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Status and Demographic Analysis of the Dusky Shark, Carcharhinus obscurus, in the Northwest Atlantic

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Status and demographic analysis of the Dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

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In Partial fulfillment
Of the Requirements for the Degree of
Master of Science

by
Jason G. Romine
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APPROVAL SHEET

This thesis is submitted in partial fulfillment of

The requirements for the degree of

Master of Science

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TABLE OF CONTENTS

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I would like to thank George Burgess of the Florida Museum of Natural History and the individuals that make up the Commercial Shark Fishery Observer Program for collecting and providing data for this study.

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I would also like to thank the WRGC and associates for their input and relief from the stressors of a graduate student's life as well as the commercial fishers I have had the pleasure of speaking with. They have provided me with a view that fishery managers must take account of if both fishers and fishery scientists are to coexist and preserve the fisheries for our future.

Last, but not least I would like to thank my immediate family; my wife, Heidi; our schnoodle, Raffles; our chocolate lab, Dusky; our Maine-coon cat, Blackbeard; and the various reptiles we may have at present. I would like to thank Heidi for her continued support through it all. She is the reason I have made it this far and the reason I look forward to each day no matter how grim the sky.

LIST OF TABLES

CHAPTER 1: Status of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

CHAPTER 2: Demographic analysis of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

LIST OF FIGURES

CHAPTER 1: Status of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

CHAPTER 2: Demographic analysis of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

ABSTRACT

The dusky shark, *Carcharhinus obscurus,* is a large coastal shark ranging from the Caribbean North to Cape Cod, U.S.A. in the Northwest Atlantic. The dusky shark has experienced drastic reductions in population size in the Northwest Atlantic due to over-fishing combined with life history parameters that result in very low annual population growth. Catches of dusky sharks comprised 20% of the Virginia Institute of Marine Science (VIMS) Shark survey total catch in the late 1970's and early 1980's and presently comprise only 2-3% of total catch. This drastic reduction in abundance has given cause to examine the status and ecology of the species in the Northwest Atlantic.

Analyses were conducted on fishery-independent, fishery-dependent, and previously published data to examine the present status and ecology of the dusky shark. All data sets depicted a decline in abundance of dusky sharks as well as a decline in catches of mature sharks. The dusky shark was recently placed on the protected species list and may no longer be taken by commercial fishers. Although the species is protected, it experiences high hooking mortality within the commercial shark fishery. Analyses were conducted to determine factors that lead to mortality of dusky sharks within the fishery.

Reproduction in the dusky shark is not well understood. Reproductive data was analyzed to provide more accurate estimates of gestation period and to determine if a resting period following parturition occurs as in other carcharhiniformes.

Previous demographic analyses of the dusky shark in the Northwest Atlantic have yielded estimates of population increase of 2.8% to 5.6%. These estimates did not include fishing mortality or the possibility of a three-year reproductive cycle. Demographic model techniques were employed to estimate population growth under conditions determined in this study and previously published data. Life tables and Leslie matrices were constructed to incorporate various levels of hooking mortality and probability distributions for vital parameter estimates. Age-0 natural mortality was determined to be the value that would create a population at equilibrium under zero fishing pressure within the models.

Elasticity analyses were conducted to determine contributions of life stages to population growth. Elasticity ratios were then analyzed to estimate the required amount of increased fecundity or survival within the age-0 group to offset increased mortality in the juvenile stage. Model sensitivities to perturbations in vital parameters were also calculated.

Catch data analyses yielded increased catches of smaller sharks despite consistency in fishing location over time within the commercial fishery. The smallest size classes of dusky sharks experienced the highest hooking mortalities within the fishery. Demographic analyses portrayed decreasing population values under minimal fishing pressure. This coupled with an evident three-year reproductive period provides a grim outlook for the species unless greater protections are enacted.

STATUS AND DEMOGRPAHIC ANALYSIS OF THE DUSKY SHARK, *Carcharhinus obscurus,* IN THE NORTHWEST ATLANTIC

CHAPTER: 1

Status of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

INTRODUCTION

The dusky shark (*Carcharhinus obscurus*) is a common coastal and pelagic shark that inhabits warm-temperate and tropical continental waters of the western North Atlantic, ranging from southern New England to the Caribbean and Gulf of Mexico to southern Brazil. This species can be found inhabiting waters within the surf zone out to depths of 400 m (Compagno 1984). The dusky shark avoids areas of lower salinity and is rarely found in estuarine environments (Compagno 1984; Musick and Colvocoresses 1986; Musick et al. 1993).

This species undertakes long temperature-related migrations along the east coast of the U.S. Individuals move north as water temperatures increase with the onset of spring and return south with the onset of fall (Musick and Colvocoresses 1986). Adults migrate farther than neonates and juveniles. Juveniles occupy highly productive coastal nurseries from New Jersey to South Carolina for several months (Castro 1993).

Tagging studies have shown the dusky shark's range in the Northwest Atlantic to extend from New England south to the Caribbean Sea and the Gulf of Mexico no farther south than the Yucatan Peninsula (Kohler et al. 1998). These data support the designation of a distinct population segment designation for the dusky shark in the Northwestern Atlantic. Tagged sharks released in the Caribbean Sea (n=4) were not recovered (Kohler et al. 1998). These sharks may have been the closely related

Galapagos shark, *Carcharhinus galapagensis*. Additional tagging of dusky sharks in this region is needed to validate the southern extent of the population.

The dusky shark attains large sizes, reaching 360 cm Total Length (TL) (Castro 1993). In the western North Atlantic, males are estimated to reach sexual maturity at 231 cm FL and 19 years of age, while females mature at 235 cm FL and 21 years of age (Natanson et al. 1995). The oldest reported dusky from vertebral centra aging studies is 37 years, but they are believed to live to a maximum age of 40 or 50 years (Natanson et al. 1995). Vertebral aging has been validated in Australian waters using OTC (oxytetracycline) marking and tag recapture data (Simpfendorfer et al. 2002).

Reproduction in this species is not well understood. Length of gestation period and time of mating are have not been determined. The dusky shark is viviparous, giving birth to litters ranging from 3-14 pups. Branstetter and Burgess (1996) suggest a gestation period of 22 to 24 months. The lack of large yolky ova in late term females suggests at least a one-year resting period following parturition (Musick 1995; Branstetter and Burgess 1996).

Dusky sharks have suffered dramatic population decreases over the past decade. Fishing mortality and lack of a management plan (prior to 1993) combined with slow growth and a long reproductive process has led to their decline in Northwestern Atlantic waters. These factors combined with a shark fishery that expanded from 135 metric tons landed in 1979 to 6452 metric tons in 1991 (Castro 1997) have been the main cause of the decline of the species. The southeast U.S. accounts for approximately 75% percent of all shark landings in the United States (Scott 1997). The fishery peaked in 1989 and has declined since then (Castro 1997). The dusky shark was one of the preferred species within this fishery along with blacktip sharks, sandbar sharks, and spinner sharks (Scott 1997).

Relative abundance of the species has declined from 20% of the total shark catch on coastal long-lines to 1-2% of the catch (Musick et al. 1993). Scott (1997) also noted a decline in the catch rate of dusky sharks by long-liners operating in the Virginia area from 1976 to 1993. Brown's (1997) standardized CPUE for rod and reel landings from the Virginia to Massachusetts region also show a decline from 1986 to 1995. Decline in numbers of dusky sharks have also been documented from pelagic long-liners. Examination of logbooks reveal a decline in the catch rate index of dusky sharks from 1.5 in 1992 to 0.8 in 1995 (Cramer 1996). Russel (1993) found a similar trend in the Northern Gulf of Mexico longline fishery from 1988-1991. Specifically, catch rate of dusky sharks declined from 0.9 sharks/100 hooks in 1988 to 0.0037 sharks /100 hooks in 1991.

Demographic analyses have generated estimates of annual intrinsic rate of population increase, r, of 2.8% (Cortés 1998) and 5.6% (Sminkey 1996). These two estimates are based on a population free of fishing mortality and a two-year reproductive cycle. The reality of heavy fishing mortality and the possibility of a three-year reproductive cycle would lead to a lower estimate of r. These consequences illustrate the need for conservative management strategies to protect this species.

Large coastal sharks were first protected in the Atlantic by a Secretarial Fishery Management Plan in 1993 (NMFS 1993). Subsequently, quotas were cut in 1997 after analyses indicated the original assessment had over estimated the intrinsic rate of increase by 2.5 to 3 times. In 2000 dusky sharks were placed on the list of prohibited species

(NMFS 2000), but by-catch mortality remains a problem. This study examines the status of dusky sharks in the Northwest Atlantic and provides recommendations for their conservation.

The objectives of this study were:

1. To determine catch rates and length frequencies of sharks landed over time in the commercial shark fishery and from the fisheries-independent VIMS shark longline survey.
2. To determine mortality rates of dusky sharks and factors causing mortality of dusky sharks within the commercial shark fishery.
3. To determine reproductive periodicity and gestation period of dusky sharks.

METHODS

Data Collection

Data collected by the Florida State Museum Commercial Shark Fishery Observer Program (CSFOP) from 1994-2000 in the South Atlantic and Florida region of the Gulf of Mexico were analyzed for catch rates, length frequencies, mortality estimates and life history parameters. Observers collected data on long-line sets and shark catches (Table 1). Observer coverage was 35-40 days within each biannual commercial shark harvest season. Data on long-line sets included depth, soak times, number of hooks, and length of set. Biological data collected included fork length (FL), total length (TL), sex, hooking mortality, and reproductive status. Fork length and total length were measured from the tip of the snout to the fork of the tail and tip of snout to the tip of the caudal fin respectively. Individuals were given a reproductive category based on clasper characteristics in males and uterine condition in females. Males were designated as juvenile, sub-adult or mature. Measurements of clasper lengths on sub-adult and mature specimens were also recorded. Females were characterized as immature, maturing, mature, post-partum, or pregnant. Number of embryos and their minimum and maximum lengths were recorded for each litter. Average number of pups per female was calculated from 51 pregnant sharks.

Table 1. Summary of annual catch data from the Commercial Shark Fishery Observer Program (CSFOP) from 1994 to 2000.

Year	Hooks set	Soak time (hours)	Number of dusky sharks
1994	85886	1531.10	74
1995	119938	2473.00	427
1996	92138	1653.00	219
1997	15117	266.70	141
1998	45438	1003.10	319
1999	51321	1184.70	297
2000	22396	536.62	10

Dusky shark data collected by the fishery-independent shark-monitoring program at the Virginia Institute of Marine Science (VIMS) from 1975-2001 (the survey did not operate outside the Chesapeake Bay in 1994) were also analyzed for catch rates, relative abundance, size frequencies, and reproductive parameters. The VIMS longline shark survey operates annually from May through October. Approximately seven 100 hook sets are made each month at set stations along the Virginia coast. Gear consists of tarred nylon mainline and steel yankee gangions (Musick et al. 1993). Throughout the period of 1975-2001, a total of 574 coastal sets were made consisting of 56,134 hooks and 2,451 soak hours (Table 2).

Data Analysis

Catch Per Unit Effort (CPUE) for five size classes was calculated from the CSFOP data set as sharks/100,000 hk hrs (hook hours). Size classes were designated as <110 cm FL, 111-169 cm FL, 170-229 cm FL, 230-269 cm FL, and >270cm FL. These same size classes were used to calculate size-specific hooking mortality. Daily frequency of hooking mortality was also calculated.

Ages were estimated for all sharks for which length data were available by using von Bertalanffy parameters established by Natanson et al. (1995). These ages were then used to establish age-specific hooking mortality. A regression was fit to age-specific hooking mortality rates for ages 0-31. Little data were available for sharks greater than 31 years of age.

Hooking mortality or state of fish upon landing was determined by the observer. Lacking any vital signs, the animal was designated as dead. If the animal was alive, the

Table 2. Summary of catch data from the Virginia Institute of Marine Science shark longline survey from 1975 to 2001.

Year	**N**	**Min. FL(cm)**	**Max. FL(cm)**	**Avg. FL(cm)**	**Total hooks set**	**Total soak time(hours)**	**Sets**	**Yearly avg. set CPUE(sharks /1000hk*hrs)**
1975	20	76	288	124	496	116	13	7.890
1976	7	79	263	111	210	40	6	8.838
1977	4	84	247	204	872	64	13	0.812
1978	10	77	93	85.2	236	11	4	17.260
1979	10	131	172	151	301	15	4	3.840
1980	117	73	183	94	3650	162	37	7.780
1981	43	75	169	102	3650	168	37	2.530
1982	3	161	264	227	478	29	5	1.580
1983	3	160	189	174	1176	51	13	0.370
1984	6	104	145	117	667	32	9	2.110
1985	1	197	197	197	380	23	5	0.950
1986	0	0	0	0	748	31	9	0.000
1987	4	146	198	169	653	42	7	1.010
1988	0	0	0	0	852	46	9	0.000
1989	1	83	83	83	566	20	6	0.450
1990	2	83	88	85	5432	229	55	0.130
1991	6	80	218	115	4768	198	49	0.350
1992	1	88	90	89	3588	127	36	0.069
1993	5	84	139	98	1995	74	19	0.660
1994		0	0	0				no sets
1995	5	80	109	95	2540	107	27	0.460
1996	24	79	172	109	3313	137.5	33	1.750
1997	1	73	0	93	4321	152	36	0.050
1998	7	81	125	96	4577	162.5	41	0.370
1999	18	74	111	91	2620	106.5	26	1.730
2000	28	81	105	90	4095	156.5	38	1.810
2001	16	73	108	93	3950	151	37	0.980
Total	**342**				**56134**	**2451**	**574**	**2.453**

observer designated the animal accordingly. Post-release mortality is unknown. Mortality estimates were calculated for each month and size class.

Correspondence analysis and multiple correspondence analyses were conducted using SAS software and the CORRESP procedure with the MCA statement to produce graphical representations of correlations between factors associated with hooking mortality within the first shark fishing season. The second season was omitted from the analysis due to the small numbers of dusky sharks landed during this time period.

Average number of pups per female was calculated from 51 pregnant sharks. Reproductive state of 98 mature female dusky sharks was examined to determine the reproductive cycle of this species. Embryo sizes from CSFOP, VIMS, and Clark and von Schmidt (1965) coupled with reproductive states were used to determine gestation period.

RESULTS

Length frequencies

Analysis of length frequencies provided by the CSFOP annually indicated a distinct shift in catch composition from a broad size distribution in 1994 to catches comprised primarily of sharks less than 110 cm FL in 1999 (Figure 1). Fifty-five percent of females caught were less than 110 cm FL and 50% of males caught were less than 110 cm FL. Using age and growth information from Natanson et al. (1995), the fishery was exploiting the 0-3 year old age classes.

The fishery independent (VIMS) data show a similar trend. The majority of animals landed were juvenile sharks (Figure 2). The average length of dusky sharks landed has declined from 200 cm PCL in 1977 to 80 cm PCL in 2001 (Figure 3). No mature animals were landed after 1982, despite increases in effort. Fishing gear has remained consistent over time and is not the cause of reduced landings of mature dusky sharks by the VIMS shark survey. This shift is indicative of a decline in abundance of mature animals within the population.

Catch rates

The VIMS CPUE data from 1974 to 2000 show a decrease in relative abundance of dusky sharks from 1980 to 1992, followed by a slight increase in abundance (1997-

Figure 1. Annual length frequencies of male and female dusky sharks from CSFOP data from 1994-1999.

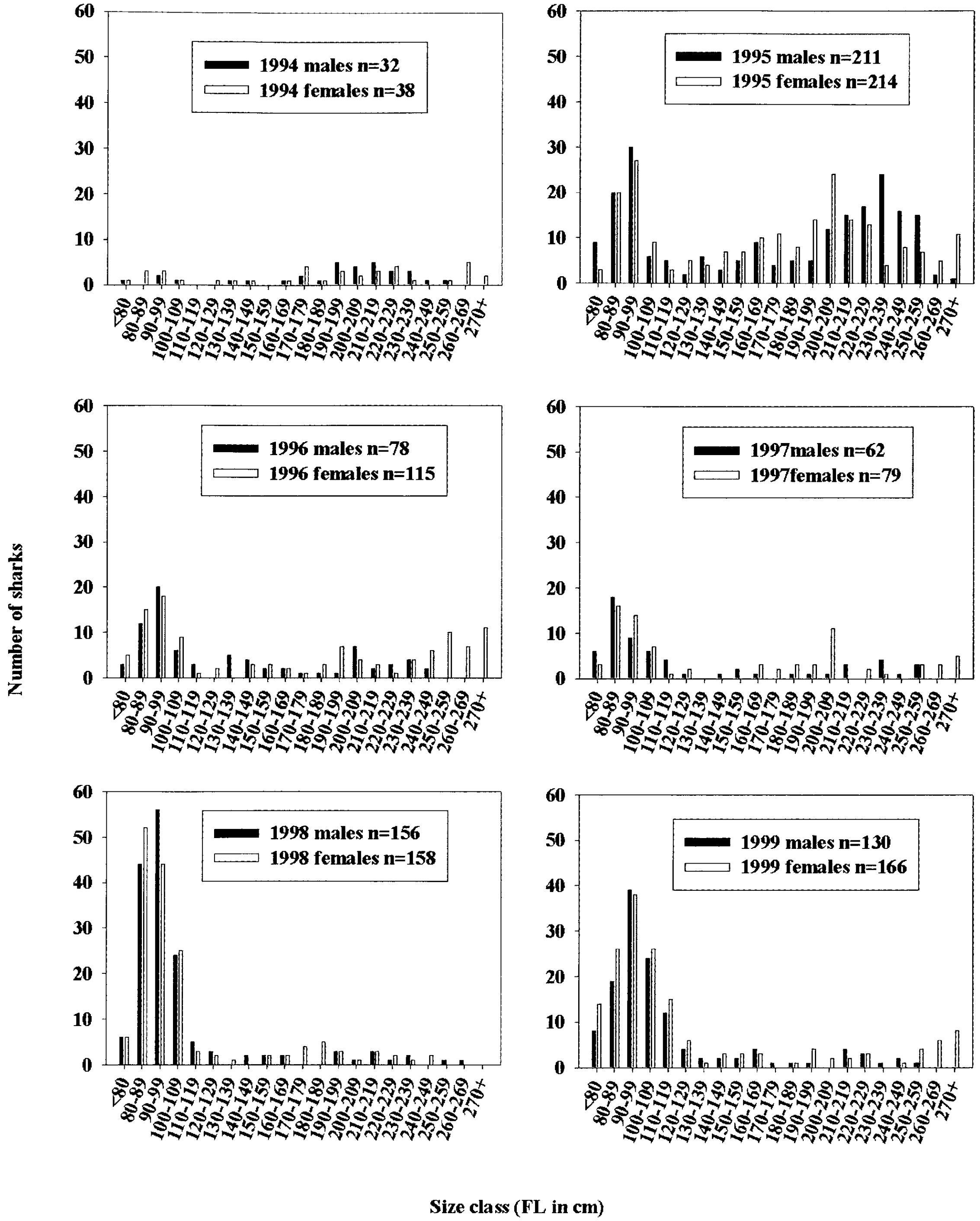


Figure 2. Length frequencies of dusky sharks sampled by the VIMS shark survey from 1975-2001.

