

# UC San Diego

## Research Theses and Dissertations

### Title

Methods for Assessment of Data-Poor Shark Species

### Permalink

<https://escholarship.org/uc/item/2j77n0zc>

### Author

Chapple, Taylor K.

### Publication Date

2009

Peer reviewed

Methods for assessment of data-poor shark species

By

Taylor Kryst Chapple  
B.A. (Boston University) 2001

DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA  
DAVIS

Approved:

Louis W. Botsford

Suzanne Kohin

A. Peter Klimley

Committee in Charge

2009

UMI Number: 3401520

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI 3401520

Copyright 2010 by ProQuest LLC.

All rights reserved. This edition of the work is protected against unauthorized copying under Title 17, United States Code.



ProQuest LLC  
789 East Eisenhower Parkway  
P.O. Box 1346  
Ann Arbor, MI 48106-1346

## ACKNOWLEDGEMENTS

I'm pretty sure no one will ever read my dissertation except those of you that are, or believe you are, in my acknowledgements. I have a list miles long of all the people who made this whole dissertation possible. No paper pages could really express my great appreciation and since no length would actually do, I'll just keep it short for your benefit.

First, I'd like to thank Loo Botsford, the only Italian who doesn't follow soccer. Loo assumed a great risk in taking me on as a graduate student. Luckily for me, Loo was in Italy when I first spoke with him. I'm guessing he may have been a few casks of wine (or grappa) in when he offered me a spot in his lab. The other option, which my lab-mate, Liz Moffitt, will fully support, is that Loo had a better chance of remembering our names collectively as 'Liz Taylor.' Whatever his reasons may have been, I am incredibly grateful; I would not be the 'male-modeler' I am today without him. Loo was a great force in my education, both academic and personal. Loo was a wealth of knowledge, sometimes intimidatingly so, and always worked to make me a better scientist. Whether it was a Beverton-Holt stock recruitment model or the difference between standard deviation and standard error, Loo could explain it in 20 different ways (on occasion I actually validated this number). Even outside of the academic education, Loo was always incredibly compassionate. I now know that everything is better in Italy (except perhaps fisheries science). Loo helped me develop, not only as a scientist, but also as a person. For his guidance and mentorship I will always be thankful.

Throughout my time at Davis I was mentored by Pete Klimley. Pete's compassion and dedication for everything (e.g., science, students, soccer, wine, etc.) has been a

source of inspiration, and his mantra to always 'have a thick skin' has kept me going on many occasions. His guidance and constant debates about who the better soccer team/player is has been invaluable to me.

Suzy Kohin at NMFS dedicated a great deal of time and effort to my dissertation and has signed off on it! Barb Block provided great amounts of financial and logistic support, but more valuably, incredible amounts of time and energy to make this white shark research (and my dissertation) so successful. She has made every effort to support me in conducting important science (I hope you agree).

One of my greatest mentors and friends has been the infamous Dr. Sal Jorgensen. Sal was a lab-mate for the first year and change of graduate school. I can't begin to explain the role he has played in my growth and education. Sal is one of those meticulous scientists that do such amazing and cool work you wonder if they ever does anything else. But, pretty quickly you learn that Sal is a master of damn near everything, from surfing to bottlerocketing to whiskey drinking. He can even claim responsibility for introducing me to my lady-friend. Nothing, and I mean nothing, would have been nearly the adventure nor the education if it were not for Sal. I owe so much, from my dissertation focus to my addiction to Baja to my current wardrobe, to his never-ending support and friendship.

This list of people could go on indefinitely, so briefly and in no specific order, I'd like to thank Paul Kanive, Jamie Barlow, Barbara and Sebastard Clucas, Tim Kuhn, Marisa Alcorta, Mesi, Dovi Kacev, Patrick Kilduff, Steve Garcia, Michelle Lee, Henry Carson, Scot Anderson, Sara Krause, Krista Jones, Wes Dowd, Karin Neff, Adri and Matt Muir, Plainfield Station, Felix Rudolph, Turd Fergusson, Mariah Meek, Steve Teo,

James Fitzgerald, Skyli McAfee, Ron Elliot, Chiqe N Focker, Dave Nothhelfer, Ben Becker, David Kaplan, Tom Hahn, John Jameson and Son, Patricia King, Joshua Tetley, John and Gillian Pagel, Richard Theiss and countless volunteers to helped me do research and survive.

Finally, I'd like to thank my family. I've known them almost all my life and am indebted to them on so many fronts: to my mom for always instilling a sense of appreciation for everything and 'life-is-good'edness, to my dad, for the incredible stubbornness and real ability to see any problem through. Keep kickin' cancer's ass! Kyle and Meghan you guys have given me amazing life lessons. I wouldn't have done this without all the bruises, scars and support you've both given me since you dropped me at a young age. Kyle all those surf-trips were awesome. Nobody can drop in like you (and thanks Milk-truck for giving him up for a few weeks each year). Aunt Tess, thank you for being such a scientific inspiration; this dissertation has been sort of like licking a banana slug. The Cornelius crew has been a source of constant laughs and support, your wonder, love and respect of the natural world has been inspiring (welcome to the world the newest member, the great Lyle shark).

Seriously, this is it. The person I most owe this dissertation to is my lady-friend, Dr Jamie McJamerton. She's kind of a big deal. She is my editor-in-residence, the water in my whiskey and pretty much the best thing ever. McJamertwin can't really be labeled as one of a kind (as the name might suggest), but I can't imagine a better person or companion. She has been riding shotgun through every bipolar moment of my graduate carrier. She and Batman have traveled near and far, missed hours of sleep, edited

countless drafts and almost baked enough pie to deserve some sort of title (or possibly a plaque mounted somewhere in Davis).

I would like to thank PEMREM, NOAA-Seagrant, the Sloan, Moore and Packard Foundations as a part of the Tagging of Pacific Pelagics (TOPP) program of the Census of Marine Life, The Monterey Bay Aquarium Foundation, Pacific Coast Science and Learning Center, Patricia King and Bodega Marine Laboratory inter-campus travel grant for funding.

## TABLE OF CONTENTS

|   |     |
|---|-----|
| TITLE PAGE.....   | i   |
| ACKNOWLEDGEMENTS .....  | ii  |
| TABLE OF CONTENTS.....  | vi  |
| ABSTRACT.....   | vii |
| INTRODUCTION .....  | 1   |
| CHAPTER 1 .....   | 10  |
| A comparison of linear demographic models and the fraction of lifetime egg production (FLEP) for assessing sustainability in sharks     |     |
| CHAPTER 2 .....   | 35  |
| Utilizing a data-poor framework to assess of the status of the common thresher shark, <i>Alopias vulpinus</i> , off southern California |     |
| CHAPTER 3 .....   | 62  |
| A first estimate of white shark, <i>Carcharodon carcharias</i> , abundance off central California using photo-identity marking          |     |



Methods for assessment of data-poor shark species

**Abstract**

Although many shark species are currently fished past sustainable levels, we lack the data to fully assess their status under traditional frameworks. There is an increasing need to develop and validate new methods to assess shark populations. In chapter one, I tested how well the *ad hoc* methods that use linear models would reflect sustainability as seen from a more conventional fisheries point of view. I compared two examples of linear demographic models to a conventional approach, that directly measures a species' sustainability, by assessing 26 shark species' vulnerability to fishing pressure using each method. I found that the linear demographic models resulted in different rankings and numerical values than the conventional approach. Because these ranking are used to inform management decisions, it is important to use approaches similar to the conventional metric, which directly measure a species' vulnerability. In chapter two, I developed a method to use catch-per-unit-effort and size-structure data from the common thresher shark, *Alopias vulpinus*, in an age-structured model to determine the fishing mortality ( $0.76 \text{ y}^{-1}$ ) and the resulting recruitment decline ( $0.20 \text{ recruits egg}^{-1}$ ). I determined the status of the population based on the fraction of current biomass (22%) and lifetime reproduction (0.47) relative to unfished levels. These values indicated that thresher sharks were overfished in 1992. This method is useful for other new fisheries with similar kinds of available data. In chapter three, I developed a new method to

estimate the population abundance of white sharks, *Carcharodon carcharias*, off central California, where no fishery data exist. Because a white shark's fin allows each individual to be uniquely identified and they showed predictable annual fidelity at coastal sites, I was able to compute a mark-recapture abundance estimate using a Bayesian algorithm. I collected 321 photographs identifying 131 unique individuals. The abundance off central California was estimated to be 251 individuals ([197,360] 2.5% and 97.5% quantiles). My methods can be readily expanded to include juvenile and young-of-the-year sharks and sharks from other locations, over extended time-series, and to monitor the status, population trends and protection needs for white sharks.

## INTRODUCTION

Worldwide, marine fishes are being heavily exploited; at the turn of the century over 25% of the world's fisheries were over-exploited or depleted (Botsford et al., 1997), and analyses suggest nearly 90% of large predatory fish biomass on continental shelves has been depleted (Myers & Worm, 2003). Management strategies have employed comprehensive methods (e.g., age-structured dynamic simulation modeling or yield per recruit modeling) for stock assessments and prediction to prevent overfishing of fished stocks and to recover those already exploited. But, because such methods require a great deal of data and, therefore, resources, these stock assessment approaches have been geared toward populations with directed fisheries, utilizing fishery-dependent indices of abundance (e.g., total landings and age or size-structure) and fishery-independent surveys when available.

Many species have not been assessed because they lack the specific data to be evaluated under these frameworks. Sharks, perhaps the best example in this group, have been heavily exploited; yet many species lack the data to be formally assessed under conventional frameworks. Sharks are often taken as bycatch in other fisheries (Smith & Aseltine-Neilson, 2001) or landed in countries without an adequate fisheries documentation infrastructure (Bonfil, 1994), therefore, many species lack adequate data for rigorous assessment and management strategies.

The main goal of my dissertation is to critically evaluate current assessment methods and to develop improved methods for data-poor species, using sharks as examples. First, I evaluate whether current methods to assess data-poor shark species actually indicate the current status and vulnerability of the assessed populations to

fishing. Second, I develop two new methods for assessing shark populations, one that uses commonly available information in data-poor situations, and a new method to acquire the necessary data. I apply these methods to the assessment of shark species that lack extensive fishery data. These analyses and new methods may prove useful in the assessment of other data-poor shark species and aid in efforts to manage and recover exploited species.

Current methods to circumvent the paucity of data include linear demographic models, which depend on life-history information (e.g. survival, fecundity, age at maturity, age of senescence) and various assumptions, rather than empirical data reflecting population status (Au & Smith, 1997; Smith et al., 1998; Smith et al., 2008; Au et al., 2008). For example, Frisk et al. (2001) unrealistically assumed no density dependent fishing response when they calculated a potential rate of population increase,  $r'$ , from existing relationships between life-history parameters. Similarly, Smith et al. (1998) applied a linear demographic model to life-history parameters obtained or derived from the literature to determine  $r_{2M}$ , a proxy for intrinsic growth rate, for 26 species of sharks. The authors artificially assumed that a density dependent response to fishing pressure only occurs in juvenile survival, but did not empirically assess how compensatory mechanisms had contributed to shark resilience at low abundance (Stevens et al., 2000; Carlson & Baremore, 2003).

A major aim of these linear demographic methods is to rank species based on their potential population growth rates at low abundance, after fishing pressure has hypothetically been removed. These growth rates are assumed to be representative of how different populations will respond to removal of fishing pressure and, thus, they are

presumed to be a measure of their resiliency. Their purpose is to highlight vulnerable species and prioritize management strategies (Smith et al., 1998), but linear demographic models give no metric of the actual persistence or current status of a population. Instead, they describe a rate of potential population growth under specific static theoretical conditions. There is neither an empirical relationship between these proxy values and the true intrinsic rate of increase or population persistence, nor any validation as to whether these values are even attainable in real populations.

For most fishery management, population status is expressed as a measure of current biomass and lifetime reproduction as compared to unfished levels. These metrics account for how density dependence leads to natural compensation at reduced population abundance. The fraction of lifetime egg production (FLEP, which is also referred to as spawning potential ratio, SPR), an established fishery metric, measures the fraction of an individual's lifetime reproduction produced at a specific level of fishing compared to unfished levels. The biological minimum of persistence requires that an individual reproduce enough to replace itself over its lifetime. Density dependent age-structured models indicate unfished populations produce higher levels of eggs than necessary for persistence (Sissenwine & Shepherd, 1987; Botsford et al., 1997). Therefore, a population can be fished down to a threshold value of FLEP, which still allows an animal to replace itself. For example, a value of FLEP=60% is proposed to be adequate for viable populations of sharks (Restrepo et al., 1998). In this sense, FLEP is a direct empirical measure of the vulnerability and persistence of a population.

In chapter one, I test how well the *ad hoc* methods that use linear models would reflect sustainability from a more conventional fisheries point of view. I use similar

assumptions and life-history parameters to compare two linear demographic models ( $r_{2M}$ , Au & Smith, 1997 and  $r'$ , Frisk et al., 2001) to FLEP, in terms of how they quantify relative vulnerability of 26 species of sharks. I compared these three methods using ordinal and numerical approaches and determine the level of fishing necessary to maintain each population at suggested target levels (FLEP=60%).

These different frameworks result in different numerical values and ordinal rankings. This is most likely a result of how each model assumes a population will respond to fishing. For example,  $r_{2M}$  assumes a compensatory response in only juvenile survival, which results in a theoretical population growth rate under specific conditions. Whether this value is attainable has yet to be validated. Conversely, FLEP measures the change in the age-structure of a population; a direct empirical measure of the current replacement ability of the average individual and, therefore, the population's sustainability.

The common thresher shark, *Alopias vulpinus*, is the most common commercially caught pelagic shark on the west coast of the US, but because of a paucity of data in terms of conventional assessment frameworks, the only evaluation of this shark used a linear demographic model similar to  $r_{2M}$  (Pacific Fishery Management Council, 2003). Although this method sought to evaluate the status of *A. vulpinus*, it did not estimate current values of fishing mortality or abundance from observed population changes to density dependence in recruitment, rather it evaluated the theoretical response to somewhat arbitrary levels of fishing.

In chapter two, I develop a method to determine the effects of fishing pressure on *A. vulpinus*. Time series of catch-per-unit-effort and size-distribution data were available

to track an index of population abundance and determine how the structure of the population was changing in response to exploitation. I use the available data over the first 12 years of commercial harvest to determine how fishing pressure affected the population. Insights into how fishing alters the population structure, in terms of the density dependent response, and the relative biomass, allow me to assess the ability of the thresher shark population to sustain certain levels of harvest.

Thresher sharks are found to have been overexploited and subjected to high levels of fishing pressure, which resulted in a precipitous decline in their population. The method I develop can be applied to other data-poor species to determine the effects of fishing pressure and changes in the population structure where catch-per-unit-effort and size-structure data are available in a new fishery (e.g., North American sea urchin; (Botsford et al., 2004), however, this method cannot be applied to species that have no fisheries data.

Though great white sharks, *Carcharodon carcharias*, occur circumglobally, no directed fishery data exist. There have been few attempts to quantify abundance estimates of white shark populations using mark-recapture techniques (Strong et al., 1996; Cliff et al., 1996), though these abundance estimates suffer from low precision, due in part to low recapture rates.

Recently, white shark distribution has been described to be comprised of at least three genetically distinct populations in Australia/New Zealand, South Africa and the northeastern Pacific (NEP; Jorgensen et al., 2009). Though estimates are available for populations in South Africa (Cliff et al., 1996) and Australia (Strong et al., 1996), no rigorous abundance estimate is available in the NEP.

Within the NEP, electronic tagging studies have shown that white sharks predictably aggregate at sites off central California (CCA) during their annual migration (Jorgensen et al., 2009). During their annual aggregation, a white shark's proclivity to investigate prey at the surface allows photographic documentation of individual dorsal fins, which can be used to uniquely identify individual white sharks (Gubili et al., 2009), similar to a human fingerprint or a whale's fluke pattern.

