

EFFECTS OF TEMPORAL CLOSURES AND GEAR MODIFICATIONS ON THE
POPULATION OF DUSKY SHARKS IN THE NORTHWESTERN ATLANTIC OCEAN

By

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To my mom, dad, Chris and Xander

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Abstract of Dissertation Presented to the Graduate School
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By

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My objectives in this study were two-fold. First, I built an age-structured model to assess the effects of fishing on population trends for dusky shark. This model included sensitivity analyses to assess the effects of time/area closures, reduced mortality as a result of reduced soak times for the bottom longline fishery, full selectivity of age-zero animals, removal of Catch Per Unit Effort (CPUE) series and changes to other model parameters on overall population sizes. My second objective was to build a spatial model that evaluated the effects time/area closures and changes to other model parameters had on the population size of three life-stages (juvenile, subadult and adult) of the dusky shark.

Results showed that the impacts of fishing already imposed on the dusky shark would be difficult to overcome even with the implementation of time/area closures, gear modifications and/or catch and discards being reduced for another 20 years. Results of the base case, all scenarios and sensitivity analyses except for one (increasing virgin biomass) of the age-structured model indicated that the population of dusky sharks in the northwestern Atlantic Ocean is at less than 60% of virgin biomass. Recent work has shown that the Maximum Sustainable Yield (MSY) for dusky sharks may be well above 50% of the carrying capacity. Fisheries managers must determine whether the high depletion rates reported in these models

suggest this species is overfished, and would therefore require long-term targets for population recovery to sustainable levels.

The base case version of the spatial model illustrated that the majority of total density (numbers) for all three stages (juvenile, subadult and adult) occurred in the closed region of the model, but the effects of fishing were still seen in the boundaries between open and closed areas. Sensitivity analyses showed that parameter values affected the densities and the redistribution of fishing effort for all three stages. However, all of the models (except for the open and closed versions) indicated that the highest densities were found in the closed portion of the model and that the redistribution of fishing effort was concentrated into a very small area on either side of the closures. Neonate densities in all models generally followed the same trends as total density, and recruitment densities varied very little throughout individual models.

Results of these models suggest that dusky shark populations have been heavily reduced and that research into the effects of time/area closures on dusky shark populations should continue. Fisheries managers should investigate new management options that will reduce the fishing mortality of dusky sharks caught as bycatch. Managers should also increase observer effort in fisheries that catch dusky sharks as bycatch and improve on recording and reporting by fishers and dealers. Future research should be aimed at determining ways to reduce fishing mortality rates for the dusky shark and improving our knowledge of parameters used in spatial modeling.

CHAPTER 1 DUSKY SHARK BACKGROUND

Background

Management of sharks in the western North Atlantic Ocean has been politically and socially contentious. Since 1993, resource managers, fishery biologists and fishers have struggled to create a management plan that would allow sustainable fishing and be economically viable for fishers. The current National Marine Fisheries Service (NMFS) Fishery Management Plan (FMP) for Atlantic sharks manages 39 species, which are separated into four management categories: large coastal, small coastal, pelagic, and prohibited sharks (NMFS, 2006). However, biologists and independent stock assessment referees have suggested that sharks be managed on a species level rather than as groups. Due to the complexity of the multi-species fishery that currently exists for large coastal sharks, this suggestion has only recently been enacted for the sandbar shark (*Carcharhinus plumbeus*) (NMFS, 2008). These new species-specific regulations include a sandbar shark “research fishery” with a heavily reduced quota and a non-sandbar large coastal shark fishery with a 33-shark/day limit (NMFS, 2008). Scientific work should continue to explore whether species-level management is possible for additional species, including the dusky shark.

Sharks are susceptible to overfishing because of their K-selected life history characteristics (Cortés, 2002a; Heppell et al., 1999; Cortés, 1999). Many species associated with commercial and recreational fisheries grow slowly, have late ages at maturation, and exhibit limited maximum reproductive capacity. It has been estimated that several shark species, such as the sandbar (*Carcharhinus plumbeus*) (Sminkey and Musick, 1994; Cortés, 1999) and dusky (*Carcharhinus obscurus*) (Simpfendorfer, 1999) shark, have a capacity to increase their population size at well below 10% per year. Musick et al. (2000) noted that species with

intrinsic rates of increase below 10% were particularly vulnerable to fishing mortality. Simpfendorfer (1999) used a demographic model for dusky sharks and found that only 4% of each age class can be caught sustainably. Similar findings have been found for sea birds and sea turtles whose populations are sensitive to juvenile and adult mortality rates, respectively and are considered long-lived species (sea turtles) (Crouse, 1999; Russell, 1999). Cortés (2002a) found through a probability-based elasticity analysis that λ (i.e., the finite population growth rate) for shark populations is most sensitive to the survival of juvenile stages. Sharks considered at the K-selected end of the spectrum, had high juvenile survival and low age-0 survival (or fertility) elasticities (used in demographic modeling to provide a measure of the effect of small alterations in single matrix vital rates or elements). The dusky shark was categorized as being in the “slow” end of the life history pattern spectrum in his study, and was shown to lack the biological traits necessary to allow a return to original population sizes after moderate exploitation (< 10%) of adult and juvenile life-stages (Cortés, 2002a). Heppell et al. (1999) also stated that long-lived marine animals, such as sharks, have low first year survival elasticities and that even a small decrease in survival of adult or juvenile age classes can substantially reduce population abundances. In addition, animals with low juvenile and adult survival are unlikely to increase fecundity or juvenile survival rate in order to compensate for low population size (Heppell et al., 1999).

The NMFS has implemented several management decisions aimed at protecting the dusky shark and several other species from becoming overfished. These include placing 19 species (including the dusky shark) on the prohibited species list, making it illegal to target and/or land these species either recreationally or commercially) (NMFS 1999), implementing a time/area closure off North Carolina from January through July to protect juvenile dusky and sandbar

sharks from longline fishing mortality (NMFS, 2003) and reducing the Total Allowable Catch for the directed large coastal non-sandbar shark fishery (NMFS, 2008). However, these actions have not prevented the dusky shark from being caught and discarded as bycatch in several fisheries (Alexia Morgan unpublished data; Beerkircher et al., 2002) or in state waters. A recent stock assessment of the dusky shark showed declines of 60-80% relative to virgin biomass (Cortés et al., 2006).

As we continue to see signs of population declines for this species, it has become apparent that additional changes to current management plans must be made. An increase in the size of the current time/area closure, gear restrictions (i.e. reducing soak time), and/or individual species management for the dusky shark are potential changes that could be implemented. These measures have been and continue to be contentious issues among researchers, resource managers, and fishers. Utilizing models to simulate the effect of these alternative management plans on the dusky shark, a prohibited species, may show that species-specific management or alternative management options can and should be implemented (Pelletier et al., 2008).

Models are essential to fisheries management because they depict and project the population in a mathematical framework using existing data, and allow inputs to be modified to explore a range of policy options. The major pitfall of models is that they are a simplified depiction of the system and thus may not include important interactions (process error), and parameter inputs to the model can have high uncertainty (observation error). Poorly designed models or well-designed models utilizing poor or limited data can lead to the implementation of incorrect management plans.

Statement of Problem and Objectives

In June 2000, the dusky shark (listed by NMFS as a Candidate Species under the Endangered Species Act (ESA), and listed as vulnerable in the northwest Atlantic and Gulf of

Mexico by the IUCN Red List of Threatened Species for 2004) and 13 additional species were placed on the prohibited species list, which disallows landing these sharks (NMFS, 1999). However, many of these species, including the dusky shark, continue to be caught and discarded as bycatch in both the commercial and recreational fisheries (Alexia Morgan, unpublished data). As a result, some populations continue to decline due to species-specific responses to capture on fishing gear (Morgan and Burgess, 2007), several age/size classes being caught (Alexia Morgan, unpublished data), discard mortality and the inability of the current quota-based management system to address these individual issues.

The dusky shark has been exposed to high fishing mortality aimed at multiple size classes over the past few decades (Cortés et al., 2006, Alexia Morgan, unpublished data). The main fishery for dusky sharks in the United States, prior to being classified as a prohibited species, was the directed shark bottom longline, which operates along the U.S. east coast and Gulf of Mexico. Dusky sharks are also caught in the U.S. pelagic longline fishery and are taken incidentally in several other fisheries as well as recreationally (Cortés et al., 2006).

The overall goal of this study was to complete a stock assessment of the dusky shark population in the northwest Atlantic Ocean and to utilize a spatial model to investigate whether time/area closures are an adequate management tool for the dusky shark. My objectives were two fold. First, I built an age-structured model for dusky shark, which included sensitivity analyses to assess effects of time/area closures, reduced mortality as a result of reduced soak times for the bottom longline fishery, a different selectivity curve, the removal of the Bottom Longline Observer Program (BLLOP) Catch Per Unit Effort (CPUE) series, combined CPUE series for all catch rates and changes to other model parameters on overall population sizes. My second objective was to build a spatial model that evaluated effects of time/area closures on the

population sizes of three life-stages (juvenile, subadult and adult) of the dusky shark. This second approach has yet to be used in a stock assessment for this species of shark but spatial modeling has been used to assess stock abundance of the school shark (*Galeorhinus galeus*) in Australia (Punt et al., 2000). Both modeling approaches were used to assess whether alternative management plans such as increased time/area closures, species specific management, or gear modifications could decrease fishing induced mortality and predict sustainable protection of dusky sharks in the northwestern Atlantic Ocean. These approaches were different than those used by Cortés et al. (2006), who used surplus production, age-structured production and catch-free models, fewer years of data, no spatial analysis, and different sensitivity analyses and target reference points.

Fisheries Management

The initial Federal Fishery Management Plan (FMP) for sharks was enacted in 1993 in reaction to concern that increased commercial and recreational fishing effort for sharks had caused over-fishing (NMFS, 1993). In 1999, sharks in the Northwest Atlantic Ocean and Gulf of Mexico became managed under the Fishery Management Plan for Atlantic Tunas, Swordfish, and Sharks and subsequent amendments (Highly Migratory Species [HMS] FMP) (NMFS, 1999). In July 2006 the Final Consolidated Fishery Management Plan for Atlantic Tunas, Swordfish and Sharks was published (NMFS, 2006). This FMP is a result of the 2002 and 2006 stock assessments of large and small coastal sharks, respectively (NMFS, 2006). The current HMS FMP manages four groups of sharks: large coastal sharks (11 species), small coastal sharks (four species), pelagic sharks (five species) and prohibited sharks (19 species, including the dusky shark), with each group managed separately (NMFS, 2006). The dusky shark has only been assessed as an individual species by Cortés et al. (2006).

Time and area closures and Marine Protected Areas (MPAs) are becoming management tools for state, federal and internationally managed fisheries (Pelletier et al., 2008). The MPA's and other closures are commonly used as a management tool to protect biodiversity, repairing demographic structure of a population and spawning stocks. The effects of the closures can be analyzed through "candidate indicators", such as enhancing fisheries yields outside of the closure and increasing the stability of the population (Pelletier et al., 2008). The results of most studies have shown that improving fishery yields within closed areas only works when the fishery is already overexploited (Apostolaki et al., 2002). Internationally, pelagic fishes (Goodyear, 1999), mollusks (Dredge, 1992), and reef fishes (Galal et al., 2002) are being managed with MPAs because they can provide protection of specific size classes, sexes, and/or species from excessive fishing mortality. The success of closures depends on their size, time period of closure, the life-stages that use the closed area (Horwood et al., 1998; Dinmore et al., 2003; Tang and Chen, 2003), movement rates of fish, and additional catch and/or effort controls that will alleviate the effect of fishing effort displacement (Walters, 2000; Rijnsdorp et al., 2001; Walters et al., 2007). Determination of which size class or sex is in need of protection depends upon the demographic attributes of the species, which size class or sex historically has been targeted, and the current status of the population in question. There has been great debate among fisheries researchers and fishers over the use and success of MPAs and time area closures as management tools (Pelletier et al., 2008).

A time/area closure was implemented in 2005 from January to July off the coast of North Carolina in an effort to protect juvenile dusky and sandbar sharks from longline fishing and discard mortality (NMFS, 2003). This closure is intended to protect dusky sharks for 7 months of the year. The closed area is small (Oregon Inlet, NC at 35°41'N offshore to 74°51'W, then

following the 60 fathom contour to 35°30'N and 74°46'W and continuing along the 60 fathom contour south to 33°51'N and 76°24'W (see Appendix A)) for a highly mobile species and will not protect dusky sharks that move out of the area during the specified closed times. No previous studies have evaluated the potential for success of this time/area closure in protecting highly migratory species, and thus there is no indication of whether this closure will be beneficial to the dusky and/or any other species of large coastal shark. This study was the first to assess the effects of time/area closures on the dusky shark through the use of both age-structured and spatial modeling.

Life History of the Dusky Shark

The dusky shark has one of the longest reproductive cycles (three years) of all shark species, can reach lengths of 360 cm fork lengths (FL) and lives between 40-50 years (Natanson et al., 1995). Age and growth estimates and length frequency analyses from the North Atlantic Ocean (Natanson et al., 1995) and Western Australia (Simpfendorfer, 2002) are reported in Appendix B. Growth parameters for males ranged from L_{∞} =345.4-373 cm FL (theoretical average maximum) and K =0.038-0.043/year (growth coefficient) and for females L_{∞} = 336.5-349 cm FL and K =0.039-0.045/year. Females and males are estimated to reach sexual maturity at 21 and 19 years of age, respectively, and litters range from 3-14 pups with a 1:1 sex ratio. The gestation period has been estimated to be as long as 24 months with a one-year resting cycle in between (Branstetter and Burgess, 1996). Dusky sharks are viviparous, giving birth to live young, ranging in size between 70-100 cm TL (Last and Stevens, 1994; Natanson et al, 1995) (Appendix A).

Mating occurs between July and September and birth occurs between May and June in nursery grounds located from South Carolina to Virginia. Juvenile dusky sharks (> 150 cm FL) also inhabit other coastal beach nursery grounds from New Jersey to South Carolina (Castro,

1996). The growth rate of juvenile dusky sharks ranges from 8 cm/year to 11 cm/year (Simpfendorfer, 2000). Females can store sperm in the oviducal glands. Time of mating and subsequent fertilization has not been defined.

Thus, the dusky shark is a long-lived fish, but previous studies have hypothesized a range of natural mortality rates. Natural mortality (M) in the dusky shark has been estimated using Hoenig's (1983) method, resulting in a value for M of 0.083/year (Romine et al., 2002) and 0.08/year (Simpfendorfer, 1999). Estimates of natural mortality using Pauly's (1980) method resulted in a value of 0.11/year (Simpfendorfer, 1999). Cortés et al. (2006) calculated M ranging from 0.02-0.1 using Rikhter and Efanov's (1976), Pauly (1980), Hoenig (1983), and Jensen (1996) methods. Size-specific natural mortality rates of 0.21 and 0.25 for age-0 sharks and 0.08 for age 40+ sharks were calculated through Peterson and Wroblewski's (1984) and Lorenzen's (1996) methods, respectively. Chen and Watanabe's (1989) method resulted in an M of 0.16 for age-0 sharks and 0.05 for age 30 sharks and an average of 0.05 for sharks age 31+ (Cortés et al., 2006) (Appendix B). Because of the late age at maturity of the dusky shark, increasing the natural mortality of age-0 animals has been shown to have little effect on population abundance (Simpfendorfer, 1999).

Distribution

The dusky shark is a coastal-pelagic species inhabiting warm-temperate and tropical inshore and offshore waters. It is found from the continental shelf to the open ocean and in depths ranging from the surface to 400 m. In western North Atlantic waters this species is found from New England to Brazil, including the Gulf of Mexico and Caribbean Sea. It also occupies the eastern Atlantic, western Mediterranean, western Indian, western Pacific, and the eastern Pacific Oceans (Compagno, 1984).

Dusky sharks are highly migratory and in the western North Atlantic moves northwards along the US east coast as the water warms during the spring and summer and southward as the waters cool during fall and winter (Musick and Colvocoresses, 1986). Tagging studies have documented a maximum distance traveled of 2,052 nautical miles, a maximum speed of 41.3 km/day and a maximum time at liberty of 15.8 years (Kohler et al., 1998). The NMFS Cooperative Shark Tagging Program has tagged dusky sharks in New England and recaptured these sharks in the southwestern Gulf of Mexico and Yucatan Peninsula. These tagging studies have also indicated that there is a single population within the North Atlantic Ocean, with no mixing with dusky sharks outside of the North Atlantic, although this has not been corroborated with any genetic work (Romine et al., 2002). Dusky sharks can be found in similar areas to the sandbar, bignose (*Carcharhinus altimus*), silky (*Carcharhinus falciformis*), whitetip (*Carcharhinus longimanus*) and Galapagos (*Carcharhinus galapagensis*) sharks (Compagno, 1984). Young sharks do not migrate as far north and south as adults do and some partial sexual segregation has been suggested (Compagno, 1984). Dusky sharks tend to avoid areas of low salinity (Compagno, 1984).

Conclusions

Management efforts over the past several years have aimed at protecting the dusky shark from overfishing. Despite these efforts a recent stock assessment (Cortés et al., 2006) has indicated this species is overfished and that management has been unable to protect this species from being caught as bycatch in several fisheries. In the following two chapters I describe the results of my analysis using an age-structured and spatial model to determine if alternative management efforts, such as increasing the time area closure and/or reducing the soak time for longline gear, could improve the status of the dusky shark population. The age-structured model

is different from ones previously used to assess this species (Cortés et al., 2006) and this is the first time a spatial model has been used to assess the dusky shark population.

CHAPTER 2 AGE-STRUCTURED MODEL

Introduction

Age-structured models divide a population into age classes and follow these cohorts separately throughout the simulation. Simpler models such as production models combine growth, reproduction and mortality, making it impossible to look at the “dynamic” interactions occurring between these processes (Hadden, 2001). Age-structured models can also incorporate multiple gear types and biological information (Simpfendorfer and Burgess, 2002). The life history patterns of the dusky shark and its exploitation in several fisheries made an age-structured model appropriate for this species. Exploitation rates for dusky sharks vary between size classes; therefore the ability of an age-structured model to follow each size class separately is a very useful tool for stock assessment and decision analysis. Cortés et al. (2006) have previously used a surplus production, catch free and age-structured production model to determine the status of the dusky shark. I used a different age-structured model, three more years of data, a different selectivity curve, removed the Bottom Longline Observer Program (BLLOP) Catch Per Unit Effort Series (CPUE), combined CPUE series for all catch rates and included analyses on the effects of time/area closures and reduced soak times.

The age-structured model used to address objective 1 was coded in Excel and utilized a Bayesian framework. A Bayesian approach allows for the incorporation of uncertainty and prior knowledge of unknown parameters during the initial stages of model development (Punt and Hilborn, 1997). The model was similar to ones used by Punt and Walker (1998) and Simpfendorfer and Burgess (2002). For my analysis the model was modified to include: age specific natural mortality rates, lognormal prior distributions for unknown parameters, and the use of fork lengths instead of pre-caudal lengths to determine weights. Multiple fisheries, gear

types and selectivities were included in the model. Catch rate data were assumed to be proportional to biomass and catch rates were compared to the exploitable biomass of specific survey gear (Simpfendorfer and Burgess, 2002). The model was used to provide estimates of the current (for 2006) and future (2025) status of the population compared to the virgin population (assumed to be around 1972 based on historical knowledge of the fishery [Simpfendorfer and Burgess, 2002]) and to analyze the impact varying parameter values and commercial and recreational catches would have on population levels. One base case model, five scenarios and six sensitivity analyses were run. Parameter values and catches used in the sensitivity analysis and scenarios can be found in Table 2-1.

Data for Model

All biological data obtained from the literature are reported in Appendix B. Size at age was taken from Natanson et al. (1995). Natural mortality rates used in this model assumed a linear decrease for age 0 to mature animals (Cortés et al., 2006).

Commercial Catches

Commercial landings for dusky sharks were collected from the following sources and provided to me by Enric Cortés (personal communication): National Marine Fisheries Service (NMFS) South East Fisheries Science Center (SEFSC) quota monitoring system (now known as pelagic dealer compliance), the Northeast (NE) and Southeast (SE) regional general canvass landings (now known as Accumulated Landings System), the SEFSC Coastal Fisheries Logbook Program (CFL) and the Pelagic Longline Logbook (PLL) (Table 2-2).

The quota monitoring system collects information from seafood dealers who 1) hold a Federal dealer permit for sharks, 2) are selected by the SEFSC to report and 3) are located in the SE region. This dataset provides species specific information. The general canvass landings data set collects data directly from all seafood dealers and is considered a more complete dataset

because it includes state landings, but tends to have poorer species specific data and a large proportion of unclassified sharks than the quota monitoring system. The CFL collects data from commercial fishers holding either a 1) Gulf of Mexico Reef Fish permit, 2) South Atlantic Snapper-Grouper permit or 3) King and Spanish mackerel or Shark permits. The PLL collects data from commercial fishers participating in the pelagic longline fishery targeting tuna and tuna-like species. Fishers must submit a logbook for any trip in which a highly migratory species was caught (Cortés et al., 2006).

The total amount of dusky sharks landed in commercial fisheries was calculated by taking the maximum amount (kg Dressed Weight [dw]) from the quota monitoring, coastal logbook and SE general canvass landings data (the maximum number is used because landings can be reported to all three databases) and adding it to the maximum amount (kg dw) from the NE general canvass landings data and pelagic longline logbook (Table 2-2) (Cortés et al., 2006). I constructed historical catches for the time period of 1972-1989 using a linear increase in catches from 0 kg in 1972 to 17,000 kg in 1989 (Table 2-3). Reported catches from the 1980s are known to be unrealistic (Enric Cortés, NOAA, personal communication) so I included those years in the historical data set in an effort to produce a more realistic catch series. Catches were increased from 0 to 17,000 kg so that catches in 1989-1991, prior to the drastic increases in catches due to the explosion of the fishery, would be similar (Tables 2-2 and 2-3).

Dead discard (animals discarded back to sea dead) estimates were collected from the PLL (Table 2-4) and BLLOP (Table 2-2) and provided to me by Enric Cortés. Discards from the BLLOP were added to the commercial landings to obtain the total commercial catches for the time period. The PLL discards were counted separately and represented the total amount of discards because they have a different selectivity curve (described below) than the BLLOP

discards and commercial catches. All weights (commercial and discard) were converted from pounds (lb) to kg for inclusion in the age-structured model. I constructed historical discards for the time period 1972 to 1991 using a linear increase in discards from 0 kg in 1972 to 30,000 kg in 1991 (Table 2-3). I ended the linear increase at 30,000 kg so that it would be near the estimated discards reported in 1991. Discard estimates varied through the years but it is unlikely that discards prior to 1991 were more than those seen during the expansion of the fishery in the 1990's.

Individual states were used to make up three broad regions (Gulf of Mexico (GOM), Mid Atlantic (MA) and South Atlantic (SA)). The GOM was made up of the west coast of Florida to Texas, the MA is all states between Virginia and New York and the SA was the Florida east coast through North Carolina.

Recreational Catches

Data were collected from the Marine Recreational Fisheries Statistic Survey (MRFSS), NMFS Headboat Survey (HBOAT) and Texas Parks and Wildlife Department Recreational Fishing Survey (TXPWD) for recreational fishing estimates (Table 2-5) and provided to me by Enric Cortés (personal communication). The total amount of dusky shark catches in recreational fisheries was calculated by adding the amount reported from the three recreational surveys (reported in estimated numbers of fish caught). Detailed information on these three datasets can be found in Shark Evaluation Annual Reports (Cortés et al., 2006). All weights were converted to kg for inclusion in the age-structured model. I constructed historical catches for the time period 1972 to 1980 using a linear increase in catches from 0 kg in 1972 to 200,000 kg in 1980 (Table 2-3). Recreational catches were highest during the 1980's and I kept the historical catch series larger in the 1970's to coincide with the expansion of the recreational fishery for sharks (George Burgess, FLMNH, personal communication).

Individual states were used to make up three broad regions (Gulf of Mexico (GOM), Mid Atlantic (MA) and South Atlantic (SA)). The GOM was made up of the west coast of Florida to Texas, the MA is all states between Virginia and New York and the SA was the Florida east coast through North Carolina.

Catch Rates

Virginia Institute of Marine Science (VIMS) Monitoring Data

The VIMS data set is a fishery-independent scientific survey, which began in 1974 and continues today. Data for the present study were available for 1974-2006. The survey uses longline gear to sample 4-5 stations during several cruises that operate predominantly in the summer in the coastal waters of Virginia. No dusky sharks were caught during 1986, 1988 and 1994 despite surveys being completed. The variables year, station, season (spring, summer, fall, winter-based on months), average depth and the time the sets were started were used for catch rate analysis of this series. Effort was the number of hooks per set multiplied by soak time (hrs. fished). I developed the catch rate series for this data set. Additional information on this data set and variables used in the catch rate analysis can be found in Cortés et al. (2006).

Bottom Longline Observer Program (BLLOP)

The BLLOP is a fishery dependent commercial data set that began in 1994 and continues today. Data for these analyses were available from 1994-2006. Fisheries observers were placed aboard commercial bottom longline vessels from New Jersey to Texas and recorded information pertaining to the number of sharks caught, size, sex, location and disposition of sharks for individual sets. The program was voluntary in nature from 1994-2001 and became mandatory in 2002. Vessels that hold a current directed shark permit are selected at random for observer coverage. The variables year, area (Gulf of Mexico, South Atlantic and Mid-Atlantic Bight), hook type (small, small J, small C, medium, medium J, medium C, large, large J, large C), set

depth, bait type (little tunny, Atlantic sharpnose shark, other shark, other teleost, skate or ray, eel, and other) season (spring, summer, fall and winter) and time of day the sets were made were used for catch rate analysis of this series. For the Catch Per Unit Effort (CPUE) analysis the dataset was divided into the two time periods (1994-2001 and 2002-2006) and two separate analyses were run (John Carlson personal communication). Effort was the number of hooks per set multiplied by the length (miles) of longline per set and the soak time (hrs.). Additional information on this data set can and variables used in the catch rate analysis can be found in Cortés et al. (2006).

Pelagic Longline Observer Program (PLLOP)

This is a fishery-dependent commercial data set, which started in 1992 and continues to this day. Data for these analyses were available for 1992-2006. Fishery observers were placed aboard commercial pelagic longline vessels targeting tuna and tuna-like species from the Grand Banks to Brazil and recorded shark bycatch. The variables year, whether it was an experimental set, whether light sticks were used, fishing quarter of a particular year, area, gear (bottom longline or pelagic longline), quartile for nominal tuna catch rate (per 1000 hooks) and quartile for nominal swordfish catch rate (per 1000 hooks) were used for catch rate analyses (Enric Cortés, NOAA, personnel communication). Effort was the number of dusky sharks caught per 1,000 hooks. Additional information on this data set can and variables used in the catch rate analysis can be found in Cortés et al. (2006).

Large Pelagic Survey (LPS)

This data set is a fishery-dependent recreational data set, which started in 1986 and continues to this day. Data for these analyses were available from 1986-2006 and consisted of angler interviews. Data on rod and reel and handline fisheries from Massachusetts to Virginia was collected for this program. The variables year, state, interview type (phone or dockside),

tournament (yes or no), boat type (private, party, headboat) and month were used for catch rate analysis of this data set. Effort was the number of dusky sharks caught per 100 trips. I developed the catch rate series for this data set. Additional information on this data set can and variables used in the catch rate analysis can be found in Brown (2002).

