all other species in the same community. The community was developed with a connectance of 25%, and five species were selected for

fishing. The five species were selected based on predefined characteristics. These species were, 1) the species with the most number of direct links, 2) the species with the fewest number of direct links, 3) a species with a high predator to prey ratio, 4) a species with a high prey to predator ratio, and 4) a randomly selected species. The single-species biological reference points of B_{MSY} and F_{MSY} were estimated using the multispecies time series as input. The ASPIC-estimated fishing mortality rates were between 10-75% lower than was expected from the L-V model. This indicates the need to incorporate buffers into fishing mortality rates to account for mortality from predator-prey interactions. A second fishing scenario was used to explore the effects of rebuilding plans on single-species and community dynamics. The same five species were fished to 20% of their virgin biomass, at which point they were considered overfished. A rebuilding plan was simulated by reducing the fishing mortality rate to half of F_{MSY} . In all but one of the simulations, the projected time required to rebuild the populations was longer in the multispecies model than the single-species model.

In Chapter 3, two additional communities were parameterized using the multispecies Lotka-Volterra model. The two communities had connectance values of 35% and 45% and the goal was to compare the two communities with the community of 25% in Chapter 2. Species with the same characteristics, e.g., species with the most direct links, species with the fewest direct links, etc., were selected for fishing. The same two fishing scenarios that were implemented in Chapter 2 were applied to each community of higher connectance. All of the estimates of fishing mortality were within the 10-75% buffer suggested from Chapter 2 results. No specific trends were evident among the species in the three different communities. However, fewer unfished species were affected by fishing in the community of 45% connectance than the other two communities. The lack of a trend among the communities is likely an effect of the

network structure used to initialize the interaction matrices. The lack of a trend may also suggest that multispecies dynamics are hard to predict and that there may be no “rule of thumb” to determine the community level responses to fishing, or other perturbations. Comparison of the L-V model to other available multi-species models may shed light on why no trends were found among community connectance in this study.

In Chapter 4, multispecies fishing scenarios were examined using the multispecies Lotka-Volterra community with 25% connectance. The goal of this chapter was to explore the effect of fishing five species simultaneously, with species that either have direct connections or have no direct connections at all. For each species selected for fishing, the single-species biological reference points were estimated in ASPIC and then applied simultaneously in a single run of the Lotka-Volterra model. In both multispecies scenarios, three of the five species increased in biomass, higher than was expected from the single-species fishery projections. This demonstrated the need to study species interactions and understand the food web dynamics when determining fishery management benchmarks.

APPENDIX A: CHAPTER 1 SUPPLEMENTARY MATERIAL

Table A.1. Number of tows by year and shrimp statistical zone for the SEAMAP summer trawl survey for dataset used for the analyses in this study. Only tows in the depth range of 10-30 fathoms were included.

Year/Zone	13	14	15	16	17	18	19	20	21	Total
1982	17	17	3	0	5	22	15	15	22	116
1983	0	2	11	11	17	16	23	19	15	114
1984	4	9	14	18	12	10	20	18	9	114
1985	9	18	5	9	5	5	23	14	42	130
1986	0	12	11	8	10	4	16	10	25	96
1987	5	21	10	16	14	7	20	14	14	121
1988	5	12	7	12	17	10	22	14	12	111
1989	6	10	8	16	5	8	20	12	17	102
1990	13	18	8	16	12	12	18	17	11	125
1991	11	19	9	11	18	12	15	14	15	124
1992	1	24	16	15	18	3	26	20	8	131
1993	14	18	11	14	17	7	27	15	12	135
1994	10	17	19	17	11	8	20	17	10	129
1995	4	17	16	12	16	7	25	17	10	124
1996	8	25	10	21	16	9	19	9	18	135
1997	2	22	10	18	16	5	24	8	21	126
1998	6	14	16	16	9	7	20	20	9	117
1999	6	23	17	10	23	5	24	16	15	139
2000	7	19	12	11	25	6	28	13	13	134
2001	12	17	17	11	3	5	6	8	14	93
2002	8	24	13	19	14	10	22	16	17	143
2003	6	21	5	2	13	13	18	19	10	107
2004	12	24	12	14	20	12	18	14	13	139
2005	8	6	17	11	16	4	23	11	22	118
2006	6	12	8	17	18	11	20	16	11	119
2007	8	9	15	11	18	3	28	13	17	122
2008	17	12	19	13	20	13	20	12	19	145
Total	205	442	319	349	388	234	560	391	421	3309
	205	761			971		1372			

Table A.2. Number of tows by year and shrimp statistical zone for the SEAMAP fall trawl survey for dataset used for the analyses in this study. Only tows in the depth range of 10-30 fathoms were included.

Year/Zone	13	14	15	16	17	18	19	20	21	Total
1986	5	16	5	22	15	21	21	10	12	127
1987	10	18	16	13	11	14	10	10	2	104
1988	5	13	19	10	19	11	18	16	13	124
1989	11	18	11	14	14	15	17	12	15	127
1990	12	11	14	15	17	10	22	11	18	130
1991	12	23	11	13	22	15	16	19	10	141
1992	5	11	11	15	17	8	21	22	10	120
1993	8	22	11	20	11	9	22	16	10	129
1994	6	9	14	16	13	8	22	12	12	112
1995	8	8	15	15	14	9	20	17	12	118
1996	6	22	14	12	17	8	20	10	20	129
1997	16	23	10	18	12	17	13	14	14	137
1998	14	36	7	20	6	9	18	14	12	136
1999	4	26	10	25	11	5	29	16	14	140
2000	16	18	17	14	15	9	24	17	13	143
2001	8	24	12	21	15	10	23	16	17	146
2002	4	9	13	11	18	8	28	19	10	120
2003	7	12	9	13	16	19	16	15	13	120
2004	6	14	15	14	19	14	18	13	16	129
2005	16	18	12	33	10	12	22	14	20	157
2006	5	15	6	11	18	14	20	22	9	120
2007	13	14	18	15	16	14	18	16	16	140
Total	197	380	270	360	326	259	438	331	288	2849
	197	650			945			1057		

Table A.3. Species present in at least 3% of all summer tows. These species were used in the community metric analyses, including the cluster analysis, multi-response permutation procedure, and nonmetric multidimensional scaling.

Scientific name	Family	Common Name	Percent of tows present
<i>Micropogonias undulatus</i>	Sciaenidae	Atlantic croaker	95
<i>Penaeus aztecus</i>	Penaeidae	Brown shrimp	91
<i>Synodus foetens</i>	Synodontidae	Inshore lizardfish	79
<i>Lutjanus campechanus</i>	Lutjanidae	Northern red snapper	79
<i>Callinectes similis</i>	Portunidae	Lesser blue crab	78
<i>Stenotomus caprinus</i>	Sparidae	Longspine porgy	75
<i>Syacium gunteri</i>	Bothidae	Shoal flounder	63
<i>Leiostomus xanthurus</i>	Sciaenidae	Spot croaker	63
<i>Centropristis philadelphicus</i>	Serranidae	Rock sea bass	61
<i>Diplectrum bivittatum</i>	Serranidae	Dwarf sand perch	59
<i>Chloroscombrus chrysurus</i>	Carangidae	Atlantic bumper	57
<i>Cynoscion nothus</i>	Sciaenidae	Silver seatrout	57
<i>Prionotus longispinosus</i>	Triglidae	Bigeye searobin	56
<i>Portunus gibbesii</i>	Portunidae	Iridescent swimming crab	55
<i>Peprilus burti</i>	Stromateidae	Gulf butterfish	53
<i>Cynoscion arenarius</i>	Sciaenidae	Sand seatrout	52
<i>Lagodon rhomboides</i>	Sparidae	Pinfish	52
<i>Squilla empusa</i>	Squillidae	Mantis shrimp (<i>S. empusa</i>)	45
<i>Cyclopsetta chittendeni</i>	Bothidae	Mexican flounder	42
<i>Lutjanus synagris</i>	Lutjanidae	Lane snapper	40
<i>Balistes capriscus</i>	Balistidae	Gray triggerfish	38
<i>Chaetodipterus faber</i>	Ephippidae	Atlantic spadefish	36
<i>Eucinostomus gula</i>	Gerreidae	Jenny mojarra	34
<i>Trachypeneus similis</i>	Penaeidae	Roughback shrimp	33
<i>Trichiurus lepturus</i>	Trichiuridae	Atlantic cutlassfish	33
<i>Halieutichthys aculeatus</i>	Ogcocephalidae	Pancake batfish	32
<i>Upeneus parvus</i>	Mullidae	Dwarf goatfish	32
<i>Penaeus setiferus</i>	Penaeidae	Northern white shrimp	31
<i>Sphoeroides parvus</i>	Tetraodontidae	Least puffer	31
<i>Porichthys plectrodon</i>	Batrachoididae	Atlantic midshipman	30
<i>Trachurus lathami</i>	Carangidae	Rough scad	28
<i>Saurida brasiliensis</i>	Synodontidae	Brazilian lizardfish	28
<i>Loligo pleii</i>	Loliginidae	Arrow squid	28
<i>Harengula jaguana</i>	Clupeidae	Scaled herring	28
<i>Lepophidium brevibarbe</i>	Ophidiidae	Shortbread cusk eel	28
<i>Serranus atrobranchus</i>	Serranidae	Blackear bass	26
<i>Lagocephalus laevigatus</i>	Tetraodontidae	Smooth puffer	26
<i>Sicyonia brevirostris</i>	Sicyoniidae	Brown rock shrimp	25
<i>Sicyonia dorsalis</i>	Sicyoniidae	Lesser rock shrimp	24

(Table A.3 continued)

<i>Etropus crossotus</i>	Paralichthyidae	Fringed flounder	24
<i>Loligo pealeii</i>	Loliginidae	Longfin inshore squid	24
<i>Larimus fasciatus</i>	Sciaenidae	Banded drum	23
<i>Citharichthys spilopterus</i>	Paralichthyidae	Bay whiff	22
<i>Arius felis</i>	Ariidae	Hardhead catfish	22
<i>Penaeus duorarum</i>	Penaeidae	Northern pink shrimp	21
<i>Selene setapinnis</i>	Carangidae	Atlantic moonfish	21
<i>Opisthonema oglinum</i>	Clupeidae	Atlantic thread herring	20
<i>Portunus spinimanus</i>	Portunidae	Blotched swimming crab	20
<i>Scorpaena calcarata</i>	Scorpaenidae	Smoothhead scorpionfish	20
<i>Calappa sulcata</i>	Clappidae	Yellow box crab	20
<i>Lolliguncula brevis</i>	Loliginidae	Atlantic brief squid	20
<i>Astropecten duplicatus</i>	Astropectinidae	Two-spined star fish	20
<i>Squilla chydrea</i>	Squillidae	Mantis shrimp (<i>S. chydrea</i>)	18
<i>Caranx crysos</i>	Carangidae	Blue runner	18
<i>Anchoa hepsetus</i>	Engraulidae	Broad-striped anchovy	18
<i>Peprilus alepidotus</i>	Stromateidae	American harvestfish	17
<i>Prionotus rubio</i>	Triglidae	Blackwing searobin	16
<i>Ancylosetta quadrocclata</i>	Bothidae	Ocellated flounders	15
<i>Symphurus plagiatus</i>	Cynoglossidae	Blackcheek tonguefish	13
<i>Callinectes sapidus</i>	Portunidae	Blue crab	12
<i>Gymnachirus texae</i>	Archiridae	Gulf of Mexico fringed sole	12
<i>Orthopristis chrysopterus</i>	Haemulidae	Pigfish	11
<i>Synodus poeyi</i>	Synodontidae	Offshore lizardfish	11
<i>Bollmannia communis</i>	Gobiidae	Ragged goby	10
<i>Portunus spinicarpus</i>	Portunidae	Longspine swimming crab	10
<i>Amusium papyraceum</i>	Pectinidae	Paper scallop	10
<i>Menticirrhus americanus</i>	Sciaenidae	Southern kingcroaker	10
<i>Sphyrna guachancho</i>	Sphyrnidae	Guachancho barracuda	10
<i>Hoplostethus macrurus</i>	Muraenidae	Freckled pikeconger	9
<i>Paralichthys lethostigma</i>	Paralichthyidae	Southern flounder	9
<i>Prionotus paralatus</i>	Triglidae	Mexican searobin	9
<i>Ophidion welschi</i>	Ophidiidae	Crested cuskeel	9
<i>Diplectrum formosum</i>	Serranidae	Sand seabass	8
<i>Monacanthus hispidus</i>	Monacanthidae	Planehead filefish	8
<i>Raja texana</i>	Rajidae	Roundel skate	8
<i>Ogcocephalus declivirostris</i>	Ogcocephalidae	Slantbrow batfish	8
<i>Renilla mulleri</i>	Renillidae	Sea pansy	8
<i>Prionotus ophryas</i>	Triglidae	Bandtail searobin	8
<i>Mullus auratus</i>	Mullidae	Red goatfish	8
<i>Pristipomoides aquilonaris</i>	Lutjanidae	Wenchman	8
<i>Rhizoprionodon terraenovae</i>	Carcharhinidae	Atlantic sharpnose shark	8
<i>Scomberomorus maculatus</i>	Scombridae	Spanish mackerel	8

(Table A.3 continued)

<i>Scomberomorus cavalla</i>	Scombridae	King mackerel	8
<i>Brevoortia patronus</i>	Clupeidae	Gulf menhaden	7
<i>Trachypeneus constrictus</i>	Penaeidae	Roughneck shrimp	7
<i>Haemulon aurolineatum</i>	Haemulidae	Tomtate grunt	7
<i>Selene vomer</i>	Carangidae	Lookdown	7
<i>Prionotus tribulus</i>	Triglidae	Bighead searobin	6
<i>Engyophrys senta</i>	Bothidae	Spiny flounder	6
<i>Polydactylus octonemus</i>	Polynemidae	Atlantic threadfin	6
<i>Luidia clathrata</i>	Luidiidae	Lined sea star	6
<i>Prionotus roseus</i>	Triglidae	Blue-spotted searobin	6
<i>Selar crumenophthalmus</i>	Carangidae	Bigeye scad	6
<i>Symphurus diomedianus</i>	Cynoglossidae	Spottedfin tonguefish	5
<i>Sphyrna tiburo</i>	Sphyrnidae	Bonnethead	5
<i>Sardinella aurita</i>	Clupeidae	Round sardinella	5
<i>Trichopsetta ventralis</i>	Bothidae	Sash flounder	5
<i>Brotula barbatum</i>	Ophidiidae	Bearded brotula	5
<i>Syacium papillosum</i>	Bothidae	Dusky flounder	5
<i>Decapterus punctatus</i>	Carangidae	Round scad	5
<i>Solenocera vioscai</i>	Solenoceridae	Humpback shrimp	4
<i>Bellator militaris</i>	Triglidae	Horned searobin	4
<i>Hepatus epheliticus</i>	Calappidae	Calico box crab	4
<i>Rhomboplites aurorubens</i>	Lutjanidae	Vermilion snapper	4
<i>Rachycentron canadum</i>	Rachycentridae	Cobia	4
<i>Astropecten cingulatus</i>	Astropectinidae	Echinoderm	4
<i>Ophiolepis elegans</i>	Ophiuridae	Brittle star	3
<i>Prionotus stearnsi</i>	Triglidae	Shortwing searobin	3
<i>Bagre marinus</i>	Arridae	Gafftopsail catfish	3
<i>Stellifer lanceolatus</i>	Sciaenidae	Star drum	3
<i>Anchoa mitchilli</i>	Engraulidae	Bay anchovy	3
<i>Libinia emarginata</i>	Majidae	Portly spider crab	3

Table A.4. Species present in at least 3% of all fall tows. These species were used in the community metric analyses, including the cluster analysis, multi-response permutation procedure, and nonmetric multidimensional scaling.

