

2008

## Age, growth, and demography of the sandbar shark, *Carcharhinus plumbeus*, over temporal and spatial scales

Jason G. Romine

*College of William and Mary - Virginia Institute of Marine Science*

Follow this and additional works at: <https://scholarworks.wm.edu/etd>



Part of the [Fresh Water Studies Commons](#), [Marine Biology Commons](#), and the [Oceanography Commons](#)

---

### Recommended Citation

Romine, Jason G., "Age, growth, and demography of the sandbar shark, *Carcharhinus plumbeus*, over temporal and spatial scales" (2008). *Dissertations, Theses, and Masters Projects*. William & Mary. Paper 1539616830.

<https://dx.doi.org/doi:10.25773/v5-dcpf-mn33>

This Dissertation is brought to you for free and open access by the Theses, Dissertations, & Master Projects at W&M ScholarWorks. It has been accepted for inclusion in Dissertations, Theses, and Masters Projects by an authorized administrator of W&M ScholarWorks. For more information, please contact [scholarworks@wm.edu](mailto:scholarworks@wm.edu).

**Age, Growth, and Demography of the sandbar shark, *Carcharhinus plumbeus*, over  
temporal and spatial scales**

---

A Dissertation  
Presented to  
The Faculty of the School of Marine Science  
The College of William and Mary in Virginia

In Partial Fulfillment  
Of the Requirements for the Degree of  
Doctor of Philosophy

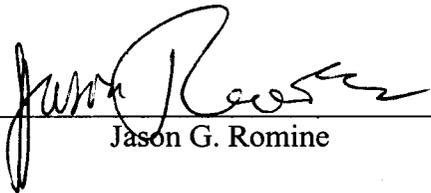
---

by

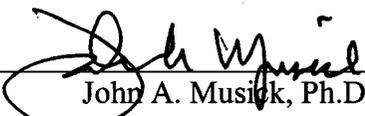
Jason G. Romine  
2008

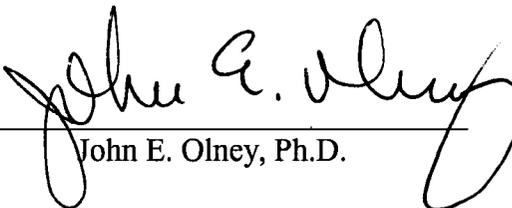
**APPROVAL SHEET**

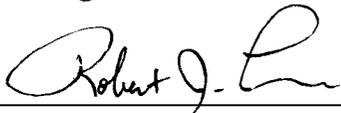
This dissertation is submitted in the partial fulfillment of  
the requirements for the degree of  
Doctor of Philosophy

  
\_\_\_\_\_  
Jason G. Romine

Approved, by the Committee, April 2008

  
\_\_\_\_\_  
John A. Musick, Ph.D.  
Committee Chairman/Advisor

  
\_\_\_\_\_  
John E. Olney, Ph.D.

  
\_\_\_\_\_  
Robert J. Latour, Ph.D.

  
\_\_\_\_\_  
Peter A. van Veld, Ph.D.

  
\_\_\_\_\_  
Kenneth J. Goldman, Ph.D.  
Alaska Department of Fish and Game  
Homer, Alaska

## **DEDICATION**

This work is dedicated to my mother, Janie Romine. As a three time cancer survivor she remains well outside the confidence intervals of the common person. She is truly an inspiration and possesses the fortitude, perseverance, and optimism that the common person may only hope to possess.

## TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	vi
LIST OF TABLES.....	vii
LIST OF FIGURES.....	viii
CHAPTER 1	
INTRODUCTION.....	2
CHAPTER 2	
Compensatory growth in the sandbar shark, <i>Carcharhinus plumbeus</i> , in the Northwest Atlantic.....	10
ABSTRACT.....	11
INTRODUCTION.....	12
METHODS.....	17
RESULTS.....	22
DISCUSSION.....	24
LITERATURE CITED.....	28
CHAPTER 3	
Growth estimates for the sandbar shark, <i>Carcharhinus plumbeus</i> , in the Northwest Atlantic through tag-recapture methods.....	41
ABSTRACT.....	42
INTRODUCTION.....	43
METHODS.....	44
RESULTS.....	48
DISCUSSION.....	48
LITERATURE CITED.....	52
APPENDICES.....	65
CHAPTER 4	
Age and growth of the sandbar shark, <i>Carcharhinus plumbeus</i> , in Hawaiian waters through vertebral analysis.....	74
ABSTRACT.....	75
INTRODUCTION.....	76
METHODS.....	77
RESULTS.....	81
DISCUSSION.....	85
LITERATURE CITED.....	90

CHAPTER 5

Demographic analyses of the sandbar shark over temporal and spatial scales.....102

ABSTRACT.....103

INTRODUCTION.....104

METHODS.....107

RESULTS.....110

DISCUSSION.....112

LITERATURE CITED.....116

## ACKNOWLEDGEMENTS

The work contained within the following pages has been made possible by countless volunteers, collaborators, fellow graduate students, and friends that contributed a great deal of their time and effort in collecting samples, participating in cruises, lab analyses and supplying constructive criticisms of these projects.

I would like to thank my parents for their support throughout all my endeavors whether they agreed with me or not. I would like to especially like to thank Patrick Richardson for introducing me to one Dr. John E. Olney, with whom this entire adventure began, from sorting a seemingly endless collection of ichthyoplankton samples, to my present position as Research Biologist with the Florida Museum of Natural History.

This all would not have been possible without Dr. Jack Musick taking me into his lab and supporting my ideas. I must thank him for all the wonderful opportunities he has afforded me during my time here.

The VIMS shark lab consisting of Wes Dowd, Julia Ellis, Chip Cotton, Dave Portnoy, Vince Saba, Josh Smith, Dean Grubbs, and Pat McGrath has continuously been the source of great times and entertainment.

There are those that one encounters in life that one can depend on in the darkest nights of your life. Jonathan Eastwood and Brian Watkins have continuously been there in the darkest hours to offer a hand up or safe harbor in the midst of the hurricanes of life.

Last but not least I would like to thank RaeMarie Johnson. RaeMarie served as second reader on all 900 or so vertebrae reads. She was a constant force in pushing me along when mired in the mud at VIMS. She is truly a wonderful person and without her support I would not be writing this now.

## LIST OF TABLES

<u>Chapter 2</u>	Page
Table 1. Model fits for 1980 (a) and 2000 (b) samples males and females. ....	32
<u>Chapter 3</u>	
Table 1. Model results of all parameterizations. Model in shaded area was the accepted model.....	54
<u>Chapter 4</u>	
Table 1. Estimates of model parameters and goodness of fit statistics for models fitted to length-at-age data for male and female sandbar sharks.....	94
Table 2. Mean size at age for male and female sandbar sharks.....	95
<u>Chapter 5</u>	
Table 1. Life history parameters and probability distributions for Hawaii model.....	119
Table 2. Life history parameters and probability distributions for NWA 1980 model.....	120
Table 3. Life history parameters and probability distributions for NWA 2000 model.....	121
Table 4. Natural mortality methods and population growth for Hawaiian sandbar sharks.....	122
Table 5. Results for analyses of all three populations based on life history parameters.....	123
Table 6. Elasticities of population growth to survival of newborns, juveniles, and adults for Hawaii, NWA 1980 and NWA 2000 models.....	124
Table 7. Stable population harvests for juvenile and adult harvest strategies.....	125

## LIST OF FIGURES

### Chapter 2

Figure 1. Number of sharks, male and females combined, sampled within five centimeter size classes for both time periods.....	34
Figure 2. All model fits for females 1980 data.....	35
Figure 3. All model fits for females 2000 data.....	36
Figure 4. All model fits for males 1980 data.....	37
Figure 5. All model fits for females 1980 data.....	38
Figure 6. Differences in mean size at age in centimeters between time periods.....	39
Figure 7. ML estimates and 95% confidence intervals for proportion females mature at age.....	40

### Chapter 3

Figure 1. Recapture locations of sandbar sharks tagged by VIMS.....	55
Figure 2. Pre-caudal length of sandbar sharks at time of release.....	56
Figure 3. Pre-caudal length of sandbar sharks at time of tagging and at time of recapture.....	57
Figure 4. Growth increments of tagged sandbar sharks during time at liberty.....	58
Figure 5. Error structures used within the model.....	59
Figure 6. Residuals of best fit model.....	60
Figure 7. Bootstrap and mean estimates for sandbar sharks tagged by VIMS....	61
Figure 8. Bootstrap results and mean estimates of growth parameters from different tag types used on sandbar sharks.....	62
Figure 9. Comparison of growth parameters estimated through tagging and vertebral analyses. Vertebral estimates are from Romine et al. (in prep).....	63

Figure 10. Comparison of growth curves estimated from tagging and vertebral aging methods.....	64
--	----

Chapter 4

Figure 1. Sampling area on the windward coast of Oahu. All sharks used for age and growth were captured within the rectangle noted as sampling area.....	96
Figure 2. Size frequency of sandbar sharks used for age and growth in this study.....	97
Figure 3. Regression of pre-caudal length and centrum radius ( $r^2=0.97$ , $n=148$ ) for males and females combined.....	98
Figure 4. Mean marginal increment ratio monthly values and standard deviation of the monthly means for both sexes combined.....	99
Figure 5. Length-at-age estimates and growth models fitted to data for male sandbar sharks ( $n= 81$ ).....	100
Figure 6. Length-at-age data and fit of growth models to the data for female sandbar sharks ( $n = 105$ ).....	101

Chapter 5

Figure 1. Maturity ogive for female Hawaii sandbar sharks.....	126
Figure 2. Yield recruit <sup>-1</sup> isopleths for age at first harvest and fraction of reproductive potential removed. Top axis depicts annual population change due to fraction of reproductive potential removed. Isopleths terminate at maximum possible F value.....	127
Figure 3. Yield recruit <sup>-1</sup> isopleths for maximum age harvested and fraction of reproductive potential removed. Top axis depicts annual population change due to fraction of reproductive potential removed.....	128

## ABSTRACT

Numbers of sandbar sharks, *Carcharhinus plumbeus*, in the Northwest Atlantic have experienced drastic declines since the early 1980's reaching their minima during the early 1990's. Catch rates in the early 1990's were a mere 25% of those during the 1980's. Such drastic reductions in other fish stocks have often caused compensatory responses, most notably the cod stocks in the Northwest Atlantic. Compensatory responses in depressed populations may include decreased natural mortality, increased fecundity, or increased growth rates. Compensation for population fluctuations below carrying capacities have been recognized for many terrestrial and oceanic r-selected organisms, but few instances have been noted for K-selected species. Due to slow-growth and late maturity, compensatory responses in K-selected species such as the sandbar shark probably require generation-scale time periods to become evident. A previous age and growth study discovered slight increases in juvenile sandbar shark growth rates when vertebral centra samples obtained in 1980-81 and 1990-1992 were compared. The Virginia Institute of Marine Science shark long-line survey reported the lowest abundance of sandbar sharks in 1992. Animals pupped during this time may display greater differences in growth rates due to drastically reduced population size. Samples obtained over the 2001-2004 time period were compared to the aforementioned time periods to investigate potential compensatory responses in the sandbar shark population in the Northwest Atlantic.

Growth estimates for the sandbar shark, *Carcharhinus plumbeus*, in the Northwestern Atlantic were estimated using a reparameterized von Bertalanffy growth model. Sharks were tagged in Virginia waters with roto-tags and double return nylon dart tags from 1992 to 2006 by the shark longline survey of the Virginia Institute of Marine Science. Captured sharks were measured, tagged, and released by VIMS scientists. Dart tags were inserted at the base of the first dorsal fin on the

left side of the animal. Over the time period, 37 recaptured sharks with reliable length at recapture information were reported. Time at liberty ranged from 26 to 3,561 days. Pre-caudal length at tagging ranged from 41 to 81 cm and pre-caudal length at recapture ranged from 43 to 147 cm. Growth increments ranged from 0.10 to 66 cm. The fitted model estimated growth rates of  $11 \text{ cm} \cdot \text{yr}^{-1}$  for 45 cm precaudal length sharks and  $7 \text{ cm} \cdot \text{yr}^{-1}$  for 75 cm pre-caudal length shark

Age and growth estimates were determined for the sandbar shark, *Carcharhinus plumbeus*, from Oahu, Hawaii in the central Pacific Ocean. Age estimates were obtained through vertebral centra analysis of 187 sharks. We verified our age estimates through marginal increment analysis of centra and oxytetracycline marking methods of at-liberty sandbar sharks. Sizes of sampled sharks ranged from 46 cm to 147 cm pre-caudal length. Four growth models were fitted to length-at-age data; two forms of the von Bertalanffy growth model, the Gompertz growth model, and a logistic growth model. Males and females exhibited statistically significant differences in growth, indicating that females grow slower and attain larger sizes than males. Growth parameter estimates revealed slower growth rates than previously estimated (based on captive specimens) for Hawaiian sandbar sharks. The von Bertalanffy growth model using empirical length-at-birth provided the best biological and statistical fit to the data. This model gave parameter estimates of  $L_{\infty}=138.5 \text{ cm PCL}$  and  $k=0.12 \text{ year}^{-1}$  for males and  $L_{\infty}=152.8 \text{ cm PCL}$ ,  $k=0.10 \text{ year}^{-1}$  for females. Male and female sandbar sharks mature at approximately 8 and 10 years of age respectively.

The population of sandbar sharks in the Hawaiian Islands is an un-fished population. The presents a unique opportunity to conduct demographic analyses on a virgin population of sandbar sharks. Most populations of sandbar sharks have been heavily exploited due to near coastal and estuarine habitat preferences and high demand for fins. Conversely the population

of sandbar sharks in the Northwest Atlantic (NWA) has suffered severe declines since the early 1980's. Previous studies have suggested compensatory growth is occurring within this population, but the true effect at the population level has not been estimated. Life history parameters estimated for the Hawaii population, the NWA population in 1980-1981 and 2000-2004 time periods were used in stochastic age-based life tables and Leslie matrices to estimate demographic parameters. Yield recruit<sup>-1</sup> relationships were estimated for the Hawaii population to determine optimal harvest strategies that would maintain a population at equilibrium. Population growth for the Hawaii population was estimated to be 1.014 year<sup>-1</sup>. Yield recruit<sup>-1</sup> analyses suggested harvest of sharks 15 years of age and older would provide the greatest yield while not causing population decline. Population growth for sandbar sharks in the NWA was 1.009 year<sup>-1</sup> for the 1980-1981 time period and 1.030 year<sup>-1</sup> for the 2000-2004 time period.

**Age, growth, and demographic analyses of the sandbar shark, *Carcharhinus plumbeus*, over temporal and spatial scales**

## Introduction

### *Sandbar shark ecology*

The sandbar shark, *Carcharhinus plumbeus*, is a common large coastal shark that inhabits temperate and subtropical waters world wide and attains lengths greater than two meters (1984). In the Northwest Atlantic (NWA) this species inhabits near-shore waters out to the edge of the continental shelf from Cape Cod to Brazil (Bigelow and Schroeder, 1948; Springer, 1960; Garrick, 1982). Tagging studies suggest that this region is composed of two unit stocks. One stock is found from Cape Cod south to the Northern Yucatan peninsula and another from Trinidad to Brazil (Springer, 1960; Kohler et al., 1998). Genetic studies conducted on specimens from Virginia waters and the Gulf of Mexico further support the existence of a single stock that utilizes the area of Cape Cod to the Northern Yucatan Peninsula (Heist et al., 1995).

The sandbar shark in the NWA undergoes seasonal migrations from the Gulf of Mexico and Florida to as far north as Cape Cod as water temperatures rise in the spring and return south as water temperatures decrease in the fall (Springer, 1960; Musick and Colvocoresses, 1988). Juvenile sharks inhabit nursery areas until the age of six to seven years (Casey et al., 1985; Musick et al., 1993). Adult sandbar sharks maintain sexual segregation except during times of mating (Springer, 1960). Adult males often inhabit waters along the edge of the continental shelf out to depths of 250 meters while juvenile and females are generally found inshore.

Females move into estuarine areas to release pups. Pups and juveniles then occupy these areas of lower salinity until cooler temperatures force them to deeper and more southerly waters (Springer, 1960; Castro, 1993). Utilization of lower salinity areas

is presumably a method to reduce neonate predation by larger sharks and provide an area of high production for growth.

The sandbar shark is viviparous giving birth to well developed live young. In the NWA pups are approximately 47 cm fork length (FL) at birth (Springer, 1960; Castro, 1993; Sminkey and Musick, 1995; Cortés, 2000), and litter sizes average nine pups per litter (Springer, 1960; Clark and von Schmidt, 1965; Sminkey and Musick, 1996; Cortés, 2000). Due to the advanced development of the pups, a long gestation period of approximately nine to 12 months is required (Springer, 1960; Clark and von Schmidt, 1965; Lawler, 1976). Maturity in both males and females is reached between 15 and 16 years of age at a length of approximately 135 cm pre-caudal length (PCL) (Springer, 1960; Casey et al., 1985; Sminkey and Musick, 1995).

#### *Age and Growth of Elasmobranchs*

Elasmobranchs lack calcified structures such as scales, otoliths, opercles, and other hard parts traditionally used for ageing teleosts (Cailliet and Goldman, 2004; Goldman, 2005). Techniques for ageing elasmobranchs have been limited to the use of vertebral centra, spines, thorns, or neural arches. The present study focused on the use of vertebral centra for age determination of sandbar sharks. Although cartilaginous, calcium is deposited within the vertebral centra as the animal grows. Workers have correlated bands of heavy mineralization to periods of reduced growth rates within the vertebral centra and have utilized these banding patterns as indicators of annual growth periods (Ishiyama, 1951; Holden and Vince, 1973; Stevens, 1975; Ferreira and Vooren, 1991; Clement, 1992; Officer et al., 1997). Causes of reduced growth can be attributed to a

suite of environmental factors such as seasonality, migration, reduced prey abundance, mating, behavior, or cooler temperatures. Natanson and Cailliet (1990) proposed ring formation was more closely related to somatic growth than annual periodicity in the pacific angel shark, *Squatina californica*.

Resorption of tissue in teleosts has presented a problem in ageing long-lived bony fishes. This is not the case in elasmobranchs. Clement (1992) discounted the possibility of resorption of mineralized tissue in chondrichthyans due to the apparent absence of osteoclasts and proposed growth can occur without resorption of previously mineralized tissue, thus layers within the vertebral centra and other mineralized structures remain unaltered throughout the life of the organism. The elegant growth system of chondrichthyans does not rely on resorption of tissue for growth and thus the use of vertebral centra as a means for ageing sandbar sharks appears appropriate.

Various researchers have validated the annual periodicity of band pairs. Holden and Vince (1973) validated the yearly periodicity of one opaque and one translucent band within the vertebral centra of the thornback skate, *Raja clavata*, using tetracycline injections. Casey et al. (1985) validated the annual periodicity of growth bands in the sandbar shark, *Carcharhinus plumbeus*, via a comparison between vertebrae obtained from sharks held in aquaria for several years to at liberty specimens. McAuley et al. (2006) validated annual periodicity of growth bands for the sandbar shark in Australian waters. Other researchers have validated annual periodicity of rings via oxytetracycline staining in sharpnose sharks, *Rhizoprionodon terranova*, and dusky sharks, *Carcharhinus obscurus* (Branstetter, 1987; Simpfendorfer et al., 2002).

### *Objectives*

The objectives of this work are to provide updated growth parameters for the sandbar shark in the NWA, estimate growth parameters for the sandbar shark in Hawaii through tag recapture methods, estimate growth parameters of the sandbar shark in Hawaii, provide demographic analyses of the sandbar shark in Hawaii, and conduct a comparative examination of the age and growth of the sandbar shark across temporal and spatial scales.

The objectives of chapter two are to estimate growth parameters of the sandbar shark in the Northwestern Atlantic through analyses of vertebral samples obtained from 2000-2004 and compare these estimates to previous estimates of growth parameters estimated from samples obtained from 1980-1981 and 1990-1992 in the Northwest Atlantic as well as other populations worldwide. Comparisons will also be made between age based ogives constructed from all time periods.

The objectives of chapter three are to estimate growth parameters through tag-recapture data for the sandbar shark in the NWA using a reparameterized form of the von Bertalanffy growth model developed by Francis(1988). Previous tag recapture models for this species in the Northwest Atlantic have underestimated growth rates and overestimated age at maturity.

The objectives of chapter four are to estimate growth parameters for the sandbar shark in Oahu, Hawaii through analyses of vertebral centra. A previous study estimated growth parameters for the sandbar shark in Hawaii from captive animals. Two methods

were used to estimate the growth parameters for the sandbar shark in this study, tooth replacement rate and observations of change in length over time of captive reared animals. The two methods disagreed greatly. The tooth replacement method estimated maturity to be reached at 13 years and the captive observation study estimated maturity to be attained at three years of age.

The objective of chapter five are to conduct demographic analyses on the sandbar shark in Hawaii using life tables and Leslie matrices. The population is assumed to experience limited fishing mortality due to longline regulations as well as cultural aspects, thus the population should be near equilibrium levels.

## References

- Bigelow, H.B. & W.C. Schroeder 1948 Sharks In: C.M.B. J. Tee-Van, S.F. Hildebrand, A.E. Parr, & W.C. Schroeder (ed.) Fishes of the Western North Atlantic. Part 1. Vol. 1., Mem. Sears Foundation for Marine Research, Yale Univ. New Haven CT.
- Branstetter, S. 1987. Age and growth validation of newborn sharks held in laboratory aquaria, with comments on the life history of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Copeia: 291-300.
- Cailliet, G.M. & K.J. Goldman 2004 Age determination and validation in chondrichthyan fishes. In: J. Carrier, J.A. Musick & M. Heithaus (ed.) The biology of sharks and their relatives, CRC Press, Boca Raton, FL pp. 399-447
- Casey, J.G., H.L. Pratt, Jr. & C.E. Stillwell 1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. Can. J. Fish. Aquat. Sci. 42: 963-975.
- Castro, J.I. 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38: 37-48.
- Clark, E. & K. von Schmidt 1965. Sharks of the Central Gulf coast of Florida. Bull Mar Sci 15: 13-83.
- Clement, J.G. 1992. Re-examination of the fine structure of endoskeletal mineralization in chondrichthyans: Implications for growth, ageing and calcium homeostasis. Sharks: Biology and fisheries. AUST. J. MAR. FRESHWAT. RES. 43: 157-181.
- Compagno, L.J.V. 1984. FAO species catalogues, vol 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis No. 125.
- Cortés, E. 2000. Life history patterns and correlations in sharks. Reviews in Fisheries Science 8: 299-344.
- Ferreira, B.P. & C.M. Vooren 1991. Age, growth, and structure of vertebra in the school shark *Galeorhinus galeus* (Linnaeus, 1758) from southern Brazil. Fish. Bull. 89: 19-31.

- Francis, R.I.C.C. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. *N. Z. J of Mar Freshw Res* 22: 42-51.
- Garrick, J.A.F. 1982. Sharks of the genus *cacharhinus*, U.S. Dept. Commer., NOAA Tech. Rep. NMFS 445.
- Goldman, K.J. 2005 Age and Growth of Elasmobranch Fishes In: e. J.A. Musick and R. Bonfil (ed.) *In: Management Techniques for Elasmobranch Fisheries.*, FAO Fisheries Technical Paper, Rome pp. 251
- Heist, E.J., J.E. Graves & J.A. Musick 1995. Population genetics of the sandbar shark (*Carcharhinus plumbeus*) in the Gulf of Mexico and Mid-Atlantic Bight. *Source Copeia*, no 3: 555-562.
- Holden, M.J. & M.R. Vince 1973. Age validation studies on the centra of *Raja clavata* using tetracycline. *J. Cons. Cons. Int. Explor. Mer* 35: 13-17.
- Ishiyama, R. 1951. Studies of the rays and and skates belonging to the family Rajidae found in Japan and adjacent regions. 2. On the age-determination of japanes black-skate *Raja fusca garman* (Preliminary Report). *Bull. Japan. Soc. Sci. Fish.* 16: 112-118.
- Kohler, N.E., J.G. Casey & P.A. Turner 1998. NMFS Cooperative Shark Tagging Program, 1962-93: An atlas of shark tag and recapture data. *Mar Fish Rev* 60: 1-87.
- Lawler, E.F. 1976. The biology of the sandbar shark, *Carcharhinus plumbeus*, (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. Virginia Institute of Marine Science Virginia Institute of Marine Science. 1976: 49.
- McAuley, R.B., C.A. Simpfendorfer, G.A. Hyndes, R.R. Allison, J.A. Chidlow, S.J. Newman & R.C.J. Lenanton 2006. Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia *Env. Bio. of Fish.* 77: 385-400.
- Musick, J.A., S. Branstetter & J.A. Colvocoresses 1993 Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast NOAA Tech. Rep. NMFS 115:1-18 pp. 115

- Musick, J.A. & J.A. Colvocoresses (ed.). 1988 Seasonal recruitment of subtropical sharks in the Chesapeake Bight, USA.
- Natanson, L.J. & G.M. Cailliet 1990. Vertebral growth zone deposition in Pacific angel sharks. *Copeia* 4: 1133-1145.
- Officer, R.A., R.W. Day, J.G. Clement & L.P. Brown 1997. Captive gummy sharks, *Mustelus antarcticus*, form hypermineralized bands in their vertebrae during winter. *Can. J. Fish. Aquat. Sci.* 54: 2677-2683.
- Simpfendorfer, C.A., R.B. McAuley, J. Chidlow & P. Unsworth 2002. Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. *Mar Freshw Res* 53: 567-573.
- Sminkey, T.R. & J.A. Musick 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* 4: 871-883.
- Sminkey, T.R. & J.A. Musick 1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.* 94: 341-347.
- Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. U. S. Fish. Wildl. Fish. Bull. 61: 38 pages.
- Stevens, J.D. 1975. Vertebral rings as a means of age determination in the blue shark (*Prionace glauca* L.). *J.Mar.Biol.Assoc.Uk* 55: 657-665.

## **CHAPTER 2**

### **Compensatory growth of the sandbar shark, *Carcharhinus plumbeus*, in the Northwest Atlantic**

**Abstract**

Numbers of sandbar sharks, *Carcharhinus plumbeus*, in the Northwest Atlantic have experienced drastic declines since the early 1980's reaching their minima during the early 1990's. Catch rates in the early 1990's were a mere 25% of those during the 1980's. Such drastic reductions in other fish stocks have often caused compensatory responses, most notably the cod stocks in the Northwest Atlantic. Compensatory responses in depressed populations may include decreased natural mortality, increased fecundity, or increased growth rates. Compensation for population fluctuations below carrying capacities have been recognized for many terrestrial and oceanic r-selected organisms, but few instances have been noted for K-selected species. Due to slow-growth and late maturity, compensatory responses in K-selected species such as the sandbar shark probably require generation-scale time periods to become evident. A previous age and growth study discovered slight increases in juvenile sandbar shark growth rates when vertebral centra samples obtained in 1980-81 and 1990-1992 were compared. The Virginia Institute of Marine Science shark long-line survey reported the lowest abundance of sandbar sharks in 1992. Animals pupped during this time may display greater differences in growth rates due to drastically reduced population size. Samples obtained over the 2001-2004 time period were compared to the aforementioned time periods to investigate potential compensatory responses in the sandbar shark population in the Northwest Atlantic.

## Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a common large coastal shark that inhabits temperate and subtropical waters world wide and attains lengths greater than 2 meters (Compagno, 1984). In the Northwest Atlantic (NWA) this species inhabits near-shore waters out to the edge of the continental shelf from Cape Cod to Brazil (Bigelow and Schroeder, 1948; Springer, 1960; Garrick, 1982). Tagging studies suggest that this region is composed of two unit stocks. One stock is found from Cape Cod south to the Northern Yucatan peninsula and another from Trinidad to Brazil (Springer, 1960; Kohler et al., 1998). Genetic studies conducted on specimens from Virginia waters and the Gulf of Mexico further support the existence of a single stock that utilizes the area of Cape Cod to the Northern Yucatan Peninsula (Heist et al., 1995).

The sandbar shark in the NWA undergoes seasonal migrations from the Gulf of Mexico and Florida to as far north as Cape Cod as water temperatures rise in the spring and return south as water temperatures decrease in the fall (Springer, 1960; Musick and Colvocoresses, 1988). Juvenile sharks inhabit nursery areas until the age of 6-7 years (Casey et al., 1985; Musick et al., 1993). Adult sandbar sharks maintain sexual segregation except during times of mating (Springer, 1960). Adult males often inhabit waters along the edge of the continental shelf out to depths of 250 meters while juvenile and females are generally found inshore.

Females move into estuarine areas to release pups. Pups and juveniles then occupy these areas of lower salinity until cooler temperatures force them to deeper and more southerly waters (Springer, 1960; Castro, 1993b). Utilization of lower salinity

areas is presumably a method to reduce neonate predation by larger sharks and provide an area of high production for growth.