Catch Rate Analyses

Catch rates for the Bottom Longline Observer Program (BLLOP), Virginia Institute of Marine Science (VIMS), Pelagic Longline Observer Program (PLLOP), and Large Pelagic Survey (LPS) data sets (Table 2-6) were included in all model runs. A Generalized Linear Model (GLM) was used to standardize these catch rates. This methodology has previously been used in the analysis of other shark species (e.g. Cortés et al., 2002; Cortés et al., 2006). The model treats the proportion of sets with positive catch (binomial error with logit function) and the sets with positive catches (Poisson error distribution and log link function) separately due to the zero inflated nature of the catch distributions. Models were fitted using a SAS GENMOD procedure (SAS Institute Inc., 1999) and a forward stepwise approach, testing each factor one at a time. A null model was run first and then individual factors were entered one at a time. The results were ranked from greatest to smallest reduction in deviance per degree of freedom when compared to the null model. The factor with the largest reduction in deviance per degree of freedom was integrated into the model if 1) the effect of the factor was significant at least at the 5% level based on results of a Type III likelihood ratio test from a Chi-Square statistic and 2) the deviance per degree of freedom was reduced by at least 1% compared to the less complex model. Year was always included as a factor because it is needed to develop a time series (Cortés, 2002b; Cortés et al, 2002; Cortés et al., 2006).

A deviance analysis table including the deviance for proportion of positive observations and the deviance for the positive catch rates was used to summarize the results. The final model

was run using a computer program that uses the SAS GLIMMIX macro. Akaike's Information Criterion (AIC), Schwarz's Bayesian Criterion and $-2 \times$ the residual likelihood (-2Res L) were used for goodness-of-fit tests. A Type III test of fixed effects was used to test the significance of each individual factor. Relative indices were calculated through the final mixed model as the product of the year effect least squares means (LSMeans) from the binomial and Poisson components, which used bias correction terms to calculate the confidence intervals (Cortés, 2002b; Cortés et al., 2002; Cortés et al. 2006). The standardized catch rates were all used in the model.

Age-structured Model

Components of the Model

The model is age (Natanson et al., 1995) and sex structured (catch divided equally between males and females) and uses a Virtual Population Analysis (VPA) type of simulation approach (equation 2-1),

$$N_{a+1, g, t+1} = \begin{cases} N_{0, g, t+1} & a = 0 \\ (N_{a, g, t} e^{-M/2} - C_{a-1, g, t}) e^{-M/2} & 1 \geq a > x_g \\ N_{a, g, t} e^{-M} - C_{a, g, t} e^{-M/2} + N_{a-1, g, t} e^{-M} - C_{a-1, g, t} e^{-M/2} & a = x_g \end{cases} \quad (2-1)$$

where $N_{a, g, t}$ is the number of individuals of age a , sex g in year t , M is instantaneous natural mortality, x_g is the maximum age of sex g and C is total catch in numbers (Simpfendorfer and Burgess, 2002). Total catch was found using equation 2-2,

$$C_{a, g, t} = \sum_j C_{a, g, t, j} \quad (2-2)$$

where $C_{a, g, t}$ is the total catch of age a , sex g , in year t summed across all j gear types (Simpfendorfer and Burgess, 2002).

The number of pups born each year was calculated using equations 2-3 and 2-4,

$$N_{0,g,t} = \left(\frac{S_t}{(b + c \cdot S_t)} \right) P_{g=f}'' e^{\varepsilon_t - \sigma_r^2 / 2} \quad (2-3)$$

$$S_t = \sum_{a=m}^x N_{a,g=f,t} \cdot P_a' \cdot P_a'' \quad (2-4)$$

where N is the number of pups of sex g , born in each year t , b and c are parameter values of the Beverton-Holt recruitment relationship, P_g'' is the proportion of pups that are female ($g=f$ indicates the sex of the pups is female, $a=m$ indicates age is mature), S_t is the egg production in year t , z is the proportion of R^* (virgin biomass) that recruits when S_t is at 20% of the virgin level (Cortés, 2004), P_a' is the number of pups per pregnant female at age a , P_a'' is the proportion of females of age a that are pregnant, e_t is an error term and σ_r^2 is the standard deviation of e_t (Simpfendorfer and Burgess, 2002). The parameter values R^* and z are estimated through the Sampling Importance Resampling (SIR) algorithm discussed in more detail below (Simpfendorfer and Burgess, 2002). Parameter values for b and c are calculated from R^* , z and S^* (unexploited egg production) using equations 2-5 and 2-6,

$$b = \frac{S^* \cdot \left(1 - \frac{(z - 0.2)}{0.8z} \right)}{R^*} \quad (2-5)$$

$$c = \frac{z - 0.2}{0.8zR^*} \quad (2-6)$$

where recruitment is assumed to be affected by process error and an error term ($\varepsilon_t \sim N(0, \sigma_r^2)$) is included (Simpfendorfer and Burgess, 2002).

The catch was found with using equations 2-7 and 2-8,

$$C_{a,g,t,j} = F_{t,j} \nu_{a,g,j} \left(N_{a,g,t} e^{-M/2} - \sum_{i=1}^{j-1} C_{a,g,t,i} \right) \quad (2-7)$$

$$F_{t,j} = C_{t,j} / B_{t,j}^e \quad (2-8)$$

where $C_{a,g,t,j}$ is the catch for sex g , age a animals at time t with gear j , $F_{t,j}$ is the fishing mortality that occurs at time t and gear type j , and $v_{a,g,j}$ is the selectivity of gear type j for animals of sex g and age a . The model assumes all catch is taken in the middle of the year after half of the natural mortality has occurred and in sequential order by fisheries (Commercial, recreational and discards)(Simpfendorfer and Burgess, 2002).

Exploitable biomass was found with equation 2-9,

$$B_{t,j}^e = \sum_g \sum_a w_{a,g} v_{a,g,j} \left(N_{a,g,t} e^{-M/2} - \sum_{i=1}^{j-1} C_{a,g,t,i} \right) \quad (2-9)$$

where $B_{t,j}^e$ is the exploitable biomass for year t , gear type j , and $w_{a,g}$ is the weight of sex g , age a animals (Simpfendorfer and Burgess, 2002). A power curve (equation 2-10) was used to calculate the weight of animals:

$$W_{a,g} = lwa \cdot L_{a,g}^{lwb} \quad (2-10)$$

where $L_{a,g}$ is the length (Natanson et al., 1995) for sex g and age a and lwa and lwb are constants of the length-weight relationship from a power curve (Simpfendorfer and Burgess, 2002).

The total and mature biomasses were found using equations 2-11 and 2-12,

$$B_t^t = \sum_g \sum_a N_{a,g,t} \cdot w_{a,g} \quad (2-11)$$

$$B_t^m = \sum_{a=m}^x N_{a,g=f,t} \cdot w_{a,g} \quad (2-12)$$

where B_t^t is the total biomass for year t and B_t^m is the mature female biomass at time t (Simpfendorfer and Burgess, 2002). The pre-exploitation population was found using equation 2-13,

$$N_{a,g,0} \begin{cases} R^* e^{e_a - \sigma_r^2} P_g^m & a = 0 \\ N_{a-1,g,0} e^{-M} & 1 \geq a > x_g \\ N_{a-1,g,0} e^{-M} / 1 - e^{-M} & a = x_g \end{cases} \quad (2-13)$$

where $N_{a,g,0}$ is pre-exploitation (Simpfendorfer and Burgess, 2002). The exploitable biomass of survey gear was found using equation 2-14,

$$B_{t,h}^e = \sum_g \sum_a w_{a,g} v_{a,g,h} \left(N_{a,g,t} e^{-M/2} - \sum_j C_{a,g,t,j} \right) \quad (2-14)$$

where $B_{t,h}^e$ is the exploitable biomass in year t for survey gear h (Simpfendorfer and Burgess, 2002).

Parameter Estimation

Selectivities were based on age frequency distributions from the Bottom Longline Observer Program (BLLOP), Virginia Institute of Marine Science (VIMS), Large Pelagic Survey (LPS) and the Pelagic Longline Observer Program (PLLOP) data sets. An age-length key (Natanson et al., 1995) was used to create age-frequency distributions from length frequency distributions. The BLLOP selectivity was used for the BLLOP CPUE series, commercial catches and BLLOP discards, VIMS selectivity was used for the VIMS CPUE, LPS selectivity was used for the LPS CPUE and recreational catches and the PLLOP selectivity was used for the PLLOP CPUE and PLL discards. The distribution was scaled to the maximum selectivity value and a double logistic distribution was fitted to age for each data set (Cortés et al., 2006) using equations 2-15 and 2-16,

$$V_a = C_a / \max(C_a) \quad (2-15)$$

$$f(x) = \frac{1}{1 + e^{-(x-a50/b)}} \cdot \left[1 - \left(\frac{1}{1 + e^{-(x-c50/d)}} \right) \right] \quad (2-16)$$

where V_a is the selectivity value at age a , C_a is the catch at age a , $f(x)$ is the double logistic function, a_{50} and c_{50} are median ages of the ascending and descending arm of the double logistic equation and the variables b and d are the slopes respectively. Selectivity curves and parameter estimates for the all models except for one sensitivity analysis (sensitivity 9) were provided by Enric Cortés (personal communication). In sensitivity 9, I adjusted the parameters of the double logistic distribution to allow for full selectivity of age 0 animals. Additional information on the methods used to construct the selectivity curves can be found in Cortés et al. (2006).

Model fit compared observed catch rates to the population size in the model using equation 2-17,

$$\ln(L_j) = \left(\left(\sum_{t(h)} [\ln I_{t,h} - \ln(q_h B_{t,h}^e)]^2 \right) \frac{1}{2\sigma_h^2} \right) - n \ln(\sqrt{\sigma_h^2} 2\pi) \quad (2-17)$$

where $\ln(L_j)$ is the log likelihood of the lognormal distribution, $I_{t,h}$ is the catch rate for year t of survey gear type h , q_h is the catchability coefficient of gear type h and σ_h^2 is the variance of the residuals from survey gear h .

Populations were projected to year 2025 to show the effects of various harvesting strategies had on the simulated population into the future. The SIR algorithm was used to estimate posterior distributions for the priors (R^* , z , q_h and σ_h^2) used in the model. The SIR algorithm worked by 1) randomly selecting a value from the prior distributions of each of the four parameters listed above, 2) the model simulated the population through time with the selected parameters, 3) the total likelihood of the model was calculated, 4) steps 1-3 were repeated 1000-7000 times, and 5) 2000 model runs with replacement (selection was based on their total likelihood) were made and used to construct the posterior distribution (Simpfendorfer and Burgess, 2002). A lognormal prior distribution with a mean of 20,000 and standard

deviation of 10,000 was used for R^* (Colin Simpfendorfer personal communication) and a lognormal prior distribution with a mean of 0.3 and standard deviation of 0.09 was used for z (Cortés 2004). The prior distribution for σ^2_h was a uniform distribution with bounds [0;0.8] (Simpfendorfer and Burgess, 2002). The prior distribution for q_h was independent and normally distributed with starting values of 0.00001 for the VIMS, LPS and PLLOP catch rates and 0.000001 for the BLLOP catch rates.

Sensitivity Analysis

Scenario 1: Commercial and recreational catches closure in the future

It is unlikely that catches of dusky sharks between now and 2025 will remain at zero, therefore I added catches and discards from 2007 to 2025 to the model. I developed this model by taking the average catches (commercial, recreational and discards) from 2002-2006 and applying them to 2007-2025. I used the years 2002-2006 because they occur after the dusky shark was placed on the prohibited species list and allow a year (2001) for the new management plan to take full effect in the fishery. The base case model was rerun including catches for 2007 to 2025, simulating continued catches of the dusky shark for the duration of the model time line.

Scenario 2: Simulated closure by removal of North Carolina catches

I simulated an increase in the current time area closure to include all of North Carolina from 2007-2025. The general canvass, CFL and recreational datasets were used to determine the average percent of total dusky shark catches caught in North Carolina between 2002 and 2006. This average percent was removed from the 2007-2025 catches used in the previous model and this model was then run with the new 2007-2025 catch series, plus the original data from 1972-2006.

Scenario 3: Simulating reduced soak times

The BLLOP average discard rates (included in total commercial catches) for 2002 to 2006 were reduced by 43% and applied to 2007-2025, in an effort to simulate the effects of reducing the soak times used in bottom longline fishing. The reduction was based on the BLLOP database and results from Morgan and Burgess (2007), which showed that reducing the soak time to less than 10 hours resulted in a reduction of initial mortality of 43%. Similar data were not available from any of the other data. This model was run with the new catch series from 2007 to 2025 (included the average commercial and recreational catches from 2002 to 2006 used in scenario 1 and applied to 2007-2025, plus these reduced discards from 2002-2006 also applied to 2007-2025) and the original catch series from 1972-2006.

Scenario 4: Increased commercial catch series

There is some uncertainty surrounding the amount of both recreational and commercial catches reported due to changes in the design of sampling programs, species identification problems and general issues with logbook compliance. Commercial catches in the early years seemed very low, scattered and unrealistic given the growth of the bottom longline fishery during those years. I therefore increased the commercial catch series from 1972-2006 by 25% for this scenario.

Scenario 5: reduced recreational catch series

The recreational catches that have been reported for the dusky shark seem very high, so I reduced the recreational catches from 1972-2006 by 25% in this scenario.

Sensitivity 1: R^* prior distribution increased

During the development of the base case model it became clear that changes made to R^* had a substantial effect on the outcome of the model. I increased the lognormal prior distribution for R^* to a mean of 60,000 with a SD of 30,000 to determine how much influence this parameter

had on the population size. The same catches used in the base case model were used in this model.

Sensitivity 2: Z increased

I increased the prior distribution of z to a lognormal distribution with an increased mean of 0.6 and a SD of 0.24. The higher values used in the prior distribution of this model are near the biological maximum estimated for this species and allow for more compensation (Simpfendorfer et al., 2000; Cortés, 2004). The same catches used in the base case model were used in this model.

Sensitivities 3-6: Parameters increased by 10%

Parameter values (R^* , Z , M and selectivities) in these four sensitivity analyses were increased by 10% from their base case values. This enabled the determination of which parameter's had the largest overall effect on the model's prediction of total and mature biomass in 2006 and 2025 when compared to virgin biomass. The same catches used in the base case model were used in this model.

Sensitivity 7: BLLOP CPUE series removed

The BLLOP catch rate series was the only series taken from the directed shark fishery. There is uncertainty as to whether the drop in CPUE seen after 1999 in this series was a factor of actual population declines for the dusky shark or an artifact of the species being placed on the prohibited species list in 2000. I removed the series from this sensitivity analysis to test whether this sharp decline from 1999 to 2000 was affecting the fit of the model. The same catches used in the base case model were used in this model.

Sensitivity 8: Combined CPUE series

I combined all four of the catch rate series into one catch rate and used only this series in this sensitivity analysis (Table 2-7 and Figure 2-1). The same catches used in the base case

model were used in this model. The series were combined using a GLM with the CPUE's as the dependent variable and year and individual series as the independent variables. The results of the GLM were divided by the mean CPUE before being used in this analysis. It should be noted that this combined series contained the entire BLLOP series and therefore, the caveats dealing with the dusky shark being placed on the prohibited species list (see above) may still apply.

Sensitivity 9: Selectivity

The age frequency distributions for two (BLLOP and VIMS) of the data sets used for the selectivity analysis showed that age-zero animals were the most commonly caught. The selectivities used in the base case and all other scenarios and sensitivity analysis assumed exploitation began at age 1. In this analysis, I changed the slope of the double logistic distribution for all four series to allow for the age-zero class to be fully exploited to fishing (Table 2-8). The same catches used in the base case model were used in this model.

Results

Catches

The highest catches of dusky sharks occurred in the 1990s with both landings and discards peaking in the mid 1990s (Figure 2-2). Commercial landings of dusky sharks were highest in 1992-2000 and peaked in 1995 and 1996 (Figure 2-2). Catches dropped off drastically in 2001 after dusky sharks were placed on the prohibited species list (Figure 2-2). Commercial discards increased from 1993 to 1995 with a very large peak in 1994 (Figure 2-3.). Recreational catches were highest during the first year of reporting (1981) but remained high through 1992 (Figure 2-4). After a very large decrease in recreational catches in 1993, catches rose in 1994-1997 and fell again in 1998 (Figure 2-4). Recreational catches have remained low since 1998. The majority of the catches come from the MRFSS survey (Figure 2-4). Total catches of dusky sharks peaked in 1995 (Figure 2-5). The amount of dusky sharks caught dropped dramatically

after 2000 (Figure 2-5). The dusky shark became officially protected in 2000; however, landings and discards were still reported after this year. Some of these reports can be attributed to misidentification, but it is also likely that dusky sharks were illegally caught and landed after 2000. This species has a high at-vessel mortality rate (Morgan and Burgess, 2007) when caught on bottom longline gear and it is possible that rather than discard the dead animals, fishers kept and landed them.

Results for the general canvass data indicate the majority of dusky sharks were landed in the MA (52.5%) followed by the SA (27.4%) and GOM (20.1%) (Table 2-9). The CFL showed the majority of dusky sharks represented in the CFL were landed in the GOM (64.4%) followed by the SA (26.5%) and MS (9.1%) and the QMS, which only covers the southeast US region, reported the majority of dusky sharks were caught in the GOM (53.8%) followed by the SA (46%) and no landings were reported for the MA region (Table 2-9). The recreational data sets showed that overall the majority of dusky sharks were caught in the MA (Table 2-9).

Catch Rates

The four catch rate series analyzed all showed decreasing trends over time (Figure 2-6). The VIMS fishery-independent data set began to show an increase in 2006; however, this was the last year of data so it is unclear whether this reflects an actual increase in dusky shark relative abundance or is due to some other factors. The two observer programs (BLLOP and PLLOP) showed declines in catch rates after 1999, with the BLLOP showing substantial declines. The BLLOP data set began to show an increase in catch rates by 2006, but these rates were still much lower than those seen in the early years of the program. More years of data will have to be collected to determine if this increasing trend continues.

Catch rates (standardized) for the VIMS data set were high at the beginning of the time series (1974) but dropped dramatically by 1981 (Figure 2-7A). Dusky shark catch rates

remained very low until 2006, when they became even higher than those seen in the first three years (Figure 2-7A). Year ($P < 0.0001$) was included in the final model for the proportion of positive catches and area ($P < 0.0001$) was significant in the model for positive catches.

The BLLOP program was a voluntary program from 1994 to 2001 and mandatory from 2002 to 2006. Catch rates were standardized separately for the two time periods in an effort to compensate for any differences between observer coverage during the two time periods (John Carlson, personal communication). Catch rates were the highest during the voluntary years (1994-1999) and dropped to the lowest in 2000 (Figure 2-7B). The program only observed vessels in the SA during this year, which may account for the very low catch rate. The mandatory years all had relatively low catch rate values with a slight increase by 2006. The factors year, area, bait type, hook were included in the final model for the proportion of positive catches and the factors year, season, area and time of day were included in the final model for the positive catches for the voluntary time period. The final models for the mandatory time period included the factors year, area and set depth for proportion of positive catches, and year for positive catches.

The PLLOP catch rates were higher in 1992 and 1994 than any other year but over the whole time series remained very low (Figure 2-7C). The lowest catch rate was in 2003 after which catch rates began to climb slowly through 2006, which was the highest catch rate since 2000. The factors area, year and the interaction between area and tuna catch rate (TQR) were included in the final model for proportion of positive catches. Year, area, swordfish catch rate (SQR), TQR, and the interactions between year and area, year and quarter and SQR and area were included in the final model for positive catches.

The LPS data set remained low for the entire time series but there was a decrease in the mid 1990s (Figure 2-7D). This decrease coincides with the decrease in recreational catches reported by the MRFSS dataset. The catch rate series started high in 1986 and had several slight increases and decreases through 1993. The catch rates have remained low since 1994, with the lowest rate occurring in 2006. The nominal catch rates were higher than the standardized catch rates through the entire time series, but both catch rates did followed a similar pattern (Figure 2-7D). The factors state and year were included in the final model for the proportion of positive sets and the factors interview type and year were included in the final model for the positive catches.

Selectivity Curves

The LPS dataset had the smallest age structure and the BLLOP dataset had the largest age structure (Appendix C). These results are most likely a factor of the sampling designs of the programs. The LPS program samples from recreational fishers and the BLLOP program observed the predominant fishery for dusky sharks and sampled from a much larger area. Age frequency distributions (Appendix C) showed that age-0 animals were most commonly caught in the BLLOP and VIMS data sets. The PLLOP and LPS data sets had the highest age frequency distributions for dusky sharks ages 0, 4 and 5 (Appendix C). Selectivity curves for the VIMS and BLLOP datasets showed a steep increase from age 0 to approximately age 5 and 7 respectively, with the BLLOP selectivity curve staying relatively steady until age 22 after which it began a decline (Appendix C). The VIMS selectivity curve remained fairly steady until age 16 followed by a decline. The LPS selectivity curve had a sharp increase from age 0 to at 5 and then began a shallow decrease after age 8 (Appendix C). The PLLOP selectivity curve also had a steady increase from age 0 to 5, at which point it remained fairly steady until age 16 when the

curve began a steady decline (Appendix C). Parameter estimates for these selectivity curves are shown in Appendix D.

Base Case Model

The base case model showed that the current median total population of dusky sharks (B_{2006}) has been reduced to 43% of the virgin biomass (B_0) and similar results (47% of B_0) were seen for the median mature biomass in 2006. Estimates of the parameters R^* and z were 20,548 and 0.35 respectively (Table 2-10). The posterior distribution was similar to the prior distribution for the parameter R^* , indicating that the data were uninformative for this parameter (Figure 2-8A). The majority of the distribution for R^* occurred around 20,000 for both the prior and posterior distributions and both distributions flattened out around 50,000 (Figure 2-8A). The prior and posterior distributions for the remainder of unknown parameters were different; suggesting the data were informative for these parameters (Figures 2-7B-F). The prior distribution for z descended from around 0.3 to 0.5, while the posterior distribution peaked around 0.6, but both distributions included similar values (Figure 2-8B). The prior distribution for $qvims$ peaked at the beginning (~ 0.1) and end (~ 1) of the distribution but remained relatively flat in between these peaks (Figure 2-8C). The posterior distribution peaked around 0.3 and then had a second smaller peak around 0.45 (Figure 2-8C). The two distributions had a similar range of values (Figure 2-8C). The prior and posterior distributions for $qbllop$ were very different and did not overlap or share a similar range of values (Figure 2-8D). The prior distribution peaked around 6, while the posterior distribution peaked around 0.3 (Figure 2-8D). The distributions for the parameter $qpllop$ had different peaks, with the prior peaking around 0.2 and 1 and the distribution continuing past 1.5 (Figure 2-8E). The posterior distribution peaked around 0.4 and did not go past 1 (Figure 2-8E). The posterior distribution for $qlps$ had several peaks throughout the distribution while the prior had two peaks around 0.5 and 1.3 (Figure 2-8F). The

distributions both had high proportions occurring around 0.7, but the prior distribution continued past 2, while the posterior distribution did not go past 1 (Figure 2-8F).

The catch data used in this model ended in 2006 and the model continued to estimate the population through 2025 (B_{2025}) (Figures 2-8 and 2-9). This simulated a fishing mortality rate of zero for the remainder of the years; however, total B_{2025}/B_0 (43% of B_0) was still similar to those levels seen in 2006 and the mature B_{2025}/B_0 (41% of B_0) was reduced even further (Table 2-10). These trends indicate long recovery times from overfishing, where 20 years of no fishing caused only slight increases in population biomass in the simulations (Figure 2-9 and 2-9).

Scenario 1: Commercial and Recreational Catches Closure in the Future

Continuing the catches through 2025 resulted in a slightly more pessimistic total (37% of B_0) and mature (36% of B_0) B_{2025}/B_0 when compared to the results of the base case model (41% and 43% of B_0 respectively) (Table 2-10). Declines in mature biomass began in 1974 and continued through 2025, with large declines occurring in the early 1980s (Figure 2-9). Thus, the model predicted that mortality due to discards and illegal landings of dusky sharks in the future would prevent recovery of dusky shark populations from the current population levels found today.

Scenario 2: Simulated Closure by Removal of North Carolina Catches

The median mature (34% of B_0) and total (35% of B_0) B_{2025}/B_0 were very similar to the results from scenario 1 (reduced by 7% and 8% respectively from the base case model) (Table 2-10). Mature biomass declined from 1974 to 2025, with the largest declines occurring in the mid 1990s (Figure 2-9). These results suggest that increasing the time/area closure to include all of North Carolina will have little effect, positive or negative, on the population size of the dusky shark.

Scenario 3: Simulating Reduced Soak Times

Reducing the soak time to less than 10 hours caused a slight decrease in median total (8%) and mature (6%) B_{2025}/B_0 (Table 2-10). These results were very similar to those found in scenarios 1 and 2 with median total and mature B_{2025}/B_0 being 35% of B_0 (Table 2-10). This would suggest that implementing a restriction on the amount of soak time for the bottom longline fishery would do little to further protect the dusky shark from population declines estimated in the base case model (Figure 2-9).

Scenario 4: Increased Commercial Catch Series

The increase in commercial catches resulted in a slightly more pessimistic outcome when compared to the base case model. Total B_{2006}/B_0 had a median value of 36% of B_0 and B_{2025}/B_0 had a median value of 35% of B_0 (Table 2-10). This was a reduction in median population size of 7% and 8% respectively from the results of the base case model. Mature B_{2006}/B_0 and B_{2025}/B_0 had median values of 43% and 34% of B_0 respectively, which was a reduction of 5% and 7% respectively from the base case model (Table 2-10). Mature biomass began to decrease in 1974 and continued through the entire time series. The most significant declines in population biomass occurred in 1974-2001 (Figure 2-9).

Scenario 5: Reduced Recreational Catch Series

Decreasing recreational catches resulted in a slightly less pessimistic outcome when compared to the base case model, with a slight increase in biomass towards the end of the time series (Figure 2-9). The median total B_{2006}/B_0 and B_{2025}/B_0 were 49% and 48% of B_0 respectively, which was an increase in median population size of 6% and 5% respectively (Table 2-10). Median mature biomass B_{2006}/B_0 (52% of B_0) was increased by 4% and by 6% in B_{2025}/B_0 (47% of B_0) (Table 2-10). Mature biomass began decreasing in 1974 with large decreases in

mature biomass starting in 1986. The biomass began to increase in 2016 and this increase continued through 2025 (Figure 2-9).

Sensitivity 1: R^* Prior Distribution Increased

Increasing the prior distribution of R^* resulted in an estimated median value of 62,247 (Table 2-10). This caused very significant changes to percent biomass (total and mature) reduction when compared to the base case model, with the median total and mature B_{2006}/B_0 and B_{2025}/B_0 being at more than 80% of B_0 , which is twice the level found in the base case model (Table 2-10). Median total B_{2006}/B_0 was 82% of B_0 and B_{2025}/B_0 was 84% of B_0 (Table 2-10). Mature median B_{2006}/B_0 and B_{2025}/B_0 was 82% of B_0 (Table 2-10). Mature biomass declined fairly steadily in 1974-2013 at which point the biomass began increasing slightly (Figure 2-10).