In chapter three, I develop a method to estimate a first ever population abundance of white sharks, *Carcharodon carcharias*, off CCA. I collect above and below water photographs of white sharks at aggregation sites off CCA for three years, and then use evidence of strong annual site-fidelity and uniquely identifiable fins to incorporate these photographs into a Bayesian mark-recapture framework. This framework was designed to yield high precision in analyses with low capture rates (Gazey & Staley, 1986), avoiding weakness of previous abundance estimates at other location.

I found the population of white sharks off central California to be low, even compared to other marine and terrestrial populations of protected species. This population estimate is the first step to quantitatively determining the status of white sharks. The framework I developed supports the use of longer time-series data to determine trends in the population. In addition, data from other locations worldwide can be incorporated into this framework to establish an estimate of global abundance and status of white sharks.

Taken together, these three chapters address a key issue in fisheries; how to assess data-poor species, and they apply the answers to a taxon whose populations are frequently data poor, sharks. Current frameworks require large amounts of data to



evaluate populations, but many fish species, and most shark species, lack sufficient data to be assessed under these conventional frameworks. Novel methods are needed to assess these data-poor species. I developed new methods to estimate abundance, assess fishing pressure and determine how well recently popular methods reflect sustainability, for data-poor species. These methods may be further applied across other fisheries to fill in gaps where conventional frameworks are not useful.

## LITERATURE CITED

- Au, D. W., Smith, S. E., & Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Fish and Aquatic Resources Series 13. Oxford, UK: Blackwell (pp. 298–308).
- Au, D. W., & Smith, S. E. 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 415–420.
- Bonfil, R. 1994. Overview of World Elasmobranch Fisheries. FAO Technical Papers No 341. Food and Agriculture Organization of the United Nations, Rome (pp 119).
- Botsford, L. W., Campbell, A., & Miller, R. 2004. Biological reference points in the management of North American sea urchin fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1325–1337.
- Botsford, L. W., Castilla, J. C., & Peterson, C. H. 1997. The management of fisheries and marine ecosystems. *Science* **277**: 509.
- Carlson, J., & Baremore, I. 2003. Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? *Marine and Freshwater Research* **54**: 227-234.
- Cliff, G., van der Elst, R. P., Govender, A., Witthuhn, T. K., & Bullen, E. M. 1996. First estimates of mortality and population size of white sharks on the South African coast. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 393-400).
- Frisk, M. G., Miller, T. J., & Fogarty, M. J. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 969–981.
- Gazey, W. J., & Staley, M. J. 1986. Population estimation from mark-recapture experiments using a sequential Bayes algorithm. *Ecology* **67**: 941–951.
- Gubili, C., Johnson, R., Gennari, E., Oosthuizen, W., Kotze, D., Meyer, M., Sims, D., Jones, C., & Noble, L. 2009. Concordance of genetic and fin photo identification in the great white shark, *Carcharodon carcharias*, off Mossel Bay, South Africa. *Marine Biology* **156**: 2199-2207.

- Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., Fritz-Cope, C., Brown, A. C., Klimley, A. P., & Block, B. A. 2009. Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B: Biological Sciences*. Retrieved November 4, 2009, from <http://rspb.royalsocietypublishing.org/content/early/2009/10/29/rspb.2009.1155.abstract>
- Myers, R. A., & Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**: 280–283.
- Pacific Fisheries Management Council. 2003. *Fishery management plan for U.S. west coast fisheries for highly migratory fisheries*. Silver Spring, MD: National Marine fishery Service.
- Restrepo, V. R., thompson, G. G., Mace, P. M., Gabriel, W. L., Low, L. L., McCall, A. D., Methot, R. D., J. E. Powers, Taylor, B. L., Wade, P. R., & Witzig, J. F. 1998. *Technical Guidance On the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act*. Silver Spring, MD: National Marine fisheries Service.
- Sissenwine, M. P., & Shepherd, J. G. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **44**: 913–918.
- Smith, S. E., & Aseltine-Neilson, D. 2001. Thresher shark. In W. S. Leet, C. M. Dewee, R. Klingbeil, & E. J. Larson (Eds.), *California's Living Marine Resources: A Status Report, California Department of Fish and Game*. University of California (pp. 339-341).
- Smith, S. E., Au, D. W., & Show, C. 2008. Intrinsic rates of increase in pelagic elasmobranchs. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Fish and Aquatic Resources Series 13. Oxford, UK: Blackwell (pp. 288–297).
- Smith, S. E., Au, D. W., & Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine & Freshwater Research* **49**: 663–678.
- Stevens, J. D., Bonfil, R., Dulvy, N., & Walker, P. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476-494.
- Strong, W. R., Bruce, B. D., Nelson, D. R., & Murphy, R. D. 1996. Population dynamics of white sharks in Spencer Gulf, South Australia. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 401-414).

**Chapter 1:**

**A comparison of linear demographic models and the fraction of lifetime egg  
production (FLEP) for assessing sustainability in sharks**

## ABSTRACT

Linear demographic models, applying life-history characteristics to Leslie matrices or life tables, have been used to determine a proxy for the sustainability status of many shark species. These proxies, sometimes based on arbitrary assumptions, are used to inform management decisions aimed at sustaining populations. To test how well these *ad hoc* methods using linear models would reflect sustainability from a more conventional fisheries point of view, we compared the application of two linear demographic models ( $r_{2M}$ , Smith et al., 1998 and  $r'$ , Frisk et al., 2001) to calculation of the fraction of lifetime egg production (FLEP) for 26 shark species. FLEP is a measure of the capacity for replacement of individuals in a population, which is commonly the basis for a reference point in fishery management. We compared the computed species status from each method in both ordinal and numerical terms, using the Spearman rank correlation and the Pearson product-moment correlation coefficient, respectively. The values of  $r'$  did not covary with FLEP (Spearman's  $\rho_s = 0.2818$ ,  $p = 0.077$ ; Pearson's  $\rho_p = 0.32$ , not significant at  $p = 0.05$ ). The values of  $r_{2M}$  and FLEP did covary ( $\rho_s = 0.647$ ,  $p = 0.00013$ ;  $\rho_p = 0.68$ , significant at  $p = 0.05$ ), but some species showed substantially different relative numerical values. Linear demographic models often do not include density dependence or, as in  $r_{2M}$ , assume a large arbitrary compensatory response in juvenile survival, to calculate a theoretical growth rate, whereas FLEP measures the change in the age-structure and the resulting reproductive capacity of average individuals in a population. These differences likely led to the differences in rankings and numerical values between methods. The goal of these rankings and values are to

inform management decisions and at the very least, calculation of FLEP from the same data provides a marginally better measure of population sustainability status.

## INTRODUCTION

Commercial and recreational harvest of sharks has led to the overexploitation of many species (Stevens et al., 2000). Because they are often taken as bycatch in other fisheries (Smith & Aseltine-Neilson, 2001; Stevens et al., 2000) or landed in countries without an adequate fisheries documentation infrastructure (Bonfil, 1994), many shark species lack adequate data for rigorous assessment and management strategies. Linear demographic models have been developed to determine the status of shark populations and their susceptibility to fishing pressure with minimal fishery data. These linear models are normally based on life tables or Leslie matrices using age or stage-specific mortality, fecundity, age of maturity and lifespan to calculate a proxy for the potential resiliency of a species. They provide a theoretical instantaneous rate of increase of a population based on static life-history and fishery parameters under specific conditions.

Many elasmobranch species have been assessed using a modified linear demographic model that artificially includes density dependence in the survival of juvenile individuals (Au & Smith, 1997; Smith et al., 1998; Cortés et al., 2002; Au et al., 2008; Smith et al., 2008). In this model, Euler's equation was applied to a population at equilibrium with natural mortality,  $M$ , as a function of maximum age,  $\omega$  (Hoenig, 1983). The authors assumed the fishing mortality,  $F$ , necessary to produce maximum sustainable yield (MSY) was equal to the natural mortality. Euler's equation was then solved for  $S_0$ , the compensatory increase in juvenile survival necessary for the fished population to remain constant ( $r=0$ ). Then, removing fishing pressure ( $F=0$ ) and holding  $S_0$  at this enhanced level, the authors solved the equation for the intrinsic rate of

increase if fishing was removed, a value they called the rebound potential,  $r_{2M}$  (Au & Smith, 1997).

Smith et al. (1998) applied this method to life-history parameters obtained or derived from the literature to determine the  $r_{2M}$  for 26 species of sharks (including two stocks of dogfish). Although these values of  $r_{2M}$  have been interpreted in the elasmobranch fisheries literature as relative metrics of risk from fishing pressure (for example Walker, 1998; Jennings, 2000; Xiao & Walker, 2000; Francis et al., 2001; Simpfendorfer et al., 2002; Mancusi et al., 2005; Campana et al., 2006; Clarke et al., 2006; Au et al., 2008; Smith et al., 2008), an empirical value of intrinsic growth (Cortés et al., 2002; Beerkircher et al., 2003; Pacific Fishery Management Council, 2003; Lage et al., 2008) and doubling time of a population (Braccini et al., 2006), there is no indication or validation of the actual relationship between these values and the true intrinsic rate of increase (Gedamke et al., 2007). In addition,  $r_{2M}$  has no empirical dependence on the current status of a population. Instead, it describes a rate of potential population growth under specific static theoretical conditions.

Another approach calculated a potential rate of population increase,  $r'$ , from existing relationships between life-history parameters (Frisk et al., 2001).  $r'$  was calculated as the natural log of fecundity divided by the age at maturity. This method was derived from a general correlation between population decline from fishing pressure and low  $r'$  values in teleosts (Jennings et al., 1998).

Although density dependence likely plays a key role in elasmobranch resilience (Stevens et al., 2000; Carlson & Baremore, 2003), these linear demographic models are based on Leslie-matrices and life tables, which by definition do not include density



dependence. Without including density dependence, populations will grow exponentially, and although exponential growth may be realistic at low abundance, in real populations the growth rate will change as the population abundance increases. Smith et al. (1998) artificially include a compensatory increase in juvenile survival at low abundance, but there is no empirical basis for assuming sharks rely solely on this source of compensation at low abundance. Sharks may increase juvenile survival, but this is likely accompanied by increases in individual growth rates (Sminkey & Musick, 1995; Stevens & West, 1997; Carlson & Baremore, 2003), decrease in age of maturity (Parsons, 1993; Castro, 1996; Carlson & Baremore, 2003) or other compensatory responses.

Results from age-structured models with density-dependent recruitment suggest the current lifetime egg production of an individual (*LEP*; analogous to eggs-per-recruit), a measure of the number of eggs (or offspring) a female produces over her lifetime, may be more appropriate as an indicator of sustainability of a population. Sissenwine and Shepherd (1987) showed that *LEP* could be compared with the stock-recruitment (*S-R*) relationship to gauge population persistence under different rates of fishing pressure. In this context, *LEP* determines the slope ( $1/LEP$ ) of the replacement line, a line passing through the origin that crosses the *S-R* line at the equilibrium condition for a given value of fishing. As fishing pressure increases, the *LEP* decreases and the slope of the replacement line steepens, decreasing the equilibrium level of recruitment and eggs. At the point where the steepness of the replacement line exceeds the slope of the *S-R* line at the origin, the population equilibrium size is zero, indicating population collapse (Sissenwine & Shepherd, 1987).

For most fishery management, population status is expressed as a measure of current biomass and lifetime reproduction, both of which are stated relative to unfished levels (i.e., depletion and FLEP, which is LEP divided by LEP with no fishing). Fishery control rules seek to maintain these quantities above certain minimal levels. In the US the stated motivation for using FLEP is as a proxy for MSY, but nonetheless a specific sustainable value is maintained. These limit reference points (LRPs) are threshold levels of fishing or biomass that are thought to guarantee population persistence while allowing maximum harvest when empirical values of MSY and fishing are not available. These minimal levels are based on empirically derived species-specific values or values for species with similar productivities (Restrepo et al., 1998). The population dynamic basis is the expression for equilibrium of a population with age-structure and density-dependent recruitment.

The metric LEP has a compelling interpretation in terms of replacement; the biological minimum of persistence requires that an individual reproduce enough to replace itself over its lifetime. Often we do not know how many eggs an individual must produce to replace itself, but density-dependent age-structured models indicate unfished populations produce higher levels than necessary for persistence (Botsford et al., 1997). Therefore, the surplus from a population can be fished down to the LRP where an individual produces enough eggs to exactly replace itself.

The problem for sharks is that, with the exception of the barndoor skate (Gedamke et al., 2009), the S-R relationships for elasmobranchs have yet to be empirically defined at low abundance. In such instances, current FLEP can be calculated as the capacity for replacement of individuals in a population, but it cannot be compared to the steepness

or slope of the S-R relationship. Because we do not know the density dependent consequences at these low abundances, FLEP is normally bounded against collapse by a LRP (i.e., FLEP=60% for elasmobranchs; Restrepo et al., 1998). Comparing the current FLEP of the fishery to the LRP can give a direct measure of the status and resiliency of a population at specific levels of fishing and can define the fishing level for maximum sustainable yield.

To test how well the *ad hoc* methods that use linear models would reflect sustainability from a more conventional fisheries point of view, we compared the status of each method to calculation from an established fisheries management framework using the life-history data from Smith et al. (1998). We compared  $r_{2M}$  and  $r'$  to FLEP to determine the effectiveness of linear demographic models in evaluating the status of shark populations. We used the assumptions and parameter values compiled by Smith et al. (1998) to determine the FLEP for 26 species of sharks. We ranked each species based on their relative exploitation susceptibility given by  $r_{2M}$ ,  $r'$  and FLEP. We then compared the values given by  $r'$  and  $r_{2M}$  with FLEP on both an ordinal and a numerical basis. We also used these parameter values to determine the level of fishing necessary to maintain each population at FLEP=60% under the assumed static conditions.

## METHODS

We evaluated 26 species of sharks (including two stocks of dogfish) with age at 50% female maturity,  $\alpha$ , maximum age,  $\omega$ , fecundity,  $m$ , and natural mortality,  $M$ , compiled by Smith et al. (1998).

We calculated the value of FLEP by integrating over all mature ages from  $\alpha$  to  $\omega$ , with natural mortality from Hoenigs (1983) expression ( $\ln[M]=1.44-0.982\ln[\omega]$ ) and  $F$  set equal to  $M$  (i.e. total mortality,  $Z=2M$ ), as in Smith et al. (1998). Fishing began with knife-edge selection at,  $\alpha$ , and continued until  $\omega$ . The value of FLEP was thus,

$$FLEP = \frac{\int_{a=\alpha}^{\omega} m e^{-(M+F)a} da}{\int_{a=\alpha}^{\omega} m e^{-Ma} da} \quad (1)$$

Where fecundity,  $m$ , is assumed to be independent of age as in Smith et al. (1998).

Integrating equation (1) results in,

$$FLEP = \frac{\frac{e^{-(M+F)\omega} - e^{-(M+F)\alpha}}{F+M}}{\frac{e^{-M\omega} - e^{-M\alpha}}{M}} \quad (2)$$

Note that in equation (2) fecundity played no role in determining the FLEP.

We ranked each species according to its value of FLEP,  $r_{2M}$  and  $r'$ , where the species with higher relative vulnerability to exploitation were assigned lower ranks. Species with the same rank score were given the average ranking between the two values. The values were compared in terms of their order, using the Spearman rank correlation. We also compared these indicators in terms of their numerical values, using the Pearson product-moment correlation coefficient.

Because all species produced a value of FLEP less than 60% assuming the given parameter values, it is unlikely that they would be fished for very long with  $F=M$ . To see how the aggregate would respond to various fishing mortality rates, we plotted the fraction of species for which FLEP exceeded 60%, vs.  $F$ . Because  $F$  is often given as a proportion of  $M$  (e.g.,  $F=.5M$ ), we also expressed the fishing mortality of each species in terms of a fraction of its corresponding natural mortality (i.e., we plotted FLEP vs.  $\mu$ , where  $F= \mu M$ ).

## RESULTS

The values of FLEP,  $r'$  and  $r_{2M}$  and their corresponding rankings are shown in Table 1.1. The null hypothesis of the Spearman rank correlation test is that the ranks do not covary between methods. The rankings of  $r'$  and FLEP did not covary significantly (Spearman's  $\rho_s = 0.2818$ ,  $p=0.077$ ). The Pearson product-moment correlation coefficient indicated that  $r'$  and FLEP had a slightly positive correlation ( $\rho_p=0.32$ , not significant at  $p=0.05$ ; Fig. 1.1).