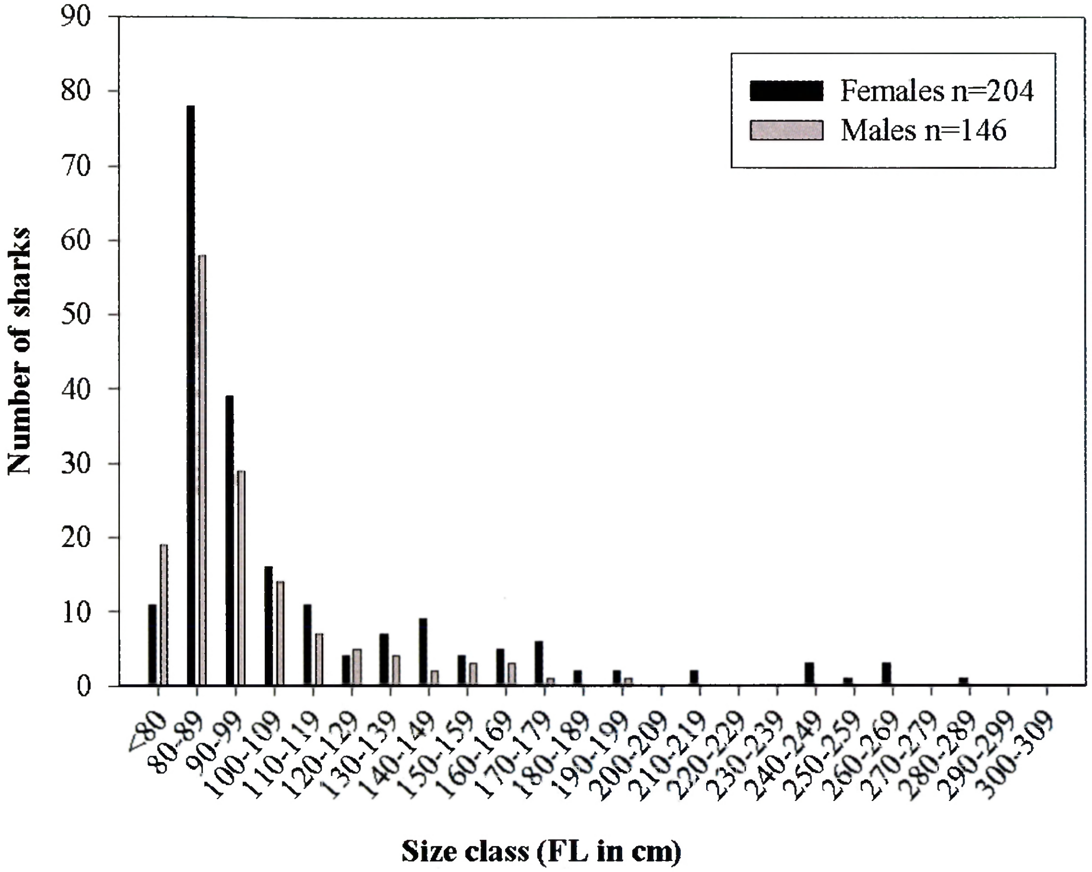
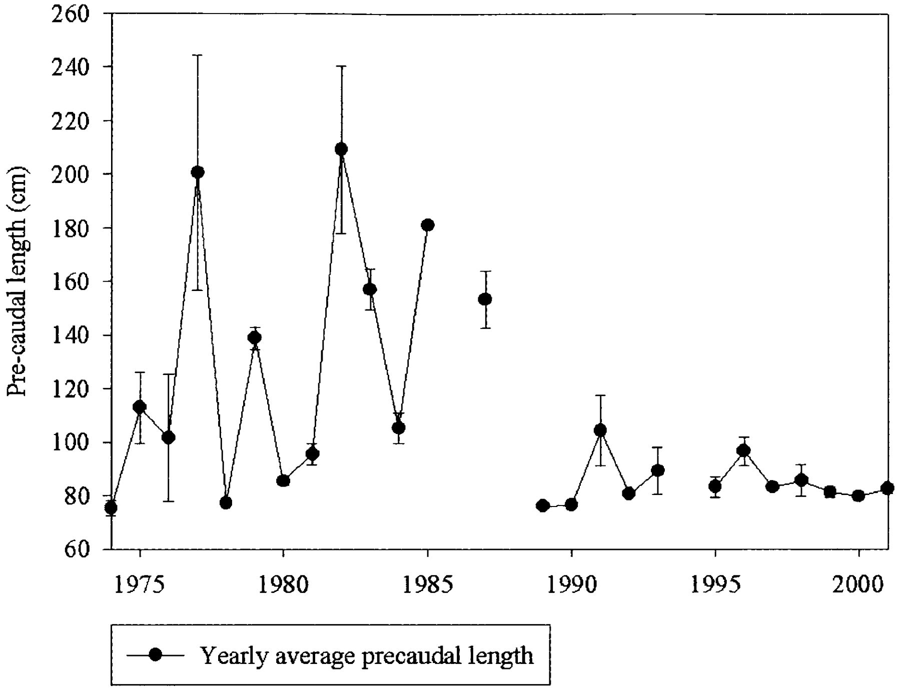


Figure 3. Average yearly pre-caudal length (PCL) of dusky sharks landed by the VIMS longline survey. (Note: No dusky sharks were landed in 1986,1988, only one dusky shark was landed in 1985, 1989, 1992, and 1997. Sampling was limited to the Chesapeake Bay in 1994.)



2000) in recent years (Figure 4). Catch rates have declined from as high as 17 dusky sharks /1000 hook hours in 1978 to less than 2 dusky sharks /1000 hook hours from 1990 to present. Recent catch rates remain much lower than catch rates in the late 1970's and early 1980's.

Catch data from CSFOP show increasing catch rates from 1994 to 1999. CPUE increased from 6.02 sharks /100,000 hook hours in 1994 to 45.07 sharks per 100,000 hook hours in 1999 (Figure 5). Catch rates from 1994 to 1999 indicate a shift toward greater numbers of small sharks being landed (Figure 6,7).

Average fork length of the North Carolina catch decreased from 180 cm FL to 120 cm FL over the time period. Catch rates for sharks greater than 170 cm FL declined over the period while catch rates for sharks below 170 cm FL showed dramatic increases. CPUE for sharks less than 110 cm FL was approximately 4 sharks /100,000 hook hrs in 1994. CPUE for this same size class increased to 110 sharks /100,000 hook hrs in 1999. The fishery appears to have become more efficient from 1994-1999, landing more dusky sharks per successful set in 1999 than in 1994 (Figure 8). This could either be a direct result of different efficiencies of different boats over the sample period, or the fishery has become more efficient at targeting the large congregations of small sharks in near-shore waters. An increase in abundance of the youngest age-classes could also explain this trend.

Winter season catches consisted of small animals caught in near-shore waters. The summer season catch consisted of larger and sharks farther offshore (Figure 9). The average FL of the catch for the winter season was 117 cm FL and the summer season average size was 189 cm FL. The largest catch of dusky sharks observed by CSFOP

Figure 4. Annual average longline set CPUE (dusky sharks/ 1000 hook hours) and total hook hours fished by the VIMS longline survey from 1975 to 2001.

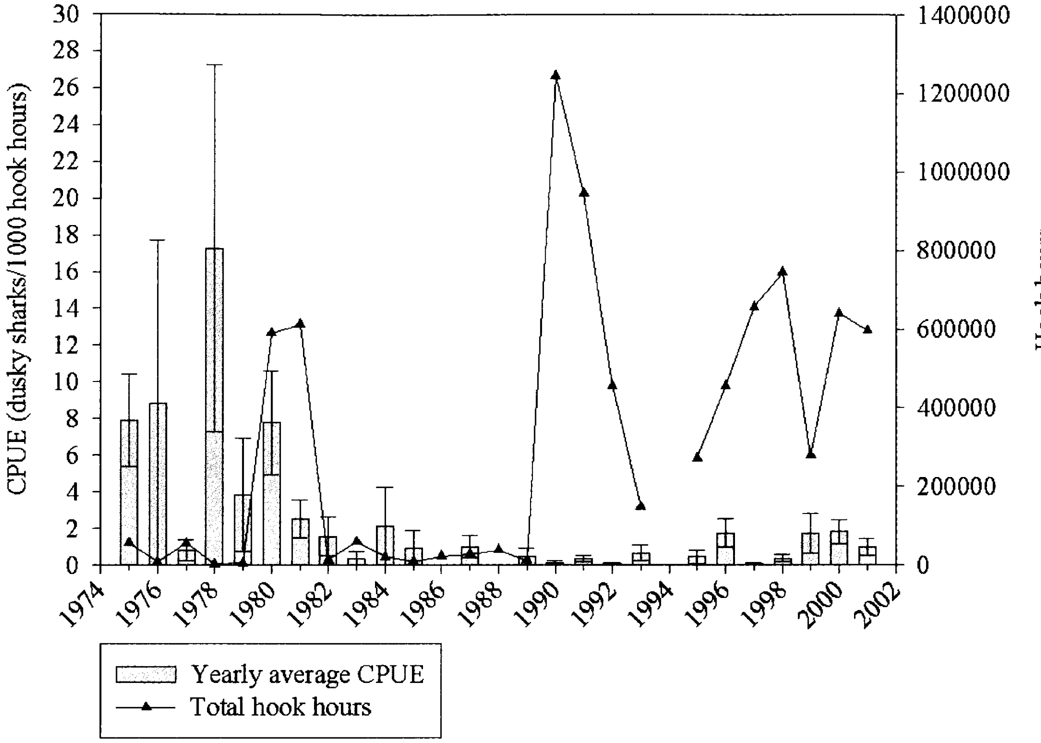


Figure 5. Annual average dusky shark CPUE calculated from CSFOP data.

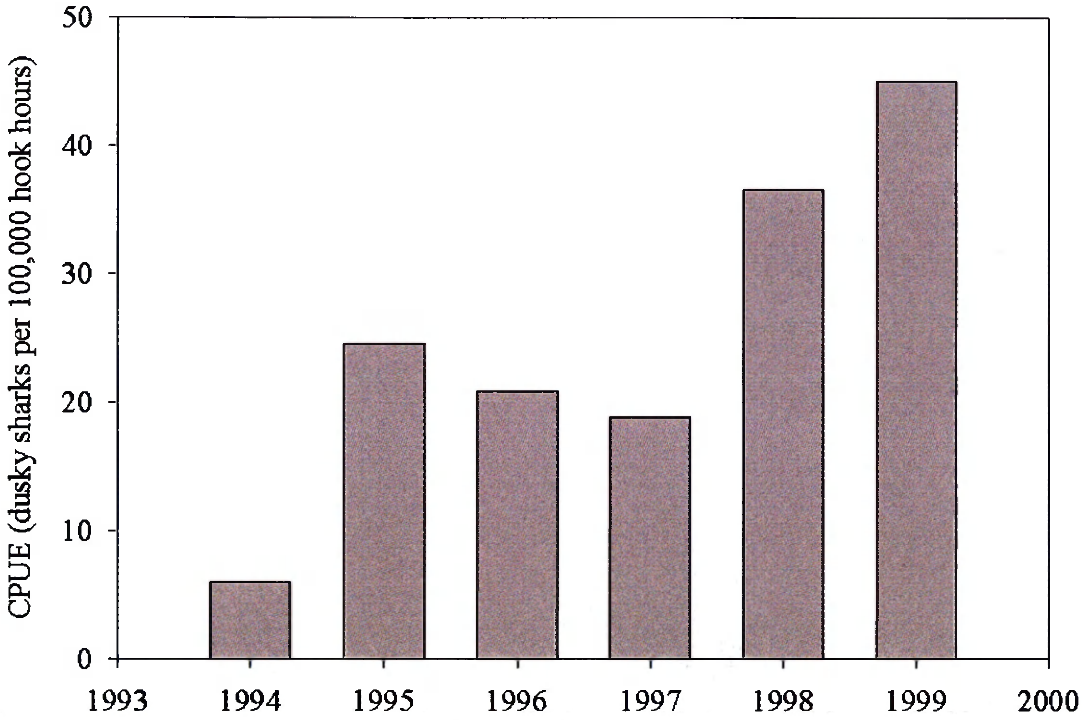


Figure 6. Size class specific dusky shark CPUE calculated from CSFOP data.

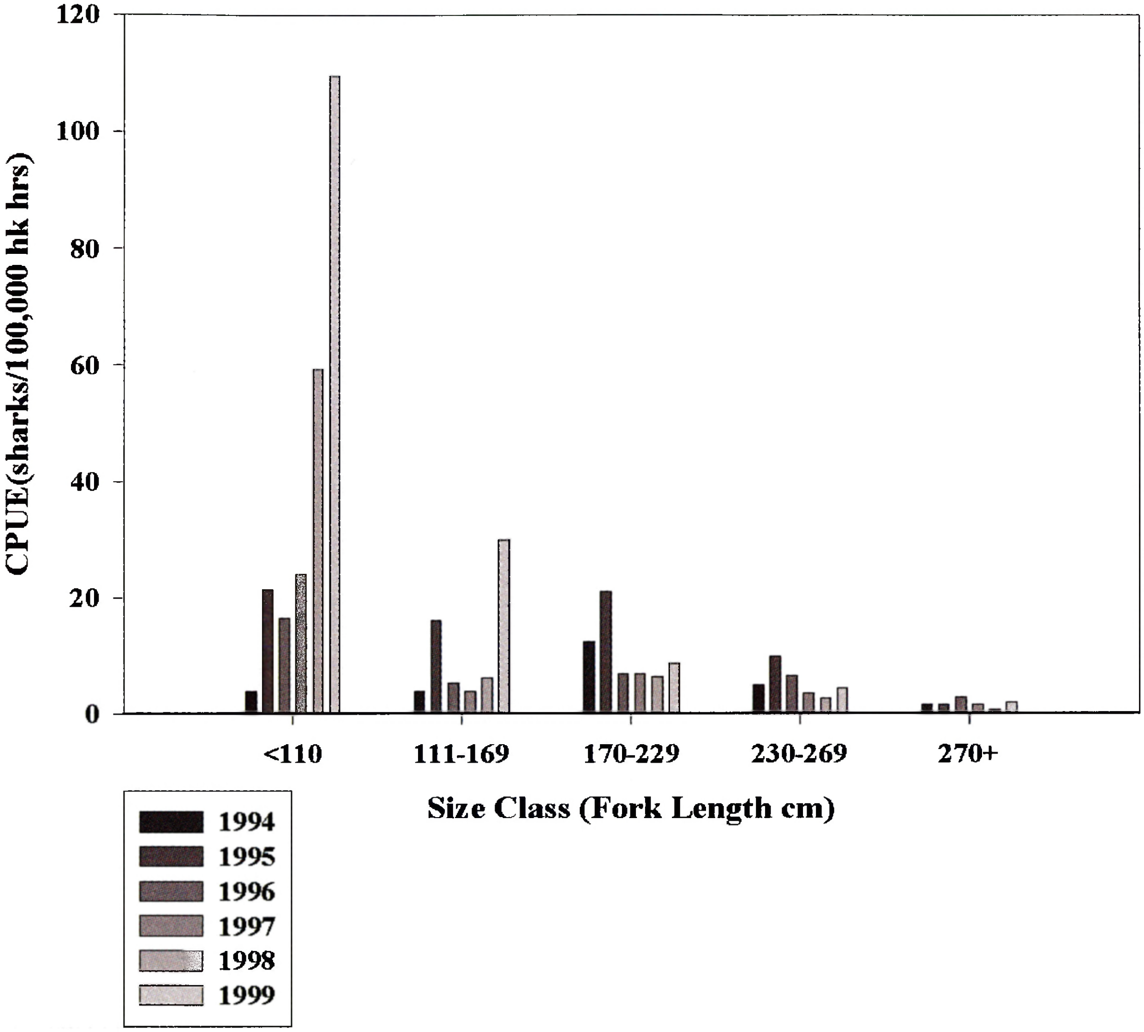
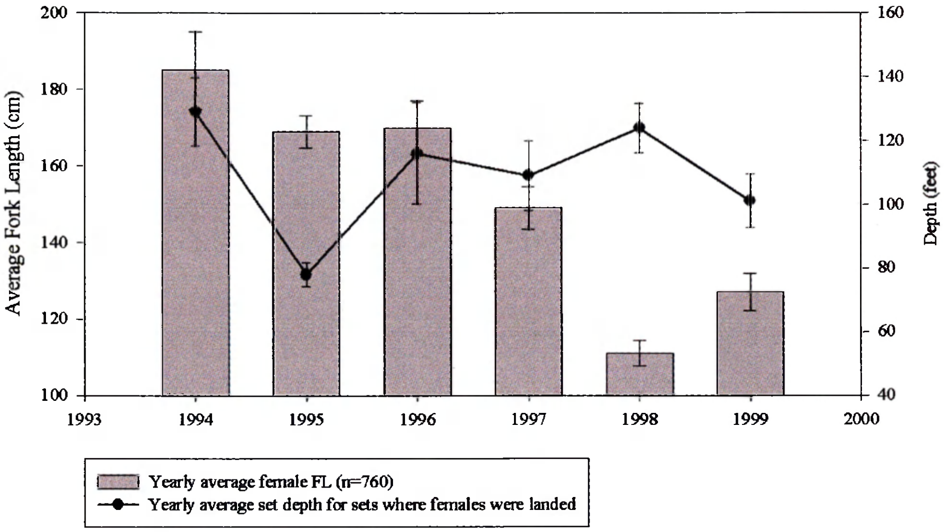


Figure 7. Annual average fork length (cm) of female and male dusky sharks and average set depth for sets where male and female dusky sharks were landed from CSFOP data.