The sandbar shark is viviparous giving birth to well developed live young. In the NWA pups are approximately 47 cm fork length (FL) at birth (Springer, 1960; Castro, 1993b; Sminkey and Musick, 1995; Cortés, 2000), and litter sizes average nine pups per litter (Springer, 1960; Clark and von Schmidt, 1965; Sminkey and Musick, 1996; Cortés, 2000). Due to the advanced development of the pups, a long gestation period of approximately 9-12 months is required (Springer, 1960; Clark and von Schmidt, 1965; Lawler, 1976). Maturity in both males and females is reached between 15 and 16 years of age at a length of approximately 135 cm pre-caudal length (PCL) (Springer, 1960; Casey et al., 1985; Sminkey and Musick, 1995).

#### *Previous work on Age and Growth of the sandbar shark*

Previous studies of the age and growth of the sandbar shark from the NWA have yielded mixed results. Lawler (1976) produced unrealistic values for maximum length (267 cm TL) and only produced von Bertalanffy growth parameters for female sandbar sharks due to a limited sample size of males. Casey et al. (1985) provided a more comprehensive study of the age and growth of the sandbar shark that consisted of a large sample size and included age validation studies, but also produced unrealistic maximum length estimates (303 cm Fork Length). Empirical maximum reported lengths are 234 cm TL and 226 cm TL for females and males respectively (Cortés, 2000). This study (Casey et al., 1985) lacked a representative sample from larger size classes, which is an inherent problem in conducting an age and growth study on long-lived species. The oldest male to

be aged was 15 years old and the oldest female to be aged was 21 years old. Casey and Natanson (1992) provided new growth parameters based on tagging experiments and proposed age at maturity to be to 30 years and maximum size to be 186 cm FL. Sminkey and Musick (1995) reexamined age and growth of the sandbar shark from samples obtained a decade apart, 1980-1981 and 1991-1992. The sample set from 1991-1992 was the most robust sample size and had the greatest size range of any study conducted on sandbar shark to date.

Age and growth studies on sandbar sharks have been carried out in other regions as well. Joung et al. (2004) examined the age and growth of the sandbar shark from Taiwanese waters using vertebral centra from the caudal peduncle. Calculations from this study produced maximum lengths of 216.3 cm TL and 201.6 cm TL for females and males respectively. Estimated age at maturity was 9 yrs for females and 10.5 years for males at lengths of 170-175 cm TL for both sexes. This contradicts general trends in elasmobranch life history, males typically attain maturity at smaller sizes and younger ages (Cortés, 2000). Annual formation of growth bands has not been validated for vertebral centra removed from the caudal peduncle and may be the cause for these discrepancies. Joung and Chen (1995) reported litter sizes ranging from 4-12 and a mean of 7.54. Size at birth was estimated as 60-65 cm TL following a 10-12 month gestation period. McAuley et al. (2006) examined the sandbar shark in Northwest Australian waters and reported von Bertalanffy growth parameters for females to be  $K=0.039 \text{ year}^{-1}$  and  $L_{\infty}=245.8$ . Male growth parameters were reported as  $K=0.044 \text{ year}^{-1}$  and  $L_{\infty}=226.3$  cm fork length. This study also reported size at birth of 42.5 cm FL. Age

at which 50% of the population was mature was estimated as 16.2 years for females and 13.8 years for males.

Protective nets off the west coast of South Africa provided the opportunity to conduct age and growth studies on the sandbar shark in the south western Indian Ocean. Cliff et al. (1988) reported size at maturity as 129 cm PCL and 130 cm PCL for male and females respectively. Litter sizes averaged 7.2 pups and pups were 40-50cm PCL. The smallest free-swimming specimen from this area was 48 cm PCL reported by Bass et al. (1973).

Romine et al. (2006) provided estimates of growth for the sandbar shark in the Hawaiian Islands. Growth parameters estimated for the von Bertalanffy growth function were:  $K=0.12 \text{ year}^{-1}$  and  $L_{\infty}=152.8 \text{ cm PCL}$  for females and  $K=0.10 \text{ year}^{-1}$  and  $L_{\infty}=138.5 \text{ cm PCL}$  for males.

### *Compensation*

The sandbar shark, *Carcharhinus plumbeus*, in the NWA has experienced drastic reductions in numbers due to over-fishing in the absence of a Fishery Management Plan (FMP). The Virginia Institute of Marine Science long-line survey has shown a steady reduction in numbers from the late 1970's to the lowest abundance in the early 1990's. A FMP for large coastal sharks was enacted in 1993 (NMFS, 1993), and numbers of sandbar sharks in the Virginia bight area have increased slightly. However, the current abundance estimates remain well below those of the early 1980's. Such drastic reductions in other fish stocks have often caused compensatory responses, most notable being cod stocks in the NWA (Trippel, 1995). Compensation for population fluctuations

below carrying capacities have been recognized for many terrestrial and oceanic r-selected organisms. These organisms demonstrate high fecundity, rapid growth and maturity at a young age. Deviations below the carrying capacity for these species often result in changes in growth parameters due to a suite of circumstances (Rose et al., 2001). Often a decrease in population density results in decreased intra-specific competition and in turn greater availability of food sources. As a result mortality rates may change or reproductive success may change. The increased availability of food sources may result in faster growth, earlier maturity, or higher fecundity. Increase in fecundity may occur via larger offspring or more offspring.

Few studies have documented changes in life history parameters for elasmobranchs before and after exploitation. Carlson and Baremore (2002) found significant increases in juvenile growth and earlier maturity in the sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico after heavy exploitation. Recently Cassoff et al. (2007) reported changes in life history parameters of the porbeagle, *Lamna nasus*, in the NWA following exploitation. Sminkey and Musick (1995) discovered slight differences between size at age in juvenile sandbar sharks when samples obtained in 1980-81 and 1990-1992 were compared. However older sharks in their 1990-1992 sample had undergone their fastest growth in the the late 1970's and early 1980's before population decline. Greater differences in growth rates may be discovered upon examination of sharks pupped during the time of lowest abundance. The VIMS long-line survey reported the lowest abundance of sandbar sharks in 1993, one year after Sminkey had conducted his research.

Natural mortality of young sandbar sharks may be decreased due to depressed numbers of large predator coastal sharks in the NWA. Catches of larger sharks such as bull (*Carcharhinus leucas*), sandtiger (*Carcharias Taurus*), lemon (*Negaprion brevirostris*), and dusky sharks (*Carcharhinus obscurus*) in Virginia waters have drastically declined since the early 1980's (Ha, 2006).

Compensation expressed as increased fecundity is unlikely due to the advanced nature and large size of sandbar shark offspring and space limitations within the uteri. Increased fecundity could only occur at the cost of reduced offspring size or drastically increased sizes of females.

A likely compensatory mechanism is an increase in growth rate due to lack of intra and inter-specific competition for food resources as a result of a depressed breeding populations of large coastal sharks in the NWA. Maturity may be reached at an earlier age as a consequence of a faster growth rate, or an increase in the rate of growth and in turn an increase in fecundity at the population level may occur.

The present study aims to continue the investigation of this phenomenon by comparing growth rates derived from vertebrae from 2000-2004 period to samples obtained in 1980-83.

## **Methods**

### *Data collection*

Vertebral centra were obtained from sandbar sharks landed by the VIMS long-line survey, Commercial Shark Fishery Observer Program (CSFOP), and NMFS long-line survey. The VIMS long-line survey operated in Chesapeake Bay, Virginia coastal waters

and North Carolina coastal waters. CSFOP and NMFS surveys operated from North Carolina south to Florida and into the Gulf of Mexico along Florida's western coast. Samples were collected during 1980-1983 and 2000-2004.

VIMS shark longline stations ranged in depth from five meters to 33 meters and were sampled once a month from May to October using longlines consisting of 100 10/0 J-hooks and 12/0 circle hooks on monofilament leader material. Hooks were baited with menhaden, *Brevoortia tyrannus*, and allowed to soak for 4 hours. Sharks landed by the VIMS longline survey were measured and euthanized. Pre-caudal length was the primary measurement used in this study and was defined as length from the tip of the snout to the deepest part of the pre-caudal notch. Once the shark was euthanized, vertebral centra were removed from directly below the first dorsal. Samples were labeled and placed in the vessel's freezer for return to the lab.

Samples were also obtained through from trawl, gillnet and recreational fishing gears within Chesapeake Bay during the 2000-2004 time period. Either the shark was sampled in the field using the aforementioned protocols or it was returned to the lab to be measured and sampled.

Samples obtained through CSFOP were removed from the anteriorad of the "log" or carcass. Removal of centra from below the first dorsal was not practical in this commercial setting because such action would reduce the value of the shark at market.

Upon return to the laboratory, samples were thawed and excess muscle tissue was removed from the sample. The sample was then placed in 75% ETOH until it could be sectioned. Vertebral centra were sectioned sagittally and longitudinally through the focus of the centrum using an isomet rotary diamond saw. These sections were then set to dry

for 24 hours. Once dry, the samples were mounted on a microscope slide via cover slip mounting medium. The samples were wet sanded using 300, 400 and 600 fine grit sandpaper progressively until light was readily transmitted through the sample and the annuli were distinguishable on a dissection microscope.

Male sharks were classified as mature if claspers were deemed fully calcified (i.e. hard) and could be rotated forward (Clark and von Schmidt, 1965; Driggers et al., 2004). Maturity status of females was determined by examination of oviducal gland size, uteri width and appearance (Castro, 1993a). Pregnant and postpartum females were classified as mature.

### ***Data analyses***

The rings or annuli counted for age estimates were defined as a band pair consisting of an opaque zone combined with a wider translucent zone in the intermedialia, which continued on to the corpus calcareum (Casey et al. 1985, Sminkey & Musick 1995). The birthmark was determined as the first band that intersected the inflection of the corpus calcareum. Mounted vertebral sections were examined for age using a dissecting microscope and an Optimas video imaging system. The principal author and another reader conducted multiple blind readings of all vertebrae. Once all vertebrae were read, Hoenig's (1995) and Evans and Hoenig's (1998) tests of symmetry were conducted to test the hypothesis that age estimates between readers did not differ significantly and were due to random error.

Age estimates for vertebrae that were not consistent between readers were reexamined by both readers until a consensus was reached. The consensus estimate was

used in the final analysis. If a consensus age estimate could not be reached the sample was removed from the study (Cailliet & Goldman 2004).

Following Carlson & Baremore (2005), we fitted five growth models to length-at-age data for male and female sharks. We fitted a modified version of the Gompertz model (Ricker, 1975):

$$L_t = L_0(e^{G(1-e^{-kt})}),$$

where  $G = \ln(L_\infty / L_0)$  (Bertalanffy, 1938). The second model that was fitted was a model proposed by Galluci and Quinn (1979):

$$L_t = \frac{\omega}{k}[1 - e^{-k(t-t_0)}],$$

where  $\omega = k * L_\infty$ . The third model fitted to the data was the logistic model (Ricker 1975) :

$$L_t = L_\infty / (1 + e^{-k(t-t_0)}).$$

Two forms of the von Bertalanffy growth model were also fitted to the data (von Bertalanffy 1938, Beverton & Holt 1957, Cailliet et al. 2006). The first form of the model (VB1) used the length-at-birth intercept rather than a theoretical age at zero length and is described as:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt},$$

where  $L_0$  = mean length-at-birth (45 cm PCL),  $L_t$  = length at time  $t$ ,  $L_\infty$  = theoretical asymptotic length, and  $k$  = coefficient of growth. Length-at-birth was estimated from observed at-term embryos and free-swimming young-of-the-year during this study. The second form, a three-parameter von Bertalanffy model (VB2) incorporating the theoretical age-at-zero ( $t_0$ ) term is described as:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where,  $t_0$  = age or time when length theoretically equals zero.

All model parameters were estimated using the Marquardt least-squares nonlinear (NLIN) procedure in SAS statistical software (SAS V.9, SAS Institute, Inc). The F-test statistic was used to determine which model provided a better description of the data. Temporal comparisons between models and model parameters were made using likelihood methods (Kimura, 1980; Haddon, 2001). Homogeneity of variance across time periods was tested using Bartlett's Test in R. Model error was assumed to be independent, normally distributed, and homoscedastic. A Shapiro-Wilks test for normality was used to test the assumption of normality.

Size and age-based maturity ogives were developed for male and female sharks from all time periods where data were available. Trippel and Harvey (1991) suggested the use of maximum likelihood or probit analysis to estimate age at which 50% (A50) of the population was mature in populations where there are successive increases in proportion of mature fish with increasing age. We used two methods to estimate A50. Logistic regression was used to fit to binomial maturity data (0=immature, 1=mature) in SAS using the GENMOD procedure and the logit link function. The error was assumed to be binomially distributed. Age at which probability of being mature was 50% was determined by dividing the estimated intercept and slope terms within the logistic function. 95% confidence intervals were also estimated.

We also used maximum likelihood (ML) methods to estimate A50. This method takes into account the sample size within each age class. The negative log-likelihood function that was minimized was:

$$-\ln(ML) = \sum_j [n_j * \ln(1 + e^{(-b*(j-A50))})^{-1}] + (N_j - n_j) * \ln(1 - (1 + e^{(-b*(j-A50))})^{-1})],$$

where  $n_j$  is the number of mature fish in age class  $j$ ,  $N_j$  is the total number of fish in age class  $j$ ,  $b$  is the instantaneous rate of fish maturation, and  $A_{50}$  is the age at which 50% of the population is mature.  $A_{50}$  and  $b$  were estimated by minimizing the negative log-likelihood using AD model builder. Bias-corrected 95% confidence intervals were constructed using bootstrap methods of estimation (Haddon, 2001). Confidence intervals were only estimated for the  $A_{50}$  value and the steepness parameter,  $b$ , was held to the value estimated from the initial fit of the model.

## ***Results***

During the period of 1980-1983, 183 sandbar sharks were sampled. 36 of which were males and 147 were females. The oldest estimated age for a female shark was 27 years at a length of 155 cm PCL. Lengths for females ranged from 52 to 164 cm PCL. Lengths for males ranged from 51 to 147 cm PCL (Figure 1). The oldest estimated age for a male sandbar shark was 20 years (147 cm PCL). Also during this time period 77 at term pups were measured from 15 litters. These sharks were included within the analysis to account for differences in gear selectivity between the two time periods. During the earlier time period circle hooks were not used to land sharks.

Over the time period of 2000-2004, 464 sandbar sharks were sampled, of these 250 were females which ranged in length from 38 cm to 167 cm PCL and 206 males that ranged from 40 cm to 162 cm PCL. The oldest estimated age for a female shark was 25 years at a length of 150 cm PCL and for males was 22 years at a length on 148 cm PCL.

Blind agreement between readers occurred for 64% of the samples. Reader estimates were within one year of each other for 95% of the samples and within two years for 98% of the samples. Estimation methods between readers were not significantly different ( $X^2=41.20$ ,  $df=33$ ,  $p=0.154$ ).

Based on MSE (Mean Square Error) the VB2 model provide the best fit for males and females for the 1980 data set (Table 1, Figures 2-5). The VB2 model provided the best fit for the 2000 female data as well. The logistic model provided the better fit for 2000 male data. The logistic model underestimated asymptotic length and returned a high growth coefficient value.

The VB1 model for the 1980 samples estimated  $L_\infty$  to be 166.9 for females and 150.3 for males. Growth coefficient estimates from the VB1 model were 0.09 for females and 0.11 for males. The VB2 model growth parameter estimates were  $L_\infty=170.7$  for females and 152.3 for males,  $K= 0.0827$  for females and 0.1044 for males, and  $t_0=-3.92$  for females and -3.48 for males. The VB1 model for the 2000 samples estimated  $L_\infty$  to be 160.7 for females and 155.8 for males. Growth coefficient estimates from the VB1 model were 0.1148 for females and 0.1236 for males. The VB2 model growth parameter estimates were  $L_\infty=163.6$  for females and 158.8 for males,  $K= 0.1055$  for females and 0.1124 for males, and  $t_0=-3.26$  for females and -3.16 for males. In all cases, except for the 1980 male data set, the VB2 model provided a better fit than the VB1 model based on an F-test at the 0.05 confidence level (Table 1).

The assumption of normally distributed error was not violated and skew and kurtosis were minimal for all model fits. Likelihood ratio tests revealed significant differences between the VB2 models for females across time periods ( $X^2=22.75$ ,  $df=3$ ,

$p < 0.005$ ). Differences in predicted length at age between time periods ranged from -3.4 to 4.78 cm (Figure 6). Comparison of the VB2 models for males revealed significant differences as well ( $X^2 = 23.07$ ,  $df = 3$ ,  $p < 0.005$ ). Likelihood ratio tests assume homogeneity of variances between data sets. A Bartlett's test was conducted to test this assumption. There was no significant difference in variances between time periods for females at the 0.05 level ( $X^2 = 2.6277$ ,  $df = 1$ ,  $p = 0.1050$ ). There was significant difference between variances for males between the two time periods at the 0.05 level but not at the 0.01 level ( $X^2 = 4.3115$ ,  $df = 1$ ,  $p = 0.03786$ ).

Ogives generated through SAS estimated age at which 50% of females to be mature was 14.9 years of age for the samples obtained in the 1980s and 11.51 years of age for the sample obtained in the 2000-2004 time period. Fitted age-based ogives for females were significantly different ( $F = 13.968$ ,  $df = 3, 42$ ,  $p < 0.0001$ ). Length at 50% maturity for females was 139 cm PCL and 132 cm PCL for 1980 and 2000 samples respectively and were found to be significantly different ( $F = 7.27$ ,  $df = 3, 157$ ,  $p = 0.0001$ ).

Maximum likelihood estimates were slightly higher for female A50 for both time periods. For samples obtained in the 1980s, A50 = 15.06 years of age and for the 2000-2004 time period A50 = 12.49 years of age (Figure 7).

## **Discussion**

We have shown a significant change in the growth parameters for the sandbar shark in the NWA between 1980-1983 and 2000-2004. Model parameters suggested a greater asymptotic length and lower  $k$  value for both male and female sharks from the earlier time period than the more recent time period. The VB2 model provided the best

logical fit for both sexes for both time periods. Age at 50% maturity (A50) was also significantly different. Difference in A50 between time periods for female sharks was approximately three years. Length at 50% maturity was also significantly different for females, but the lengths differed by a mere four centimeters, suggesting size or length required to pup may be the limiting constraint to compensatory responses at the population level for the sandbar shark.

Few studies have illustrated significant changes in growth of K selected species (Sminkey and Musick, 1995; Carlson and Baremore, 2002; Sosebee, 2005; Cassof et al., 2007). This study is the fourth study involving elasmobranchs to demonstrate changes in growth rates following exploitation. Critics of these studies abound, questioning methods and assumptions of statistical tests, and whether the results have true biological meaning that may impact management decisions. We have attempted to avoid violating any assumptions that may discount the viability of our findings, but given the long term nature of the study certain problems are inherent and unavoidable.

Most animals caught during both time periods were landed with identical gear within the same locales. Some sharks from the more recent time period were landed using smaller hooks (9/0 J vs 12/0 circle) with monofilament leaders on the same braided nylon mainline. Samples were also collected from gill-nets, recreational gear, and trawl nets. The selectivity of the larger hooks is obviously low for neonates and small juvenile sharks. This was evident for the sample set for the earlier time period. At term pups were included within the earlier time set to account for a lack of neonates within that sample set. The models which incorporated empirical length at birth were not used

because they did not describe maximum length as well, nor did they provide a better statistical fit than the more complex models that employed theoretical size at birth.

Some mature animals in the earlier data set were collected from port sampling and research cruises, whereas the more recent samples from mature animals were collected by observers in the commercial shark longline fishery observers and from research cruises. Although different gear configurations were used to land sharks, the variances in these data were not significantly different.

Cassof et al. (2007) explored the possibility of temperature playing a role in the differing growth rates of *Lamna nasus*, porbeagle shark, in the NWA, but found comparable temperature across both time periods in the study. Examination of temperature data from VIMS standard longline stations between 1980-1981 and 2000-2002 did not show differences in temperature across the time periods.

Our growth estimates are generally similar to those reported by Sminkey and Musick (1994) and McCauley et al. (2006). Parameters reported by Joung et al. (2004) depict much faster growth than what we have found for sandbar sharks in the NWA over both time periods, as well as for sandbar sharks in the Hawaiian Islands (Romine et al. 2006). Given the number of studies conducted on sandbar sharks and the general similarity among reported values except for the Taiwan study suggest the latter may be in error given the unvalidated nature of the small vertebrae from the caudal peduncle and limited length range used.

Researchers have shown that multi-stage growth models may provide a more accurate description of growth of fishes (Porch et al., 2002; Hearn and Polachek, 2003). Various factors such as onset of maturity, long migrations to and from pupping and

mating areas, and food resources invariably impact growth. A twelve month gestation period coupled with a one year resting period in sandbar sharks further complicates their growth pattern. The effect of migration or lack thereof on an annual basis was not examined in modeling the growth of the sandbar shark in the present study. Once mature, females remain in southern waters during their resting year and only migrate north in to pupping areas such as Chesapeake and Delaware Bays in alternate years when pregnant. Thus more energy may be put into growth during their resting year. Determining the existence and the magnitude of oscillatory growth patterns should be the next step in providing the best possible description of sandbar shark growth.

We have demonstrated compensation in the form of slightly faster growth for sandbar sharks in the NWA. As a result earlier age at maturity appears to be occurring. These revised estimates still depict a fish that is slow growing and easily susceptible to overfishing. Age at length studies should be continued to monitor the status of this population and to provide managers with updated and accurate life history parameters for use in future stock assessments.

## References

- Bass, A.J., J.D. D'Aubrey & N. Kistnasamy 1973. Sharks of the east coast of southern Africa. 1. The genus *Carcharhinus* (Carcharhinidae). South African Association for Marine Biological Research Investigational Report 33: 168.
- Bertalanffy, L.v. 1938. A quantitative theory of organic growth(inquiries on growth laws. II). Hum. Biol. 10: 181-213.
- Bigelow, H.B. & W.C. Schroeder 1948 Sharks In: C.M.B. J. Tee-Van, S.F. Hildebrand, A.E. Parr, & W.C. Schroeder (ed.) Fishes of the Western North Atlantic. Part 1. Vol. 1., Mem. Sears Foundation for Marine Research, Yale Univ. New Haven CT.
- Carlson, J.K. & I.E. Baremore 2002. Changes in biological parameters of Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, in the Gulf of Mexico: evidence for density-dependent regulation? Sci Coun Res Doc NAFO 2: 8.
- Casey, J.G., H.L. Pratt, Jr. & C.E. Stillwell 1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. Can. J. Fish. Aquat. Sci. 42: 963-975.
- Cassof, R.M., S.E. Campana & S. Myklevoll 2007. Changes in the baseline growth and maturation parameters of the Northwest Atlantic porbeagle, *Lamna nasus*, following heavy exploitation. Can J Fish Aquat Sci 64.
- Castro, J.I. 1993a. The biology of the finetooth shark, *Carcharhinus isodon*. Environmental Biology of Fishes 36: 219-232.
- Castro, J.I. 1993b. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38: 37-48.
- Clark, E. & K. von Schmidt 1965. Sharks of the Central Gulf coast of Florida. Bull Mar Sci 15: 13-83.
- Cliff, G., S.F.J. Dudley & B. Davis 1988. Sharks caught in the protective gill nets off Natal, South Africa. 1. The sandbar shark *Carcharhinus plumbeus* (Nardo). S Afr J Mar Sci 7: 255-256.

- Compagno, L.J.V. 1984. FAO species catalogues, vol 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis No. 125.
- Cortés, E. 2000. Life history patterns and correlations in sharks. *Reviews in Fisheries Science* 8: 299-344.
- Driggers, W., J.K. Carlson, B. Cullum, J.M. Dean, D. Oakley & G. Ulrich 2004. Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. *Env. Bio. of Fish.* 71: 171-178.
- Gallucci, V.F. & T.J. Quinn II 1979. Reparameterizing, fitting, and testing a simple growth model. *Transactions of the American Fisheries Society* 108: 14-25.
- Garrick, J.A.F. 1982. Sharks of the genus *cacharhinus*, U.S. Dept. Commer., NOAA Tech. Rep. NMFS 445.
- Ha, D.S. 2006. Ecology and conservation of Virginia shark species: analysis of thirty years of Virginia long-line shark census data, 1974-2004. Dissertation, The College of William & Mary, School of Marine Science, Virginia Institute of Marine Science.
- Haddon, M. 2001. *Modelling and Quantitative Methods in Fisheries*. Chapman & Hall, CRC Press, Boca Raton, FL.
- Hearn, W.S. & T. Polachek 2003. Estimating long-term growth-rate changes of southern bluefin tuna (*Thunnus maccoyii*) from two periods of tag-return data. *Fishery Bulletin* 101: 58-74.
- Heist, E.J., J.E. Graves & J.A. Musick 1995. Population genetics of the sandbar shark (*Carcharhinus plumbeus*) in the Gulf of Mexico and Mid-Atlantic Bight. *Source Copeia*, no 3: 555-562.
- Joung, J.S. & C.T. Chen 1995. Reproduction in the sandbar shark, *Carcharhinus plumbeus*, in the waters off northeastern Taiwan. *Copeia* 3: 659-665.

- Joung, J.S., Y.Y. Liao & C.T. Chen 2004. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in northeastern Taiwan waters. *Fisheries Research* 70: 83-96.
- Kimura, D.K. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77: 765-776.
- Kohler, N.E., J.G. Casey & P.A. Turner 1998. NMFS Cooperative Shark Tagging Program, 1962-93: An atlas of shark tag and recapture data. *Mar Fish Rev* 60: 1-87.
- Lawler, E.F. 1976. The biology of the sandbar shark, *Carcharhinus plumbeus*, (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. Virginia Institute of Marine Science Virginia Institute of Marine Science. 1976: 49.
- McAuley, R.B., C.A. Simpfendorfer, G.A. Hyndes, R.R. Allison, J.A. Chidlow, S.J. Newman & R.C.J. Lenanton 2006. Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia. *Env. Bio. of Fish.* 77: 385-400.
- Musick, J.A., S. Branstetter & J.A. Colvocoresses 1993 Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast NOAA Tech. Rep. NMFS 115:1-18 pp. 115
- Musick, J.A. & J.A. Colvocoresses (ed.). 1988 Seasonal recruitment of subtropical sharks in the Chesapeake Bight, USA.
- NMFS 1993. Fishery management plan for sharks of the Atlantic Ocean. NOAA/NMFS, U.S. Department of Commerce Department of Commerce, Feb. 25, 1993.
- Porch, C.E., C.A. Wilson & D.L. Nieland 2002. A new growth model for red drum (*Sciaenops ocellatus*) that accomodates seasonal and ontogenic changes in growth rates. *Fish. Bull.* 100: 149-152.
- Ricker, W.E. 1975. Computation and Interpretation of Biological Statistics of fish Populations. *Bulletin of the Fisheries Research Board Canada* 191: 1-382.

- Romine, J.G., R.D. Grubbs & J.A. Musick 2006. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in Hawaiian waters through vertebral analysis. *Envir Bio Fish* 77: 229-239.
- Rose, K.A., J.H. Cowan, K.O. Winemiller, R.A. Myers & R. Hilborn 2001. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. *Fish and Fisheries* 2: 293-327.
- Sminkey, T.R. 1994. Age, Growth and Population Dynamics of the Sandbar Shark, *Carcharhinus Plumbeus*, At Different Population Levels. Ph.D. Dissertation, College of William and Mary. 116 pp.
- Sminkey, T.R. & J.A. Musick 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* 4: 871-883.
- Sminkey, T.R. & J.A. Musick 1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.* 94: 341-347.
- Sosebee, K. 2005. Are density-dependent effects on elasmobranch maturity possible? *J Northw Atl Fish Sci* 35: 115-124.
- Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. U. S. Fish. Wildl. Fish. Bull. 61: 38 pages.
- Trippel, E.A. 1995. Age at maturity as a stress indicator in fisheries. *BIOSCIENCE* 45: 759-771.
- Trippel, E.A. & H.H. Harvey 1991. Comparison of methods used to estimated age and length of fishes at sexual maturity using populations of white sucker (*Catostomous commersoni*). *Can. J. Fish. Aquat. Sci.* 48: 1446-1459.

Table 1. Model fits for 1980 (a) and 2000 (b) samples males and females. (MSE=Mean square error, RSS= residual sums of squares, NA=not applicable)

a.

<b>Year</b>		<b>MSE</b>					
<b>1980</b>	<b>Model</b>		<b>RSS</b>	<b>Linf</b>	<b>K</b>	<b>t0</b>	<b><math>\omega</math></b>
<b>Female</b>	Gompertz	56.9611	9968.19	155.577	0.16032	NA	NA
<b>Female</b>	GQ	45.2328	7870.50	NA	0.08395	-3.88145	14.4924
<b>Female</b>	Logisitc	57.0919	9933.99	154.500	0.19575	3.61136	NA
<b>Female</b>	VB1	47.7674	8359.30	168.329	0.09271	NA	NA
<b>Female</b>	VB2	45.2328	7870.50	172.634	0.08395	-3.88144	NA
<b>Male</b>	Gompertz	33.1950	2257.26	137.314	0.20001	NA	NA
<b>Male</b>	GQ	24.4702	1639.50	NA	0.10853	-3.44948	16.3214
<b>Male</b>	Logistic	35.9203	2406.66	134.848	0.26029	2.29618	NA
<b>Male</b>	VB1	26.4675	1799.79	147.192	0.11878	NA	NA
<b>Male</b>	VB2	24.4702	1639.50	150.385	0.10853	-3.44948	NA

b.