Scientific name	Family	Common Name	Percent of tows present
<i>Penaeus aztecus</i>	Penaeidae	Brown shrimp	88
<i>Stenotomus caprinus</i>	Sparidae	Longspine porgy	86
<i>Callinectes similis</i>	Portunidae	Lesser blue crab	80
<i>Synodus foetens</i>	Synodontidae	Inshore lizardfish	72
<i>Centropristis philadelphic</i>	Serranidae	Rock sea bass	65
<i>Peprilus burti</i>	Stromateidae	Gulf butterfish	62
<i>Diplectrum bivittatum</i>	Serranidae	Dwarf sand perch	55
<i>Saurida brasiliensis</i>	Synodontidae	Brazilian lizardfish	52
<i>Upeneus parvus</i>	Mullidae	Dwarf goatfish	51
<i>Syacium gunteri</i>	Bothidae	Shoal flounder	50
<i>Squilla empusa</i>	Squillidae	Mantis shrimp (<i>S. empusa</i>)	48
<i>Prionotus longispinosus</i>	Triglidae	Bigeye searobin	47
<i>Trachurus lathami</i>	Carangidae	Rough scad	45
<i>Portunus gibbesii</i>	Portunidae	Iridescent swimming crab	44
<i>Sicyonia dorsalis</i>	Sicyoniidae	Lesser rock shrimp	44
<i>Lutjanus campechanus</i>	Lutjanidae	Northern red snapper	43
<i>Micropogonias undulatus</i>	Sciaenidae	Atlantic croaker	42
<i>Loligo pleii</i>	Loliginidae	Arrow squid	40
<i>Loligo pealeii</i>	Loliginidae	Longfin inshore squid	38
<i>Chloroscombrus chrysurus</i>	Carangidae	Atlantic bumper	37
<i>Trachypeneus similis</i>	Penaeidae	Roughback shrimp	37
<i>Sicyonia brevirostris</i>	Sicyoniidae	Brown rock shrimp	36
<i>Sphoeroides parvus</i>	Tetraodontidae	Least puffer	36
<i>Lagodon rhomboides</i>	Sparidae	Pinfish	34
<i>Serranus atrobranchus</i>	Serranidae	Blackear bass	34
<i>Porichthys plectrodon</i>	Batrachoididae	Atlantic midshipman	33
<i>Cynoscion arenarius</i>	Sciaenidae	Sand seatrout	33
<i>Lepophidium brevibarbe</i>	Ophidiidae	Shortbread cusk eel	32
<i>Trichiurus lepturus</i>	Trichiuridae	Atlantic cutlassfish	31
<i>Pristipomoides aquilonaris</i>	Lutjanidae	Wenchman	31
<i>Etropus crossotus</i>	Paralichthyidae	Fringed flounder	30
<i>Lagocephalus laevigatus</i>	Tetraodontidae	Smooth puffer	29
<i>Halieutichthys aculeatus</i>	Ogcocephalidae	Pancake batfish	28
<i>Prionotus stearnsi</i>	Triglidae	Shortwing searobin	28
<i>Anchoa hepsetus</i>	Engraulidae	Broad-striped anchovy	27
<i>Cyclopsetta chittendeni</i>	Bothidae	Mexican flounder	27
<i>Lolliguncula brevis</i>	Loliginidae	Atlantic brief squid	27
<i>Cynoscion nothus</i>	Sciaenidae	Silver seatrout	26
<i>Prionotus paralatus</i>	Triglidae	Mexican searobin	25

(Table A.4 continued)

<i>Squilla chydæa</i>	Squillidae	Mantis shrimp (<i>S. chydæa</i>)	24
<i>Selene setapinnis</i>	Carangidae	Atlantic moonfish	24
<i>Penaeus duorarum</i>	Penaeidae	Northern pink shrimp	23
<i>Callinectes sapidus</i>	Portunidae	Blue crab	23
<i>Leiostomus xanthurus</i>	Sciaenidae	Spot croaker	21
<i>Portunus spinimanus</i>	Portunidae	Blotched swimming crab	21
<i>Calappa sulcata</i>	Clappidae	Yellow box crab	21
<i>Portunus spinicarpus</i>	Portunidae	Longspine swimming crab	21
<i>Harengula jaguana</i>	Clupeidae	Scaled herring	20
<i>Symphurus plagiatus</i>	Cynoglossidae	Blackcheek tonguefish	20
<i>Monacanthus hispidus</i>	Monacanthidae	Planehead filefish	20
<i>Astropecten duplicatus</i>	Astropectinidae	Two-spined star fish	17
<i>Lutjanus synagris</i>	Lutjanidae	Lane snapper	17
<i>Synodus poeyi</i>	Synodontidae	Offshore lizardfish	16
<i>Bollmannia communis</i>	Gobiidae	Ragged goby	16
<i>Penaeus setiferus</i>	Penaeidae	Northern white shrimp	16
<i>Prionotus rubio</i>	Triglidae	Blackwing searobin	15
<i>Citharichthys spilopterus</i>	Paralichthyidae	Bay whiff	15
<i>Amusium papyraceum</i>	Pectinidae	Paper scallop	14
<i>Balistes capriscus</i>	Balistidae	Gray triggerfish	13
<i>Eucinostomus gula</i>	Gerreidae	Jenny mojarra	12
<i>Etrumeus teres</i>	Clupeidae	Round herring	12
<i>Engyophrys senta</i>	Bothidae	Spiny flounder	12
<i>Renilla mulleri</i>	Renillidae	Sea pansy	11
<i>Hoplunnis macrurus</i>	Muraenesocidae	Freckled pike-conger	11
<i>Syacium papillosum</i>	Bothidae	Dusky flounder	10
<i>Ancylopsetta quadrocellata</i>	Bothidae	Ocellated flounders	10
<i>Scorpaena calcarata</i>	Scorpaenidae	Smoothhead scorpionfish	10
<i>Sardinella aurita</i>	Clupeidae	Round sardinella	9
<i>Sphyræna guachancho</i>	Sphyrænidae	Guachanche barracuda	9
<i>Prionotus tribulus</i>	Triglidae	Bighead searobin	9
<i>Polydactylus octonemus</i>	Polynemidae	Atlantic threadfin	9
<i>Urophycis floridanus</i>	Phycidae	Southern codling	9
<i>Brotula barbatum</i>	Ophidiidae	Bearded brotula	9
<i>Opisthonema oglinum</i>	Clupeidae	Atlantic thread herring	8
<i>Raja texana</i>	Rajidae	Roundel skate	8
<i>Larimus fasciatus</i>	Sciaenidae	Banded drum	7
<i>Antennarius radiosus</i>	Antennariidae	Big-eyed frogfish	7
<i>Gymnachirus texae</i>	Archiridae	Gulf of Mexico fringed sole	7
<i>Priacanthus arenatus</i>	Priacanthidae	Atlantic bigeye	7
<i>Rhynchoconger flava</i>	Congridae	Yellow conger	6
<i>Peprilus alepidotus</i>	Stromateidae	American harvestfish	6
<i>Decapterus punctatus</i>	Carangidae	Round scad	6

<i>Bregmaceros atlanticus</i>	Bregmacerotidae	Antenna codlet	6
<i>Hepatus epheliticus</i>	Calappidae	Calico box crab	6
<i>Menticirrhus americanus</i>	Sciaenidae	Southern kingcroaker	6
<i>Trachypeneus constrictus</i>	Penaeidae	Roughneck shrimp	6
<i>Solenocera vioscai</i>	Solenoceridae	Humpback shrimp	6
<i>Paralichthys lethostigma</i>	Paralichthyidae	Southern flounder	6
<i>Ophidion welshi</i>	Ophidiidae	Crested cuskeel	6
<i>Selar crumenophthalmus</i>	Carangidae	Bigeye scad	6
<i>Diplectrum formosum</i>	Serranidae	Sand seabass	6
<i>Trichopsetta ventralis</i>	Bothidae	Sash flounder	5
<i>Mullus auratus</i>	Mullidae	Red goatfish	5
<i>Ogcocephalus declivirostri</i>	Ogcocephalidae	Slantbrow batfish	5
<i>Anchoa mitchilli</i>	Engraulidae	Bay anchovy	5
<i>Ancylopsetta dilecta</i>	Bothidae	Three-eye flounder	5
<i>Luidia clathrata</i>	Luidiidae	Lined sea star	5
<i>Rhizoprionodon terraenovae</i>	Carcharhinidae	Atlantic sharpnose shark	5
<i>Haemulon aurolineatum</i>	Haemulidae	Tomtate grunt	5
<i>Prionotus roseus</i>	Triglidae	Bluespotted searobin	5
<i>Caulolatilus intermedius</i>	Malacanthidae	Anchor tilefish	4
<i>Scomberomorus maculatus</i>	Scombridae	Spanish mackerel	4
<i>Prionotus ophryas</i>	Triglidae	Bandtail searobin	4
<i>Bellator militaris</i>	Triglidae	Horned searobin	4
<i>Caranx crysos</i>	Carangidae	Blue runner	4
<i>Libinia emarginata</i>	Majidae	Portly spider crab	4
<i>Orthopristis chrysopterus</i>	Haemulidae	Pigfish	4
<i>Anasimus latus</i>	Majidae	Stilt spider crab	4
<i>Symphurus diomedianus</i>	Cynoglossidae	Spottedfin tonguefish	3
<i>Selene vomer</i>	Carangidae	Lookdown	3

Table A.5. Results from the indicator species analysis for the prevalent species in the summer SEAMAP trawl survey. The maximum group is the region where the species shows the highest relative abundance over the entire survey period. The p -value, is from the Monte Carlo simulations of the indicators values and significant p -value less than 0.05 indicates a statistically significant indicator value.

Species	Maximum Group	Indicator Values				Monte Carlo		
		Zone 13	East	Mid	West	Mean	s.d.	p
Atlantic brief squid	Zone 13	40	3	0	6	8.3	1.01	0.0002
Atlantic cutlassfish	Zone 13	51	4	1	2	11.9	2.22	0.0002
Bay anchovy	Zone 13	18	1	0	0	2.2	0.61	0.0002
Bay whiff	Zone 13	24	6	0	1	4.9	0.83	0.0002
Bearded brotula	Zone 13	12	6	0	0	3.1	0.60	0.0002
Bigeye searobin	Zone 13	37	17	3	2	14.9	2.00	0.0002
Big-eyed frogfish	Zone 13	6	1	0	2	2.9	0.70	0.0068
Blackcheek tonguefish	Zone 13	23	11	0	1	6.4	0.90	0.0002
Blackwing searobin	Zone 13	10	2	1	0	6.8	1.58	0.0394
Blue crab	Zone 13	18	7	2	3	7.7	1.22	0.0002
Bluespotted searobin	Zone 13	4	1	1	0	2.1	0.61	0.0234
Broad-striped anchovy	Zone 13	14	11	1	5	9.1	1.40	0.0080
Freckled pike-conger	Zone 13	10	2	1	1	3.5	0.60	0.0002
Mantis shrimp (<i>S. chydrea</i>)	Zone 13	14	4	1	7	8.2	1.28	0.0024
Mantis shrimp (<i>S. empusa</i>)	Zone 13	41	14	4	5	14.2	1.26	0.0002
Northern white shrimp	Zone 13	18	5	2	2	6.2	1.35	0.0002
Ragged goby	Zone 13	30	2	0	1	6.0	1.20	0.0002
Rock sea bass	Zone 13	29	19	7	9	18.3	1.70	0.0010
Roughback shrimp	Zone 13	26	11	2	5	11.3	1.27	0.0002
Sand seatrout	Zone 13	41	5	1	4	10.3	1.53	0.0002
Shortbread cusk eel	Zone 13	12	9	6	5	9.6	0.99	0.0256
Silver seatrout	Zone 13	15	6	3	5	8.3	1.15	0.0002
Atlantic croaker	East	9	25	12	4	13.2	1.61	0.0004
Banded drum	East	0	5	2	2	2.8	0.63	0.0138
Blackear bass	East	5	16	4	8	10.0	1.07	0.0010
Crested cuskeel	East	1	9	1	0	2.8	0.72	0.0002
Fringed flounder	East	17	27	2	1	9.5	1.18	0.0002
Iridescent swimming crab	East	15	37	5	2	13.9	1.77	0.0002
Atlantic bumper	Mid	2	7	20	10	12.1	1.86	0.0070
Atlantic midshipman	Mid	8	9	13	4	10.0	1.06	0.0332
Atlantic sharpnose shark	Mid	0	1	4	0	1.9	0.46	0.0036
Bandtail searobin	Mid	0	0	6	0	1.6	0.43	0.0002
Brown rock shrimp	Mid	0	1	45	6	13.6	2.62	0.0002
Dusky flounder	Mid	2	1	5	2	3.5	0.65	0.0202

(Table A.5 continued)