Females



Males

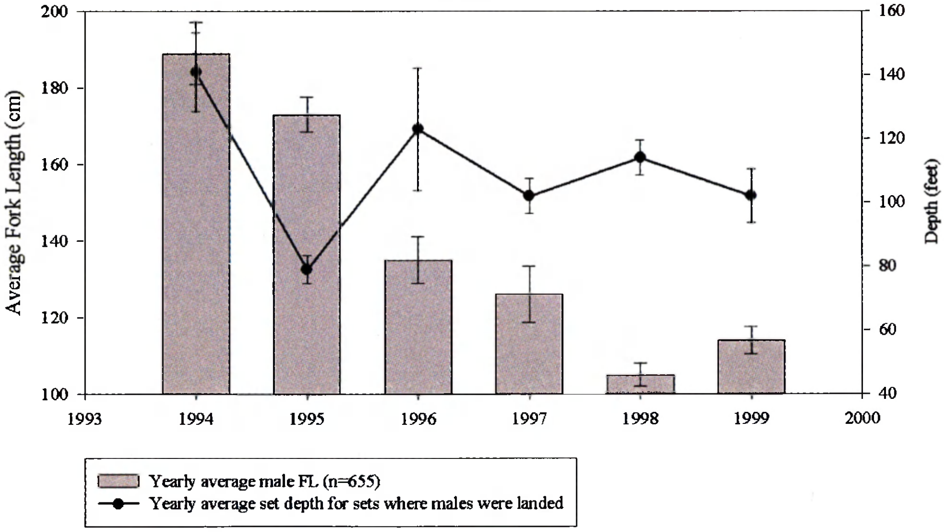


Figure 8. Annual average number of dusky sharks landed per successful set and average number of hook hours per successful set observed by CSFOP from 1994 to 1999.

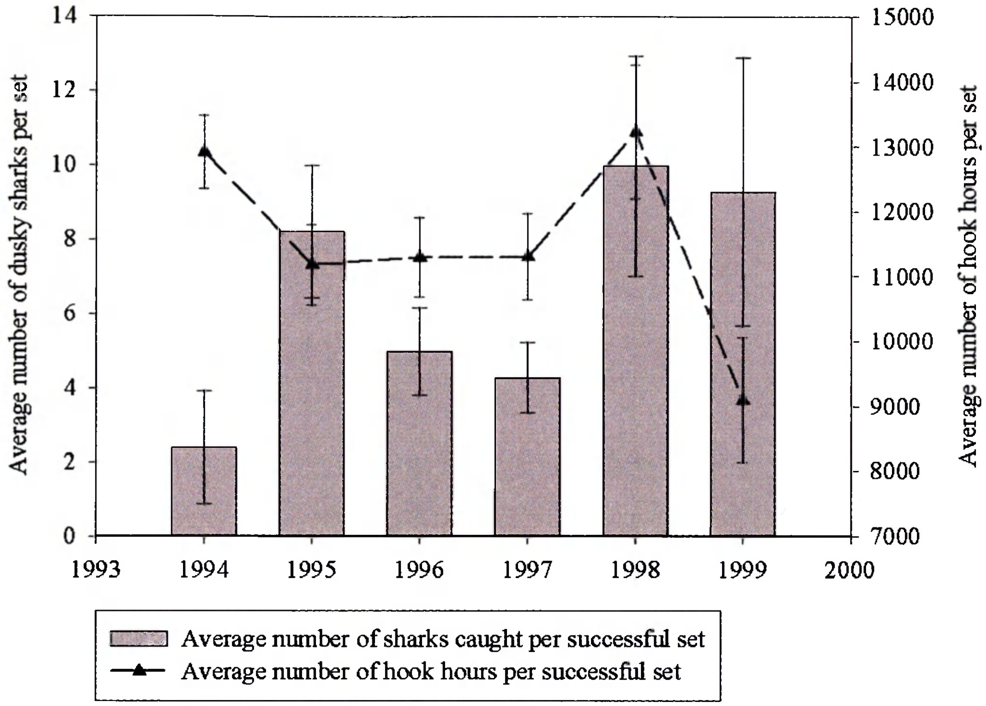
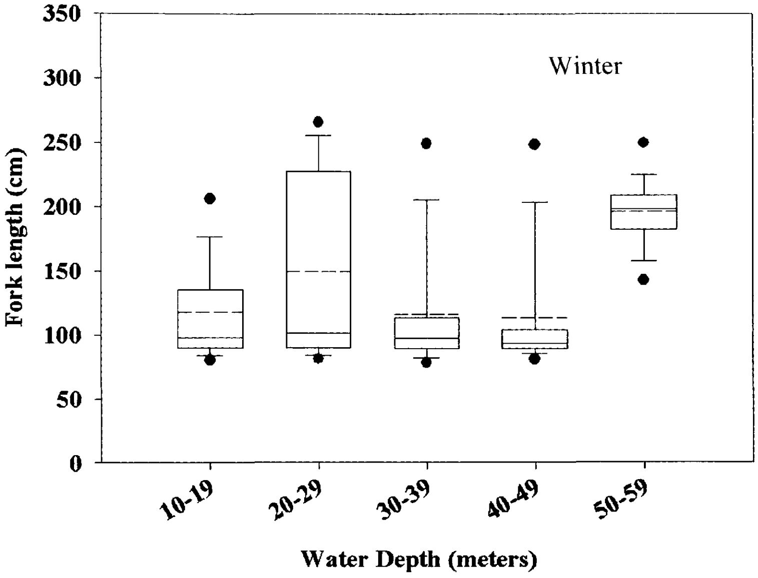
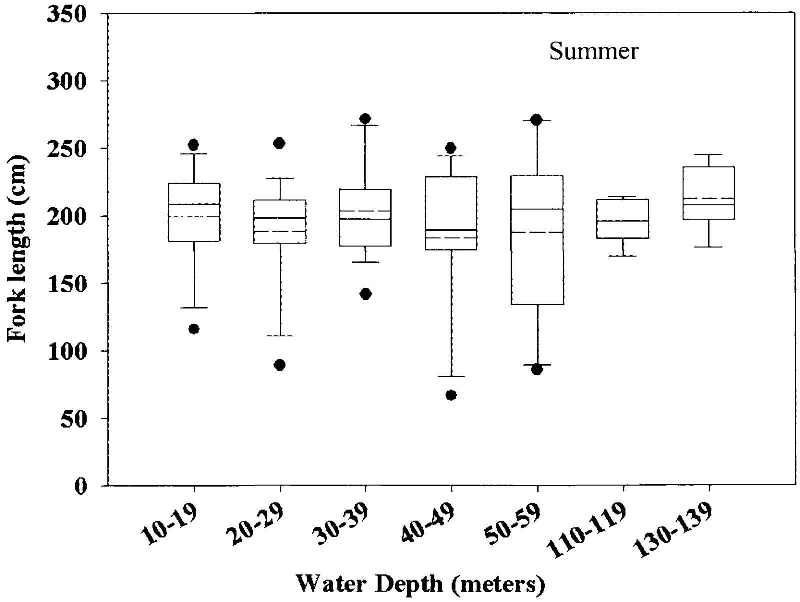


Figure 9. Winter and summer size composition of dusky sharks landed and associated water depth from CSFOP data from 1994-1999.





occurred in March even though more hook hours were observed in January, February, and July (Table 3, Figure 10). During the winter months, aggregations of small sandbar sharks are located in the inshore waters of North Carolina, and are targeted (Branstetter and Burgess 1996). Small dusky sharks occur there as well and are thus vulnerable to fishing mortality by vessels targeting sandbar sharks.

Hooking Mortality

Hooking mortality increased as shark size decreased (Table 4). Hooking mortality for dusky sharks less than 110 cm FL was 79%. Mature animals (>230 cm FL) experienced the lowest hooking mortality (37%). Soak time also influenced hooking mortality (Table 5). Mortality for North Carolina winter sets (January –April) was 79% when soak times were greater than 15 hours. Mortality increased to 85% for soak times greater than 20 hours. Mortality was 57% when soak times were less than 15 hours. Soak times of less than 10 hours had the lowest hooking mortality (5%).

Correspondence analysis of soak time with alive or dead observations yielded similar results. Longer soak times associated with dead sharks and the shorter soak times associated with live sharks (Figure 11). Spring months associated with the highest proportions of dead sharks (Figure 12). The smallest two size classes were also associated with dead sharks, while the largest size classes were located in the same quadrant as live sharks. Figure 13 illustrates the relationship between region and size of dusky sharks landed. The smallest size classes closely corresponded to catches in North Carolina.

Table 3. Summary of CSFOP monthly catch data.

	Total alive	**Avg FL alive (cm)**	**Avg soak time for alive sharks (hrs)**	**Total dead**	**Avg FL dead (cm)**	**Avg soak time for dead sharks (hrs)**	**Total catch (numbers of sharks)**	**Hooking mortality (% dead)**
Jan	69	156	16.13	174	116.6	16.91	241	72.20
Feb	68	132.3	14.44	119	104.7	15.76	187	63.64
Mar	71	121.2	13.10	236	99.49	16.04	307	76.87
Apr	22	194.6	17.92	112	119.4	18.50	134	83.58
May	2	83.5	15.35	0	NA	NA	2	0.00
Jun	0	NA	NA	0	NA	NA	0	NA
Jul	39	205.6	14.24	92	187.25	16.14	131	70.23
Aug	0	NA	NA	4	172.5	13.60	4	100.00
Sep	1	NA	NA	3	169.7	15.68	4	75.00
Oct	0	NA	NA	6	133	17.29	6	100.00
Nov	0	NA	NA	0	NA	NA	0	NA
Dec	0	NA	NA	0	NA	NA	0	NA
Total	273			744			1017	73.16

Figure 10. Total number of hook hours observed each month by CSFOP from 1994 to 1999.

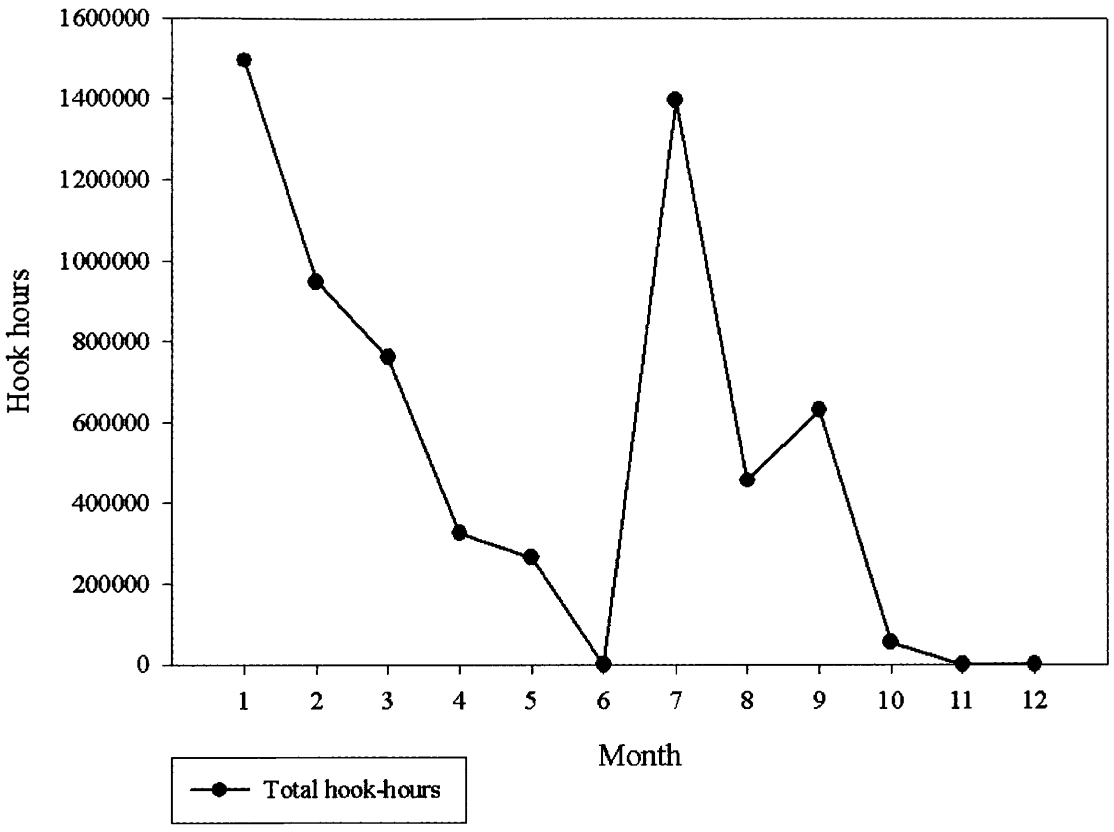


Table 4. Observed number and percent of dusky sharks landed that were dead from CSFOP from 1994 to 2000.

	<110 cm	**110-169 cm**	**170-229 cm**	**230-269 cm**	**270+ cm**
N	508	92	77	32	10
%	79%	71%	69%	43%	37%

Table 5. Soak time associated mortality calculated from CSFOP data from 1994 to 2000.

Soak times for Jan -Apr				
Soak time (hours)	Number alive	% Alive	Number dead	% Dead
<10	21	95	1	5
10.62 -14.85	84	38	138	62
15.05-19.77	110	21	407	79
>20	12	15	66	85
<15	105	43	139	57
>15	122	21	473	79

Figure 11. Multiple correspondence analysis of soak times, fork length, and dead or alive variables from CSFOP from 1994-1999.

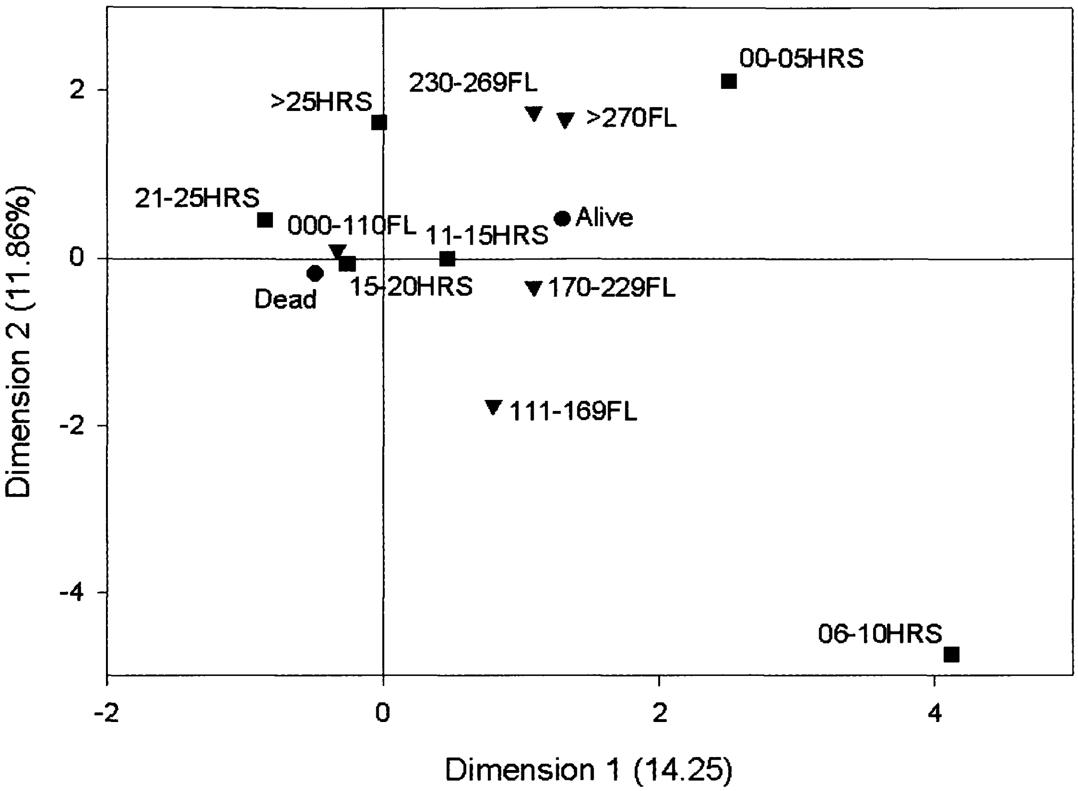


Figure 12. Multiple correspondence analysis of month, fork length, and dead or alive variables from CSFOP dusky shark data from 1994-1999.