Sensitivity 2: Z Increased

Increasing the prior of Z resulted in a median estimate of $Z= 0.54$ (Table 2-10) and had the opposite effect of increasing R^* and median total and mature biomasses were significantly reduced when compared to the base case model. The median mature and total B_{2006}/B_0 (37% and 28% of B_0 respectively) and B_{2025}/B_0 (35% and 28% of B_0 respectively) were reduced by over 10% when compared to the base case model (Table 2-10). Mature biomass decreased from 1974 to 2006, increased slightly in 2008 and 2009 and then continued to decrease through 2025. Larger decreases in mature biomass were seen in the early and mid 1990s (Figure 2-10).

Sensitivity 3: R^* Increased by 10%

This sensitivity analysis (R^*) was the only one of the four that resulted in higher total and mature B_{2006}/B_0 and B_{2025}/B_0 biomasses compared to the results of the base case model (Table 2-10). Total and mature B_{2006}/B_0 were 50% of B_0 and B_{2025}/B_0 were 46% and 44% of B_0 respectively, which were increases of 7%, 2%, and 3%, respectively, when compared to the base

case model (Table 2-10). Mature biomass was larger but followed a similar trend to that seen in the base case model (Figure 2-10).

Sensitivity 4: Z Increased by 10%

Increasing Z caused total and mature B_{2006}/B_0 and B_{2025}/B_0 to decrease compared to the results of the base case model (Table 2-10). Biomasses were reduced from ~40% in the base case model to around 20% of B_0 for total B_{2006}/B_0 and B_{2025}/B_0 and for the mature B_{2025}/B_0 (Table 2-10). The mature B_{2006}/B_0 was slightly higher (29% of B_0) but was still reduced with respect to the base case model (48% of B_0) (Table 2-10). Mature biomass estimates followed a trend similar to that of the base case model but appeared to drop off more rapidly in the late 1990's (Figure 2-10).

Sensitivity 5: M Increased by 10%

Increasing M lead to the largest change in biomass estimates when compared to the base case model and resulted in the most pessimistic outcome of all sensitivity and scenario analyses (Table 2-10). Total B_{2006}/B_0 and B_{2025}/B_0 and mature B_{2025}/B_0 were all reduced from ~40% of B_0 (base case) to less than 10% of B_0 (Table 2-10). Mature B_{2006}/B_0 was reduced from 48% of B_0 in the base case model to 16% of B_0 in this model (Table 2-10). Mature biomass had a much more dramatic drop off in the mid to late 1990s, when compared to the base case model (Figure 2-10).

Sensitivity 6: Selectivities Increased by 10%

Changing the selectivity values caused the smallest changes to the overall population size when compared to the results of the base case model (Table 2-10). The results were very similar to those predicted by the base case model. Total B_{2006}/B_0 and B_{2025}/B_0 was reduced by 3% (39% of B_0) and 5% (38% of B_0) compared to the base case model respectively and mature B_{2006}/B_0 and B_{2025}/B_0 was reduced by 4% (44% and 37% of B_0) when compared to the base case model

(Table 2-10). Mature biomass followed a very similar trend to that seen in the base case model (Figure 2-10).

Sensitivity 7: BLLOP CPUE Series Removed

Removal of the BLLOP CPUE series resulted in slightly higher total and mature B_{2006}/B_0 and B_{2025}/B_0 compared to the results of the base case model (Table 2-10). The mature B_{2006}/B_0 and B_{2025}/B_0 was reduced to 52% and 47% of B_0 respectively. This was an increase of 5% of B_{2006}/B_0 and 6% of B_{2025}/B_0 compared to the base case model (Table 2-10). Total B_{2006}/B_0 and B_{2025}/B_0 was reduced to 48% of B_0 , which was an increase of 5% compared to the base case model (Table 2-10). Mature biomass through the time series was similar to those levels from the base case model (Figure 2-10).

Sensitivity 8: Combined CPUE Series

The use of a single catch rate series did not change the results from the base case model, except for mature B_{2006}/B_0 , which was 1% higher than in the base case model (Table 2-10). However, the confidence intervals of the series (Table 2-7) were very poor and may suggest combining the catch rate series is not the most appropriate method. Mature biomass through the time series was also the same as in the base case model (Figure 2-10).

Sensitivity 9: Selectivity

Allowing for full exploitation of the age-zero age class caused the population to be more reduced compared to the base case model for all results except for mature B_{2006}/B_0 . Total median B_{2006}/B_0 and B_{2025}/B_0 was reduced to 39% of B_0 and mature B_{2025}/B_0 was reduced to 37% of B_0 , which were reductions of 5% and 4% respectively of the base case model (Table 2-10). Mature B_{2006}/B_0 was increased to 49% of B_0 , which was an increase of 2% compared to the base case model (Table 2-10). Mature biomass declined through the time series until the last few years, when it began to increase slightly (Figure 2-10).

Discussion

My results show that the impacts of previous fishing on the dusky shark would be difficult to overcome, even with the implementation of time/area closures, gear modifications and/or catches being reduced for another 20 years. The base case model, all scenarios and all sensitivities except for one (sensitivity 1) resulted in the dusky sharks in the northwestern Atlantic Ocean being at less than 60% of virgin biomass. Recent work has shown that the Maximum Sustainable Yield (MSY) for the dusky shark and other shark species may be well above 50% of the carrying capacity, due to a low value of z and the high inflection point of the population growth curve (Cortes, 2008; Simpfendorfer et al., 2008; Cortes et al., 2006). This would suggest that the dusky shark could sustain much less fishing pressure than previously thought, under the assumption that MSY occurs at 50% of the carrying capacity. Fisheries managers must consider whether MSY should be increased for the dusky shark and whether the results of these models indicate the population is overfished.

The declines seen here are similar to those seen in the school shark population (13-45% of B_{1995}/B_{1927}) in southern Australia (Punt and Walker, 1998). Increasing the parameter values for M resulted in the most significant changes in percent biomass (total and mature) reduction when compared to the base case model. The scenarios that looked at the effects of alternative management plans such as increasing the time/area closure or reducing the soak time did not provide very encouraging results and indicated that biomass reductions would continue into 2025. The impacts of fishing already placed on this species may be difficult to overcome even with catches being reduced for another 20 years. The reductions in biomass seen in these models are due to both commercial and recreational fishing that increased in the 1980s and 1990s and continues today, albeit at much reduced levels combined with the life history patterns of the dusky shark. This species has a long lag time between birth and age at sexual maturity, as well

as a very long reproductive life cycle (three years), with only 1/3 of all females reproducing in a single year. This long lag between life-stages and their low reproductive effort makes it very difficult for this species to quickly replace animals lost to fishing mortality. Generations may be needed for this species to fully recover despite efforts to protect it by placing it on the prohibited species list, instituting a larger time/area closure and/or gear restrictions.

Cortés et al.'s (2006) dusky shark assessment used similar data but three different models (Bayesian surplus production, age-structured production model and catch-free age-structured production model). The results from that assessment were more pessimistic overall than those presented herein, with the surplus production model indicating a decline of greater than 80% in 2003 relative to virgin biomass, and the age-structured model showing declines of 62-80% of virgin biomass. Three sensitivity analyses in the present assessment-increasing the prior distributions for Z and M -resulted in a reduction in biomass similar to those found in Cortés et al. (2006). Despite the differences, both assessments indicated that the dusky shark biomass has been greatly reduced with respect to virgin levels. The decline in population size seen in both assessments is a consequence of declining catch rates, increased fishing mortality during the 1990s, a decrease in biomass over time and multiple age classes being represented in the catch. These factors when combined with the dusky shark's life history characteristics (slow growth, late age at maturity, long reproductive cycles), make this species very susceptible to overfishing.

The differences between these two stock assessments are most likely due to the use of different models and parameter estimates and indicate the importance of model selection during the assessment process. Age-structured models differ from production models in that they consider cohorts and follow these cohorts separately throughout the simulation. Production models combine growth, reproduction and mortality, making it impossible to look at the

“dynamic” interactions occurring between these processes (Haddon, 2001). Age-structured models allow multiple gear types and biological information to be included, whereas production models do not (Simpfendorfer and Burgess, 2002). Bayesian modeling allows for the incorporation of uncertainty during the initial stages of the development of the model and the use of historical fishing data (Punt and Hilborn, 1997). Ludwig and Walters (1985) suggested that the selection of a model used in a stock assessment should be dependent on how much information is available and that in some instances simpler production models can provide better estimates. The life history patterns of the dusky shark, its exploitation in several fisheries and the availability of catch and catch rate data, fishery selectivities, growth, fecundity and maturity made an age-structured model appropriate for this species. Exploitation and natural mortality rates for dusky sharks vary between size classes; therefore the ability of an age-structured model to follow each size class separately is a useful tool for stock assessment and decision analysis. However, because of the uncertainty in many model parameters for this species, the use of several different models and assessment techniques likely adds to the strength of the overall findings and provides more insight to fishery managers.

Simpfendorfer and Burgess (2002) used a similar model to the one used in this assessment to assess the population of small coastal sharks in the northwest Atlantic Ocean. The results of their sensitivity analysis showed that the model was not very susceptible to changes in input parameters, catches and/or catch rates. However, they suggested that the high level of uncertainty for all of the results made it difficult to identify individual factors affecting the model. The results of all models in this assessment were also surrounded by a large level of uncertainty, except for sensitivity analysis 1 in which R^* was significantly increased. The reduction in uncertainty found in this sensitivity analysis suggests that R^* is a very important

parameter and that the input values for this parameter greatly drive the outcome of the model.

However, if one assumes the higher value of R^* is more realistic, then the outcome of the model sharply contrasts with the results of the base case scenario and those of Cortés et al. (2006).

Therefore it is unlikely that this higher value of R^* is applicable to the dusky shark.

Simpfendorfer et al.'s (2000) sensitivity analyses of an age and sex-structured model of the whiskery shark (*Furgaleus macki*), which used a similar model, showed that the results were most influenced by changes in catch and effort data. This was largely driven by the availability and accuracy problems (mis-identification and non-reporting) associated with these data and similar issues are thought to exist in the U.S. dusky shark fishery. Scenarios where commercial catches were increased and recreational catches were decreased to compensate for these issues resulted in changes to the reduction in percent biomass when compared to virgin levels. As would be expected, increasing the commercial catches resulted in a more pessimistic model outcome and decreasing recreational catches lead to a more optimistic model outcome. The results of the sensitivity analyses where parameters were increased by 10% showed that this model was most susceptible to changes made to the natural mortality (M) rates. Natural mortality rates for this species are already very high and increasing them by 10% drove the population size down to approximately 10% of virgin biomass. The fact that changes to M had such a large impact on the model outcomes is very important since the original values used were estimated through indirect methods and therefore there is a certain level of uncertainty surrounding them. Direct estimates of M could be determined through tagging and telemetry studies, but these can be expensive and time consuming. Tagging studies can become biased if information on tag recapture, tag shedding rates and tag reporting rates is missing or incomplete. Catch curve analysis can be used when tagging and telemetry studies are not practical but this

analysis comes with a number of assumptions that may not be a realistic representation of the population. As technology continues to improve, the use of tagging and telemetry studies for species such as the dusky shark will become more realistic (Simpfendorfer, 2005).

Two of the model scenarios (1 and 2) can be used to assess the utility of time/area closures in protecting the dusky shark. Scenario 1 can be used to simulate the current time/area closure into the future because it is based on the average amount of catches that have occurred since the closure was put into place. The results showed slightly lower biomass levels than in the base case model, which had no catches past 2006. This would suggest that the reduction in catches likely to be caused by the current time/area closure combined with the prohibited species classification, would not be able to stop the reduction in the population size over time. Scenario 2 where catches for 2007-2025 were reduced by removing North Carolina catches, gave results very similar to those from scenario 1. This suggests that the reduction in catches resulting from increasing the size of the time/area closure in the future (to include all of North Carolina) would do little to further protect the dusky shark. The apparent inability of time/area closures to protect dusky sharks is related to historically high fishing mortality rates, the time period of the closure (6 months), size of the closure, high movement rates and the biology of this species.

Morgan and Burgess (2007) suggested that placing a restriction on the length of soak time in the bottom longline fishery may reduce fishing mortality rates suffered by obligate ram ventilators such as the dusky shark. The length of soak time has also been found to be important in several other fisheries. Ward and Myers (2002) determined that the total mortality associated with increased soak time in pelagic longline fisheries might be fairly underestimated. They suggested this was due to animals being consumed while caught on a long line during long soak times or the catch falling off of the gear. The number of harbor porpoises caught in gillnet

fisheries in the Northwest Atlantic Ocean was found to be directly associated with soak time, with the longer soak-times catching more porpoises (Hood, 2002). In New Zealand a limit on the amount of soak time for set-net fisheries was implemented in order to reduce the number of fish destroyed by sea lice, and to reduce the amount of fishing gear lost during fishing operations (Francis, 1999). The calculations I made using the BLLOP dataset indicated that reducing the soak time in the bottom longline fishery to less than 10 hours would reduce the mortality of dusky sharks by 43%. Scenario 3 that used these data resulted in similar biomass reductions to those found in scenario 1. This would suggest that implementing a reduction in soak time on bottom longline gear would add little protection to the dusky shark and that their population will continue to decline over time.

The BLLOP catch rate series showed large declines after the dusky shark was placed on the prohibited species list (2000). This dataset reports observed catches and it is more realistic that fishers were able to change their fishing techniques to avoid catching dusky sharks once they became prohibited, then it is that the population dropped so substantially within a year or two. Due to the uncertainty of the accuracy of dusky shark catch rates in the last few years of data for this series, I conducted a sensitivity analysis where the BLLOP series was removed and a sensitivity analysis where the four catch rate series were combined into a single series. The removal of the BLLOP series caused only a slight increase in population size compared to the base model. The use of a single catch rate series provided the same results as the base case model. This would indicate that the three other catch rates series show a similar downward trend in catch rates over the time series and that including the BLLOP series in the base case model was appropriate and did not substantially affect the model outcome.

Age-zero and juvenile sharks were the most frequently caught according to the four datasets that included length data that was assigned to ages using an age length key (BLLOP, VIMS, PLLOP and LPS). Age length keys are useful when direct ageing of animals represented in the catch is not possible. However, errors in ageing can occur, leading to incorrect age length keys, which could in turn impact the results of an age-structured model. Errors in ageing could lead to incorrect growth rate estimates, age at sexual maturity estimates, selectivities and the subsequent partitioning of catch to incorrect ages. In these analyses, multiple ages were caught in all of the fisheries but very few adult animals were ever represented in the catch. Representation of multiple ages in both the commercial and recreational fisheries targeting dusky sharks should be of concern to fisheries managers because previous research has shown that low level exploitation of age-zero dusky sharks can be sustained only if no other age classes were caught (Simpfendorfer, 1999). This was highlighted in the sensitivity analysis that allowed for full exploitation of the age-zero age class. Increasing the exploitation of this age-class, while still allowing other age classes to be exploited, lead to a reduction in biomass compared to the base case model. The high exploitation of age-zero and juveniles in both the recreational and commercial fisheries appears to have a substantial impact on the ability of this population to increase in size (in terms of biomass).

Future work should include additional research into at-vessel mortality rates by soak time for the pelagic longline fishery, mark/recapture programs, post-release survivability, spatial distribution of different age classes and movement. Management should continue improving on species identification workshops for fishers and dealers and work on improving the quality of reported data. It may also be beneficial to investigate the effects that changes in the

methodologies of reporting to various datasets have had. Additional models that require fewer data could also be used to assess this species.

Table 2-1. Five alternative scenarios and nine sensitivity analyses of the base case model for the age-structured model (R^* = virgin biomass, z = steepness parameter, M = natural mortality, sd = standard deviation, BLLOP = Bottom Longline Observer Program, VIMS = Virginia Institute of Marine Science, LPS = Large Pelagic Survey, PLLOP = Pelagic Longline Observer Program and CPUE = Catch Per Unit Effort).

Model	Parameter
Scenario 1 Catch continues through 2025	Average commercial catches, BLLOP discards and recreational discards for 2002-2006 applied to 2007-2025
Scenario 2 Time/area closure	Average North Carolina catches (commercial and recreational) removed from 2007-2025 catch series used in scenario 1
Scenario 3 Reduced soak time/fishing mortality	Reduce bottom longline discards used in 2007-2025 catch series from scenario 1 by 43%
Scenario 4 Commercial catch series increased	Commercial catches increased by 25%
Scenario 5 Recreational catch series lowered	Recreational catches reduced by 25%
Sensitivity 1 R^* increased	Lognormal distribution: 60,000 (mean) /30,000 (sd)
Sensitivity 2 Z increased	Lognormal distribution: 0.6 (mean) /0.24 (sd)
Sensitivity 3 10% increase in R^*	Lognormal distribution: 22,000 (mean) /11,00 (sd)
Sensitivity 4 10% increase in z	Lognormal distribution: 0.33 (mean) / 0.01(sd)
Sensitivity 5 10% increase in M	Increased for each age
Sensitivity 6 10% increase in Selectivities	Increased for each data set (BLLOP, VIMS, LPS and PLLOP)
Sensitivity 7 Removal of one CPUE Series	Removed BLLOP CPUE series from model
Sensitivity 8 Combined CPUE series	Combined all four series into one single series
Sensitivity 9 Selectivity	Allowed age-0 animals to be fully exploited

Table 2-2. Total amount (kg) of dusky sharks reported landed and discarded in commercial fisheries from the following sources: Canvass South East (SE), Canvass North East (NE), Quota Monitoring System (QMS), Commercial Fisheries Logbook (CFL), Bottom Longline Observer Program (BLLOP) (discards) and Pelagic Longline Logbook (PLL).

Year	Canvass SE	Canvass NE	QMS	CFL	PLL	BLLOP discards	Total
1982					18		18
1983					5		5
1984					0		0
1985	2,251				0		2,251
1986	0				0		0
1987	38				5		43
1988	767				61		828
1989	451				240		691
1990	18,122				418		18,540
1991	15,031			0	321		15,353
1992	64,289		1,051	756	505	4,057	70,658
1993	27,455	17,134	1,248	898	1,606	1,732	50,073
1994	39,043	16,530	14,219	10,230	12,782	2,464	95,268
1995	44,924	13,956	148,581	106,893	26,061	9,375	349,791
1996	42,724	9,407	122,756	88,314	20,236	7,746	291,183
1997	16,467	3,484	33,226	23,904	11,448	2,097	90,626
1998	19,631	872	35,928	25,847	9,623	2,267	94,168
1999	31,779	20,602	26,566	19,113	6,951	2,005	107,017
2000	11,262	57,739	36,382	26,174	10,890	2,296	144,743
2001	66	370	66	47	255	57	861
2002	1,893	2,089	517	372	92	258	5,221
2003	3,677	6,886	128	92	66	269	11,118
2004	447	18	0	0	0	226	691
2005	289	107	0	0	0	18	415
2006	1814	83	0	0	0	114	2,012

Table 2-3. Constructed historical catch series (kg) for commercial and recreational landings and commercial (Pelagic Longline Logbook) discards of the dusky shark.

Year	Commercial	Recreational	Discards
1972	0	0	0
1973	1,000	28,000	2,000
1974	2,000	52,000	3,500
1975	3,000	78,000	5,000
1976	4,000	100,000	6,500
1977	5,000	125,000	8,000
1978	6,000	152,000	9,500
1979	7,000	175,000	11,000
1980	8,000	200,000	12,500
1981	9,000		14,000
1982	10,000		15,500
1983	11,000		17,200
1984	12,000		19,000
1985	13,000		20,500
1986	14,000		22,000
1987	15,000		23,500
1988	16,000		25,000
1989	17,000		26,500
1990			28,000
1991			30,000

Table 2-4. Total amount (kg) of dusky sharks reported discarded in the Pelagic Longline Logbook (PLL).

Year	PLL
1992	31,811
1993	16,663
1994	125,496
1995	14,577
1996	6,838
1997	12,835
1998	17,587
1999	5,469
2000	13,750
2001	1,347
2002	0
2003	0
2004	0
2005	0
2006	0

Table 2-5. Total amount (kg) of dusky sharks reported caught in recreational fisheries from the following sources: Marine Recreational Fisheries Statistical Survey (MRFSS), Headboat and Texas Parks and Wildlife Department (TXPWD).

Year	MRFSS	Headboat	TXPWD	Total
1981	225,432			225,432
1982	53,829			53,829
1983	132,814			132,814
1984	225,492			225,492
1985	117,196		4,009	117,196
1986	121,963	646	807	126,618
1987	152,322	534	0	153,663
1988	98,983	456	770	99,438
1989	72,173	672	0	73,615
1990	69,029	165	0	69,194
1991	90,768	386	0	91,154
1992	168,298	1,701	489	169,999
1993	17,122	1,983	0	19,593
1994	55,427	829	0	56,256
1995	46,568	967	0	47,536
1996	88,746	1,540	104	90,286
1997	81,575	1,085	81	82,763
1998	25,867	707	0	26,656
1999	29,548	1,666	0	31,214
2000	16,227	868	725	17,094
2001	35,550	147	0	36,423
2002	5,739	369	0	6,108
2003	15,791	221	400	16,012
2004	0	156	392	556
2005	19,168	74	130	19,634
2006	346	95	4,009	571

Table 2-6. Catch rate series (CPUE) and coefficient of variations (CV) used in analyses from the following four data sets: Virginia Institute of Marine Science (VIMS) (product of hooks per set and soak time (hrs.) per set), Large Pelagic Survey (LPS) (number of dusky sharks caught per 100 trips), Bottom Longline Observer Program (BLLOP) (number of hooks per set multiplied by the length of the longline (miles) per set and soak time (hrs.) per set)(provided by John Carlson, personal communication) and Pelagic Longline Observer Program (PLLOP) (number of dusky sharks caught per 1,000 hooks) (provided by Enric Cortés, personal communication).

Year	VIMS		LPS		BLLOP		PLLOP	
	CPUE	CV	CPUE	CV	CPUE	CV	CPUE	CV
1974	2.40	2.02						
1975	2.93	0.1						
1976	3.03	1.76						
1977	0.39	6.03						
1978	2.16	1.69						
1979	1.78	1.90						
1980	2.05	0.59						
1981	0.93	1.04						
1982	0.20	9.09						
1983	0.29	6.94						
1984	0.46	4.70						
1985	0.18	11.09						
1986			1.86	0.32				
1987	0.67	3.20	2.55	0.22				
1988			1.46	0.61				
1989	0.11	14.01	2.32	0.28				
1990	0.03	16.30	1.39	0.32				
1991	0.13	4.13	1.71	0.29				
1992	0.01	41.68	0.45	0.99			3.60	2.50
1993	0.11	7.38	1.35	0.49			1.71	1.19
1994			0.43	1.35	11.96	0.29	2.71	1.88
1995	0.08	9.28	0.66	0.88	18.76	0.24	1.11	0.77
1996	0.24	2.54	0.94	0.96	15.51	0.24	0.96	0.67
1997	0.00	77.62	0.68	1.19	23.79	0.25	0.46	0.32
1998	0.07	7.91	0.85	1.23	18.05	0.29	1.29	0.90
1999	0.28	2.99	0.77	1.80	19.21	0.36	0.35	0.24
2000	0.39	1.95	0.50	1.63	4.52	0.75	0.72	0.50
2001	0.19	3.68	0.41	2.40	7.82	0.44	0.28	0.20
2002	0.55	1.66	0.74	1.60	3.16	0.52	0.16	0.11
2003	0.27	3.21	0.52	1.13	5.11	0.36	0.08	0.06
2004	0.48	1.71	0.56	1.02	5.06	0.38	0.47	0.32
2005	0.52	1.48	0.58	1.09	6.30	0.49	0.37	0.26
2006	9.09	0.33	0.26	2.29	6.74	0.55	0.72	0.50

Table 2-7. Combined Catch Per Unit Effort (CPUE) series, upper confidence intervals (UCI) and lower confidence intervals (LCI).

Year	Combined		
	CPUE	LCI	UCI
1974	2.88	0.002	3921.45
1975	4.89	0.004	6662.28
1976	5.41	0.004	7362.95
1977	0.39	0.000	525.43
1978	2.26	0.002	3084.72
1979	1.55	0.001	2109.52
1980	2.03	0.001	2763.40
1981	0.66	0.000	901.64
1982	0.32	0.000	434.51
1983	0.35	0.000	475.43
1984	0.41	0.000	563.53
1985	0.31	0.000	425.91
1986	2.14	0.002	2856.09
1987	4.27	0.003	5694.24
1988	1.44	0.001	1914.50
1989	3.39	0.003	4524.26
1990	0.02	0.000	3.09
1991	0.02	0.000	3.82
1992	0.01	0.000	0.69
1993	0.01	0.000	0.51
1994	0.01	0.000	0.90
1995	0.10	0.002	5.50
1996	0.01	0.000	0.35
1997	0.06	0.002	2.14
1998	0.02	0.000	0.67
1999	0.02	0.000	0.73
2000	<0.00	0.000	0.02
2001	<0.00	0.000	0.04
2002	<0.00	0.000	0.01
2003	<0.00	0.000	0.02
2004	<0.00	0.000	0.02
2005	<0.00	0.000	0.03
2006	<0.01	0.000	0.30

Table 2-8. Selectivity parameters for the double logistic distribution fitted to age data allowing for full exploitation of age-zero animals, for the following four data sets: Bottom Longline Observer Program (BLLOP), Virginia Institute of Marine Science (VIMS), Large Pelagic Survey (LPS) and Pelagic Longline Observer Program (PLLOP) (Enric Cortés personal communication).

Data set	Parameter estimates			
	a_{50}	b	c_{50}	d
BLLOP	4	5250	32	4
VIMS	2	440	28	5
LPS	2	600	24	5
PLLOP	1.5	440	28	5

Table 2-9. Regional landings of dusky shark (GOM = Gulf of Mexico, SA = South Atlantic, MA = Mid-Atlantic region and UNK= unknown) from the general canvass (GC), quota monitoring (QMS), Coastal Fisheries Logbook (CFL) and recreational data sets for all years combined.

Region	Data set	Percent
GOM	General canvass	20.1
MA	General canvass	52.5
SA	General canvass	27.4
GOM	QMS	53.8
SA	QMS	46.0
UNK	QMS	0.2
GOM	CFL	64.4
MA	CFL	9.1
SA	CFL	26.5
GOM	Recreational	24.9
MA	Recreational	53.7
SA	Recreational	21.4

Table 2-10. Parameter outputs (R^* = virgin biomass, z = steepness parameter, $qvims$ = catchability of Virginia Institute of Marine Science (VIMS) survey gear, $qbllop$ = catchability of Bottom Longline Observer Program (BLLOP) fishing gear, $qlps$ = catchability of Large Pelagic Survey (LPS) fishing gear and $qppl$ = catchability of Pelagic Longline Logbook (PLL) fishing gear) from the Sampling Importance Resampling algorithm (median estimates with 95% confidence intervals (in parenthesis)) and population status for total and mature B2006/B0 (biomass in 2006/virgin biomass (1972)) and B2025/B0 (biomass in 2025/virgin biomass (1972)) (median estimates with 95% confidence intervals (in parenthesis)) for the base case model, five scenarios and nine sensitivity analysis.