Dwarf sand perch	Mid	3	8	20	17	15.0	1.11	0.0038
Gray triggerfish	Mid	0	2	8	4	4.3	0.73	0.0048
Horned searobin	Mid	0	0	9	0	1.6	0.44	0.0002
Inshore lizardfish	Mid	3	18	27	21	19.4	0.98	0.0002
Jenny mojarra	Mid	0	2	9	3	4.4	0.81	0.0018
Lane snapper	Mid	0	2	26	0	5.5	0.89	0.0002
Longspine porgy	Mid	1	26	35	23	22.9	1.24	0.0002
Longspine swimming crab	Mid	0	1	20	4	7.4	1.34	0.0002
Mexican searobin	Mid	0	4	13	9	7.7	1.00	0.0020
Northern red snapper	Mid	1	4	31	8	12.3	1.23	0.0002
Ocellated flounders	Mid	0	3	8	1	3.3	0.56	0.0002
Paper scallop	Mid	0	0	18	3	4.7	0.74	0.0002
Pigfish	Mid	0	0	4	1	1.5	0.44	0.0018
Planehead filefish	Mid	0	3	18	4	7.5	1.50	0.0002
Red goatfish	Mid	0	0	7	1	2.2	0.61	0.0002
Round scad	Mid	0	0	7	2	3.2	0.84	0.0010
Roundel skate	Mid	0	0	12	1	2.6	0.53	0.0002
Sand seabass	Mid	0	0	10	0	2.2	0.53	0.0002
Smoothhead scorpionfish	Mid	0	0	20	0	3.3	0.59	0.0002
Spot croaker	Mid	1	6	10	5	7.3	1.17	0.0260
Spottedfin tonguefish	Mid	0	0	4	1	1.4	0.39	0.0010
Tomtate grunt	Mid	0	0	11	0	1.8	0.47	0.0002
Arrow squid	West	1	5	11	22	11.4	0.97	0.0002
Atlantic bigeye	West	0	0	1	7	2.5	0.57	0.0002
Atlantic threadfin	West	0	1	1	10	3.6	0.82	0.0002
Bigeye scad	West	0	0	0	6	2.3	0.59	0.0016
Brazilian lizardfish	West	2	11	10	25	15.1	1.32	0.0002
Brown shrimp	West	9	12	11	58	24.6	1.53	0.0002
Dwarf goatfish	West	0	2	11	53	15.2	1.46	0.0002
Lesser blue crab	West	26	17	7	32	23.7	2.26	0.0102
Lesser rock shrimp	West	9	10	1	28	16.0	2.88	0.0040
Lined sea star	West	0	0	1	6	2.1	0.55	0.0002
Longfin inshore squid	West	4	7	8	17	11.1	1.03	0.0004
Northern pink shrimp	West	0	1	5	17	9.5	1.99	0.0084
Offshore lizardfish	West	0	2	6	8	5.6	0.99	0.0252
Pinfish	West	1	1	13	21	10.7	1.27	0.0002
Rough scad	West	2	1	0	4	2.5	0.61	0.0434
Roughneck shrimp	West	1	6	14	24	13.7	1.40	0.0002
Round herring	West	1	3	1	7	4.5	0.90	0.0336
Round sardinella	West	0	0	1	12	4.6	1.21	0.0004
Sash flounder	West	1	1	0	4	2.5	0.69	0.0496
Scaled herring	West	2	4	2	12	6.9	1.12	0.0024
Sea pansy	West	0	0	0	24	4.1	0.85	0.0002
Shoal flounder	West	11	12	4	22	16.6	2.34	0.0346

(Table A.5 continued)

Shortwing searobin	West	0	2	5	25	8.8	1.18	0.0002
Smooth puffer	West	1	3	8	17	9.0	1.15	0.0004
Spiny flounder	West	0	1	4	7	3.9	0.66	0.0024
Two-spined star fish	West	0	0	2	23	6.4	1.27	0.0002
Wenchman	West	1	3	11	16	9.2	1.00	0.0004
Pancake batfish	<i>NS</i>	5	11	8	4	9.0	1.20	0.0508
Antenna codlet	<i>NS</i>	2	1	0	3	2.3	0.53	0.0560
Calico box crab	<i>NS</i>	3	3	1	1	2.4	0.54	0.0562
Bighead searobin	<i>NS</i>	7	3	0	0	5.4	1.29	0.0636
Slantbrow batfish	<i>NS</i>	0	0	2	3	2.0	0.46	0.0642
Blotched swimming crab	<i>NS</i>	0	4	4	13	10.9	2.16	0.0926
Yellow conger	<i>NS</i>	3	2	1	1	2.5	0.57	0.0988
Yellow box crab	<i>NS</i>	1	4	7	6	6.3	0.77	0.1006
Southern kingcroaker	<i>NS</i>	3	2	0	1	2.5	0.61	0.1060
Southern flounder	<i>NS</i>	0	4	1	2	2.9	0.79	0.1066
Guachanche barracuda	<i>NS</i>	0	4	3	2	3.2	0.59	0.1078
Atlantic moonfish	<i>NS</i>	2	4	8	6	7.3	1.00	0.1626
Least puffer	<i>NS</i>	8	14	6	7	12.4	2.06	0.1762
Gulf butterfish	<i>NS</i>	5	20	15	20	18.8	1.98	0.2014
Atlantic thread herring	<i>NS</i>	1	1	3	4	3.6	0.90	0.2835
Three-eye flounder	<i>NS</i>	0	1	2	2	2.0	0.53	0.2847
Portly spider crab	<i>NS</i>	1	2	0	1	1.6	0.45	0.2965
Southern codling	<i>NS</i>	0	2	3	3	3.1	0.61	0.3393
Humpback shrimp	<i>NS</i>	2	0	1	2	2.4	0.54	0.3679
Gulf of Mexico fringed sole	<i>NS</i>	0	2	1	2	2.5	0.54	0.3929
Lookdown	<i>NS</i>	1	0	1	1	1.4	0.41	0.3995
American harvestfish	<i>NS</i>	2	0	2	1	2.5	0.63	0.4249
Anchor tilefish	<i>NS</i>	1	1	0	2	1.8	0.49	0.4657
Blue runner	<i>NS</i>	1	1	1	0	1.7	0.49	0.5929
Stilt spider crab	<i>NS</i>	0	1	1	1	1.5	0.45	0.6161
Mexican flounder	<i>NS</i>	3	8	7	8	8.4	1.15	0.7489
Spanish mackerel	<i>NS</i>	0	1	1	1	1.7	0.48	0.8440

Table A.6. Results from the indicator species analysis for the prevalent species in the fall SEAMAP summer survey. The maximum group is the region where the species shows the highest relative abundance over the entire survey period. The p -value, is from the Monte Carlo simulations of the indicators values and significant p -value less than 0.05 indicates a statistically significant indicator value.

Species	Indicator Value					Monte Carlo		
	Maximum Group	Zone 13	East	Mid	West	Mean	s.d.	p
Atlantic brief squid	Zone 13	34	1	1	6	6.4	0.86	0.0002
Atlantic cutlassfish	Zone 13	52	6	1	1	10.1	1.19	0.0002
Atlantic midshipman	Zone 13	35	3	2	3	9.1	1.10	0.0002
Bay whiff	Zone 13	31	4	0	5	7.2	1.16	0.0002
Bearded brotula	Zone 13	9	1	0	0	1.9	0.45	0.0002
Blackcheek tonguefish	Zone 13	9	2	1	4	4.3	0.68	0.0006
Blue crab	Zone 13	12	2	0	1	5.5	1.30	0.0004
Blue-spotted searobin	Zone 13	4	1	1	0	2.4	0.63	0.0464
Broad-striped anchovy	Zone 13	10	3	1	8	6.0	1.00	0.0034
Crested cuskeel	Zone 13	4	2	1	2	3.0	0.60	0.0324
Freckled pikeconger	Zone 13	8	1	1	2	3.2	0.58	0.0002
Gulf menhaden	Zone 13	11	1	0	0	3.3	0.85	0.0002
Iridescent swimming crab	Zone 13	37	11	3	16	16.0	1.49	0.0002
Least puffer	Zone 13	20	6	4	7	9.2	0.98	0.0002
Lesser blue crab	Zone 13	42	14	7	20	21.5	1.39	0.0002
Lookdown	Zone 13	5	1	1	1	2.5	0.56	0.007
Mantis shrimp (<i>S. chydæa</i>)	Zone 13	14	1	0	8	5.7	0.86	0.0002
Mantis shrimp (<i>S. empusa</i>)	Zone 13	46	4	2	10	13.0	1.18	0.0002
Northern white shrimp	Zone 13	64	5	1	4	9.4	1.05	0.0002
Pinfish	Zone 13	23	11	9	10	15.4	1.57	0.002
Ragged goby	Zone 13	24	0	0	2	3.7	0.77	0.0002
Roughback shrimp	Zone 13	32	1	1	12	10.1	1.26	0.0002
Roughneck shrimp	Zone 13	9	0	0	2	2.9	0.69	0.0002
Sand seatrout	Zone 13	42	19	4	4	15.1	1.35	0.0002
Shortbread cusk eel	Zone 13	21	4	5	3	8.3	0.91	0.0002
Silver seatrout	Zone 13	22	15	8	13	16.5	1.50	0.0088
Southern flounder	Zone 13	8	7	1	0	3.1	0.56	0.0002
Star drum	Zone 13	3	1	0	1	1.3	0.39	0.0042
Wenchman	Zone 13	13	0	0	2	2.9	0.60	0.0002
Atlantic croaker	East	25	53	13	3	31.6	4.62	0.0002
Atlantic sharpnose shark	East	0	7	3	0	2.8	0.55	0.001
Banded drum	East	1	11	5	6	7.0	0.87	0.0042
Bigeye searobin	East	19	34	12	1	17.1	2.06	0.0002
Fringed flounder	East	12	16	2	2	7.2	0.87	0.0002

(Table A.6 continued)

Portly spider crab	East	0	3	0	0	1.6	0.53	0.0166
Rock sea bass	East	13	21	16	9	16.7	1.06	0.007
Spot croaker	East	23	30	16	3	18.2	1.62	0.0004
Bandtail searobin	Mid	0	0	7	3	2.8	0.55	0.0002
Bonnethead	Mid	0	0	6	1	2.0	0.48	0.0002
Brittle star	Mid	0	0	3	1	1.6	0.50	0.0136
Brown rock shrimp	Mid	0	0	39	2	7.7	0.95	0.0002
Cobia	Mid	0	1	2	1	1.6	0.41	0.0454
Dusky flounder	Mid	0	0	4	1	1.9	0.50	0.0152
Gray triggerfish	Mid	0	10	29	4	12.2	1.73	0.0002
Gulf butterfish	Mid	2	8	23	20	15.2	1.24	0.0008
Hardhead catfish	Mid	4	8	11	1	7.3	1.09	0.0106
Horned searobin	Mid	0	0	7	0	1.7	0.46	0.0002
Inshore lizardfish	Mid	4	17	33	24	21.1	1.01	0.0002
Lane snapper	Mid	0	3	43	5	11.8	1.13	0.0002
Longspine porgy	Mid	3	18	50	10	20.5	1.15	0.0002
Mexican searobin	Mid	0	0	11	1	3.2	0.62	0.0002
Ocellated flounders	Mid	0	8	10	1	4.9	0.69	0.0006
Pancake batfish	Mid	3	5	13	10	9.8	1.08	0.0254
Paper scallop	Mid	0	1	12	2	3.4	0.64	0.0002
Pigfish	Mid	0	0	10	5	4.0	0.81	0.0004
Planehead filefish	Mid	0	1	14	0	3.1	0.62	0.0002
Red goatfish	Mid	0	0	16	0	2.8	0.55	0.0002
Rough scad	Mid	1	3	14	11	8.9	1.12	0.0012
Round scad	Mid	0	0	6	0	1.9	0.49	0.0002
Roundel skate	Mid	0	0	16	0	2.9	0.56	0.0002
Sand seabass	Mid	0	0	24	0	3.0	0.58	0.0002
Smooth puffer	Mid	1	0	13	13	7.4	0.77	0.0004
Smoothhead scorpionfish	Mid	2	0	22	3	6.3	0.84	0.0002
Spottedfin tonguefish	Mid	0	0	4	2	2.0	0.47	0.0082
Tomtate grunt	Mid	0	0	12	1	2.9	0.73	0.0002
Vermilion snapper	Mid	0	0	7	1	1.7	0.45	0.0002
American harvestfish	West	3	1	2	14	5.9	1.11	0.0002
Arrow squid	West	3	3	2	22	8.3	1.00	0.0002
Atlantic bumper	West	1	2	8	62	17.7	2.06	0.0002
Atlantic moonfish	West	4	2	4	9	6.4	0.87	0.029
Atlantic thread herring	West	3	3	3	10	6.8	1.07	0.0154
Atlantic threadfin	West	0	0	0	10	2.5	0.63	0.0002
Blackear bass	West	13	2	1	14	8.1	1.06	0.0014
Blotched swimming crab	West	1	2	3	14	6.4	0.96	0.0002
Blue runner	West	2	2	6	7	5.7	0.81	0.047
Brazilian lizardfish	West	1	1	2	34	8.3	0.98	0.0002
Brown shrimp	West	25	22	16	27	23.9	1.00	0.007
Calico box crab	West	0	1	1	3	1.6	0.42	0.0144

(Table A.6 continued)

Dwarf goatfish	West	0	1	18	20	9.5	1.05	0.0002
Dwarf sand perch	West	6	3	8	47	16.4	1.20	0.0002
Echinoderm	West	0	1	0	3	1.7	0.53	0.0204
Gulf of Mexico fringed sole	West	1	0	1	14	3.8	0.63	0.0002
Humpback shrimp	West	1	0	1	3	1.8	0.50	0.038
King mackerel	West	0	0	2	5	2.7	0.57	0.0038
Lesser rock shrimp	West	4	1	1	29	7.4	1.01	0.0002
Lined sea star	West	0	0	1	8	2.9	0.74	0.0008
Mexican flounder	West	8	6	7	15	12.1	1.22	0.0248
Northern pink shrimp	West	1	2	2	21	6.9	1.05	0.0002
Northern red snapper	West	18	5	16	33	21.5	1.31	0.0002
Offshore lizardfish	West	0	0	1	15	3.6	0.66	0.0002
Round sardinella	West	0	0	0	12	2.2	0.57	0.0002
Scaled herring	West	2	5	1	25	9.0	1.26	0.0002
Sea pansy	West	0	0	0	21	3.8	0.95	0.0002
Shoal flounder	West	11	10	6	33	17.7	1.46	0.0002
Slantbrow batfish	West	0	0	2	11	2.8	0.54	0.0002
Southern kingcroaker	West	0	1	0	11	3.6	0.72	0.0002
Spiny flounder	West	0	0	1	9	2.2	0.50	0.0002
Two-spined star fish	West	0	0	1	31	6.9	1.34	0.0002
Atlantic spadefish	<i>NS</i>	10	14	14	2	11.5	1.66	0.0586
Bay anchovy	<i>NS</i>	2	1	0	0	1.5	0.50	0.1988
Bigeye scad	<i>NS</i>	0	0	3	2	2.5	0.68	0.1308
Bighead searobin	<i>NS</i>	2	3	1	0	2.7	0.71	0.1992
Blackwing searobin	<i>NS</i>	3	3	5	2	5.3	0.86	0.6231
Gafftopsail catfish	<i>NS</i>	2	1	0	1	1.5	0.46	0.3275
Guachanche barracuda	<i>NS</i>	2	1	3	3	3.3	0.60	0.7481
Jenny mojarra	<i>NS</i>	10	8	3	10	10.6	1.37	0.5591
Longfin inshore squid	<i>NS</i>	5	5	4	7	7.4	0.99	0.4275
Longspine swimming crab	<i>NS</i>	5	0	5	1	3.8	0.86	0.1076
Sash flounder	<i>NS</i>	2	1	0	2	2.0	0.52	0.225
Shortwing searobin	<i>NS</i>	0	0	2	2	1.6	0.51	0.0822
Spanish mackerel	<i>NS</i>	1	1	2	4	2.9	0.61	0.0972
Yellow box crab	<i>NS</i>	3	3	6	6	6.0	0.74	0.3751

Table A.7. Species identified as being in the ten most abundance species based upon average biomass by DFC and survey.