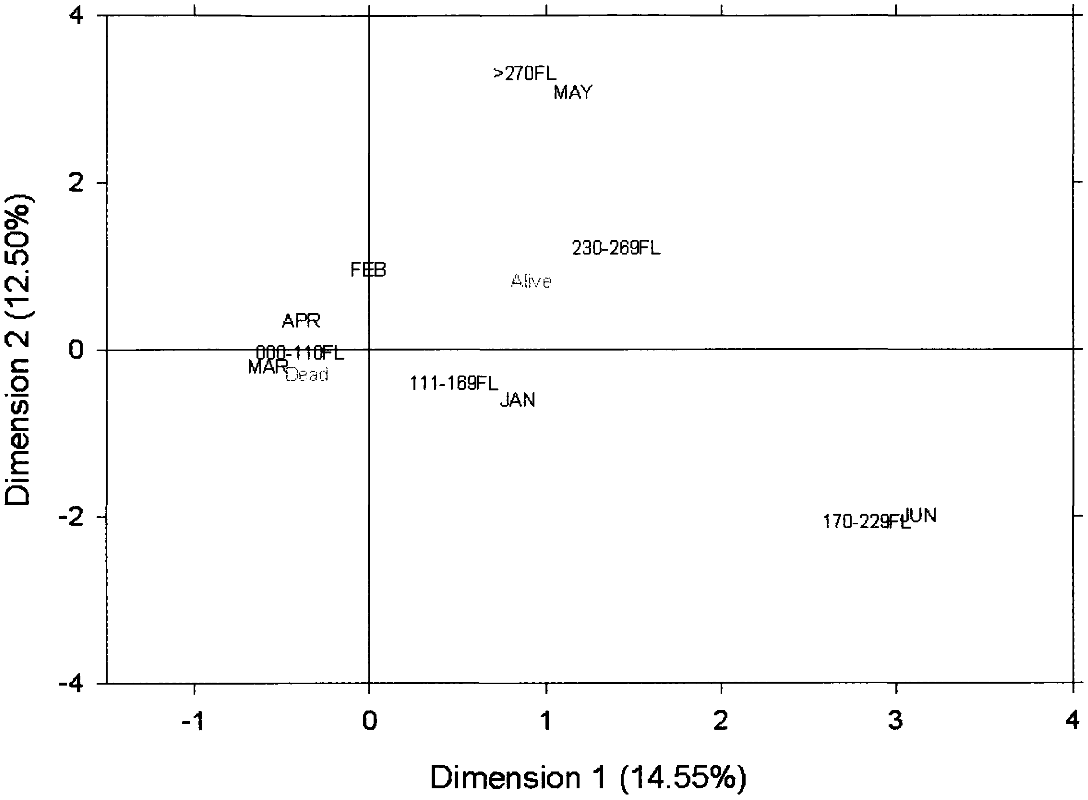
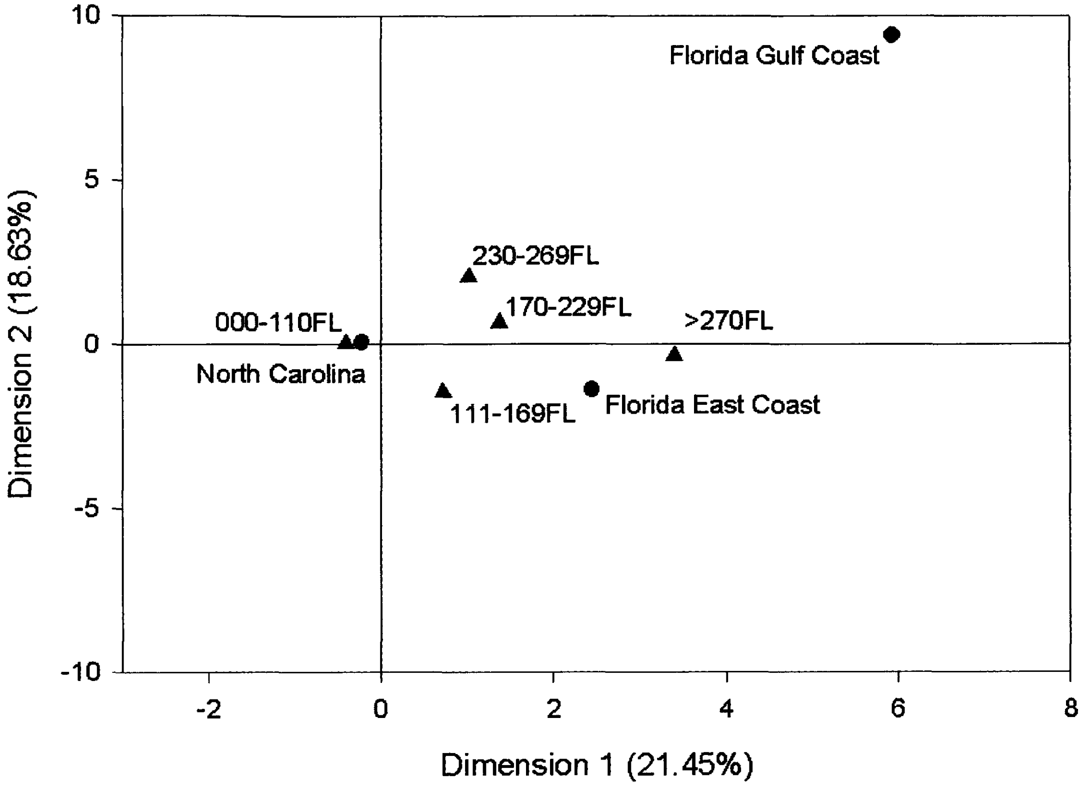


Figure 13. Correspondence analysis of dusky shark size and region variables from CSFOP data from 1994 to 1999.



A quadratic equation was fit to age specific hooking mortality and was weak but significant ($y = -0.00049856x^2 - 0.00048872 + 0.75$, $r^2 = 0.52$) (Figure 14). Hooking mortality decreased exponentially with increase in age.

Reproduction

Females averaged 7.13 (n=51) pups per litter and ranged from 3-12 pups (Figure 15). Observers indicated on one occasion that a female released pups as the animal was being landed. Pups may be aborted by late term females following hooking and preceding landing, and as such the physical presence of pups may not be adequate for accurate determination of fecundity. Cliff et al. (1988) noted similar occurrences with sandbar sharks, *Carcharhinus plumbeus,* caught in protective gill-nets. Four pups were released from a term female upon extraction from the net. Placental scars were evident from the four released pups. Examination of placental scarring may provide a more accurate estimate of fecundity for late term females that may have released pups due to the stress of being hooked. This method was not employed within the present study.

Embryo size throughout the year indicated a gestation period of approximately 20 months (Figure 16, 17). Development appeared to last for 20-22 months following fertilization sometime between July and September and ending with birth between May and June. Time of mating is still not known and may not indicate time of fertilization due to the ability of this species to retain viable spermatozoa in the oviducal glands (Pratt 1993).

Springer (1940) recorded 5 litters in the month of January and March from Englewood, Florida. The average total length of the January and March litters was 80.5

Figure 14. Age specific catch frequency and age specific hooking mortality from CSFOP data from 1994 to1999. A quadratic equation (y =-0.00049856x^2 –0.00048872 + 0.75) was fit to age specific hooking mortality (r^2 =0.53).

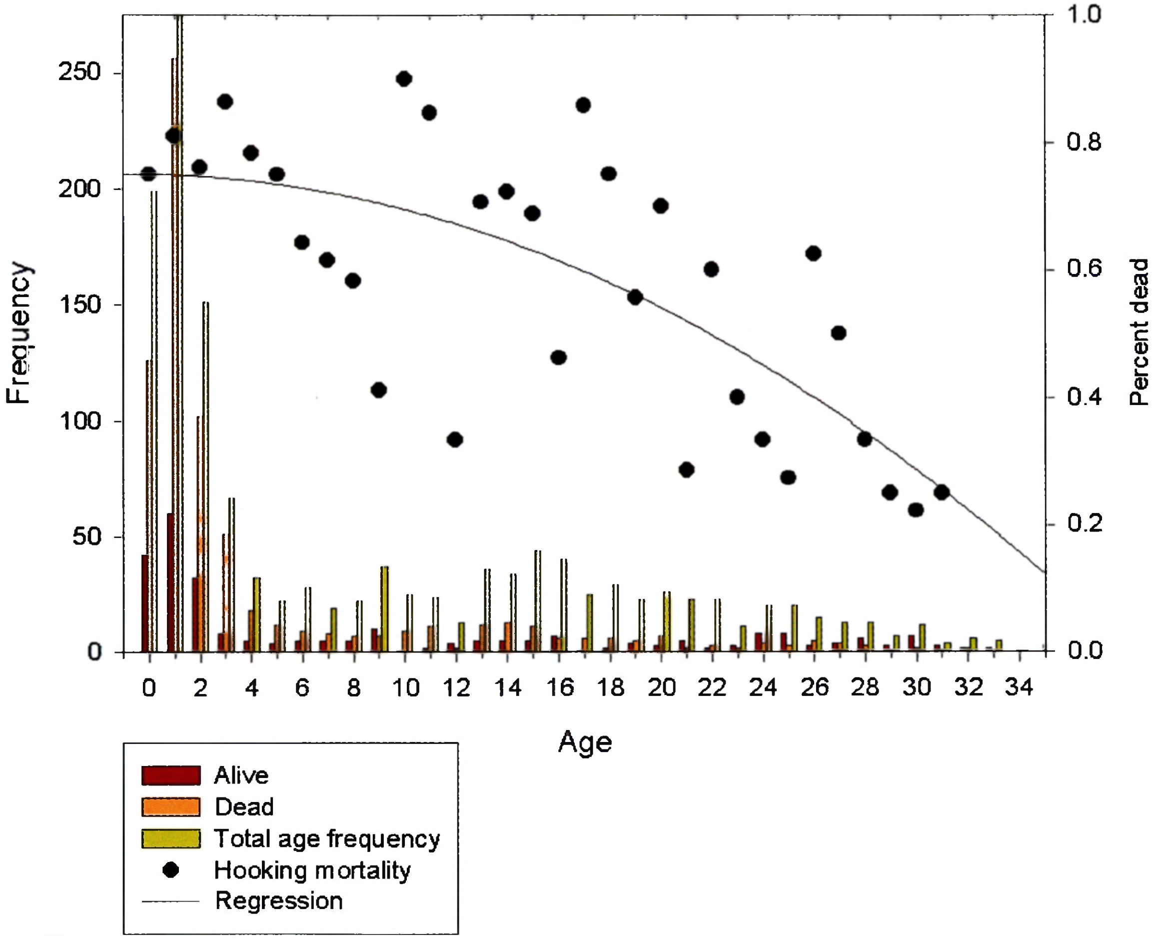


Figure 15. Frequency of dusky shark litter sizes calculated from VIMS and CSFOP data.

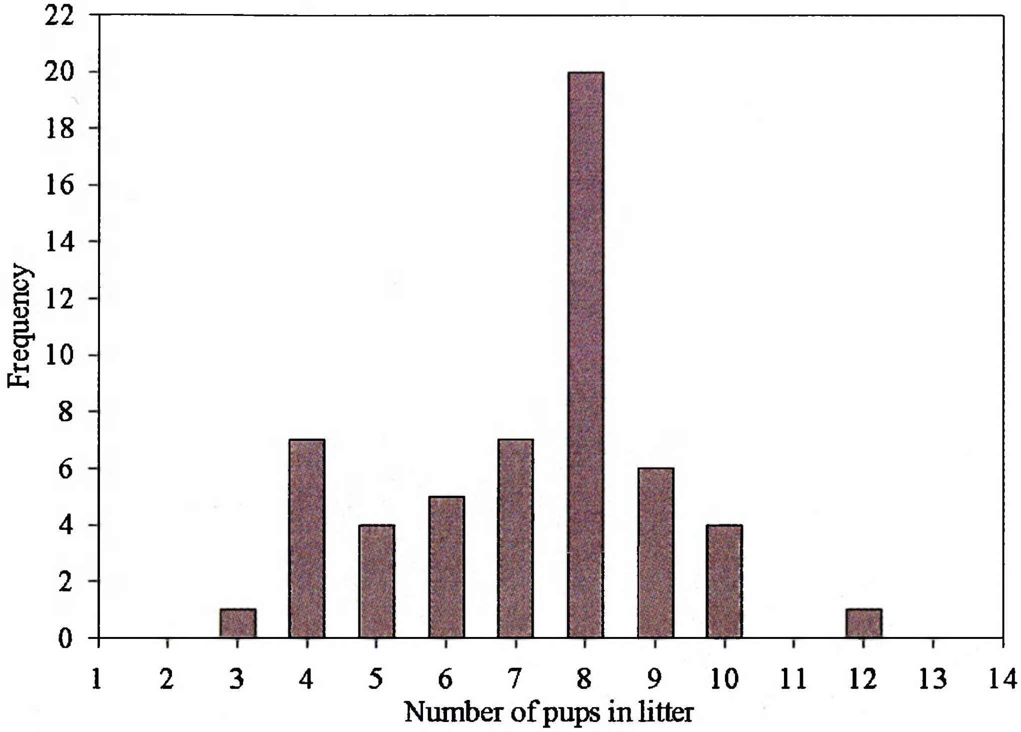


Figure 16. Minimum and maximum fork lengths of pups in each litter vs. time from CSFOP, VIMS, and Clark and von Schmidt (1965).

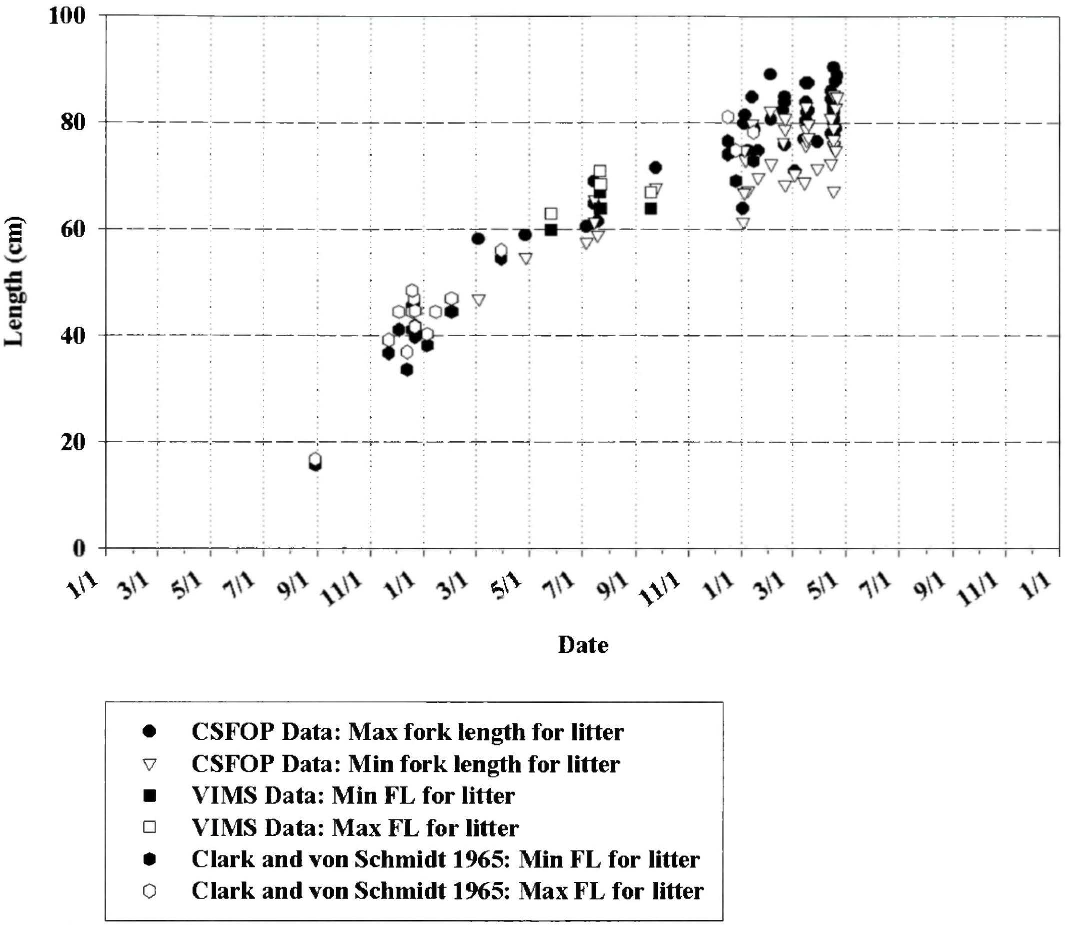
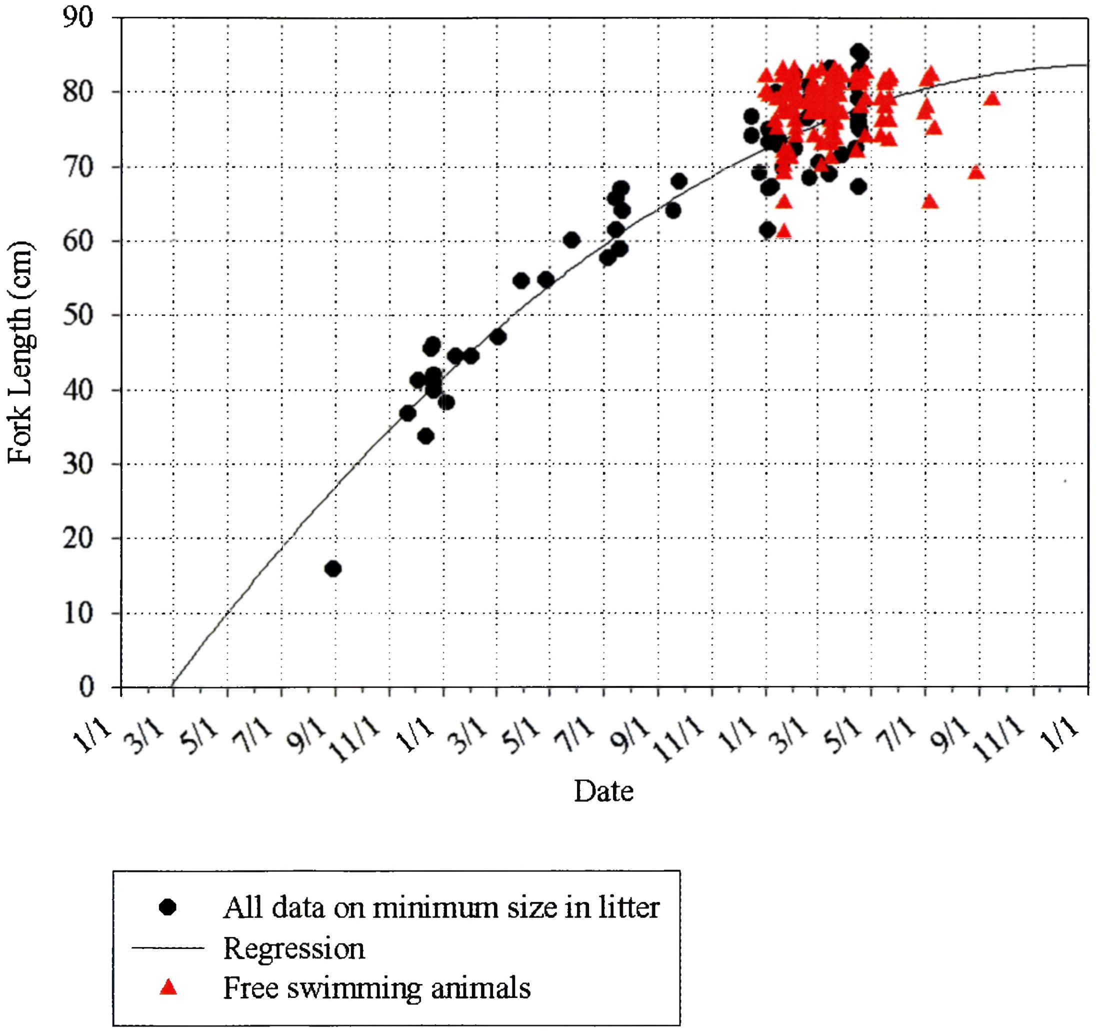


Figure 17. Minimum embryo lengths of dusky sharks and free-swimming dusky sharks from VIMS, CSFOP, and Clark and von Schmidt (1965).