<b>Year</b>		<b>MSE</b>					
<b>2000</b>	<b>Model</b>		<b>RSS</b>	<b>Linf</b>	<b>K</b>	<b>t0</b>	<b><math>\omega</math></b>
<b>Female</b>	Gompertz	36.2491	8881.03	150.734	0.19619	NA	NA
<b>Female</b>	GQ	31.8758	7777.70	NA	0.10611	-3.23893	17.3238
<b>Female</b>	Logisitic	33.7897	8244.68	149.902	0.23594	2.75959	NA
<b>Female</b>	VB1	32.9359	8069.29	160.582	0.11500	NA	NA
<b>Female</b>	VB2	31.8758	7777.70	163.260	0.10611	-3.23893	NA
<b>Male</b>	Gompertz	35.5325	7106.50	146.428	0.21053	NA	NA
<b>Male</b>	GQ	34.4020	6845.99	NA	0.11239	-3.16713	17.8476
<b>Male</b>	Logistic	31.0317	6175.31	145.127	0.25915	2.46751	NA
<b>Male</b>	VB1	35.8962	7179.24	155.755	0.12355	NA	NA
<b>Male</b>	VB2	34.4020	6845.99	158.797	0.11239	-3.16713	NA

Figure 1. Number of sharks, male and females combined, sampled within five centimeter size classes for both time periods.

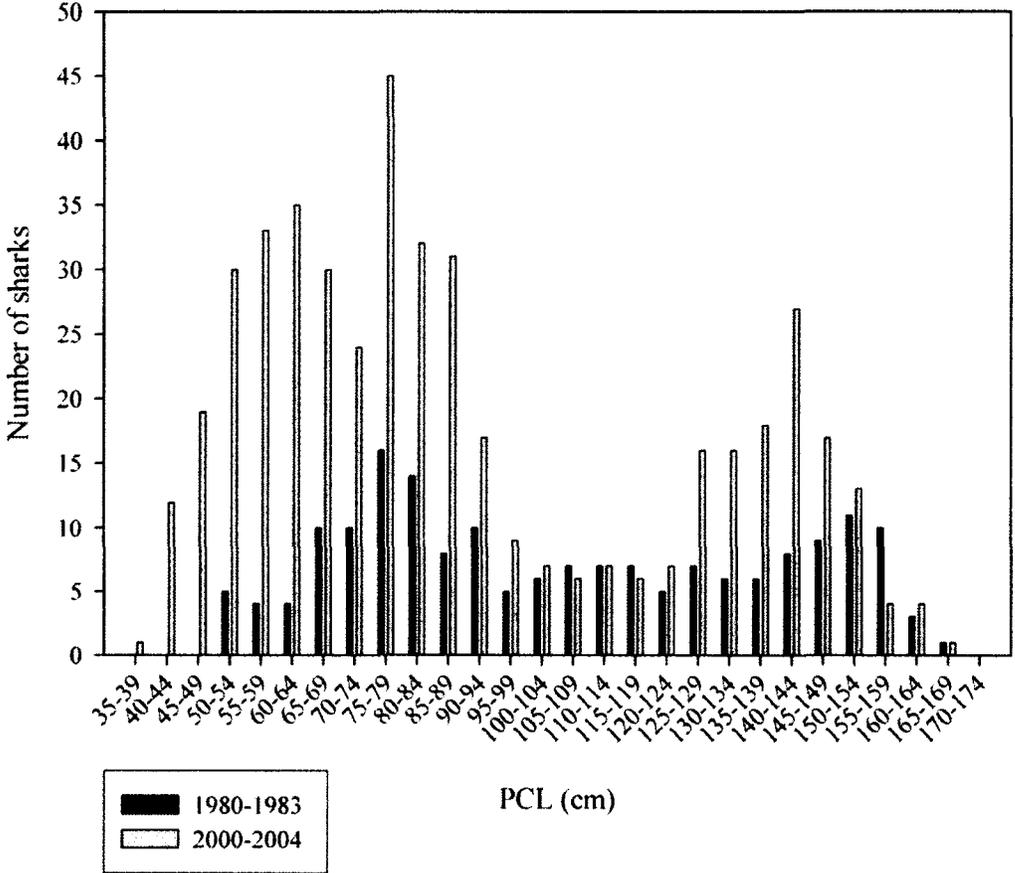


Figure 2. All model fits for females 1980 data.

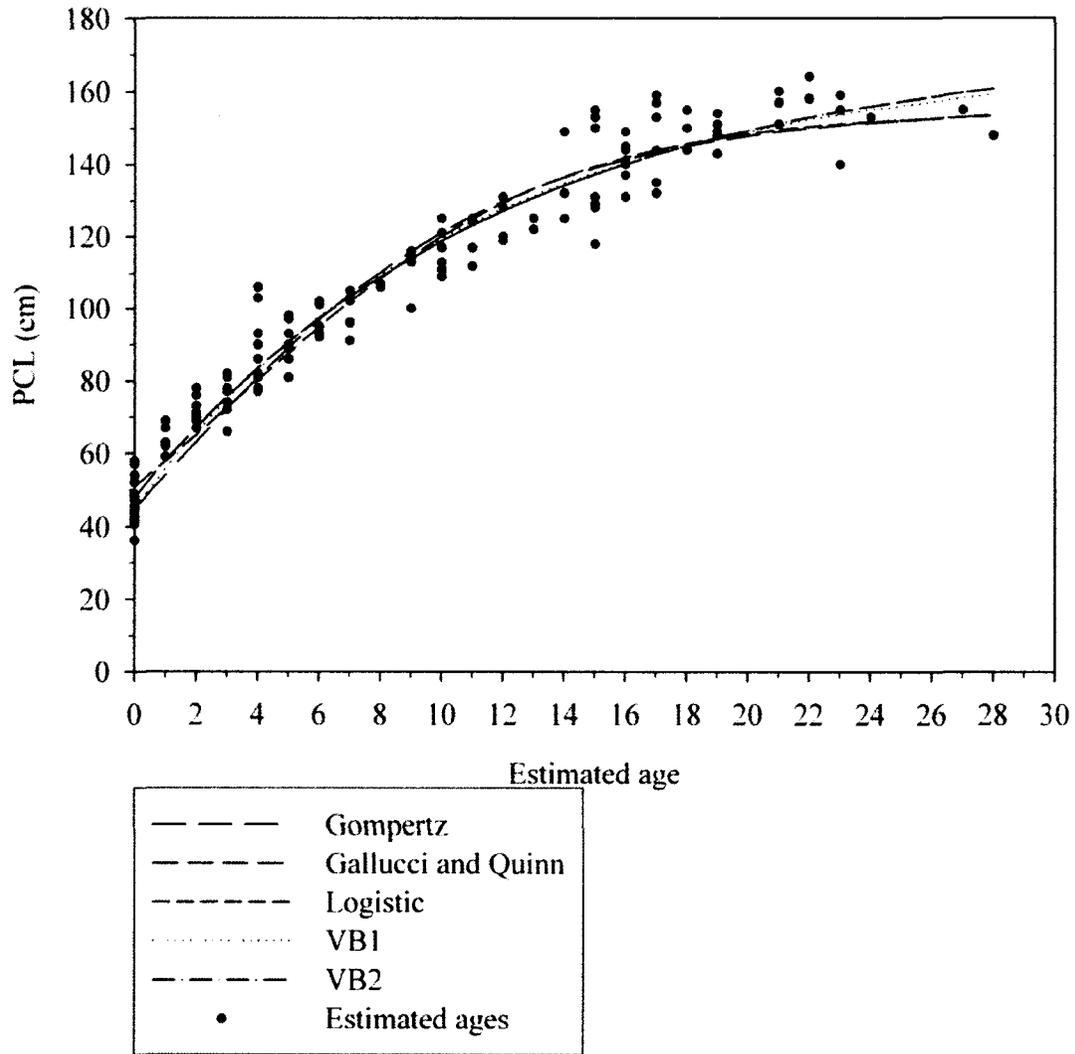


Figure 3. All model fits for females 2000 data.

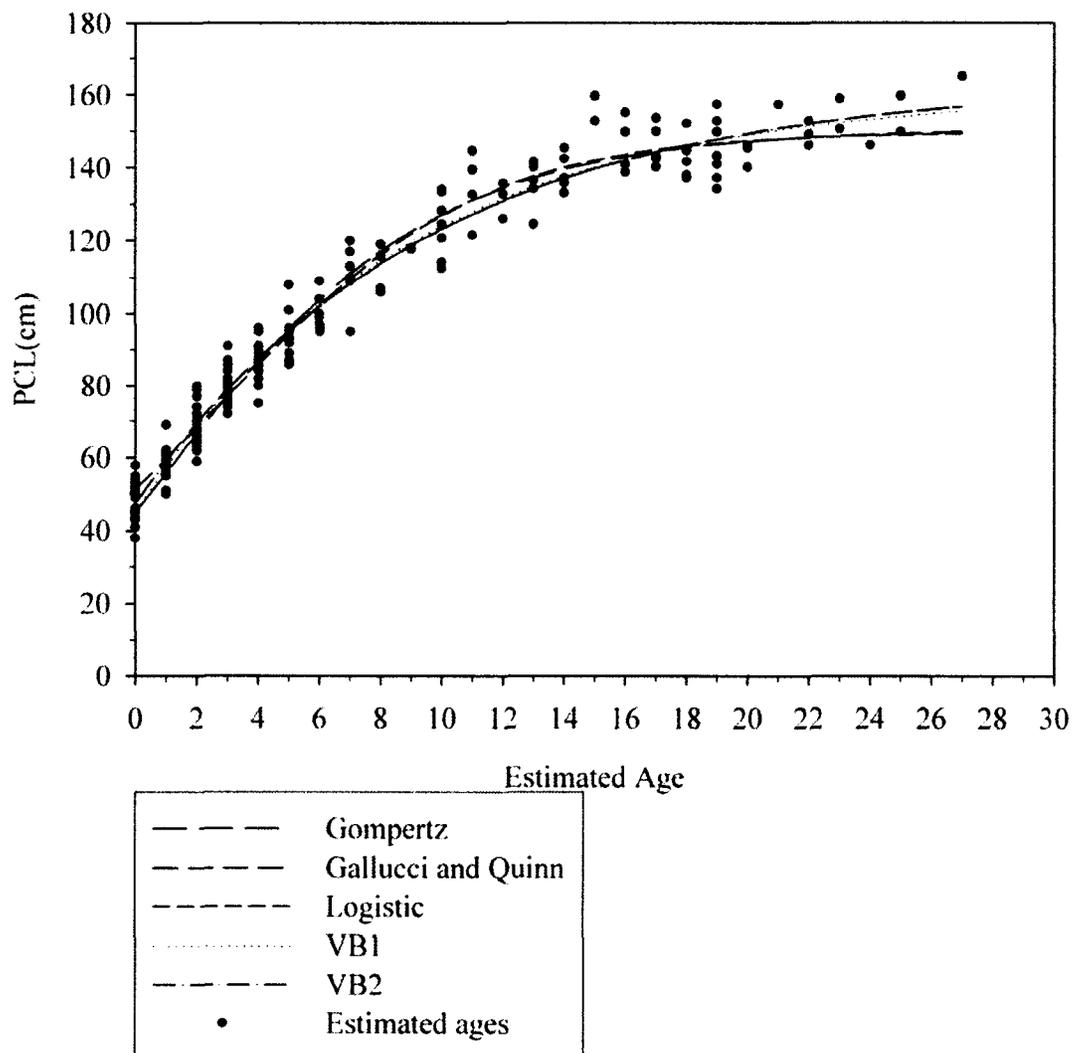


Figure 4. All model fits for males 1980 data.

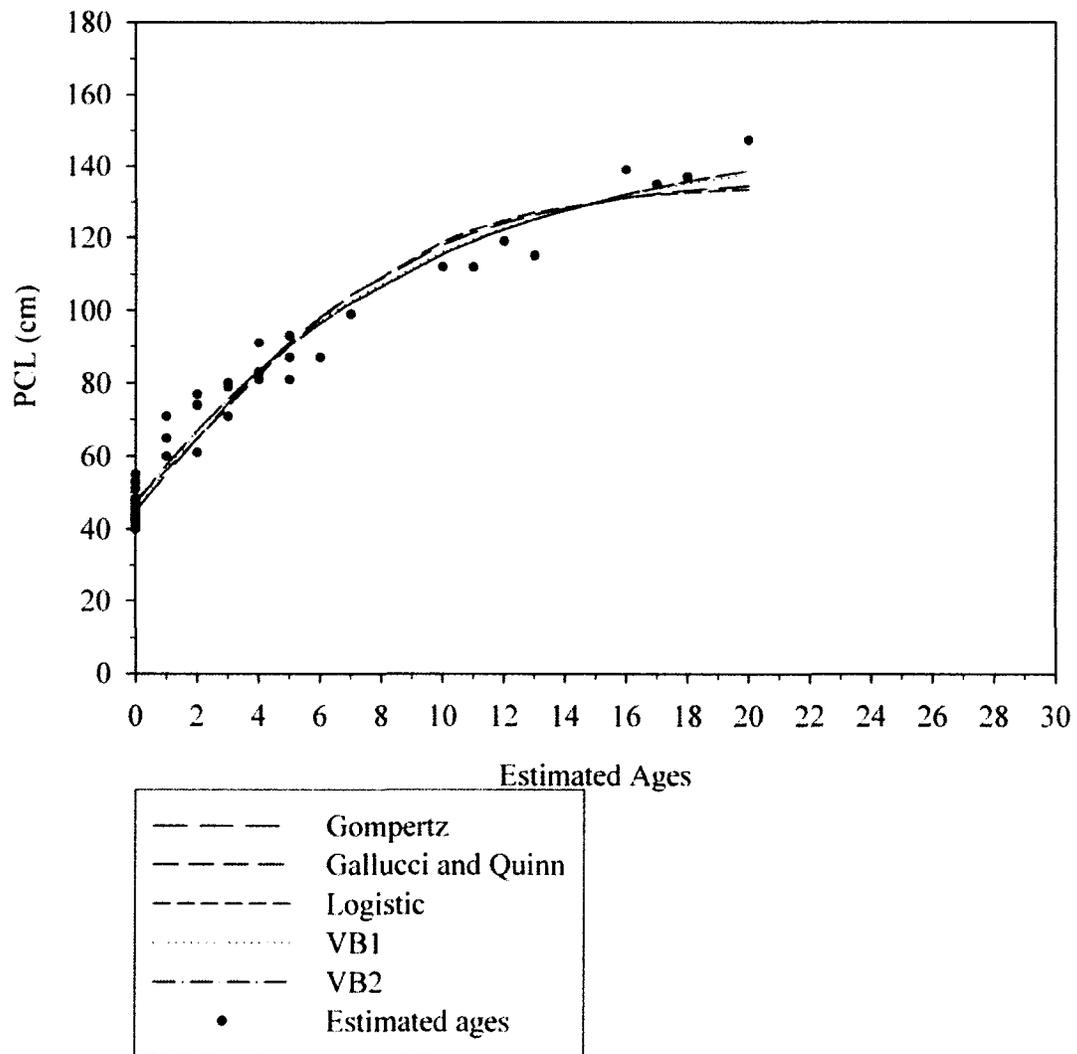


Figure 5. All model fits for females 1980 data.

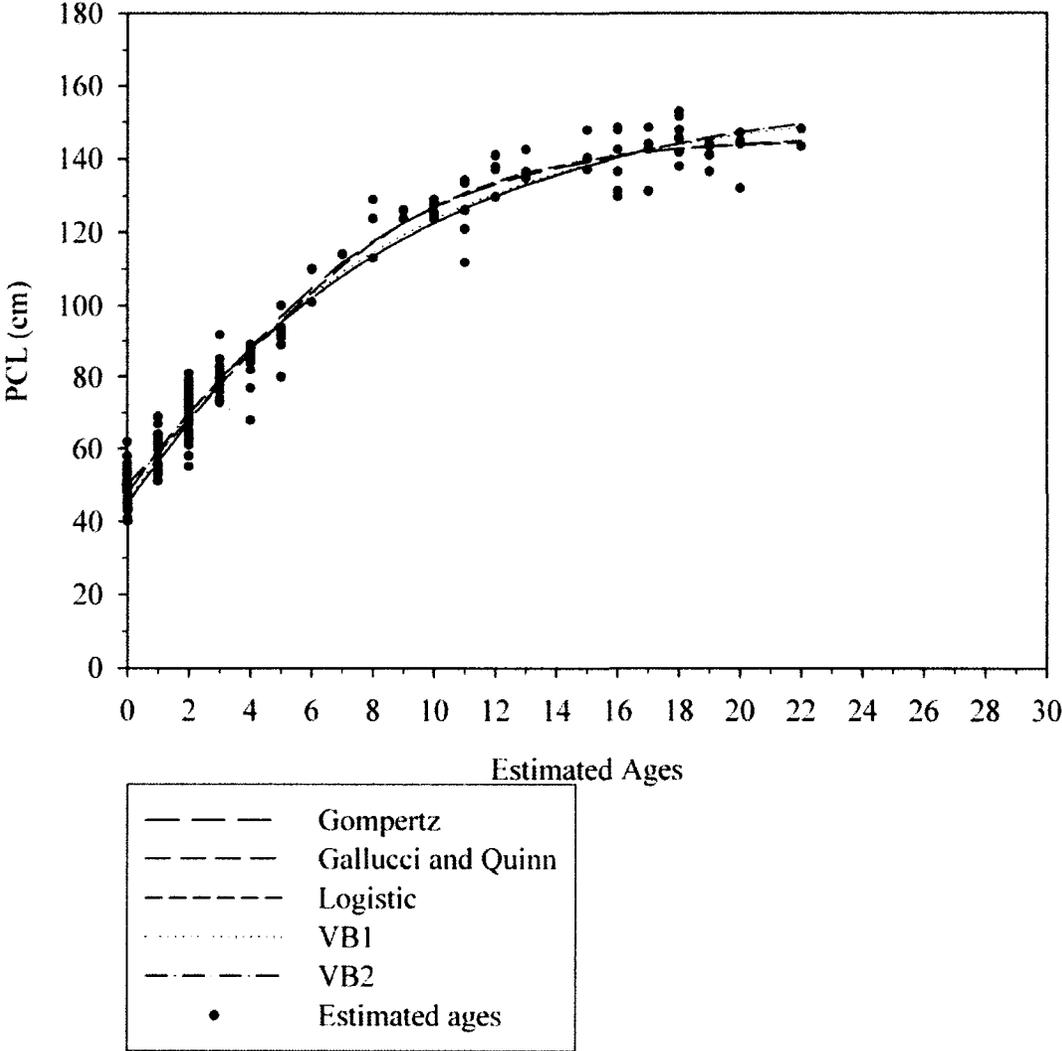


Figure 6. Differences in mean size at age in centimeters between time periods.

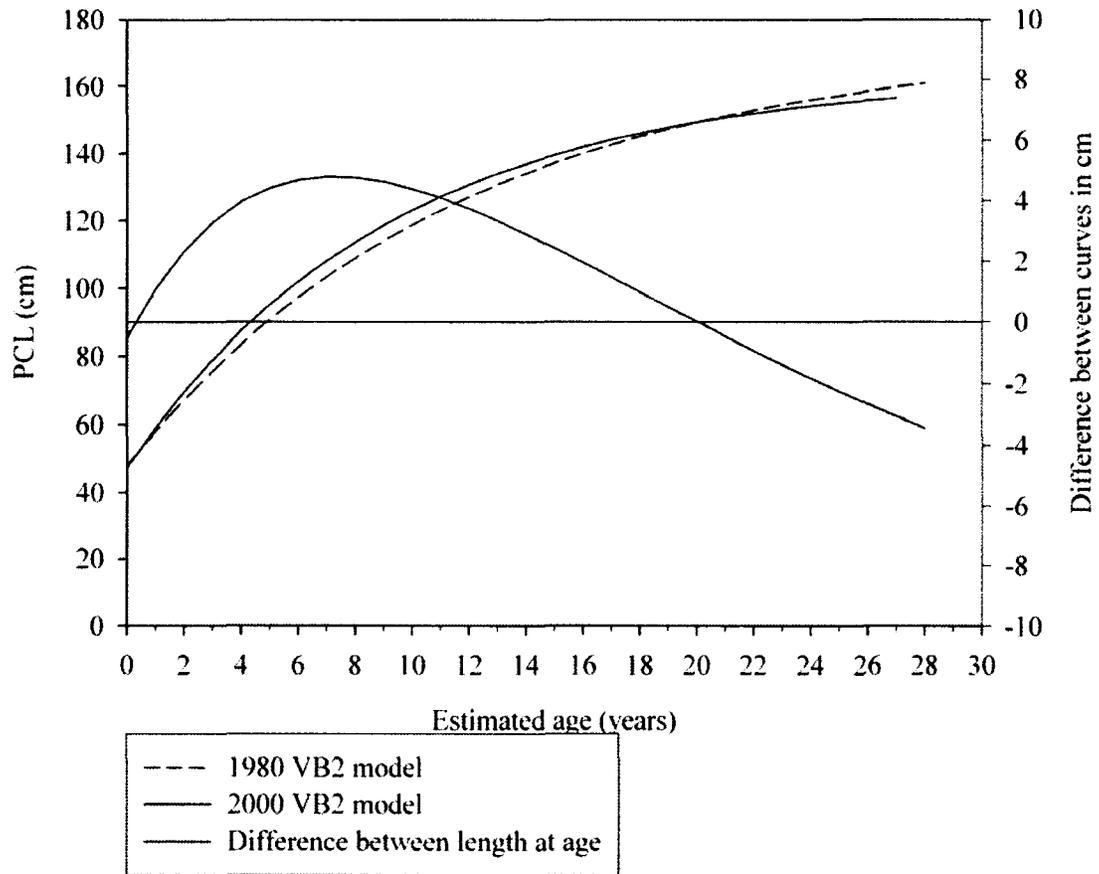
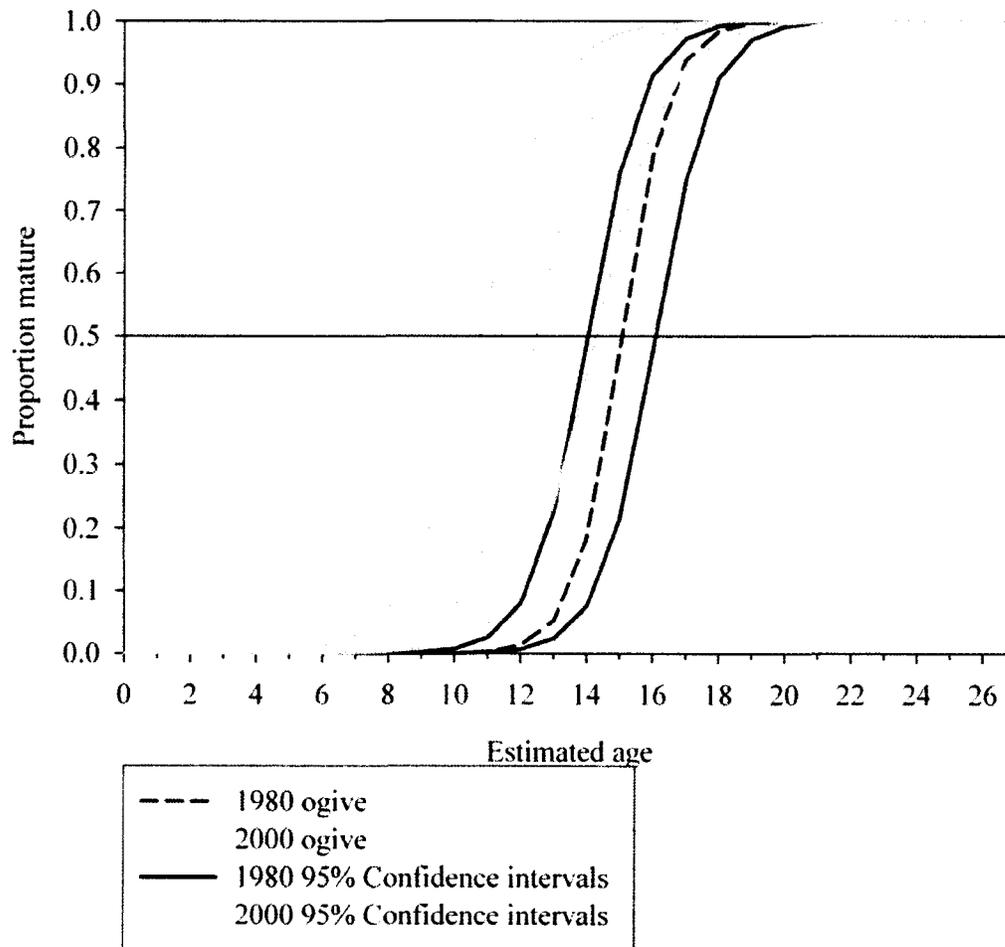


Figure 7. ML estimates and 95% confidence intervals for proportion females mature at age.



### **Chapter 3**

**Length based model for estimating growth of sandbar shark in the Northwest  
Atlantic through tag recapture methods**

## Abstract

Growth estimates for the sandbar shark, *Carcharhinus plumbeus*, in the Northwestern Atlantic were estimated using a reparameterized von Bertalanffy growth model. Sharks were tagged in Virginia waters with roto-tags and double return nylon dart tags from 1992 to 2006 by the shark longline survey of the Virginia Institute of Marine Science. Captured sharks were measured, tagged, and released by VIMS scientists. Dart tags were inserted at the base of the first dorsal fin on the left side of the animal. Over the time period, 37 recaptured sharks with reliable length at recapture information were reported. Time at liberty ranged from 26 to 3,561 days. Pre-caudal length at tagging ranged from 41 to 81 cm and pre-caudal length at recapture ranged from 43 to 147 cm. Growth increments ranged from 0.10 to 66 cm. The fitted model estimated growth rates of  $11 \text{ cm} \cdot \text{yr}^{-1}$  for 45 cm precaudal length sharks and  $7 \text{ cm} \cdot \text{yr}^{-1}$  for 75 cm pre-caudal length shark

## Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a large coastal shark inhabiting subtropical to temperate waters along the east coast of North America from the Gulf of Mexico north to Cape Cod (Compagno, 1984). The species undergoes seasonal northward migrations as water temperatures increase in the late spring and early summer then returns south as water temperatures cool in the late fall and winter months (Musick et al., 1993). The species attains maximum lengths of approximately 240 cm total length (TL) and attains maturity at approximately 140 cm TL.

Many methods for determining size-at-age of fishes have been utilized to describe growth of fishes. Fisheries scientists typically use hard parts of fishes to estimate ages of known length fishes and fit growth models to these data. The von Bertalanffy growth model is most frequently used to describe growth of fishes. This method often lacks validation for the species in question and may lead to spurious results if the entire growth range of the fish in question is not contained within the sample set (Knight, 1968). Thus tag recapture methods are important in that they may either support or reject growth estimates determined through hard part analyses.

Francis (1988) utilized a reparameterized form of the von Bertalanffy growth model for tag recapture data to include measurement error, individual growth variability, proportion of outliers, and seasonal variation. A maximum likelihood model that incorporated estimates of these and three models of variance structure were proposed (Francis, 1988). The use of likelihood methods allows simple and quick comparison between nested models of varying complexity. The reparameterized von Bertalanffy

growth model provides estimates of growth rate at size providing greater insight into the growth of the study specimen.

This method of analyzing tag-recapture data has been widely used in teleost fishes and elasmobranchs (Francis, 1988; Francis, 1997; Simpfendorfer, 2000; Welsford and Lyle, 2005). Casey and Natanson (1992) used Faben's growth model for tag-recapture data to describe the growth of the sandbar shark in the Northwest Atlantic and estimated  $L_{\infty}$  of 167 cm PCL and  $k=0.046 \text{ cm yr}^{-1}$ . Sminkey and Musick (1995) estimated  $k$  from vertebral analyses methods to be 0.057 and 0.089 derived from samples collected from 1980 to 1981 and 1991 to 1992 respectively. The discrepancies between the two methods may be due to the effect of the tag on the animal. Manire and Gruber (1991) found significant differences between annual growth rates between sharks tagged with M-dart tags and pit tagged animals.

The objectives of this paper are to estimate growth rates of the sandbar shark in the Northwest Atlantic (NWA) through length-based models using tag recapture data from the Virginia Institute of Marine Science Shark longline survey. Growth models will also be fit to previously published data for the sandbar shark in the NWA for comparative purposes.