DFC	Fall Survey Only	Summer Survey Only	Both Surveys
Zone 13	Northern white shrimp Pinfish Silver seatrout Spot croaker	Atlantic brief squid Fringed flounder Iridescent swimming crab Rock sea bass	Atlantic croaker Atlantic cutlassfish Bigeye searobin Brown shrimp Lesser blue crab Sand seatrout
East	Hardhead catfish Silver seatrout	Atlantic bumper Lesser blue crab	Atlantic croaker Bigeye searobin Brown shrimp Gulf butterfish Inshore lizardfish Longspine porgy Sand seatrout Spot croaker
Mid	Hardhead catfish Sand seatrout	Dwarf sand perch Rock sea bass	Atlantic croaker Atlantic bumper Brown shrimp Gulf butterfish Inshore lizardfish Longspine porgy Silver seatrout Spot croaker
West	Atlantic bumper Silver seatrout Spot croaker	Arrow squid Longfin inshore squid Rough scad	Atlantic croaker Brown shrimp Gulf butterfish Inshore lizardfish Lesser blue crab Longspine porgy Shoal flounder Sand seatrout

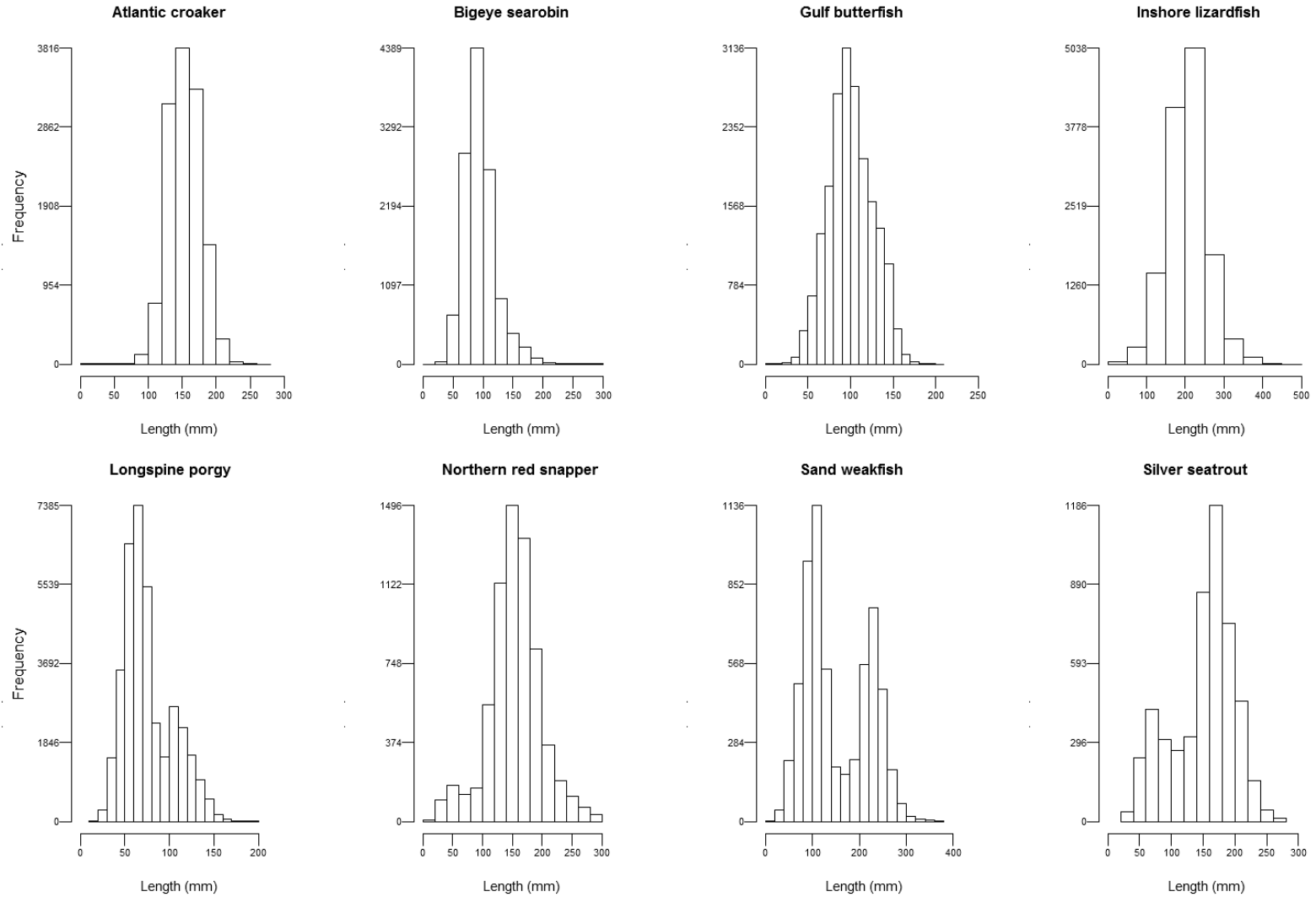


Figure A.1. Length distribution for select species from the Summer SEAMAP bottomfish trawl survey. The Atlantic croaker, bigeye searobin, sand weakfish, and silver seatrout were measured using total length, and the other four species using fork length.

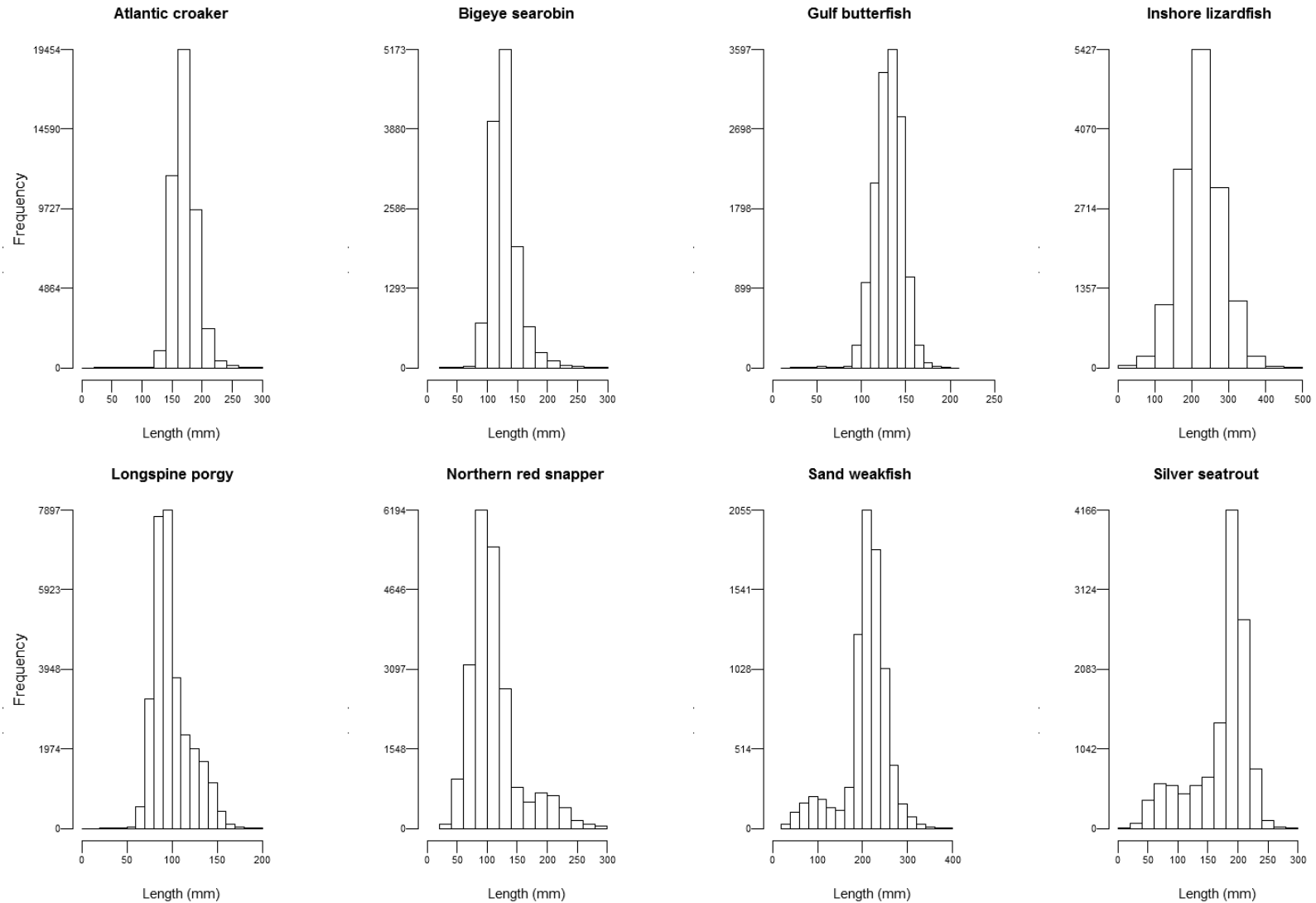


Figure A.2. Length distribution for select species from the Fall SEAMAP bottomfish trawl survey. The Atlantic croaker, northern red snapper, sand weakfish, and silver seatrout were measured using total length, and the other four species using fork length.

APPENDIX B: CHAPTER 2 SUPPLEMENTARY MATERIAL

Table B.1. Point estimates and the 80% confidence interval from the 1,000 bootstrap trials in ASPIC. The * indicates if a parameter was fixed at the true value for the ASPIC runs.

Parameter name	Point Estimate	Estimated relative bias	80% lower	80% upper
Species A				
F_{MSY}	0.093	2.33%	0.078	0.122
B_{MSY}	40.430	0.86%	30.380	48.460
MSY	3.767	0.36%	3.583	3.951
K	80.850	0.86%	60.750	96.920
q	0.006	2.16%	0.005	0.008
Species B				
F_{MSY}	0.108	2.48%	0.086	0.134
B_{MSY}	34.220	0.97%	27.430	43.490
MSY	3.686	0.32%	3.500	3.877
K	68.440	0.97%	54.870	86.990
q	0.004	2.39%	0.003	0.005
Species C				
F_{MSY}	0.379	0.46%	0.361	0.402
B_{MSY}	26.270	0.13%	24.120	28.440
MSY	9.957	0.37%	9.442	10.420
K	52.530	0.13%	48.230	56.870
q^*	0.005	0.00%	0.005	0.005
Species D				
F_{MSY}	0.122	1.80%	0.103	0.147
B_{MSY}	305.500	0.31%	252.900	364.800
MSY	37.200	0.19%	35.830	38.560
K	611.000	0.31%	505.700	729.700
q	0.005	1.74%	0.005	0.007
Species E				
F_{MSY}	0.205	0.09%	0.200	0.211
B_{MSY}	164.000	0.03%	156.100	173.000
MSY	33.670	0.06%	32.650	35.020
K	327.900	0.03%	312.200	346.000
q^*	0.005	0.00%	0.005	0.005

APPENDIX C: CHAPTER 3 SUPPLEMENTARY MATERIAL

Table C.1. Point estimates and the 80% confidence interval from the 1,000 bootstrap trials in ASPIC. The * indicates if a parameter was fixed at the true value for the ASPIC runs.