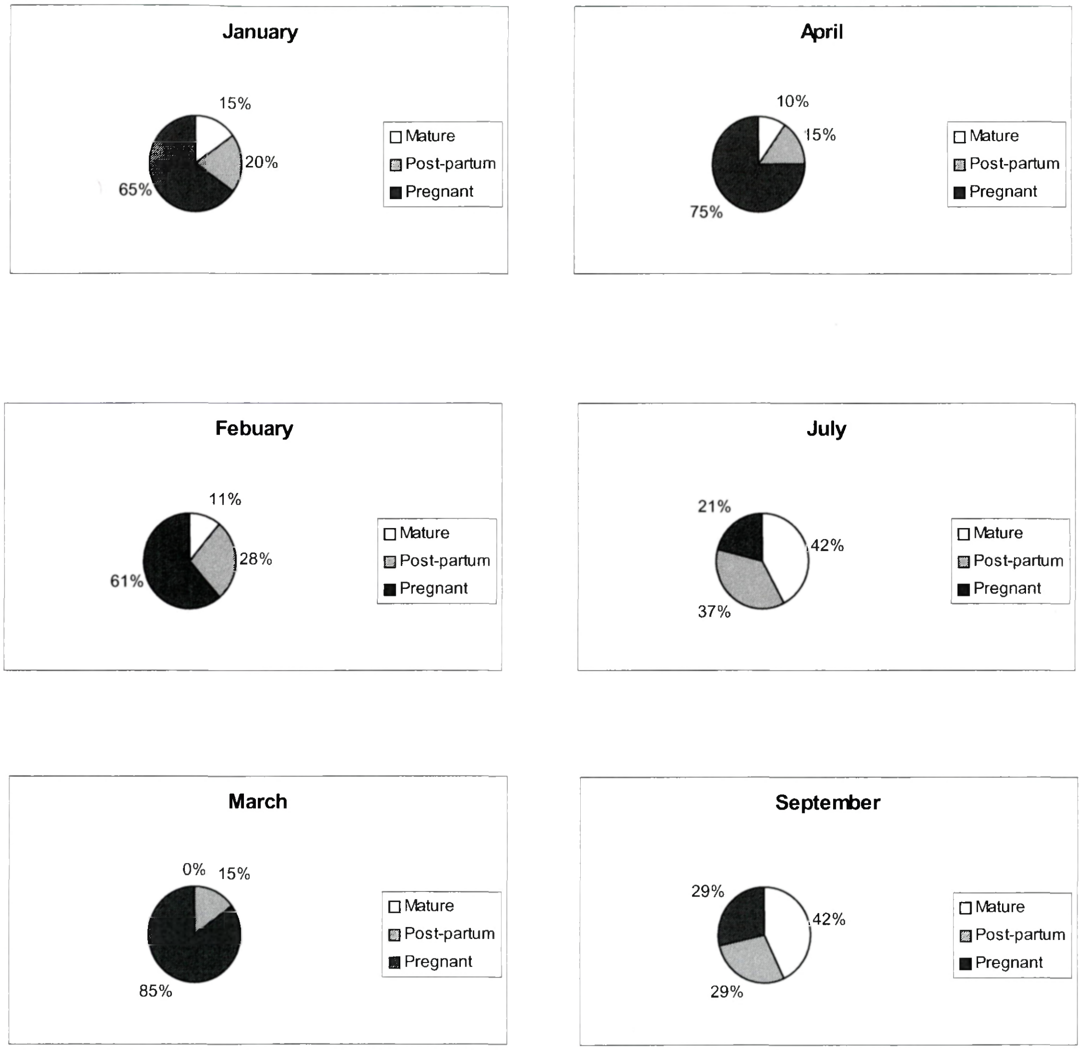
cm and 60.0 cm, respectively. The former pups would have been pupped the following spring while the latter pups would have been pupped 12-14 months later.

Clark and von Schmidt (1965) found a similar phenomenon of two distinct groups of pups. One group of pups examined from August- March ranged from 21.6 cm FL – 69.9 cm FL. These pups would have been pupped in a year's time. The second group of pups examined in December and January ranged from 85.5cm FL-96.5cm FL. This group of pups would have been pupped the following spring. These litters averaged 7.7 pups and the sex ratio was approximately 1:1.

CSFOP data on uterine condition show approximately 66% of mature females were pregnant from January through April (Figure 18). Post-partum females accounted for 37% and 29% of the mature animals in July and September respectively. Pregnant females accounted for 21% and 29% of mature animals in July and September respectively. This suggests a resting period of a year following parturition and a three-year reproductive cycle. Little or no data were available for the months of May, June, August, and October-December. This is due to the fishery-dependent nature of the data set examined.

The largest immature female was 225 cm FL. The smallest mature female was 221 cm FL. All females greater than 226 cm FL were classified as mature. Springer (1960) reported a larger size at maturity (231 cm FL).

Figure 18. Uterine condition of mature female dusky sharks from CSFOP data from 1994 to 1999.



Uterine Condition				
	Mature	Post-partum	Pregnant	n
Jan	3	4	13	20
Feb	2	5	11	18
March	0	2	11	13
Apr	2	3	15	20
Jul	8	7	4	19
Sept	3	2	2	7

DISCUSSION

Litter sizes of dusky sharks found in this study agreed with previously published observations. Clark & von Schmidt (1965) reported litters averaging 7.7 pups and ranged from 6-10 pups. This study found litter sizes to average 7.11 pups and range from 3-12 pups based on 56 litters. Pups may be aborted following hooking and preceding landing, thus biasing fecundity estimates. Little data exist for free swimming specimens.

Two size classes of embryos were found during the first half of the year, a finding that is consistent with previously published observations. The presence of two size classes of embryos combined with available uterine condition data suggests a two-year gestation period. This finding is plausible when one considers the large size of pups at parturition, 70-90 cm FL. One-third of the mature female population displayed resting ovaries prior to pupping season and two-thirds of the mature females were pregnant during this same time period. The pregnant proportion of the population contained two size classes of embryos. Following the pupping season one-third of the sharks sampled consisted of pregnant females. Embryo lengths coupled with uterine conditions of mature females suggest a gestation period of approximately 20-22 months beginning in July and ending sometime between April and June. The absence of large yolky ova in at term females supports a resting period of some nature (Musick 1995; Branstetter and Burgess 1996). The proposed gestation period coupled with a theoretical one-year resting period increases the total reproductive cycle of this species to 3 years or longer.

Mortality in the commercial long-line fishery on dusky sharks off the Southeastern U.S. is greatest in the winter season. This coincides with high concentrations of small sharks, which experience higher hooking mortality than larger sharks. A limit on soak times to less than 15 hours could reduce hooking mortality in the winter season by 20%. The average soak time for the winter season was 14.58 hours and ranged from 1.92-42.58 hours.

Summer long-line catches of dusky sharks off the southeastern U.S. were lower and consisted of larger animals. The average fork length of the summer season catches was 189 cm compared to 117 cm FL for the winter season. This is indicative of larger sharks moving into the system to pup and the smaller sharks moving north into the mid-Atlantic Bight due to warming water temperatures in late spring and early summer as shown in the VIMS data set (Musick and Colvocoresses 1986; Musick et al. 1993).

Throughout 1994-1999, catch rates for small sharks (<170 cm FL) increased dramatically. Catch rates for sharks larger than 170 cm FL decreased. The increase in catch rates of small sharks does not appear to have been caused by a shift of the fishery to more inshore waters where small sharks are more abundant (Figure 9). The average water depth of set locations increased for the time period, suggesting that the increased catches of smaller sharks were due to an increase in abundance.

Catch rates for small sharks (<170 cm FL) increased in both data sets while catch rates of older mature animals declined in both data sets. The lack of an increase in adult dusky sharks in the VIMS data set, and a marked decline in adult dusky sharks in the CSFOP data set are a cause for concern. Simpfendorfer (1999) found that limited exploitation of the youngest year class of dusky sharks could be sustainable as long as older age classes were not exploited. If mortality on the early age classes continues even through by-catch (the species has recently come under federal protection) a lack of mature animals could quickly lead to recruitment failure.

If recovery of this species is to be sustained, hooking mortality (73.16%) should be decreased to ensure that younger age classes reach maturity. Hooking mortality estimates do not include the possible mortality of post release animals.

Post hooking mortality should remain a concern even if the population recovers and becomes harvestable again. The most effective way to accomplish this without closing the longline fishery in months where hooking mortality is the highest (March and April) is to decrease longline set times to 10 hours or less. After the dusky shark population recovers, limited harvest of age 0-2 sharks may be sustainable if larger sharks are protected.

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CHAPTER 2:

Demographic analysis of the dusky shark, *Carcharhinus obscurus,* in the Northwest Atlantic

INTRODUCTION

Many tools exist for estimating the status of populations of fishes and the amount of exploitation a population may sustain. Management recommendations for well studied and exploited fish populations are often reached through complex fishery models. When data on catch rates, abundances, fishing effort, immigration and emigration rates, and other data are not available, life-table analysis or matrix models are often used to provide information for management recommendations (Simpfendorfer 2004). This is often the case with elasmobranch populations due to their migratory nature, life-history traits, and lack of availability of general fisheries data.

Life-tables and matrix models utilize life-history parameters to produce estimates of the intrinsic rate of population increase (r) and population growth (λ, where $\ln(\lambda)=r$) respectively. Parameters employed in these analyses are survivorship (empirical or theoretical), fecundity, and age-specific growth rates. A multitude of researchers have shown the usefulness of these two methods for modeling elasmobranch populations (Cortes 1995; Cortés 1998; Smith et al. 1998; Simpfendorfer 1999; Brewster-Geisz and Miller 2000; Cortés 2002; Goldman 2002; Mollet and Cailliet 2002).

Matrix models provide additional information regarding the importance of specific age-classes or life stages to population growth through elasticity analysis. Elasticity analysis measures the effect of proportional changes in age-specific or stage-specific vital parameters on population growth, or ranks ages or stages at which the smallest changes in life-history parameters will result in the greatest change in population growth. This information has proven useful for providing guidance for conservation and management decisions because it enables managers to enact measures that protect the most important age-class or stage within a population (Mills et al. 1999; Brewster-Geisz and Miller 2000; Heppell et al. 2000; Cortés 2002). Elasticity ratios have also been used to estimate required responses in fecundity or age-zero survival to return a population to equilibrium following reductions in juvenile or adult survival (Heppell et al. 1999; Cortés 2002).

Few researchers have modeled populations of dusky sharks through these methods. Simpfendorfer (1999) assessed the dusky shark fishery in Australia using standard demographic analysis in the form of life-table analysis. His findings revealed population growth was possible if fishing mortality (*F*) was limited to only the youngest age classes. This fishery is strictly a gill-net fishery and thus size of animals landed can generally be controlled through appropriate selection of mesh size. The shark fishery in the southeast U.S. is predominantly a long-line fishery in which size-selectivity is minimal (Branstetter and Burgess 1996).

Smith et al. (1998) produced a demographic model for 26 species of sharks, including the dusky shark, that incorporated density- dependent compensation in the form of increased survivorship in juvenile ages as a response to mortality in the mature age classes. Cortés (2002) produced a demographic model for the dusky shark which incorporated uncertainty in demographic parameters by using probability distributions for vital parameters which were re-sampled through Monte Carlo simulations. His study included a fecundity distribution of 6-12 pups in each litter, and did not include density-dependent compensatory mechanisms or fishing mortality estimates.

Models created by Simpfendorfer (1999) and Smith et al. (1998) utilized time invariant model parameters and only Smith et al. (1998) accounted for the possibility of density-dependent compensation in the form of a specific level of increased juvenile survivorship for each species in their study. Cortés (2002) is the only work to have included uncertainty for vital parameters within his model in order to account for the likely flux in parameter values as population growth changes over time.

Few researchers have included fishing mortality in demographic analyses. The inclusion of fishing mortality within the models provided more precise estimates of population growth under realistic conditions. The dusky shark is a protected species that only experiences fishing mortality in the form of hooking mortality. Values for age-specific hooking mortality, calculated in chapter 1, were included in the models as fishing mortality.

Precise estimates of parameters for life tables are typically difficult to obtain for many elasmobranch species due to their migratory nature and life-history traits. To account for this lack of precision, Cortés (2002) included uncertainty estimates of life table parameters. Uncertainty was incorporated using Monte Carlo simulations and probability distributions for input values. This technique has proven to be useful for management due to error estimates generated from this type of analysis (Cortés 2002). This method also overcomes flaws in deterministic demographic models that can lead to errors in ranking of life stages due to the inherent variation in vital parameters (Mills et al. 1999; Heppell et al. 2000; Cortés 2002).

The objectives of this study were:

1. To create demographic models which included: total mortality (*Z*) based on hooking mortality estimates calculated in chapter 1, values for fecundity and reproductive period calculated from chapter 1, uncertainty in vital parameters, and estimates of age-0 natural mortality which would create a population at equilibrium over time in the absence of fishing mortality.

2. To examine elasticity ratios to provide estimates of required compensatory response under fishing scenarios following the methods of Heppel et al. (1999) and Cortés (2002).

METHODS

Age structured life tables that included probability distributions for demographic parameters were used to estimate population growth rates, generation times, and elasticities under various levels of exploitation following the methods of Cortés (2002) and Goldman (2002). Monte Carlo simulations and probability distributions were used to incorporate uncertainty in demographic parameters and to supply estimates of error in output values using Microsoft Excel software with Crystal Ball (Decisioneering Inc., Denver, CO) risk assessment software coupled with Microsoft Visual Basic macros. Incorporating uncertainty in vital parameters appears to be a valid approach for highly-migratory species due to the range of values reported in the literature for various demographic parameters and the difficulty in obtaining exact values for long-lived, migratory species. These circumstances are indicative of a stochastic population that is subject to environmental and human induced perturbations.

Contributions of specific life-stages and ages to population growth were estimated using elasticity analyses (Heppell et al. 1999). Sensitivities of the model to perturbations in demographic parameters were also calculated. These estimates are valuable to managers for the construction of management plans involving size limits, exploitation rates and closed areas.

Life-tables were constructed for females using a yearly time step to produce estimates of population growth (λ, when $\lambda = 1$ the population is stable with no loss or increase in size) and intrinsic rate of increase (***r***, where $\lambda = e^r$), generation times $\bar{A}$, net reproductive rate R_0, reproductive value (v_x), and stable age distribution (c_x). Population doubling or halving time was also calculated as

$$t_2 = \frac{\ln 2}{r} \text{ or} \qquad \text{Equation (1)}$$

$$t_{.05} = \frac{\ln .5}{r} \text{ .} \qquad \text{Equation (2)}$$

Demographic parameters used in the model were those found in the literature and those produced by this study.

Uncertainty was included in the model to compensate for possible variation in reported life history parameters (Cortés 2002; Goldman 2002). It is unlikely that parameters remain constant over time due to changes in population size, especially a population that has undergone severe reductions and is likely to exhibit some compensatory response. Mills et al. (1999) suggested incorporating a range of values for life history parameters when conducting elasticity analysis combined with simulation techniques to avoid the problems associated with elasticity analyses of mean matrices. This method also produces confidence intervals for output values such as population growth and population doubling time. Probability distributions were created for the following parameters: maximum age (ω), age at first reproduction (α), fecundity (m_x= number of female pups per female/ length of reproductive cycle) and survivorship at age (S_x). Probability distributions for maximum age (ω) and age at first reproduction (α) were centered on reported values and were bounded by values 10% greater and lesser than the reported value.

A triangular probability distribution was used for maximum age (ω). Natanson et al. (1995) used tag recapture data to produce a value of 45 years as maximum age (ω), thus 45 was given the greatest probability and was bounded by 40 and 50. Age at first reproduction used in the model was 21 years of age. A triangular probability distribution bounded by 19 and 23 years of age was used.

Fecundity estimates used in the model were derived from this study and other published data. A best-fit normal probability distribution was fit to litter size frequency data from this study (Figure 19). Minimum and maximum values for litter sizes were 3 pups and 12 pups respectively. Litter sizes of 8 pups were given the highest probability. Female specific fecundity or m_x was calculated as the number of females per female/ reproductive cycle, in this case 3 years.

Many methods for estimating natural mortality are found in the literature. Six methods were used for determining the range of survivorship for all age classes except the age-0 cohort in model simulations. The following methods were used: Peterson and Wroblewski (1984), Hoenig (1983), Pauly (1980), Chen and Watanabe (1989), Jensen based on age at maturity (t_{mat}) and based on k (Jensen 1996) (Table 6). Probability distributions for survivorship were bounded by minimum and maximum values calculated from the six methods.

These methods did not address age-0 survivorship and little data exists for survivorship of young of the year elasmobranchs nor do they address the possibility of decreased survivorship at maturity due to reproductive costs. Gruber et al. (2001) estimated juvenile annual survival rates for lemon sharks, *Negaprion brevirostris*, to range from 38% to 65% under greater and lesser population densities respectively.

Table 6. Methods used to estimate natural mortality (*M)* in previously published life table analyses of dusky sharks. Where k and L_∞ are von Bertalanaffy growth curve parameters, T is the average water temperature, $\boldsymbol{t_{mat}}$ is age at maturity, $\boldsymbol{t_{max}}$ is maximum age, Z is total mortality and w is wet weight.

Method	**Relationship**
Pauly (1980)	$\ln(M) = -0.0066 - 0.297\ln(L_\infty) + 0.6543\ln(k) + \ln(T)$
Hoenig (1983)	$\ln(Z) = .941 - .873\ln(t_{\max})$
Peterson and Wroblewski (1984)	$M(w) = 1.92(w*1000)^{-0.25}$
Chen and Wantanabe (1989)	$\overline{M}(t,t+\Delta) = \frac{1}{\Delta}\ln\frac{e^{k(t+\Delta)} - e^{kt_0}}{e^{kt} - e^{kt_0}}$
Jensen (1996)	$M = 1.65 / t_{mat}$
Jensen (1996)	$M = 1.5k$

Heupel and Simpfendorfer (2002) estimated natural mortality for young blacktip sharks, *Carcharhinus limbatus*, to range from 0.70 to 0.32 over a three-year period. Theoretical estimates of mortality for dusky sharks are well below these values, thus an age-0 survivorship value that would create a population growth rate of $\lambda = 1$ in scenario one was used in this study to account for this discrepancy (Vaughan and Saila 1976; Hoenig and Gruber 1990; Saether and Bakke 2000). A uniform probability distribution was then centered on this value (Figure 19). All other estimates for natural mortality were assumed to be within the correct range.