The ordinal rankings of  $r_{2M}$ , on the other hand, were not significantly different than FLEP (Spearman's  $\rho_s = 0.647$ ,  $p=0.00013$ ), indicating that the order of FLEP and  $r_{2M}$  covary. The Pearson product-moment correlation coefficient indicated that there was positive covariability ( $\rho_p=0.68$ , significant at  $p=0.05$ ), but some species show substantially different relative numerical values (Fig. 1.2). For example, the numerical values of  $r_{2M}$  for the whitetip reef and sand tiger sharks suggest similar levels of vulnerability (0.048 and 0.052, respectively), yet FLEP values indicate the whitetip reef shark is nearly four times more vulnerable than the sand tiger shark (0.060 and 0.236,

respectively). Conversely,  $r_{2M}$  values indicate the sand tiger shark is nearly three times more vulnerable than the gray smoothhound (0.052 and 0.136, respectively), whereas the FLEP values of sand tiger and gray smoothhounds are nearly equal (0.236 and 0.246, respectively).

Similar to  $r_{2M}$  (Smith et al., 1998; Au et al., 2008; Smith et al., 2008), FLEP showed a significant correlation with  $\alpha$  ( $p=0.0002$ ; Fig 1.3), but not  $\omega$  ( $p=0.64$ ). FLEP is likely correlated with  $\alpha$  because Hoenig's (1983) relationship between  $\omega$  and  $M$  was used. Figure 1.4 shows the age-structures, determined by  $M$ , of each species from the time of first reproduction through the maximum age. The potentially artificial effect of using Hoenig's (1983) equation to determine  $M$  is obvious. The lines representing age-structures never cross because the species that are longer lived have lower natural mortality resulting in a more gradual slope. Thus, there were essentially only two independent variables,  $\alpha$  and  $\omega$ , in the calculation of FLEP.

Setting  $F=M$  as in Smith et al. (1998) resulted in FLEP values in the range of 0.047 to 0.28, well below 60%. Values of  $\mu$  required to allow FLEP=60%, are given in Table 1.1 ( $F=\mu M$ ). Figures 1.5 and 1.6 show the fraction of shark species that would remain above FLEP=60% and 35% (threshold for most teleosts; Restrepo et al., 1998) at specific values of  $\mu$  and  $F$ , respectively. Shark populations fall below FLEP=60% and 35% a low levels of fishing ( $F=0.015$  to  $0.11$ ) under the assumed specific conditions.

## DISCUSSION

The ultimate goal of using growth potentials is to provide quantitative values and rankings of sharks to inform management strategies (Smith et al., 1998). The relative

rank of species' vulnerabilities can therefore have significant bearing on how species are managed. The two linear demographic models in this study produced rankings and numerical values that were different from FLEP and were not directly informative of fishery status. In this capacity it appears that FLEP provides a substantially better assessment than linear demographic models to rank or inform management strategies regarding the vulnerability of shark species.

The differences in rankings and numerical values between these linear demographic models and FLEP are likely a result of how fishing is assumed to affect a population in each framework. For example, with  $r_{2M}$  fishing pressure results in only a compensatory increase in  $S_0$ , but there is no guarantee that this level of  $S_0$  is attainable or even realistic. At best, the level of growth explained by  $r_{2M}$  is an upper theoretical threshold, resulting from arbitrary compensation in  $S_0$  when fishing pressure is removed. Conversely, FLEP is a measure of how the age-structure of the population will change with fishing pressure. The shape of the age-structure is directly informative regarding how much reproduction an individual (or population) can produce. Therefore, FLEP is a direct measure of the capacity for an individual to replace itself, a metric that specifies the vulnerability of a population at given levels of fishing.

It should be stressed that the values calculated here for FLEP or  $r'$  and  $r_{2M}$  are not empirically based on current population status in the same sense as conventional calculations of FLEP. Values, at best, represent the relative rank of these species under explicit assumptions, specifically, the assumed values of  $F$ . These values of  $F$ , and even lower values determined to be more appropriate for sharks ( $F=.5M$ ; Au et al., 2008), may be misleading because they appear to be too high to allow persistence of these

species at suggested critical thresholds (Table 1.1). Implications throughout the literature that  $r_{2M}$  empirically represents the persistence status of a population (Cortés et al., 2002) or available biomass in a population (Pacific Fishery Management Council, 2003) may be misleading. However,  $r_{2M}$  does, in a distorted sense represent doubling time (Braccini et al., 2006) (i.e., with artificially elevated juvenile survival that does not decline with increasing density).

More appropriate values of FLEP can be calculated from variable information about specific fisheries (e.g., gear selectivity; Beerkircher et al., 2003) or empirically. For example, the S-R relationship for the barndoor skate was empirically determined from trawl survey data (Gedamke et al., 2009). At the origin, the data fitted to both Ricker and Beverton-Holt S-R models indicated a slope of 4.99 and 5.26, respectively. This equates to a FLEP of nearly 20%. Though this value is much lower than 60%, the barndoor skate has been found to be highly resilient with an intrinsic rate of increase of  $0.45y^{-1}$  (Gedamke et al., 2009).

In general, many shark species lack enough data to be formally assessed and while linear demographic models have become a popular method by which to assess the potential resiliency of a group of species, these methods are useful only under specific conditions and lack the ability to be directly informative in a fishery management setting. Only in the few cases where these values are empirically derived can they be used in a formal assessment framework. Therefore, the use of  $r_{2M}$  and  $r'$  as empirical assessments of population status can have serious consequences for achieving the goals of management strategies and guidelines for sharks. Instead, fisheries managers should rely on a more direct way to evaluate the current status and resilience of shark species.



At the very least, calculation of FLEP from the same data provides a marginally better measure of population sustainability status.

### **ACKNOWLEDGEMENTS**

I would like to thank J Cornelius, P Kilduff, S Kohin and AP Klimley for assistance in with this manuscript. I would also like thank MKC Chapple, B Clucas, S Jorgensen, B Cornapple, B Davis, T Hahn and countless other for their roles in completing this manuscript. Funding for this project was provided by PEMREM and the NMFS-Sea Grant Population Dynamics Fellowship.

## LITERATURE CITED

- Au, D. W., Smith, S. E., & Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Fish and Aquatic Resources Series 13. Oxford, UK: Blackwell (pp. 298–308).
- Au, D. W., & Smith, S. E. 1997. A demographic method with population density compensation for estimating productivity and yield per recruit of the leopard shark (*Triakis semifasciata*). *Canadian Journal of Fisheries and Aquatic Sciences* **54**: 415–420.
- Beerkircher, L., Shivji, M., & Cortés, E. 2003. A Monte Carlo demographic analysis of the silky shark (*Carcharhinus falciformis*): implications of gear selectivity. *Fishery Bulletin* **101**: 168–174.
- Bonfil, R. 1994. Overview of world elasmobranch fisheries. In *Overview of World Elasmobranch Fisheries. FAO Technical Papers No 341*. Rome: Food & Agriculture Organization of the UN (FAO) (p. 119).
- Botsford, L. W., Castilla, J. C., & Peterson, C. H. 1997. The management of fisheries and marine ecosystems. *Science* **277**: 509.
- Braccini, J. M., Gillanders, B. M., & Walker, T. I. 2006. Hierarchical approach to the assessment of fishing effects on non-target chondrichthyans: case study of *Squalus megalops* in southeastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 2456–2466.
- Campana, S. E., Marks, L., Joyce, W., & Kohler, N. E. 2006. Effects of recreational and commercial fishing on blue sharks (*Prionace glauca*) in Atlantic Canada, with inferences on the North Atlantic population. *Canadian Journal of Fisheries and Aquatic Sciences* **63**: 670–682.
- Carlson, J., & Baremore, I. 2003. Changes in biological parameters of Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the Gulf of Mexico: evidence for density-dependent growth and maturity? *Marine and Freshwater Research* **54**: 227–234.
- Castro, J. I. 1996. Biology of the blacktip shark, *Carcharhinus limbatus*, off the southeastern United States. *Bulletin of Marine Science* **59**: 508–522.
- Clarke, S. C., McAllister, M. K., Milner-Gulland, E. J., Kirkwood, G. P., Michielsens, C. G., Agnew, D. J., Pikitch, E. K., Nakano, H., & Shivji, M. S. 2006. Global estimates of shark catches using trade records from commercial markets. *Ecology Letters* **9**: 1115–1126.

- Cortés, E., Brooks, L., & Scott, G. 2002. *Stock Assessment of Large Coastal Sharks in the U.S. Atlantic and Gulf of Mexico*. Silver Spring, MD: NMFS.
- Francis, M. P., Griggs, L. H., & Baird, S. J. 2001. Pelagic shark bycatch in the New Zealand tuna longline fishery. *Marine and Freshwater Research* **52**: 165–178.
- Frisk, M. G., Miller, T. J., & Fogarty, M. J. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* **58**: 969–981.
- Gedamke, T., Hoenig, J. M., DuPaul, W. D., & Musick, J. A. 2009. Stock-Recruitment Dynamics and the Maximum Population Growth Rate of the Barndoor Skate on Georges Bank. *North American Journal of Fisheries Management* **29**: 512–526.
- Gedamke, T., Hoenig, J. M., Musick, J. A., DuPaul, W. D., & Gruber, S. H. 2007. Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: Pitfalls, advances, and applications. *North American Journal of Fisheries Management* **27**: 605–618.
- Hoenig, J. M. 1983. Empirical use of longevity data to estimate mortality rates. *Fishery Bulletin* **82**: 898–903.
- Jennings, S. 2000. Patterns and prediction of population recovery in marine reserves. *Reviews in Fish Biology and Fisheries* **10**: 209–231.
- Jennings, S., Reynolds, J. D., & Mills, S. C. 1998. Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society B: Biological Sciences* **265**: 333.
- Lage, C. R., Petersen, C. W., Forest, D., Barnes, D., Kornfield, I., & Wray, C. 2008. Evidence of multiple paternity in spiny dogfish (*Squalus acanthias*) broods based on microsatellite analysis. *Journal of Fish Biology* **73**: 2068–2074.
- Mancusi, C., Clò, S., Affronte, M., Brada, M. N., Hemida, F., Serena, F., Soldo, A., & Vacchi, M. 2005. On the presence of basking shark (*Cetorhinus maximus*) in the Mediterranean Sea. *Cybium* **29**: 399-405.
- Pacific Fishery Management Council. 2003. *Fishery Management Plan and Environmental Impact Statement for U.S. West Coast Fisheries for Highly Migratory Species*. Portland, Oregon. Portland, OR.
- Parsons, G. R. 1993. Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environmental Biology of Fishes* **38**: 25–35.

- Restrepo, V. R., Thompson, G. G., Mace, P. M., Gabriel, W. L., Low, L. L., McCall, A. D., Methot, R. D., J. E. Powers, Taylor, B. L., Wade, P. R., & Witzig, J. F. 1998. *Technical Guidance On the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act*. Silver Spring, MD: National Marine Fisheries Service.
- Simpfendorfer, C. A., McAuley, R. B., Chidlow, J., & Unsworth, P. 2002. Validated age and growth of the dusky shark, *Carcharhinus obscurus*, from Western Australian waters. *Marine and Freshwater Research* **53**: 567–574.
- Sissenwine, M. P., & Shepherd, J. G. 1987. An alternative perspective on recruitment overfishing and biological reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **44**: 913–918.
- Sminkey, T. R., & Musick, J. A. 1995. Age and growth of the sandbar shark, *Carcharhinus plumbeus*, before and after population depletion. *Copeia* **1995**: 871–883.
- Smith, S. E., & Aseltine-Neilson, D. 2001. Thresher shark. In W. S. Leet, C. M. Dewee, R. Klingbeil, & E. J. Larson (Eds.), *California's Living Marine Resources: A Status Report, California Department of Fish and Game*. University of California (pp. 339-341).
- Smith, S. E., Au, D. W., & Show, C. 2008. Intrinsic rates of increase in pelagic elasmobranchs. In M. D. Camhi, E. K. Pikitch, & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Fish and Aquatic Resources Series 13. Oxford, UK: Blackwell (pp. 288–297).
- Smith, S. E., Au, D. W., & Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine & Freshwater Research* **49**: 663–678.
- Stevens, J. D., Bonfil, R., Dulvy, N., & Walker, P. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476-494.
- Stevens, J. D., & West, G. J. 1997. *Investigation of School and Gummy Shark Nursery Areas in South Eastern Australia*. 77 pp. CSIRO Marine Research: Hobart.
- Walker, T. L. 1998. Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* **49**: 553–572.
- Xiao, Y., & Walker, T. L. 2000. Demographic analysis of gummy shark (*Mustelus antarcticus*) and school shark (*Galeorhinus galeus*) off southern Australia by applying a generalized Lotka equation and its dual equation. *Canadian Journal of Fisheries and Aquatic Sciences* **57**: 214–222.

| Species                    | FLEP Rank | $r_{2M}$ Rank | $r'$ Rank | FLEP  | $r_{2M}$ | $r'$ | FLEP <sub>.5M</sub> | $\mu$ |
|----------------------------|-----------|---------------|-----------|-------|----------|------|---------------------|-------|
| Bull                       | 1         | 4             | 4         | 0.047 | 0.027    | 0.08 | 0.21                | 0.16  |
| Dusky                      | 2         | 2             | 3         | 0.052 | 0.02     | 0.07 | 0.22                | 0.17  |
| Sandbar                    | 3         | 5.5           | 6         | 0.058 | 0.028    | 0.1  | 0.23                | 0.17  |
| Sevengill                  | 4         | 3             | 20        | 0.059 | 0.026    | 0.24 | 0.23                | 0.17  |
| Whitetip reef              | 5         | 15.5          | 1         | 0.060 | 0.048    | 0.03 | 0.24                | 0.17  |
| Lemon                      | 6         | 9.5           | 10        | 0.064 | 0.034    | 0.13 | 0.24                | 0.18  |
| Leopard                    | 7         | 7             | 13        | 0.077 | 0.032    | 0.14 | 0.27                | 0.19  |
| Scalloped hammerhead       | 8         | 5.5           | 16        | 0.078 | 0.028    | 0.16 | 0.27                | 0.19  |
| Sharpnose                  | 9         | 24            | 21        | 0.092 | 0.084    | 0.26 | 0.29                | 0.20  |
| Gray reef                  | 10.5      | 19.5          | 10        | 0.095 | 0.054    | 0.13 | 0.30                | 0.20  |
| Blacktip                   | 10.5      | 19.5          | 13        | 0.095 | 0.054    | 0.14 | 0.30                | 0.20  |
| Spinydogfish <sup>B</sup>  | 12        | 1             | 2         | 0.104 | 0.017    | 0.04 | 0.31                | 0.21  |
| Silky                      | 13        | 13.5          | 15        | 0.106 | 0.043    | 0.15 | 0.31                | 0.21  |
| Galapagos                  | 14        | 15.5          | 17.5      | 0.119 | 0.048    | 0.21 | 0.33                | 0.22  |
| Tiger                      | 15        | 13.5          | 24        | 0.124 | 0.043    | 0.3  | 0.34                | 0.23  |
| School/Soupfin             | 16        | 8             | 19        | 0.134 | 0.033    | 0.22 | 0.35                | 0.24  |
| Blue                       | 17        | 21            | 26        | 0.137 | 0.061    | 0.55 | 0.35                | 0.24  |
| Angel                      | 18        | 11            | 6         | 0.143 | 0.038    | 0.1  | 0.36                | 0.24  |
| Common thresher            | 19        | 23            | 13        | 0.161 | 0.069    | 0.14 | 0.38                | 0.26  |
| White                      | 20        | 12            | 10        | 0.168 | 0.04     | 0.13 | 0.39                | 0.26  |
| Mako                       | 21        | 17            | 17.5      | 0.169 | 0.051    | 0.21 | 0.39                | 0.27  |
| Bonnethead                 | 22        | 25            | 27        | 0.172 | 0.105    | 0.6  | 0.40                | 0.27  |
| Oceanic whitetip           | 23        | 22            | 25        | 0.187 | 0.067    | 0.32 | 0.41                | 0.28  |
| Spiny dogfish <sup>A</sup> | 24        | 9.5           | 8         | 0.207 | 0.034    | 0.12 | 0.43                | 0.30  |
| Sand tiger                 | 25        | 18            | 6         | 0.236 | 0.052    | 0.1  | 0.46                | 0.32  |
| Gray smoothhound           | 26        | 27            | 22.5      | 0.246 | 0.136    | 0.28 | 0.47                | 0.33  |
| Brown smoothhound          | 27        | 26            | 22.5      | 0.283 | 0.127    | 0.28 | 0.51                | 0.37  |

<sup>A</sup>North-western Atlantic

<sup>B</sup> British Columbia

Table 1.1 26 species of sharks (including two stocks of dogfish) are ranked according to their FLEP,  $r_{2M}$  (Smith et al., 1998) and  $r'$  (Frisk et al., 2001). FLEP<sub>1.5M</sub> is the value of FLEP calculated where  $F=.5M$  rather than  $F=M$ .  $\mu$  is the fraction of  $M$  ( $F=\mu M$ ) that is required to keep the population at or near FLEP=60%.