Parameter name	Point Estimate	Estimated relative bias	80% lower	80% upper
Species A				
F_{MSY}	0.027	0.86%	0.024	0.029
B_{MSY}	83.190	0.34%	74.820	94.170
MSY	2.222	0.74%	1.997	2.427
K	166.400	0.34%	149.600	188.300
q	0.003	0.82%	0.003	0.004
Species B				
F_{MSY}	0.135	14.41%	0.104	0.209
B_{MSY}	17.710	0.58%	15.940	20.040
MSY	2.386	10.95%	2.054	3.402
K	35.430	0.58%	31.880	40.080
q^*	0.005	0.00%	0.005	0.005
Species C				
F_{MSY}	0.123	12.78%	0.088	0.179
B_{MSY}	33.080	-3.17%	22.550	46.340
MSY	4.051	0.68%	3.769	4.324
K	66.170	-3.17%	45.100	92.670
q	0.004	12.52%	0.003	0.005
Species D				
F_{MSY}	0.134	3.44%	0.107	0.174
B_{MSY}	256.700	0.53%	197.100	323.700
MSY	34.340	0.24%	33.240	35.470
K	513.400	0.53%	394.300	647.400
q	0.006	3.33%	0.005	0.008
Species E				
F_{MSY}	0.217	0.21%	0.174	0.268
B_{MSY}	107.900	2.54%	87.500	134.900
MSY	23.390	0.11%	22.610	23.980
K	215.800	2.54%	175.000	269.800
q	0.007	0.20%	0.006	0.009

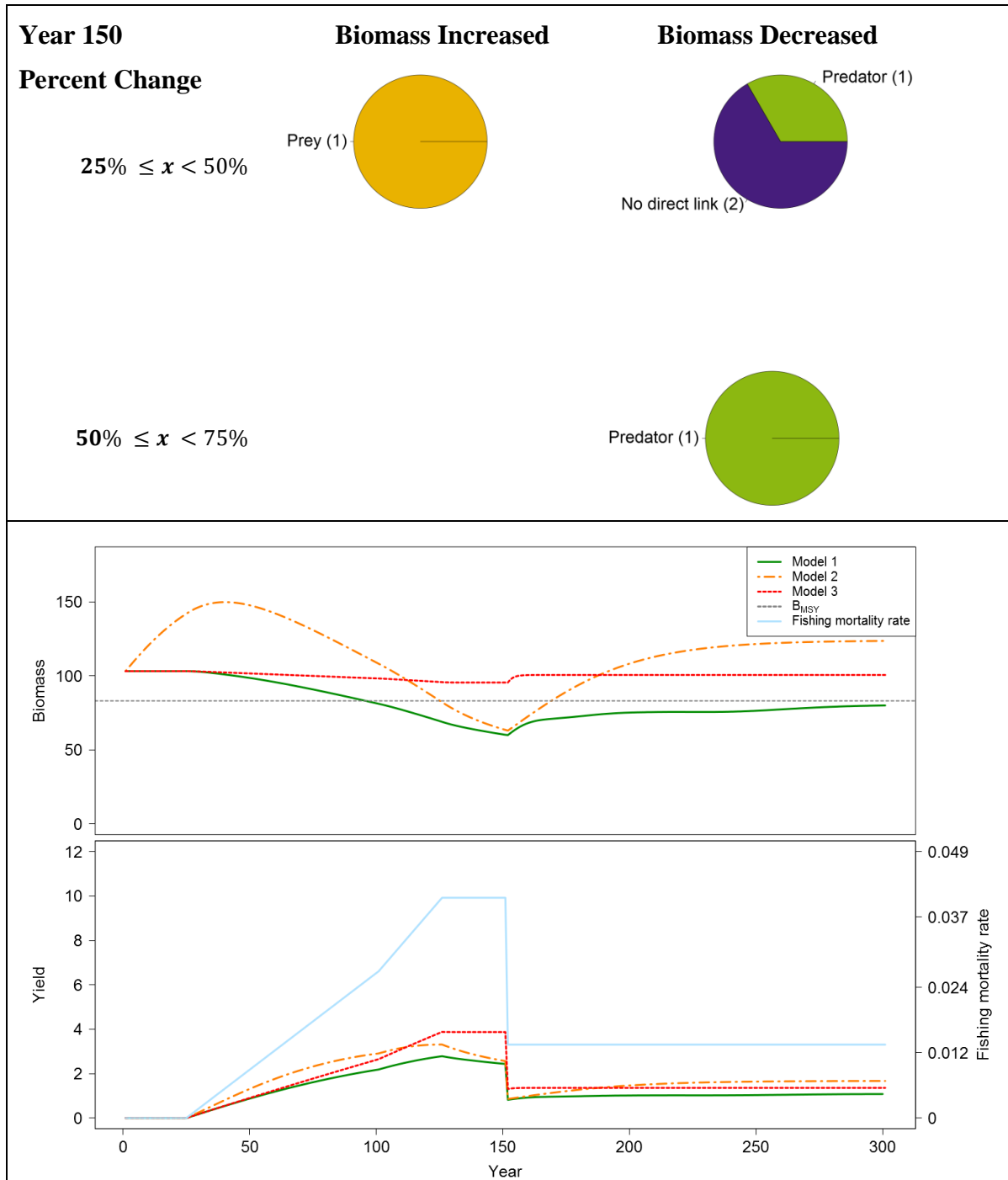


Figure C.1. Model results for Species A_{35} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A_{35} , the prey of Species A_{35} , and species with no direct link to Species A. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

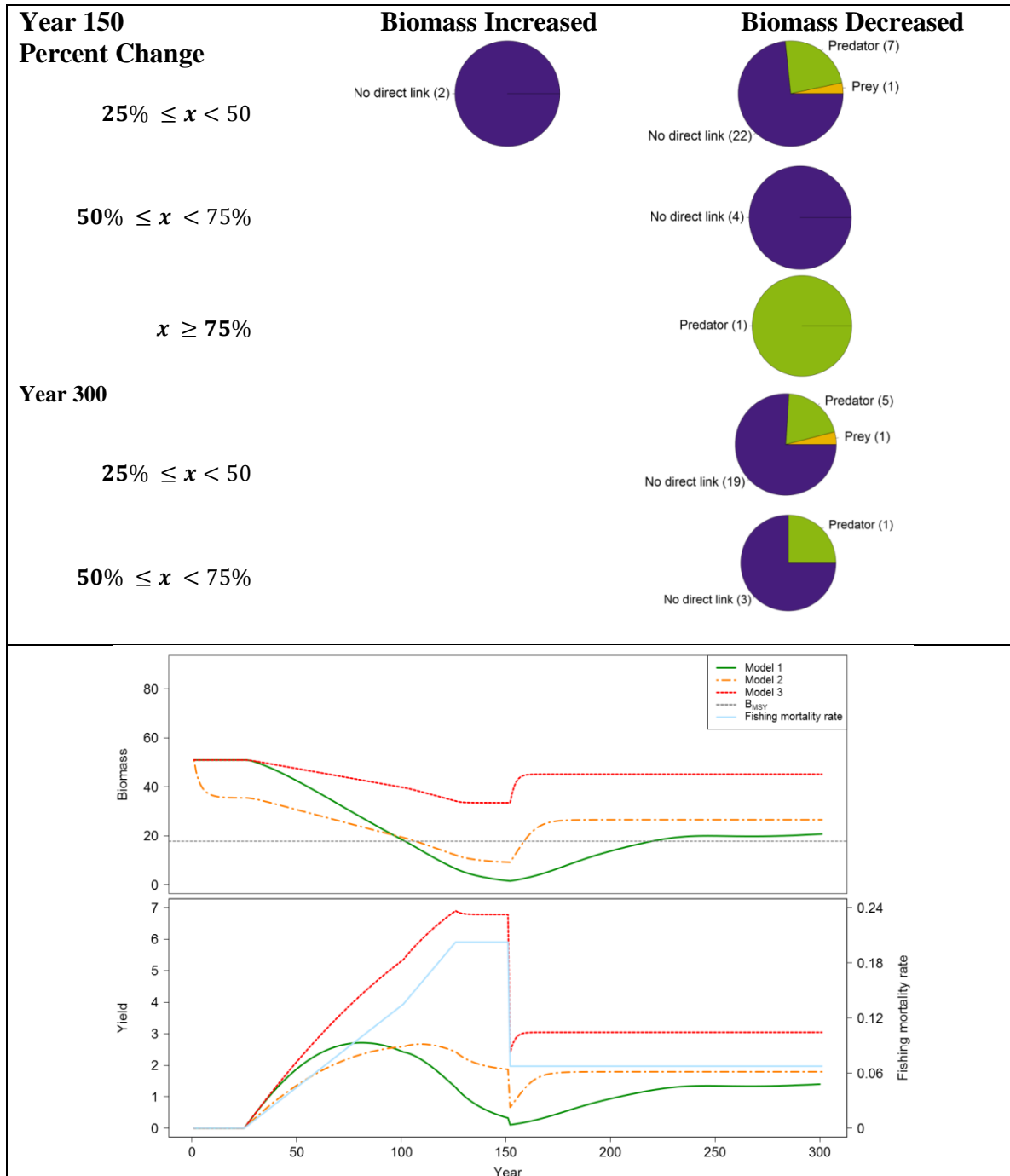


Figure C.2. Model results for Species B₃₅ when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species B₃₅, the prey of Species B₃₅, and species with no direct link to Species B₃₅. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

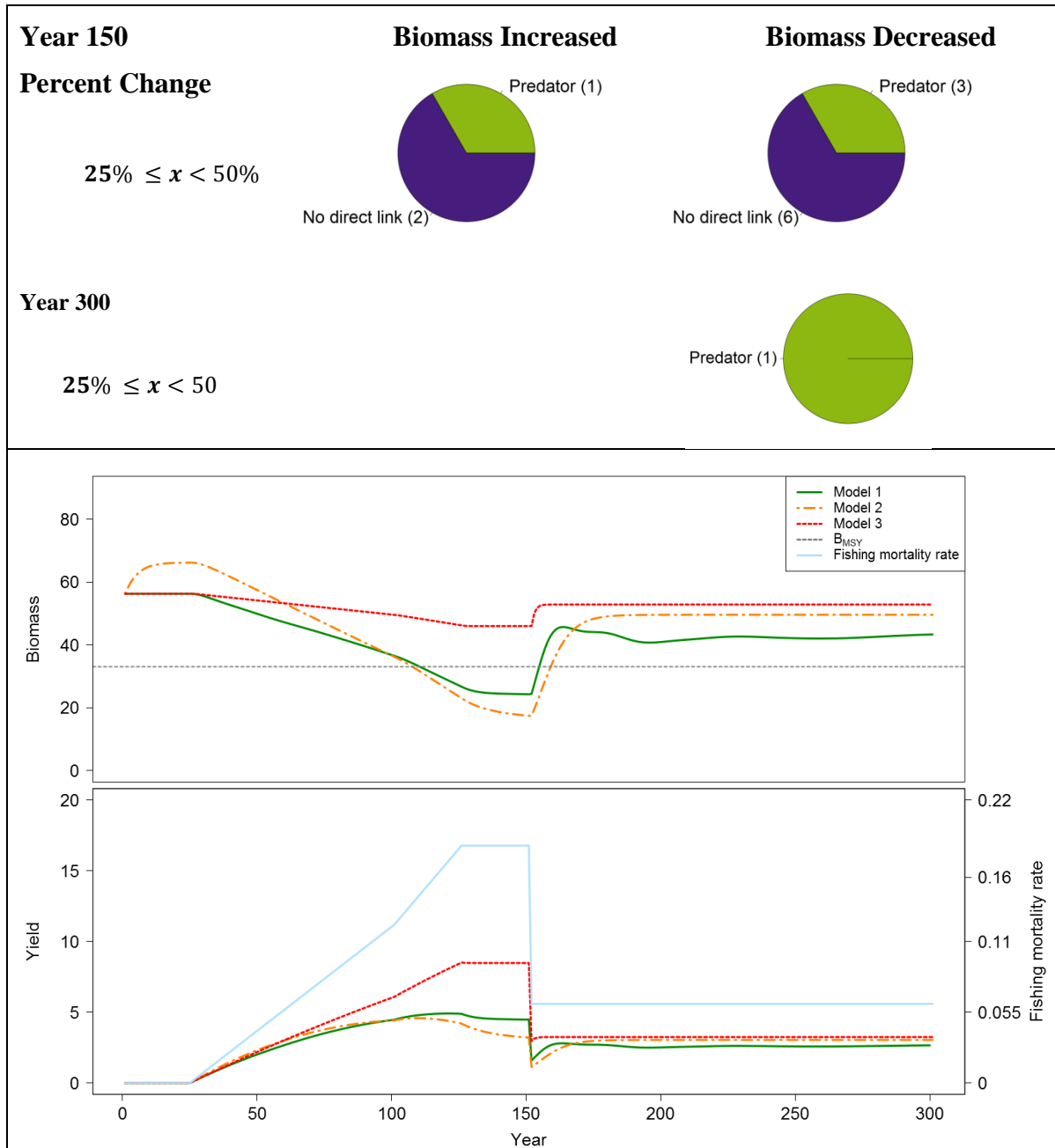


Figure C.3. Model results for Species C_{35} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C_{35} , the prey of Species C_{35} , and species with no direct link to Species C_{35} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

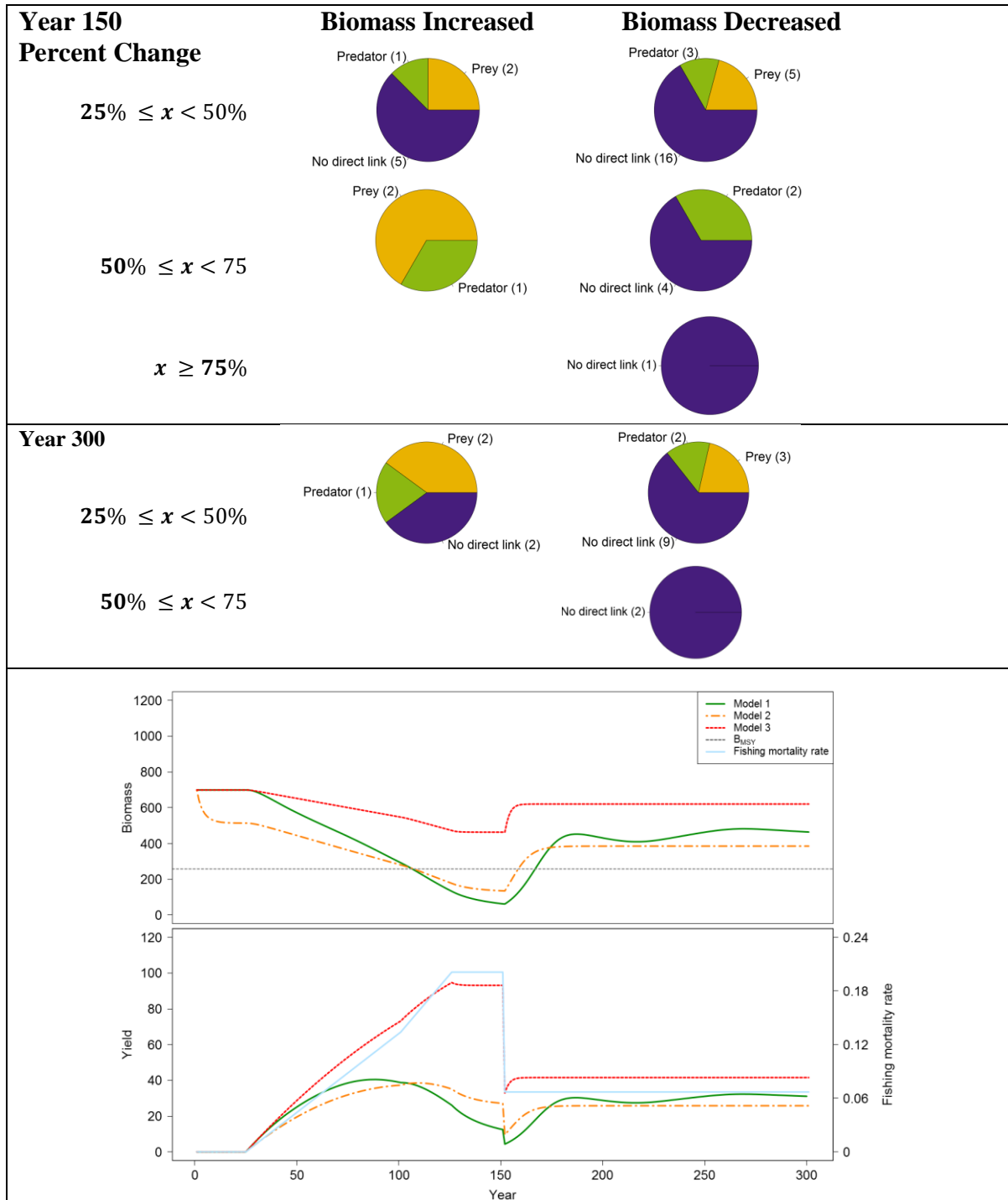


Figure C.4. Model results for Species D₃₅ when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D₃₅, the prey of Species D₃₅, and species with no direct link to Species D. The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