## **Methods**

### *Data collection*

Sandbar sharks were caught on longlines within Chesapeake Bay, coastal lagoons of Virginia's eastern shore and coastal Virginia waters fished by the Virginia Institute of

Marine Science Shark longline survey. Longline sets consisted of 80-100 hooks covering approximately 2km. Two types of gangions were used during the study. The first type consisted of 2m tarred nylon attached to steel cable via a barrel swivel. A 10/0 J-hook was then attached to the end of the steel cable. The second type of gangion used consisted of 4m of 136kg test monofilament with a 12/0 circle hook. Depths at location of capture ranged from three to 40m. Sharks were measured, then tagged with Hallprint nylon tipped double return dart tags inserted into the musculature at the base of the first dorsal fin and released (Grubbs et al., 2007). Condition of animal upon release was recorded.

#### *Data Analyses*

A modified version of Faben's method (Francis, 1988) for analyzing tag-recapture data was used to model tag recapture data from the VIMS Shark Research Program as well as data from Casey and Natanson (1992). Casey and Natanson (1992) used roto-tags and M-dart tags for sandbar sharks in the NWA. Models were fit to these data to provide a means for comparison and to determine if deleterious effects may be caused from tag type. Inputs to the model included length at initial capture ( $L_1$ ), change in length between captures ( $\Delta L$ ), time at initial capture ( $T_1$ ), time at recapture ( $T_2$ ), and time at liberty in years ( $\Delta T$ ):

$$\Delta L = \left[ \frac{\beta g_\alpha - \alpha g_\beta}{g_\alpha - g_\beta} \right] \left[ 1 - \left( 1 + \frac{g_\alpha - g_\beta}{\alpha - \beta} \right)^{\Delta T + (\phi_2 - \phi_1)} \right],$$

Where  $g_\alpha$  is the mean growth in  $\text{cm yr}^{-1}$  at length  $\alpha$ ,  $g_\beta$  is the mean growth in  $\text{cm yr}^{-1}$  at length  $\beta$ , and  $\alpha < \beta$ .  $\alpha$  and  $\beta$  were set to minimum and maximum values of  $L_i$ .

Seasonal growth may be incorporated in the model as:

$$\phi_i = u \frac{\sin[2\pi(T_i - w)]}{2\pi}, \text{ for } i=1,2.$$

Where  $0 \leq u \leq 1$  and depicts the extent of seasonal growth. When  $u$  is equal to zero there is no seasonal growth. Annual timing of maximum growth is characterized by  $w$  which is expressed as time of year.

Likelihood methods were used to fit the model to the data by minimizing the negative log-likelihood function using AD Model builder (Otter research):

$$\lambda = \sum_i \ln[(1-p)\lambda_i + p/R],$$

$$\text{where, } \lambda_i = \exp \frac{-0.5(\Delta L_i - \mu_i - m)^2 / (\sigma_i^2 + s^2)}{[2\pi(\sigma_i^2 + s^2)]^{0.5}};$$

Measurement error was assumed to be normally distributed and have a mean,  $m$ , and standard deviation,  $s$ . Estimated mean growth increment,  $u_i$  of the  $i^{\text{th}}$  fish,  $\Delta L_i$ , was assumed to be normally distributed with standard deviation  $\sigma_i$ . Error was modeled using linear, power, and lognormal functions. The linear function used was

$$\sigma_i = v\mu_i,$$

where  $\nu$  is a scaling factor to compensate for increased variability in growth of individuals as expected growth increment increases. The power function used in the model was

$$\sigma_i = \nu \mu_i^\tau,$$

where  $\tau$  is a scaling parameter. The lognormal function used was

$$\sigma_i = \tau(1 - e^{-\nu \mu_i}).$$

Given the nature of tag-recapture data Francis (1988) included a term to describe the probability of outlier contamination  $p$ , within the observed range of growth increments,  $R$ .

A stepwise approach to fitting models to the data was taken. The least complex model was fit to the data  $(g_\alpha, g_\beta, p)$  and then additional parameters were included in the model. A likelihood ratio test was used to determine if the addition of parameters significantly improved the fit of the model. If number of parameters in the model were equal then the model that produced the lowest negative log-likelihood was chosen.

The model that provided the best fit to the data was then bootstrapped 5000 times and corrected 95% confidence intervals for model parameters were estimated using AD Model builder (Haddon, 2001).

Von Bertalanffy growth parameters were estimated from the following functions:

$$L_\infty = (\beta g_\alpha - \alpha g_\beta)(g_\alpha - g_\beta)$$

$$e^{-k} = 1 + (g_\alpha - g_\beta)/(\alpha - \beta).$$

Growth rate at length was estimated following the methods of Attwood and Swart (2000),

$$\frac{dPCL}{dt} = L_\infty * K * \left(1 - \frac{PCL}{L_\infty}\right).$$

## Results

Over the time period 98 sandbar sharks were recaptured from Maryland, U.S. south to Port Aransas, Texas, U.S. (Figure 1). Time at liberty ranged from 26 to 3,561 days at liberty. Length at time of tagging ranged from 41 to 96cm PCL (Figure 2). Measurement information at recapture was obtained from 43 sharks (Figure 3). Of these, 38 had viable length data. Sharks used in the data analyses consisted of 22 females and 16 males. Growth increments ranged from 0.10 to 66 cm PCL (Figure 4).

The best fit model was the simplest model which did not incorporate seasonal and outlier contamination terms (Table 1). Model error was normally distributed and lacked skew and kurtosis when the lognormal error structure was used (Figures 5,6). Mean growth rates for sharks at 41cm PCL and 96 cm PCL were 11.2 and 7.15 cm year<sup>-1</sup>. This model estimated  $L_{\infty}$  to be 192 cm PCL and  $k$  to be 0.077 (Figure 7). The optimally parameterized model from Casey and Natanson (1992) tagging data from rototags revealed lower growth estimates (Figure 8).

## Discussion

Using methods described by Francis (1988) we have modeled growth of the sandbar shark in the Northwest Atlantic Ocean. Comparisons between age-at-length and tag-recapture models yielded similar results (Figures 9,10). This is the first time this has been accomplished for the sandbar shark in the NWA. Previous estimates of growth and growth rates through tag-recapture methodologies have proven spurious, yielding unrealistic maximum lengths and longevity. There are many possible reasons for these

spurious results. Stevens (1990) first suggested tags may slow growth of blue sharks in the Northeast Atlantic. Various researchers have reported negative growth from shark tagging studies (Pratt and Casey, 1983; Davenport and Stevens, 1988). Manire and Gruber (1991) illustrated this for lemon sharks, *Negaprion brevirostris*, in Bimini, Bahamas. M-dart style tags were found to stunt growth and significant differences in growth were found between sharks that were tagged using internal pit-tags and sharks tagged with-M-dart tags.

Tag insertion and the subsequent open wound may place the shark in a greater struggle to maintain ion balance, thus stunting growth (Manire and Gruber 1991). Drag is also a likely component that may influence growth of the tagged animal. This is especially true when sharks occupy highly productive estuarine environments. Annual emigrations into these areas by juvenile sandbar sharks lead to fouling of tags and thus increase drag. The effect of tag drag and fouling becomes less of an issue once sandbar sharks reach greater sizes and move to less productive coastal habitats.

Growth variability for our model (0.12) was less than that determined for juvenile dusky sharks in Southwest Australia 0.24 to 0.40 (Simpfendorfer, 2000). This study used jumbo roto-tags similar to those used by Casey and Natanson (1992) and may have been a contributor to higher growth variability. Skomal and Natanson (2003) estimated growth variability for the blue shark, *Prionace glauca*, to be 0.26 and 0.44 depending on parameterization of the model. Our lower values may be a product of our tag type and tagging methodology. Greater growth variability has been noted in teleosts. Welsford and Lyle (2005) estimated growth variability to range from 0.29 to 0.88 for the purple

wrasse, *Notolabrus furcicola*. The biology and ecology are likely contributors to these differences.

Although Welsford and Lyle (2005) did estimate greater growth variability, estimates of measurement error were lower than our estimates (-0.07 to -0.12). When the measurement error term was used in our model it was estimated to be -0.22 and 0.62. The greater measurement error estimate is similar to that found by Simpfendorfer (2000). Skomal and Natanson (2003) estimated measurement error to be -2.03. Although our sample size was similar to this study our measurement error estimate was an order of magnitude less.

Interestingly, seasonal parameters did not significantly improve the model. The sandbar shark is highly migratory, as seen from our tagging data as well as other researchers, and likely experiences fluctuations in annual growth due to migration, temperature and prey availability. Greatest growth is hypothesized to occur in the summer months when juveniles occupy highly productive estuarine habitats (Dowd et al., 2006; Conrath and Musick, 2007; Grubbs and Musick, 2007).

Along with tag type, other factors may confound the issue of stunted growth. These include measurement error and data transcription errors. Several reported recapture lengths appeared to be incorrect and were removed from the data set used. Other researchers have encountered similar and unrealistic recapture lengths. Pratt and Casey (1983) reported growth rates of  $-144.3 \text{ cm year}^{-1}$  to  $161.2 \text{ cm year}^{-1}$ . These estimates are not empirically possible and may be due to the aforementioned factors.

Given our results as well as others, researchers should consider the primary focus of their research. If movement is the primary focus of the study and growth data are not

needed, then tags which have the lowest possible shed rates should be used. However the cost of using these types of tags is the possible subsequent loss of accurate growth data despite large sample sizes. Quantifying these biases should be the next step to improving tag-recapture based growth models.

## References

- Attwood, C.G. & L. Swart 2000. Discrepancy between otolith and tag-recovery estimates of growth for two South African surf-zone teleost species. *S Afr J Mar Sci* 22: 9-15.
- Casey, J.G. & L.J. Natanson 1992. Revised estimates of age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. *Can. J. Fish. Aquat. Sci.* 49: 1474-1477.
- Compagno, L.J.V. 1984. FAO species catalogues, vol 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. FAO Fisheries Synopsis No. 125.
- Conrath, C.L. & J.A. Musick 2007. The sandbar shark nursery within bays and lagoons of the eastern shore of Virginia. *Trans Am Fish Soc* 136: 999-1007.
- Davenport, S. & J.D. Stevens 1988. Age and growth of two commercially important sharks (*Carcharhinus tilstoni* and *C. sorrah*) from northern Australia. *Aust J Mar Freshw Res* 39: 417-433.
- Dowd, W.W., R.W. Brill, P.G. Bushnell & J.A. Musick 2006. Estimating consumption rates of juvenile sandbar sharks (*Carcharhinus plumbeus*) in Chesapeake Bay, Virginia, using a bioenergetics model. *Fish Bull* 104: 332-342.
- Francis, M.P. 1997. Spatial and temporal variation in the growth rate of the elephantfish (*Callorhincus milii*). *N.Z. J Mar Freshw Res* 31: 9-23.
- Francis, R.I.C.C. 1988. Maximum likelihood estimation of growth and growth variability from tagging data. *N. Z. J of Mar Freshw Res* 22: 42-51.
- Grubbs, R.D. & J.A. Musick 2007. Spatial delineation of summer nursery areas for juvenile sandbar sharks, *Carcharhinus plumbeus*, in the Mid-Atlantic Bight. American Fisheries Society. Bethesda, MD.
- Grubbs, R.D., J.A. Musick, C.L. Conrath & J.G. Romine 2007. Long-term movements, migration, and temporal delineation of summer nurseries for juvenile sandbar sharks in the Chesapeake Bay region. In: C.T. McCandless, N.E. Kohler and H.L.

- Pratt, Jr. (editors). Shark nursery grounds of the Gulf of Mexico and the East Coast waters of the United States. American Fisheries Society. Bethesda, MD. .
- Haddon, M. 2001. Modelling and Quantitative Methods in Fisheries. Chapman & Hall, CRC Press, Boca Raton, FL.
- Knight, W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. J. Fish, Res. Bd. Canada 25: 1303-1307.
- Manire, C.A. & S.H. Gruber 1991. Effect of M-type dart tags on field growth of juvenile lemon sharks. Trans Amer Fish Soc 120: 776-780.
- Musick, J.A., S. Branstetter & J.A. Colvocoresses 1993 Trends in shark abundance from 1974 to 1991 for the Chesapeake Bight region of the U.S. Mid-Atlantic coast NOAA Tech. Rep. NMFS 115:1-18 pp. 115
- Pratt, H.L., Jr. & J.G. Casey 1983. Age and growth of the shortfin mako, *Isurus oxyrinchus*, using four methods. Can J Fish Aquat Sci 40: 1944-1957.
- Simpfendorfer, C. 2000. Growth rates of juvenile dusky sharks, *Carcharhinus obscurus* (Lesueur, 1818), from southwestern Australia estimated from tag- recapture data. Fish Bull 98: 811-822.
- Skomal, G.B. & L.J. Natanson 2003. Age and growth of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Fish Bull 101: 627-639.
- Sminkey, T.R. & J.A. Musick 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. Copeia 4: 871-883.
- Stevens, J.D. 1990. Further results from atagging study of pelagic sharks in the north-east Atlantic. Mar Bio Assoc United Kingdom 70: 707-720.
- Welsford, D.C. & J.M. Lyle 2005. Estimates of growth and comparisions of growth rates determined from length- and age-based models for populations of purple wrasse (*Notolabrus fucicola*). Fish Bull 103: 697-711.

Table 1. Model results of all parameterizations. Model in shaded area was the accepted model.

<b>Model</b>	<b>f</b>	<b>ga</b>	<b>gb</b>	<b>v</b>	<b>p</b>	<b>m</b>	<b>s</b>	<b>u</b>	<b>w</b>	<b>tau</b>	<b>#</b>	<b><math>L_{\infty}</math></b>	<b>k</b>
ga,gb,v,tau	117.4	11.2	7.15	0.12	-	-	-	-	-	7.60	4	192	0.077
ga,gb,v,p,tau	117.4	11.2	7.15	0.12	0.0	-	-	-	-	7.60	5	192	0.077
ga,gb,v,m,s,tau	117.4	11.48	7.20	0.11	-	-0.22	0.00	-	-	7.68	6	189	0.081
ga,gb,v,p,m,s,tau	117.4	11.48	7.20	0.11	0	-0.22	0.00	-	-	7.68	7	189	0.081
ga,gb,v,u,w,tau	116.8	11.16	7.07	0.12	0.0	-	-	0.52	0.00	7.53	6	191	0.077
ga,gb,v,p,u,w,tau	116.8	11.16	7.07	0.12	0.0	-	-	0.52	0.00	7.53	7	191	0.077
ga,gb,v,m,s,u,w,tau	114.4	10.44	6.86	0.14	-	0.62	0.00	1.00	0.01	7.39	8	201	0.067
ga,gb,v,p,m,s,u,w,tau	114.4	10.44	6.86	0.13	0.0	0.62	0.00	1.00	1.0	7.39	9	201	0.067

Figure 1. Recapture locations of sandbar sharks tagged by VIMS.

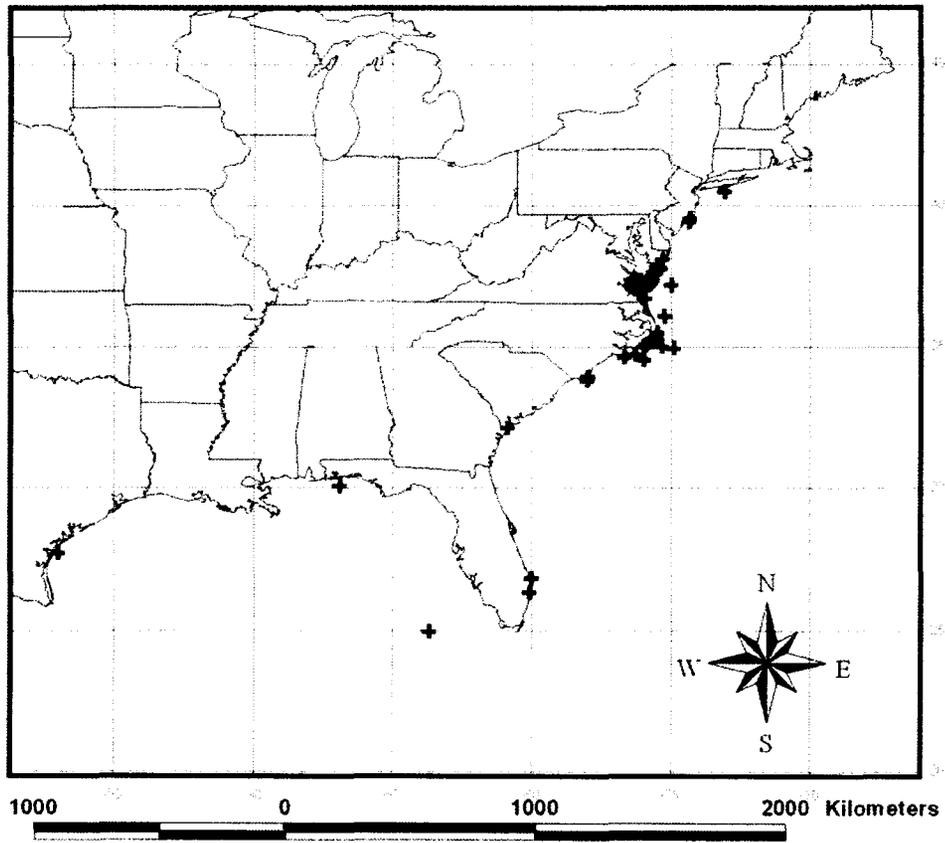


Figure 2. Pre-caudal length of sandbar sharks at time of release.

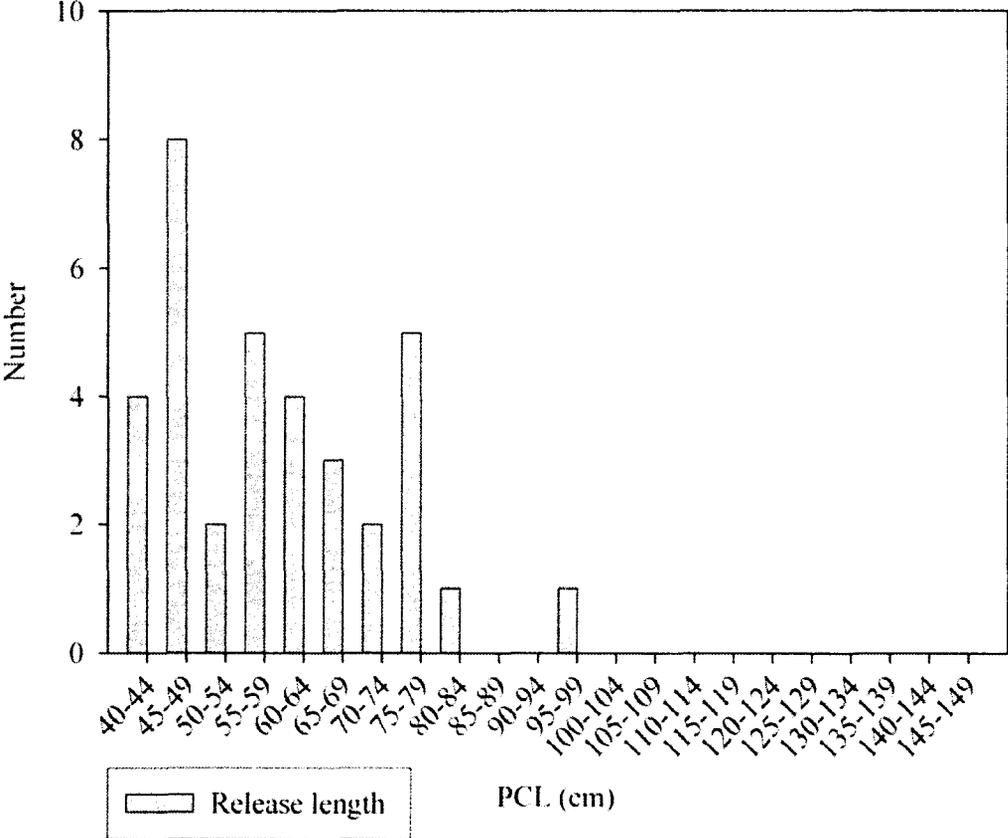


Figure 3. Pre-caudal length of sandbar sharks at time of tagging and at time of recapture.

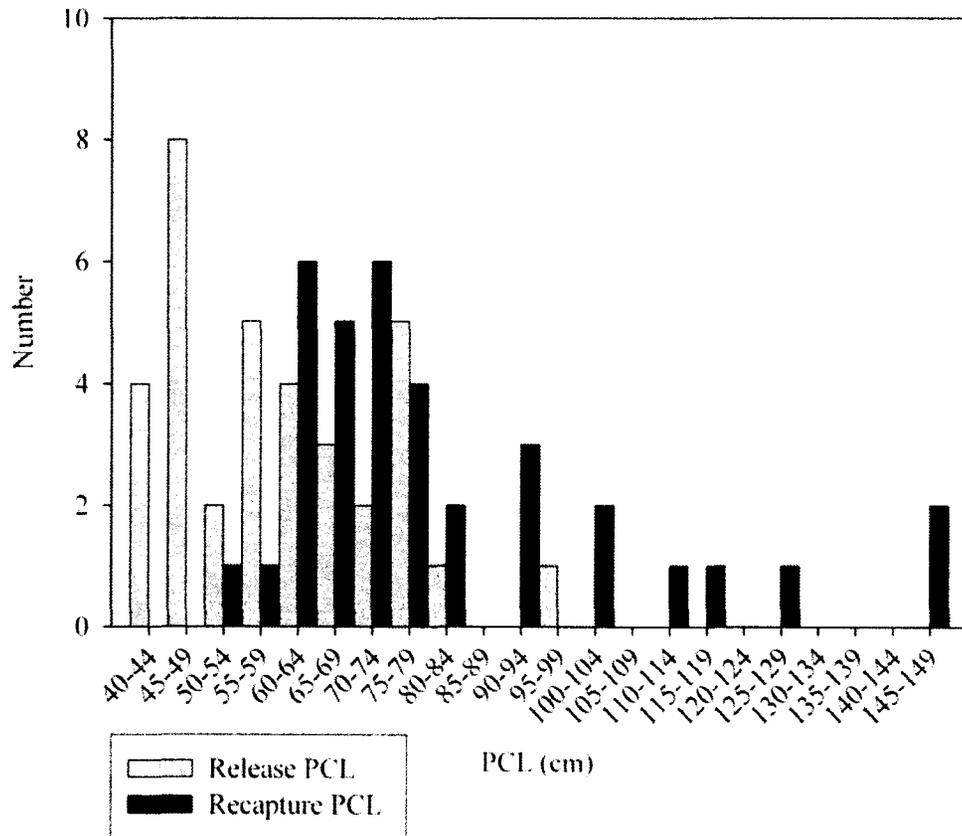


Figure 4. Growth increments of tagged sandbar sharks during time at liberty.

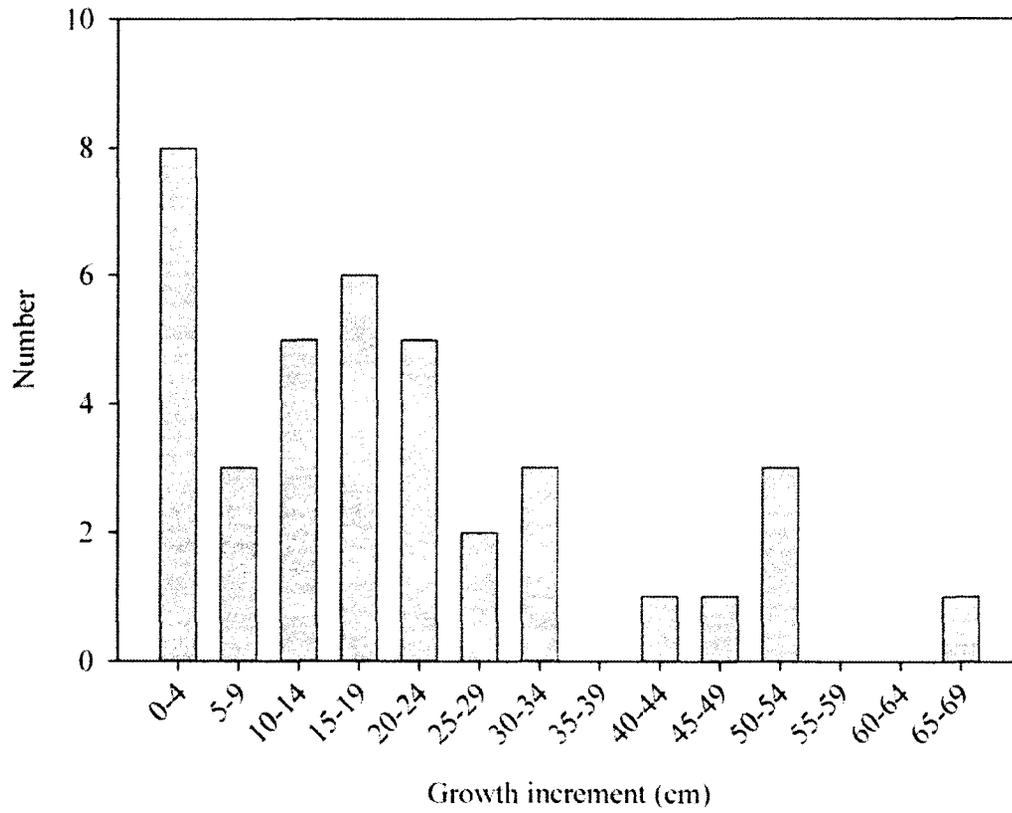


Figure 5. Error structures used within the model.

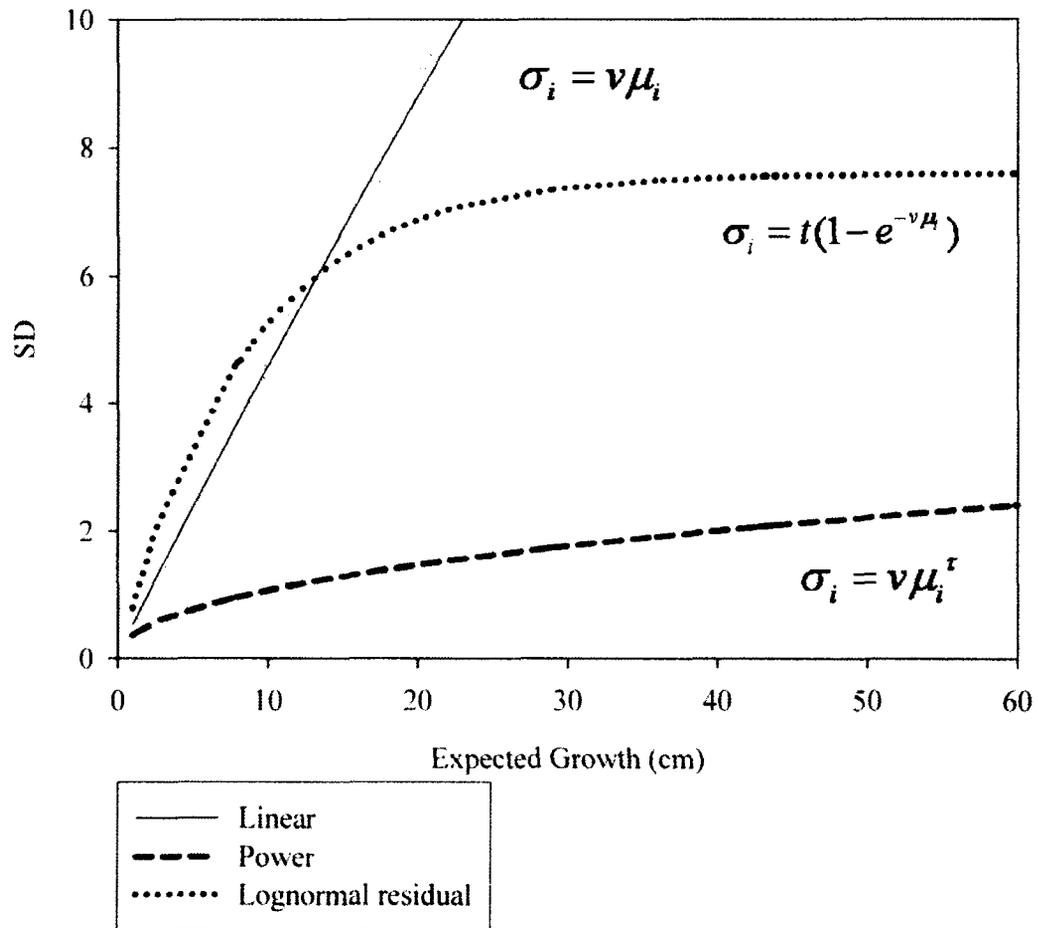


Figure 6. Residuals of best fit model.