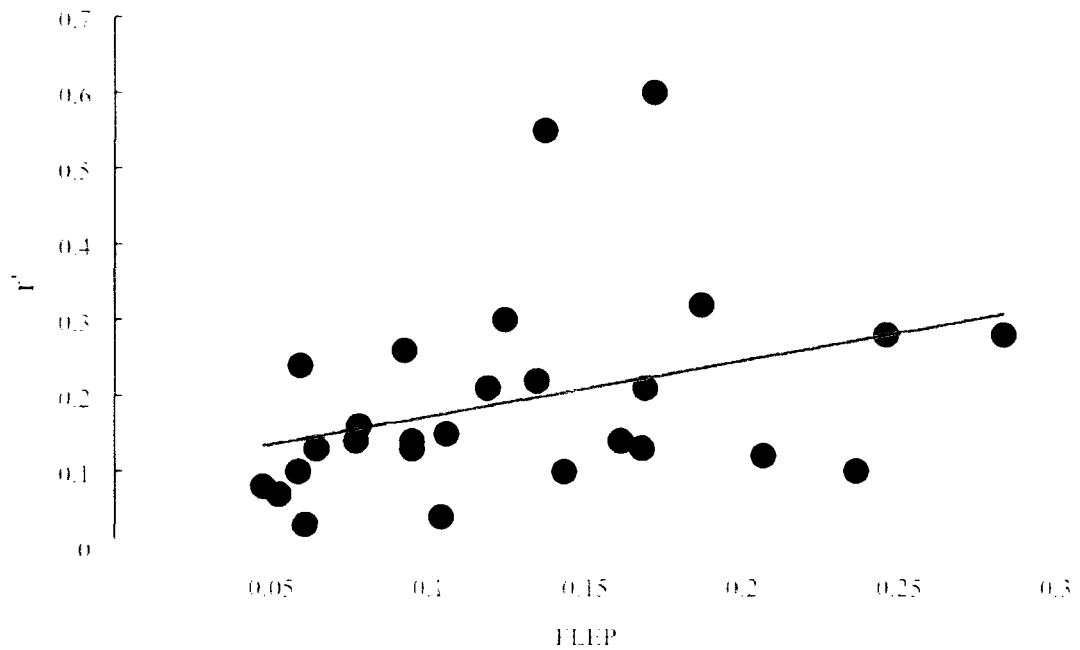


Figure 1.1. Regression of  $r'$  (Frisk et al., 2001) vs. FLEP for 26 species of sharks. The ordinal rank relationship does not significantly covary ( $\rho_s=0.28$ ), and individual species' numerical values vary ( $\rho_p=0.32$ , significant at  $p=0.05$  level).

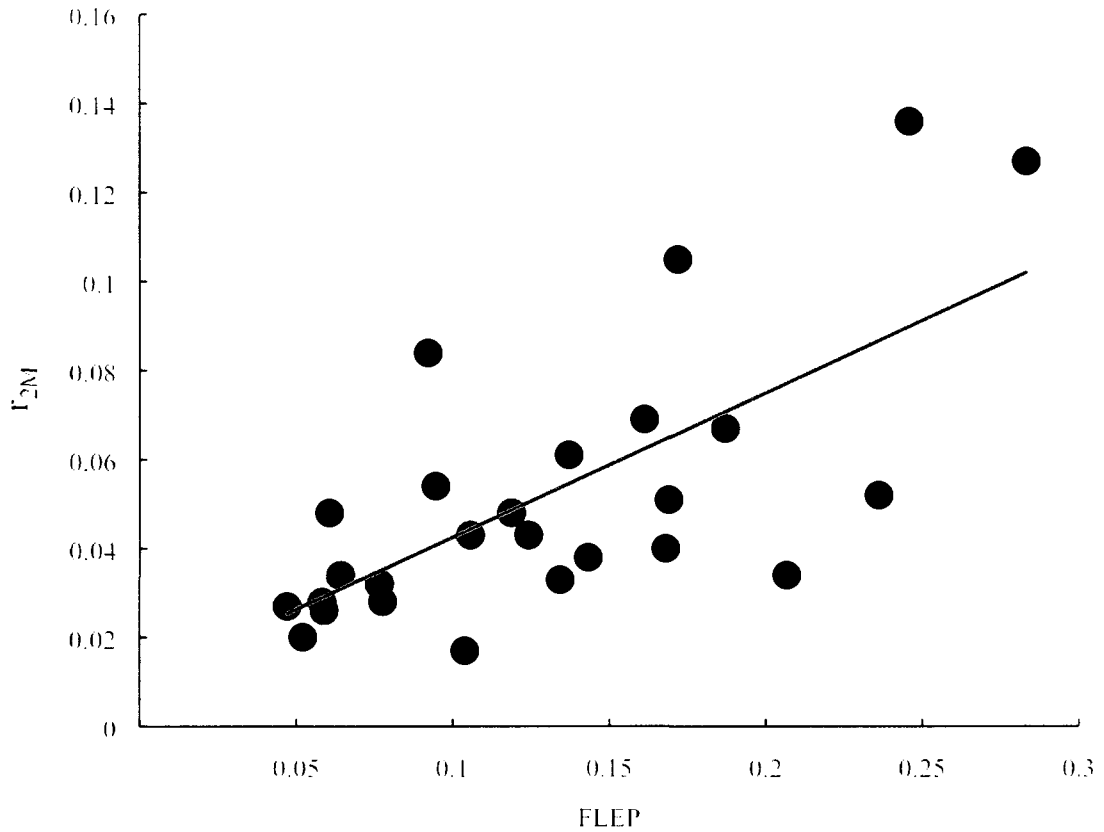


Figure 1.2. Regression of  $r_{2M}$  (Smith et al., 1998) and FLEP for 26 species of sharks calculated from the same data. The rank relationship covaries ( $\rho_s=0.0013$ ) and numerical values are not significantly different ( $\rho_p=0.69$ , not significant at  $p=0.05$  level), yet many species' ranks change.



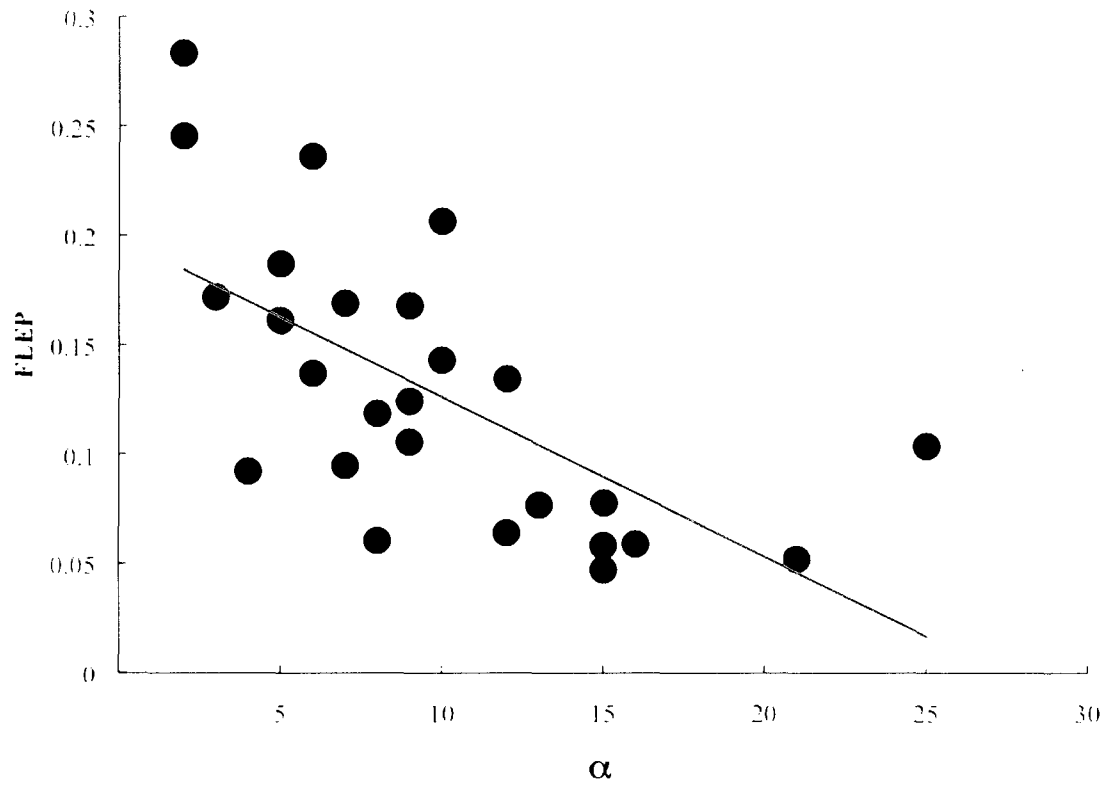


Figure 1.3. Regression of FLEP vs. age of maturity,  $\alpha$ , for 26 species of sharks. Age of maturity significantly predicts FLEP ( $p=0.0002$ ).

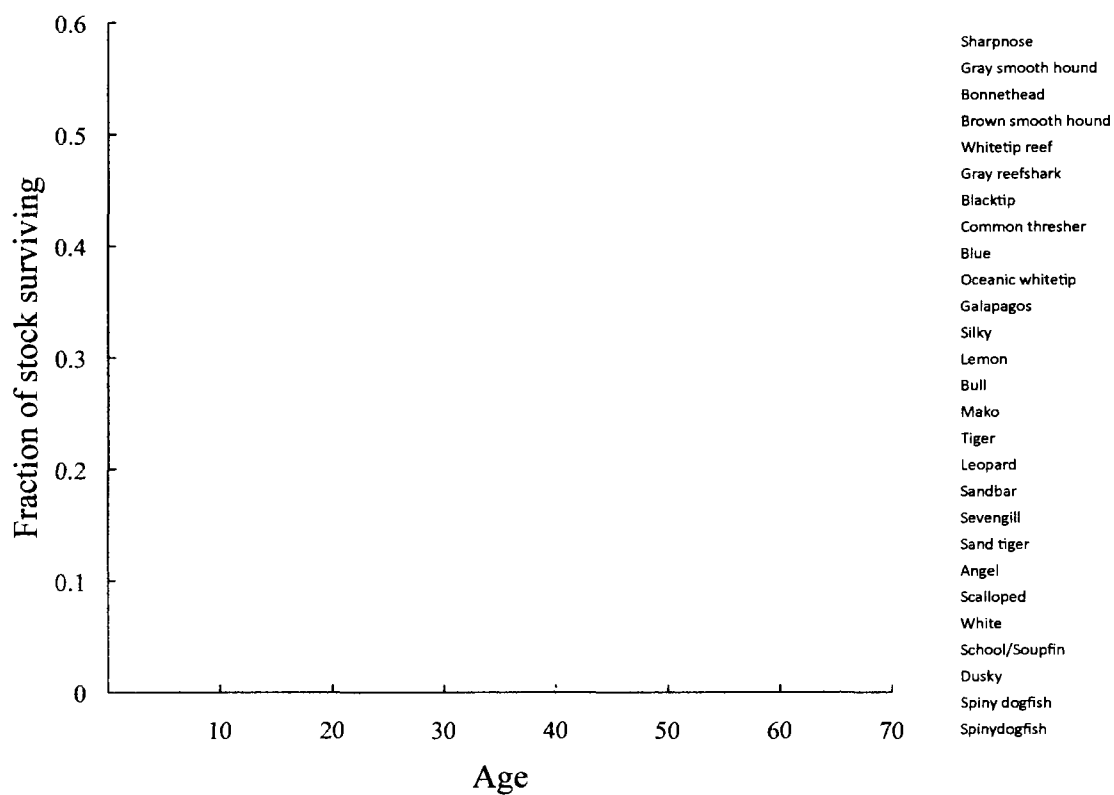


Figure 1.4. The age-structure of 26 species of sharks. The lines do not overlap because the fraction of individuals alive is dependent on  $M$ , calculated from maximum age. Longer-lived species have lower natural mortality and thus, shallower slopes. Species are identified by color (A- North-western Atlantic; B- British Columbia), the legend from top to bottom correlates to sharks from left to right

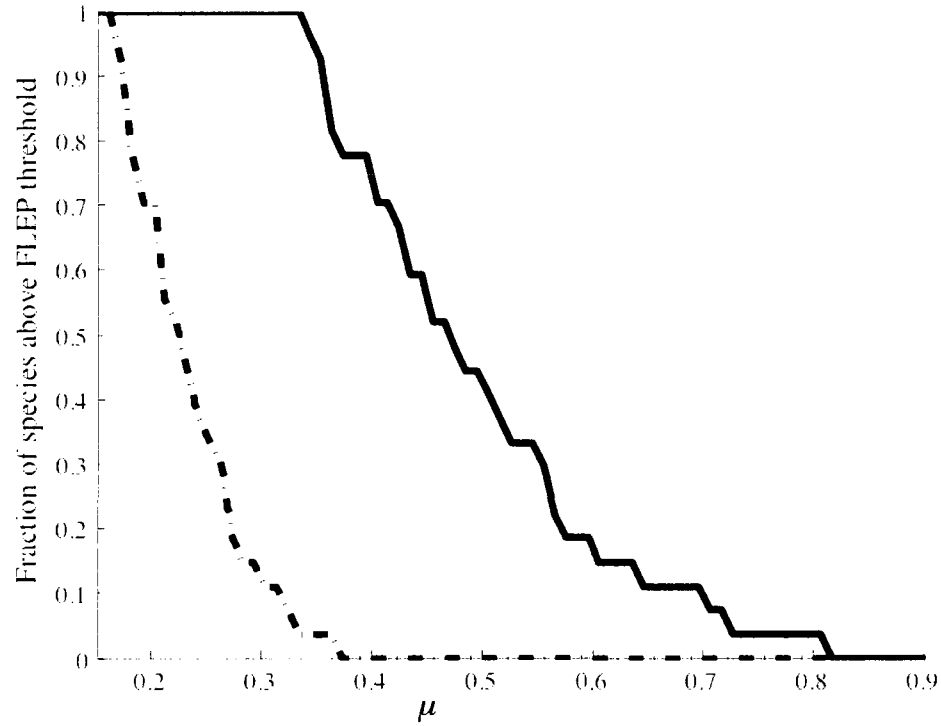


Figure 1.5. The fraction of 26 species of sharks that would be persistent under LRP of FLEP=35% (—), recommended for teleosts, and FLEP=60% (---), recommended for elasmobranchs (Restrepo et al., 1998), at increasing increments of fishing mortality. Fishing mortality is given as a fraction,  $\mu$ , of the natural mortality, where  $F = \mu M$ .