	Model	R^* (CI)	z (CI)	$qvims$ (CI)	$qbllop$ (CI)	$qlps$ (CI)	$qppl$ (CI)	Total B ₂₀₀₆ /B ₀ (CI) %	Total B ₂₀₂₅ /B ₀ (CI) %	Mature B ₂₀₀₆ /B ₀ (CI) %	Mature B ₂₀₂₅ /B ₀ (CI) %
Base case	Base case	20,548 (8,813-33,656)	0.35 (0.23-0.57)	0.22 (0.01-0.60)	0.25 (0.14-0.66)	0.31 (0.01-0.66)	0.39 (0.13-0.64)	43 (0-65)	43 (0-65)	47 (0-70)	41 (0-64)
Scenario 1	Catch 2006-20025	19,426 (8,219-34,937)	0.33 (0.21-0.42)	0.41 (0.03-0.76)	0.36 (0.09-0.73)	0.48 (0.11-0.65)	0.44 (0.03-0.77)	40 (0-65)	37 (0-63)	45 (6-68)	36 (0-63)
Scenario 2	Removal of North Carolina catches	16,065 (6,686-31,453)	0.28 (0.2-0.45)	0.39 (0.06-0.72)	0.41 (0.01-0.76)	0.43 (0.03-0.7)	0.34 (0.03-0.7)	38 (0.60)	35 (0-59)	44 (18-63)	34 (0-58)
Scenario 3	Reduced discard mortality by 43%	17,618 (6,970-25,894)	0.26 (0.20-0.35)	0.27 (0.01-0.58)	0.65 (0.27-0.74)	0.55 (0.19-0.77)	0.54 (0.1-0.78)	38 (0-68)	35 (0-68)	45 (0-69)	35 (0-66)
Scenario 4	High commercial catch	19,814 (11,616-31,493)	0.29 (0.2-0.45)	0.52 (0.07-0.75)	0.36 (0.11-0.76)	0.23 (0.08-0.67)	0.46 (0.07-0.75)	36 (0-61)	35 (0-62)	43 (1-66)	34 (0-61)
Scenario 5	Low recreational catch	19,164 (10,860-29,338)	0.36 (0.2-0.69)	0.17 (0.001-0.65)	0.52 (0.06-0.70)	0.32 (0.08-0.73)	0.51 (0.03-0.72)	49 (5-68)	48 (4-69)	52 (15-68)	47 (5-67)
Sensitivity 1	R^* increased	62,247 (46,972-83,437)	0.40 (0.30-0.40)	0.55 (0.41-0.64)	0.47 (0.04-0.69)	0.68 (0.44-0.76)	0.46 (0.03-0.59)	82 (75-88)	84 (76-90)	82 (74-88)	82 (74-88)
Sensitivity 2	Z increased	16,350 (9,216-37,019)	0.54 (0.31-0.97)	0.49 (0.01-0.69)	0.60 (0.02-0.77)	0.50 (0.01-0.75)	0.34 (0.01-0.79)	28 (0-71)	28 (0-72)	37 (0-71)	35 (0-70)

Table 2-10. Continued

	Model	R* (CI)	Z (CI)	qvims (CI)	qbllop (CI)	qlps (CI)	qpll (CI)	Total B2006/B0 (CI) %	Total B2025/B0 (CI) %	Mature B2006/B0 (CI) %	Mature B2025/B0 (CI) %
Sensitivity 3	10% increase R	21,345 (13,340- 24,164)	0.28 (0.21- 0.46)	0.49 (0.05- 0.79)	0.46 (0.05- 0.75)	0.38 (0.32- 0.50)	0.1 (0.08- 0.70)	50 (8-55)	46 (8-55)	50 (11-56)	44 (7-53)
Sensitivity 4	10% increase Z	15,218 (13,263- 38,052)	0.23- 0.21- 0.55)	0.34 (0.13- 0.67)	0.27 (0.13- 0.60)	0.25 (0.2- 0.54)	0.27 (0.15- 0.71)	22 (8-69)	21 (7-68)	29 (12-70)	20 (7-68)
Sensitivity 5	10% increase M	21,085 (11,182- 24,193)	0.28 (0.2- 0.38)	0.67 (0.26- 0.76)	0.54 (0.20- 0.73)	0.55 (0.07- 0.76)	0.23 (0.02- 0.78)	9 (0-20)	8 (0-1)	16 (0-29)	9 (0-20)
Sensitivity 6	10% increase selectivity	19,186 (18,808- 23,462)	0.34 (0.2- 0.36)	0.36 (0.18 -0.5)	0.23 (0.01- 0.43)	0.13 (0.1- 0.45)	0.31 (0.16- 0.36)	39 (35-49)	38 (33-49)	44 (43-53)	37 (33-48)
Sensitivity 7	Bottom Longline Observer Program Catch Per Unit Effort removed	21,751 (10,980- 28,499)	0.31 (0.28- 0.50)	0.54 (0.28- 0.75)	0.37 (0.10- 0.71)	0.36 (0.05- 0.65)	0.26 (0.13- 0.71)	48 (12-61)	48 (12-62)	52 (19-62)	47 (13-60)
Sensitivity 8	Combined Catch Per Unit Effort series	20,372 (10,654- 26328)	0.30 (0.2- 0.45)	0.34 (0.09- 0.61)	0.08 (0.02- 0.60)	0.68 (0.06- 0.77)	0.44 (-0.07- 0.70)	43 (0-58)	43 (0-58)	48 (0-59)	41 (0-56)
Sensitivity 9	Selectivity	19,653 (6,013- 33,008)	0.20 (0.2- 0.41)	0.38 (0.18- 0.69)	0.50 (0.08- 0.77)	0.47 (0.09- 0.78)	0.31 (0.02- 0.66)	39 (0-65)	39 (0-65)	49 (0-69)	37 (0-64)

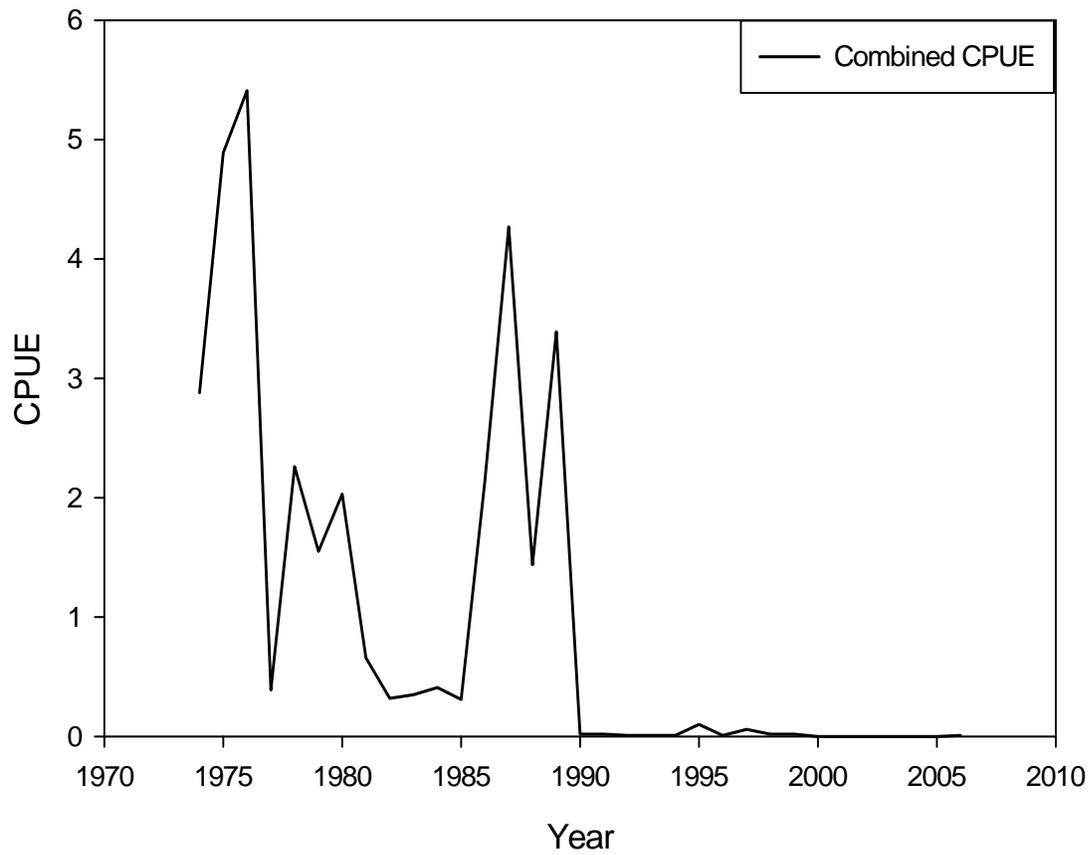


Figure 2-1. Combined Catch Per Unit Effort (CPUE) series. The single series includes the following four series; Virginia Institute of Marine Science (VIMS), Bottom Longline Observer Program (BLLOP), Pelagic Longline Observer Program (PLLOP) and Large Pelagic Survey (LPS).

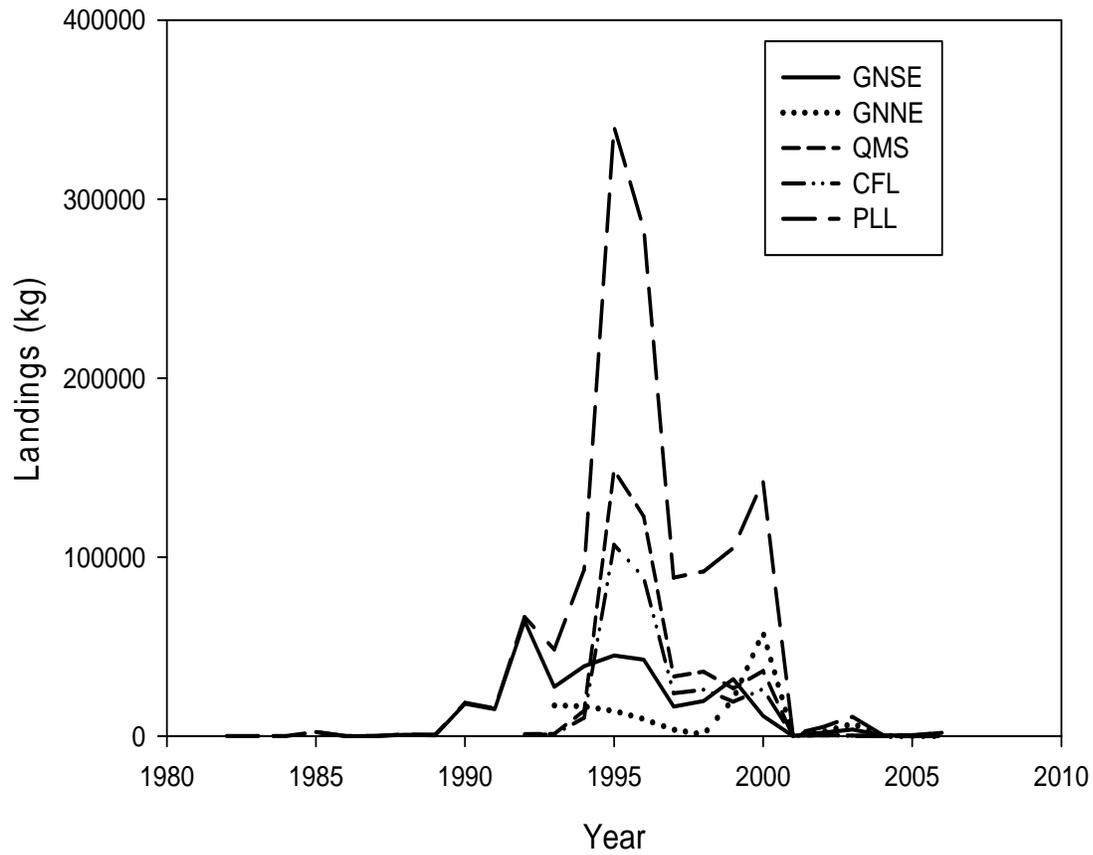


Figure 2-2. Dusky shark commercial landings (kg) from the general canvass SE and NE (GNSE and GNNE), quota monitoring system (QMS), Coastal Fisheries Logbook (CFL) and Pelagic Longline Logbook (PLL).

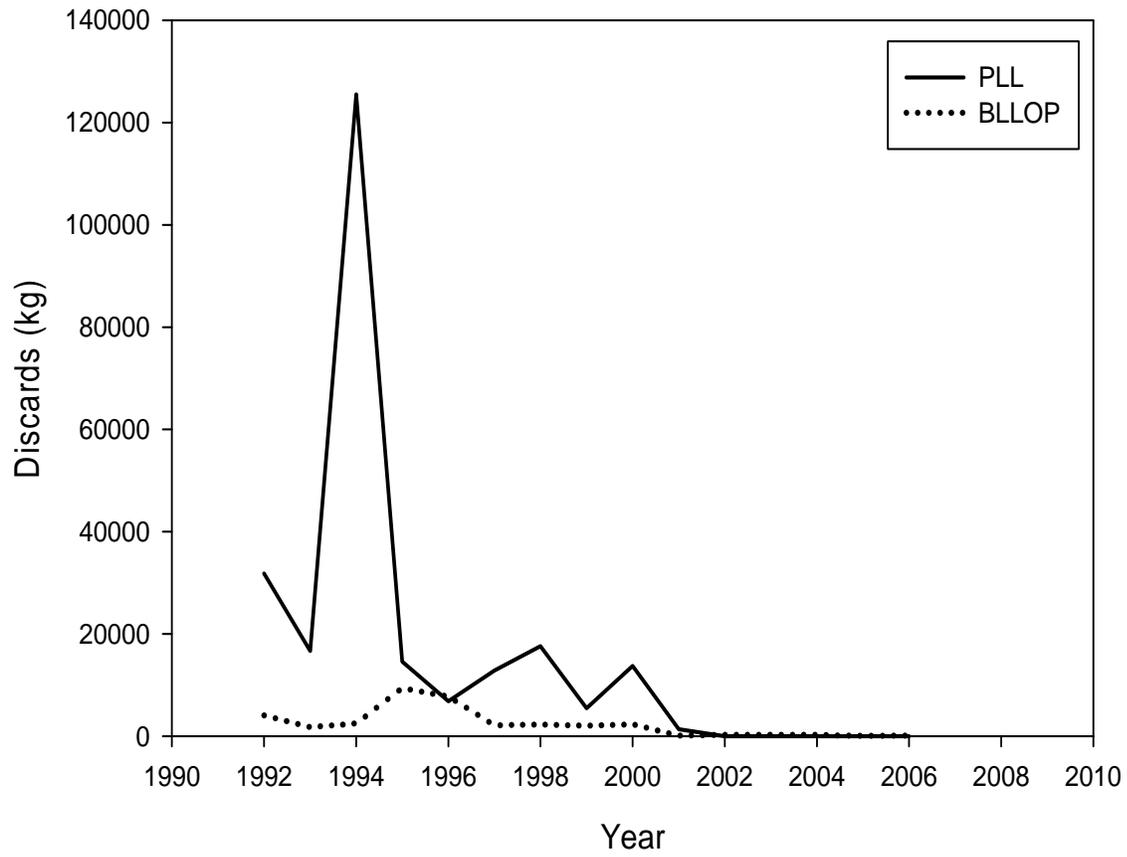


Figure 2-3. Dusky shark commercial discards (kg) from the Pelagic Longline Logbook (PLL) and Bottom Longline Observer Program (BLLOP).

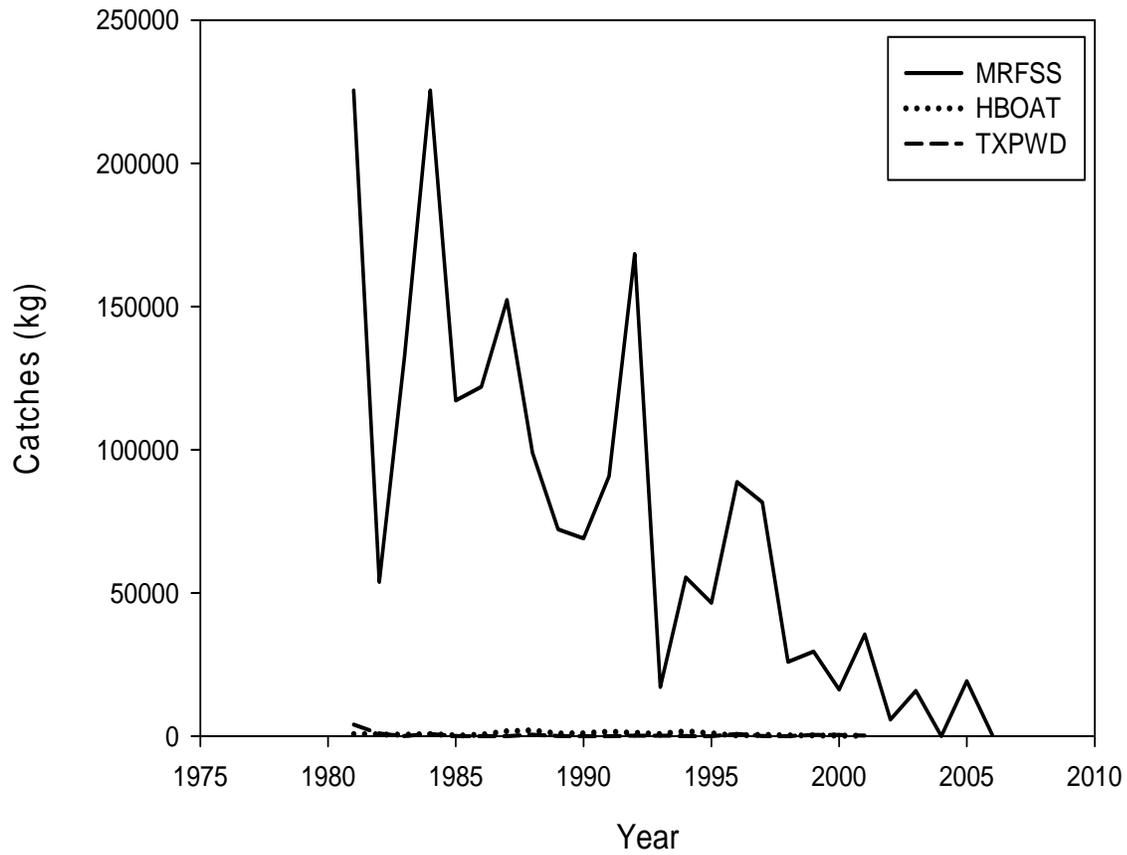


Figure 2-4. Dusky shark recreational catches and dead discards (kg) from the Marine Recreational Fishery Statistics Survey (MRFSS), Headboat (HBOAT) and Texas Parks and Wildlife Department (TXPWD).

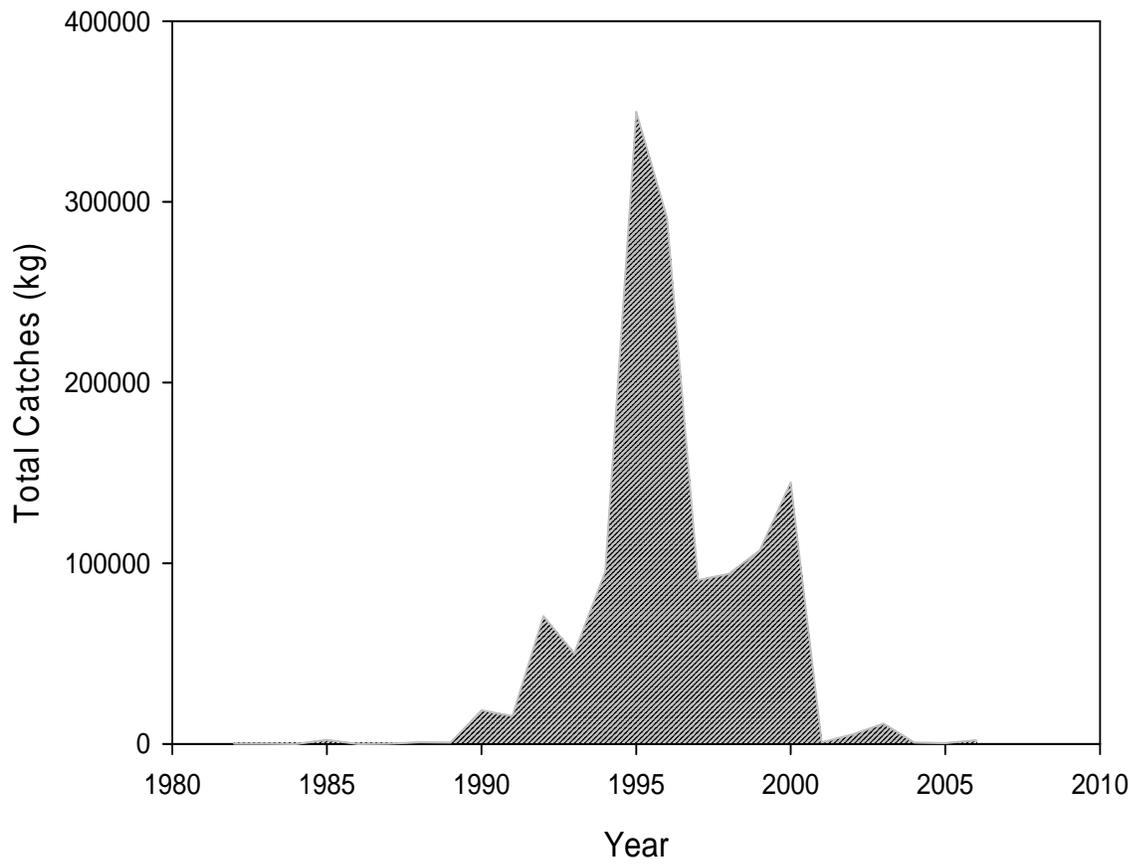


Figure 2-5. Total amount (kg) of dusky shark commercial catches and Bottom Longline Observer Program discards.

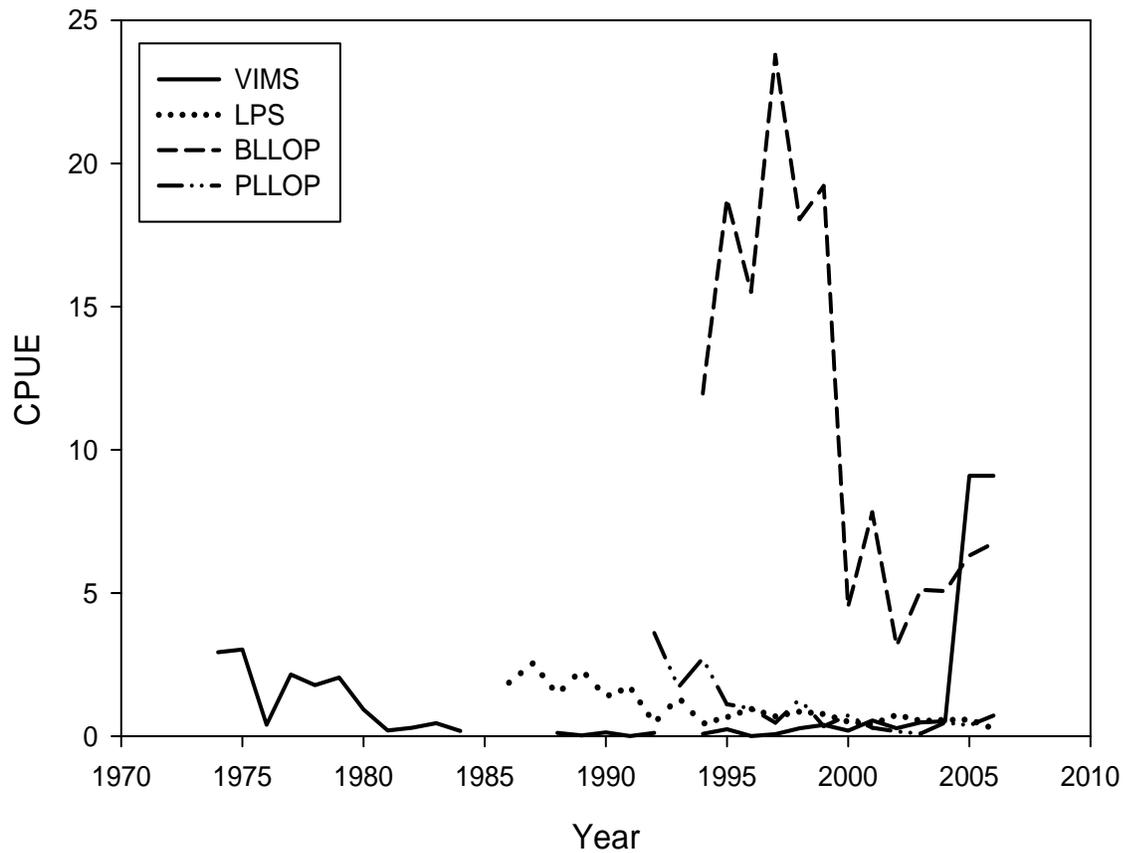


Figure 2-6. Combined Catch Per Unit Effort (CPUE) indices for the Virginia Institute of Marine Science (VIMS) (product of hooks per set and soak time (hrs.) per set), Large Pelagic Survey (LPS) (number of dusky sharks caught per 100 trips), Bottom Longline Observer Program (BLLOP) (number of hooks per set multiplied by the length of the longline (miles) per set and soak time (hrs.) per set)(John Carlson, personal communication) and Pelagic Longline Observer Program (PLLOP) (number of dusky sharks caught per 1,000 hooks) (provided by Enric Cortés, personal communication).