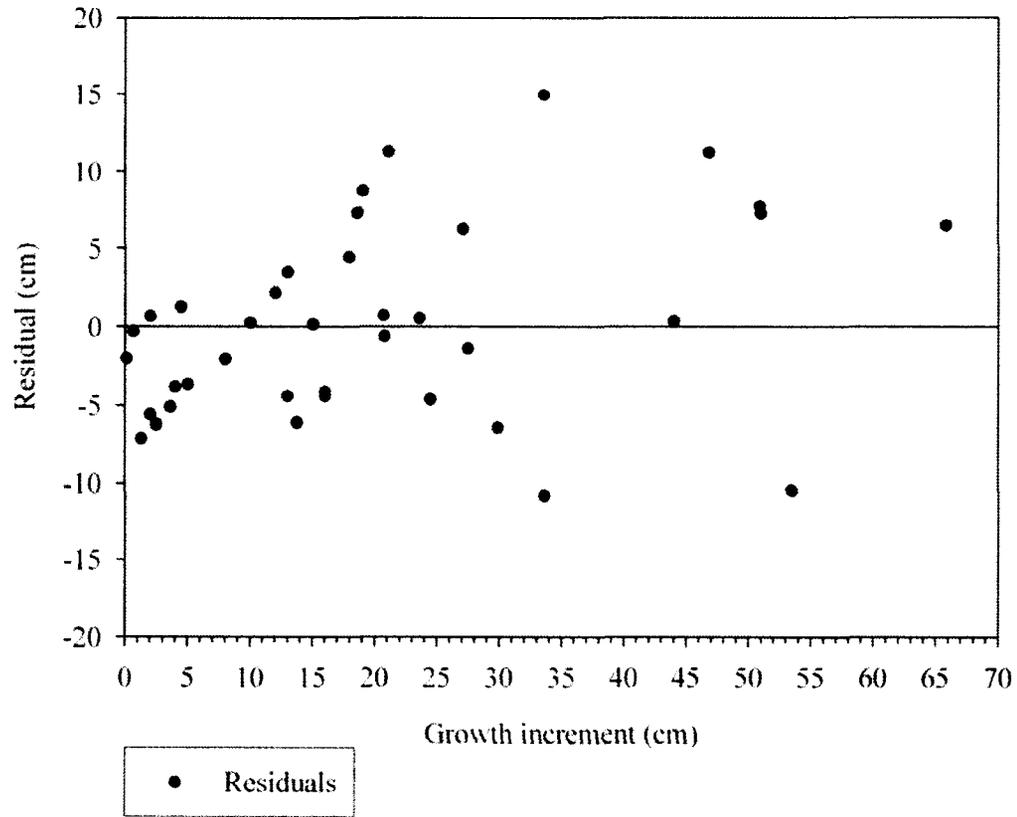


Figure 7. Bootstrap estimates and mean for sandbar sharks tagged by VIMS.

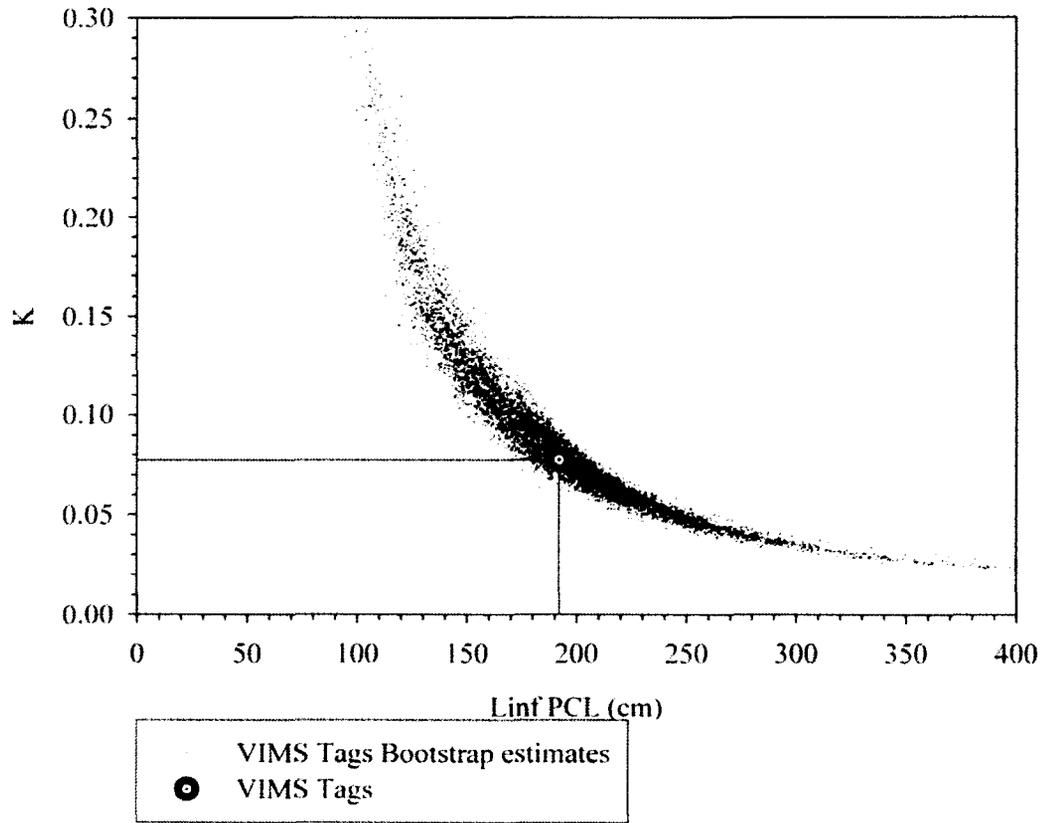


Figure 8. Bootstrap results and mean estimates of growth parameters from different tag types used on sandbar sharks.

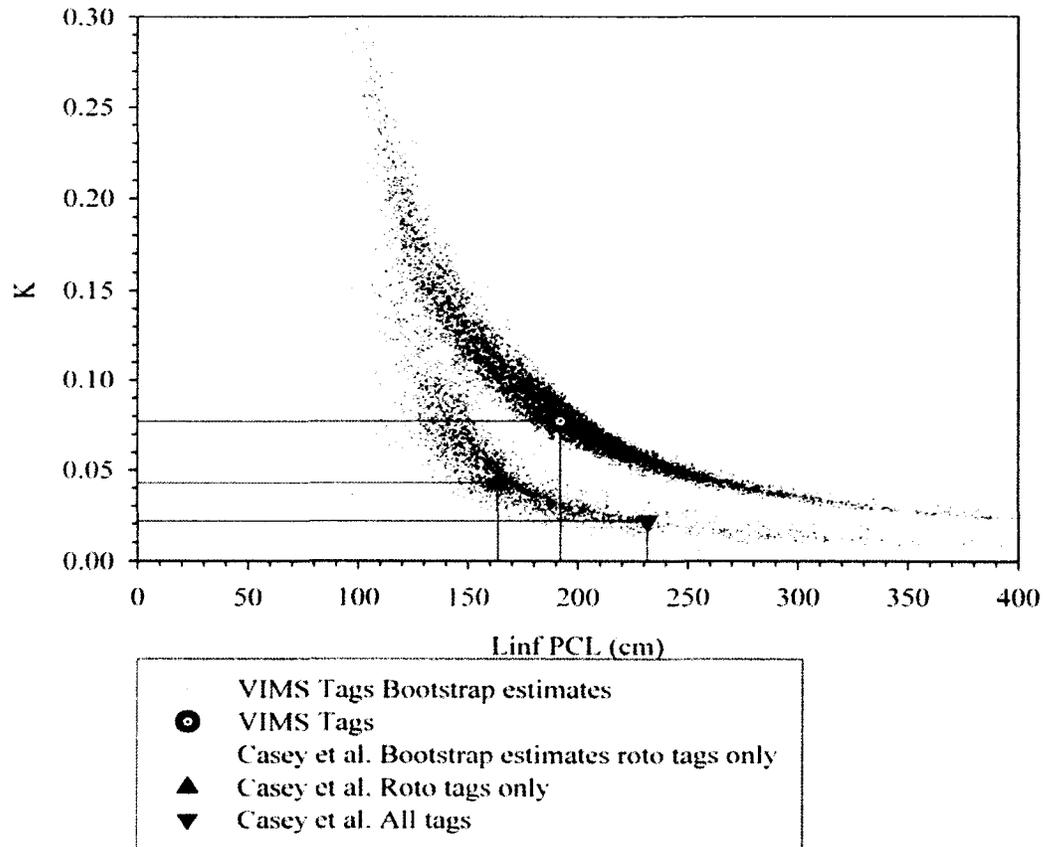


Figure 9. Comparison of growth parameters estimated through tagging and vertebral analyses. Vertebral estimates are from Romine et al. (in prep).

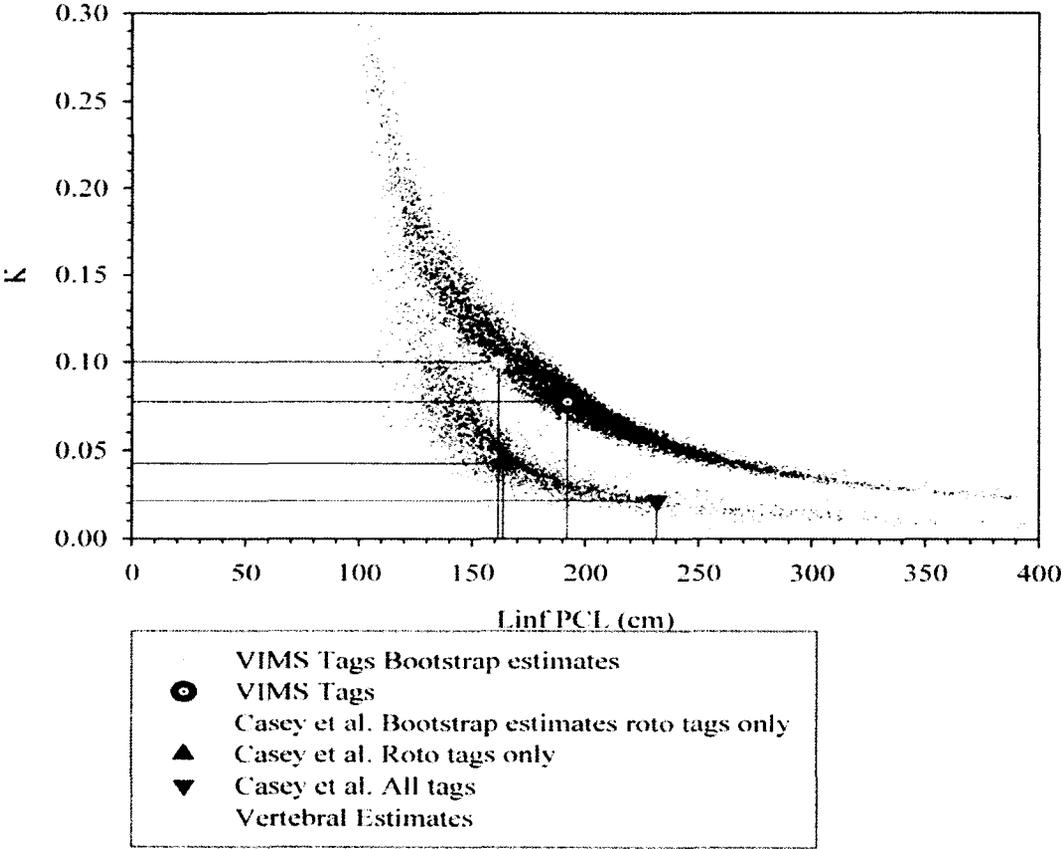
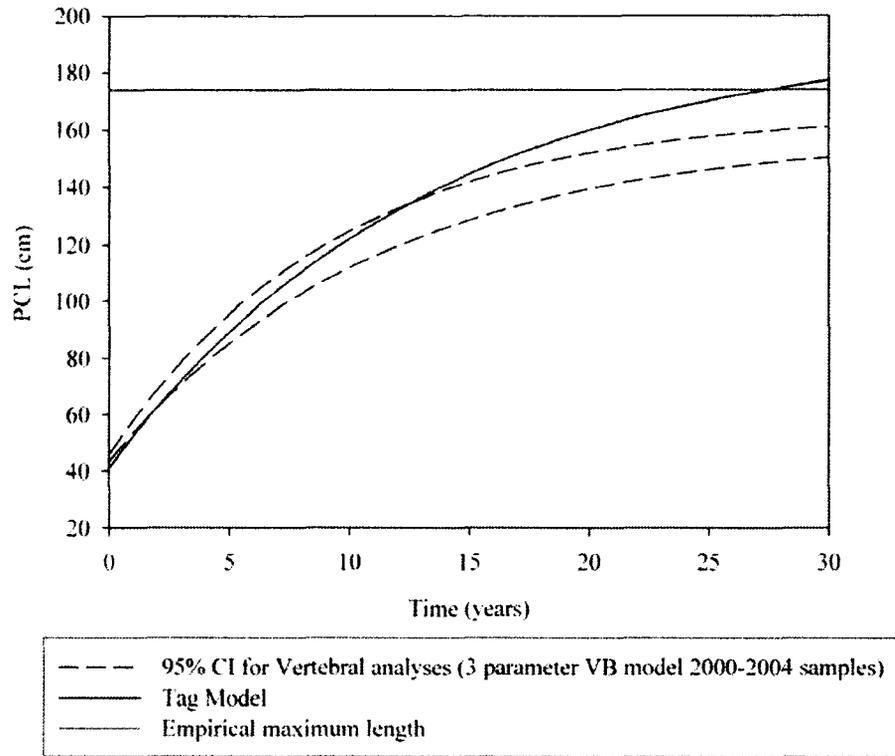


Figure 10. Comparison of growth curves estimated from tagging and vertebral aging methods.



## Appendix I. ADMB Code used for growth model fits and bootstrap parameter estimation.

```

/*****
//      Programmer: Jason Romine
//      Project Name:
//      Date:
//      Version:
//      Comments: Estimate initial Francis tag-recapture growth model
//
/*****/

DATA_SECTION
init_int nobs;
init_matrix data(1,nobs,1,6);
vector len(1,nobs);
vector dl(1,nobs);
vector dt(1,nobs);
vector time1(1,nobs);
vector time2(1,nobs);

LOC_CALCS
      len=column(data,2);
      dl=column(data,3);
      dt=column(data,4);
      time1=column(data,5);
      time2=column(data,6);
END_CALCS

PARAMETER_SECTION

init_number ga;          //Mean annual growth rates for fishes at length A
and B
init_number gb;
//init_number v;
init_bounded_number v(0,100);    //Degree of individual variabilty in growth
rates

//init_number p(-1);
init_bounded_number p(0,1); //outlier probability

//Measurement error terms;
init_number m(-1);
//init_number m;          //mean of the measurement error in observed
growth increment
init_number s(-1);
//init_number s;          //standard deveiation of the mesurement error

```

```

//SEASONAL TERMS;
//init_bounded_number u(0,1);           //intensity of seasonal variation in
growth
init_number u(-1);
//init_bounded_number w(0,1);           //Phase term, time of year associated
with maximum growth
init_number w(-1);

init_number tau;

!!ga=10;
!!gb=5;
!!v=0.1;
!!p=0;
!!m=0;
!!s=0;
!!u=0;
!!w=0;
!!tau=7.45;

objective_function_value f;
number A;
number B;
number R;
vector ui(1,nobs);//predicted dl
vector resid(1,nobs);
vector residsqr(1,nobs);
vector sigsqr(1,nobs);
vector lam(1,nobs);
vector phi1(1,nobs);
vector phi2(1,nobs);
vector sig(1,nobs);
number Linf;
number K;
number g45;
number g80;

PROCEDURE_SECTION
  calc_obj_fun();
  calc_vb_parms();

FUNCTION calc_obj_fun

  A=min(column(data,2));
  B=max(column(data,2));

```

```

R=max(column(data,3));
double pi=3.14593;

dvar_vector phi1=u*(sin(2*pi*(time1-w)))/(2*pi);
dvar_vector phi2=u*(sin(2*pi*(time2-w)))/(2*pi);

dvar_vector t1=(((B*ga)-(A*gb))/(ga-gb))-len;
//dvar_vector t2=1.-pow((1.+((ga-gb)/(A-B))),dt);
dvar_vector t2=1.-pow((1.+((ga-gb)/(A-B))),dt+phi2-phi1);
ui=elem_prod(t1,t2);
resid=dl-ui;
cout<<"resid\n"<<resid<<endl;
residsqr=elem_prod(resid-m,resid-m);
//residsqr=elem_prod(resid,resid); //w/out measurement error
cout<<"residsqr\n"<<residsqr<<endl;

sigsqr=elem_prod(v*ui,v*ui);
//cout<<"sigsqr\n"<<sigsqr<<endl;
//sig=v*pow(ui,tau);
//sigsqr=elem_prod(sig,sig);
//cout<<"tau\n"<<tau<<endl;
//sigsqr=elem_prod((v*pow(ui,tau)), (v*pow(ui,tau)));//alt variance model
//sigsqr=elem_prod(( tau*(1-exp(-v*ui))), (tau*(1-exp(-v*ui))));//alt variance
model

//dvar_vector N=mfexp(elem_div((-0.5*residsqr),(sigsqr))); //w/out measurement
error
dvar_vector N=mfexp(elem_div((-0.5*residsqr),(sigsqr+s*s))); //w/measurement
error
cout<<"N\n"<<N<<endl;

//dvar_vector D=pow((2.*pi*sigsqr),0.5); //w/o measurement error
dvar_vector D=pow((2.*pi*(sigsqr+s*s)),0.5);//w/measurement error
cout<<"D\n"<<D<<endl;

lam=elem_div(N,D);
cout<<"lam\n"<<lam<<endl;
//f=-1.*sum(log((1)*lam));
f=-1.*sum(log((1-p)*lam)+p/R);

FUNCTION calc_vb_parms
Linf=((B*ga)-(A*gb))/(ga-gb);
K=(log(1+(ga-gb)/(A-B)))-1.;
g45=(((45-A)*gb)+((B-45)*ga))/(B-A);
g80=(((80-A)*gb)+((B-80)*ga))/(B-A);

```

## REPORT\_SECTION

```
report<<"len\n"<<len<<endl;
report<<"A\n"<<A<<endl;
report<<"B\n"<<B<<endl;
report<<"lam\n"<<lam<<endl;
report<<"ui\n"<<ui<<endl;
report<<"dl\n"<<dl<<endl;
report<<"resid\n"<<resid<<endl;
report<<"ga\n"<<ga<<endl;
report<<"gb\n"<<gb<<endl;
report<<"v\n"<<v<<endl;
report<<"sigsqr\n"<<sigsqr<<endl;
//report<<"tau\n"<<tau<<endl;
//report<<"resids\n"<<resid<<endl;
report<<"p\n"<<p<<endl;
report<<"fn"<<f<<endl;
//report<<"A\n"<<A<<endl;
//report<<"B\n"<<B<<endl;
//report<<"data\n"<<data<<endl;
report<<"Linf\n"<<Linf<<endl;
report<<"K\n"<<K<<endl;
report<<"Dt\n"<<Dt<<endl;
report<<"g45\n"<<g45<<endl;
report<<"g80\n"<<g80<<endl;
```

## Appendix II. Bootstrap estimation of Francis model and von Bertalanffy growth parameters.

```

/*****
//      Programmer: Jason Romine
//      Project Name:
//      Date:
//      Version:
//      Comments: Bootstrap estimation of model parameters
//
/*****/
DATA_SECTION
    int seed;
    init_number nobs;
    init_matrix data(1,nobs,1,6);
    vector len(1,nobs);
    vector dl(1,nobs);
    vector dt(1,nobs);
    vector time1(1,nobs);
    vector time2(1,nobs);

    LOC_CALC
        ifstream ifs("seed.txt");
        ifs>>seed;

    END_CALC

PARAMETER_SECTION
    LOC_CALC
        //use in data or parameter sections only.
        dvector indtmp(1,nobs);    //temporary index where we generate
random numbers
        ivector indFrom(1,nobs);    //indices from where we move
        ivector indTo(1,nobs);    //indices to where we move
        random_number_generator rng(seed);    // random number
generator with seed = 999
        //cout<<"original data ... \n"<<data<<endl; //print

        for(int y=1;y<=2;y++)
            {
                indtmp.fill_randu(rng);    //fill
random uniform numbers
                indtmp= 1.+indtmp*nobs; //get the
unif numbers on the right scale (from 1 to 10 eg)
                if(y==1)indFrom = ivector(indtmp);
//fill from vector with integers

```

```

else indTo=ivector(indtmp); //fill to
vector with integers
    }
    //cout<<endl<<indtmp<<endl;
    //cout<<endl<<indFrom<<endl;    //print them
    //cout<<endl<<indTo<<endl;
    for(y=1;y<=nobs;y++)    //substitute to row with from row
        {
            data[indTo[y]] =data[indFrom[y]];
        }
    //cout<<"\nbootdata ...\n"<<data<<endl;    //print*/
    len=column(data,2);
    dl=column(data,3);
    dt=column(data,4);
    time1=column(data,5);
    time2=column(data,6);

```

END\_CALCS

```

init_number ga;    //Mean annual growth rates for fishes at length A
and B
init_number gb;
//init_number v(-1);
init_number v;//Degree of individual variabilty in growth rates
init_number p(-1);
//init_bounded_number p(0,1); //outlier probability

//Measurement error terms;
//init_number m(-1);
init_number m;    //mean of the measurement error in observed
growth increment
//init_number s(-1);
init_number s;    //standard deveiation of the mesurement error

//SEASONAL TERMS;
//init_bounded_number u(0,1);    //intensity of seasonal variation in
growth
init_number u(-1);
//init_bounded_number w(0,1);    //Phase term, time of year associated
with maximum growth
init_number w(-1);

init_number tau;
//init_number log_sigma(1);

!!ga=10;

```

```

!!gb=5;
!!v=1.4;
!!p=0;
!!m=.60;
!!s=2;
!!u=0;
!!w=0;
!!tau=7.5;

```

```

objective_function_value f;
number A;
number B;
number R;
number Linf;
number K;
number g45;
number g80;

```

```

vector ui(1,nobs);//predicted dl
vector resid(1,nobs);
vector residsqr(1,nobs);
vector sigsqr(1,nobs);
vector lam(1,nobs);
vector phi1(1,nobs);
vector phi2(1,nobs);
vector sig(1,nobs);

```

#### PROCEDURE\_SECTION

```

calc_obj_fun();
calc_vb_parms();

```

#### FUNCTION calc\_obj\_fun

```

A=min(column(data,2));
B=max(column(data,2));
R=max(column(data,3));
double pi=3.14593;
//dvar_vector phi1=u*(sin(2*pi*(time1-w)))/(2*pi);
//dvar_vector phi2=u*(sin(2*pi*(time2-w)))/(2*pi);
dvar_vector t1=(((B*ga)-(A*gb))/(ga-gb))-len;
dvar_vector t2=1.-pow((1.+(ga-gb)/(A-B)),(dt));
//dvar_vector t2=1.-pow((1.+(ga-gb)/(A-B)),(dt+phi2-phi1));
ui=elem_prod(t1,t2);
resid=dl-ui;
residsqr=elem_prod(resid-m,resid-m);
//residsqr=elem_prod(resid,resid);//w/o error

```

```

//cout<<"residsqr\n"<<residsqr<<endl;
//Variance models
//sigsqr=elem_prod(v*ui,v*ui);
//sigsqr=elem_prod((v*pow(ui,tau)),(v*pow(ui,tau)));
sigsqr=elem_prod(( tau*(1-exp(-v*ui))), (tau*(1-exp(-v*ui))));//alt variance
model

//dvar_vector N=mfexp(elem_div((-0.5*residsqr),(sigsqr))); //w/out measurement
error
dvar_vector N=mfexp(elem_div((-0.5*residsqr),(sigsqr+s*s))); //w/measurement
error
//dvar_vector D=pow((2.*pi*sigsqr),0.5); //w/o measurement error
dvar_vector D=pow((2.*pi*(sigsqr+s*s)),0.5); //w/measurement error
lam=elem_div(N,D);
f=-1.*sum(log((1-p)*lam)+p/R);

```

#### FUNCTION calc\_vb\_parms

```

Linf=((B*ga)-(A*gb))/(ga-gb);
K=(log(1+(ga-gb)/(A-B)))/-1.;
g45=(((45-A)*gb)+((B-45)*ga))/(B-A);
g80=(((80-A)*gb)+((B-80)*ga))/(B-A);

```

#### REPORT\_SECTION

```

//report<<"A\t"<<A<<endl;
//report<<"B\t"<<B<<endl;
//report<<"data\t"<<data<<endl;
dump_pars();

```

#### FUNCTION dump\_pars

```

ofstream ofs("caseyrotoparmests.txt",ios::app);
//ofs<<A<<"\t"<<B<<"\t"<<ga<<"\t"<<gb<<"\t"<<v<<"\t"<<tau<<"\t"<<endl;
//ofs<<A<<"\t"<<B<<"\t"<<ga<<"\t"<<gb<<"\t"<<v<<"\t"<<p<<"\t"<<m<<"\t"<<
s<<"\t"<<u<<"\t"<<w<<"\t"<<endl;
ofs<<A<<"\t"<<B<<"\t"<<ga<<"\t"<<gb<<"\t"<<v<<"\t"<<p<<"\t"<<m<<"\t"<<
s<<"\t"<<tau<<"\t"<<Linf<<"\t"<<K<<"\t"<<g45<<"\t"<<g80<<endl;

```

## Appendix III. Master code to run bootstrap estimation.

```

/*****
//      Programmer: Jason Romine
//      Project Name:
//      Date:
//      Version:
//      Comments: Run bootstrap code
//
/*****/
DATA_SECTION
    init_int nsims;
    int seed;
    LOC_CALC
        //use in data or parameter sections only.
        ofstream ofs2("caseyrotoparmests.txt");//delete par samples file w/append
        statement should append

        ofs2<<"A\t"<<"B\t"<<"ga\t"<<"gb\t"<<"v\t"<<"p\t"<<"m\t"<<"s\t"<<"tau
\t"<<"Linf\t"<<"K\t"<<endl;//writes header to parsamples.txt
        seed=999;

        for(int y=1;y<=nsims;y++)
        {
            system("caseyrotoboot.exe -est -nox");//-est stops the estimation of
the hession or use nohess
            ofstream ofs("seed.txt");
            ofs<<seed<<endl;
            seed++;
        }
    END_CALC
PARAMETER_SECTION
    !!exit(1);
    objective_function_value f;

PROCEDURE_SECTION

REPORT_SECTION

```

## **CHAPTER 4**

Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in Hawaiian waters  
through vertebral analysis

## Abstract

Age and growth estimates were determined for the sandbar shark, *Carcharhinus plumbeus*, from Oahu, Hawaii in the central Pacific Ocean. Age estimates were obtained through vertebral centra analysis of 187 sharks. We verified our age estimates through marginal increment analysis of centra and oxytetracycline marking methods of at-liberty sandbar sharks. Sizes of sampled sharks ranged from 46 cm to 147 cm pre-caudal length. Four growth models were fitted to length-at-age data; two forms of the von Bertalanffy growth model, the Gompertz growth model, and a logistic growth model. Males and females exhibited statistically significant differences in growth, indicating that females grow slower and attain larger sizes than males. Growth parameter estimates revealed slower growth rates than previously estimated (based on captive specimens) for Hawaiian sandbar sharks. The von Bertalanffy growth model using empirical length-at-birth provided the best biological and statistical fit to the data. This model gave parameter estimates of  $L_{\infty} = 138.5$  cm PCL and  $k = 0.12 \text{ year}^{-1}$  for males and  $L_{\infty} = 152.8$  cm PCL,  $k = 0.10 \text{ year}^{-1}$  for females. Male and female sandbar sharks mature at approximately 8 and 10 years of age respectively.

## Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a common large-coastal shark that inhabits temperate and subtropical waters world-wide and attains lengths greater than two meters (Bigelow & Schroeder 1948, Compagno 1984). In Hawaiian waters, sandbar sharks most frequently occur between depths of 10 and 50 meters (Wass 1973). The species is not commercially important in the central Pacific, which provides a unique opportunity to examine age and growth of a late maturing carcharhiniform shark that has not been greatly affected by fishing mortality.

Male and female sandbar sharks in Hawaiian waters have historically been shown to reach maximum sizes of 132 cm and 146 cm precaudal length (PCL), respectively (Wass 1973). The sandbar shark is viviparous via yolk-sac placenta, giving birth to well-developed live young following a gestation period of approximately 9-12 months (Springer 1960, Clark & von Schmidt 1965, Wass 1973, Lawler 1976). In Hawaiian waters, pups are approximately 47 cm PCL at birth and litter sizes average 5.5 pups per litter (Wass 1973). Wass (1973) estimated maturity to occur at 110 cm PCL for males and at 115 cm PCL for females.