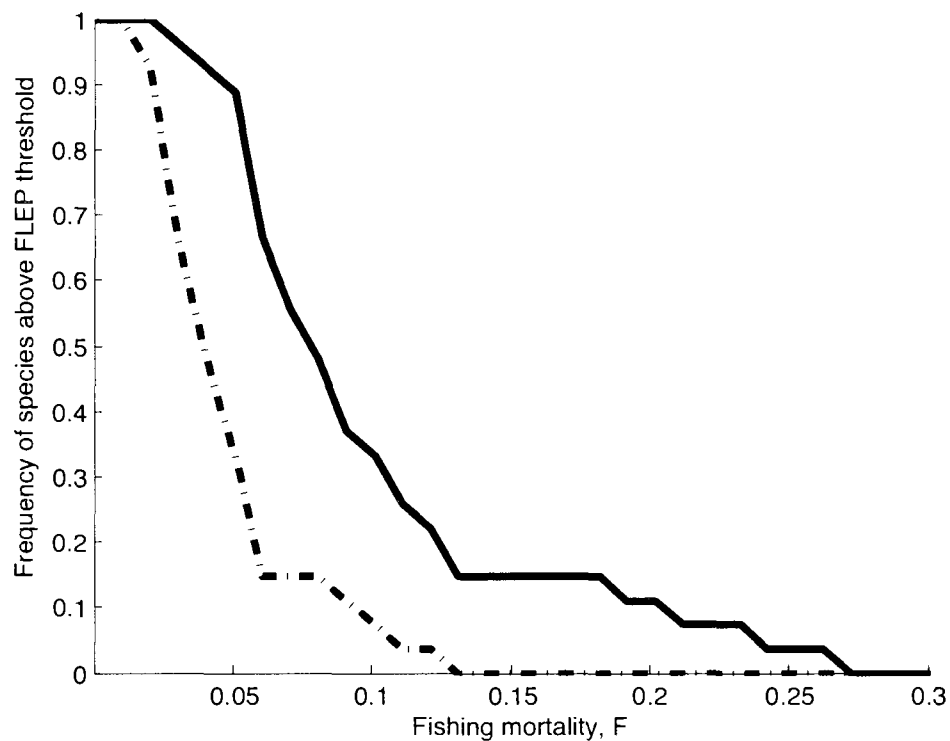


Figure 1.6. The fraction of 26 species of sharks that would be persistent under LRP of FLEP=35% (—), recommended for teleosts, and FLEP=60% (---), recommended for elasmobranchs (Restrepo et al., 1998), at increasing values of fishing mortality, F.

**CHAPTER 2:**

**Utilizing a data-poor framework to assess of the status of the common thresher  
shark, *Alopias vulpinus*, off southern California**

## ABSTRACT

Limited data on many species constrains the opportunity for adequate assessment under traditional frameworks. By assuming constant mortality and linear recruitment decline, we were able to use a combination of two available data types, catch per unit effort and size distribution data, in an age-structured model to determine the fishing mortality rate ( $0.76 \text{ y}^{-1}$ ) and the rate of recruitment decline with egg production ( $0.20 \text{ recruits egg}^{-1}$ ) for the common thresher shark, *Alopias vulpinus*, briefly exposed to targeted fishing pressure. From these results we determined the status of the local thresher shark population based on (1) the fraction of lifetime egg production and (2) the ratio of fished to unfished biomass. In 1992 the value of lifetime egg production ( $0.47$ ) was below acceptable value for sharks. The biomass had declined by 78%, indicating an overfished population. For new fisheries where catch-per-unit-effort and size data are available, the methods we use here can be applied to other data-poor species to determine the effects of fishing pressure and changes in the population structure.

## INTRODUCTION

Sharks and rays (elasmobranchs) are critical to many marine systems (Robbins et al., 2006) and are more prone to overexploitation than bony fish (teleosts; Klimley, 1999), with only a few species able to support fisheries (Cortés, 1998). There is increasing evidence that over-harvesting, from both targeted and incidental catch, has resulted in recent declines in a number of shark populations (see Bonfil, 1994; Cortés et al., 2002). In 2008, the World Conservation Union's Red List of Threatened Species included 126 chondrychthian species (21.3% of 591 assessed) as globally threatened (22-critically endangered, 29-endangered and 75-vulnerable) (IUCN, 2008). Recently, 16 oceanic sharks were added to the list of sharks at risk of extinction, including the common thresher shark, *Alopias vulpinus* (Dulvy et al., 2008). Because sharks are apex predators, significant declines in their populations can negatively impact marine ecosystems (Bascompte et al., 2005). In part to prevent overfishing of pelagic shark stocks and to ensure recovery of some already exploited on the west coast of the United States, the Pacific Fisheries Management Council (PFMC) implemented a Highly Migratory Species Fisheries Management Plan (FMP). The PFMC FMP relies on simple logistic and demographic population models for stock assessments and management is based on the predicted effects of fishing on those stocks. Under the FMP, harvest is federally managed for five species of pelagic sharks, including thresher sharks, and prohibited for three others.

Historically, stock assessment approaches have been geared toward populations with directed fisheries, utilizing fishery data such as total landings, fishery-dependent indices of abundance and age or size-structure when available. However, many species

lack adequate data for such management (Pilling et al., 2008). Although they are still taken in large numbers as bycatch in other fisheries (e.g. drift longline and gillnet) (Smith & Aseltine-Neilson, 2001), many pelagic shark species on the west coast of the US lack robust fishery data because they have not been subject to targeted fishing effort or were targeted only briefly (Smith & Aseltine-Neilson, 2001). Formal assessments of these species are either not possible or require novel methods for low data situations.

The common thresher shark, *A. vulpinus*, is the most common commercially caught pelagic shark on the west coast but lacks a formal assessment due to a paucity of data for traditional assessment frameworks. *A. vulpinus* was first targeted in 1978 in California waters during a springtime drift gillnet fishery. The California Department of Fish and Game (CDFG) collected thresher shark data through the California logbook system, landing receipts and length measurements from market samples during fishing seasons from 1981 through 1999. Over the first 11 years (1981-1991) there was a significant decline in the catch-per-unit-effort (CPUE) (Holts et al., 1998). In response, California implemented various seasonal and area closures following this period to protect reproductive females. By 1990, drift gillnet fishing was either completely prohibited or severely limited in the months that had previously provided 50% of shark catch (Bedford, 1987; Hanan et al., 1993). The associated effort was shifted to the more valuable swordfish, *Xiphias gladius*, with thresher sharks only incidentally caught or secondarily targeted during periods of low swordfish availability (Hanan et al., 1993).

The CPUE data from the fishery were used in the development of the PFMC Highly Migratory Species FMP to derive a proxy for the local maximum sustainable yield of the common thresher shark population on the west coast (Pacific Fisheries Management



Council, 2007). Data from the brief period of apparently constant CPUE near 1992 was used in a linear population model to derive a production function from the estimate of sustainable productivity based on the life history of the thresher shark (Pacific Fisheries Management Council, 2003). Current methods for assessing most shark populations depend on estimated life history information, rather than observations of responses to fishing. The value of juvenile survival is adjusted to provide zero population growth ( $r=0$ ) in Euler's equation for linear population models, with an assumed amount of fishing ( $F=M$  or  $F=0.5M$ ), and the juvenile mortality is adjusted to make  $r=0$ . Fishing is then removed, and the resulting value of  $r$  that solves the equation is used as an intrinsic rebound potential (Au & Smith, 1997; Smith et al., 1998; Pacific Fisheries Management Council, 2007; Au et al., 2008; Smith et al., 2008). These methods do not estimate current values of fishing mortality or abundance from observed population changes to density dependence in recruitment, rather they evaluate the theoretical response to somewhat arbitrary levels of fishing.

Because thresher sharks were targeted only briefly, the fishery lacks robust data from which to fully assess the population under conventional frameworks. Time series of catch and effort data are frequently available and they can be used to track an index of population abundance, but they support little other analysis. However, with the addition of size distribution data over a period of constant fishing pressure, we can determine how the structure of the population was changing in response to exploitation.

Our goal was to develop a method to determine the degree of fishing pressure reflected in the resulting change in the age and size-structure and the abundance of the data-poor thresher shark population. Insights into the fishing pressure and the

consequent underlying structure of the population allowed us to assess the ability of the population to sustain current (and other) levels of harvest. The methods we developed here may be applicable to other fisheries that undergo dramatic increases in fishing but lack the data to be assessed under current frameworks.

We made use of both size distribution and CPUE data in this approach. We used a size and age-structured estimation model to estimate the fishing mortality rate and decline in recruitment of the thresher shark due to fishery pressure. We then used the results to determine the overfishing status in 1992 in terms of: (1) the fraction of lifetime egg production (FLEP), an index of the spawning potential ratio of a population, and (2) the fraction of unfished biomass present. These reflect whether the population is undergoing overfishing, and whether the population is overfished, respectively (Restrepo et al., 1998).

## MATERIALS AND METHODS

To estimate parameters of the thresher shark fishery, we fit an age and size structured model to two sources of data; CPUE and size distribution. Annual CPUE values were calculated by Au and Show (*unpublished data*) from CDFG logbook entries on drift gillnet catches from 1981-1999. After the removal of erroneous data (e.g. unrealistic soak times, net lengths and catch numbers), these CPUE data were determined for uniform blocks in the California economic exclusion zone between the Farallon Islands and Cortez Bank. CPUE was calculated for the winter fishery (Aug-Jan) only, which was not affected by early changes in the springtime near-shore fishery. A unit of effort was described as the net length x hours soaked. We assumed that these

data were an adequate index of the abundance of sharks in the population; they appeared to be consistent with the decline expected of a new fishery (Fig. 2.1).

### **Age-structured model**

We first developed an age-structured model of *A. vulpinus* to estimate fishing mortality rate and population status from data for the first 12 years of the fishery. Though the first experimental offshore net fishery was initiated in 1977 we began our analysis in 1981, as that was when a logbook program providing reliable catch and effort data and length sampling began. The end of the useful part of the CPUE data series for this analysis was taken to be 1992, when restrictions and management decisions (e.g. limited entry, time/area closures, shortened season) caused the previously declining CPUE to level off and then begin to increase. We assumed  $F$  was constant over this time period (1981-1992).

We used life history values available in the literature (Smith et al., 2008a, 2008b) for the parameters of the population model. We assumed that females represented a constant portion of the catch throughout the fishery. Though the catch of males and females may not be equal, there were no data to suggest the sex ratio changed throughout this time period. Maturity was assumed to occur at age 5 y with a fecundity of 2 female pups.

We used the maximum age to be 25 y and a natural mortality rate,  $M$ , of  $0.179 \text{ y}^{-1}$  as estimated by Smith et al. (2008). Following Smith et al. (1998) we assumed no difference in the survivorship of adults and juveniles.

We assumed the population was at equilibrium before fishing began in 1981. To set the initial population to a constant equilibrium we normalized the replacement value,  $R_0$ , to equal 1 by adjusting first year survival and setting the age structure of the population to the stable age distribution (SAD).

When fishing began, population abundance declined because of two factors: (1) change in the age-structure due to the removal of older age classes, and (2) a possible decline in recruitment due to that change in the age-structure. The effect of the decline in age-structure is included in the standard Leslie matrix model, but the decline in recruitment would likely be density dependent, hence would depend on the stock-recruitment relationship, which is not included in a standard, linear form of the Leslie matrix. To account for the potential effects of population decline on recruitment we allowed recruitment to decline linearly with the decline in population reproduction represented by the changing age-structure and fecundity-at-age. We represented the slope of that decline in recruitment with production by a recruitment decline factor (RDF) that accounted for a linear decline in recruitment with declining stock size. This assumes that a portion of the stock recruitment relationship is linear. This assumption can be illustrated in terms of a general Beverton-Holt stock recruitment relationship (Fig. 2.2). For the ease of explanation and terminology we used the common fishery nomenclature of ‘eggs’ and ‘recruits’ rather than terminology specific to sharks (i.e. pups). Eggs are the independent variable in the egg-recruitment relationship, here computed from the age-structure and fecundity. The population at an initial time,  $t=0$ , will have had a specific egg production,  $E_1$ , and a corresponding recruitment,  $R_1$ . When fishing occurs, the age structure of the population would change and reduce the egg

production value to  $E_2$ . This new  $E_2$  would cause a drop in the recruitment to  $R_2$ . We refer to the assumed constant slope between these two points as the RDF:

$$RDF = \frac{(R_2 - R_1)}{(E_2 - E_1)} \quad (1)$$

This equation allows us to account for a decline of recruitment in the estimate as a result of the density dependence of recruits on egg production. Note that obtaining a value of  $RDF = 0$  would indicate constant recruitment, while a value of 1.0 would indicate that recruitment declined linearly in direct proportion to egg production (i.e., as in the standard Leslie matrix).

We were primarily interested in estimating the fishing mortality,  $F$ , which would cause the decline observed in the CPUE (Fig 2.1). However, to account for the possible effects of a decline in recruitment we also had to estimate the value of RDF that best fit our model to the available CPUE data. We chose values of  $F$  and RDF that minimized the loglikelihood error,  $\theta_1$ , between the CPUE data and the model,

$$\theta_1 = -2 \ln \left( \frac{\sum_{t=1981}^{1992} \left( \sum_{a=1}^{25} N_{a,t} - CPUE_t \right)^2}{\sum_{t=1981}^{1992} (CPUE_{mean} - CPUE_t)^2} \right)^n \quad (2)$$

where  $N_{a,t}$  is the number of individuals of age  $a$  at time  $t$ ,  $n$  is the number of samples and  $CPUE_{mean}$  is the mean value of the CPUE data.

To determine the values of  $F$  and RDF that minimize  $\theta_1$  we ran our age-structured model allowing  $F$  and RDF to vary over all reasonable values. Preliminary runs of the

Leslie matrix using coarse grain parameter values for F (0 to 3) and RDF (0 to 5) resulted in the likely ranges of 0.1 to 2.5 and 1 to 1.2, respectively. Each parameter was iterated with 100 values in an exhaustive search over these ranges.

### **Size-structured model**

Our initial finding from the fit of the age structure model to the CPUE data resulted in a similar value of the criterion ( $\Theta_1$ ) over a broad range of values of RDF and F. To resolve this remaining uncertainty we incorporated a second source of data reflecting the change in the size distribution with harvest. We used CDFG alternate length (AL) measurements recorded at commercial docks. Because animals were dressed by removing the head and tail prior to dockside measurements, actual lengths were not available. Total lengths (TL) were calculated by dividing AL by 0.175, the determined relationship between TL and AL (Hanan et al., 1993). Overall, 9,646 individuals were measured between 1981-1990 (Hanan et al., 1993).

To fit the model to the size data we computed the size distribution implied by the age distribution from our age-structured model. We did this by assigning each age a Gaussian distribution of sizes centered at the mean size at that age, calculated from the von Bertalanffy growth equation, and a standard deviation ( $\sigma$ ) of 10% of the mean. The Gaussian distribution was truncated at  $3\sigma$ . In this way, the size at a specific age was given as a Gaussian distribution to account for stochasticity in the growth of an individual. Parameters for the von Bertalanffy equation were taken from Smith et al. (2008b) with  $L_\infty=465$  cm,  $k=0.129$  and  $L_0=135$  cm. The resulting size distribution

showed a typical distribution of a long-lived species with a low natural mortality, with a peak of large individuals near  $L_\infty$ .

There were no size limits in this fishery (Hanan et al., 1993); hence all sizes were considered available to the fishery. However, gillnets are commonly considered to have an abrupt selectivity based on the size of the mesh used. In addition, recent findings by D Cartamil (*pers comm.*) suggest that the smaller individuals do not use the pelagic environment as readily as adults and are therefore less likely to be caught in the pelagic fishery. Because of the unknown selectivity at lower sizes, we compared the size distributions of the model and data only over a range of sizes that we believe had constant selectivity. This range was 350-560 cm TL.