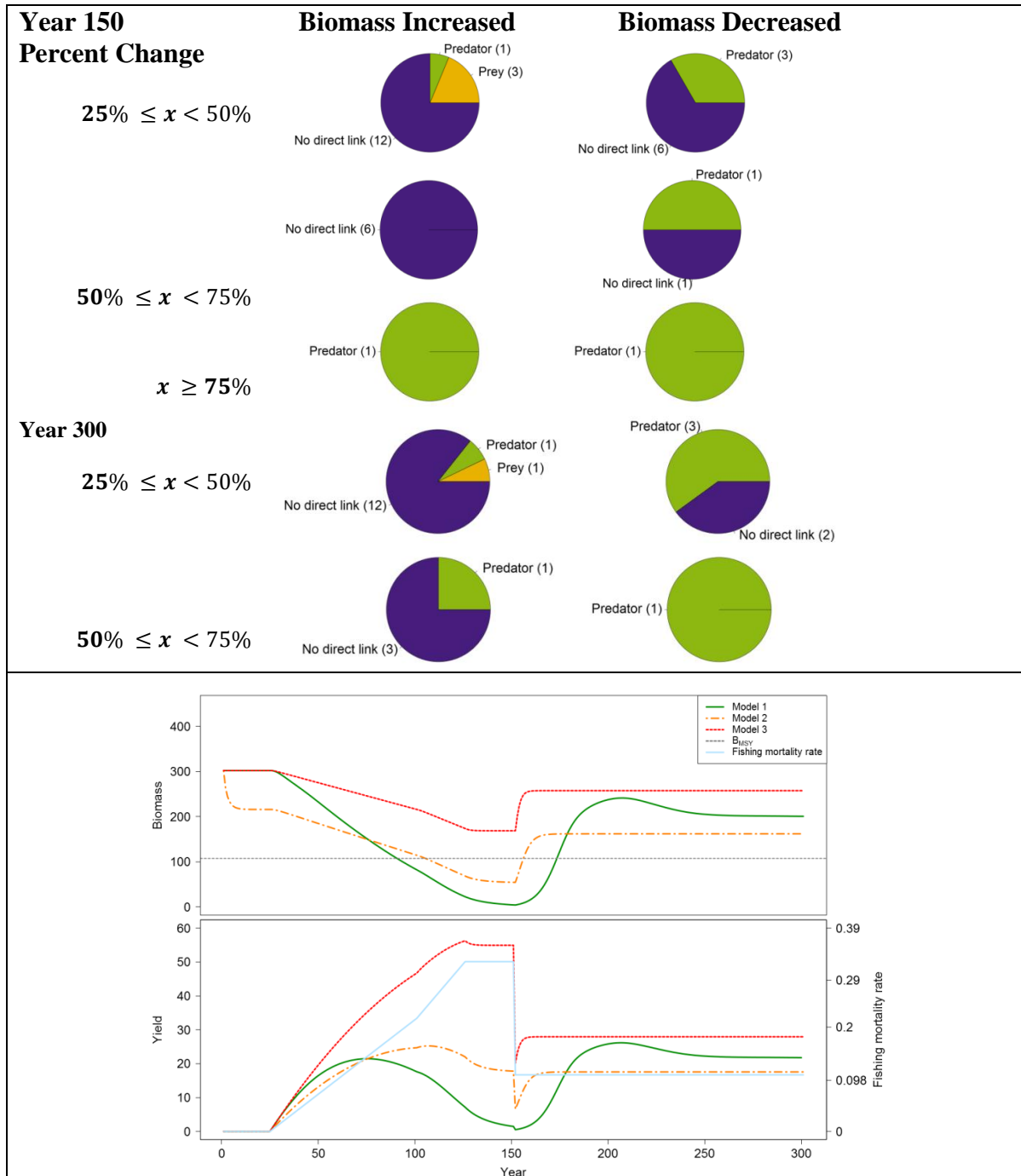


Figure C.5. Model results for Species E_{35} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E_{35} , the prey of Species E_{35} , and species with no direct link to Species E with the number of species in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

Table C.2. Point estimates and the 80% confidence interval from the 1,000 bootstrap trials in ASPIC. The * indicates if a parameter was fixed at the true value for the ASPIC runs.

Parameter name	Point Estimate	Estimated relative bias	80% lower	80% upper
Species A				
F_{MSY}	0.096	0.79%	0.081	0.118
B_{MSY}	52.080	1.82%	41.890	61.920
MSY	4.991	0.41%	4.805	5.158
K	104.200	1.82%	83.770	123.800
q	0.005	0.80%	0.004	0.006
Species B				
F_{MSY}	0.077	4.24%	0.061	0.097
B_{MSY}	38.290	-0.03%	30.520	49.210
MSY	2.941	0.49%	2.809	3.064
K	76.580	-0.03%	61.050	98.410
q	0.003	4.39%	0.002	0.004
Species C				
F_{MSY}	0.143	0.90%	0.131	0.158
B_{MSY}	21.490	0.76%	19.230	25.050
MSY	3.067	0.87%	2.917	3.242
K	42.970	0.76%	38.460	50.100
q^*	0.005	0.00%	0.005	0.005
Species D				
F_{MSY}	0.100	1.43%	0.084	0.121
B_{MSY}	343.000	0.69%	285.900	416.200
MSY	34.240	0.09%	32.980	35.470
K	686.000	0.69%	571.700	832.400
q^*	0.005	1.37%	0.004	0.006
Species E				
F_{MSY}	0.141	1.02%	0.130	0.160
B_{MSY}	147.300	1.03%	127.200	164.800
MSY	20.760	1.26%	19.200	21.850
K	294.500	1.03%	254.400	329.600
q^*	0.005	0.00%	0.005	0.005

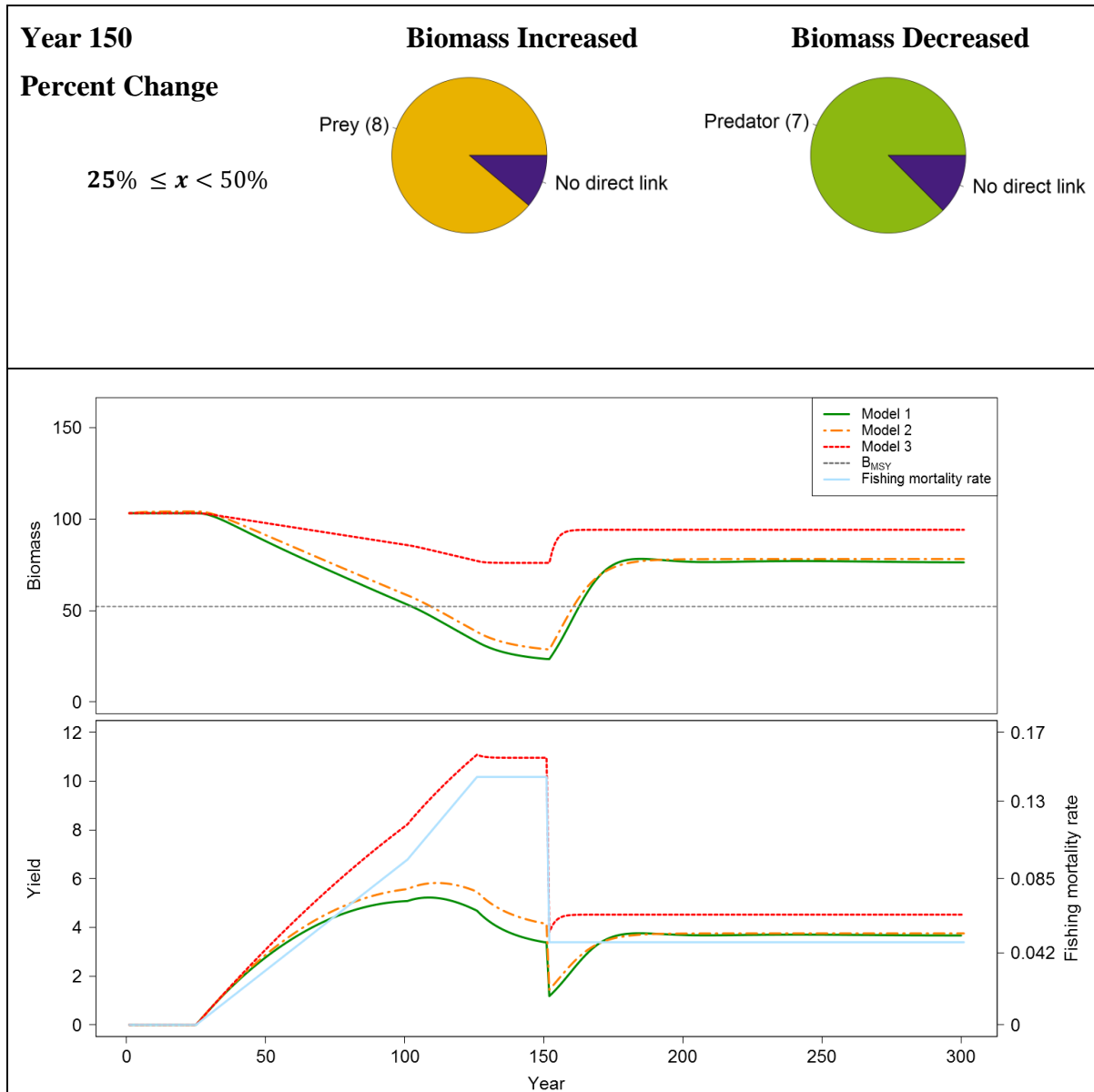


Figure C.6. Model results for Species A_{45} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species A_{45} , the prey of Species A_{45} , and species with no direct link to Species A_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

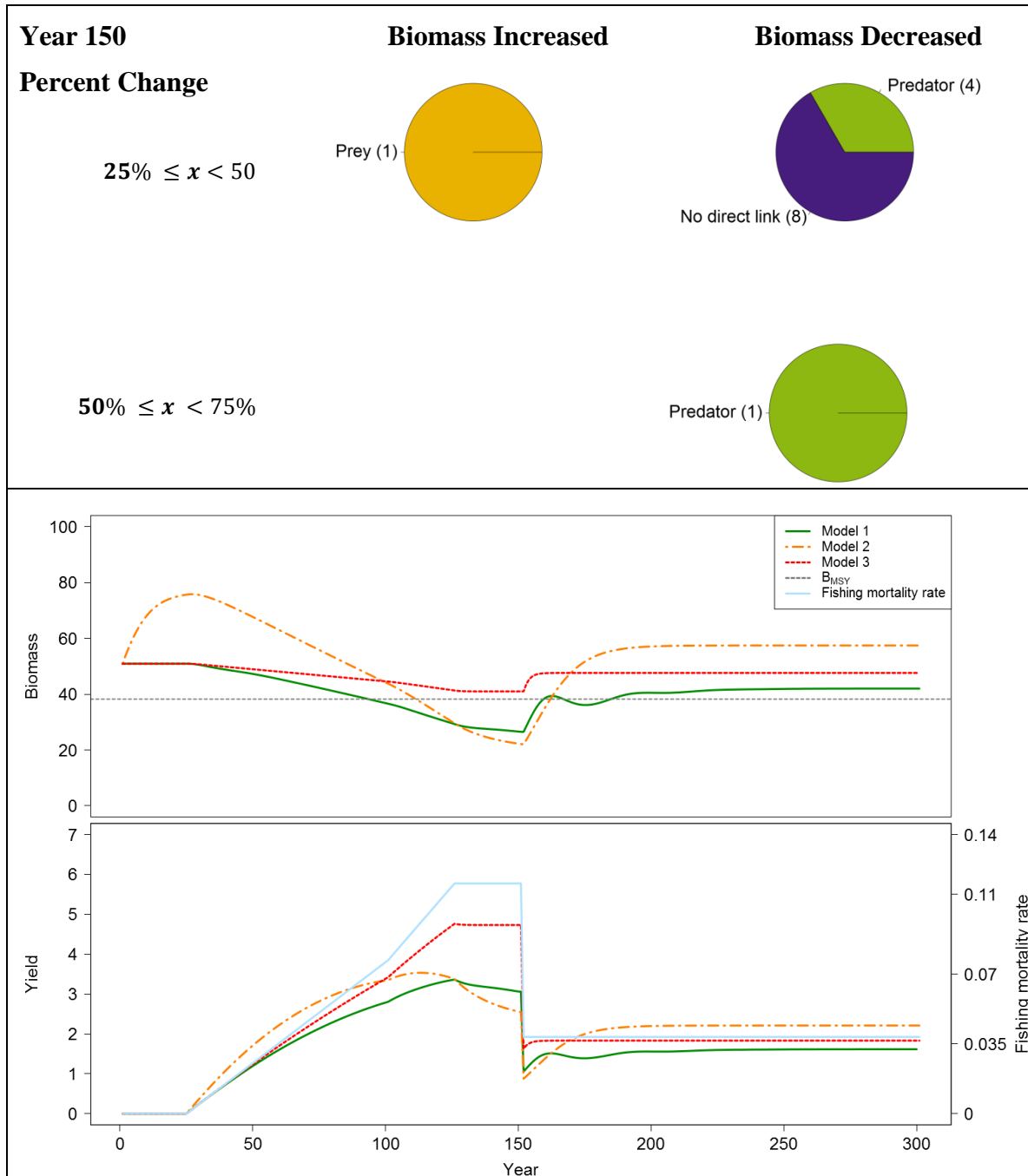


Figure C.7. Model results for Species B_{45} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species B_{45} , the prey of Species B_{45} , and species with no direct link to Species B_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