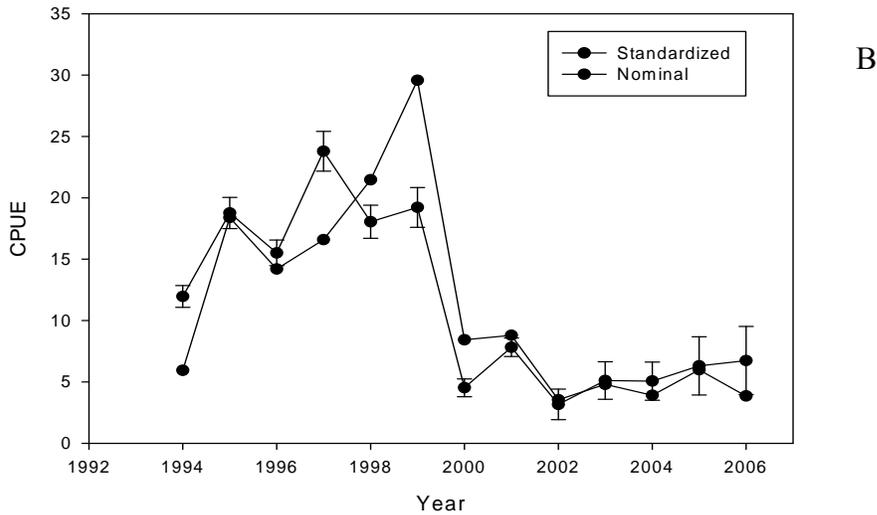
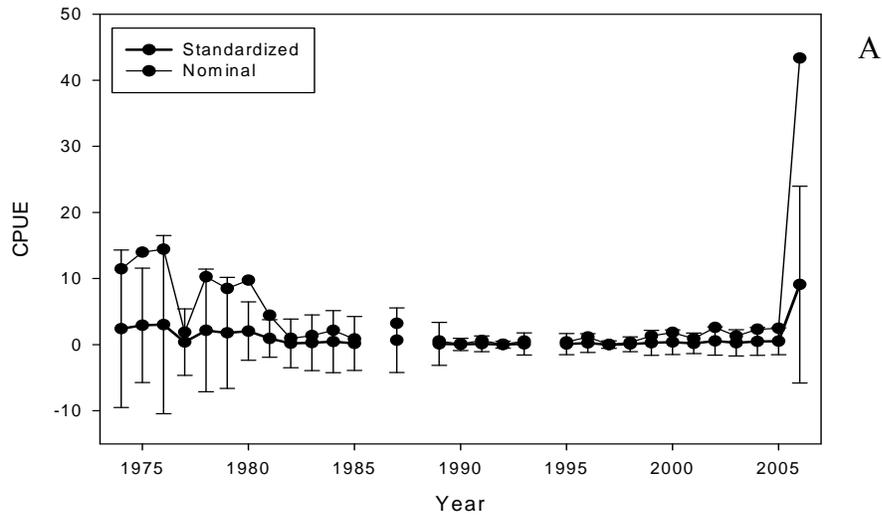
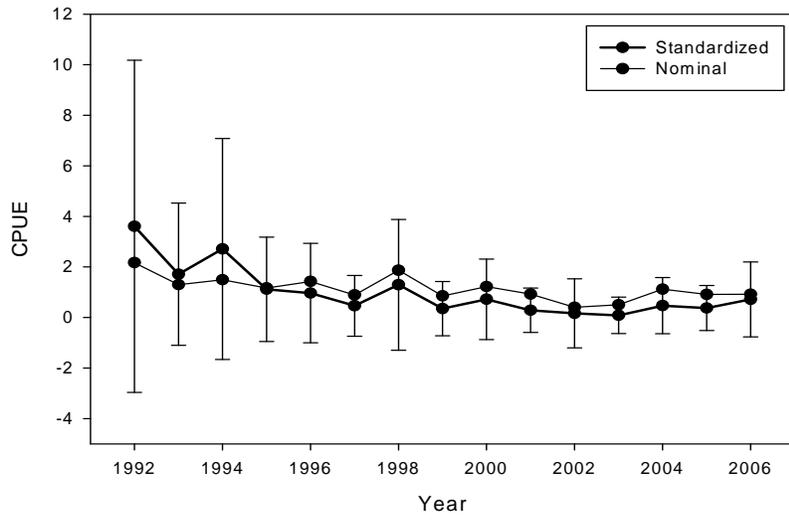
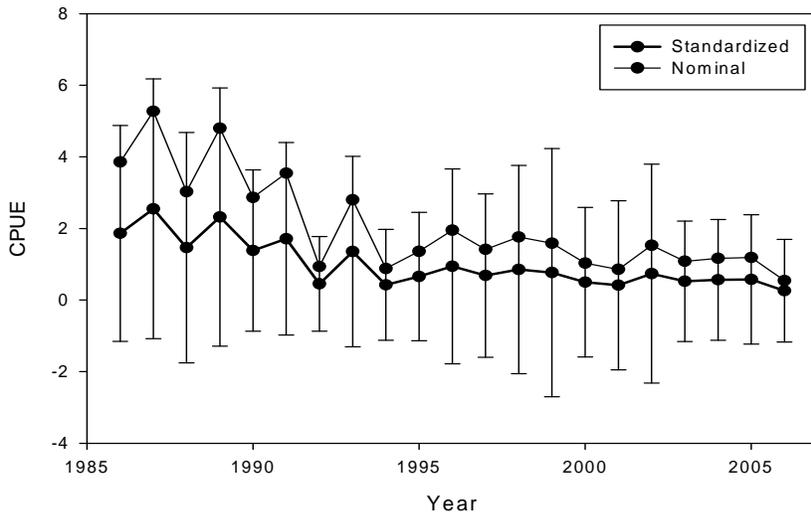


Figure 2-7. Standardized (with 95% confidence intervals) and nominal Catch Per Unit Effort (CPUE) indices. A) Virginia Institute of marine Science (VIMS) (product of hooks per set and soak time (hrs.) per set). B) Bottom Longline Observer Program (BLLOP) (number of hooks per set multiplied by the length of the longline (miles) per set and soak time (hrs.) per set) (John Carlson, personal communication). C) Pelagic Longline Observer Program (PLLOP) (number of dusky sharks caught per 1,000 hooks) (Enric Cortés personal communication). D) Large Pelagic Survey (LPS) (number of dusky sharks caught per 100 trips).

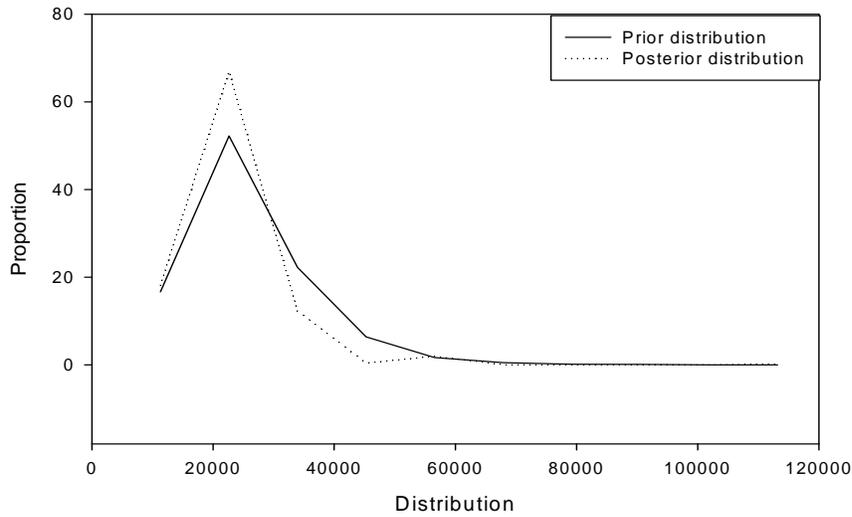


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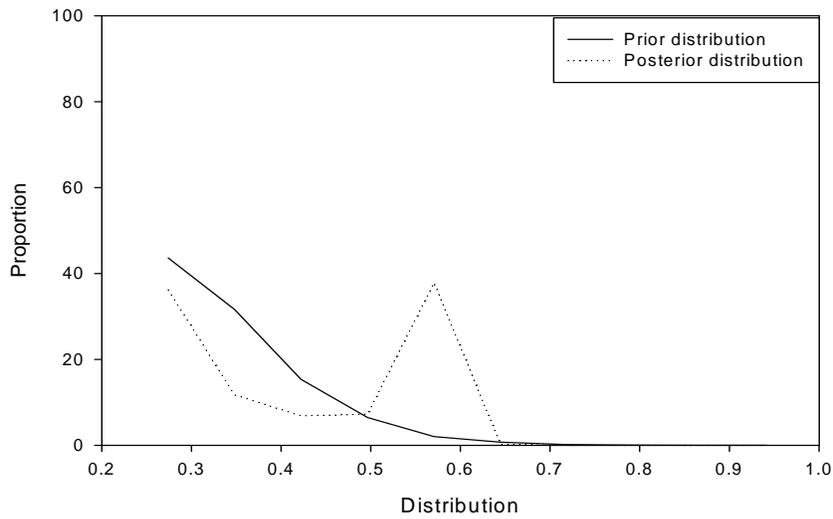


D

Figure 2-7. Continued.



A



B

Figure 2-8. Prior vs. posterior distributions for unknown parameters A) R^* (virgin biomass), B) z (steepness parameter), C) $qvims$ (catchability of Virginia Institute of Marine Science (VIMS) survey gear), D) $qbllop$ (catchability of Bottom Longline Observer Program (BLLOP) fishing gear), E) $qpllop$ (catchability of Pelagic Longline Observer Program (PLLOP) fishing gear), and F) $qlps$ (catchability of Large Pelagic Survey (LPS) fishing gear).

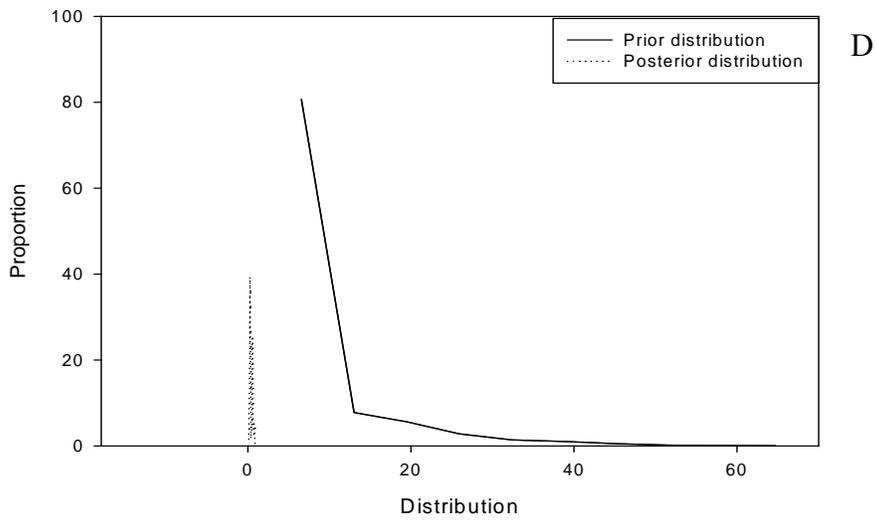
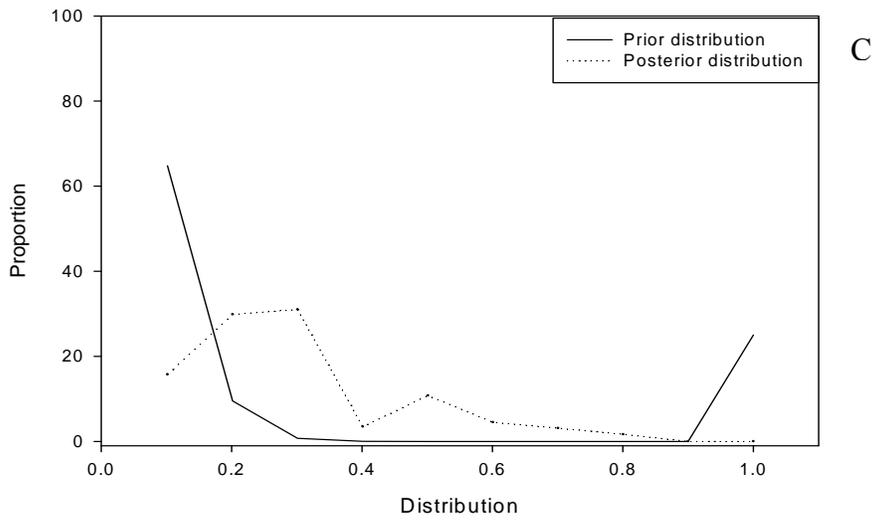


Figure 2-8. Continued.

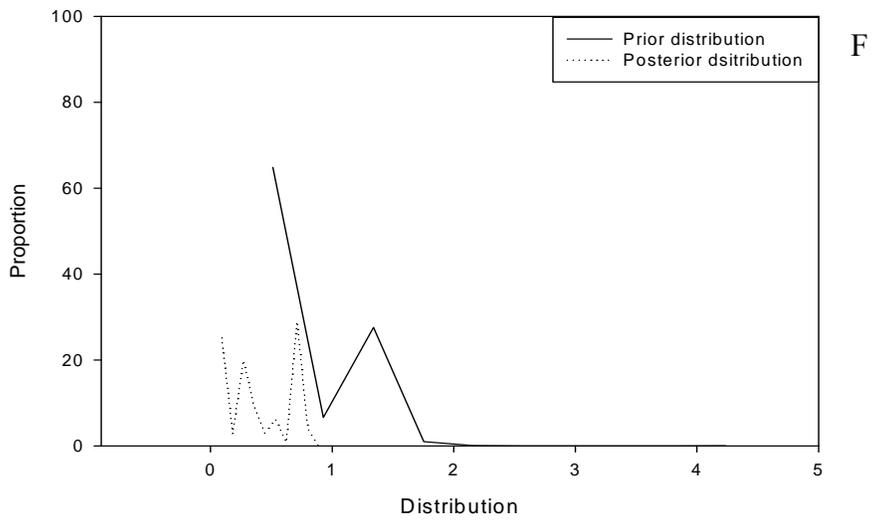
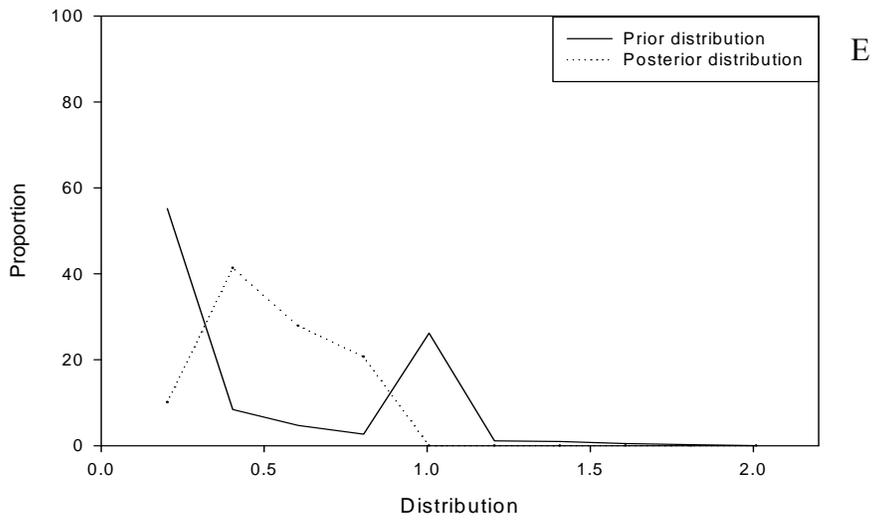


Figure 2-8. Continued.

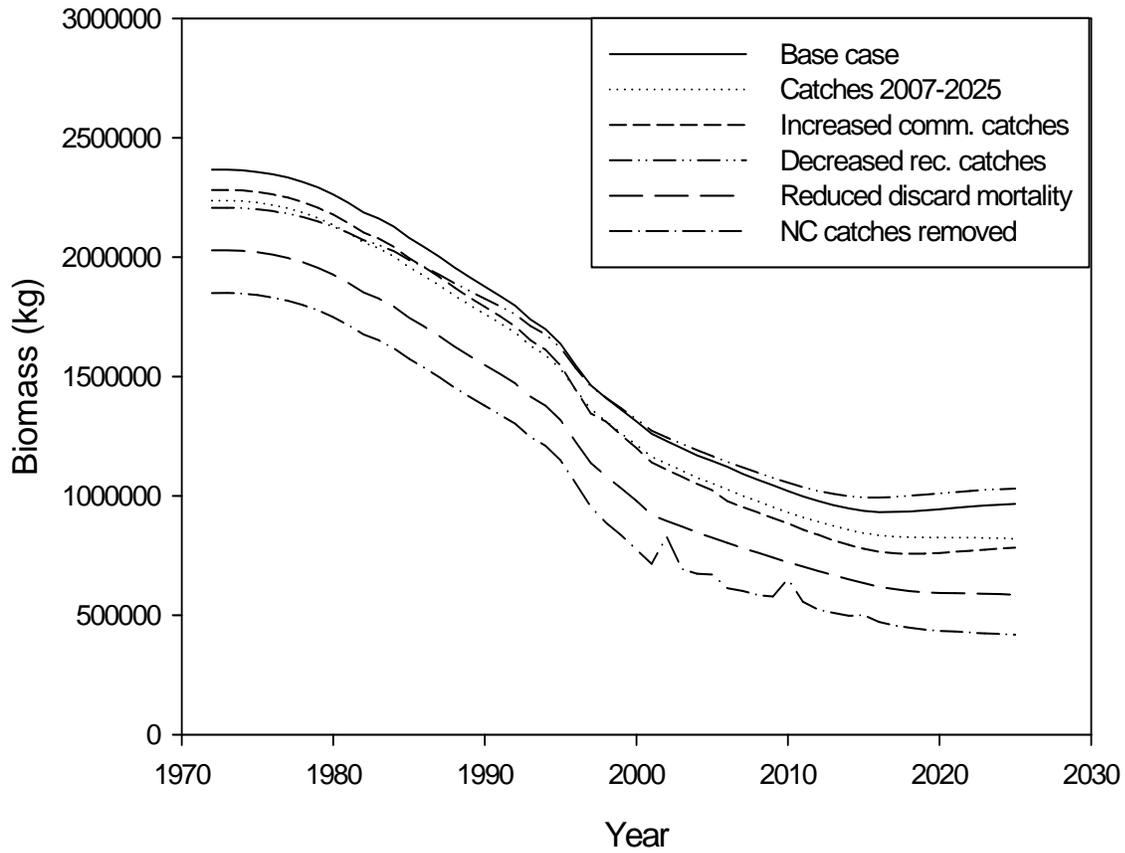


Figure 2-9. Mature median biomass (kg) for the base case and five scenarios (catches continued from 2007-2025, commercial catches increased by 25%, recreational catches decreased by 25%, reduced discard mortality and North Carolina catches removed) of the base case model.

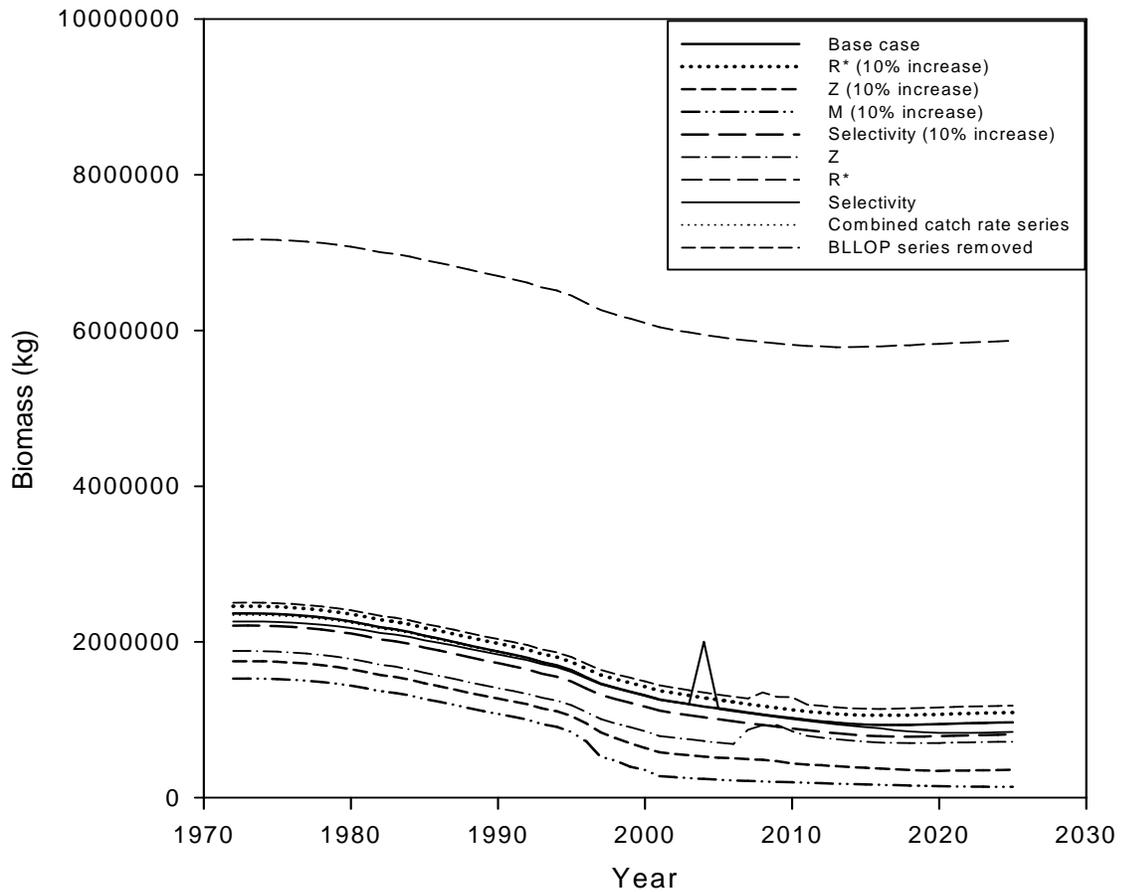


Figure 2-10. Mature median biomass (kg) for the base case and nine sensitivity analyses (R^* (virgin biomass) increased by 10%, z (steepness parameter) increased by 10%, M (natural mortality) increased by 10%, selectivities increased by 10%, z mean and standard deviation increased, R^* mean and standard deviation increased, selectivities allowed for full exploitation of age-zero class, four Catch Per Unit Effort (CPUE) series combined into one and Bottom Longline Observer Program (BLOP) CPUE series removed) of the base case model.

CHAPTER 3 SPATIAL MODEL

Introduction

Spatially explicit models can be used to investigate and evaluate the usefulness and success of time/area closures or marine protected areas in protecting marine species. The complexity of spatial models can range from simple one-dimensional models to complex models that combine movement, fishing and population dynamics (Pelletier and Mahevas, 2005). A spatially explicit model has been used for a stock assessment of the school shark in Australia (Punt et al., 2000) but has never been used for the dusky shark.

A one-dimensional spatial model was adapted from Walters and Hilborn (2007) and used to evaluate the effects of time/area closures on the population sizes of three life-stages (juvenile, subadult and adult) of the dusky shark. This approach has yet to be used in a stock assessment for any species of shark. The new model was modified to include these three life-stages (juvenile, subadult and adult) with different natural mortality rates and movement rates and was used to model the time/area closure off the coast of North Carolina. This model allows the user to identify marine protected areas using spatial cells that are connected through the dispersal of neonates and adult animals determine changes in the compensation of juvenile post-settlement survival, identify how displaced fishing effort will affect the abundance of fish outside the model area, identify long-term changes in abundance and harvest and changes in mean fecundity (Walters et al., 2007). The size of the protected area and parameters within the model can be changed, giving the user the ability to test various hypotheses. Since this type of model has not previously been used on elasmobranchs, many parameter values were unknown and I used this opportunity to investigate what effect different parameter values would have on the model outputs as well as the effects of increasing/decreasing the size of the time/area closure.

Ages were used to develop the stages (both sexes combined) were juvenile (ages 2-6), subadult (ages 7-19) and adult (ages 20+) based on Natanson et al. (1995). The effort or number of cells (1 nautical mile) modeled was 200 (50 open cells (northern area), 130 closed cells and 20 open cells (southern area) in that order), based on assuming the closed area off the coast of North Carolina is approximately 370 km long. The following coordinates outline the time/area closure: 35° 41' N to 30° 51' N and west of 74° 46' W, roughly following the 60 fathom contour line, diagonally south to 76° 24' W and north to 74° 51' W (Appendix A).

Spatial Model

Components of the Model

The spatial aspect of the model was created by identifying n spatial cells (i) that each extend for 1 nautical mile along the shore and offshore far enough to protect the entire life cycle of the animal, in theory. Cells that were closed to fishing were given the value 0 and those open to fishing were given the value 1 (Walters et al., 2007). The models used in these analyses represent the entire coast of North Carolina and the closed area within that area (Appendix A). Movement only occurred within the modeled area and the movement of animals outside of this area was not accounted for.

The long-term impact of protection to animals in each of these cells was calculated through a procedure that converged within 20 iterations. Each cell was related to other cells so that numerical equations were solved using a procedure termed “successive over-relaxation”, which also helps eliminate “chatter” within the iteration process. The initial estimate of the number of animals in each cell is given in equation 3-1,

$$N_i^{(1)} = \frac{R_o}{F \cdot area_j + M} \quad (3-1)$$

where N_i is the number of older animals in an individual cell summed over all ages, R_o is the average natural recruitment rate per cell (scaling parameter that indicates unit of measurement for N_i), F is fishing mortality rate absent any closures, $area_j$ is 1 or 0 depending on whether the individual cell is open or closed, respectively, and M is natural mortality (Walters et al., 2007).

Equation 3-1 was held constant and estimates were used to solve equations 3-3, 3-4 and 3-5 and update the mixing effects (see below). Iterations updated the values for these three equations. The results were considered fixed constants and were combined with a relaxation weight to determine a new iterative estimate using equation 3-2,

$$N_i^{(2)} = sortwt \cdot \frac{\left(r(L_i) + emig \cdot N_j^{(1)} \cdot \left(\frac{N_j^{(1)}}{N_i^{(1)}} \right)^{dpow} \right)}{\left(q \cdot F_i + m + emig \cdot \left(\frac{N_i^{(1)}}{N_j^{(1)}} \right)^{dpow} \right)} + (1 - sortwt) \cdot N_i^{(1)} \quad (3-2)$$

where $sortwt$ is the relaxation weight, $emig$ is the movement rate into $area_j$ per year, q is all fishing mortality that would occur if the whole area was open, which has been concentrated into only open areas, and $dpow$ is an empirical power parameter used to predict mean fecundity, F_i is the fishing effort redistribution and $r(L_i)$ is local recruitment rate, which is a function of the neonate settlement rate L_i (assumed to be normally distributed) (Walters et al., 2007). The equilibrium age structure for each cell was calculated by determining a rate at which cohorts could die off in each cell. Dispersal to and from other cells was calculated using the $emig$ parameter (Walters et al., 2007). These steps were repeated until N_i converged on a fixed value (Walters et al., 2007):

The Beverton-Holt (BH) recruitment function was calculated using equation 3-3,

$$r(L_i) = \frac{h_i \cdot \alpha L_i}{1 + \beta L_i} \quad (3-3)$$

where h_i is the habitat quality for the individual cell, α is the maximum survival rate of neonates from settlement to recruitment ([compensation ratio*avg. natural recruitment)/neonates per recruit]), and α/β is the maximum recruitment rate, (β =[compensation ratio – 1]/neonates per recruit). The compensation ratio is the ratio of maximum neonate survival at low densities to survival at unfished natural abundances (Walters et al., 2007). This parameter is typically used for teleost fish but is similar to the steepness parameter (z) used in Chapter 2. I used a different equation than that used in Chapter 2 in an effort to provide more estimates of the unknown parameters from this function. Neonate contributions to the model were calculated using equation 3-4,

$$L_i = jper \left(\sum N_i^{(t)} e^{\frac{-0.5(1-j)}{sdldist^2}} \right) \quad (3-4)$$

where $jper$ is a scaling constant for total neonate settlement from each individual cell, and $sdldist$ is the standard deviation of the spatial distribution of neonate settlement (Walters et al. 2007).

The recruitment function and neonate contribution equations affect the dispersal of neonates by determining the sum of neonate contributions from other cells, and identify post-settlement density dependence. The exponential term in the neonate contribution equation allows for neonate settlement to follow a normal distribution, while the parameter $jper$ is a scaling constant for neonate settlement and $sdldist$ identifies an area beyond an individual cell where settlement rates drop off. For example, if $sdldist$ equals 5 then neonate settlement would drop off five miles from the cell. The habitat quality for neonates of each spatial cell is incorporated into the Beverton-Holt recruitment function equation. Cells with unsuitable habitat were given a value of $h_i = 0$ and cells with suitable habitat, $h_i = 1$. The inclusion of this term also lead to the assumption that emigration rates (per year) increased to $emig/h_i$ and immigration rates decreased to $h_i/emig$ (Walters et al., 2007).

Fishing effort redistribution (F_i) within the model was calculated using equation 3-5,

$$F_i = effort \cdot \frac{e^{\left(\frac{c_i \cdot N_i^{(1)}}{effpow}\right)}}{\sum C_i \cdot e^{\frac{N_i^1}{effpow}}} \quad (3-5)$$

where *effort* is the total number of spatial cells, C_i is the spatial cell and *effpow* is the standard deviation of the gravity model (Walters et al., 2007).