The effect of changes in age-0 survivorship on population growth rates was calculated using a Leslie matrix to calculate intrinsic rates of population increase under a range of natural mortality estimates and levels of fishing mortality. Natural mortality estimates used ranged from 0.0-0.8. Fishing mortality was applied to all age classes equally and ranged from 0.0-0.5.

Annual population growth rates ($\lambda = e^{r}$) (Table 7) were calculated from rates of population increase (r) by iteratively solving the Euler equation:

$$1 = \sum_{x=1}^{\omega} l_x m_x e^{-rx} \qquad \text{Equation (3)}$$

Generation time ($\overline{A}$) was calculated as

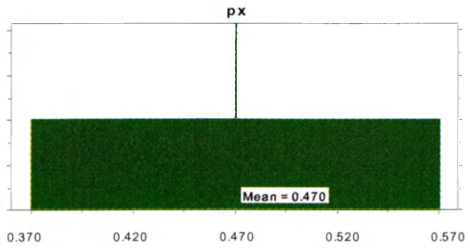
$$\overline{A} = \sum_{x=1}^{\omega} x l_x m_x e^{-rx} . \qquad \text{Equation (4)}$$

The distribution of reproductive values (v_x) was calculated as

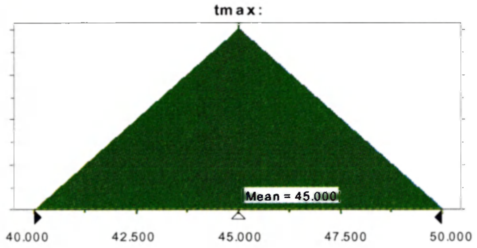
$$\frac{v_x}{v_0} = \frac{e^{rx}}{l_x} \sum_{t=x}^{\omega} e^{-rt} l_t m_t , \qquad \text{Equation (5)}$$

Figure19. Probability distributions employed in demographic models. a) Distribtuion for age-0 survivorship, b) maximum age, c) total fecundity, d) age at first reproduction, e) example of distribution for survivorship of age-1.

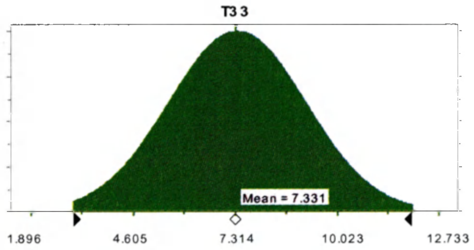
a)


px
Mean = 0.470
0.370
0.420
0.470
0.520
0.570

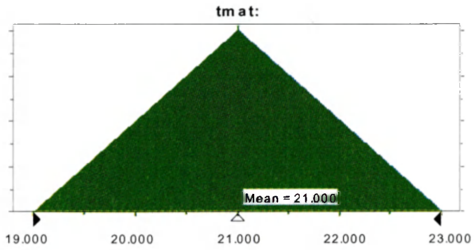
b)


tmax:
Mean = 45.000
40.000
42.500
45.000
47.500
50.000

c)


T33
Mean = 7.331
1.896
4.605
7.314
10.023
12.733

d)


tmat:
Mean = 21.000
19.000
20.000
21.000
22.000
23.000

e)

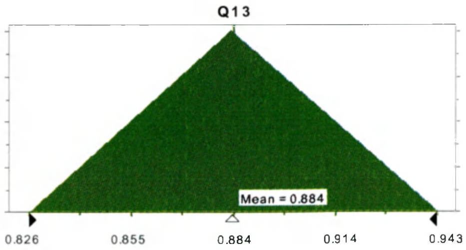

Q13
Mean = 0.884
0.826
0.855
0.884
0.914
0.943

Table 7. Symbols and definitions used in demographic analyses.

Symbol	**Definition**
r	Intrinsic rate of population increase
x	Age
ω	Maximum reproductive age
l_x	Survival to age x
m_x	Fecundity(female pups/female/reproductive cycle)at age x
c_x	Stable age distribution
P_x	Mean survivorship of the probability distribution for age x
R_0	Net reproductive rate
$\overline{X}$	Mean life expectancy
t_2	Population doubling time
$\overline{A}$	Generation time or mean age of parents of the offspring produced by a population at the stable age distribution
$\lambda = e^r$	Annual population growth rate
v_0	Reproductive value at birth =1
v_x	Reproductive value distribution
S_x	Surviviorship at age x

where v_o is the reproductive value at birth (v_o=1) and t represents all ages a female will attain through x to ω. The stable age distribution (c_x) was calculated as

$$c_x = \frac{l_x e^{-rx}}{\sum_{x=1}^{\omega} l_x e^{-rx}}. \qquad \text{Equation (6)}$$

Elasticities were calculated as

$$e_{ij} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathrm{w}, \mathrm{v} \rangle} \qquad \text{Equation (7)}$$

following the methods of Caswell (2001) and Cortés (2002). Elasticities were calculated for young of year or fertility, 1-3 age classes, 4-9 age classes, 10-20 age classes, 21-28 age classes and 29-50 age classes. The sensitivity of λ to changes in model parameters was calculated as

$$s_{ij} = \frac{v_i w_j}{\langle \mathrm{w}, \mathrm{v} \rangle} \qquad \text{Equation (8)}$$

following the methods of Caswell (2001). Mean life expectancy was calculated as follows

$$\overline{X}_{life expectancy} = \frac{1}{-\ln(\sum_{x=0}^{\omega} P_x)}. \qquad \text{Equation (9)}$$

P_x is the mean survivorship of the probability distribution for age x. The net reproductive rate (R_0) was calculated as

$$R_0 = \sum_{x=0}^{\omega} l_x m_x \,.$$ Equation (10)

Monte Carlo simulation was used to randomly sample from probability distributions created for demographic parameters that possessed a level of uncertainty within the reported values. Confidence intervals were reported as the 2.5th and 97.5th percentiles after simulations had been run.

Three scenarios were established to examine the effects of fishing mortality. Scenario one assumed a population at equilibrium and no fishing mortality was included in this scenario. Fishing mortality was included in scenarios two and three to estimate the effect of certain levels of fishing mortality on population growth and to simulate age specific fishing mortality induced by the commercial shark fishery. Although the species is federally protected it may still be landed within certain state waters. It also experiences high rates of hooking mortality within federal waters during the winter shark-fishing

□□□□□□□□□′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′ □′

Recent stock assessments of the shark fishery for the large coastal complex estimated F to range from F=0.07-0.21 (NMFS 2003). These estimates of fishing mortality were included in the models in scenarios two and three. In scenario two 0.07 was divided by two and in scenario three 0.21 was divided by two. Fishing mortality estimates were halved to compensate for F being applied to the first six months of the year. Hooking mortality and catch of is greatest in the winter season. These values were then multiplied by percent dead for each age-class to establish age-specific fishery mortality rates. Ages were assigned using the age-growth relationship derived by Natanson et al. (1995) through vertebral analyses. Fishing mortality was applied only to ages 0-31 due to the lack of hooking mortality data for animals greater than 31 years of age. Not applying fishing mortality to ages greater than 31 appears plausible due to the reduced hooking mortality experienced by dusky sharks as they increase in size. In doing so scenarios two and three simulated the effects of the fishery on population growth (See appendix 1 for life tables).

Ratios of juvenile survival elasticity to age-zero survival elasticity were calculated to provide estimates of required compensatory responses following increased juvenile mortality following the methods of Heppell et al. (1999) and Cortés (2002).

Deterministic post-breeding projection matrices were used to display responses to conditions set in the models. An initial population of 1,000,0000 animals was created following the stable age distribution calculated in scenario one. The population was projected over 100 years for each scenario beginning at equilibrium conditions.

RESULTS

Intrinsic rates of population increase

Under zero fishing mortality and a P_0 value of 0.473, intrinsic rate of increase was 0%. This translated to a natural mortality rate of 0.75 (Figure 20). This was the greatest value for age-0 natural mortality that the population could sustain given the conditions established in the model. The greatest rate of population increase under zero fishing pressure attainable was 2.6% year^{-1}. This assumed zero natural mortality at age-0 and a population free of fishing mortality. Given these conditions, the maximum sustainable fishing mortality across all age classes was 0.0433. This would result in an *r*- value of zero (Figure 20).

Given the variability in parameters employed in the model under zero fishing pressure, intrinsic rates of population increase ranged from –1.2% and 0.8% year^{-1}. The fishing scenarios investigated yielded negative rates of population increase for both fishing mortality scenarios (Table 8). Under the conditions of scenario two (F=0.07), the intrinsic rate of population increase ranged from -1.1% to -3.2%. Under the conditions in the scenario three (F=0.21) intrinsic rates of population increase ranged from -5.9% to -7.2%.

Figure 20. Intrinsic rate of population increase under various levels of age-0 natural mortality and fishing pressure across all age classes.

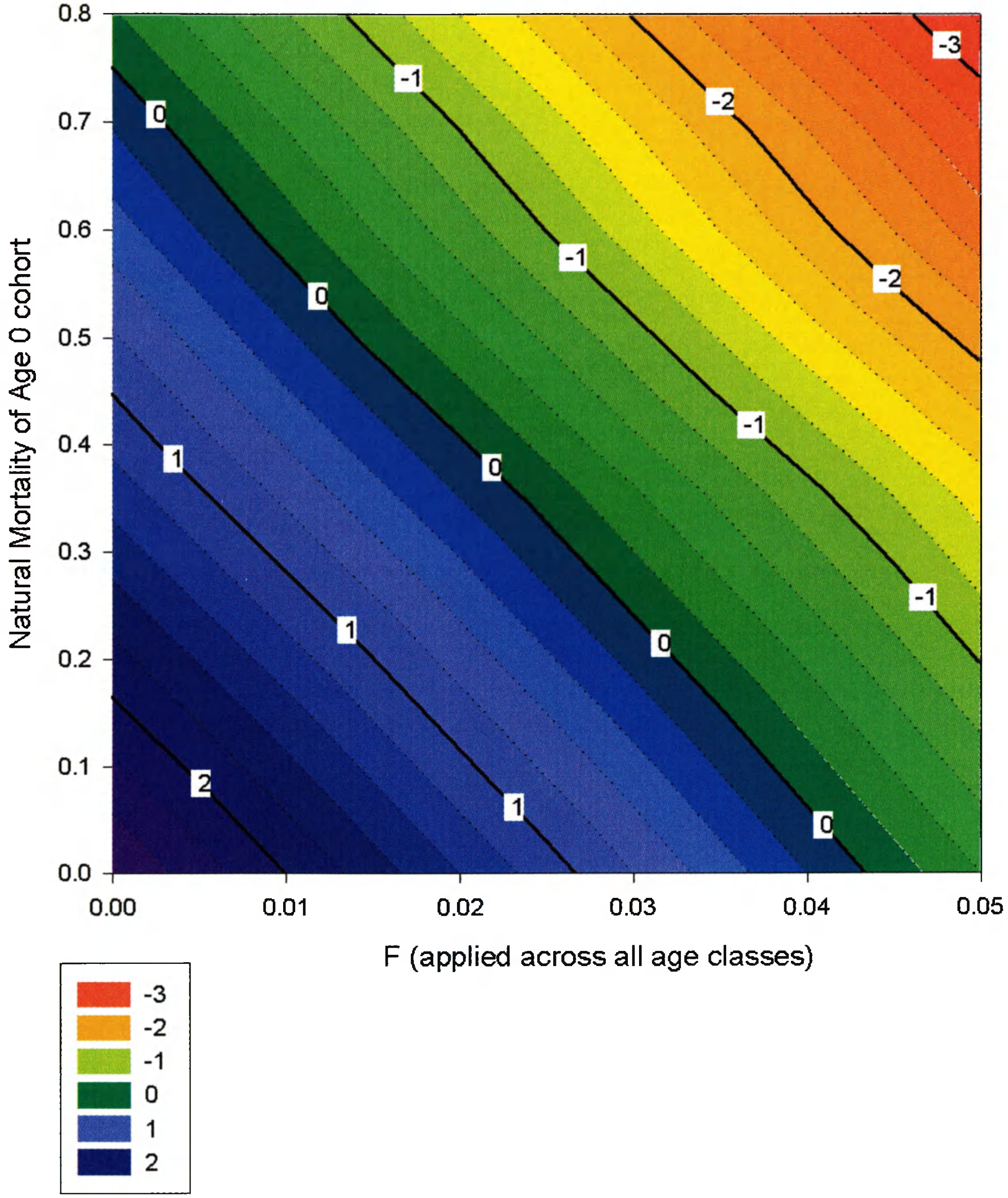


Table 8. Results of demographic analyses under no fishing mortality (F=0.00) and for F=0.07 (scenario two) and F=0.21 scenario (scenario three).

F	λ	r	$\overline{A}$	R_0	**Mean Life expectancy**
0.00	0.998 (0.99- 1.008)	-0.002 (-0.012-0.008)	29.69 (27.34-31.99)	0.943 (0.69-1.24)	10.87 (10.43-11.34)
0.07	0.978 (0.97-0.99)	-0.022 (-0.011- -0.032)	30.18 (27.68-32.69)	.34 (0.21-0.50)	9.50 (9.13-9.88)
0.21	0.940 (.931-.948)	-0.062 (-0.053- -0.072)	31.362 (28.55-34.22)	0.16 (0.11-0.22)	7.63 (7.42-7.86)

	Elasticity					
F	**Fertility**	**1-3 age classes**	**4-9**	**10-20**	**21-28**	**29-50**
0.00	3.26 (3.03-3.53)	9.79 (9.09-10.58)	19.59 (18.19-21.17)	35.91 (33.34-38.81)	19.97 (17.95-21.20)	11.49 (7.79-15.35)
0.07	3.21 (2.97-3.49)	9.64 (8.91-10.46)	19.28 (17.81-20.92)	35.35 (32.66-38.35)	20.01 (18.17-21.16)	12.50 (8.41-16.83)
0.21	3.10 (2.84-3.39)	9.29 (8.52-10.18)	18.58 (17.05-20.36)	34.06 (31.25-37.33)	20.03 (18.64-20.91)	14.94 (10.06-19.94)

Life expectancy

Mean life expectancy changed from 10.87 years in scenario 1 (F=0) to 7.63 in the F=0.21 scenario. Under fishing mortality conditions the probability of surviving to maturity was extremely low. Population halving time for Scenario 2 was 34 years. Population halving time for scenario 3 was 11.5 years.

Stable age distribution

Age-0 accounted for 16-18% of the population in all three scenarios. Contributions decreased with each increase in age (Figure 21). Assuming age at maturity is 21 and maximum age is 45, the female breeding population accounted for 13% of the total population and immature females accounted or 87% of the population.

Elasticities

Summed elasticities were greatest for the juvenile stage under all model scenarios. Elasticities for mature females decreased with age. The importance of the breeding population increased as fishing mortality increased and the contribution of younger ages classes to population growth decreased (Figure 22).

Mean elasticities for juvenile survival and age-zero survival under conditions set in scenario one were 65.29 and 3.26 respectively. The mean elasticity ratio of juvenile survival to age-zero survival is 65.29 / 3.26 = 20.02. The two fishing mortality scenarios represent an average decrease in juvenile survival of 2.4% (scenario two) and 7.2% (scenario three) from the equilibrium population. Under the conditions in scenario two, age-zero survival or fecundity would have to increase by 48%

Figure 21. Stable age distributions for all 3 scenarios.

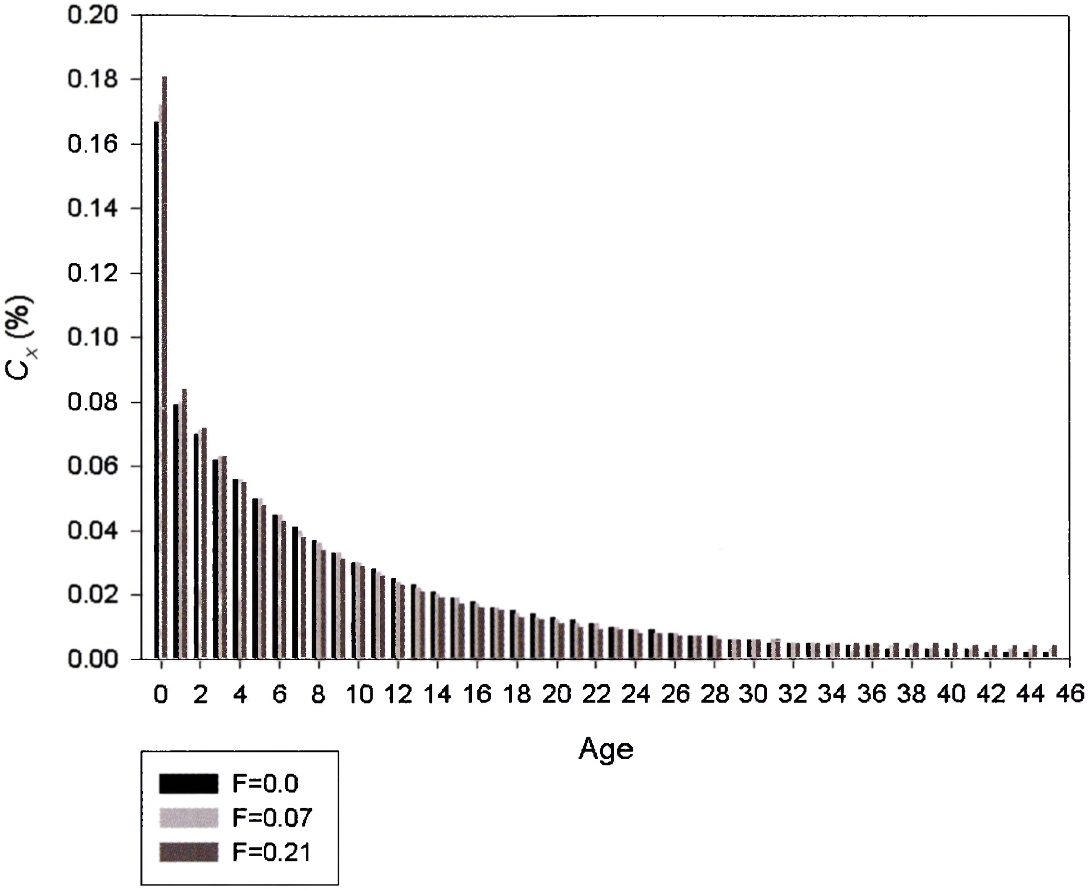
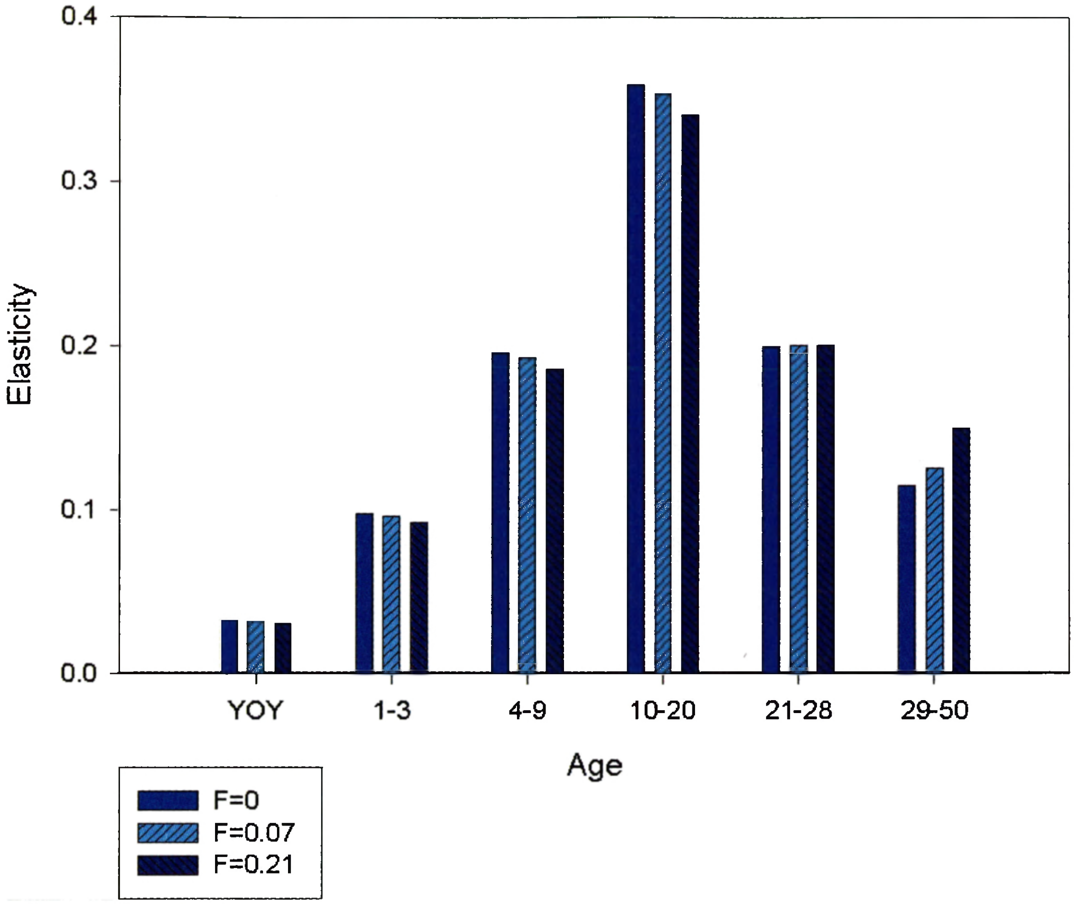