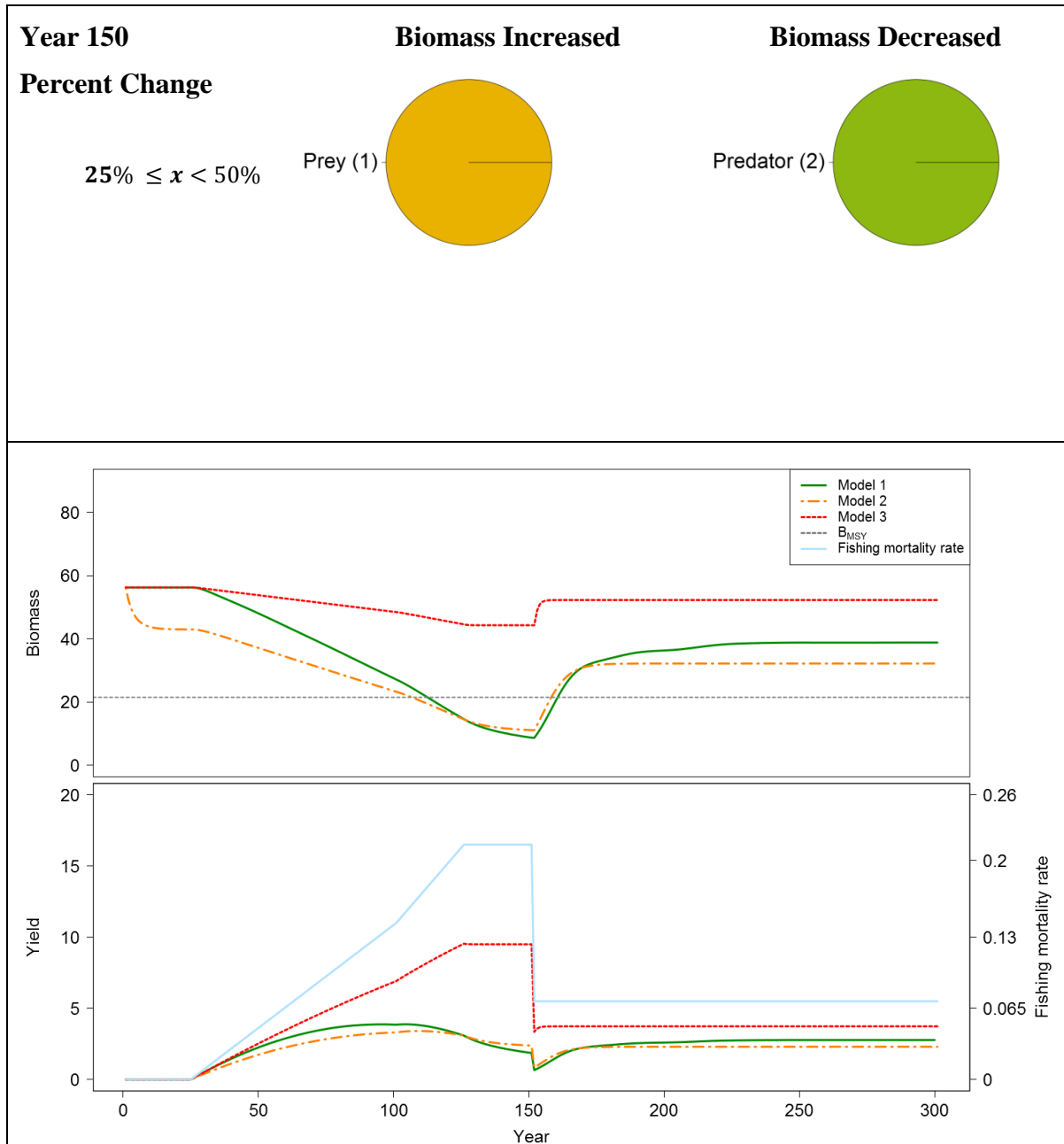


Figure C.8. Model results for Species C_{45} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species C_{45} , the prey of Species C_{45} , and species with no direct link to Species C . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

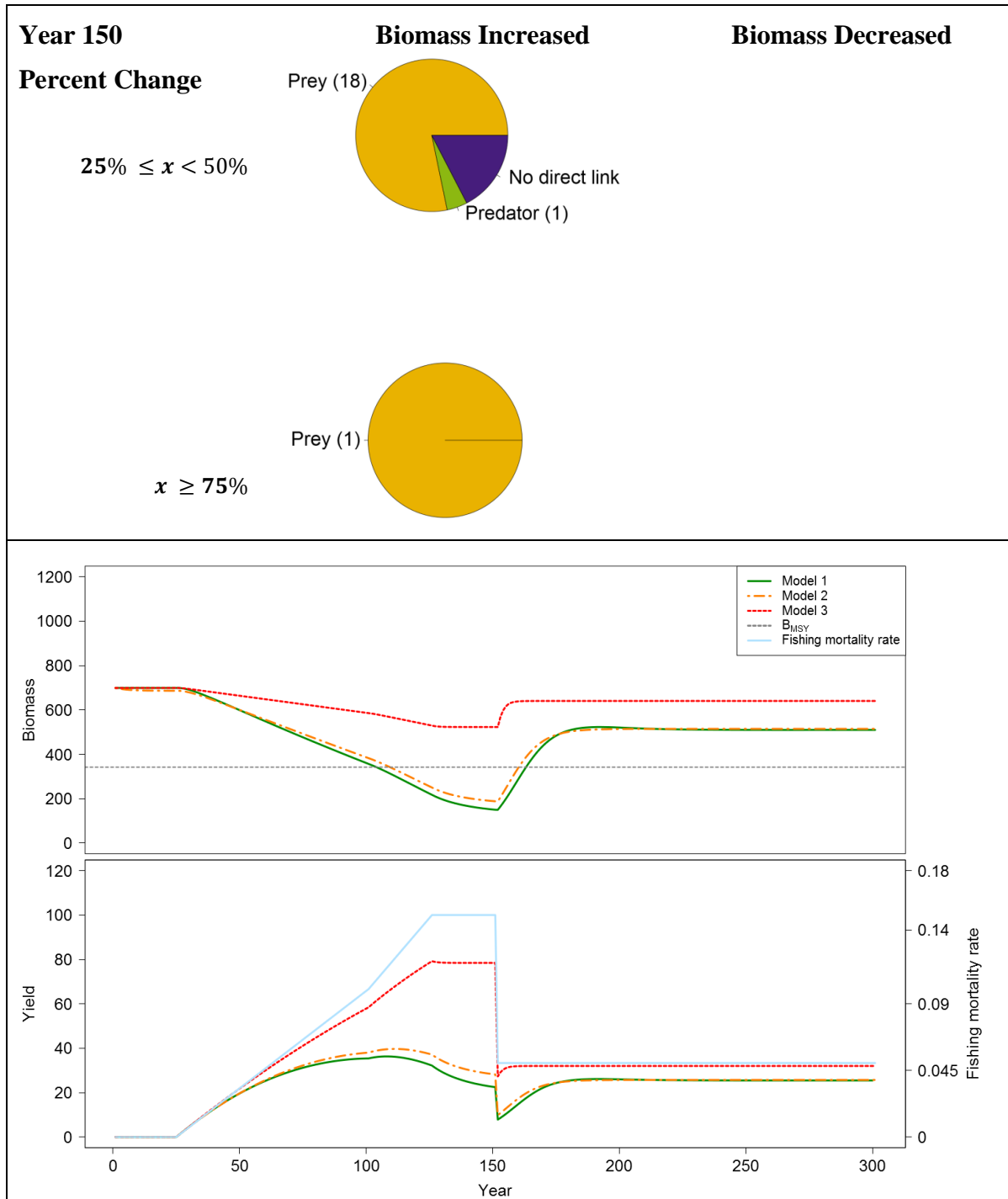


Figure C.9. Model results for Species D_{45} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species D_{45} , the prey of Species D_{45} , and species with no direct link to Species D_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

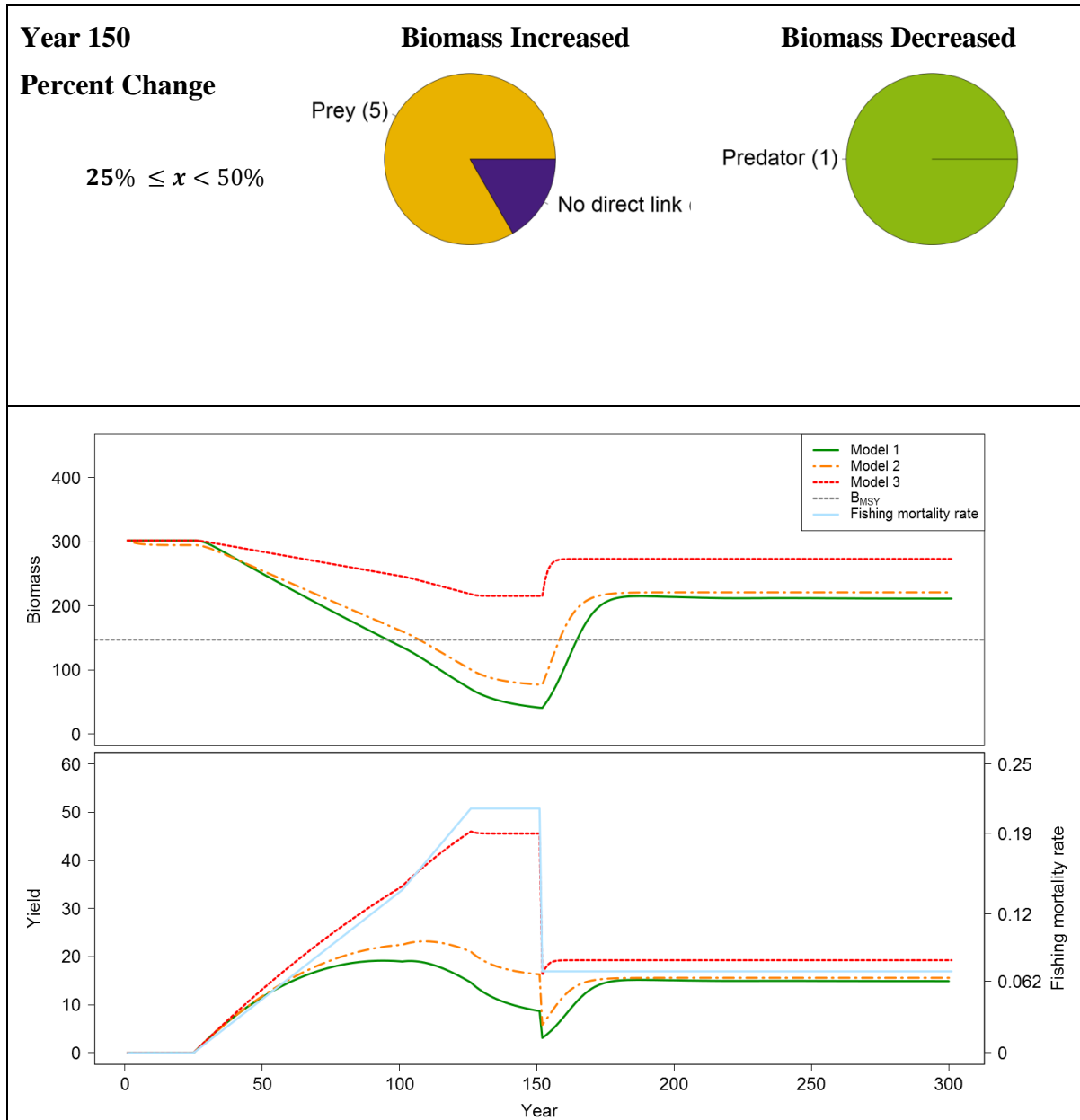


Figure C.10. Model results for Species E_{45} when overfished and rebuilt. Top panel: Pie charts of the percent change in absolute biomass of unfished species from Model 1. The pie chart wedges are the predators of Species E_{45} , the prey of Species E_{45} , and species with no direct link to Species E_{45} . The numbers of species that fall in each category are in parentheses. Bottom panel: The time series of biomass and yield are represented for all three models using the same fishing regime. Model 1 is the LV model; Model 2 is a surplus production model using the ASPIC estimates of r and K ; Model 3 is a surplus production model using r_{LV} and B_0 as a representation of K .

APPENDIX D: CHAPTER 4 SUPPLEMENTARY MATERIAL

Table D.1. Point estimates and the 80% confidence interval from the 1,000 bootstrap trials in ASPIC. The * indicates if a parameter was fixed at the true value for the ASPIC runs.