A multinomial logit model was used to predict the redistribution of fishing effort when individual cells were closed to fishing. This allowed the model to identify areas near the boundaries of an MPA where concentrations of fishing effort may occur, by assuming the likeliness of a fisher to fish in a particular cell (i.e. *effpow*: the higher the value the more evenly spread out fishing effort is) is proportional to the logarithm of abundance in that particular area. The number of animals at these locations could also be affected by “spillover” (when animals from protected areas move into non-protected areas) but this would be dependent upon their movement rates (Walters et al., 2007).

Parameters

The fishing mortality rate absent any closures (F) was taken from Cortés et al., (2006) and annual juvenile, subadult and adult natural mortality rates were taken from the values provided in Chapter 2. The average natural mortality for each stage was calculated from the assumed linear decrease for age 0 to mature animals used in Chapter 2. The parameter effort used to calculate fishing effort within the model was the total number of cells modeled, which was 200. The parameter for all mortality that would occur if the entire area was open, which has been concentrated into only areas that are open (q) was calculated by multiplying F by the effort and dividing by the sum of all cells (0 if closed and 1 if open) (Walters et al., 2007). Movement (*emig*) rates for juveniles were based on dusky sharks tagged in Western Australia (Colin

Simpfendorfer personal communication) and rates for subadult and adult animals were estimated based on these rates and knowledge of the movement patterns of larger dusky sharks (Colin Simpfendorfer, personal communication). The compensation ratio (*reck*) was set slightly higher than the maximum value (1) of the steepness parameter (*z*) to allow for the lower levels of compensation, compared to teleosts, expected for this species. Information on the standard deviation of the spatial distribution of neonate settlement (*sldist*), average recruitment rate (*Ro*), power parameter (*dpow*) and standard deviation of the gravity model (*effpow*) does not exist for sharks. I therefore used a starting value of the base case model and used the sensitivity analysis to investigate alternative values. The relaxation weight (*sorwt*) was estimated based on information provided in Walters et al., 2007. The scaling constant for total neonate settlement from each source cell (*jper*) was calculated using equation 3-6 (Walters et al., 2007).

$$\frac{1}{(sldist \cdot \sqrt{2 \cdot 3.14})} \quad (3-6)$$

The two Beverton Holt parameters α and β were calculated as mentioned above. Habitat (*hi*) areas for recruits (in terms of individual cells) were given the value 1 indicating they were of good quality (Walters et al., 2007).

This type of model has yet to be applied to highly migratory species and many of the parameters were unknown for this species. Base case parameter values were generally estimated based on knowledge of the species or calculated through the use of other parameters within the model. All parameters and parameter values used in the base case model are listed in Table 3-1. In order to fully understand the impact these estimates had on the outcome of the model, several sensitivity analysis were run. I investigated the impact of changes made to the fishing and natural mortality rates, movement rates, the compensation ratio and the standard deviations of the gravity model and spatial distribution of neonate settlement. Additionally, I investigated the

effects of opening and closing the entire model to fishing. The parameter values used in each of the sensitivity analyses are presented in Table 3-2. The ability to easily run many sensitivity analyses investigating the effects of various parameter estimates was a key benefit of this approach.

Sensitivity Analysis

I ran one base case scenario and 11 sensitivity analyses models (described below) (Table 3-2).

Sensitivity 1: Closed area/no fishing mortality

The entire area was closed to fishing in this model by setting all of the cells to 0. This sensitivity analysis simulated a time/area closure for the entire coast of North Carolina instead of the small closure currently in effect, which was represented in the base case model.

Sensitivity 2: Open area model

The entire area was opened to fishing in this model by setting all of the cells to 1. This allowed the model to simulate that there was no time/area closure in effect.

Sensitivity 3: Fishing mortality rate set to Fmsy

The fishing mortality rate was reduced to the value of Fmsy presented in Cortés et al. (2006).

Sensitivity 4: High standard deviation of the gravity model (*effpow*)

The standard deviation of the gravity model (*effpow*) was increased to investigate what effect this would have on the densities and/or redistribution of fishing effort within the model. There are no published values of this parameter for shark species.

Sensitivity 5: High compensation ratio (*reck*)

I used a higher value, which allowed for additional compensation due to increased neonate survival.

Sensitivity 6: High natural mortality rates (M)

The highest natural mortality rates for each stage were taken from the values used in Chapter 2 (Appendix B) and applied to this model.

Sensitivity 7: Low natural mortality rates (M)

The lowest natural mortality rates for each stage were taken from the values used in Chapter 2 (Appendix B) and applied to this model.

Sensitivity 8: High standard deviation of the spatial distribution of neonate settlement (sdldist)

Similar to the *effpow* parameter, there is no published estimate for the standard deviation of the spatial distribution of neonate settlement for sharks. I used an estimated higher value than the one used in the base case model for this sensitivity analysis. This allowed neonates to spread out more throughout the modeled area.

Sensitivity 9: Low standard deviation of the spatial distribution of neonate settlement (sdldist)

Similar to the *effpow* parameter, there is no published estimate for the standard deviation of the spatial distribution of neonate settlement for sharks. I used an estimated lower value than the one used in the base case model for this sensitivity analysis. This caused neonates to spread out less throughout the modeled area.

Sensitivity 10: High movement rates (emig)

The data presented by Colin Simpfendorfer (personal communication) was based primarily on juvenile animals from a different region and the movement rates observed varied substantially for juveniles. I increased the movement rates in this model using data provided by Colin Simpfendorfer (personal communication) and by making educated assumptions.

Sensitivity 11: Low movement rates (emig)

The data presented by Colin Simpfendorfer (personal communication) was based primarily on juvenile animals from a different region and the movement rates observed varied substantially for juveniles. I decreased the movement rates in this model using data provided by Colin Simpfendorfer (personal communication) and by making educated assumptions.

Results

The model outputs include the total densities (number) for each stage (juvenile, subadult and adult), as well as the amount of neonates and recruits found with that stage in the model and the amount of effort that is redistributed throughout the modeled area. These results give a visual representation of how and where dusky shark densities build up and decrease within the modeled area. Additionally, I calculated the total number of animals found in each of the three areas (northern closed, open and southern closed) for the base case and sensitivity analysis, allowing for a comparison of how closing and opening the area to fishing and changing other parameters effected the total number of dusky sharks found in each area of the model.

Base Case

The total number of juvenile dusky sharks found in the closed area was over 6 times that found in the northern closed area and over 10 times that found in the southern open area (Table 3-3). The density of juvenile dusky sharks remained low throughout the northern area of open fishing and began to increase slightly during the first section of the closed area. A large increase in density was not seen until approximately 18 nm into the closed area. This increase in density continued for 65 nm at which point it leveled. The density remained at this level throughout the remainder of the closed area and then drastically declined to levels somewhat above those of the northern open fishing area, once the southern area became open to fishing again (Figure 3-1). Neonate density within this stages model gradually increased at the beginning of the closed area

when compared to juvenile density. The decrease in density as the closed area became open again in the southern area was also more gradual than what was seen in the juvenile density curve. Additionally, neonate density began to increase quicker approximately 19 nm before the closed area began and started to decrease approximately 56 nm before the closed area ended (Figure 3-2). Recruitment density within this stages model remained very flat throughout the open and closed areas (Figure 3-3). Redistribution of fishing effort was concentrated for 4 nm on the outside edge of the southern section of the closed area (Figure 3-4).

Subadult density followed a similar trend to that seen with juvenile dusky sharks but with overall density being higher (Figure 3-5). The total number of subadult animals found in the northern open area was close to 10 times less than the amount found in the closed area and just slightly less than in the southern open area (Table 3-3). This was the opposite of the results from the juvenile and adult models, where the total number of animals was higher in the northern open area than in the southern (Table 3-3). Density began to increase approximately 28 nm into the closed area, remained steady after 128 nm into the closed area and then dropped off significantly once the southern open area began. Density in the southern open area remained higher than 3333 in northern open area (Figure 3-5). Neonate density within this stages model had a slow steady increase in density from the beginning of the northern open area and continuing to a peak about 139 nm into the closed area. The curve then began a steady decrease until 19 km into the southern open area, at which point density declines drastically (Figure 3-6). Recruitment density within this model was flat through the entire area (Figure 3-7), similar to what was seen in the juvenile stage and fishing effort was concentrated into the first 4 nm of the southern open area (Figure 3-8).

Adult density was higher than juvenile and subadult densities. There were over 11 and 17 times more adults found in the closed area than in the northern and southern open areas respectively (Table 3-3). Density increased slowly for the first 56 nm of the northern open area and then began a large increase that plateaued around 50 nm into the closed area and continued for 143 nm. After the plateau, there was a large decline in density throughout the remainder of the southern open area, resulting in densities similar to those in the northern open area (Figure 3-9). Neonate density within this stages model, increased from the start of the northern open area into the closed area and reached a plateau 107 nm into the closed area, continued for 26 nm, and then began to decrease again (Figure 3-10). Recruitment density within this stages model, remained fairly steady throughout the whole area (Figure 3-11). The redistribution of fishing effort was maximized in the last nm of the northern open area directly before the closed area began. This was in sharp contrast to what was seen in the previous two stages (Figure 3-12).

This model converged quickly for the redistribution of fishing effort for both the juvenile (Figure 3-4) and subadult (Figure 3-8) stages but not for the adult (Figure 3-12) stage. The majority of this effort switched for each of the iterations and alternated between the last open cell in the northern area and the first cell of the southern open area. There was also instability in the convergence of total adult density in the cells surrounding the start and finish of the closed area. These convergence issues are likely related to the high fishing mortality, high movement rates and natural mortality rates of the adult stage combined with the *effpow* parameter. The convergence issues did not occur in sensitivity analyses where fishing mortality (sensitivity 3) and/or the movement rate was reduced (sensitivity 11), when natural mortality was increased/decreased (sensitivities 6 and 7) or when the parameter *effpow* was increased (sensitivity 4). These issues were not seen in any of the model runs for the juvenile and/or

subadult stages. Despite this, it did appear that the redistribution of fishing effort for the adult stage became concentrated around the northern and southern end of the closed area.

Sensitivity 1: Closed Area/no Fishing Mortality

The closed area model resulted in a very flat total density curve for all three life-stages, when compared to the base case model. The total number of animals found in the northern area increased from those found in the base case model but the numbers found in the original “closed” area remained similar but slightly higher, than those found in the base case model (Table 3-3). The lower numbers found in the northern area, compared to the “closed” area, was due to the high movement rates that allowed the animals to move out of the modeled area but the model did not allow for them to move back in. This was a result of their lower natural mortality rates compared to the other two stages. Densities seen in these three life-stages were very similar to those seen during the plateaus/peaks of the base case model, with subadult density (Figure 3-5) being higher than juvenile density (Figure 3-1), and adult density (Figure 3-9) being the highest overall. Neonate density within all three model stages showed a large increase for the first 35 nm, compared to the long steep increase seen in the base case model. This was followed by a plateau that lasted for ~110 nm, at which point density began to drop to levels seen at the beginning of the model (Figures 3-2, 3-6, and 3-10). Recruitment densities in all three modeled stages remained very similar throughout the model and were similar to the base case models. Fishing effort was redistributed to the outskirts of the modeled area for all three stages (Figures 3-4, 3-8, and 3-12). This was in sharp contrast to what was seen in the base case model.

Sensitivity 2: Open Area Model

In the open area model, densities for all three stages were much lower than those seen in the closed area/no fishing mortality model but followed a very similar flat trend (Figures 3-1, 3-5 and 3-9). Total numbers of animals in the northern area were very similar to those found in the

base case model, while those in the “closed” and southern area were very reduced compared to the base case model (Table 3-3). Total numbers were lower in the northern and southern areas compared to the “closed” area because of movement out of the modeled area without replacement. Juvenile, subadult and adult densities were approximately three, four and ten times lower (respectively) than the values seen in the closed area model. Neonate and recruitment densities within each stages model also followed similar trends to those seen in the previous model. The redistribution of fishing effort was similar for juvenile (Figure 3-4) and subadult (Figure 3-8) stages. The majority of effort was evenly distributed throughout the model, which was in direct contrast to the results of the base case model (Figure 3-4, 3-8 and 3-12).

Sensitivity 3: Fishing Mortality Rate Set to F_{msy}

The reduction in the fishing mortality rate caused the total density curves for all three stages to become very flat throughout the model instead of curved as seen in the base case model (Figures 3-1, 3-5 and 3-9). The total number of animals found in all three areas and stages was very similar to those found in sensitivity 1 (Table 3-3). The densities were very similar to the peak densities seen in the base case model. Adult density was the highest of all three stages and increased much more in the closed area compared to the previous two stages but was still very similar to the values seen in the base case model. Neonate densities found within each stage started higher and increased more quickly when compared to the base case (Figures 3-2, 3-6 and 3-10). The peak densities were similar to those seen in the base case model. Recruitment densities followed similar trends to the base case model but were slightly higher in value. Fishing efforts for juvenile (Figure 3-4) and subadults (Figure 3-8) were redistributed (when compared to the base case model) to the southern open area with the majority of effort falling within the first open cell of that area. Adult fishing effort was redistributed (when compared to

the base case model) to the two cells directly before and after the closed area, with no fishing occurring in the closed area (figure 3-13).

Sensitivity 4: High Standard Deviation of the Gravity Model (effpow)

Density curves for juvenile, subadults and adults followed very similar trends to what was seen in the base case model. The total number of animals found in all stages and areas was similar to, but slightly less than those found in the base case model (Table 3-3). Densities were slightly lower for juveniles and subadults compared to the base case model but were nearly the same for adults. Neonate and recruitment curves also followed similar patterns to the base case model, with slightly lower densities found in the juvenile and subadult stage models. The redistribution of fishing effort was different for all three stages compared to the base case model and overall effort was much less. Effort for juveniles (Figure 3-4) and subadults (Figure 3-8) was redistributed primarily into the southern open area but also to a lesser extent into the northern open area. Adult effort was primarily redistributed to the cells directly before and after the closure and was slightly more distributed than in the base case model (Figure 3-12).

Sensitivity 5: High Compensation Ratio (reck)

The change in this parameter value only slightly effected juvenile, subadult and adult total numbers (Table 3-3). Neonate density and the redistribution of fishing effort were not changed when compared to the base case model. The number of recruits was increased for the juvenile and subadult stages and decreased slightly for adults, when compared to the base case model (Figures 3-3, 3-7 and 3-11).

Sensitivity 6: High Natural Mortality Rates (M)

The curves for juvenile, subadult and adult density, neonate density, and recruitment density were all similar to those seen in the base case model. The total number of animals for all three stages and areas were lower than those found in the base case model (Table 3-3). The

densities were lower for all curves, with adult density being affected the most. The redistribution of fishing effort for juvenile and subadult stages was the same as seen in the base case model. However, in the adult stage effort was redistributed to the first cell in the southern open area (Figure 3-12) compared to the last cell in the northern closure in the base case model.

Sensitivity 7: Low Natural Mortality Rates (M)

Low natural mortality rates had the opposite effect as seen in the model where high natural mortality rates were used, with regard to total density and the redistribution of fishing effort in the adult stage. The total number of animals in all three regions was higher than those found in the base case model, except for subadult animals in the southern open region, which only decreased slightly in numbers (Table 3-3). The curves for juvenile, subadult and adult densities, neonate density and recruitment density all remained similar to the curves in the base case model. Densities increased for all stages but the subadult density increased the most. The redistribution of fishing effort for the adult stage did change from the base case model (Figure 3-12). Effort was redistributed to the cells immediately prior to the closed area in the northern section and immediately after the closed area in the southern section. Fishing effort in the adult stage was also much lower in this model when compared to the base case scenario. Effort redistribution did not change for the juvenile or subadult stages.

Sensitivity 8: High Standard Deviation of the Spatial Distribution of Neonate Settlement (sdlldist)

The increase in this parameter led to a decrease in neonate densities found within each of three stages models (Figures 3-2, 3-6 and 3-10) and an increase in recruitment densities within the models for the juvenile (Figure 3-3) and subadult stages (Figure 3-7) with respect to the base case model. Recruitment densities found in the adult stage model became lower (Figure 3-11) and the redistribution of fishing effort for juveniles decreased (Figures 3-4) when compared to

the base case model. The curves for all four graphs remained very similar to the base case model, with neonate density being decreased the most within the adult stages model (Figure 3-10) and recruitment densities being increased the most within the juvenile stages model (Figure 3-3).

Sensitivity 9: Low Standard Deviation of the Spatial Distribution of Neonate Settlement (sdldist)

Lowering this parameter resulted in changes to the curves for neonate (Figure 3-2, 3-6 and 3-10) and recruitment (Figures 3-3, 3-7 and 3-11) densities found within all three stages with respect to the base case model. The highest neonate densities in the closed area remained the same as densities seen in the base case model. Recruitment densities were higher in the juvenile (Figure 3-3) and subadult (Figure 3-7) stages modes, compared to the base case model but lower in the adult stages model (Figure 3-11). The redistribution of fishing effort changed in the juvenile (Figure 3-4) and adult (Figure 3-12) stages when compared to the base case model. Effort was reduced in the juvenile stage and became concentrated into the first cell of the southern closure in the adult stage (Figure 3-8).

Sensitivity 10: High Movement Rates (emig)

The change to this parameter did not affect the curves for total, neonate or recruitment densities for the three stages when compared to the base case model. The total number of juvenile animals was reduced slightly in all three regions, and the total number of subadult and adult animals was increased slightly in the northern open area and the closed area of the model compared to the base case model (Table 3-3). Total numbers of subadults was reduced in the southern open area and increased slightly for adult animals compared to the base case model (Table 3-3). The redistribution of fishing effort for the adult stage was moved to the first cell of the southern open area (Figure 3-12) but did not change for the juvenile or sub adult stages.

Sensitivity 11: Low Movement Rates (emig)

Juvenile total (Figure 3-1) density and the neonate (Figure 3-2) and recruitment (Figure 3-3) densities found within this model, were all lower and the redistribution of fishing effort (Figure 3-4) was higher in this model compared to the previous and base case models. The total number of animals of all three life-stages found in the three regions was reduced compared to the base case model (Table 3-3). Total and neonate density (Figures 3-5 and 3-6) were slightly lower in the subadult and adult stage models but recruitment densities did not change. The redistribution of fishing effort did not change in the subadult stage but was slightly higher in the juvenile stage (Figure 3-4) and was much lower in the adult stage (Figure 3-12) and became concentrated in the last cell of the northern open area and first cell of the southern open area.

Discussion

The base case model showed that the majority of total and neonate density for all three life-stages of the dusky shark occurred in the closed region of the model but that the effects of fishing were still seen in the boundaries between open and closed areas. This fishing effect was predicted by Walters (2000) and Walters et al., (2007) due to dispersal imbalance within the model. Fish that are lost via dispersal near the closure boundary are not replaced through immigration. Juvenile and subadult densities took longer to build up in the closed area, which was most likely a factor of their slower movement rates when compared to the adult stage. Sensitivity analysis showed that parameter values affected the densities and the redistribution of fishing effort for all three stages. However, all of the models (except for sensitivities 1 and 2) indicated that the highest densities were found in the closed portion of the model and that the redistribution of fishing effort was concentrated into very few cells on either side of the closures. Highly concentrated redistribution of fishing effort has also been reported in the “plaice box” closure for beam trawlers (Pastoors et al., 2000) and cod box closures (Rijnsdorp et al., 2001).

Neonate densities within all models generally followed the same trends as the total densities in those models and recruitment densities varied very little.

The sensitivity analysis (3) with a reduction in fishing mortality (set to F_{msy}) resulted in the least changes to total densities between the closed and open areas, except for the sensitivity analyses that were entirely open (2) and/or closed (1) to fishing. In these models, densities remained flat throughout the entire model. These results coincide with other studies that have suggested time/area closures are most effective when overall mortality is also reduced (Horwood et al., 1998; Rijnsdorp et al., 2001; Chapman et al., 2005) and studies that showed larger reserves provide more protection to shark species (Chapman et al., 2005; Heupel and Simpfendorfer, 2005). In the reduced fishing mortality model, neonate densities built up more quickly and earlier prior to the closed area and decreased more slowly and later after the closed areas, when compared to the base case model. This occurred because of the moderate, if any, changes to total densities seen in the model. Neonate densities were very low in the open area model because of the low total densities in the model. Additionally, in the reduced fishing mortality model, fishing effort was much lower and was redistributed to more nm's for juveniles and subadults than in the base case model. The number of animals was able to build up in the closed area and was reduced only slightly once the area became open to fishing. This allowed the redistribution of fishing effort to be more evenly spread out into the southern open area. In the adult stage of this model, total densities were similar into the northern and southern closed regions and therefore the redistribution of fishing effort built up on either side of the closure. As would be suspected, the redistribution of fishing effort in the open model stayed around one for the entire model and zero for the model that was completely closed to fishing. With the entire area open to fishing, effort

could be evenly spread out between fishers and when the entire area was closed effort could not be redistributed within the model.

Guenette and Pitcher (1999) suggested that marine reserves provide protection to managed fish stocks but that these advantages are reduced for highly mobile species. Rapid movement of fish into and out of closed areas is thought to hinder the protection offered by a closed area (Horwood et al., 1998) because the fish become vulnerable to fishing once outside of the protected area. Changes made to movement rates in the sensitivity analyses (10 and 11) of this model only had slight effects on the outcome of the model when compared to the base case model. This was because movement rates were so high in the original model that increasing them did not affect the total outcome of the model. Horwood et al. (1998) suggested that a combination of closed area management and a reduction in fishing mortality outside of the closed area should be implemented to provide the most adequate protection. Chapman et al. (2005) suggested that the best way to protect highly mobile shark species was through the use of an ecosystem-based management approach that includes a closed area surrounded by an area with regulated fishing activities. These two management techniques have been implemented for the dusky shark but do not appear (Cortés et al., 2006) to be enough to allow the population to recover from exploitation.

Lowering the natural mortality rates (sensitivity analyses 6 and 7) allowed for the populations of each stage to build up in density and increasing the natural mortality rates lead to a reduction in total density. Natural mortality rates were decreased the most for the juvenile stage and the least for the adult stage. Attempts to reduce the natural mortality rates more in the adult stage resulted in the model not working and resulting in a number error. Therefore, I only reduced the rate as much as the model would allow (Table 3-2) and did use the lowest rates

presented in Chapter 2. This caused the largest change in density being seen in the subadult stage because of the larger original densities and larger change to the natural mortality rates. Fishing effort was lower in the adult stages because it was spread out between two nm's instead of being concentrated into one nm.

Neonate densities were changed when the spatial distribution of neonate settlement rates were altered (sensitivity analyses 8 and 9). Spreading out neonate settlement (increasing the parameter value) resulted in a decrease in total neonate numbers in the closed area because neonates were spread out more throughout the entire area of the model. Lowering this parameter caused the neonates to become more concentrated into the closed area. The redistribution of fishing effort was lower for juveniles in these two models because total density in the southern open area was much lower than in the base case model. Increasing the standard deviation of the gravity model reduced total fishing effort because it spread the effort out between more cells in the open areas. Increasing the compensation ratio allowed for increased compensation in the form of increased survival of neonates, therefore leading to increases in recruitment densities within the models. The value of 1.5 used in the base model indicates a slight change in neonate mortality when the spawning biomass changes. In teleosts this ratio is highest for species with a high maximum number of spawners per recruit (Goodwin et al., 2006). This ratio is thought to be lower for dusky sharks and similar species, because increased compensation is more likely going to be a factor of increased growth rates and subsequent earlier ages at maturity. The already low natural mortality rates for neonates of this species would make increased compensation in the form of increased survival for neonates unlikely.

Spatial modeling of the dusky shark is hampered by our lack of knowledge of their movement patterns, movement rates and spatial structure (Conroy et al., 1995). The data

presented by Colin Simpfendorfer (personal communication) were helpful in creating possible movement rates but were based primarily on juvenile animals from a different region. Colin Simpfendorfer (personal communication) also indicated that the movement rates they observed varied substantially for juveniles. While the models show a build up of density within the closed area, the high movement rates of this species makes it very likely that dusky sharks move in and out of the area during the 7 month closure. Movement out of the area into open fishing areas still leaves them susceptible to fishing pressure as does the 5 months the time/area closure is not in effect. An increase in numbers within closed areas has been reported in many Marine Protected Area (MPA) studies (Halpern and Warner, 2002). Walters et al. (2007) suggested that this phenomenon does not provide very useful information because it is only a snapshot of a small area and because there is no indication of how long it will take for these effects to be seen. This model was also unable to incorporate the temporal closure aspect of this time/area closure. In the future, more work (e.g., tag/recapture and satellite tagging studies) on the movement of dusky sharks in the northwest Atlantic Ocean needs to be completed. This information may allow for the use of a more advanced spatial model that can also incorporate the seasonal aspect of the time/area closure (Pelletier et al., 2008). Without all of this information the full effect of time/area closures on the population of this species can not be completely analyzed without great uncertainty (Conroy et al., 1995).

Additional research should also be completed on the redistribution of fishing effort to the areas surrounding a closed area, because successful management of species protected by time/area closures is dependent on this redistribution (Apostolaki et al., 2002). Apostolaki et al. (2002) showed that short-term losses associated with the implementation of a reserve can be reduced if the redistribution of fishing effort is spread out over the remainder of the fishing area.

The results of this study show that the redistribution of fishing effort becomes highly concentrated in the outskirts of the closure, which would suggest that short-term losses may be high in this closure. Redistribution of fishing effort is likely influenced by the location of the closure (distance from dock), season, market prices of targeted species and fuel costs.

Information on the long term effects of this redistribution and whether this change in fishing practice negatively impacts other species or relocates fishing to areas previously not fished needs to be investigated (Dinmore et al., 2003).

Table 3-1. Parameter values (F = fishing mortality rate absent any closure, M = natural mortality, effort = total kilometers modeled, q = fishing mortality concentrated into only areas that are open to fishing, R = average natural recruitment rate per cell, $emig$ = movement rate, $reck$ = compensation ratio, $sldist$ = standard deviation of spatial distribution of neonate settlement, $jper$ = scaling constant for total neonate settlement from each source cell, α and β = parameters from Beverton Holt stock recruitment function, $effpow$ = standard deviation of gravity model, $dpow$ = power parameter, $sort$ = relaxation weight and Hi = habitat quality for individual cells) for the base case version of the spatial model.

Parameter	Juvenile	Subadult	Adult	Reference
F	0.4	0.4	0.4	Cortés et al., 2006
M	0.21	0.13	0.05	Cortés et al., 2006
$Effort$	200	200	200	
q	1.14	1.14	1.14	Walters et al., 2007
Ro	50	50	50	
$Emig$	240	400	1000	Colin Simpfendorfer (personal communication); Simpfendorfer personal communication
$Reck$	1.5	1.5	1.5	Enric Cortés personal communication; Simpfendorfer et al., 2000; Cortés, 2004
$sldist$	20	20	20	
$Jper$	0.02	0.02	0.02	Walters et al., 2007
α	13.8	1.8	2.2	Walters et al., 2007
β	0.85	1.07	1.06	Walters et al., 2007
$Effpow$	2	2	2	
$Dpow$	0.4	0.4	0.4	Walters et al., 2007; Walters personal communication
$Sort$	0.5	0.5	0.5	Walters et al., 2007; Walters personal communication
Hi	1	1	1	Walters et al., 2007

Table 3-2. Parameter values for the sensitivity analysis of the spatial model (Fmsy = fishing mortality rate that would produce maximum sustainable yield (MSY), *effpow* = standard deviation of the gravity model and *sldist* = standard deviation of the spatial distribution of neonate settlement).