Size distribution data, both simulated and observed, were binned into 10 cm bins, representing the available sizes within this selectivity. The observed size distribution was smoothed using a “lowess” linear least squares fitting method in MATLAB. We used a criterion developed by Schnute and Fournier (1980) to determine the goodness of fit,  $\theta_2$ , between the fraction predicted,  $P$ , and observed,  $O$ , size distributions in each size bin,  $i$ , and year,  $y$ ,

$$\theta_2 = -2 \ln \left( \frac{\sum_{i=350}^{560} \sum_{y=1981}^{1990} O_{y,i} \ln \left[ \frac{O_{y,i}}{P_{y,i}} \right]}{\sum_{i=350}^{560} \sum_{y=1981}^{1990} O_{y,i} \ln \left[ \frac{O_{y,i}}{O_{mean,i}} \right]} \right) \quad \text{for all } O_i > 0 \quad (3)$$

where  $O_{mean}$  is the mean value of the distribution of a given bin over all years. Our estimation model sought to maximize the sum of the log likelihoods of the CPUE and size data.

$$\theta_3 = \theta_1 + \theta_2 \quad (4)$$

### Fraction of Lifetime Egg Production (FLEP)

We also determined the fraction of lifetime egg production (FLEP) for the best-fit parameters:

$$FLEP = \frac{\sum_{a=1}^{25} l_a e^{-Fa} m_a}{\sum_{a=1}^{25} l_a m_a} \quad (5)$$

where  $m_a$  is the fecundity and  $l_a$  is the survival of the unfished population at age,  $a$ , and  $F$  is the fishing mortality and current biomass,  $B_c$ :

$$B_c = \frac{B_t}{B_o} \quad (6)$$

where  $B_o$  is initial biomass and  $B_t$  is the biomass at time,  $t=1992$ , from the estimation model with the estimated parameter values.

## RESULTS

Published values of survival and fecundity resulted in a value of  $\lambda > 1$ . We therefore reduced fecundity to 0.548 pups  $y^{-1}$  to obtain a population that was constant with time in the unfished state. This reduction represented the unknown early mortality that must be present for the population to be constant at the 1981 abundance.

Initial fits to the CPUE data produced a broadly defined maximum (Fig. 2.3), which indicated the best estimates of RDF and  $F$  are 0.16 (-0.11,0.42; 95% confidence



intervals) recruits  $\text{egg}^{-1}$  and 0.81 (0.59,1.13; 95% confidence intervals)  $\text{y}^{-1}$ , respectively. The surface is a narrow maximum band declining from upper left to lower right. The shape of the surface illustrates that the values of RDF and F are confounded in the sense that higher estimates of F are associated with lower estimates of RDF. This likely results from the fact that lowering F would require a decline in recruitment to account for the overall decline in the population (Fig. 2.1).

Using the size criterion (eq. 3) to fit the size distributions from the model to the size data, we found that the shape of the size distribution at low F values did not depend greatly on RDF. But as F increased, an increase in RDF resulted in a better fit (Fig. 2.4). The results do not suggest a conclusive maximum. Instead, the values of RDF and F (0.20 recruits  $\text{egg}^{-1}$  and 0.44  $\text{y}^{-1}$ , respectively) are again confounded, but in a different way. Increasing RDF would result in a lower recruitment, flattening the size structure of the population. Therefore, F must increase with this decrease in recruitment to maintain the decline with size of the size-structure. Figure 2.5 shows the observed and simulated size-structure across the 25 bins within the fishing selectivity. The simulated size distribution shows a good fit to the observed size distribution in all years except for the years 1986-87, which shows a flatter distribution in the data than in the model. Therefore, we did not use the size-distribution in 1986-1987 in our analyses.

Using the two criteria together (eq.4) gave a better estimate of the parameter values in part because the errors in the two criteria were confounded in opposite directions (Fig. 2.6). The error surface indicated a better-defined maximum with steeper sides than in either of the criteria independently. The estimates for RDF and F were 0.2

(0.57,1.044; 95% confidence intervals) recruits  $\text{egg}^{-1}$  and 0.76 (-0.07,0.44; 95% confidence intervals)  $\text{y}^{-1}$ , respectively.

The FLEP (eq. 5) indicated the spawning potential dropped to 0.47 of the unfished level. This is below the limit of  $F_{50\%}$ - $F_{60\%}$  recommended by Restrepo et al. (1998) for elasmobranch species. From equation 6, abundance had dropped to 22% of  $B_0$ . This is below acceptable values, and indicates an overfished population.

## DISCUSSION

The initial trend observed in the thresher shark CPUE data is common in heavily exploited new fisheries and is indicative of the fishing-up effect (Ricker, 1975). We can see from the observed data that significant decay occurred over a very brief period. It is therefore not surprising that our estimate indicates a high value of  $F$  ( $0.76 \text{ y}^{-1}$ ). This could have been fit with a linear model, such as a Leslie matrix, assuming some constant level of catchability. Such a linear assessment would not allow for density dependence and abundance would tend toward zero instead of a new non-zero equilibrium. In order to account for changes in the size-structure we need to include the RDF that accounts for a change in recruitment allowing the population to settle at a non-zero equilibrium.

The error in fitting the size-structure model to size data depends on RDF and  $F$  in a different way (Fig. 2.4) than fitting CPUE data (Fig. 2.3). The error in the combination (Fig. 2.6) could be viewed as the intersection of those two, yielding a better estimate than would be possible with either alone because of their different dependencies of errors on parameter values. The value of  $F$  from the combination was lower and the

estimate of RDF suggests that near this level of egg production a certain relative change in recruitment requires a nearly five-fold change in stock.

From the estimates of  $F$  and RDF we were able to quantify the sustainability status of the thresher shark in terms of FLEP and  $B_c$ . The value of FLEP (0.47) indicates the stock is overfished based on suggested critical thresholds for elasmobranch species (Restrepo et al., 1998). Fishing at this value of FLEP apparently induced a decline in sharks to 22% of unfished levels. This steep decline suggests *A. vulpinus* may be more prone to overexploitation than indicated by such recommended critical thresholds. Thresher sharks do not appear to be able to sustain even moderate levels of fishing pressure (i.e., a reasonably high value of FLEP). Similar trends have been observed in some long-lived teleost species on the west coast, which reportedly may require 50-70% of unfished levels to remain sustainable (Dorn, 2002).

FLEP may be biased low because we do not take fishing selectivity into account when determining the fished LEP (numerator in eq. 5). The first three reproductively mature age groups (5,6 and 7 y) were not subject to fishing pressure in our simulated fishing model but their continued reproductive input is not accounted for in the numerator of equation 5. Therefore, an even smaller reduction in FLEP may have resulted in the observed decline in biomass; thresher sharks may be even less resilient than suggested from this study.

Indicators of shark populations (e.g. catch records, logbook data) have suggested declines in shark population, but many sharks remain data deficient under current strategies (IUCN, 2009) and we are only now beginning to focus new strategies to fully assess these stocks. The methods applied here are unique way to incorporate different

forms of data to gain useful information from such data-poor stocks. These methods can be more broadly applied to other species with limited data to determine the effects of fishing pressure on the structure and the level of recruitment production. The techniques we developed for the thresher shark can be more broadly applied to other new fisheries with rapid declines, which lack robust data to determine their status under traditional frameworks such as North American sea urchin (Botsford et al., 2004). In addition, there are increasing sources of non-traditional data for shark catches on the west coast (e.g. angler blogs). It is important to determine a framework to include these diverse sources of data to better understand the current status of the stock. Similarly novel methods were implemented by Baum et al. (2003) to incorporate data from multiple sources to determine the status of Atlantic shark stocks. Developing frameworks to incorporate multiple sources of data is crucial to determine the status of these “data-poor” fisheries.

Following increased regulations, including area and time closures, directed fishing pressure on thresher sharks was eliminated (Hanan et al., 1993) and CPUE has been increasing since 1992 (PFMC, 2003). Though the population appears to be rebounding, our analyses suggest that thresher sharks are highly susceptible to overfishing. This population is susceptible to severe declines due to even moderate fishing pressure. We recommend continued precautionary limits on take of this species.

### **ACKNOWLEDGEMENTS**

I would like to thank J Cornelius, D Kaplan, W White, S Teo, L Moffitt, P Kilduff for assistance in model development and analysis. S. Smith, G Cailliet and D Au provided data. I would also like thank MKC Chapple, B Clucas, S Jorgensen, B Cornapple and countless other for their help in completing this manuscript. Funding for this project was provided by PEMREM and the NMFS-Sea Grant Population Dynamics Fellowship.

**LITERATURE CITED**

- Au, D.W., Smith, S.E. and Show, C. 2008. Shark productivity and reproductive protection, and a comparison with teleosts. In M. D. Camhi, E. K. Pikitch & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Oxford: Blackwell Publishing (pp. 298-308).
- Bascompte, J., Melian, C.J., and Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* **102**: 5443-5447.
- Baum, J.K., Myers, R.A., Kehler, D.G., Worm, B., Harley, S.J., and Doherty P.A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**: 389-392.
- Bedford, D. 1987. Shark management: A case history – the California pelagic shark and swordfish Fishery. In S. Cook, (Ed.), *Sharks-An Inquiry into biology, behavior, Fisheries, and use*. Oregon State Univ. Extension Publishing (pp 161-171).
- Bonfil, R. 1994. Overview of World Elasmobranch Fisheries. FAO Technical Papers No 341. Food and Agriculture Organization of the United Nations, Rome (pp 119).
- Botsford, L.W., Campbell, A. and Miller, R. 2004. Biological reference points in the management of North American sea urchin fisheries. *Canadian Journal of Fisheries and Aquatic Sciences* **61**: 1325-1337.
- Cortés, E. 1998. Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research* **39**:199–208.
- Cortés, E., Brooks, L. and Scott, G. 2002. Stock assessment of large coastal sharks in the U.S. Atlantic and Gulf of Mexico. National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Sustainable Fisheries Division Contribution SFD-2/03-177.
- Dorn, M.W. 2002. Advice on West Coast rockfish harvest rates from Bayesian meta-analysis of stock recruitment relationships. *North American Journal of Fisheries Management* **22**: 280-300.
- Dulvy, N.K., et al. 2008. You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18**: 459-482.
- Hanan, D.A., Holts, D.B. and Coan, Jr, A.L. 1993. The California drift gill net fishery for sharks and swordfish 1981-82 through 1990-91. *California Department of Fish and Game Fishery Bulletin* **175**: 1-95.

- Holts, D.B., A. Julian, Sosa-Nishizaki, O. and Bartoo, N. W. 1998. Pelagic shark fisheries along the west coast of the United States and Baja California, Mexico. *Fisheries Research* **39**: 115-125.
- IUCN. 2009. IUCN Red List of Threatened Species. Retrieved November 16, 2009, from <http://www.iucnredlist.org>
- Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629-638.
- Klimley, P. 1999. Sharks beware. *American Scientist* **87**: 488-491.
- Pacific Fisheries Management Council. 2003. Fishery Management Plan and Environmental Impact Statement for U.S. West Coast Fisheries for Highly Migratory Species. Portland, Oregon.
- Pilling, G. M., Apostolaki, P., Failler, P., Floros, C. P., Large, A., Morales-Nin, B., Reglero, P., Stergiou, K. I. and Tsikliras, A.C. 2008. Assessment and management of data-poor fisheries. In J. Cotter & T. Potter (Eds.), In *Advances in Fisheries Science: 50 years on from Beverton and Holt*. Oxford: Blackwell Publishing (pp 280-305).
- Restrepo, V. R., et al. 1998. Technical Guidance On the Use of Precautionary Approaches to Implementing National Standard 1 of the Magnuson-Stevens Fishery Conservation and Management Act. NOAA Technical Memorandum NMFS-F/SPO-31, US Department of Commerce, Washington, D.C.
- Ricker, W. E. 1975. Computation and Interpretation of Biological Statistics of Fish Populations. *Bulletin of the Fisheries Research Board of Canada* **191**: 382.
- Robbins, W. D., Hisano, M., Connolly, S. R., and Choat, J. H. 2006. Ongoing collapse of coral-reef shark populations. *Current Biology* **16**: 2314-2319.
- Schnute, J. and Fournier, D. 1980. A new approach to length-frequency analysis: growth structure. *Canadian Journal of Fisheries and Aquatic Sciences* **37**:1337-1351.
- Smith, S. E., and Aseltine-Neilson, D. 2001. Thresher shark. W. S. In Leets, C. M. Dewes, R. Klingbeil & E. J. Larson (Eds.), *California's Living Marine Resources: A status report*. University of California (pp. 339-341).
- Smith, S.E., Au, D.W. and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* **49**: 663-678.
- Smith, S.E., Au, D.W. and Show, C. 2008a. Intrinsic rates of increase in pelagic elasmobranchs. In M. D. Camhi, E. K. Pikitch & E. A. Babcock (Eds.), *Sharks*

*of the Open Ocean: Biology, Fisheries and Conservation*. Oxford: Blackwell Publishing (pp 288-297).

Smith, S. E., Rasmussen, R. C., Ramon, D. A. and Cailliet, G. M. 2008b. The biology and ecology of thresher sharks (Alopiidae). In M. D. Camhi, E K Pikitch & E. A. Babcock (Eds.), *Sharks of the Open Ocean: Biology, Fisheries and Conservation*. Oxford: Blackwell Publishing (pp 60-68).



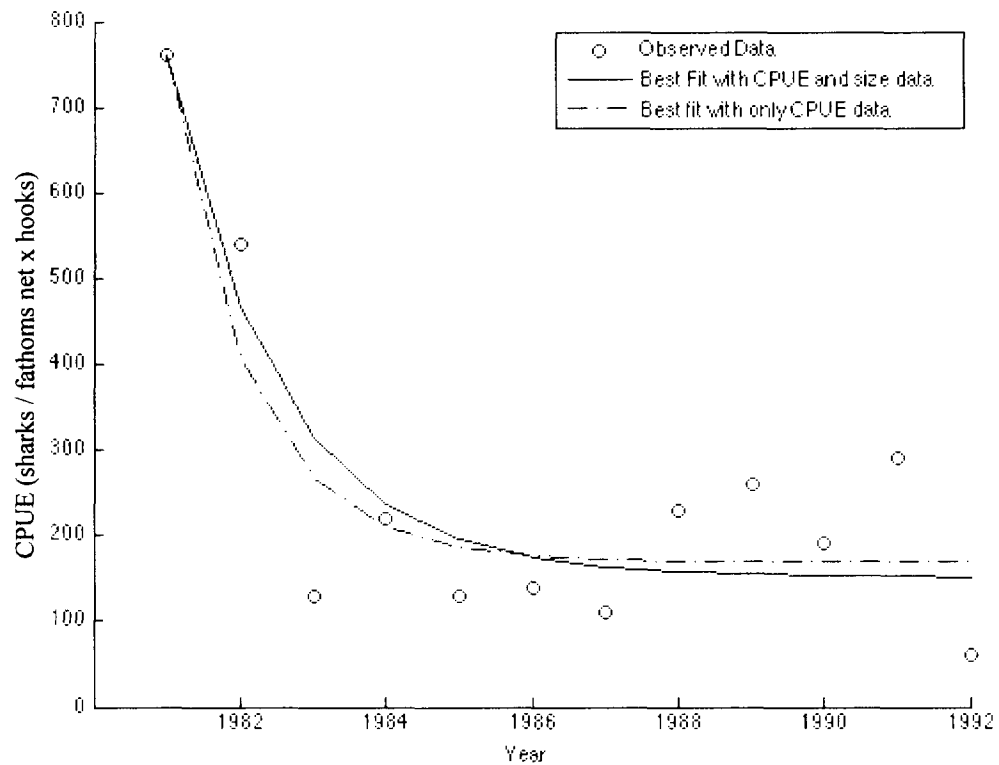


Figure 2.1. Observed CPUE data (o) from 1981-1992 with the best fit using only the CPUE data (— ·) and the best fit using a combination of CPUE and size distribution data (—). CPUE was defined as the number of sharks caught per net length x hours soaked.