Parameter name	Point Estimate	Estimated relative bias	80% lower	80% upper
Species 8				
F_{MSY}	9.28E-02	1.58%	7.67E-02	1.11E-01
B_{MSY}	9.69E+01	0.83%	8.13E+01	1.18E+02
MSY	8.99E+00	0.31%	8.60E+00	9.33E+00
K	1.94E+02	0.83%	1.63E+02	2.36E+02
q	4.77E-03	1.62%	3.98E-03	5.65E-03
Species 22				
F_{MSY}	1.14E-01	0.23%	1.10E-01	1.19E-01
B_{MSY}	1.24E+01	0.15%	1.16E+01	1.33E+01
MSY	1.42E+00	0.25%	1.36E+00	1.48E+00
K	2.48E+01	0.15%	2.32E+01	2.66E+01
q	5.00E-03	0.00%	5.00E-03	5.00E-03
Species 39				
F_{MSY}	6.50E-02	0.61%	5.80E-02	7.26E-02
B_{MSY}	1.91E+02	0.61%	1.68E+02	2.17E+02
MSY	1.24E+01	0.41%	1.18E+01	1.30E+01
K	3.81E+02	0.61%	3.37E+02	4.35E+02
q	5.43E-03	0.68%	4.89E-03	6.04E-03
Species 71				
F_{MSY}	1.06E-01	0.31%	1.02E-01	1.10E-01
B_{MSY}	3.62E+01	-0.07%	3.39E+01	3.87E+01
MSY	3.83E+00	0.11%	3.66E+00	3.97E+00
K	7.24E+01	-0.07%	6.77E+01	7.74E+01
q	5.00E-03	0.00%	5.00E-03	5.00E-03
Species 83				
F_{MSY}	1.12E-01	0.16%	1.09E-01	1.16E-01
B_{MSY}	3.26E+01	0.02%	3.07E+01	3.46E+01
MSY	3.64E+00	0.09%	3.50E+00	3.78E+00
K	6.51E+01	0.02%	6.15E+01	6.92E+01
q	5.00E-03	0.00%	5.00E-03	5.00E-03

APPENDIX E: COMPUTER CODE FOR THE LOTKA-VOLTERRA SIMULATIONS

```
#-----#
# Program to take VB LV Simdat data file, import to a workable matrix for #
# input into the R LV code, then a plotting program                      #
# number can be a single number, a list or consecutive files             #
# Melissa Hedges Monk 6.11                                              #
#-----#

graphics.off()
rm(list=ls(all=TRUE))

library(deSolve)

#-----#
# Change everything in this section                                     #
#-----#

nrowp = 1    # number of rows for plots
ncolp = 1    # number of columns for plots

pred.num = 6  #,9,16)
prey.num = 9  #,14,19)
pred.prey = cbind(pred.num,prey.num)
lv.num = '2.fishing.79' # folder name;
ex. 1,2,3 or '2.fishing.##'
run.num = c(3.3) #c(2.1,2.2,2.3,2.4)#,3.2,3.3,3.4,3.5)

#####
for (pp in 1:length(pred.num)) {
  for (w in 1:length(lv.num)) { # LV matrix 1 or 2

folder =
paste('C:/LV/RESULTS/pred',as.character(pred.prey[pp,1]),'.prey',as.character
(pred.prey[pp,2]),'.m4/',as.character(lv.num[w]),sep='')

#-----#
## all of the statistics for connectivity
connect.stats = matrix(0,nrow=18,ncol=30)

rownames(connect.stats) =
c('maxtime','nspec','StartT','pbar','sigmap','preyg',
'preyinc','predg','predinc','method','S','L',
'L.noaii','L.5noaii','Connect','L.S','Cdir','C.S')

## counter for connectivity statistics file
connect.cnt = 1
graphics.off()

for(i in 1:5){

## windows for biomass over time dev(2,3,4,5,6)
windows(width=70,height=50); par(mfrow=c(nrowp,ncolp),
mai=c(.65,.5,.5,.5), oma=c(1,1,1,1))
} # end i
```

```

#-----#
# number is the list of files 1, 1.1, etc                                     #
# Set the working directory location of the new R output,                   #
# od is the directory in which to save the plots from LV Plotting and      #
# source is the location of the R code of LVPlotting code                  #
#-----#

for (number in 1:length(run.num)) {

  setwd ( paste(folder,"/input",sep='') )
  od = paste(folder,"/output/",sep='')
  source(file = "C:/LV/LV in R/LV_R_MHM_6.11.r")

  setwd (paste(folder,"/output",sep=''))
  od = paste(folder,"/plots/",sep='')
  source(file = "c:/LV/LV in R/LV_Plots.r", keep.source=F )

# plot number of pred/prey per species
  connect.stats[,connect.cnt] = input[1:18,1]

  dev.set(2)
  plot.Btime.one1(BioT)
  connect.cnt = connect.cnt+1

  dev.set(3)
  plot.BBmean(BioT)

  dev.set(4)
  plot.BioF(BioT,FishT)

  dev.set(5)
  plot.Btime.one2(BioT,FishT)

  dev.set(6)
  plot.Catch(BioT,FishT)

  } # end number

# add titles
dev.set(2)
title('Biomass through Time (mean biomass in black)',outer=TRUE)
mtext('Year',outer=T, side=1,cex=1.4)
mtext('Biomass', outer=1.4, side=2,cex=1.4)

dev.set(3)
title('Biomass / Mean Biomass',outer=TRUE)
mtext('B/Bmean',outer=T, side=1,cex=1.4)
mtext('Density', outer=1.4, side=2,cex=1.4)

dev.set(4)
title('Biomass of Fished Species through Time',outer=TRUE)
mtext('Year',outer=T, side=1,cex=1.4)
mtext('Biomass', outer=1.4, side=2,cex=1.4)

```

```

dev.set(5)
title('Biomass through Time (fished species in bold)',outer=TRUE)
mtext('Year',outer=T, side=1,cex=1.4)
mtext('Biomass', outer=1.4, side=2,cex=1.4)

dev.set(6)
title('Biomass of Catch',outer=TRUE)
mtext('Year',outer=T, side=1,cex=1.4)
mtext('Biomass', outer=1.4, side=2,cex=1.4)

write.csv(connect.stats,paste(od, 'connect.stats',as.character(run.num[number]
),'.csv',sep=''))

savePlot(paste(od, 'BioT_',as.character(run.num[number]),'.png',sep=''),type='
png',dev.set(2))

savePlot(paste(od, 'B.Bmean',as.character(run.num[number]),'.png',sep=''),type
='png',dev.set(3))

savePlot(paste(od, 'BioF',as.character(run.num[number]),'.png',sep=''),type='p
ng',dev.set(4))

savePlot(paste(od, 'BioF.boldF',as.character(run.num[number]),'.png',sep=''),t
ype='png',dev.set(5))

savePlot(paste(od, 'Catch',as.character(run.num[number]),'.png',sep=''),type='
png',dev.set(6))

    } # end w, lv matrix to use
    } # end pred.prey

#-----#
# Lotka-Volterra Multispecies model #
# MHM 6.14.11 #
# **CHANGE** TimeStart, TimeEnd, steps if you want them any different #
#-----#

# read data and turn into matrix
input = as.matrix(read.csv(paste('LVDatIn_',as.character(run.num[number]),
'.csv',sep=''),row.names=1))

Alpha.stats =
as.matrix(read.csv(paste('Alpha.stats_',as.character(run.num[number]),
'.csv',sep=''),row.names=1))

nspec = input[2,1]
ntime = input[1,1]

```



```

## species names
spec.names = matrix(nrow=nspec,ncol=1)
  for (nam in 1:nspec){
    spec.names[nam,1] = c(paste('Spec',as.character(nam),sep=''))
  }
spec.names1 = as.character(spec.names)

#-----#
#       Define the model function and update r       #
#-----#

model <- function(t,x,parms){
  with(as.list(x),{
# use floor()+1 to find the correct columns corresponding to the
# annual year time step

    espec = which( x == 0)
    for(k in 1:length(espec)){
      a[, espec[k]] = 0
      a[espec[k],] = 0
    } # end espec

# update r with environmental variability and fishing mortality
R.new1 <- r.new + env.update[,floor(t)+1] - fmort[,floor(t)+1]

# derivative of the LV ODE
dx <- ( r.new1 + (a %*% x)) * x
# list dx for output
list(c(dx))
}) # close and end with
} # end model

## eventfun checks to see if the biomass is below the tolerance level
eventfun <- function(t, y, parms){
  with(as.list(y),{
    # check if species extinct
    espec = which(y < tol)
    y[espec] = 0
    return(c(y))
  }) # end and close with
} # end function

#-----#
#       Model parameters   read from LV Simdat R program       #
#-----#

# start and end times of simulation and number of steps
TimeStart = as.numeric(input[3,1])
TimeEnd   = ntime-1
steps = TimeEnd*12      # do 20 iterations per year

## define the sime series for the ODE
times <- seq(TimeStart,TimeEnd,length = steps)

```

```

## to find correct columns for input
cols = nspec + 3*ntime + 3
    cntr = 1                # input nspec, ntime,
    cntr1 = cntr + 1        # r
    cntr2 = cntr1 + 1       # initial Biomass
    cntr3 = cntr2 + 1       # F start
    cntr4 = cntr3 + ntime - 1 # F end
    cntr5 = cntr4 + 1       # Env start
    cntr6 = cntr5 + ntime - 1 # Env end
    cntr7 = cntr6 + 1       # alpha start
    cntr8 = cntr7 + nspec - 1 # alpha end
    cntr9 = cntr8 + 1       # BioT start
    cntr10 = cols           # BioT end

## Number of Species, read from LVsimdat.R file
n <- nspec

## vector of initial biomass from LVSimdat import
## find column numbers

init.x <- apply(as.matrix(input[, 'init.B']), c(1,2), as.numeric)

## vector of r values from LVSimdat import
r.new = apply(as.matrix(input[, 'r']), c(1,2), as.numeric)

## fmort matrix; used in event function
fmort = apply(as.matrix(input[, cntr3:cntr4]), c(1,2), as.numeric)

## matrix of environmental variability from LVSimdat import
env.update = apply(as.matrix(input[, cntr5:cntr6]), c(1,2), as.numeric)

## matrix of alpha values from LVSimdat import
a = apply(as.matrix(input[, cntr7:cntr8]), c(1,2), as.numeric)

## tolerance level for minimum biomass
tol = 0.00001

#-----#
#   RUNNING the model                               #
#-----#

# run the ODE solver
out <- lsoda(times=times, func=model, parms=NULL, y=init.x,
             events=list(func=eventfun, time=times))

## Create out matrix on annual time steps
# delete times column
new.out = out[, -1]
out.annual = matrix(0, nrow=(ntime), ncol=nspec)
tt = length(times)

```

```

        counter = 1
        for (rows in 1:(ntime)) {
            counter = ifelse(counter>tt,tt,counter)
            out.annual[rows,] = new.out[counter,]
            counter = counter + (length(times)/(TimeEnd))
        }

## Add biomass over time to data.mat
input[,cntr9:cntr10] = t(out.annual)

## Add Bmean in last year to column 1
Bmeanlast = out.annual[ntime,]
input[19,cntr] = mean(Bmeanlast)

## Add number extinct in last year to column 1
Extinct.num = length(which(out.annual[ntime,]==0))
input[20,cntr]= Extinct.num

write.csv(input,paste(od,'LVDatOut_',as.character(run.num[number]),'.csv',sep
=''))

#-----#
#      Alpha matrix information and written out in a file      #
#-----#
Bb = t(out.annual)
ex.mid = which(Bb[, (ntime/2)]==0) #species are extinct in the midpoint
ex.last = which(Bb[,ntime]==0) #species are extinct in the last year

alpha.mid = a
alpha.mid[ex.mid,]=NA
#make all aij elements in the row 0 if species extinct midpoint year only
alpha.mid[,ex.mid]=NA
#make all aij elements in the column 0 if species extinct midpoint year only
sum.alpha.mid = as.matrix(apply(alpha.mid,1,sum,na.rm=T))
sum.alpha.mid[which(sum.alpha.mid==0)]=NA

alpha.last = a
alpha.last[ex.last,]=NA
#make all aij elements in the row 0 if species extinct last year only
alpha.last[,ex.last]=NA
#make all aij elements in the column 0 if species extinct last year only
sum.alpha.last = as.matrix(apply(alpha.last,1,sum,na.rm=T))
sum.alpha.last[which(sum.alpha.last==0)]=NA

p.vector.start = matrix(Alpha.stats[,8])
# add initial p without env or F
env.f = env.update + fmort
env.fl = env.f[,c(1,(floor(ntime/2)),ntime)] #150
p.time = matrix(0,nrow=nspec,ncol=5)
sim.t = c((floor(ntime/2)),ntime) #149 because counting 0
r.vec = as.matrix(Alpha.stats[,6])
r.vec = apply(r.vec,c(1,2),as.numeric)

```

```

p.vector.start = apply(p.vector.start,c(1,2),as.numeric)
p.time[,1] = r.vec + sum.alpha.mid #pmid
p.time[,2] = r.vec + sum.alpha.last #plast
p.time[,3] = p.vector.start + env.f1[,1] #pstart + env + f
p.time[,4] = r.vec + sum.alpha.mid + env.f1[,2] #pmid + env + f
p.time[,5] = r.vec + sum.alpha.last + env.f1[,3] #plast + env + f

colnames(p.time) = c('pmid','plast','pstart.envf','pmid.envf','plast.envf')
Alpha.stats = cbind(Alpha.stats,p.time)

## calculate the ending r values
end.r = matrix(nrow=nspec,ncol=4,0)
end.r[,1] = r.new

for(a.row in 1:nspec){
  pos.end = which(a[a.row,] >0)

  # which alpha ij's are positive
  alpha.pos = a[a.row,pos.end]
  Bio.end = as.matrix(input[,cntr10])
  Bio.end1 = Bio.end[pos.end,1]
  end.r[a.row,2] = sum(alpha.pos*Bio.end1)
  } # end a.row

  end.r[,3] = end.r[,1] + end.r[,2]
  end.r[,4] = Bio.end
  colnames(end.r) = c('r.new','gi.end','total.r.end','Bio.end')
  Alpha.stats = cbind(Alpha.stats,end.r)

## write out Alpha.stats
write.csv(Alpha.stats,paste(od,'Alpha.stats_',as.character(run.num[number]),
'.csv',sep=''))

```

VITA

Melissa Hedges Monk was born in California in 1981. She graduated from Langley High School while living in Great Falls, Virginia. She has a B.S. in Wildlife Science from Virginia Tech in Blacksburg, Virginia. While attending Virginia Tech, she studied abroad for a semester at Victoria University in New Zealand where she took classes in the marine sciences. Melissa was a member of the Virginia Tech/National Marine Fisheries Service Recruiting, Training and Research Unit during her Master's program in Fisheries Science. Under the guidance of advisor Dr. Jim Berkson, Melissa estimated a survival rate for the northern population of loggerhead sea turtles and developed a population dynamics model. Melissa worked during her Master's program at the Bald Head Island Conservancy, where she was the Sea Turtle Program Coordinator and Naturalist.

After Melissa graduated from Virginia Tech she continued her education at Louisiana State University in Baton Rouge. At LSU under the guidance of Dr. Joseph Powers, she has conducted research for her doctoral requirements in the Oceanography and Coastal Sciences department with a focus in quantitative fisheries. Melissa was involved in a number of graduate student activities, including holding the position of vice president of the graduate organization CEGO in 2009. Melissa also co-founded and coordinated the LSU Chapter of EnvironMentors, an environmental science college access and mentoring program for high school students.