Sensitivity	Parameter	Reference
1. Entire habitat closed to fishing	cells=0	
2. Entire habitat open to fishing	cells=1	
3. Fishing mortality reduced to Fmsy	0.006	Cortés et al., 2006
4. <i>effpow</i> increased	5	
5. Compensation ratio (<i>reck</i>) increased	2.5	
6. Natural mortality rates increased	juvenile=0.226, subadult=0.176, adult=0.083	Cortés et al., 2006
7. Natural mortality rates decreased	juvenile=0.185, subadult=0.087, adult=0.046	Cortés et al., 2006
8. <i>sldist</i> increased	50	
9. <i>sldist</i> decreased	1	
10. Increased movement rates	juvenile=400, subadult=600, adult=1200	Colin Simpfendorfer (personal communication); Simpfendorfer personal communication
11. Decreased movement rates	juvenile=120, subadult=200, adult=500	Colin Simpfendorfer (personal communication); Simpfendorfer personal communication

Table 3-3. Total number of dusky sharks found in three areas (northern open, closed, southern open) and three life-stages (juvenile, subadult and adult) for the base case and sensitivity analysis of the spatial model.

Model	Area	Total (Numbers)		
		Juvenile	Subadult	Adult
Base case	Northern open area	4,091	4,678	10,604
	Closed area	27,088	43,245	125,192
	Southern open area	2,557	7,688	7,295
Sensitivity 1	Northern open area	11,723	19,085	49,942
	Closed area	30,486	49,626	129,851
	Southern open area	4,690	7,635	19,976
Sensitivity 2	Northern open area	3,921	4,574	5,498
	Closed area	10,197	11,894	14,296
	Southern open area	1,569	1,830	2,199
Sensitivity 3	Northern open area	11,377	18,241	44,968
	Closed area	30,324	49,222	129,026
	Southern open area	4,648	7,570	18,216
Sensitivity 4	Northern open area	3,187	4,248	10,312
	Closed area	23,884	41,504	125,102
	Southern open area	3,256	5,606	7,039
Sensitivity 5	Northern open area	4,150	4,683	10,605
	Closed area	27,245	43,258	125,191
	Southern open area	2,574	5,017	7,293
Sensitivity 6	Northern open area	3,958	4,291	7,039
	Closed area	25,157	32,173	74,490
	Southern open area	2,362	3,680	3,968
Sensitivity 7	Northern open area	4,248	5,101	12,452
	Closed area	30,582	64,123	137,227
	Southern open area	2,910	7,544	9,171
Sensitivity 8	Northern open area	3,656	4,681	10,604
	Closed area	26,309	43,134	125,192
	Southern open area	1,484	5,008	7,296
Sensitivity 9	Northern open area	3,655	4,680	10,567
	Closed area	26,311	43,134	125,179
	Southern open area	1,483	523	7,318
Sensitivity 10	Northern open area	3,943	4,689	10,654
	Closed area	26,464	43,349	125,339
	Southern open area	1,655	5,616	7,402
Sensitivity 11	Northern open area	2,680	4,635	10,207
	Closed area	24,093	42,916	124,688
	Southern open area	1,135	3,865	6,930

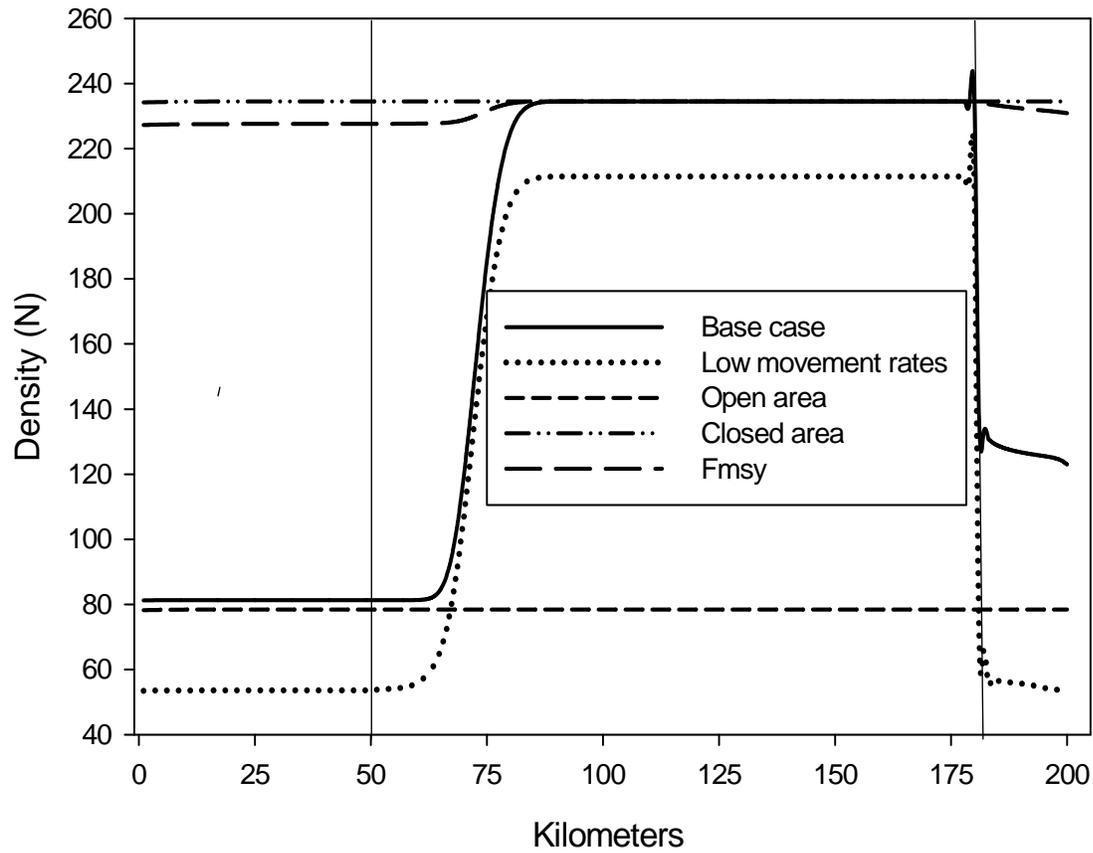


Figure 3-1. Densities (N) of juvenile dusky sharks from the base case and sensitivity analyses (low movement rates, entire area open to fishing, entire area closed to fishing, fishing mortality reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY)) of the base case model). Vertical lines represent the closed area of the model.

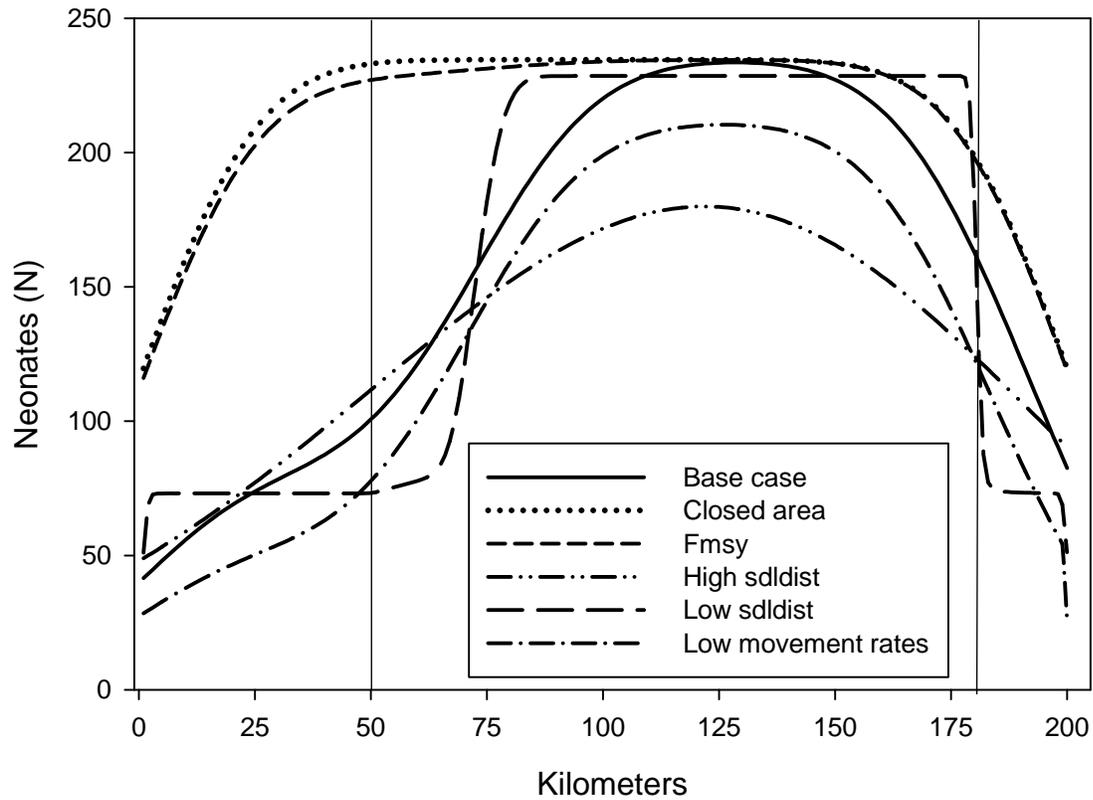


Figure 3-2. Neonate densities (N) found within the juvenile dusky shark life-stage model for the base case and sensitivity analyses (entire area closed to fishing, fishing mortality reduced to F_{msy} , (fishing mortality rate that would produce Maximum Sustainable Yield (MSY), high standard deviation of the spatial distribution of neonate settlement (*sldist*), low *sldist* and low movement rates) of the base case model. Solid vertical lines represent the closed area of the model.

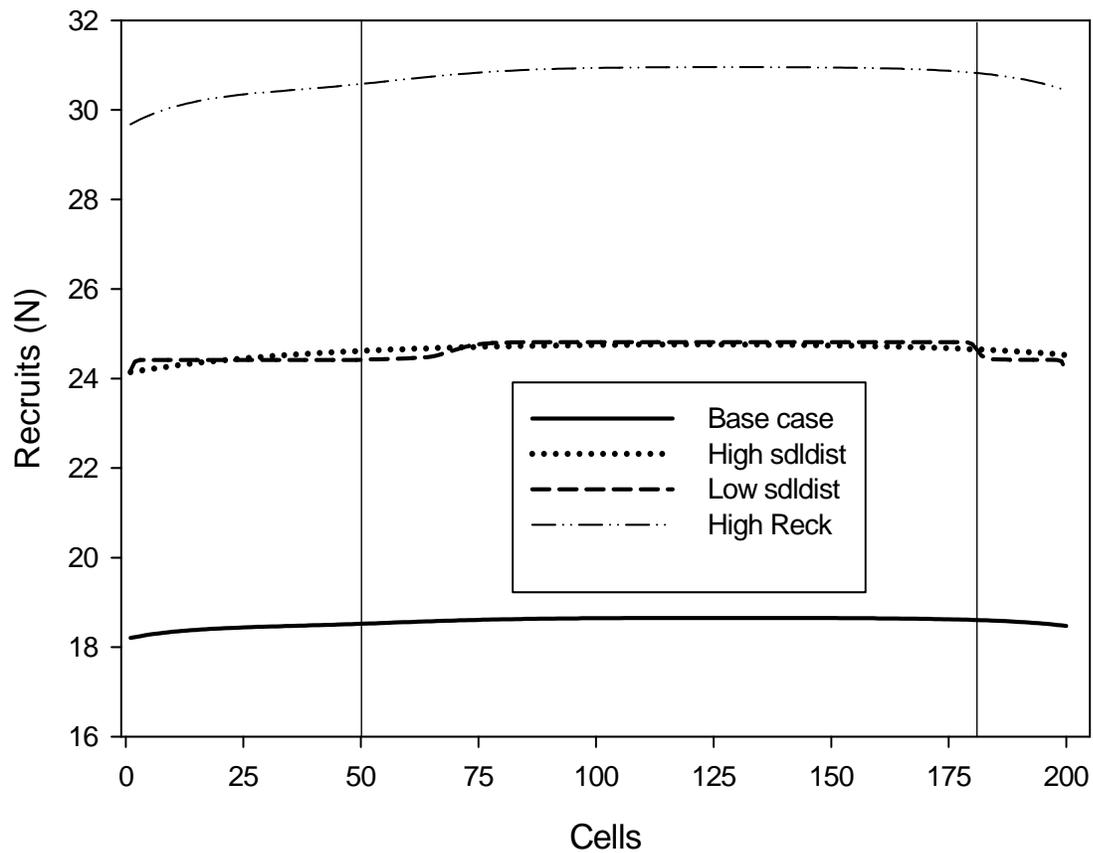


Figure 3-3. Recruit densities (N) found within the juvenile dusky shark life-stage model for the base case and sensitivity analyses (high standard deviation of the spatial distribution of neonate settlement (*sldist*), low *sldist*, high compensation ration (*reck*) increased) of the base case model. Solid vertical lines represent the closed area of the model.

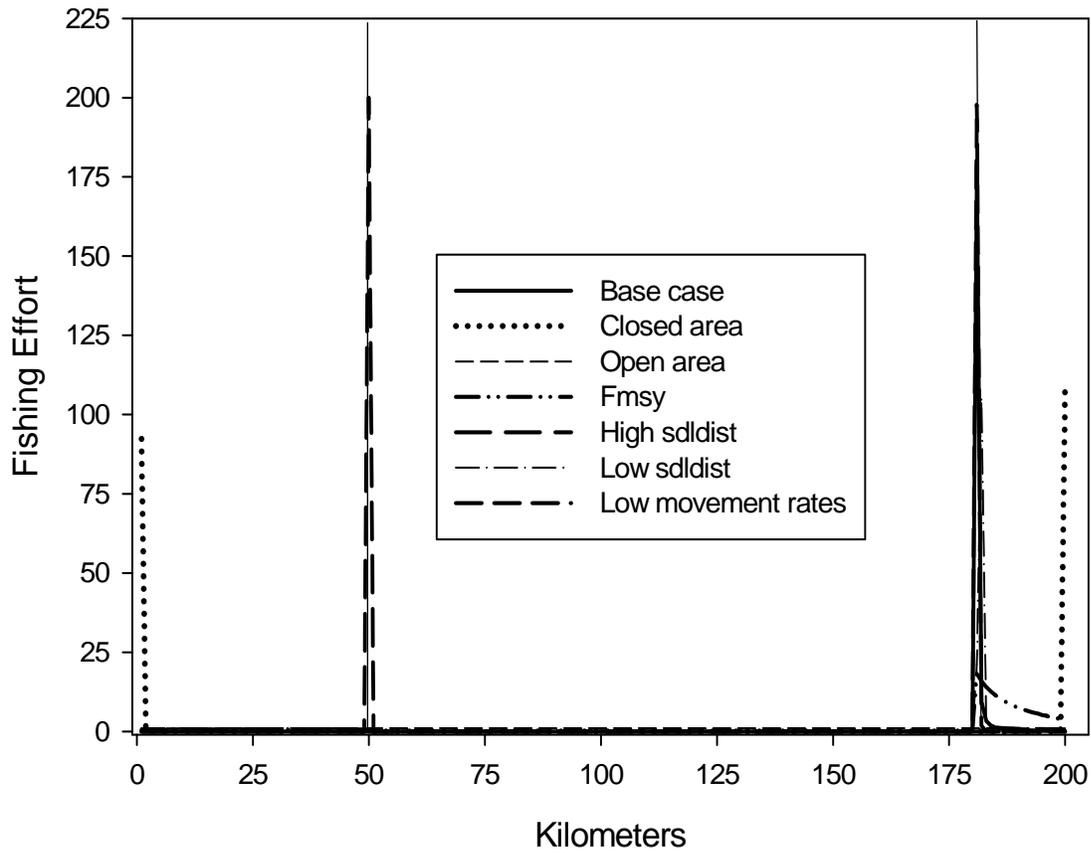


Figure 3-4. Redistribution of fishing effort for juvenile dusky sharks from the base case and sensitivity analyses (entire area closed to fishing, entire area open to fishing, fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY), high standard deviation of spatial distribution of neonate settlement (*sldist*), low *sldist* and low movement rates) of the base case model. Solid vertical lines represent the closed area of the model.

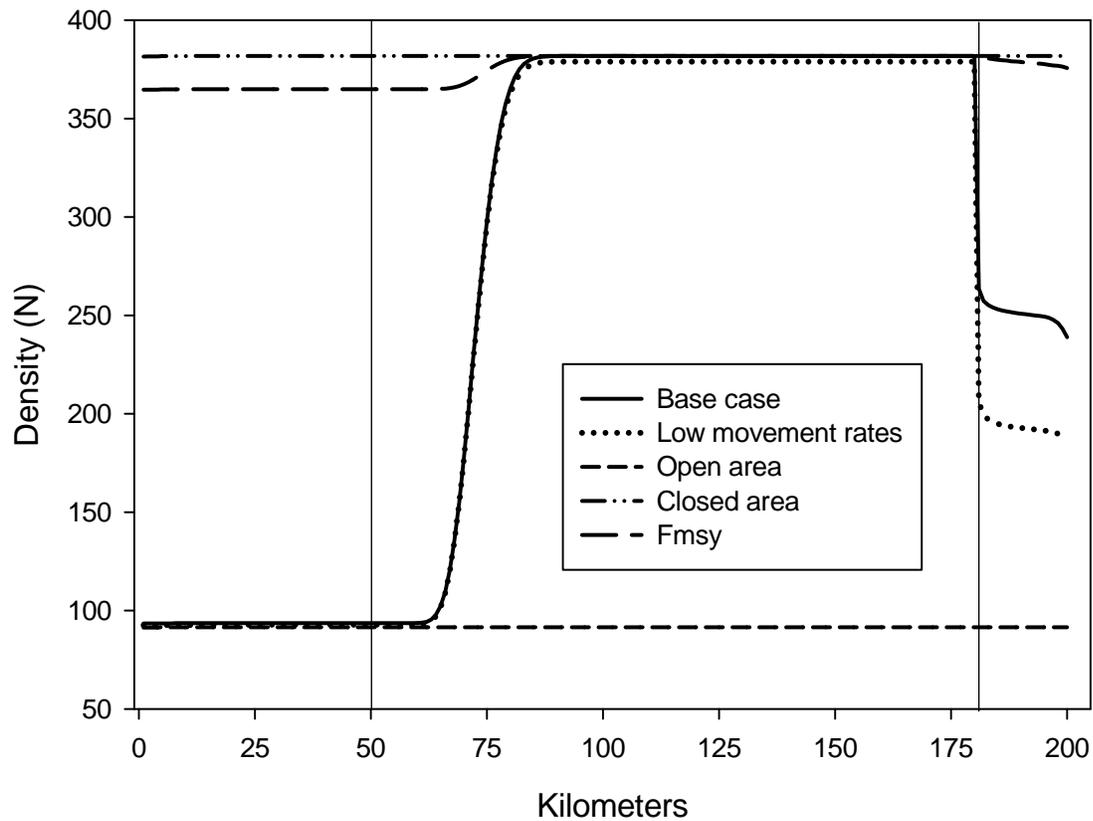


Figure 3-5. Densities (N) of subadult dusky sharks from the base case and sensitivity analyses (low movement rates, entire area open to fishing, entire area closed to fishing and fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY)) of the base case model. Solid vertical lines represent the closed area of the model.

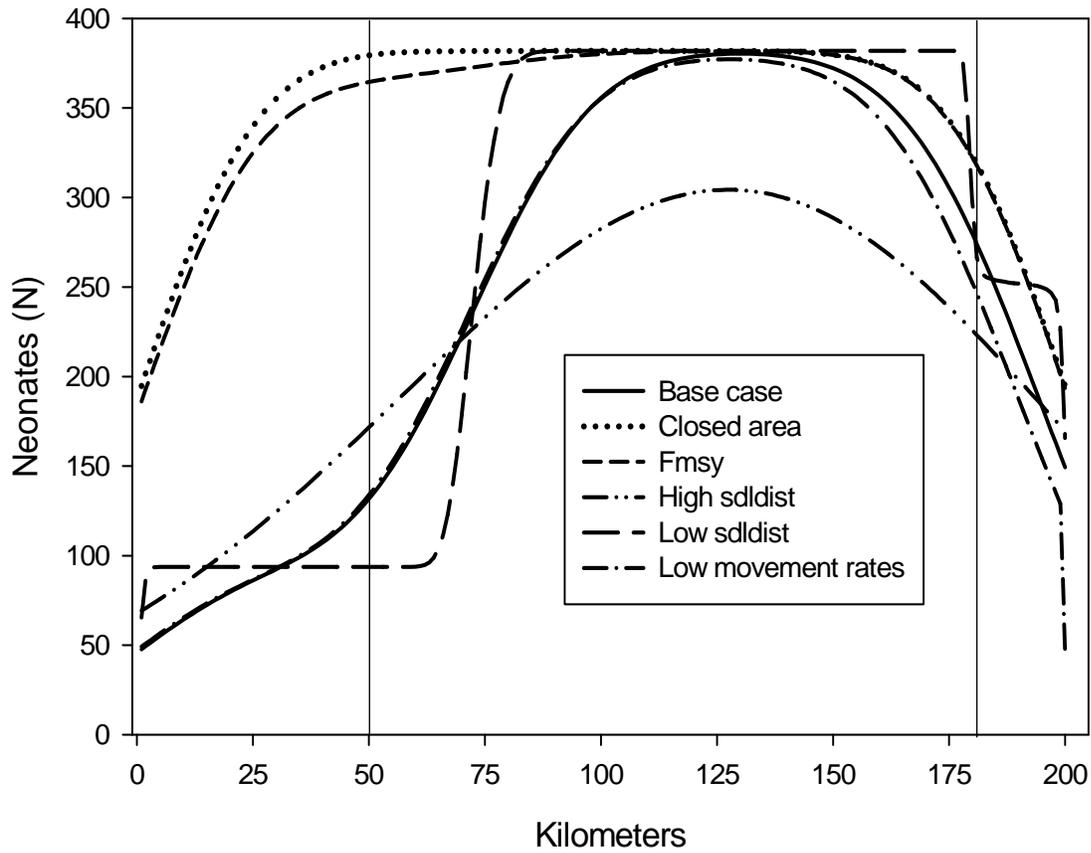


Figure 3-6. Neonate densities (N) found within the subadult dusky shark life-stage model for the base case and sensitivity analyses (entire area closed to fishing, fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY), high standard deviation of spatial distribution of neonate settlement (*sldist*), low *sldist* and low movement rates) of the base case model. Solid vertical lines represent the closed area of the model.

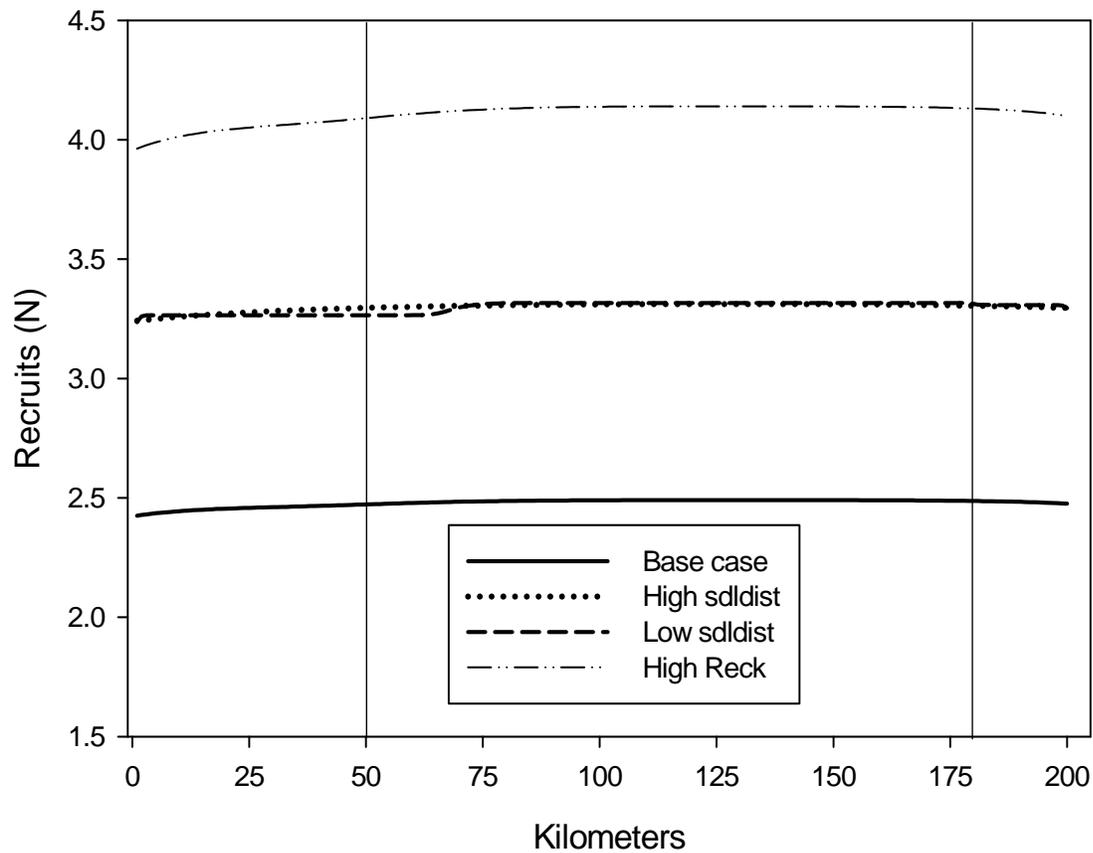


Figure 3-7. Recruit densities (N) found within the subadult dusky shark life-stage model for the base case and sensitivity analyses (high standard deviation of spatial distribution of neonate settlement (*sldist*), low *sldist* and high compensation ratio (*reck*)) of the base case model. Solid vertical lines represent the closed area of the model.

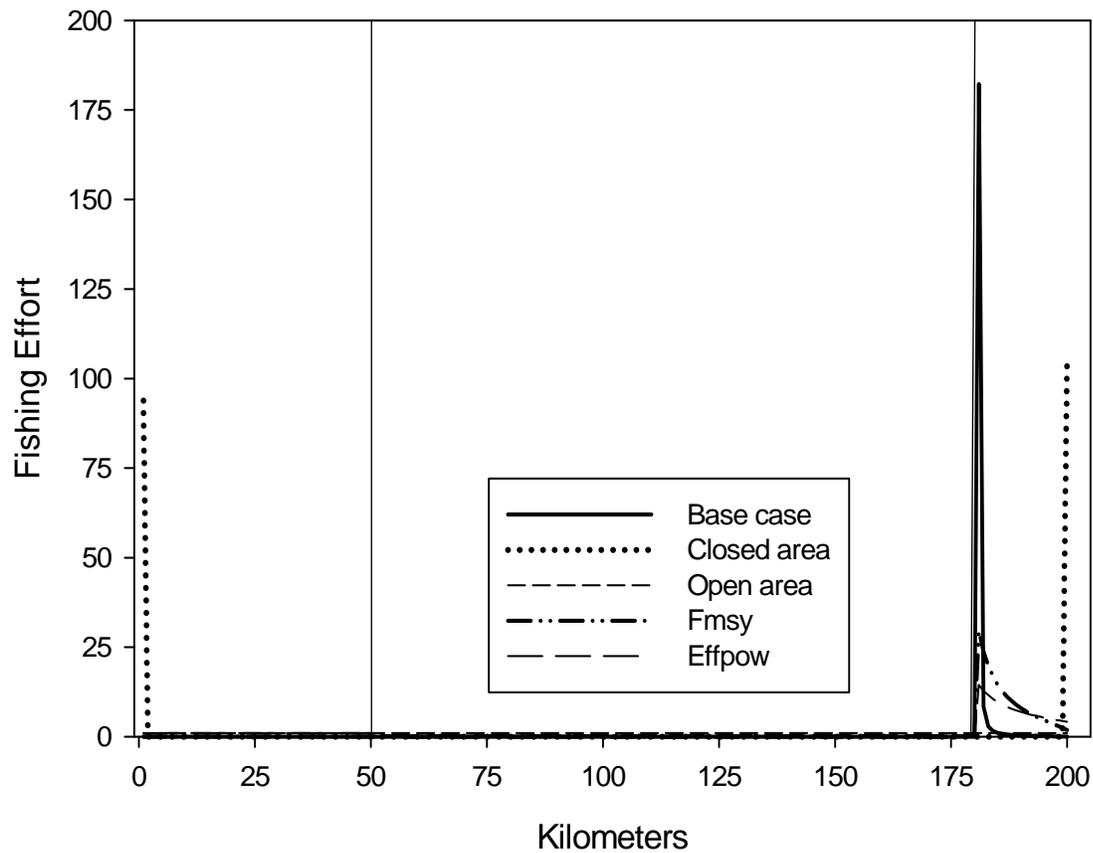


Figure 3-8. Redistribution of fishing effort for subadult dusky sharks from the base case and sensitivity analyses (entire area closed to fishing, entire area open to fishing, fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY) and high standard deviation of the gravity model (*effpow*)) of the base case model. Solid vertical lines represent the closed area of the model.