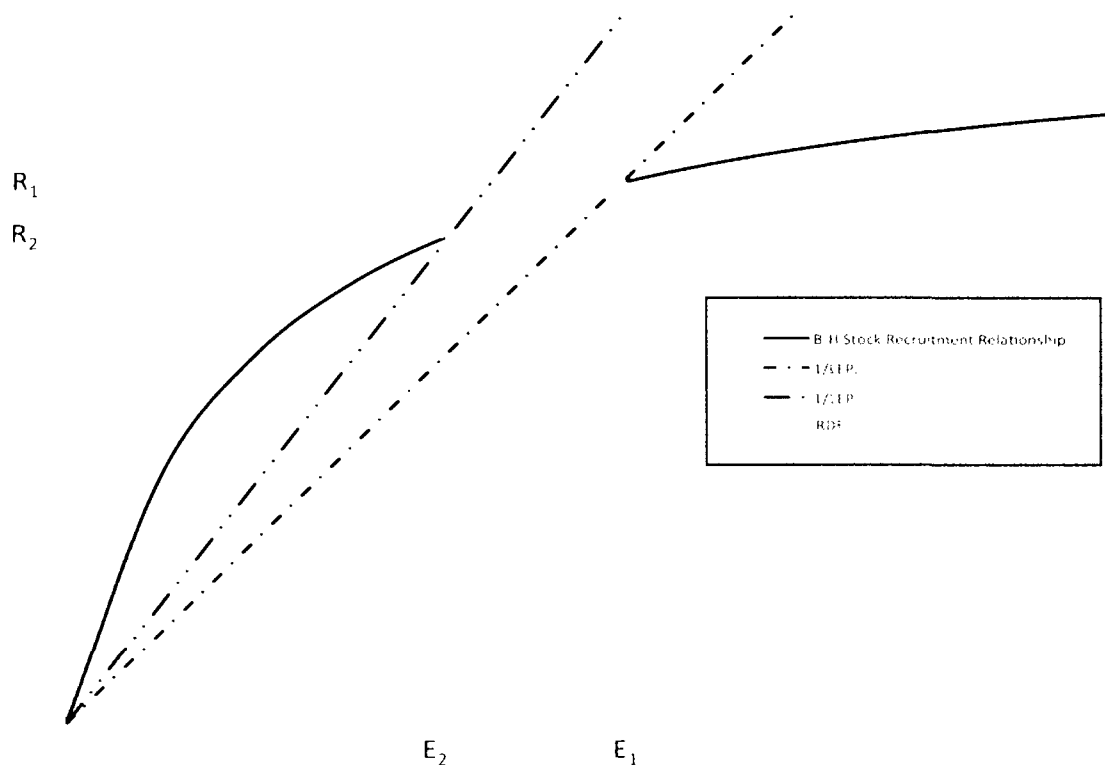


Figure 2.2. As the lifetime egg production (LEP) decreases, the slope of the line  $1/LEP_1$  ( — · ) increases and becomes  $1/LEP_2$  ( — · · ). The Beverton-Holt stock recruitment relationship ( — ), between the two points where it is intersected by each  $1/LEP$  line, can be represented by a straight line ( ——— ). This relationship illustrates the decline in the number of recruits ( $R_1-R_2$ ) with this decline in stock size ( $E_1-E_2$ ) or RDF.

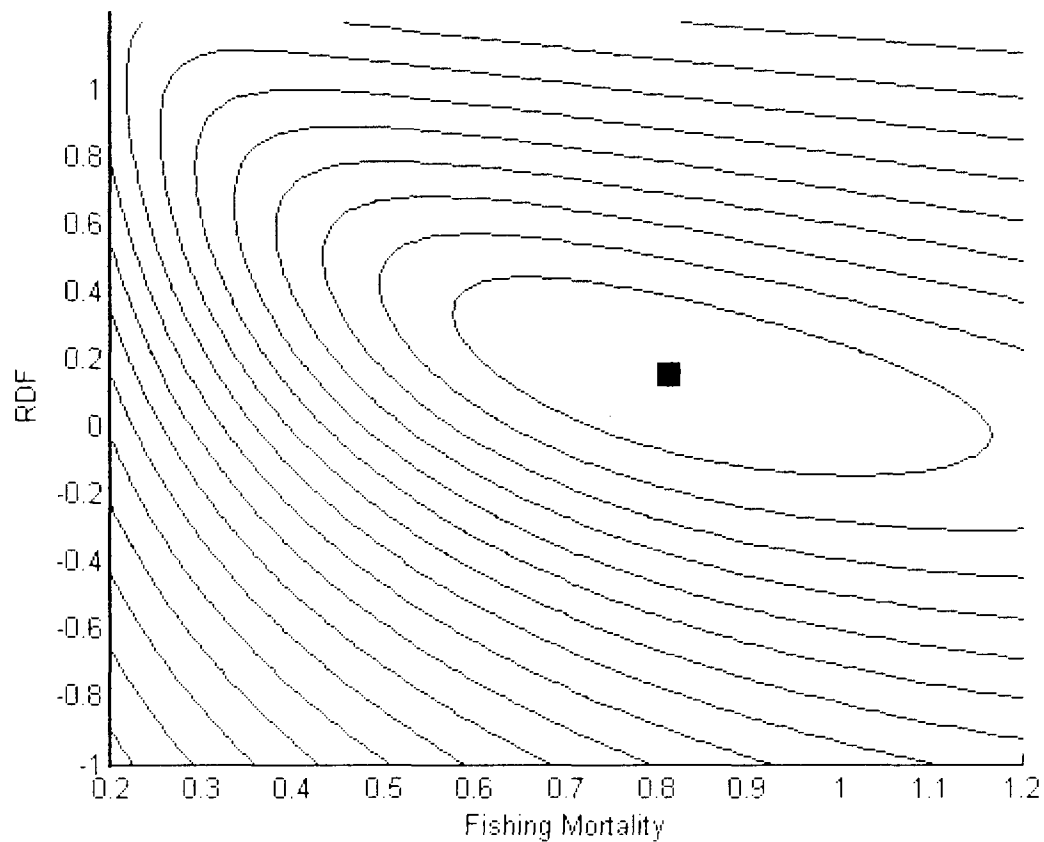


Figure 2.3. The contour lines represent the log likelihood error using only the CPUE data to determine the best fishing mortality and RDF. As the fishing mortality is increased the RDF decreases. The ■ indicates the location of the maximum and the shaded area represents the 95% confidence interval. The maximum contour line represents a value of 18 with each line an increment of 2.15.

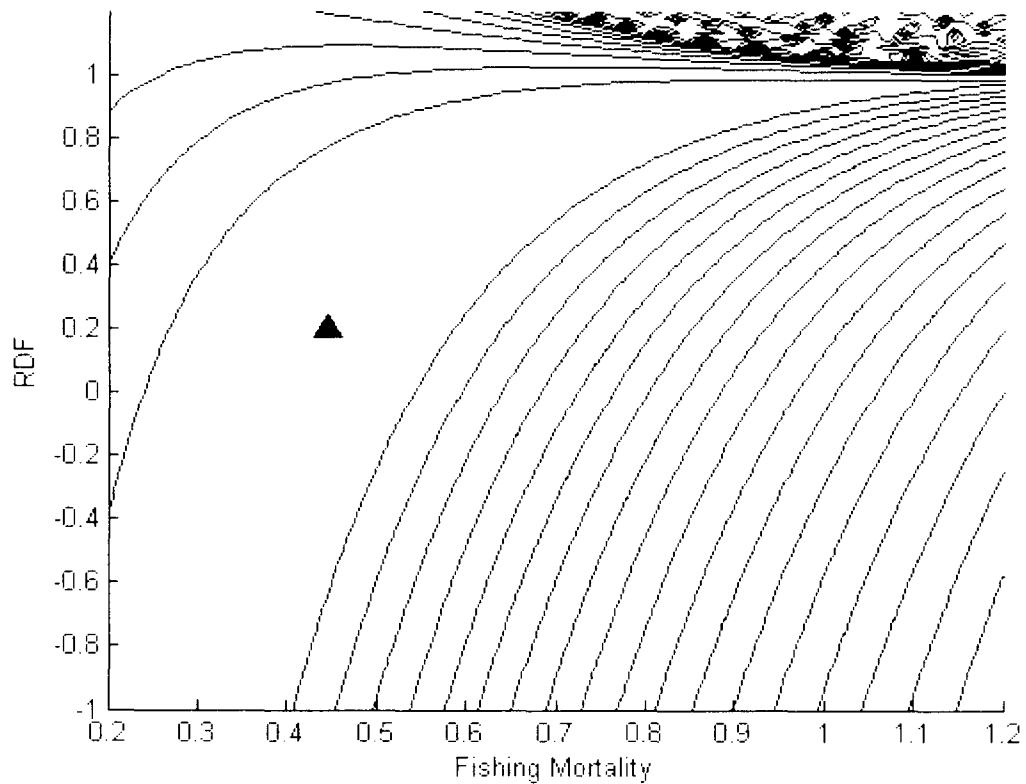
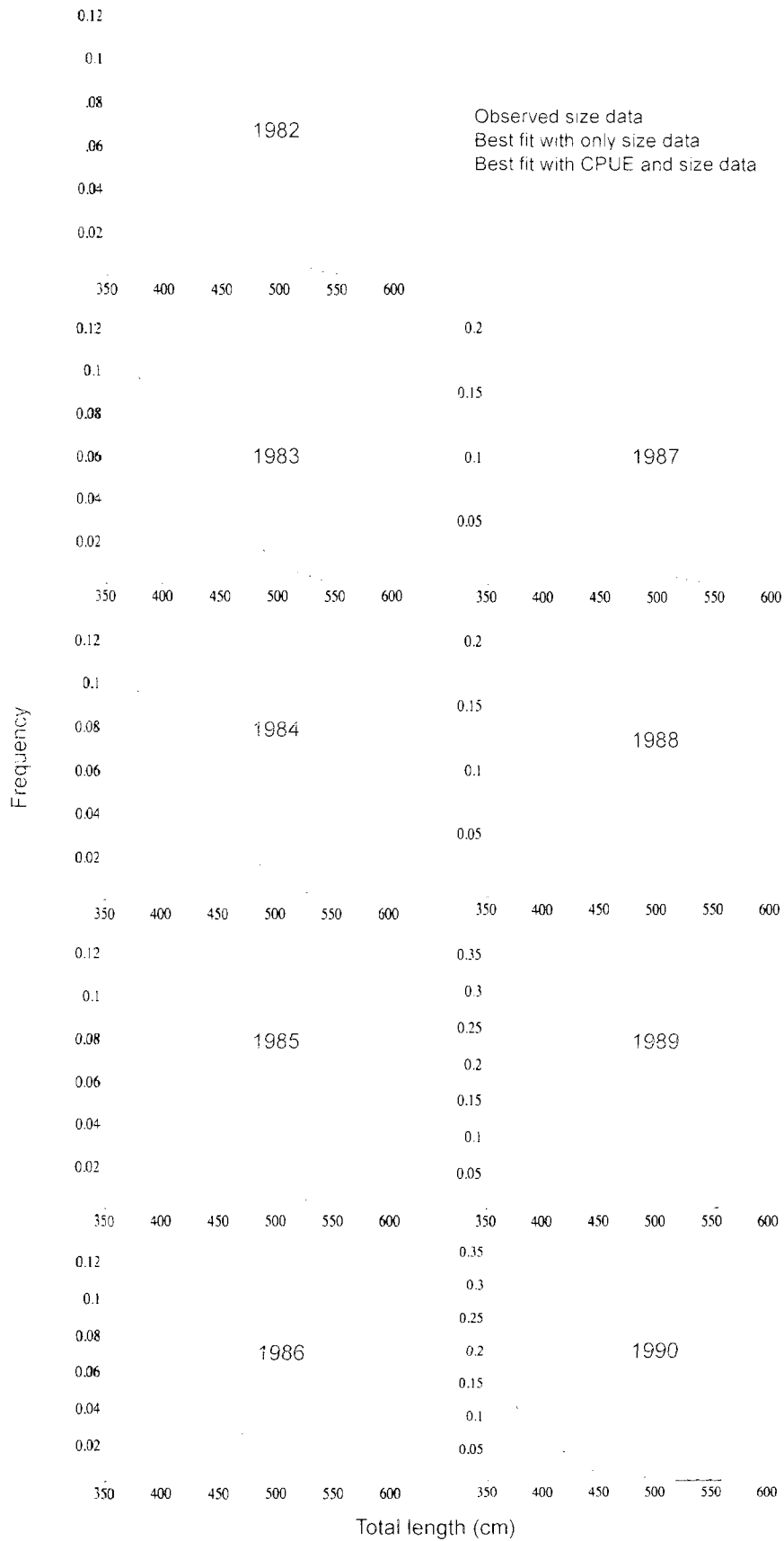


Figure 2.4. The contour lines represent the log likelihood error using only the size distribution data to determine the best fishing mortality and RDF. Size data was only used from 350-560 cm to represent those most likely caught in the fishery. The  $\blacktriangle$  indicates the location of the maximum and the entire surface is within 95% confidence interval. The maximum contour line represents a value of 10.3 with each line an increment of 0.1.

Figure 2.5. The observed and simulated size structure across the 22 bins within the fishing selectivity. Each year is plotted individually with the observed size distribution ( — ) and the best fit simulated distribution only using size-distribution ( — · ) and using both size distribution and CPUE data (— —).



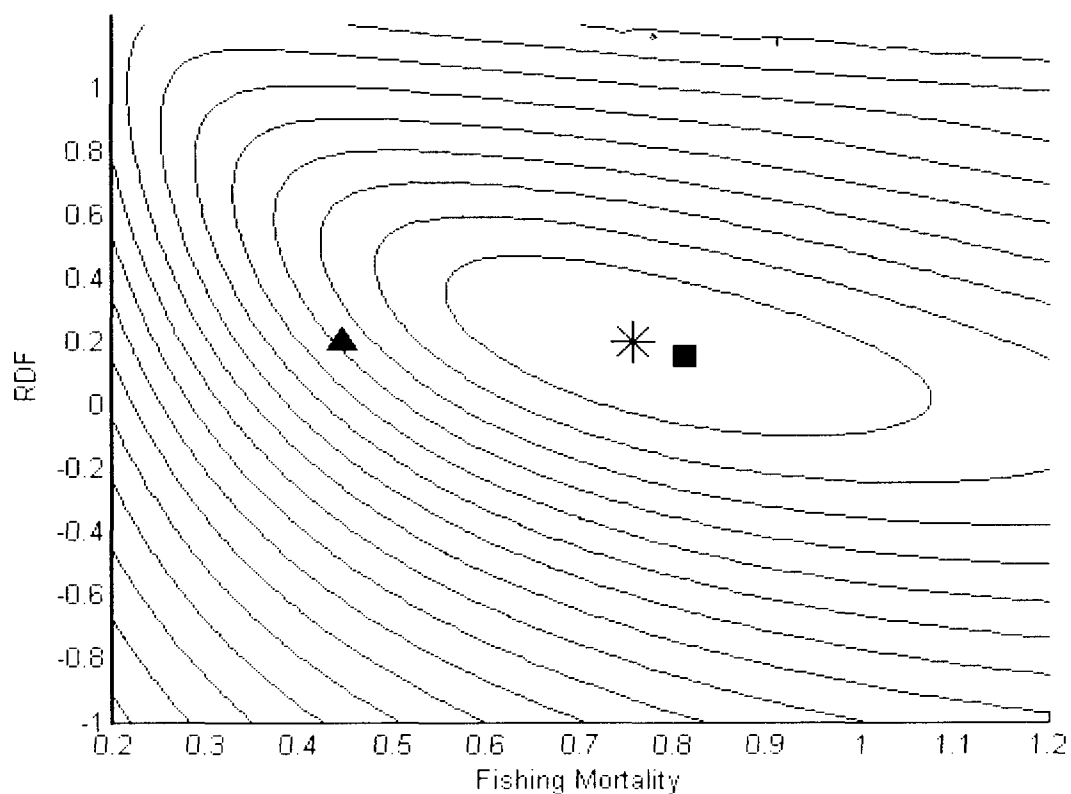


Figure 2.6. The contour lines represent the total log likelihood associated with the model using both CPUE data and the size data. The maximum is more defined than in each error plot alone. The \* in this plot indicates the location of the maximum, and the shaded area represents the 95% confidence interval. The ■ and ▲ indicate the maximum for the log likelihood for the CPUE and size distribution data, respectively. The maximum contour line represents a value of 7.3 with each line an increment of 2.17.