The age and growth of the sandbar shark off Hawaii has been previously investigated. However, dissimilarities in some parameter estimates such as growth rates and age-at-maturity exist. Using data from captive sharks, Wass (1973) reported very fast growth rates ( $k=0.4015 \text{ year}^{-1}$  for males,  $k= 0.3745 \text{ year}^{-1}$  for females) and indicated that sandbar sharks in Hawaii reached maturity at three years of age. Conversely, growth rate estimates obtained from tooth replacement calculations suggested maturity occurred at 13 years of age. The discrepancy between the two methods may be due to the use of

captive animals, which may not be indicative of growth rates in the Hawaiian wild population. Furthermore, the results based on tooth-replacement rates are comparable other sandbar shark populations around the world. For example, sandbar sharks in the Northwest Atlantic Ocean attain maturity between 12 and 15 years of age (Casey et al. 1985, Sminkey & Musick 1996). Additionally, Joung et al. (2004) estimated age-at-maturity to be between 7.5 and 8.2 years of age for females and 8.2 years of age for males for sandbar sharks in Taiwanese waters. Given the variability in growth estimates calculated by Wass (1973), we used vertebral centra from wild sandbar sharks to re-estimate growth-rates in the Hawaiian population.

## **Materials and Methods**

### ***Sample collection and preparation***

We collected sandbar sharks using demersal longlines outside of Kaneohe Bay, Hawaii at depths between 70 and 100 meters (Figure 1). Longlines were set perpendicular to the shoreline and baited with sardines (*Sardinops sagax*), chub mackerel (*Scomber japonicus*), yellowfin tuna (*Thunnus albacares*), skipjack tuna (*Katsuwonus pelamis*), barracuda (*Sphyrnaena barracuda*), and mahi-mahi (*Coryphaena hippurus*). Gangions consisted of a stainless-steel snap-clip attached to three meters of monofilament followed by a one-meter stainless-steel leader that was attached to a circle hook. We used two sizes of gangions. Smaller gangions included 250 kg monofilament, 1.6 mm stainless-steel leaders, and 14/0 galvanized circle hooks, whereas large gangions included 410 kg monofilament, 2.2 mm stainless-steel leaders, and 18/0 stainless-steel circle hooks. Hooks were allowed to fish for 3 hours before being retrieved. Captured sharks were

landed, measured, and euthanized if needed for samples. At least five male and female sharks within each 5 cm size class between 45 cm PCL and 150 cm PCL were euthanized and vertebral samples were removed from below the first dorsal fin. Once the required vertebral samples had been collected, subsequently caught sharks were injected with oxytetracycline (OTC, 25 mg kg body weight<sup>-1</sup>), tagged with Hallprint dart tags, and released for age-validation purposes.

Vertebral samples were frozen after collection. We cleaned the thawed vertebrae of excess tissue and stored five centra from each specimen in 75% ETOH. Using a Beuhler Isomet rotary diamond saw, we sectioned vertebral centra sagittally through the focus of the centrum. Sections were then dried for 24 hours. Once dry, samples were mounted on a microscope slide via mounting medium. Samples were polished using a Metaserv 2000 grinder polisher until light was readily transmitted through the samples and rings were distinguishable using a dissection microscope. Vertebrae of sharks that were recaptured and sacrificed were examined under ultraviolet light for OTC marks.

#### *Maturity*

We determined maturity of males and females using macroscopic methods. Male sharks were classified as mature if claspers were deemed fully calcified (i.e. hard) and could be rotated forward (Clark & von Schmidt 1965, Driggers et al. 2004). Females were classified as mature if they were pregnant or had enlarged oviducal glands and well developed uteri (Castro 1993).

#### *Age Assignment and Validation*

The rings or annuli counted for age estimates were defined as a band pair consisting of an opaque zone combined with a wider translucent zone in the intermedialia, which

continued on to the corpus calcareum (Casey et al. 1985, Sminkey & Musick 1995). The birthmark was determined as the first band that intersected the inflection of the corpus calcareum. If annuli were not readily distinguishable, samples were stained with a 0.01% crystal violet solution to enhance readability.

Mounted vertebral sections were examined for age using a dissecting microscope and the Optimas video imaging system. The principal author and another reader conducted multiple blind readings of all vertebrae. Once all vertebrae were read, Hoenig's (1995) and Evans and Hoenig's (1998) tests of symmetry were conducted to test the hypothesis that age estimates between readers did not differ significantly and were due to random error.

Age estimates for vertebrae that were not consistent between readers were reexamined by both readers until a consensus was reached. The consensus estimate was used in the final analysis. If a consensus age estimate could not be reached the sample was removed from the study (Cailliet & Goldman 2004).

A relative marginal increment analysis was conducted to determine periodicity of ring formation (Branstetter & Musick 1994, Natanson et al. 1995, Goldman & Musick 2006). The Marginal Increment Ratio (MIR) is defined as:

$$MIR = (VR - R_n) / (R_n - R_{n-1}),$$

where  $VR$  = centrum radius,  $R_n$  = distance from the focus to the last complete narrow band, and  $R_{n-1}$  = the distance to the penultimate complete narrow band. All measurements were made along the corpus calcareum using an Optimas imaging system. We plotted monthly mean MIR values to determine the periodicity of band pair formation and tested for statistically significant differences for all months and seasons via one-way

analysis of variance. Young-of-the-year sharks were not used in MIR analyses as they have no fully formed rings. We used centrum radius measurements to estimate the relationship between radius and pre-caudal length.

### ***Growth Models***

Following Carlson & Baremore (2005), we fit four growth models to length-at-age data for male and female sharks. Two forms of the von Bertalanffy growth model were fit to the data (von Bertalanffy 1938, Beverton & Holt 1957, Cailliet et al. this volume). The first form, a three-parameter von Bertalanffy model (VB) incorporating the theoretical age-at-zero ( $t_0$ ) term is described as:

$$L_t = L_\infty(1 - e^{-k(t-t_0)}),$$

where  $t_0$  = age or time when length theoretically equals zero. The second form of the model (VB2) used the length-at-birth intercept rather than a theoretical age at zero length and is described as:

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt},$$

where  $L_t$  = length at time  $t$ ,  $L_\infty$  = theoretical asymptotic length,  $k$  = coefficient of growth, and  $L_0$  = mean length-at-birth (47 cm PCL). Length-at-birth was estimated from observed at-term embryos and free-swimming young-of-the-year during this study as well as previously reported data by Wass (1973). A modified version of the Gompertz growth model (Ricker 1975) was also fitted to the data:

$$L_t = L_0(e^{G(1-e^{-kt})}),$$

where  $G = \ln(L_\infty / L_0)$  (von Bertalanffy 1938). These lengths were determined from empirical data from this study and confirmed by Wass (1973). Finally, a logistic model (Ricker 1975) was fitted to the data:

$$L_t = L_\infty / (1 + e^{-k(t-t_0)})$$

All model parameters were estimated using the Marquardt least-squares nonlinear (NLIN) procedure in SAS statistical software (SAS V.9, SAS Institute, Inc). Growth parameter estimates for males and females were compared for statistically significant differences following the methods of Bernard (1981), Quinn and Deriso (1999), and Wang and Milton (1999) with a generalized  $T^2$ -statistic:

$$T^2 = (\beta_1 - \beta_2)' V^{-1} (\beta_1 - \beta_2),$$

where  $\beta_1$  and  $\beta_2$  are vectors of growth-model parameter estimates,  $V$  is the variance-covariance matrix of  $[\beta_1 - \beta_2]$ :

$$\beta_1 - \beta_2 = \begin{bmatrix} L_{\infty(1)} - L_{\infty(2)} \\ k_{(1)} - k_{(2)} \\ t_{0(1)} - t_{0(2)} \end{bmatrix}.$$

The coefficient of determination ( $r^2$ ), residual mean square error (MSE), Akaike's Information criteria (AIC) (Akaike 1973), and standard deviation of the residuals were used as measures of goodness-of-fit for all models. A Shapiro-Wilks test and a normal probability plot of the residuals were used to test for normality, excessive skew or excessive kurtosis using the univariate procedure in SAS statistical software (SAS V.9, SAS Institute, Inc)

## Results

### *Sample collection*

We captured a total of 320 sandbar sharks as a part of this study. Vertebral samples were obtained from 194 sharks (Figure 2) while the remainder of sharks were measured, tagged, injected with OTC and released. Size ranges for females and males captured were 46 cm to 147 cm PCL and 46 cm to 132 cm PCL respectively. Sharks were captured in all months except March.

### *Vertebral radius and length analysis*

The relationship between vertebral radius and shark length ( $PCL=12.0VR+8.12$ ) was significantly correlated ( $n=148$ ,  $r^2=0.97$ , Figure 2). No significant difference between males and females was found ( $Z=0.109$ ,  $P=0.55$ ), thus vertebral radius measurements were combined to estimate the regression.

### *MIR analysis*

For combined sexes, MIR analysis suggests a single growth band pair is formed annually with the narrow opaque band being formed in winter months. Marginal increment ratios increased from spring to winter (Figure 4). Differences in monthly marginal-increment ratios were not significant between all months in which samples were collected, (ANOVA,  $n=120$ ,  $F=0.64$ ,  $df=8$ ,  $P=0.74$ , Figure 4). The periodicity of band formation was also supported from one recaptured shark. This shark measured 60 cm PCL at its release on 26 June, 2004 and 62 cm PCL at its recapture on 20 January, 2005. An OTC stained opaque growth band was present at the very margin of the centra, suggesting ring formation had recently begun during the winter months.

### *Age estimation*

After our initial readings, we reached consensus age estimates for 187 (105 females, 82 males) samples. Consensus could not be reached for seven samples which were removed from all analyses. Agreement between blind readings of readers was reached 43.1% of the time. Reader agreement was 71.2% within one band and 84.3% within two bands. We could not reject the hypothesis of symmetry between ages assigned by both readers ( $X^2=38.64$ ,  $df = 39$ ,  $P=0.488$ , Hoenig 1995) indicating that differences between readers were due to random error.

### *Growth Models*

We found significant differences between male and female von Bertalanffy growth-model parameters, when using the form of the model that incorporated the theoretical age at zero length ( $T^2 = 8.48 > T_0^2 = 8.11$ ,  $P < 0.05$ ). Therefore, all models were subsequently fitted to male and female length-at-age data for each sex separately.

All growth models fitted to observed length-at-age data were significant ( $P < 0.0001$ , Table 1, Figures 5 & 6). Coefficients-of-determination were all greater than 0.94. The residuals of all models were normally distributed and no excessive skew or kurtosis was detected.

The von Bertalanffy growth model that included the theoretical  $t_0$  term provided the best statistical fit to the observed size-at-age data for male sandbar sharks. This model had the lowest residual mean square error (MSE), and the lowest AIC values (Table 1). The von Bertalanffy growth model that included the theoretical  $t_0$  term and the logistic model provided the best statistical fits to the observed size-at-age data for female sandbar sharks. These models had the lowest AIC and MSE values, respectively.

The three-parameter von Bertalanffy model produced the highest estimates for asymptotic maximum length for both males (151.1 cm PCL) and females (164.9 cm PCL, Table 1). The Gompertz model produced the lowest estimates for asymptotic length for males (130.4 cm PCL) and females (143.5 cm PCL). Observed maximum lengths for males (132 cm PCL) and females (147 cm PCL) fell within the 95% confidence intervals of all models. The three-parameter von Bertalanffy model produced the lowest estimates of the growth coefficient ( $k$ ) for males ( $0.09 \text{ year}^{-1}$ ) and females ( $0.08 \text{ year}^{-1}$ ). The Gompertz and logistic models produced the highest estimates of the growth coefficient for males ( $0.19 \text{ year}^{-1}$ ) and females ( $0.17 \text{ year}^{-1}$ ).

Six sharks were recaptured over the time period of this study. Time at liberty ranged from 7 to 526 days. Lengths of recaptured sharks ranged from 60 to 77 cm PCL at release. The average growth rate was  $6.97 \text{ cm year}^{-1}$  for the five sharks that were at liberty for more than 100 days. This value agreed with growth rates for sharks in this size range estimated from vertebral analyses.

Mean length-at-age estimates determined from the three-parameter von Bertalanffy model differed between males and females (Table 2). Females were generally larger at a given age and attained older ages than males. Males attained maturity between 100 and 110 cm PCL and females attained maturity between 110 and 120 cm PCL. These sizes correspond to 8 and 10 years of age for males and females respectively as determined by the two-parameter von Bertalanffy model. Maximum observed age was 19 years for male and 23 years for females.

*Discussion*

Wass (1973) estimated maturity to occur at 3 years of age and produced  $k$  estimates of  $0.4015 \text{ year}^{-1}$  for males and  $0.3745 \text{ year}^{-1}$  for females by observing the growth rates of captive sharks. Wass also estimated maturity to occur at 10.2 and 13.1 years of age for males and females respectively using tooth replacement methodology and hypothesized the true value for the wild population to lie somewhere between the estimates from both methods used in his study. Using vertebral analyses, our estimated ages-at-maturity determined from the two-parameter von Bertalanffy models were 8 and 10 years of age for males and females respectively and produced  $k$  estimates of  $0.12 \text{ year}^{-1}$  and  $0.10 \text{ year}^{-1}$  for males and females respectively.

Although all models fit the data well; statistically, the three-parameter von Bertalanffy model described the male size-at-age data better than the other three models. This model overestimated observed maximum size, but observed maximum size fell within the confidence intervals for this model. Size at birth was also overestimated by this model (47 cm PCL observed vs. 52 cm PCL predicted). The overestimate of size-at-birth could be due to the lack of newborns sampled during this study. The smallest male sampled was 46 cm PCL and only two females under 50 cm PCL were sampled. Despite the statistical ranking of the two-parameter von Bertalanffy model amongst the other models we feel the two-parameter von Bertalanffy growth model should be used when describing growth of the male sandbar shark in Hawaii. This model provided a biologically realistic fit to the observed data. Predicted maximum asymptotic length agreed closely to observed data (132cm PCL observed and 138.5 cm PCL predicted, Table 1) and it incorporated observed size at birth.

All models fit the female size-at-age data well. Statistically, the logistic and three-parameter von Bertalanffy models fit the data better than the other models. The asymptotic length estimate from the logistic model agreed with observed maximum size (147 cm PCL). The logistic model overestimated the size-at-birth (47 cm PCL observed vs. 56 cm predicted). The three-parameter von Bertalanffy model overestimated asymptotic length and size-at-birth. As with the male data, we feel the two-parameter von Bertalanffy growth model provided a more biologically realistic fit to the female data and should be employed when describing the growth of the female sandbar shark in Hawaii.

The Gompertz models fit the data well for both sexes, but underestimated the maximum asymptotic length. This inherently increased the rate at which asymptotic length was approached and, therefore, these models provided the highest growth coefficients. The logistic models for both males and females provided high growth coefficient values due to the overestimation of the size-at-birth and estimate of asymptotic maximum size. The combination of these factors effectively increased the rate at which asymptotic length was approached.

The three-parameter von Bertalanffy growth model overestimated both size-at-birth and asymptotic maximum length for both sexes. Both estimates were unrealistic and caused the estimated growth coefficients to be the lowest amongst all models.

Given the variability of growth rates within and between populations it is imperative to conduct rigorous examination of all possible methods to describe length-at-age data. As illustrated in this study, models fitted to size-at-age data can produce variable estimates of growth parameters. In this study, the growth coefficient estimates

ranged from 0.09-0.19 year<sup>-1</sup> for males and 0.08-0.17 year<sup>-1</sup> for females between all models. Growth coefficients are often used in demographic analyses for stock assessment purposes. Researchers must consider statistical results and observed biological data when determining which model provides the best fit to the data. Often the two viewpoints do not agree, as in this study. Although the three-parameter von Bertalanffy model, which is often the only model used to describe the growth of fishes, provided the best statistical fit to these data, it produced unrealistic asymptotic lengths and sizes-at-birth. Thus, we suggest the use of the growth parameters estimated by the two-parameter von Bertalanffy model.

Age and growth of sandbar sharks in Hawaii differ from other populations that have been studied. Growth coefficients in Hawaii ( $K=0.09-0.19$  year<sup>-1</sup> for males and 0.08-0.17 year<sup>-1</sup> for females) are much higher than those reported for the northwest Atlantic Ocean ( $k=0.057$  year<sup>-1</sup>, combined sexes, Sminkey & Musick 1995). Hawaiian sandbar sharks obtain smaller maximum sizes (132 cm PCL for males and 147 cm PCL for females, observed) and reach maturity earlier (8 years for males and 10 years for females) than those in the northwest Atlantic (172 cm PCL, observed and 15 years at maturity, sexes combined). Sandbar sharks in Taiwanese waters also reach larger maximum sizes (209 cm TL for males and 219 cm TL for females, observed – Joung et al. 2004) than those in Hawaii (179 cm TL for males and 196 cm TL for females, observed). Joung et al. (2004) estimated the growth coefficient for sandbar sharks in Taiwanese waters to be  $k=0.17$  year<sup>-1</sup> for both sexes combined and the onset of maturity to occur at 8 years of age for both sexes. The youngest sharks sampled in the Taiwanese study were four years-of- age which led to estimates of length-at-birth (80.8-85.8 cm TL)

that were much larger than observed (60-65 cm TL) for this population. Therefore, the estimated growth coefficients may have been overestimated by the use of the three-parameter von Bertalanffy model, which incorporated the  $t_0$  parameter, and the age-at-maturity underestimated. It is likely that the life history parameters of the Taiwanese population are intermediate between the Hawaiian and northwest Atlantic populations.

Vertebrae from larger sharks were more difficult to read due to decreased band pair widths near the margin of the vertebrae. This contributed to the increased variability in age estimates between readers as shark size increased. This also contributed to discrepancies in mean size-at-age estimates for older ages of male and female sandbar sharks (Table 2). The low sample sizes for older male sharks also contributed to these discrepancies. Although there were difficulties in assigning age estimates to specimens, the oldest sharks estimated blind consensus was 22 years for females and 12 years for males.

Our ageing methodology was supported via OTC mark recapture, but tagging and OTC validation has only been shown for one at liberty shark under 78cm PCL. A more robust tag recapture data set is needed to obtain empirical data on the growth rates of sandbar sharks in Hawaii and to investigate the long-term movements of sharks in Hawaii. During the period of the study seven tagged sharks were recaptured. Time at liberty ranged from 7 to 526 days. Growth of these sharks during time at liberty supported our growth models for sharks between 60 and 83 cm PCL. All recaptured sharks were under 100 cm PCL and thus do not offer any support of our models for maturing or mature sandbar sharks in Hawaii.

The age and growth estimates for this population of sandbar sharks in Hawaii supports the generalization that sharks are slow growing and have low reproductive output. Currently, a legal fishery does not exist for this population. Should a fishery open, caution in management of the fishery should be exercised. The life history parameters of this population, as with other populations of slow growing, late maturing and low fecundity fishes, render it extremely vulnerable to overfishing even at low levels of fishing effort (Musick 1999).

#### *Acknowledgements*

We thank NOAA/NMFS for funding to the National Shark Research Consortium from which this study was supported. We thank the anonymous reviewers for their constructive comments. We thank Dr. John Carlson and Dr. Ken Goldman for their comments and for editing this volume. We thank the Hawaii Institute of Marine Biology for graciously allowing us the use of vessels and lab space. We would be remiss not to thank the students, staff, and volunteers that assisted in sample collection and preparation, Dr. Kim Holland, Toby Daly-Engel, Nick Whitney, Yannis Papastamatiou, RaeMarie Johnson, Kanesa Duncan, Dave Itano, Amanda Southwood, Amy Long, Todd Gedamke, Christina Conrath, and Demetria Christo. This paper is Contribution No. 2709 of the Virginia Institute of Marine Science, The College of William and Mary. This is Contribution No. 1209 of the Hawaii Institute of Marine Biology.

### References

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. *In* B.N. Petrov and F. Csaki (eds.), p. 267-281. Second International Symposium on Information Theory, Akademiai Kiado, Budapest.
- Bernard, D.R. 1981. Multivariate Analysis as a means of comparing growth in fish. *Can. J. Fish. Aquat. Sci.* 38: 233-236.
- Bertalanffy, L.v. 1938. A quantitative theory of organic growth(inquiries on growth laws. II). *Hum. Biol.* 10: 181-213.
- Beverton, R.J.H. & S.J. Holt. 1957. On the dynamics of exploited fish populations. Ministry of Agriculture. Fisheries and Food Fishery Investigation Series II XIX. 533 pp.
- Bigelow, H.B. & W.C. Schroeder. 1948. Sharks. *In*: C.M.B. J. Tee-Van, S.F. Hildebrand, A.E. Parr, & W.C. Schroeder (ed.) *Fishes of the Western North Atlantic. Part 1. Vol. 1.*, Mem. Sears Foundation for Marine Research, Yale Univ. New Haven CT.
- Branstetter, S. & J.A. Musick. 1994. Age and growth estimates for the sand tiger in the northwestern Atlantic Ocean. *Transactions of the American Fisheries Society* 123: 242-254.
- Cailliet, G.M. & K.J. Goldman. 2004. Age determination and validation in chondrichthyan fishes. pp. 399-447. *In*: J. Carrier, J.A. Musick & M. Heithaus (ed.) *The biology of sharks and their relatives*, CRC Press, Boca Raton, FL.
- Cailliet, G.M., W.D. Smith, H.F. Mollet & K.J. Goldman. 2006 . Age and growth studies of chondrichthyan fishes: an overview stressing terminology, verification, validation, and growth function fitting. *Env. Bio. of Fish. Special Volume: Age*

- and growth of chondrichthyan fishes: new methods, techniques, and analyses. *Envir Bio Fish* 77:211-228.
- Carlson, J.K. & I.E. Baremore. 2005. Growth dynamics of the spinner shark (*Carcharhinus brevipinna*) off the United States southeast and Gulf of Mexico coasts: a comparison of methods. *Fish. Bull.* 103: 280-291.
- Casey, J.G., H.L. Pratt, Jr. & C.E. Stillwell. 1985. Age and growth of the sandbar shark (*Carcharhinus plumbeus*) from the Western North Atlantic. *Can. J. Fish. Aquat. Sci.* 42: 963-975.
- Castro, J.I. 1993. The biology of the finetooth shark, *Carcharhinus isodon*. *Environmental Biology of Fishes* 36: 219-232.
- Clark, E. & K. von Schmidt. 1965. Sharks of the Central Gulf coast of Florida. *Bull. Mar. Sci.* 15: 13-83.
- Compagno, L.J.V. 1984. FAO species catalogues. Vol. 4. Sharks of the World. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO fisheries synopsis, (125)4, Pt. 2, 251-655. 251-655 pp.
- Driggers, W.B., III, D.A. Oakley, G. Ulrich, J.K. Carlson, B.J. Cullum & J.M. Dean. 2004. Reproductive biology of *Carcharhinus acronotus* in the coastal waters of South Carolina. *Journal of Fish Biology* 64: 1540-1551.
- Evans, G.T. & J.M. Hoenig. 1998. Testing and viewing symmetry in contingency tables, with application to readers of fish ages. *Biometrics* 54: 620-629.
- Goldman, K.J. & J.A. Musick. 2006. Growth and Maturity of salmon sharks in the eastern and western North Pacific, with comments on back-calculation methods. *Fish. Bull.* 104: 278-292.

- Hoening, J.M. 1995. Analysing differences between two age determination methods by tests of symmetry. *Can. J. Fish. Aquat. Sci.* 52: 364-368.
- Joung, J.S., Y.Y. Liao & C.T. Chen. 2004. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in northeastern Taiwan waters. *Fish Res* 70: 83-96.
- Lawler, E.F. 1976. The biology of the sandbar shark, *Carcharhinus plumbeus*, (Nardo, 1827) in the lower Chesapeake Bay and adjacent waters. Virginia Institute of Marine Science Virginia Institute of Marine Science. 1976: 49.
- Musick, J.A. 1999. Ecology and Conservation of Long-Lived Marine Animals. Pages 1-10 in J.A. Musick, editor. *Life in the slow lane: Ecology and Conservation of Long Lived Marine Animals. Symposium 23.* American Fisheries Society, Bethesda, Maryland.
- Natanson, L.J., J.G. Casey & N.E. Kohler. 1995. Age and growth estimates of the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fish. Bull.* 93: 116-26.
- Quinn II, J.T. & R.B. Deriso. 1999. *Quantitative fish dynamics.* Oxford University Press, Oxford, England.
- Ricker, W.E. 1975. Computation and Interpretation of Biological Statistics of fish Populations. *Bulletin of the Fisheries Research Board Canada* 191: 1-382.
- Sminkey, T.R. & J.A. Musick. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* 4: 871-883.
- Sminkey, T.R. & J.A. Musick. 1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.* 94: 341-347.

Springer, S. 1960. Natural history of the sandbar shark, *Eulamia milberti*. U. S. Fish.

Wildl. Fish. Bull. 61: 38 pages.

von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth

laws. II). Hum. Biol. 10: 181-213.

Wass, R.C. 1973. Size, growth and reproduction of the sandbar shark, *Carcharhinus*

*milberti*, in Hawaii. Pacific Science 27: 305-318.

*Table 1.* Estimates of model parameters and goodness of fit statistics for models fitted to length-at-age data for male and female sandbar sharks. All length values are for pre-caudal length (PCL) in cm. Values in parentheses are 95% confidence intervals. (VB= von Bertalanffy 3- parameter model with  $t_0$  term, VB2= von Bertalanffy 2-parameter model with empirical length at birth ( $L_0$ ),  $L_0$ = average measured length at birth used in VB2 and Gompertz growth models only, AIC=Aikake's Information Criteria, MSE=Mean Square Error, SD=standard deviation, na= not applicable)

	Model	$L_\infty$ (cm)		$t_0$	$L_0$ (cm)		$r^2$	MSE	SD of residuals
		PCL)	$k$ (year <sup>-1</sup> )		PCL)	AIC			
<b>Males</b>	VB	151.1(±16.3)	0.09(±0.03)	-5.01(±1.02)	na	2639	0.951	33.75	5.74
	VB2	138.5(±9.7)	0.12(±0.02)	na	47	3381	0.994	42.74	6.31
	Gompertz	130.4(±6.6)	0.19(±0.03)	na	47	3780	0.993	47.80	6.58
	Logistic	134.3(±7.5)	0.19(±0.03)	1.98(±0.66)	na	2740	0.995	35.05	5.85
<b>Females</b>	VB	164.9 (±14.9)	0.08(±0.02)	-5.26(±1.08)	na	5307	0.943	51.97	7.14
	VB2	152.8(±8.8)	0.10(±0.02)	na	47	6406	0.994	62.16	7.72
	Gompertz	143.5(±5.6)	0.17(±0.02)	na	47	6976	0.995	67.69	7.98
	Logistic	146.4(±6.4)	0.17(±0.02)	2.66(±0.61)	na	5278	0.995	51.69	7.12

*Table 2.* Mean size at age for male and female sandbar sharks. All lengths are PCL (cm), SD=standard deviation, and na=not applicable.

	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
<b>Females</b>																								
PCL (cm)	53.5	63.9	72.0	79.6	74.5	88.5	90.9	103.7	99.0	105.3	117.4	124.3	124.3	124.3	121.7	131.1	139.0	135.0	137.0	133.0	142.0	137.0	141.0	146.0
SD	5.3	3.4	6.1	7.6	2.1	4.4	6.5	10.0	10.3	7.6	13.5	7.3	12.3	11.9	2.3	4.3	na	3.4	6.0	na	na	na	8.5	na
<i>n</i>	11	8	11	5	2	4	8	3	4	4	5	4	4	3	3	8	1	4	7	1	1	1	2	1
<b>Males</b>																								
PCL (cm)	50.9	63.4	70.3	76.5	81.3	83.5	89.3	93	99.6	100	114	120	118	117	132	119	131	128	125	128				
SD	3.12	3.52	5.05	9.47	4.86	4.8	6.89	na	8.26	na	5.77	na	6.8	10.4	na	na	na	1.41	na	na				
<i>n</i>	14	12	9	4	4	4	6	1	5	1	5	1	5	3	1	1	1	2	1	1				

*Figure 1.* Sampling area on the windward coast of Oahu. All sharks used for age and growth were captured within the rectangle noted as sampling area.