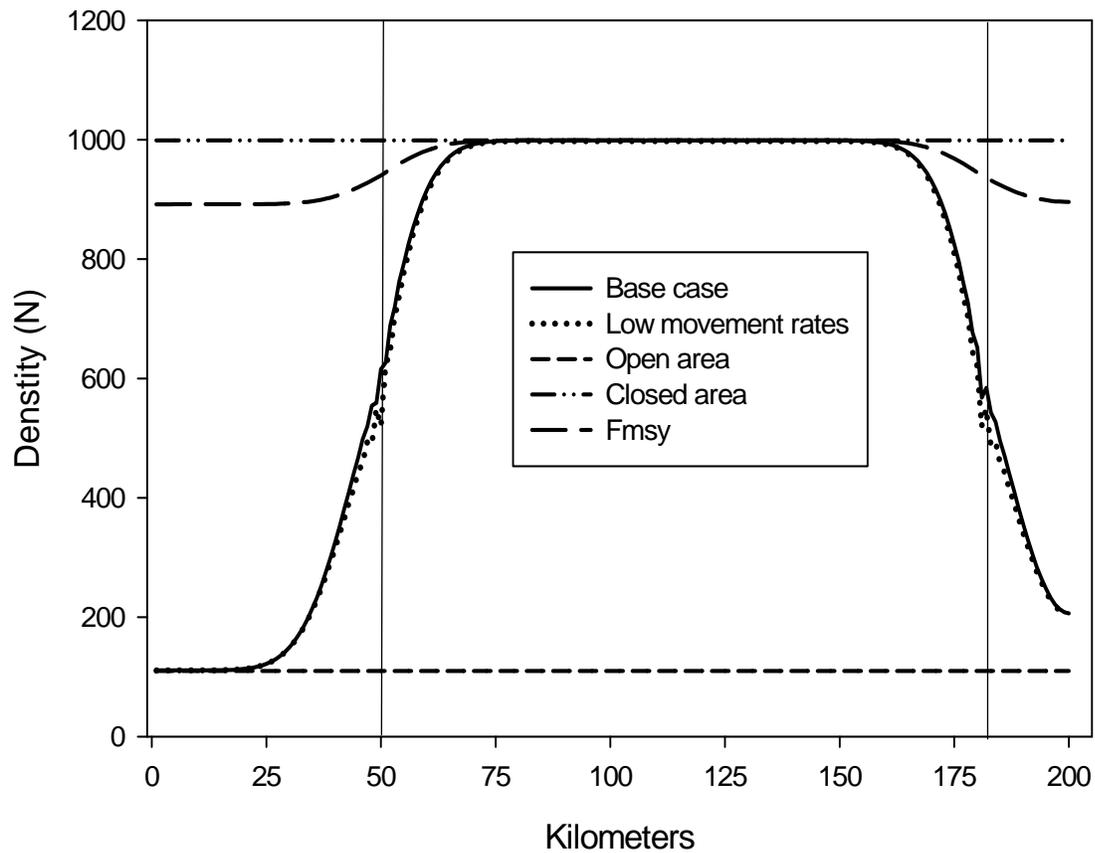


Figure 3-9. Densities (N) of adult dusky sharks from the base case and sensitivity analyses (low movement rates, entire area open to fishing, entire area closed to fishing and fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY)) of the base case model. Solid vertical lines represent the closed area of the model.

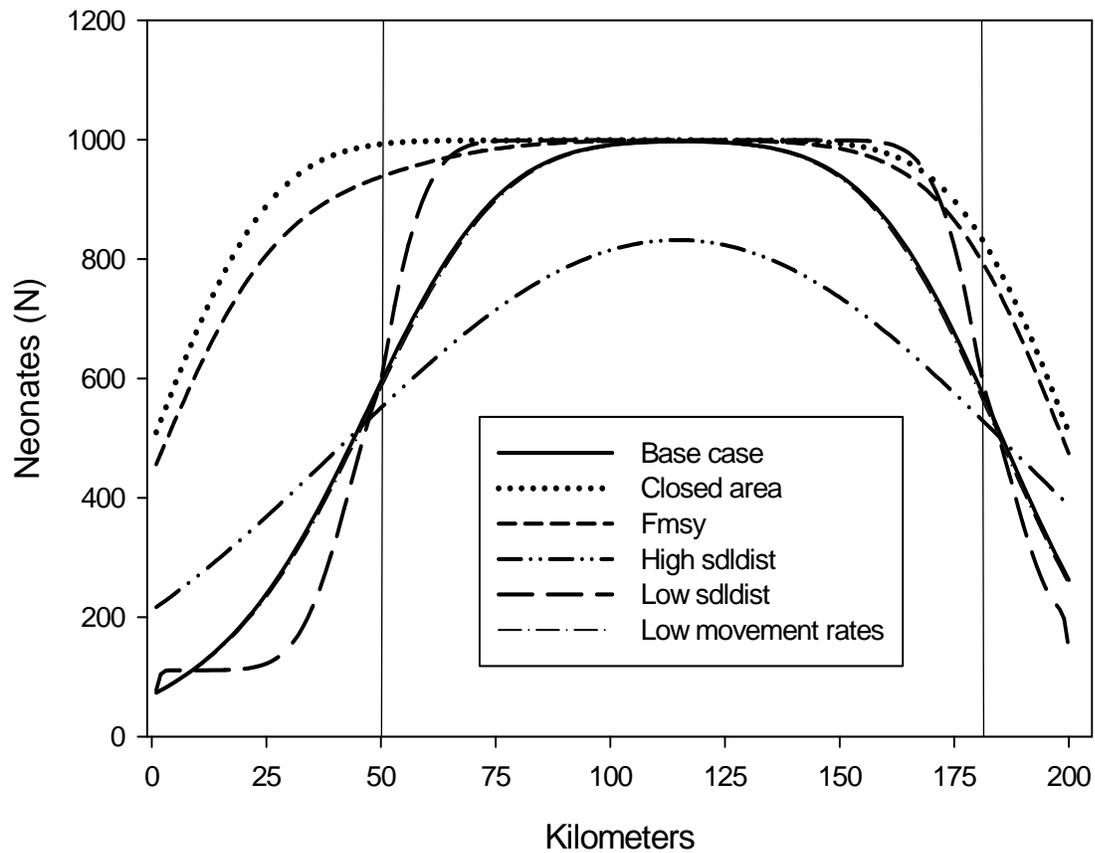


Figure 3-10. Neonate densities (N) found within the adult dusky shark life-stage model for the base case and sensitivity analyses (entire area closed to fishing, fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY), high standard deviation of spatial distribution of neonate settlement (*sldist*), low *sldist* and low movement rates) of the base case model. Solid vertical lines represent the closed area of the model.

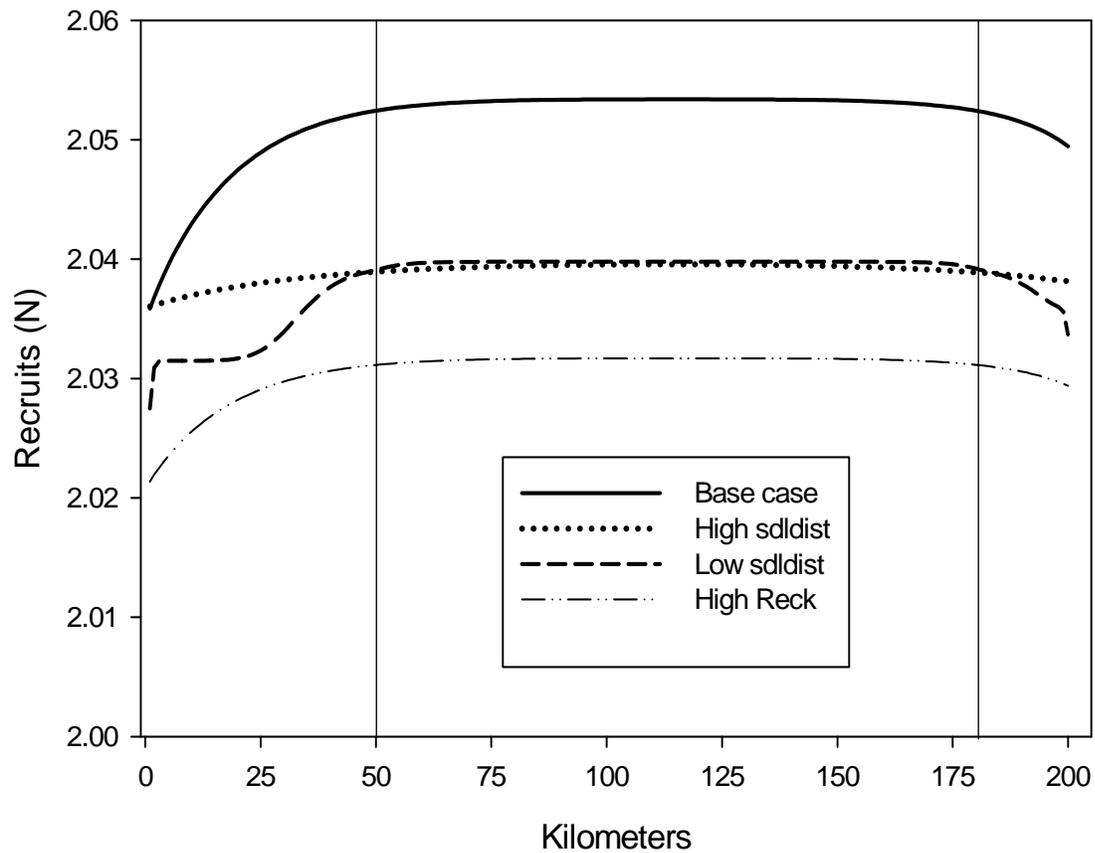


Figure 3-11. Recruit densities (N) found within the adult dusky shark life-stage model for the base case and sensitivity analyses (high standard deviation of spatial distribution of neonate settlement (*sldist*), low *sldist* and high compensation ratio (*reck*)) of the base case model. Solid vertical lines represent the closed area of the model.

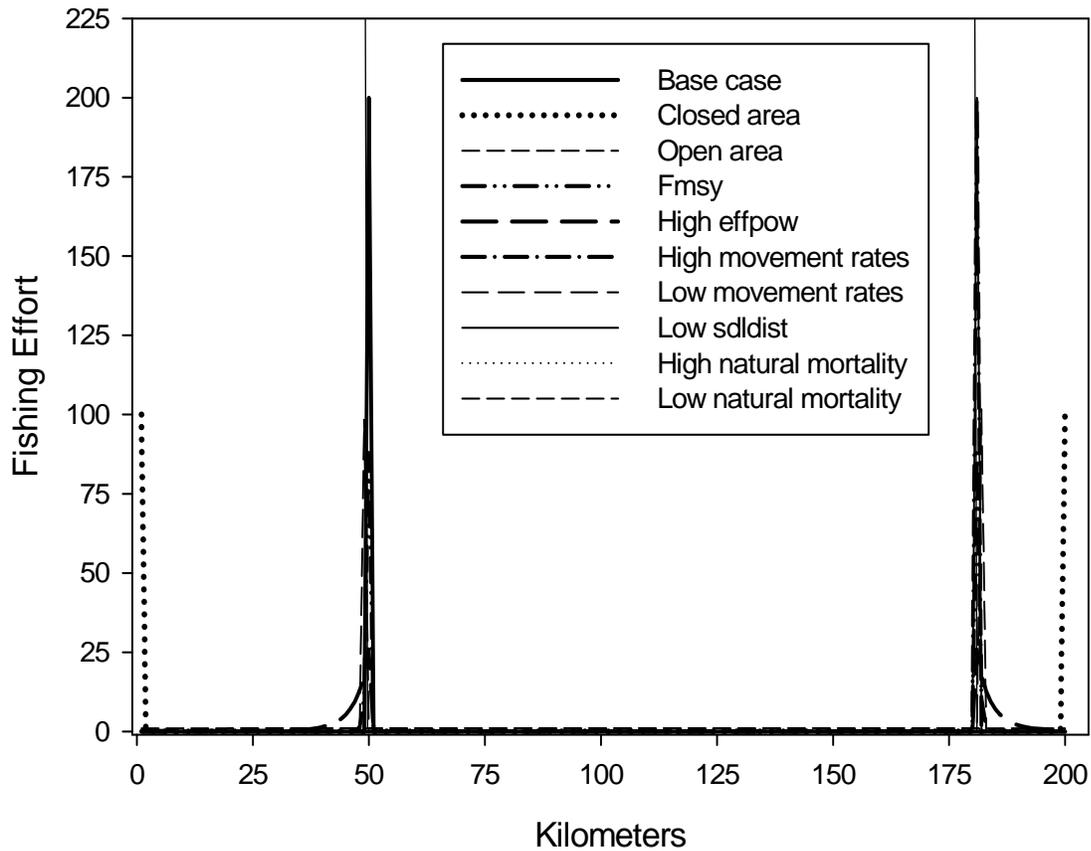


Figure 3-12. Redistribution of fishing effort for adult dusky sharks from the base case and sensitivity analyses (entire area closed to fishing, entire area open to fishing, fishing effort reduced to F_{msy} (fishing mortality rate that would produce Maximum Sustainable Yield (MSY), standard deviation of gravity model (*effpow*) increased, high movement rates, low movement rates, low standard deviation of spatial distribution of neonate settlement (*sddist*), high natural mortality rates and low natural mortality rates) of the base case model. Solid vertical lines represent the closed area of the model.

CHAPTER 4 CONCLUSIONS, MANAGEMENT AND RESEARCH RECOMENDATIONS

Conclusions

Results from the age-structured model showed that fishing mortality, even at reduced levels, will lead to the dusky shark continuing to be reduced to levels of less than 60% of virgin biomass. The results also indicated that if catches have been underestimated and/or underreported through the years that the stock could already be considered more heavily reduced with respect to virgin biomass. Management efforts already in place, including placing the species on the NMFS prohibited species list and time/area closures, are not likely to result in zero fishing mortality over the next 20 years. This inability of management measures to fully protect this species is largely due to the dusky shark being caught as bycatch in several fisheries (Beerkircher et al., 2002; Alexia Morgan, unpublished data). It is likely that the population of dusky sharks in the northwestern Atlantic Ocean will remain heavily reduced during the next 20 years. Fisheries managers must be extremely proactive in determining additional management options and research needs that will help reduce and preferably eliminate fishing mortality for this species in the future.

The results of the spatial model offer a general understanding of the theoretical effects time/area closures would have on the dusky shark population but a more complex model incorporating a temporal component and better data are needed for a full analysis. Simulated area closures caused the density of dusky sharks to become concentrated within the closed area. However, Walters et al. (2007) suggest caution when drawing conclusions based on “inside-outside” density comparisons, because the model does not include baselines with which to compare the abundances to. A more complex model that can combine population dynamics with the seasonal aspect of the time area closure, spatial movement, historical fishing effort, and

length at catch data and can simulate the closure through time would provide more reliable results. Such a complex model was not used in this assessment because this information is either lacking for this species or the historical time frame is too short at this point in time for use in such complex models.

Management and Research Recommendations

Managers should focus on trying to reduce the fishing mortality dusky sharks suffer as a result of being caught as bycatch. To help reduce or eliminate this type of fishing mortality managers should attempt to reduce the number of vessels involved in these fisheries, therefore reducing the number of interactions between fishing gear and this species. Fishing effort could be reduced by decreasing the quotas for targeted species in these fisheries, instituting by-back vessel programs or directing fishers towards fisheries that do not encounter this species. Managers should also increase observer effort in these fisheries and improve on recording and reporting by fishers and dealers, which will improve the data used in future assessments.

Future research aimed at reducing fishing mortality and/or improving our knowledge of the effects of time/area closures should include; cross checking logbook data with observer data and dealer landings to determine any discrepancies that may affect the total catches used in this and other models, develop direct estimates for natural mortality rates, investigate at-vessel mortality rates by soak time for the pelagic longline fishery, initiate mark/recapture tagging programs, investigate post release survivability in gillnet, trawl, pelagic longline, bottom longline and recreational fisheries, develop direct selectivity estimates for these same fisheries, collect length at capture data for these fisheries and determine the spatial distribution and movement rates of different age classes. Information gleaned through such additional research could be used to improve upon future assessments.

APPENDIX A
TIME AREA CLOSURE MAP

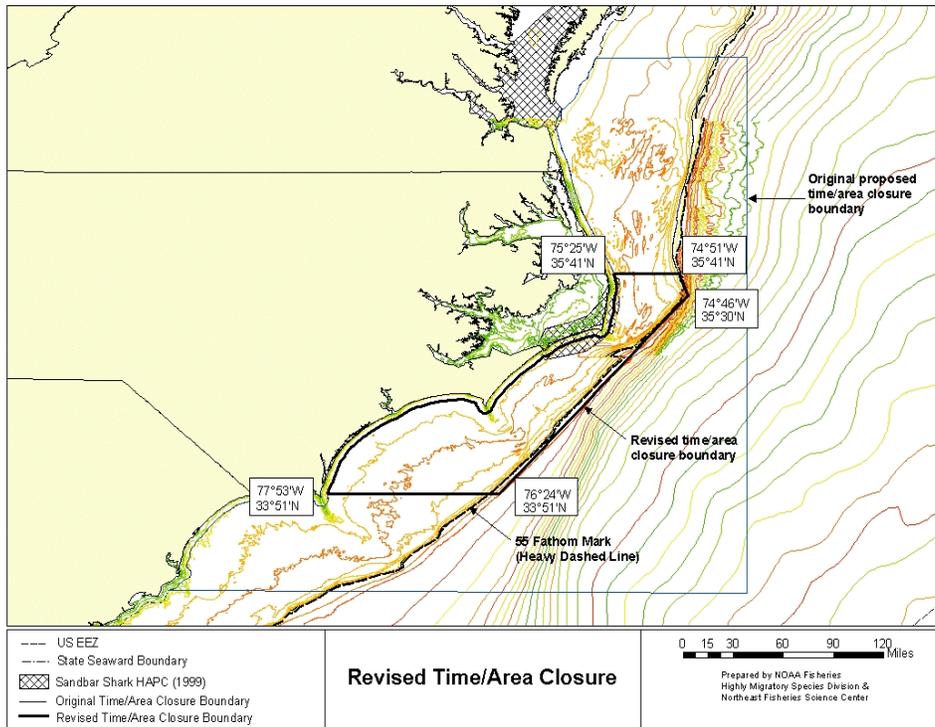


Figure A-1. Map of the time/area closure currently in effect off the coast of North Carolina. (NMFS. 2003. Final Amendment 1 to the fishery management plan for Atlantic tunas, swordfish and sharks. National Marine Fisheries Service, Highly Migratory Species Division, Silver Spring, MD. Figure 4-1, p. 4-110.).

APPENDIX B
DUSKY SHARK BIOLOGICAL DATA

Table B-1. Life history parameters for the dusky shark (Enric Cortés, personal communication).

Parameter	Definition	Value		Units	Reference
		males	females		
K	Brody growth coefficient	0.038-0.043	0.039-0.045	yr ⁻¹	Natanson et al., 1995; Simpfendorfer, 2002a Natanson et al., 1995;
L_{inf}	Theoretical maximum length	345-373	336-349	cm fork length	
t₀	Age at zero length	-6.28	-7.04	yr	Natanson et al., 1995
t_{mat}	Age at maturity	19	21	yr	Cortés et al., 2006
L_{mat}	Length at maturity	231	235	cm fork length	Cortés et al., 2006
t_{max}	Lifespan	>25	>33	yr	Natanson et al., 1995
L_{max}	Maximum observed length	299	308	cm fork length	Natanson et al., 1995;
L₀	Size at birth		68-81	cm fork length	Natanson et al., 1995
	Reproductive frequency		2 or 3	yr	Branstetter and Burgess, 1996
	Sex ratio at birth		1 to 1	dimensionless	
m_x	Mean number of pups		7.1	pups	Branstetter and Burgess, 1996
a	Scalar coefficient of weight on length	3.2415x10 ⁻⁵	sexes combined	dimensionless	Kohler et al., 1995
b	Power coefficient of weight on length	2.7862	sexes combined	dimensionless	Kohler et al., 1995
M₀ range	Age-0 instantaneous natural mortality rate		0.248	yr ⁻¹	Cortés et al., 2006
S₀ range	Age-0 annual survivorship		0.78-0.98	yr ⁻¹	Cortés et al., 2006
M_{1-mat} range	Age-1 to maturity M		0.087-0.238	yr ⁻¹	Cortés et al., 2006
S_{1-mat} range	Age-1 to maturity S		0.80-0.98	yr ⁻¹	Cortés et al., 2006
M_{ad} range	Adult instantaneous natural mortality rate		0.026-0.083	yr ⁻¹	Simpfendorfer, 1999; Romine et al.
S_{ad} range	Adult annual survivorship		0.90-0.98	yr ⁻¹	Cortés et al., 2006

APPENDIX C SELECTIVITY CURVES

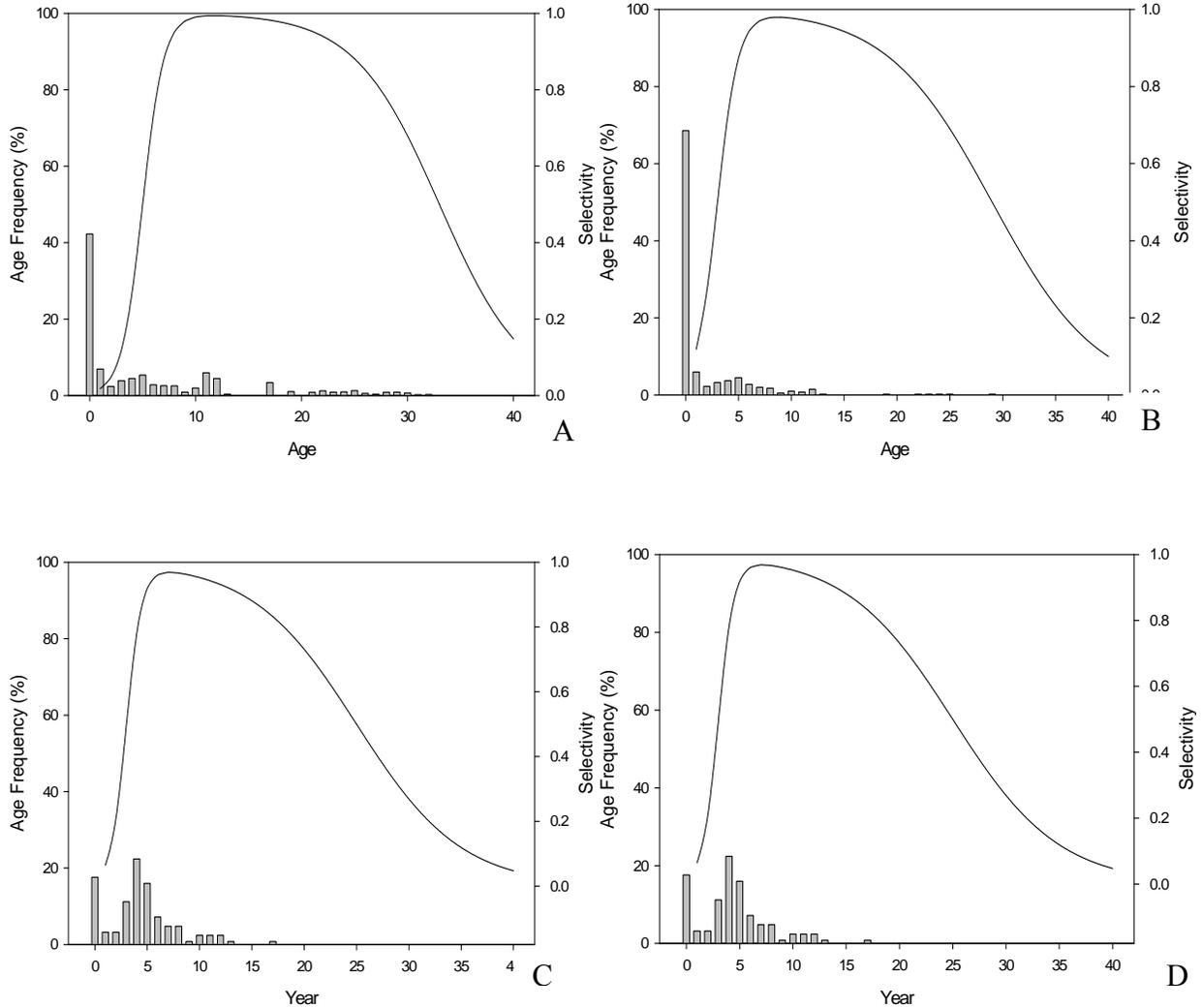


Figure C-1. Selectivity curves fit to age distributions for the following four data sets: A) Bottom Longline Observer Program (BLLOP), B) Virginia Institute of Marine Science (VIMS), C) Large Pelagic Survey (LPS) and D) Pelagic Longline Observer Program (PLLOP) (Enric Cortés personal communication).

APPENDIX D
SELECTIVITY PARAMETERS

Table D-1. Selectivity parameters for the double logistic distribution fitted to age data for the following four data sets: Bottom Longline Observer Program (BLLOP), Virginia Institute of Marine Science (VIMS), Large Pelagic Survey (LPS) and Pelagic Longline Observer Program (PLLOP) (Enric Cortés personal communication).

Data set	Parameter estimates			
	a_{50}	b	c_{50}	d
BLLOP	4	1	32	4
VIMS	2	1	28	5
LPS	2	0.75	24	5
PLLOP	1.5	1	28	5

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BIOGRAPHICAL SKETCH

I graduated from Nova Southeastern University's Oceanographic Center in 2001 with a Master of Science degree. After completing my master's degree I began working for the Florida Program for Shark Research located at the University of Florida's Museum of Natural History. In 2003 I began working toward my Ph.D. with the Department of Fisheries and Aquatic Sciences at the University of Florida.