Figure 22. Summed elasticities for all scenarios.



(Heppell et al. 1999; Cortés 2002). A 48% increase in fecundity represents an increase of four pups from mean litter size, eight. The possibility of 12 pups per litter is reasonable and recovery may be possible. Scenario three represents a decrease in juvenile survival of 7.2%. Age-zero survival or fecundity would have to increase by 144%. This is not possible given mean values for fecundity and survivorship. An increase of 144% in fecundity translates to 19 pups per litter. Increase of 144% for survival and fecundity is greater than what is physically possible.

Model sensitivity

Population growth rate was most sensitive to perturbations in survivorship of the youngest age classes, age at maturity and maximum age (Figures 23,24,25). As fishing mortality increased the model became less sensitive to age at maturity and maximum age. Sensitivity decreased as age increased for all juvenile ages (Figure 26).

Although the models were most sensitive to age-0 survival, when values for age-0 natural mortality were varied within the models, little change occurred in population growth rates. When natural mortality was completely removed from the model, population increase for scenario two increased to 0.6% (Figure 27). When natural mortality was removed from the age-0 cohort in scenario two, rate of population increase was –3.6%.

Deterministic matrix projections

The numerical projection of population size under the three scenarios is grim. Under scenario three the population decreased by 80% over 30 years and placed the

Figure 23. Sensitivity of population growth to changes in model parameters at F=0. Where t_{mat} is age at maturity, t_{max} is maximum age, and p0 is survivorship for age 0.

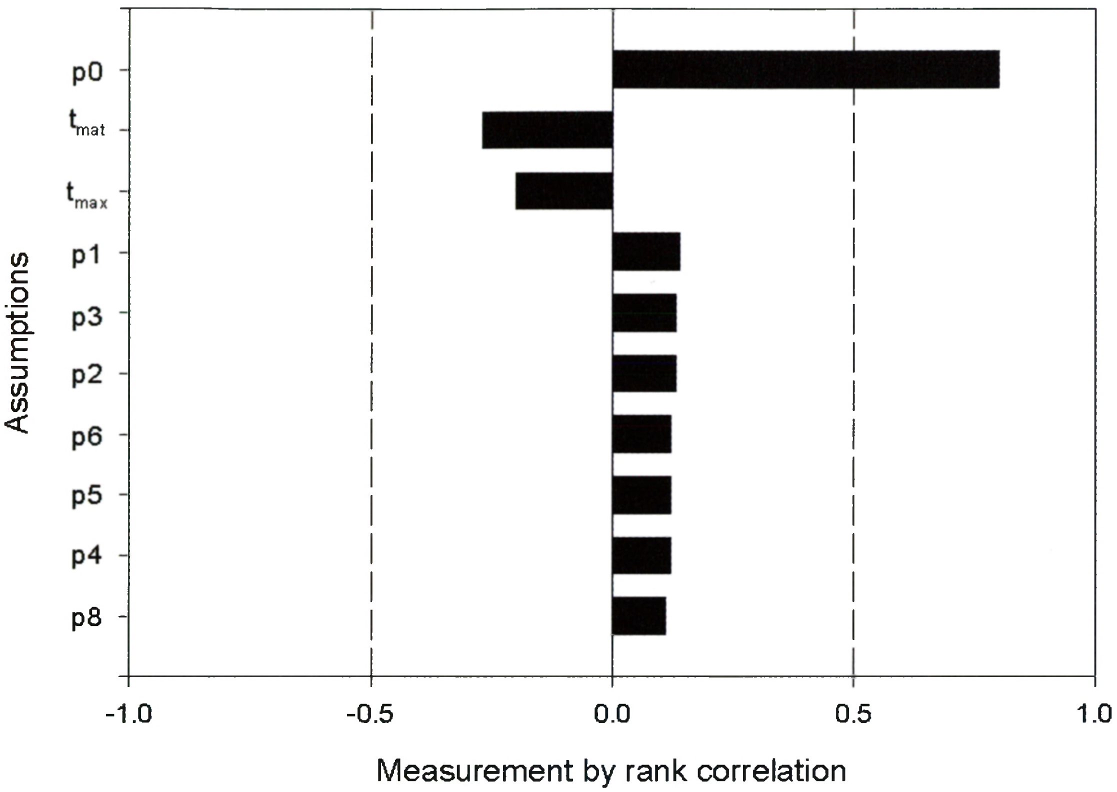


Figure 24. Sensitivity of population growth to changes in model parameters in scenario 2. Where t_{mat} is age at maturity, t_{mat} is maximum age, and p0 is survivorship for age 0.

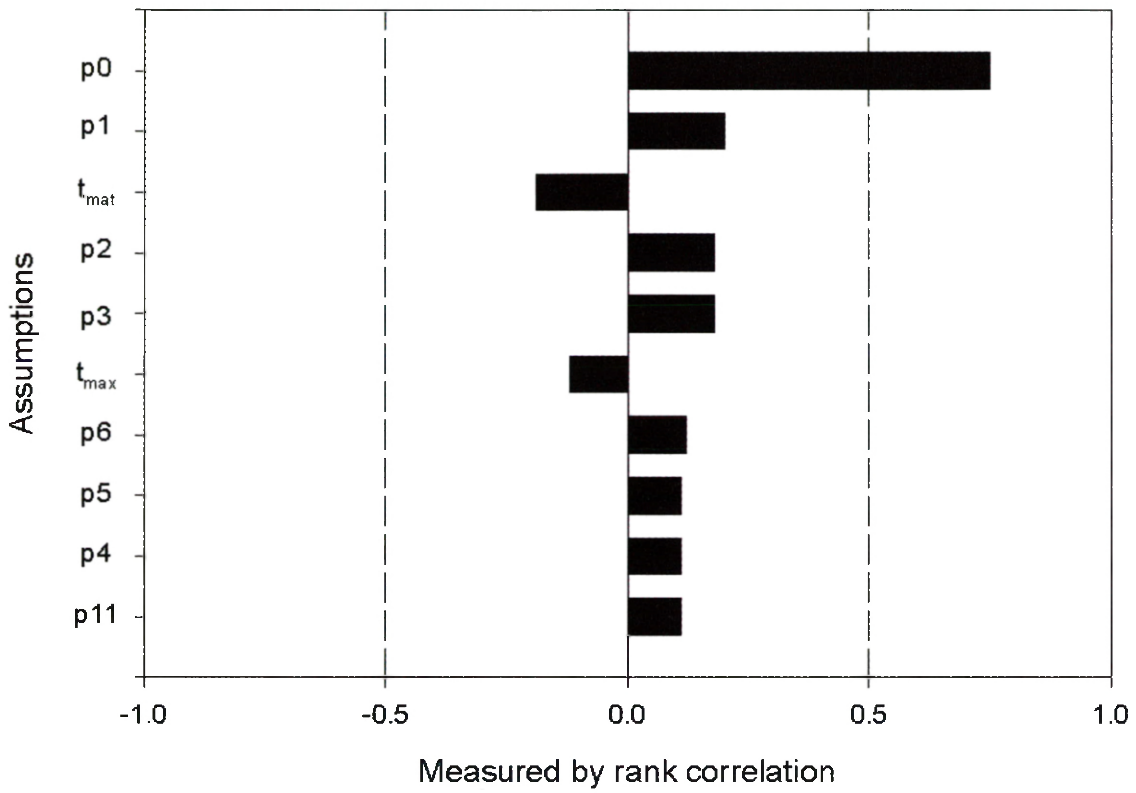


Figure 25. Sensitivity of population growth to perturbations in model parameters for scenario 3. Where pX is survivorship at age X.

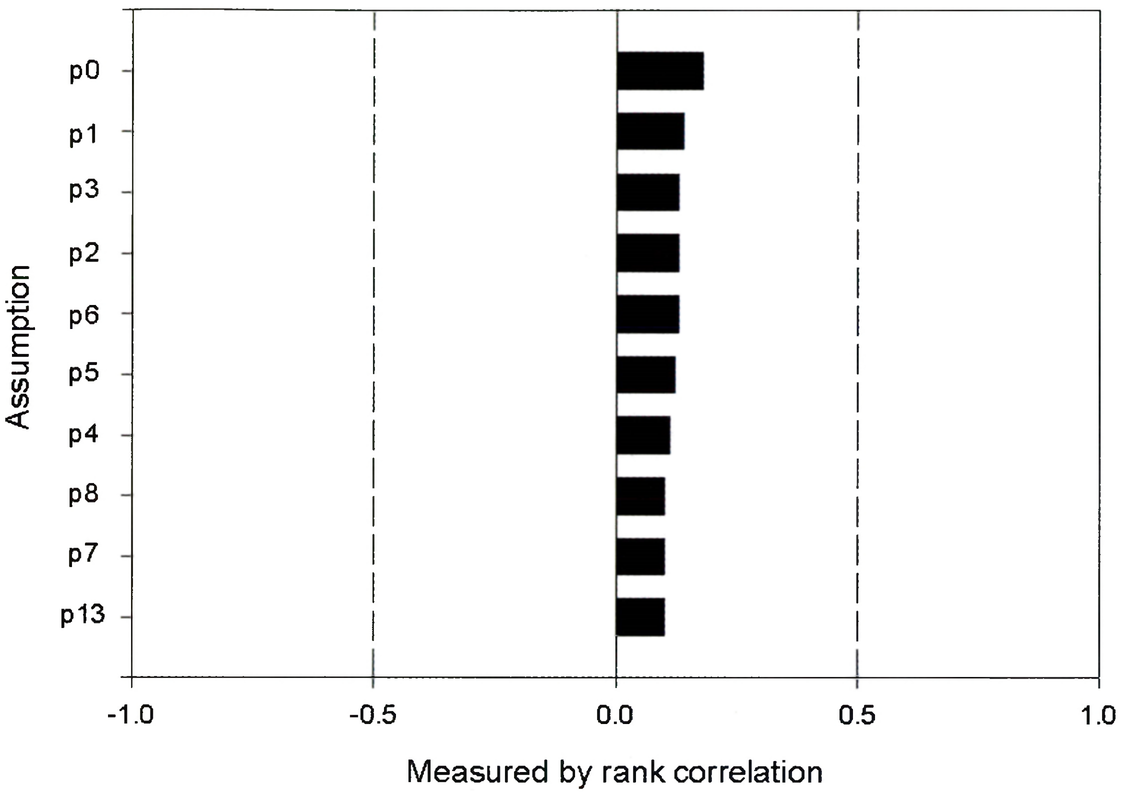


Figure 26. Sensitivity of population growth rate to perturbations in age specific survival rates for all three scenarios.

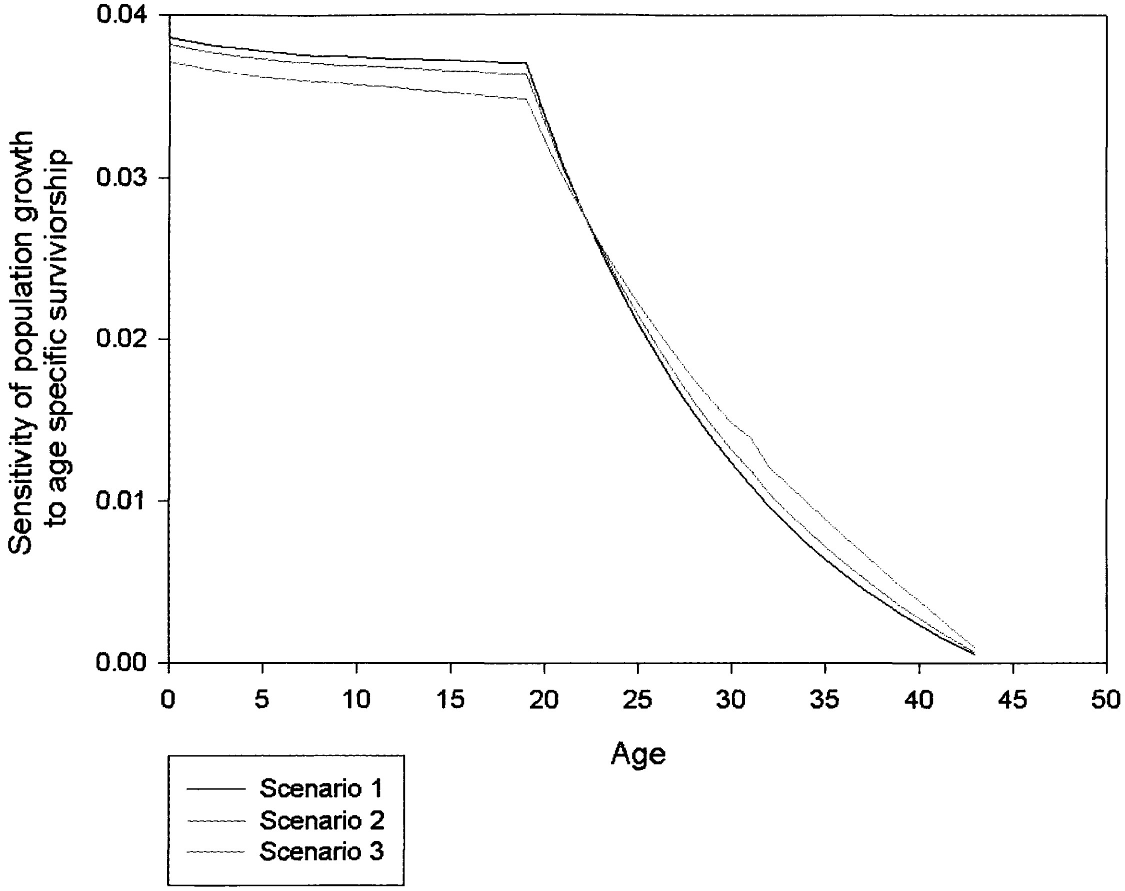
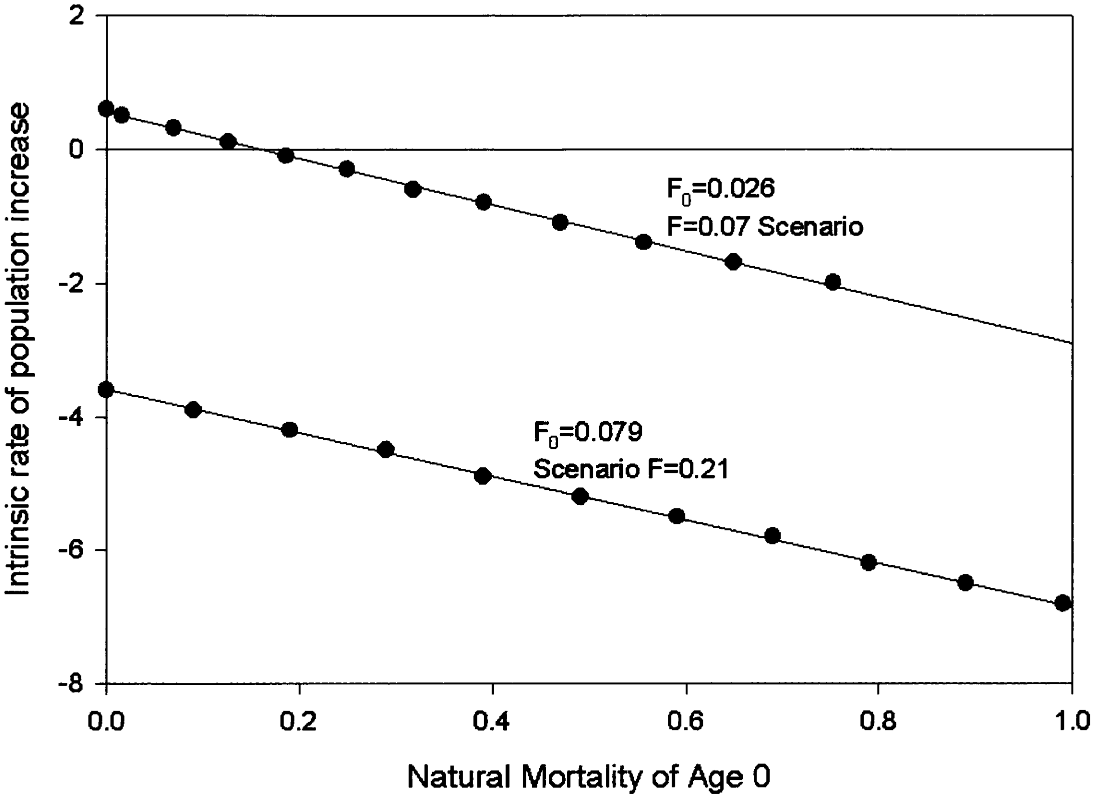
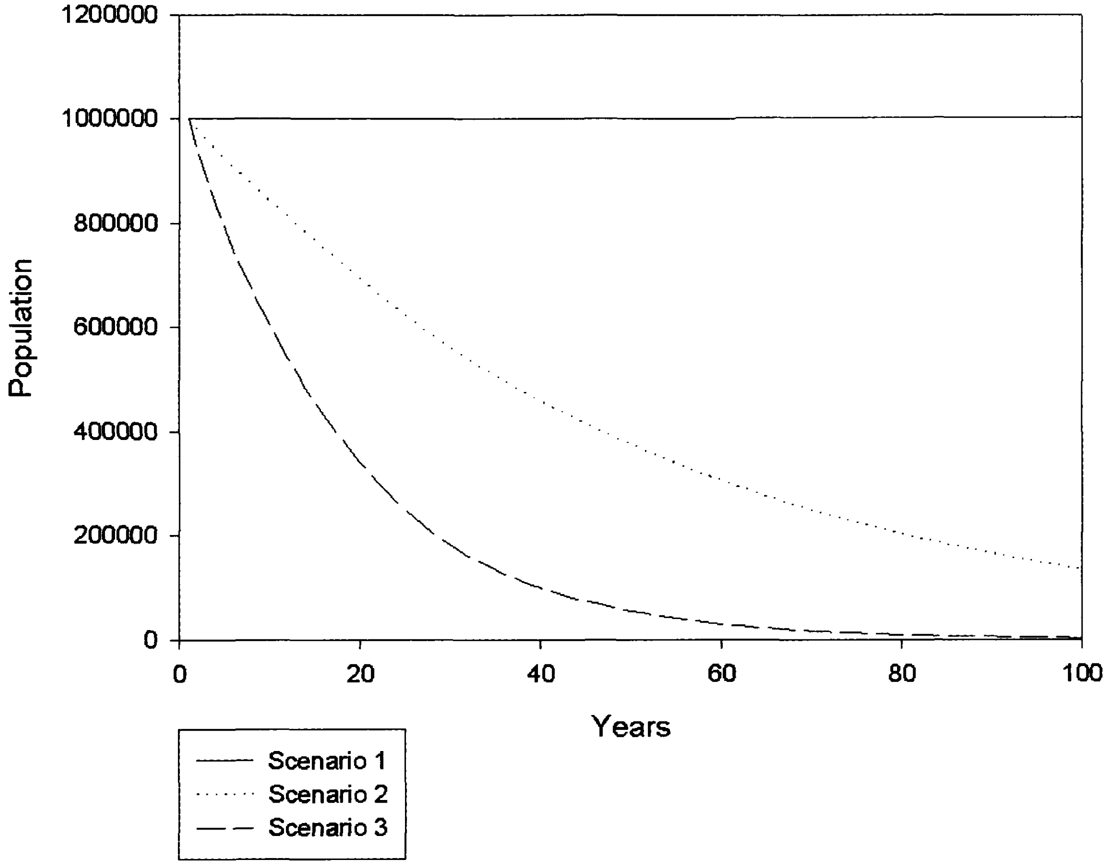