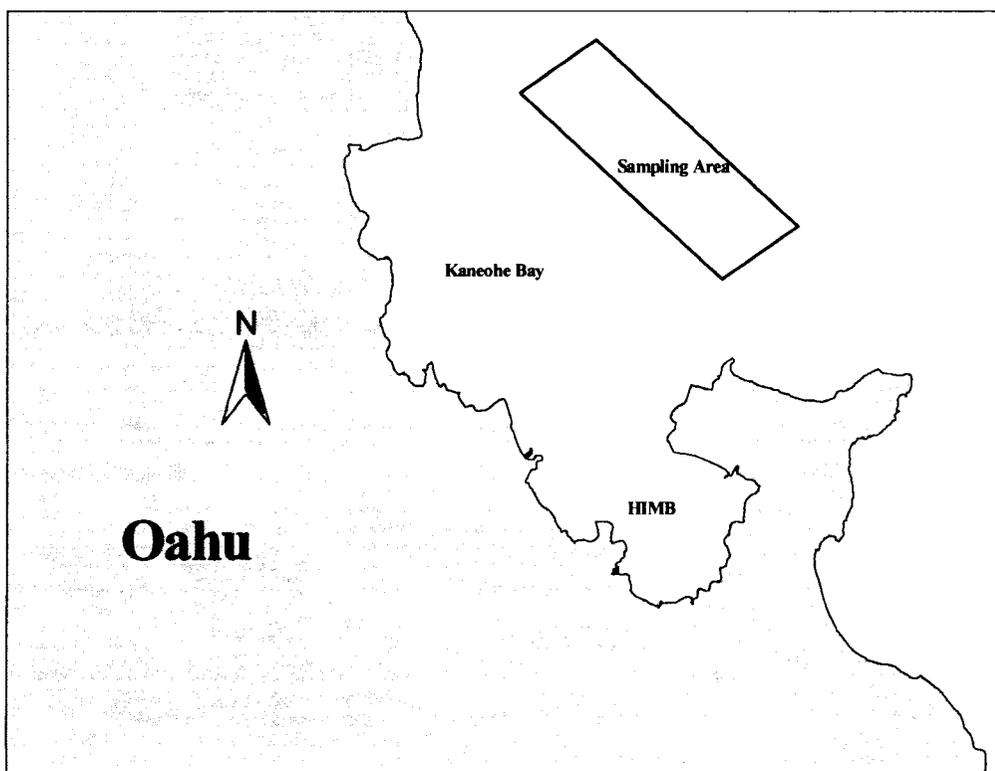
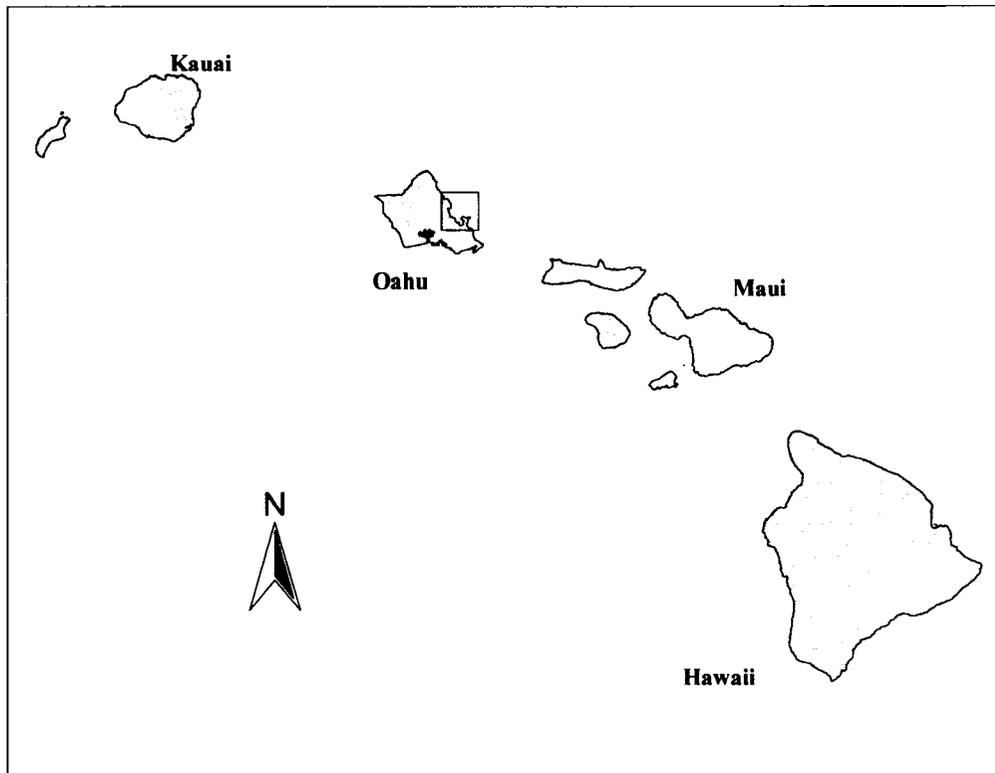


Figure 2. Size frequency of sandbar sharks used for age and growth in this study.

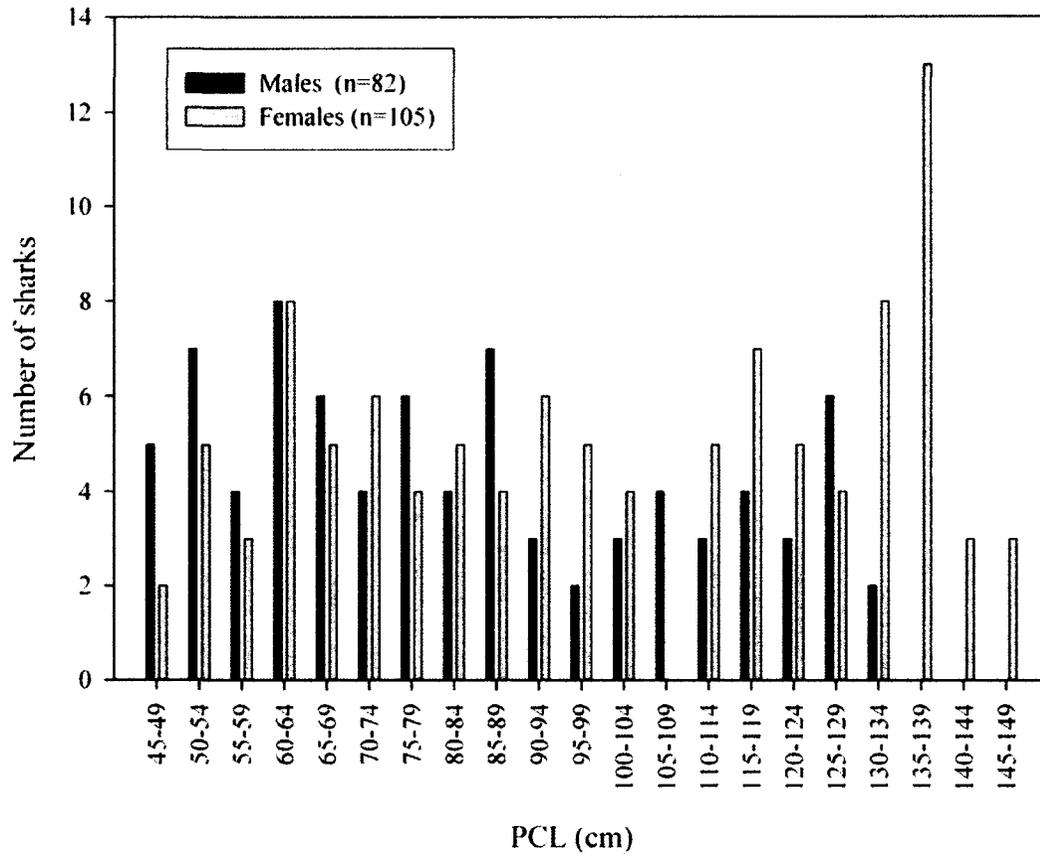


Figure 3. Regression of pre-caudal length and centrum radius ( $r^2=0.97$ ,  $n=148$ ) for males and females combined.

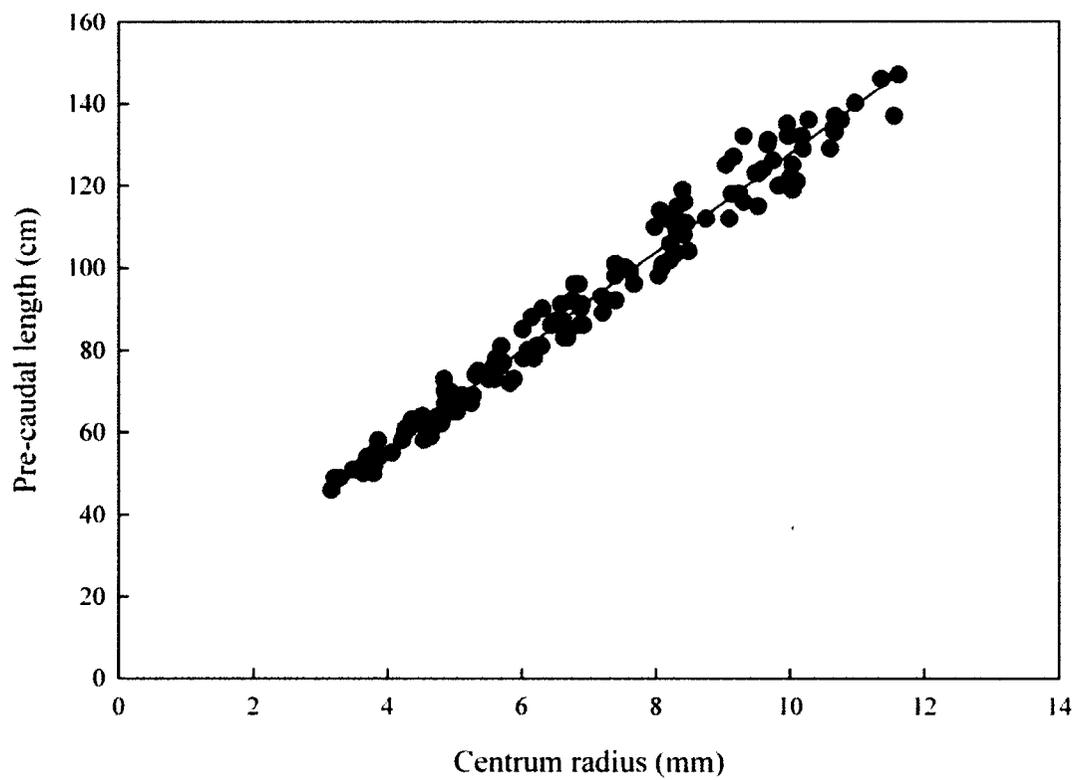


Figure 4. Mean marginal increment ratio monthly values and standard deviation of the monthly means for both sexes combined.

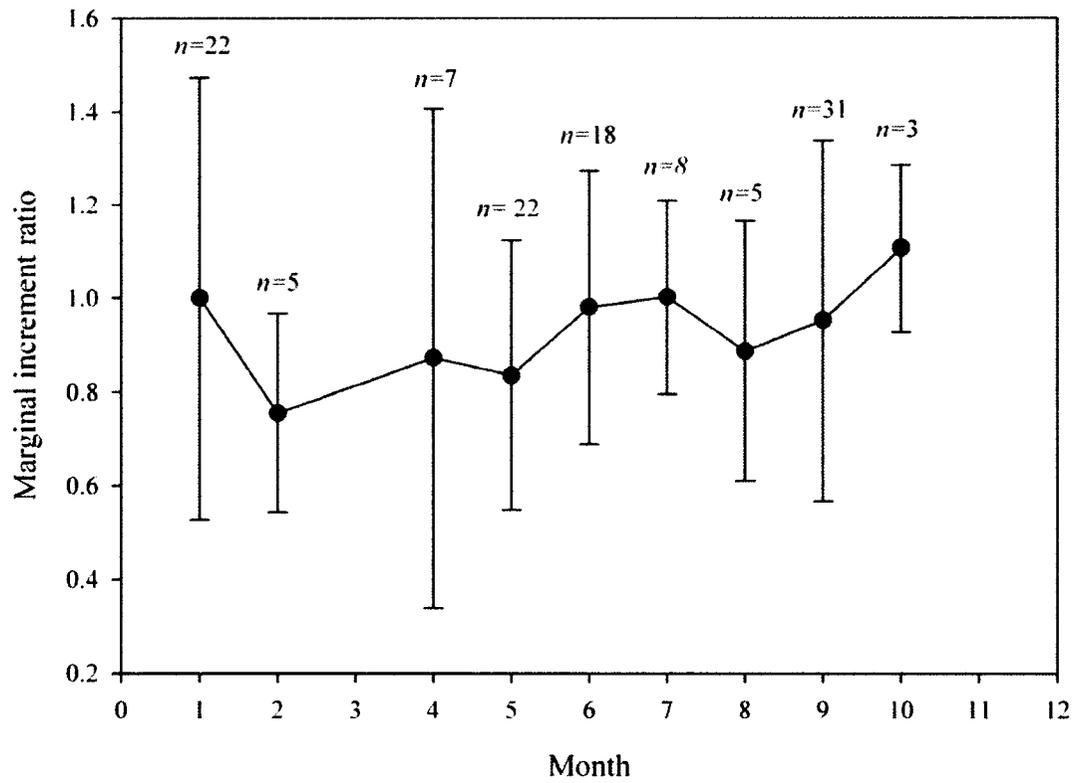


Figure 5. Length-at-age estimates and growth models fitted to data for male sandbar sharks ( $n=81$ ).

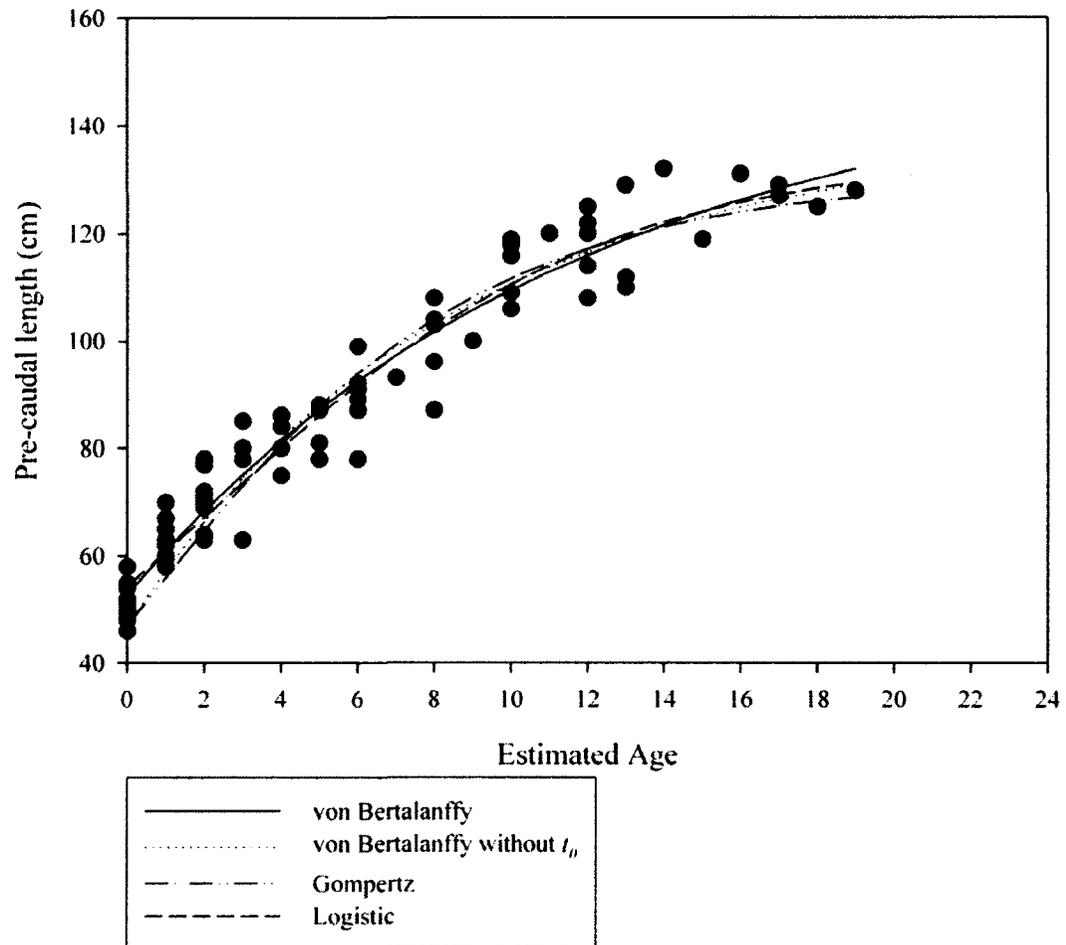
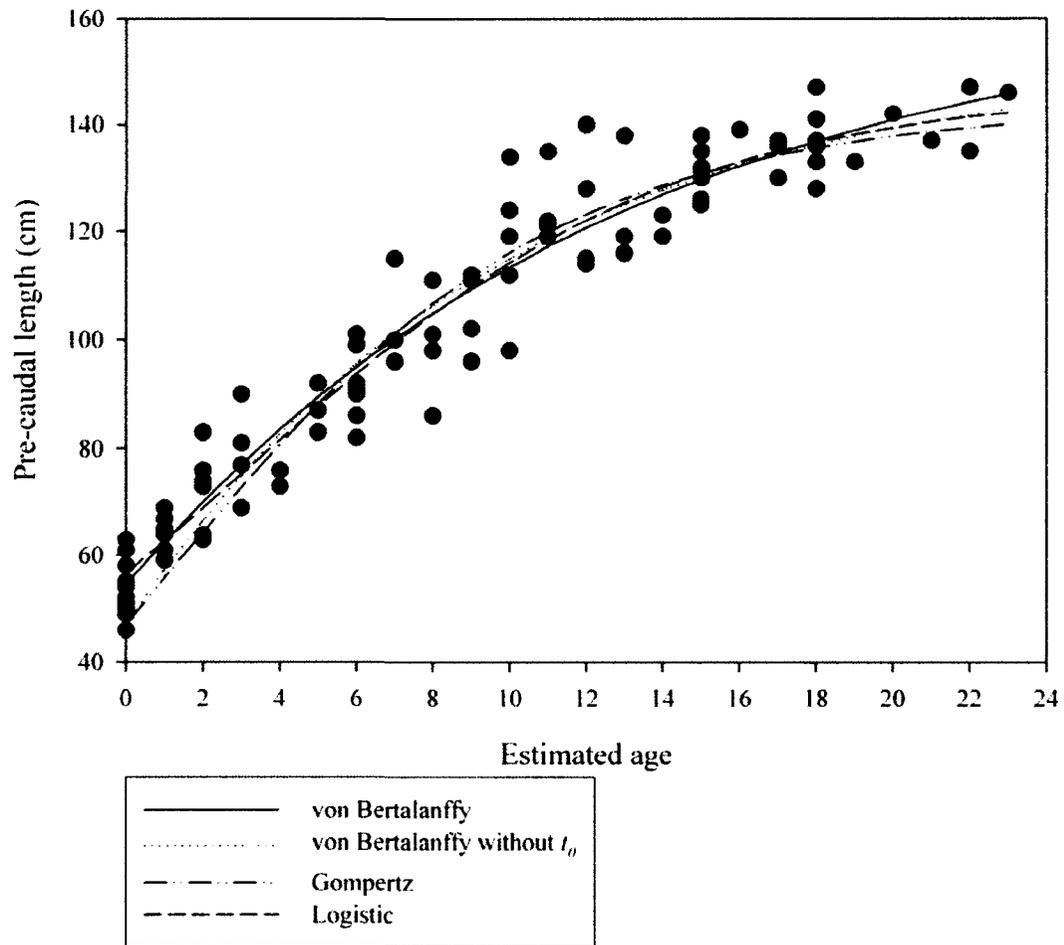


Figure 6. Length-at-age data and fit of growth models to the data for female sandbar sharks ( $n = 105$ ).



## **Chapter 5**

**Demographic analyses of the sandbar shark over temporal and spatial scales.**

**Abstract**

The population of sandbar sharks in the Hawaiian Islands is an unfished population. This presents a unique opportunity to conduct demographic analyses on a virgin population of sandbar sharks. Most populations of sandbar sharks have been heavily exploited due to near coastal and estuarine habitat preferences and high demand for fins. Conversely the population of sandbar sharks in the Northwest Atlantic (NWA) has suffered severe declines since the early 1980's. Previous studies have suggested compensatory growth is occurring within this population, but the true effect at the population level has not been estimated. Life history parameters estimated for the Hawaii population, the NWA population in 1980-1981 and 2000-2004 time periods were used in stochastic age-based life tables and Leslie matrices to estimate demographic parameters. Yield recruit<sup>-1</sup> relationships were estimated for the Hawaii population to determine optimal harvest strategies that would maintain a population at equilibrium. Population growth for the Hawaii population was estimated to be 1.014 year<sup>-1</sup>. Yield recruit<sup>-1</sup> analyses suggested harvest of sharks 15 years of age and older would provide the greatest yield while not causing population decline. Population growth for sandbar sharks in the NWA was 1.009 year<sup>-1</sup> for the 1980-1981 time period and 1.030 year<sup>-1</sup> for the 2000-2004 time period.

## Introduction

The sandbar shark, *Carcharhinus plumbeus*, is a common large coastal shark inhabiting near coastal waters throughout its tropical to subtropical worldwide distribution (Compagno et al., 2005). The species inhabits insular shelf habitats to depths of approximately 250m. Little is known of the species inhabiting waters adjacent to the Hawaiian Islands in the central Pacific. Wass (1973) studied life history aspects as well as growth rates of captive animals. Romine et al. (2006) investigated the age and growth of these sharks through vertebral analyses. Still, little is known regarding seasonal movements around or between islands.

Throughout most the sandbar shark's range the species is commercially harvested due to its rather large fins, ease of accessibility, and marketability of its flesh. The Hawaii population of sandbar shark is one of the few populations that is not commercially harvested due to the prohibition of longlining within the near coastal waters of Hawaii, of which this species appears to be constrained to. Although there is no present directed shark fishery the species accounted for a high percentage of catch during the shark removal programs which operated for six years between 1959 and 1976, but since that time have not experienced any substantial fishing mortality (Wetherbee et al., 1994). The lack of a directed fishery creates a unique opportunity to conduct demographic analyses on a supposed virgin sandbar shark population. Standard stock assessment models are not a viable method of assessment given the lack of catch and effort data. Data that do exist for sandbar abundance in Hawaii are biased due to the nature of the shark control programs. Given that the population is not subjected to fishing mortality, population increase should be approximately zero or in an equilibrium state where losses are

countered by replacements. This is a rarity among sandbar shark stocks given the high value of shark fins.

Demographic analyses of elasmobranchs are often undertaken to provide estimates of population growth and vulnerability to fishing mortality to managers when little data exist for population parameters (Cailliet, 1992; Mollet and Cailliet, 2002; Simpfendorfer, 2004; Cortes, 2007; Gedamke et al., 2007). Often estimates generated from demographic analyses are used as priors for more complex stock assessment models. These analyses also attempt to provide guidelines as to which portions of the population need greatest protection (Mills et al., 1999; Heppell et al., 2000; Cortés, 2002). Although these studies are important and provide some insight into the productivity, often many factors complicate the interpretation of the results. Namely, studies often examine exploited populations where density-dependent responses to exploitation are assumed to occur, yet life table analysis assumes density-independence and constant values for life history parameters across time. This is an inherent problem with these type of analyses (Cortes, 2007; Gedamke et al., 2007). The largest unknown in these types of analyses is that of natural mortality schedule across ages. Many theoretical estimates of natural mortality assume constant levels of mortality across all age classes despite obvious changes in size that likely lead to reduction in mortality. Also increased mortality in the late adult stage of life is often not accounted for in many studies. Walker (1998) produced one of the few studies on elasmobranchs to incorporate higher mortality levels at the youngest and oldest ages.

Gallucci et al. (2006) utilized Reproductive Potential (RP) removal to compare juvenile and adult harvest strategies that would lead to stationary populations. This

method is similar to elasticity analysis, but the use of RP allows for application to abundance and may be used in place of fishing effort due to its direct relationship with population change. This method also enables comparison of yield recruit<sup>1</sup> and the cost in terms of fraction of RP removed from the population due to harvest.

Little is known about the sandbar shark population in the Hawaiian Island chain. Catch data that exist are biased due to the lack of random and consistent effort during the shark control programs time period. Knowledge of the movements and natural mortality of the sandbar shark is non-existent and can only be hypothesized from shark control program data. These factors make a demographic analysis of the sandbar shark the only available method to estimate population parameters and the effects of fishing on this population. Prior estimates are necessary should a fishery open for sandbar sharks in Hawaii.

Opposite to the sandbar shark population in Hawaii, the population in the Northwest Atlantic has been severely overfished and fishery closures have recently been put in place. The catch of the commercial shark fishery along the eastern U.S. was primarily sandbar shark and blacktips shark, *Carchachrinus limbatus*. Due to its commercial value and the extensive fishery, many researchers have conducted population analyses on the sandbar shark in the Northwest Atlantic. Sminkey and Musick ( ) found differences in length at age for juvenile age classes when between times of high and low shark abundance. Romine et al. (in prep) found significant differences in growth parameters between the 1980-1981 and 2000-2004 times periods, suggesting compensatory responses to fishing. Although significant differences were found it is not apparent whether these differences have any true affect on population growth.

In this study we estimate demographic parameters for the sandbar shark in Hawaii from published and unpublished life-history parameters using both Life-tables and Leslie matrices. We will also use various levels of fishing mortality applied to the Hawaii population to investigate possible response to fishing if a fishery was to develop. We will also conduct demographic analyses of the sandbar shark in the Northwest Atlantic using life history parameters estimated during levels of greater and lesser abundances to examine the possible effects of compensatory changes in life history parameters and their effect on population growth.

### ***Materials and Methods***

Age structured life tables and Leslie matrices that included probability distributions for demographic parameters were used to estimate population growth rates, generation times, and elasticities for all three populations 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 produce error estimates for these parameters.

Life-tables were constructed for females using a yearly time step to produce estimates of annual population growth ( $\lambda = e^r$ ), calculated from rates of population increase ( $r$ ) by iteratively solving the Euler equation. Net reproductive rate ( $R_0$ ), Generation time ( $\bar{A}$ ), distribution of reproductive values ( $v_x$ ), stable age distribution ( $c_x$ ), mean life expectancy, and population doubling or halving time were also calculated.

Demographic parameters used in life-table analyses were those produced by this study, published, and unpublished data. Probability distributions were created for demographic parameters to compensate for variation in following parameters: maximum age ( $T$ ), fecundity ( $m_x$ ), survivorship at age ( $S_x$ ), and maturity ogive function location parameter ( $a$ ) (Mills et al., 1999; Cortés, 2002; Goldman, 2002). The incorporation of variability within model inputs produces confidence intervals for output values (Table 1,2,3).

Maximum age was assumed to be normally distributed about the maximum estimated age. Female sandbars sharks were designated as mature or immature based on uterine width, egg size, and presence of embryos. The logistic function,

$$\text{Proportion mature}_x = \frac{1}{(1 + e^{-(a+bx)})},$$

was fit to binomially distributed data where  $a$  and  $b$  are location and shape parameters (Mollet et al., 2002). Within model simulations the location parameter ( $a$ ) of the logistic function was assumed to be normally distributed. The slope parameter ( $b$ ) was held constant. Fecundity estimates used in the models were derived from this study. A best-fit normal probability distribution was fit to litter size frequency data. Female specific fecundity or  $m_x$  was calculated as the number of females born per female per reproductive cycle. A two-year reproductive cycle was used in these analyses.

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), Jensen based on age at

maturity ( $t_{mat}$ ) and based on  $k$  (Jensen, 1996). Uniform probability distributions for survivorship were bounded by minimum and maximum values calculated from the 5 methods. Both uniform and beta probability distributions were used for survivorship for the Hawaii model.

A uniform probability distribution was created for the age-0 cohort. The lower bound of this distribution was the survival value that would create a population at equilibrium given mean estimates of other model parameters. The upper bound of the distribution was set equal to the mean survivorship of the age-1 cohort (Gedamke et al., 2007). Monte Carlo simulations were used to randomly sample from probability distributions created for demographic parameters that possessed a level of uncertainty within the reported values using Crystal Ball software. Confidence intervals were reported as the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentiles after simulations had been run.

Leslie matrices were used to estimate sensitivities of population growth to changes in model parameters. Elasticity of  $\lambda$  to survival of newborns, juveniles, and adults were also estimated (Caswell, 2001). The effect of fishing on population growth of the Hawaii population was estimated in terms of annual fraction of Reproductive Potential (RP) removed,  $\Phi$ , following methods Gallucci et al. (2006). RP was estimated by summation of the inner product (Reproductive Value) of the projection matrix. The projection matrix was multiplied by a harvest matrix to produce a projection matrix which included fishing mortality. Yield recruit<sup>-1</sup> isopleths were constructed for varying harvest strategies at stable age distributions for various levels of  $\Phi$ . Matrix manipulations were run in Microsoft excel with the Poptools and Solver add-ins.

## Results

### *Maturity Hawaii*

Age at 50% maturity was estimated from 82 female sandbar sharks. Age at which 50% of the female sharks were mature was 9.09 years of age and 115cm PCL (Figure 1). Litter size averaged 5.5 pups female<sup>-1</sup> and the sex ratio was approximately 1:1. The relationship between length and litter size was not significant.

### *Hawaii Demography*

All methods of natural mortality estimation portrayed a population close to equilibrium (Table 4). Population growth rate estimates varied between natural mortality estimation methods. The Peterson and Wroblewski (1984) method estimated the lowest annual population growth (1.010 year<sup>-1</sup>) and the Jensen (1996) growth coefficient method estimated the highest population growth (1.055 year<sup>-1</sup>). When mortality methods for each age class were averaged and  $S_0$  was set to the average of  $S_0$  that would place the population at equilibrium and the median  $S_l$  value, population growth was 1.014 year<sup>-1</sup>.