Figure 27. Effects of natural mortality estimates on population growth rates under conditions set in scenarios two and three.



population near extinction in 100 yrs (Figure 28). The conditions of scenario one project slight increases in population over 100 years.

Figure 28. Deterministic population projections for all three scenarios based on the stable age distribution of an equilibrium population of 1,000,000 sharks.



DISCUSSION

Previous works

There are many shortcomings in demographic analysis of long-lived, highly migratory species. Accurate, empirical mortality rates are extremely difficult to derive and have been calculated for few elasmobranchs. In place of measured mortality rates, theoretical values for elasmobranch mortality are typically used. As well as mortality estimates, other vital parameters are likely to have some natural variation over time. Variation or uncertainty in model parameters was accounted for by including probability distributions for model parameters based on available data. In doing so, confidence intervals were created for population responses under the various scenario conditions. Incorporating a level of uncertainty in model parameters appears to be a reasonable method for addressing this shortcoming and has been suggested by other researchers (Mills et al. 1999; Cortés 2002).

Few elasmobranch models account for fishery removals and their impact on population growth or the subsequent compensatory reactions of the population. Fishing mortality was incorporated in the models to investigate what levels of fishing mortality the population could withstand. Under minimal fishing pressure models returned negative values for population increase. Population growth was most sensitive to age-0 mortality in the fishing scenarios. When natural mortality of this age class was set at zero, population growth was 0.6% within the scenario two (F=0.07). Although population growth was most sensitive to age-0 mortality within the fishery scenarios, reducing natural mortality to zero did not compensate for fishing mortality in scenario three (F=0.21) and moved population growth to slightly above zero in scenario two (F=0.07).

Previous studies of the demography of the dusky shark have calculated r-values of 2.0% (Smith et al. 1998), 2.8% (Cortés 2002), and 5.57% (Sminkey 1996). Only one of these studies has accounted for the variability in natural mortality rates and none have included the effects of fishing mortality within the analysis (Cortés 2002). Most researchers have employed a single method for calculating natural mortality across all age classes. This approach does not account for differences in natural mortality as the species in question grows. A shark of 2 meters will likely have a lower natural mortality than a shark of lesser length (Peterson and Wroblewski 1984). Under zero fishing mortality a population should be at equilibrium, $\lambda = 1$.

Age-0 natural mortality

Survivorship of the age-0 cohort was established assuming the demographic parameters employed within the model represent a virgin population at equilibrium and did not account for compensatory mechanisms that likely result from fishing mortality. As such it does not account for the possibility that currently observed demographic parameters may have already changed in a compensatory role to recover from fishing induced mortality and may not be indicative of the virgin population. Exploitation of the dusky shark was greatest in the early 1980's. Compensatory responses to fishing pressure are likely to be slow and would not be realized until 2000-2004 due to the late age at maturity and slow growth rates. Growth rate parameters employed in the models were derived in the mid 1990's and may not represent the current status of the population (Sminkey and Musick 1995). Given this possibility the models may have underestimated the population growth potential due to changes in growth rate and survivorship estimates over the past decade. The models did not account for the probable compensatory changes in growth rates and increased survivorship of the youngest age classes due to decreases in population densities (Gruber et al. 2001).

Heppel et al.(2000) suggested utilizing demographic parameters of like species when demographic parameters for the study animal are difficult to determine or unavailable. Unfortunately, data for age-0 survivorship of elasmobranchs are scarce due to a multitude of factors. Empirical mortality estimates for lemon sharks, blacktip sharks, and Cetaceans were used to verify age-0 survivorship estimates. Both groups are K-selected and thus put effort into few well-formed offspring. For example, mortality of neonate killer whales, *Orcinus orca*, was estimated to be 43% (Olesiuk et al. 1990). Given their large size at birth, 2.5 m, compared to the size at birth of dusky sharks, 80cm FL, the estimate of age-0 survivorship appears reasonable and is within mortality estimates for juvenile lemon sharks and juvenile blacktip sharks (Gruber et al. 2001; Heupel and Simpfendorfer 2002).

Elasticity and Sensitivity analysis

The contribution of the juvenile stage to population growth is directly related to the length of the juvenile stage (Heppell et al. 2000). Summing elasticities across age classes for each stage to estimate the importance of stages within the life history of species is biased when stages of disproportionate length are compared. Elasticity analysis within my models ranked age-0 and age-20 as being equally important to population growth. Sensitivity analysis appears to be a more appropriate method of estimating the importance of stages or age classes of long-lived species especially when a fished population that regularly experiences perturbations is involved. It follows that sensitivity analysis should be used for establishing management decisions when specific size ranges or age classes are in need of protection. Under fishing scenarios where multiple age classes were impacted, population growth was most sensitive to age-0 survival or fecundity.

Analyses of elasticity ratios yielded grim results for dusky sharks. The population may rebound to equilibrium if fecundity increased to 12 pups per litter under conditions set in scenario two. This is possible given the fecundity values previously reported and those values determined in the present study. Under the conditions in scenario three the population may not be able to compensate for fishing mortality unless management measures are taken to reduce juvenile mortality.

Conservation measures

Dusky sharks have slow growth and mature later than most other sharks (Natanson et al. 1995). In addition, they have a longer reproductive cycle than most other sharks. These characteristics result in a very low intrinsic rate of population increase and extreme vulnerability to over-fishing and population collapse. Demographic models suggest that even under modest levels of F, the dusky shark population is on the edge of collapse. Better estimates of fishing mortality are needed to obtain a more accurate estimate of the effect of the commercial shark fishery on the population. Although the greatest hooking mortality occurs in the youngest age classes, all year classes experience hooking mortality at some level. Simpfendorfer (1999) indicated that intrinsic rates of population increase would remain above zero if fishing mortality was restricted to the youngest year class.

The target for fishing mortality on the large coastal complex is F=0.05-0.08 (NMFS 2003). If juvenile survival increases, the population may increase at very low levels of fishing mortality if fishing mortality is only experienced as hooking mortality. A directed fishery across all age classes is not sustainable even at the lowest levels of fishing mortality. Dusky sharks require greater protections from hooking mortality for the population to recover from intense fishing pressure.

Appendix. Life table construction for all three scenarios. Probability distributions were created for survivorship, total fecundity, maximum age, and age at first reproduction. The tables below illustrate values under the most probable estimates for these values. Thus the zero value for m_x at ages greater than 45. As the probability distributions are resampled via Monte Carlo simulation the reproductive and survivorship values will reflect changes in the associated values via if/then statements included in the model.

Model setup for scenario 1

	Age	**Survivorship**			
F	x	P_x	l_x	**Total Fecundity**	m_x
0	0	0.473	1	0	0
0	1	0.884	0.473	0	0
0	2	0.89	0.418	0	0
0	3	0.894	0.372	0	0
0	4	0.898	0.333	0	0
0	5	0.901	0.299	0	0
0	6	0.904	0.269	0	0
0	7	0.906	0.243	0	0
0	8	0.908	0.221	0	0
0	9	0.91	0.2	0	0
0	10	0.912	0.182	0	0
0	11	0.913	0.166	0	0
0	12	0.915	0.152	0	0
0	13	0.916	0.139	0	0
0	14	0.917	0.127	0	0
0	15	0.918	0.117	0	0
0	16	0.919	0.107	0	0
0	17	0.92	0.099	0	0
0	18	0.921	0.091	0	0
0	19	0.922	0.084	7.331	0
0	20	0.922	0.077	7.331	0
0	21	0.923	0.071	7.331	1.222
0	22	0.924	0.066	7.331	1.222
0	23	0.924	0.061	7.331	1.222
0	24	0.925	0.056	7.331	1.222

Model setup for scenario 1 continued

F	Age x	Survivorship P_x	l_x	**Total Fecundity**	m_x
0	25	0.925	0.052	7.331	1.222
0	26	0.926	0.048	7.331	1.222
0	27	0.926	0.044	7.331	1.222
0	28	0.927	0.041	7.331	1.222
0	29	0.927	0.038	7.331	1.222
0	30	0.927	0.035	7.331	1.222
0	31	0.928	0.033	7.331	1.222
0	32	0.928	0.03	7.331	1.222
0	33	0.928	0.028	7.331	1.222
0	34	0.929	0.026	7.331	1.222
0	35	0.929	0.024	7.331	1.222
0	36	0.929	0.023	7.331	1.222
0	37	0.929	0.021	7.331	1.222
0	38	0.93	0.019	7.331	1.222
0	39	0.93	0.018	7.331	1.222
0	40	0.93	0.017	7.331	1.222
0	41	0.93	0.016	7.331	1.222
0	42	0.93	0.015	7.331	1.222
0	43	0.931	0.014	7.331	1.222
0	44	0.931	0.013	7.331	1.222
0	45	0.931	0.012	7.331	1.222
0	46	0.931	0.011	7.331	0
0	47	0.931	0.01	7.331	0
0	48	0.931	0.009	7.331	0
0	49	0.932	0.009	7.331	0
0	50	0.932	0.008	7.331	0

Model setup for scenario 2

	Age	Survivorship			
F	x	P_x	l_x	Total Fecundity	m_x
0.026	0	0.473	1.000	0	0
0.028	1	0.884	0.459	0	0
0.027	2	0.89	0.395	0	0
0.030	3	0.894	0.342	0	0
0.027	4	0.898	0.297	0	0
0.026	5	0.901	0.259	0	0
0.023	6	0.904	0.228	0	0
0.022	7	0.906	0.201	0	0
0.020	8	0.908	0.178	0	0
0.014	9	0.91	0.159	0	0
0.032	10	0.912	0.143	0	0
0.030	11	0.913	0.126	0	0
0.012	12	0.915	0.113	0	0
0.025	13	0.916	0.103	0	0
0.025	14	0.917	0.092	0	0
0.024	15	0.918	0.082	0	0
0.016	16	0.919	0.074	0	0
0.030	17	0.92	0.067	0	0
0.026	18	0.921	0.059	0	0
0.019	19	0.922	0.053	7.331	0.000
0.025	20	0.922	0.048	7.331	0.000
0.010	21	0.923	0.043	7.331	1.222
0.021	22	0.924	0.040	7.331	1.222
0.014	23	0.924	0.036	7.331	1.222
0.012	24	0.925	0.033	7.331	1.222
0.010	25	0.925	0.030	7.331	1.222

Model setup for scenario 2 continued

F	Age x	Survivorship P_x	l_x	Total Fecundity	m_x
0.022	26	0.926	0.027	7.331	1.222
0.018	27	0.926	0.025	7.331	1.222
0.012	28	0.927	0.023	7.331	1.222
0.009	29	0.927	0.021	7.331	1.222
0.008	30	0.927	0.019	7.331	1.222
0.009	31	0.928	0.018	7.331	1.222
0.018	32	0.928	0.016	7.331	1.222
0.000	33	0.928	0.015	7.331	1.222
0.000	34	0.929	0.014	7.331	1.222
0.000	35	0.929	0.013	7.331	1.222
0.000	36	0.929	0.012	7.331	1.222
0.000	37	0.929	0.011	7.331	1.222
0.000	38	0.93	0.010	7.331	1.222
0.000	39	0.93	0.009	7.331	1.222
0.000	40	0.93	0.009	7.331	1.222
0.000	41	0.93	0.008	7.331	1.222
0.000	42	0.93	0.007	7.331	1.222
0.000	43	0.931	0.007	7.331	1.222
0.000	44	0.931	0.006	7.331	1.222
0.000	45	0.931	0.006	7.331	1.222
0.000	46	0.931	0.006	7.331	0.000
0.000	47	0.931	0.005	7.331	0.000
0.000	48	0.931	0.005	7.331	0.000
0.000	49	0.932	0.004	7.331	0.000
0.000	50	0.932	0.004	7.331	0.000

Model setup for scenario 3

	Age	Survivorship			
F	x	P_x	l_x	Total Fecundity	m_x
0.079	0	0.436	1.000	0	0
0.085	1	0.813	0.436	0	0
0.080	2	0.822	0.354	0	0
0.091	3	0.817	0.291	0	0
0.082	4	0.827	0.237	0	0
0.079	5	0.833	0.196	0	0
0.068	6	0.845	0.164	0	0
0.065	7	0.850	0.138	0	0
0.061	8	0.855	0.117	0	0
0.043	9	0.872	0.100	0	0
0.095	10	0.830	0.087	0	0
0.089	11	0.836	0.073	0	0
0.035	12	0.884	0.061	0	0
0.074	13	0.851	0.054	0	0
0.076	14	0.850	0.046	0	0
0.072	15	0.854	0.039	0	0
0.048	16	0.876	0.033	0	0
0.090	17	0.841	0.029	0	0
0.079	18	0.852	0.024	0	0
0.058	19	0.870	0.021	7.331	0.000
0.074	20	0.857	0.018	7.331	0.000
0.030	21	0.896	0.015	7.331	1.222
0.063	22	0.868	0.014	7.331	1.222
0.042	23	0.886	0.012	7.331	1.222
0.035	24	0.893	0.011	7.331	1.222
0.029	25	0.900	0.010	7.331	1.222

Model setup for scenario 3 continued

F	Age x	Survivorship P_x	l_x	Total Fecundity	m_x
0.066	26	0.867	0.009	7.331	1.222
0.053	27	0.879	0.007	7.331	1.222
0.035	28	0.895	0.007	7.331	1.222
0.026	29	0.903	0.006	7.331	1.222
0.023	30	0.906	0.005	7.331	1.222
0.026	31	0.903	0.005	7.331	1.222
0.053	32	0.880	0.004	7.331	1.222
0.000	33	0.928	0.004	7.331	1.222
0.000	34	0.928	0.004	7.331	1.222
0.000	35	0.928	0.003	7.331	1.222
0.000	36	0.928	0.003	7.331	1.222
0.000	37	0.928	0.003	7.331	1.222
0.000	38	0.928	0.003	7.331	1.222
0.000	39	0.928	0.002	7.331	1.222
0.000	40	0.928	0.002	7.331	1.222
0.000	41	0.928	0.002	7.331	1.222
0.000	42	0.928	0.002	7.331	1.222
0.000	43	0.928	0.002	7.331	1.222
0.000	44	0.928	0.002	7.331	1.222
0.000	45	0.928	0.002	7.331	1.222
0.000	46	0.928	0.001	7.331	0.000
0.000	47	0.928	0.001	7.331	0.000
0.000	48	0.928	0.001	7.331	0.000
0.000	49	0.928	0.001	7.331	0.000
0.000	50	0.928	0.001	7.331	0.000

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