Mean estimate of population growth from 5,000 Monte Carlo simulations was 1.014 year<sup>-1</sup> (Table 5). The Net reproductive rate was 1.2 year<sup>-1</sup>. The age zero cohort comprised 18% to 20% of the stable age distribution when fishing mortality was absent. The nine to 15 age classes comprised only 12% of the population, but accounted for 46%

of the RP. When the beta probability distribution was used for survivorship population growth was  $1.024 \text{ year}^{-1}$ .

Population growth was most sensitive to changes in the logistic maturity function location parameter ( $a$ , 0.88) and  $S_0$  (0.33). The mean elasticity of population growth to survival was highest for juveniles (58.73%, Table 6). Mean adult elasticity was 34.17% and mean fertility elasticity or survival of the age-zero cohort was 7.11%.

### *Hawaii Reproductive potential*

Using Hoenig's (1983) method of age invariant estimates of natural mortality, the fraction of reproductive potential removed that would leave the population at equilibrium was 0.022 (Table 7). The greatest Y/R attainable under equilibrium conditions was 2.1. This was attained by applying  $F = 1.64 \text{ year}^{-1}$  to ages 15 to 23 (Figure 2). Adult harvest strategies estimated Y/R values that were approximately twice the values of Y/R values from juvenile harvest strategies (Figure 3). The population could withstand greater fishing mortality and remain at equilibrium under adult harvest strategies. Maximum Y/R was attained when  $t_c = 6$  and  $\Phi$  was greater than 0.12 signifying a declining population under this harvest strategy.

Age variant estimates of natural mortality were also used in RP analyses. The level of  $\Phi$  that could be removed under conditions set was 0.015. The greatest Y/R attainable under equilibrium conditions was 1.64 and accomplished by harvesting 17 to 23 age classes at  $F = 2.87 \text{ year}^{-1}$ .

### *NWA Demography*

Mean population growth for the 1980 and 2000 models were  $1.009 \text{ year}^{-1}$  and  $1.030 \text{ year}^{-1}$  respectively (Table XX). Net reproductive rate,  $R_0$ , was 1.22 for 1980 and 1.70 for 2000 models. Mean life expectancy for the 1980 model was 19.4 years and 17.3 for the 2000 model. Elasticity analyses yielded similar results for both time periods. The mean elasticity of population growth to survival was highest for juvenile survival and lowest for survival of the age-zero cohort. Population growth was most sensitive to changes in the location parameter of the logistic growth function and age-zero survivorship. Mean age at 50% maturity for the 1980 model was 14.98. Minimum and maximum values were 12.48 and 17.47. Mean age at 50% maturity for the 2000 model was 12.49 years. Minimum and maximum values were 9.26 and 15.71 years.

### **Discussion**

In this paper we provided demographic population estimates for the sandbar shark in Hawaii. This population is free from fishing and thus should be representative of a population near equilibrium condition. As such we examined all methods of mortality estimation to determine which method would place the population at equilibrium given other life history parameters. Many of these methods are static and do not account for changes in length and size over the life span of the organism which likely correlate to changes in survival. Application of the Peterson and Wroblewski (1984) method to all ages estimated population growth to be near stationary. This method estimated

population growth to be  $1.010 \text{ year}^{-1}$ . Other methods estimated population growth to be in excess of  $1.021 \text{ year}^{-1}$ .

Estimates of finite rate of population growth for the sandbar shark in the NWA were  $0.009$  and  $0.024 \text{ year}^{-1}$  for the 1980 and 2000 models respectively. Our estimates fall within the range of other studies conducted on this population. Previous estimates of  $r$  for the NWA have ranged from  $-0.019$  –  $0.119$  (Hoff and Musick, 1990; Sminkey and Musick, 1996; Au and Smith, 1997; Cortés, 1998; Cortés, 1999). Romine et al. (in prep) found significant differences in growth and reproductive parameters between the 1980 and 2000 time periods. Placing these values in demographic models resulted in a  $0.015 \text{ year}^{-1}$  difference in finite rate of population growth. Although small, this difference translates to a large difference over greater time periods. These models were most sensitive to the location parameter of the logistic growth function and age-0 survival, followed by survival and fecundity in the late juvenile ages. The difference between the two population growth rates is likely due to the shift in age at 50% mature.

We used two distributions to depict age specific survivorship. McAllister et al. (2001) suggesting using the beta probability distribution to depict survivorship instead of a uniform distribution. Our results show that use of the uniform distribution actually led to a more conservative estimate of  $r$ , despite equality of means for both distributions. The parameterization of the beta distribution was similar to that used by McAllister et al. (2001) for the sandbar shark in the Northwest Atlantic. It is likely that different parameterization for the beta distribution would produce widely different results on estimates of population growth. Using an unbounded beta distribution allows for potentially unrealistic survivorship estimates even though these will have low

probabilities. Given the uncertainty and probable inter-annual variation in survivorship giving equal probabilities to a range of survivorship estimates based on theoretical methods may provide a more reasonable approach. Other researchers have advocated the use a triangular distribution to describe survivorship probability distributions when conducting stochastic demographic analyses with little justification (Cortés, 2002; Aires-da-Silva and Gallucci, 2007).

McAuley et al. (2007) conducted deterministic demographic analyses on the sandbar shark found in the waters of Western Australia. This study estimated population growth of  $1.025 \text{ year}^{-1}$  in the absence of fishing. The population is subject to fisheries that primarily harvest sharks three to nine years of age. When fishing mortality was incorporated into their analyses population change was negative for all scenarios investigated. This is intuitive from our analyses of RP removals on the sandbar shark in Hawaii. Fishing mortality greater than  $0.04 \text{ year}^{-1}$  on ages three to nine would result in population decline for the Hawaii population as well. McAuley et al. (2007) estimated fishing mortalities to range from  $0.10$  to  $0.28 \text{ year}^{-1}$  over three time periods.

As with many populations of long-lived elasmobranchs, the sandbar shark in Hawaii may not withstand levels fishing pressure applied across all age classes. Juveniles and young adults had the greatest contribution to population growth as estimated through both elasticity analyses and RP analyses. Protection of juveniles and young adults until they have reproduced appears to be the best management strategy for this population of sandbar sharks.  $F$  greater than  $0.14 \text{ year}^{-1}$  applied to two or more juvenile age classes resulted in population decline. Sminkey and Musick (1996) suggested a minimum size limit of 135 cm PCL and  $F=0.24 \text{ year}^{-1}$  for the sandbar shark

in the Northwest Atlantic would be a sustainable harvest strategy. Gallucci et al. (2006) suggested harvest strategies which removed adults rather than juveniles were more advantageous in terms of Y/R for both the spiny dogfish, *Squalus ancanthias*, and the Australian sharpnose shark, *Rhizoprionodon taylori*. These species are at opposite ends of the growth and longevity spectrum. Simpfendorfer (1999) showed that fishing the youngest age class of the dusky shark, *Carcharhinus obscurus*, may also be an appropriate harvest strategy. It should be noted that this strategy is only applicable if the youngest age classes are harvested. Additional minimal mortality of older age classes would lead to population decline. Targeting older age classes, although conservative, may provide the greatest benefit to fishers and preservation of this stock.

Future population dynamics studies on the sandbar shark in Hawaii would greatly improve our knowledge of shark stocks elsewhere by providing a base for natural mortality estimates which could be applied to other populations. The literature is extremely lacking in terms of empirical mortality estimates for elasmobranchs. The population is easily accessible, not fished, and is constrained to near shore waters of the Hawaiian Islands.

## References

- Aires-da-Silva, A.M. & V.F. Gallucci 2007. Demographic and risk analyses applied to management and conservation of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. *Mar Fish Res* 58: 570-580.
- Au, D.W. & S.E. Smith 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Can. J. Fish. Aquat. Sci.* 54: 415-420.
- Cailliet, G.M. 1992. Demography of the central California population of leopard shark (*Triakis semifasciata*). *Aust J Mar Freshw Res* 43: 183-193.
- Caswell, H. 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Sunderland, Massachusetts. 722 pp.
- Compagno, L., M. Dando & S. Fowler 2005. *Sharks of the world*. Princeton University Press, Princeton, NJ, USA. 368 pp.
- Cortes, E. 2007. Chondrichthyan demographic modelling: an essay on its use, abuse and future. *Marine & Freshwater Research* 58: 4-6.
- Cortés, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fish Res* 92: 199-208.
- Cortés, E. 1999. A Stochastic Stage-Based Population Model of the Sandbar Shark in the Western North Atlantic. Pages 115-136 in J.A. Musick, editor. *Life in the slow lane: Ecology and Conservation of Long Lived Marine Animals*. Symposium 23. American Fisheries Society, Bethesda, Maryland.
- Cortés, E. 2002. Incorporating Uncertainty into Demographic Modeling: Application to Shark Populations and Their Conservation. *Conserv Biol* 16: 1048-1062.
- Gallucci, V.F., I.G. Taylor & K. Erzini 2006. Conservation and management of exploited shark populations based on reproductive value. *Can J Fish Aquat Sci* 60: 931-942.

- Gedamke, T., J.M. Hoenig, J.A. Musick, W.D. DuPaul & S.H. Gruber 2007. Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. *N Am J Fish Mgmt* 27: 605-618.
- Goldman, K.J. 2002. Aspects of age, growth, demographics and thermal biology of two lamniform shark species. Dissertation, The College of William & Mary, School of Marine Science, Virginia Institute of Marine Science.
- Heppell, S., C. Pfister & H. de Kroon 2000. Elasticity analysis in population biology: Methods and applications. *Ecol* 81: 605-606.
- Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish Bull* 82: 898-903.
- Hoff, T.B. & J.A. Musick 1990 Western North Atlantic shark-fishery management problems and informational requirements In: J. H.L. Pratt, S.H. Gruber, & T. Taniuchi (ed.) *Elasmobranchs as Living Resources: Advances in the biology, ecology, systematics, and the status of the fisheries*, NOAA Tech. Rep. NMFS 90
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can J Fish Aquat Sci* 53: 820-822.
- McAllister, M.K., E.K. Pikitch & E.A. Babcock 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Can J Fish Aquat Sci* 58: 1871-1890.
- McAuley, R.B., C.A. Simpfendorfer & N.G. Hall 2007. A method for evaluating the impacts of fishing mortality and stochastic influences on the demography of two-long-lived shark stocks. *ICES J Mar Sci* 64: 1710-1722.
- Mills, L.S., D.F. Doak & M.J. Wisdom 1999. Reliability of conservation actions based on elasticity analysis of matrix models. *Conserv Biol* 13: 815-829.
- Mollet, H.F. & G.M. Cailliet 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. *Mar Freshw Res* 53: 503-516.

- Mollet, H.F., J.M. Ezcurra & J.B. O'Sullivan 2002. Captive biology of the pelagic stingray, *Dasyatis violacea* (Bonaparte, 1832). *Mar. Freshwater. Res.* 53: 531-541.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil International pour l'Exploration de la Mer* 39: 175-192.
- Peterson, I. & J.S. Wroblewski 1984. Mortality rate of fishes in the pelagic ecosystem. *Can J Fish Aquat Sci* 41: 1117-1120.
- Romine, J.G., R.D. Grubbs & J.A. Musick 2006. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, in Hawaiian waters through vertebral analysis. *Envir Bio Fish* 77: 229-239.
- Simpfendorfer, C. 1999 Demographic analysis of the dusky shark in southwestern Australia. In: J.A. Musick (ed.) *Life in the slow lane: Ecology and conservation of long-lived marine animals*, American Fisheries Society, Bethesda pp. 149-160
- Simpfendorfer, C. 2004 Demographic Models: Life Tables, Matrix Models and Rebound Potential. Pages 187-203. In J.A. Musick and R. Bonfil, editors. *Elasmobranch Fisheries Management Techniques*, Asia Pacific Economic Cooperation, Singapore:370 pp. (electronic publication available at: [www.flmnh.ufl.edu/fish/organizations/ssg/ssg.htm](http://www.flmnh.ufl.edu/fish/organizations/ssg/ssg.htm))
- Sminkey, T.R. & J.A. Musick 1996. Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic. *Fish. Bull.* 94: 341-347.
- Walker, T.I. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* 49: 553-572.
- Wass, R.C. 1973. Size, growth and reproduction of the sandbar shark, *Carcharhinus milberti*, in Hawaii. *Pacific Science* 27: 305-318.
- Wetherbee, B.M., C.G. Lowe & G.L. Crow 1994. A review of shark control in Hawaii with recommendations for future research. *Pac. Sci.* 48: 95-115.

Table 1. Life history parameters and probability distributions for Hawaii model.

	<b>Parameter</b>	<b>Mean</b>	<b>S.D.</b>	<b>Range</b>	<b>Distribution</b>
<b>Asymptotic length</b>	$L_{\infty}$	153 cm PCL			Held constant
<b>Growth Coefficient</b>	$k$	0.1			Held constant
<b>Age at zero length</b>	$L_0$	47			Held Constant
<b>Maximum Age</b>	$\omega$	23	1.2	19-28	Lognormal
<b>Age at 50% mature</b>	$t_{mat}$	9.09	1.65		Normal
<b>Logistic maturity function</b>	$a$	-7.0438	1.7479	-9.63- -4.46	Normal
	$b$	0.7745	0.1975		Held constant
<b>Fecundity</b>	$m$	5.5	1.450	1-8	Normal distribution
<b>Sex ratio in litters</b>		1:1			Held constant
<b>Survivorship</b>	Age 0	0.693 year <sup>-1</sup>		0.570-0.815	Uniform
<b>Survivorship</b>	Age 23	0.855year <sup>-1</sup>		0.834-0.876	Uniform

Table 2. Life history parameters and probability distributions for NWA 1980 model.

	<b>Parameter</b>	<b>Mean</b>	<b>S.D.</b>	<b>Range</b>	<b>Distribution</b>
<b>Asymptotic length</b>	$L_{\infty}$	173cm PCL			Held constant
<b>Growth Coefficient</b>	$k$	0.084 year <sup>-1</sup>			Held constant
<b>Age at zero length</b>	$t_0$	-3.88			Held constant
<b>Maximum Age</b>	$\omega$	28 years	1.4	25-35	Lognormal
<b>Age at 50% mature</b>	$t_{mat}$	15.035 years	1.42	12.5-17.5	Normal
<b>Logistic maturity function</b>	$a$	-18.01	5.4177	-21- -15	Normal
	$b$	1.2019	0.3523		Held constant
<b>Fecundity</b>	$m$	8.4	2.3	1-14	Normal
<b>Sex ratio in litters</b>					Held constant
<b>Survivorship</b>	Age 1	0.864		0.775-0.896	Uniform
<b>Survivorship</b>	Age 28	0.879		0.862-0.896	Uniform

Table 3. Life history parameters and probability distributions for NWA 2000 model.

	<b>Parameter</b>	<b>Mean</b>	<b>S.D.</b>	<b>Range</b>	<b>Distribution</b>
<b>Asymptotic length</b>	$L_{\infty}$	163.26			Held constant
<b>Growth Coefficient</b>	$k$	0.10 year <sup>-1</sup>			Held constant
<b>Age at zero length</b>	$t_0$	-3.24			Held constant
<b>Maximum Age</b>	$\omega$	28	1.4	25-35	Lognormal
<b>Age at 50% mature</b>	$t_{mat}$	12.48			Normal
<b>Logistic maturity function</b>	$a$	-11.6018	4.75075	-14.6- -8.6	Normal
	$b$	0.9294	0.3763		Held constant
<b>Fecundity</b>	$m$	8.4	2.3	1-14	Normal
<b>Sex ratio in litters</b>		1:1			Held constant
<b>Survivorship</b>	Age 1	0.852		0.771-0.881	Uniform
<b>Survivorship</b>	Age 28	0.870		0.858-0.883	Uniform

Table 4. Natural mortality methods and population growth for Hawaiian sandbar sharks.

	Peterson and Wroblewski	Hoenig	Jenson ( $t_{mat}$ )	Jensen ( $k$ )
M	0.739 - 0.876	0.834	0.833956	0.860708
$\lambda$	1.010	1.022	1.022	1.055

Table 5. Results for analyses of all three populations based on life history parameters.

	$\lambda$	$r$	$\bar{A}$	$R_0$	Mean Life expectancy
<b>Hawaii</b>	1.014 (0.974-1.059)	0.013 (-0.026, 0.057)	13.098 (10.57, 15.65)	1.207 (0.673, 1.91)	13.3 (11.4, 15.4)
<b>NWA 1980</b>	1.009 (0.982, 1.04)	0.009 (-0.018, 0.038)	19.28 (16.94, 21.55)	1.22 (0.683, 1.97)	19.4 (17.5, 21.5)
<b>NWA 2000</b>	1.030 (0.983, 1.083)	0.029 (-0.018, 0.079)	16.739 (13.40, 19.86)	1.70 (0.712, 3.17)	17.3 (14.8, 19.8)

Table 6. Elasticities of population growth to survival of newborns, juveniles, and adults for Hawaii, NWA 1980 and NWA 2000 models.

	<b>Elasticities</b>		
<b>F</b>	<b>Newborns</b>	<b>Juvenile</b>	<b>Adults</b>
<b>Hawaii</b>	7.105 (5.93, 8.59)	58.73 (47.15, 69.43)	34.169 (24.61, 44.91)
<b>NWA 1980</b>	4.95 (4.43, 5.57)	70.91 (64.53, 77.19)	24.15 (18.17, 30.09)
<b>NWA 2000</b>	5.70 (4.79, 6.95)	66.45 (58.57, 73.69)	27.76 (22.49, 33.50)

Table 7. Stable population harvests for juvenile and adult harvest strategies.

Harvest	$t_c$	$t_e$	$F$	$\lambda$	Y/R	$\Phi$
<b>Unfished</b>	0	0	0	1.022	0	0
<b>Juvenile</b>	0	0	0.285	1	0.402	0.022
	0	1	0.143	1	0.492	0.022
	0	2	0.095	1	0.579	0.022
	0	3	0.071	1	0.656	0.022
	0	4	0.057	1	0.722	0.022
	0	5	0.048	1	0.776	0.022
	0	6	0.041	1	0.820	0.022
	0	7	0.036	1	0.855	0.022
	0	8	0.032	1	0.883	0.022
<b>ALL</b>	0	23	0.022	1	1.133	0.022
<b>Adults</b>	9	23	0.074	1	1.614	0.022
	10	23	0.096	1	1.711	0.022
	11	23	0.131	1	1.814	0.022
	12	23	0.187	1	1.917	0.022
	13	23	0.287	1	2.009	0.022
	14	23	0.515	1	2.074	0.022
	15	23	1.644	1	2.105	0.022
	16	23	**	1	**	**
	17	23	**	1	**	**
	18	23	**	1	**	**
	19	23	**	1	**	**
20	23	**	1	**	**	

Figure 1. Maturity ogive for female Hawaii sandbar sharks.

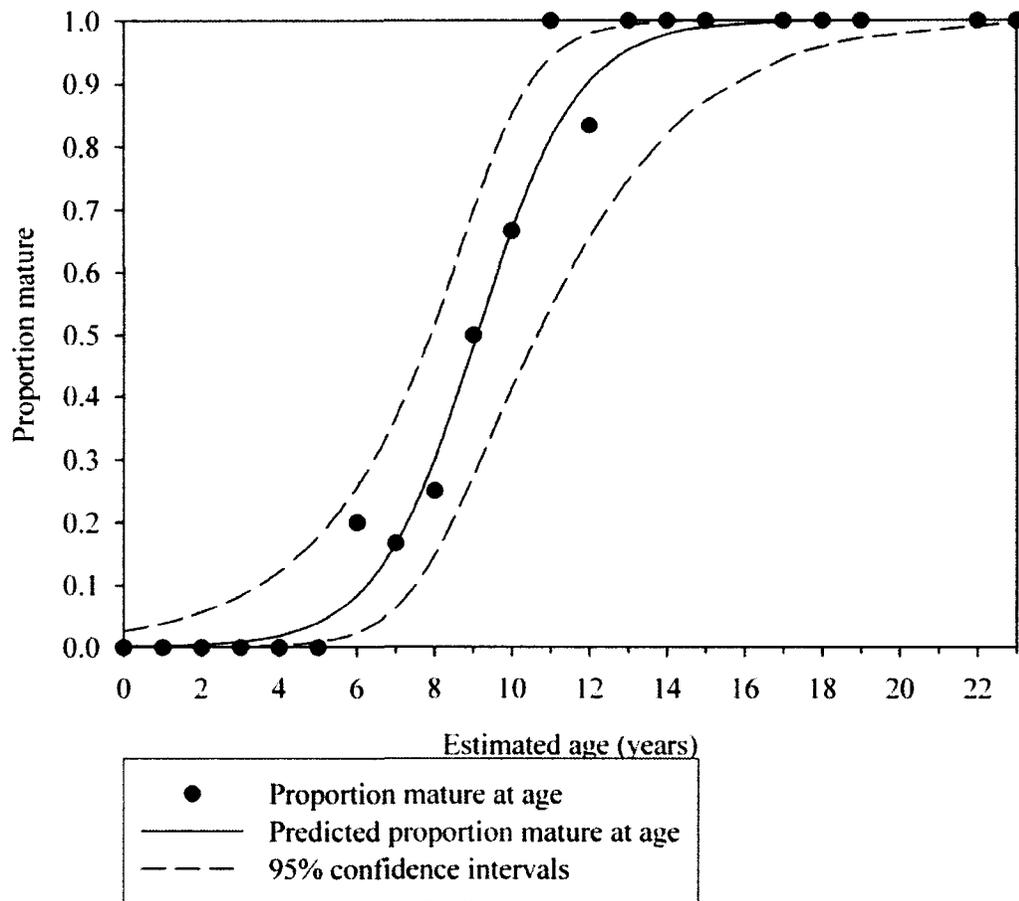


Figure 2. Yield recruit<sup>-1</sup> isopleths for age at first harvest and fraction of reproductive potential removed. Top axis depicts annual population change due to fraction of reproductive potential removed. Isopleths terminate at maximum possible F value.

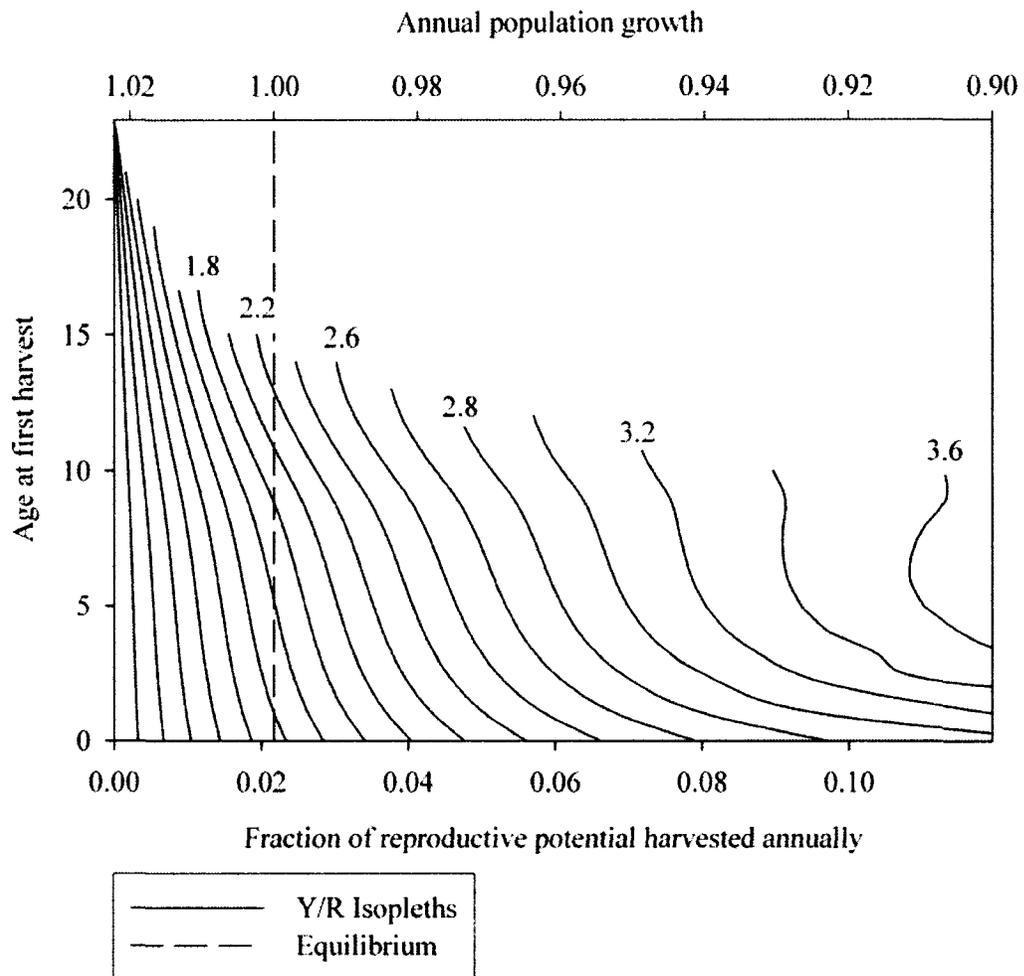
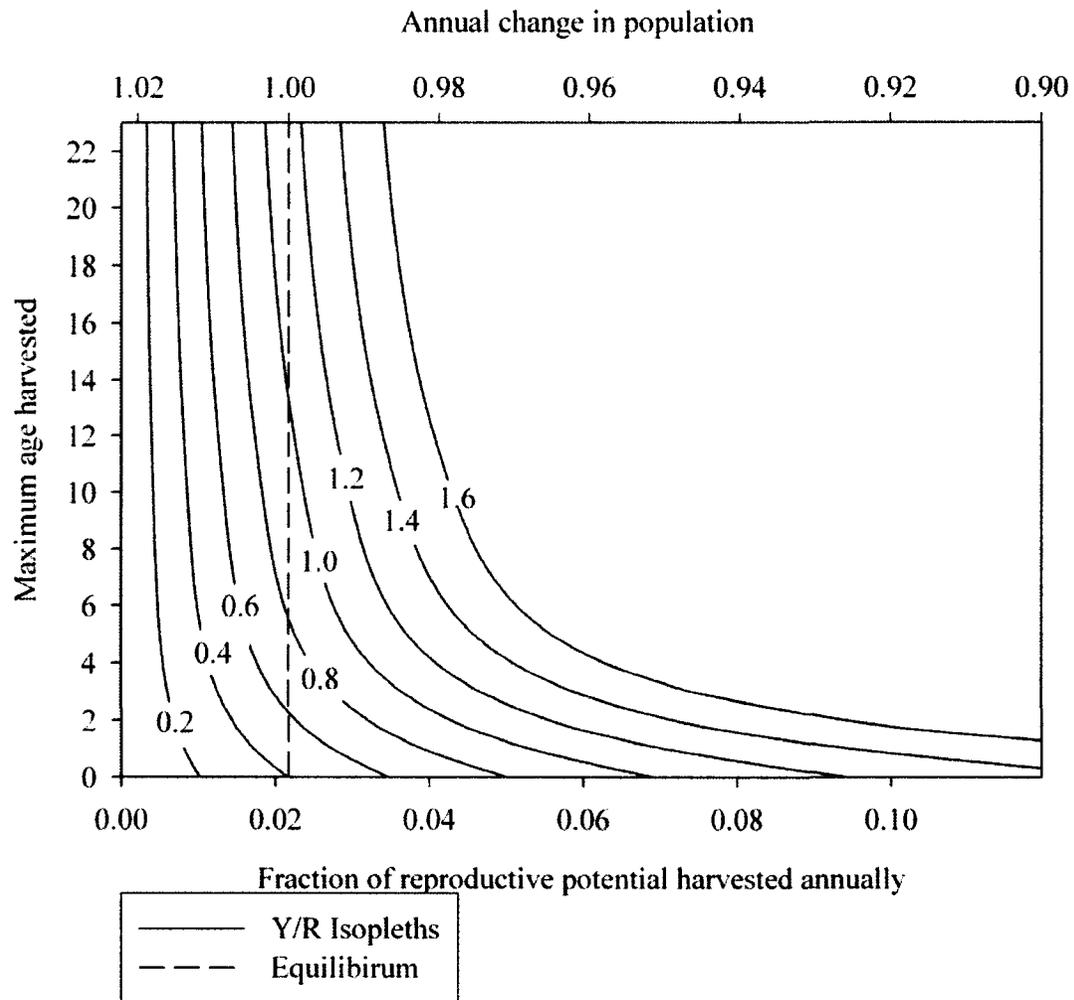


Figure 3. Yield recruit<sup>-1</sup> isopleths for maximum age harvested and fraction of reproductive potential removed. Top axis depicts annual population change due to fraction of reproductive potential removed.



**VITA**

Jason G. Romine

Born in Weisbaden, Germany on January 5, 1975. Graduated from Fauquier High School in Warrenton, Virginia in June 1993. Earned Bachelor of Science in Biology from the College of William & Mary in May 1997. Entered Master of Science program at the College of William and Mary, School of Marine Science in August 2000. Earned M.S. in August 2004. Entered PhD program at the College of William and Mary, School of Marine Science in August 2004.