**CHAPTER 3:**

**A first estimate of white shark, *Carcharodon carcharias*, abundance off central**

**California using photo-identity marking**



## ABSTRACT

The catastrophic decline of apex predators such as large sharks in the global oceans underscores the need for careful assessment and monitoring of the remaining populations. Three genetically distinct populations of white sharks, *Carcharodon carcharias*, have recently been described in Australia/New Zealand, South Africa and the northeastern Pacific. Abundance estimates for Australian and South African populations suffer from low precision because of low recapture rates from conventional tagging. There is no abundance estimate in the northeastern Pacific, which is mostly comprised of aggregation sites in central California and Guadalupe Island, Mexico. We used photo identification of dorsal fins in a sequential Bayesian mark-recapture algorithm aimed at assessing white shark abundance off central California. We collected 321 photographs identifying 131 unique individuals. The model abundance off central California is estimated to be 251 individuals ([197,360] 2.5% and 97.5% quantile), an order of magnitude smaller than populations of other large marine and terrestrial predators currently protected internationally. This model quantifies the abundance with as much as a 90% increase in precision over previous methods used at other locations. Our methods can be readily expanded to include juvenile and young of the year sharks and sharks from other locations, over extended time-series, to monitor the status, population trends and protection needs of these globally distributed predators.

## INTRODUCTION

Chondrichthyan fishes (sharks and rays) play an important role in the health and function of ecosystems and, as apex predators, maintain stability in trophic systems (Bascompte et al., 2005). The life history and demographic characteristics of many sharks (e.g. delayed maturity, long gestation periods, low fecundity and long-life) indicate high susceptibility to exploitation when compared to teleosts (Myers & Worm, 2003; Myers & Worm, 2005; Schindler et al., 2002). Consequently, commercial, recreational and artisanal harvest of chondrichthyans has led to the overexploitation of many species (Stevens et al., 2000). In 2008, the World Conservation Union's Red List of Threatened Species included 126 chondrichthyan species (21.3% of 591 assessed) as globally threatened (22-critically endangered, 29-endangered and 75-vulnerable species; IUCN, 2009).

Perhaps the best known chondrichthyan, the great white shark, *Carcharodon carcharias*, is highly susceptible to overexploitation and has been listed internationally under the Convention on International Trade in Endangered Species (Appendix II) and the World Conservation Union's Red List (IUCN, Category VU A1cd+2cd). Though white sharks occur circumglobally, their distribution has recently been described to be comprised of at least three genetically distinct populations in Australia/New Zealand, South Africa and the northeastern Pacific (NEP; Jorgensen et al., 2009). These populations are small relative to other large marine predators and thus vulnerable to overexploitation and bycatch (Cliff et al., 1996; Strong et al., 1996; Klimley & Anderson, 1996).

There have been few attempts to quantify white shark abundance and the precision of those estimates has been limited by low capture rates or abbreviated observation time. Studies in South Australia (Strong et al., 1996) and South Africa (Cliff et al., 1996) used a mixture of conventional tagging and natural body markings to mark individuals. An open-population Jolly-Seber framework in South Australia yielded two estimates ( $N_1=191.7$  to  $N_2=18$ ), though their 95% confidence intervals ([36.5,1612.2] and [3.9,157.6], respectively) were wide and included values fewer than the number of animals tagged ( $n=67$ ; Strong et al., 1996). Similarly, researchers in South Africa used a modified Peterson estimate for closed-populations, with less than 8% recapture rate, and estimated an average abundance of 1,279 individuals (839,1843; 95% confidence intervals; Cliff et al., 1996).

Within the NEP (Fig. 3.1a), adult and sub-adult white sharks aggregate at sites off central California (CCA), USA (Fig. 3.1b) and Guadalupe Island (GI), Mexico (Fig. 3.1c), but there has not been a rigorous attempt to estimate the size of the population at any aggregation site in the CCA or the NEP as a whole. In CCA, there have been no fisheries specifically targeting white sharks and they have only historically been taken as bycatch for sport or trophy or as an occasional incidental component of targeted shark fisheries (Pacific Fishery Management Council, 2003). In 1982, a fisherman killed four large female white sharks at the Farallon Islands (FAR), a known aggregation site in CCA. These removals were followed by a significant decline in predation events on marine mammals at FAR (Pyle et al., 1996), which suggests the CCA population may be small and highly susceptible to exploitation. The minimum

number of individual white sharks present at FAR was determined based on unique markings between 1988-1992 ( $n=18$ ; Klimley & Anderson, 1996).

Electronic tagging studies over the past decade have rapidly advanced our knowledge of white shark movements and residency patterns (Boustany et al., 2002; Weng et al., 2007a, 2007b; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2009;). Sub-adult and adult white sharks in the NEP show a different habitat use strategy than young of the year (YOY) and juvenile animals. In the NEP, researchers used pop-up satellite archival tags to determine that YOY and juvenile white sharks (~3 year old) frequently use California Current waters off southern California, USA, and Baja California, Mexico, as nursery grounds (Weng et al., 2007b), whereas adult and sub-adult sharks consistently utilize three core areas throughout their yearly migration focusing on 1) North American shelf or coastal waters in central California from late July-February, and 2) the slope and offshore waters around Hawaii and/or 3) the eastern Pacific offshore waters, an area called the ‘White Shark Café’ (fig. 3.1a) (Jorgensen et al., 2009; Boustany et al., 2002; Weng et al., 2007a). These studies indicate that white sharks of this region have a philopatric behavior, with annual cycles from inshore to offshore and back, that results in a genetically discernible population structure (Boustany et al., 2002; Weng et al., 2007a; Jorgensen et al., 2009). Within the CCA, both observational and acoustic tagging data have shown that during their coastal period, white sharks are present mainly from September to November at three aggregation sites, when large numbers of juvenile elephant seals (*Mirounga angustirostris*) are nearby on the islands or beaches (Fig. 3.1b): 1) Tomales Point/Point

Reyes (TOM), 2) FAR and 3) Año Nuevo (ANI) (Ainley et al., 1980; Klimley & Anderson, 1996; Jorgensen et al., 2009).

Acoustic tagging data have provided more detail of these local movements and indicate that white sharks show localized preferences for regions on the coastal shelves, returning year after year to the same region (FAR, ANI, TOM; Jorgensen et al., 2009). These high-resolution positions (250m radius) indicate white sharks patrol the regional area of preference on the shelf, maintaining visitations and durations of residency of 1 to 75 days with repeatable visits to the same region for up to three years (Jorgensen et al., 2009). Satellite tag data from the entire California Current region where white sharks occur has also indicated that during this coastal period sharks tagged off GI do not travel to CCA and those tagged in CCA do not travel to GI (Boustany et al., 2002; Weng et al., 2007; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2009). Taken together, the electronic tagging data reveal high fidelity to specific locations in the coastal home range area for individuals.

A white shark's proclivity to investigate prey at the surface during this period allows visual identification of individual dorsal fins. The trailing edge of the dorsal fin is analogous to a humpback whale fluke pattern or fingerprint and can be used to uniquely identify an individual shark (Gubili et al., 2009) (Fig. 3.2). Other techniques, used at offshore islands, identifying pigment patterns along the trunk (Domeier & Nasby-Lucas, 2007) are often not applicable in coastal areas where high productivity or suspended particles reduce water clarity. This prohibits clear underwater video or pictures. Similar dorsal fin identification techniques have been described to identify nurse sharks, *Ginglymostoma cirratum*, (Castro & Rosa, 2005) and marine mammals

(Würsig & Jefferson, 1990). In white sharks, these markings appear to be conserved over long periods (>20 yrs) and even after rare instances of significant damage to fins, old markings are still identifiable (S D Anderson *unpublished data*, Fig 3.3). Such photographic evidence uniquely identified individual white sharks and was the first data that demonstrated long-term (i.e. 2-23 yrs) seasonal site fidelity at these aggregation sites (S D Anderson *unpublished data*). More recently acoustic tagging demonstrated that frequent movements between the sites occur, with high residency during the coastal period (Jorgensen et al., 2009).

Quantitative baseline abundance data for white sharks in CCA are not currently available, but strong site fidelity at the coastal aggregation sites and the availability of a method for individual identification supports use of mark-recapture frameworks to quantify their population abundance. Obtaining this information is critical for the proper management of this vulnerable but protected species. Any application of adaptive management or assessment for probability of extinction will require baseline information on population numbers.

The goal of this study was to collect above- and below-water photo identification of individual white sharks at seasonal aggregation sites over three years in CCA. These data were incorporated into a Bayesian mark-recapture framework, designed for estimates at low capture rates (Gazey & Staley, 1986), to determine a population estimate of sub-adult and adult white sharks in the CCA. The resulting estimate of white sharks in CCA can be combined with future estimates at GI to determine the population in the entire NEP and would function as a baseline for future studies concerning the

health of the white shark population supporting efforts to quantify their status, population trends and protection needs.

## MATERIALS AND METHODS

To obtain high quality photographs of sharks, individuals were attracted to the research vessel using a seal-shaped decoy attached by 80lb test monofilament. This activity was conducted under regulations by the California Department of Fish and Game, Gulf of the Farallones Marine Sanctuary, Point Reyes National Seashore and the National Marine Fisheries Service. A small (<2 kg) piece of bait obtained from dead marine mammal carcasses (*Mirounga angirostris*, *Physeter catodon* or *Zalophus californianus*) was introduced to the water to create a localized scent. The purpose of this bait was to sustain a shark's interest in the areas near the research vessel and increase the length of the interaction and, thereby, the probability of successful data collection. The sharks were not offered the bait for consumption. As soon as the dorsal fin emerged, high-resolution photographs were taken for quantitative identification using visual techniques with a Nikon D40X (55-200 mm lens with 10.1 megapixels). Sharks were lured closer to the boat by slowly retrieving the decoy (Goldman et al., 1996). Once near the boat, individuals were sexed according to the presence (♂) or absence (♀) of claspers using an underwater camera and sized via reference markings on the gunwale of the boat or parallel reference lasers. If animals came within several meters of the research vessel they were tagged with an Amirix V-16 ultrasonic transmitter and/or a Wildlife Computers pop-off archival tag (PAT Mk10). A small DNA plug was also retained using an aluminum pole. Weather and sea-state conditions

were taken at least every day and often following individual sighting events. This study was conducted each fall (i.e. September-January) in 2006, 2007 and 2008.

ID's were determined from digital photographs of a full lateral view of the entire dorsal fin, though some instances did not permit such ideal quality photos (see below). If the animal did not surface and water clarity permitted, images were taken from high-definition underwater video. The highest quality fin photograph of each shark (defined below) was entered into a photo database at the conclusion of each day. Fin photographs were matched visually using natural notches on the trailing edge and, if possible, pigmentation patterns. All photographs were printed with the entire fin 20cm in height. Fins were compared by lining up valleys and peaks within the trailing edge. If a fin had a large wound or was missing a section, the undamaged portion was used to match. We assumed animals could gain notches over time, but could not lose them (except to be made larger; S D Anderson *unpublished data*).

To determine error rates of false identification we ran experimental matching trials. Four experts experienced with shark dorsal fin identification blindly matched 20 randomly chosen photographs from 12 sharks. Results from each expert were compared to the true matches based on known secondary characteristics (i.e. acoustic tags, body scars). Experts accurately identified individuals and matches 98% of the time with no false positives and only one false negative. Similarly, Gubili et al. (2009) used genetic data to show nearly 85% accuracy in individual identification using dorsal fin photographs. Attempts to use available software (e.g. DARWIN, FINSCAN) designed to identify marine mammal dorsal fins resulted in unacceptable levels of error (T K Chapple *unpublished data*).



We assumed mixing between sites (Jorgensen et al., 2009), therefore, fin photos from all locations were pooled. Logistical difficulties at ANI resulted in few unique ID's. Because animals have been found to move between the three study locations (Jorgensen et al., 2009), we assumed animals at ANI were likely to be encountered at the other locations. In fact, six of eight sharks identified from ANI were encountered at other locations and 15 of 21 sharks passively detected via acoustic tags at ANI were detected at other locations. Data from ANI is not included in the following analyses. Exclusion of these ANI data reduced our estimate by <3%.

Each photograph was compared to all other photographs within the entire dataset to determine matches. Each photo was also evaluated for image quality. Images were given a quality rank (maximum score of 7 points) based on 4 criteria: 1) Angle- If an image view was nearly lateral ( $90^{\circ}$ ) it was given two points. A trailing edge at a non- $90^{\circ}$  angle but still readable was given one point (e.g. normally  $>45^{\circ}$ ). All others were given zero points. 2) Size- If  $\geq \frac{3}{4}$  of the fin was photographed then two points were given. If only  $\frac{1}{2}$ - $\frac{3}{4}$  was photographed then one point was given and zero points were given for  $< \frac{1}{2}$  fin. 3) Focus- Two points were given to a non-pixelated focused photo and one point to a photograph slightly out of focus but still identifiable. Zero points were allocated if the photograph was unidentifiable because of blurriness or graininess or if the fin was only identifiable by some large distinguishing characteristics as this may violate necessary assumptions for analysis. 4) Contrast- One point was given for a fin that was distinct from the background. Zero points were given if portions of the fin were not discernable from the background.

Images were then binned by image quality score: 1) images  $\geq 6$ , 2) images with scores  $\geq 5$  and 3) all images. Each bin was analyzed in the mark-recapture framework to assess the effect of image quality on results.

### **Assumption of the Model**

The general assumptions of mark-recapture models discussed below have been presented by a number of authors (e.g., Seber, 1973; Gazey & Staley, 1986).

- **Closed Population**

Animals were assumed to not enter or leave the system. Because this study was conducted across a very small proportion of the assumed lifespan of the animals (3/36+ yrs) and because white sharks have low estimated natural mortality and fecundity (Smith et al., 1998; Cailliet et al., 1985), we assumed the population did not change significantly during the three-year study period. In addition, targeted fishing for white sharks is not permitted in US waters where these animals spend most of their time. However, they do move through international waters where unintentional hooking on longlines set for tuna might occur. Because this gear is not designed to catch large white sharks, we assumed that white sharks would break any leaders being used for these smaller species. Thus, for this analysis we assumed fishing mortality was negligible.

- **Every individual, marked or unmarked, has equal probability of being caught**

Klimley and Anderson (1996) suggested determination of population size using baiting methods has potential to be biased because they heterogeneously attract animals depending on the direction of the odor plume. We did not chum or actively attract

sharks with olfactory stimuli. The bait that we used created a small, localized scent that acted as a means to overcome an animal's natural apprehension to approach or remain near the boat once they had investigated the decoy.

In our study, every shark tagged in a previous year that was detected on the ultrasonic monitors in a subsequent year was also visually detected in that year. This suggests that the animals did not have negative association with the marking processes and were therefore equally likely to be identified/marked in subsequent years. Conversely, sharks did not consume any meat or other material that might cause positive association with the attraction process, thus, we assumed that there was no change in the capture probability.

- **Marking individuals does not alter their survival probability**

Photo-identification techniques employed to *mark* each individual in this study did not alter or affect the sharks in any way. Thus, we assumed there was no survival probability consequence of the photo ID. Some animals were tagged, however these tags have the capability to indicate mortality and in no case did this occur. Similar studies on epaulette sharks (< 75cm total length) found that tags were not detrimental to the long-term health of the animals (Heupel & Bennett, 1997). To date, attaching external tags to the significantly larger white sharks has not had any effect on survival probability as measured directly by our pop up satellite tagging program (zero mortality).

- **Individuals do not lose their marks**

Marking an individual involves visually identifying the unique characteristic on the trailing edge of the dorsal fin. Gubili et al. (2009) used genetic data and photo ID's to

show the accuracy of fin identification over a short period and S D Anderson (*unpublished data*) showed that dorsal fins were conspicuous and conserved over long time periods. Similar techniques have been employed in extensive time-series studies with other marine (Currey et al., 2008) and terrestrial organisms (Heilbrun et al., 2003).

- **Sampling time is instantaneous**

The sampling period was a small fraction of time in relation to the mixing time allowed marked and unmarked individuals. Sampling occurred from September through January. All individuals are allowed to mix for the remainder of the year before the next sampling period occurred.

- **Animals do not leave the population and return**

Observations of females has suggested that they are present every other year (Anderson & Pyle, 2003). During our brief study period we saw no evidence of a two year cycle. Ultrasonic tags allowed us to passively monitor the presence of the sharks. All animals that were passively detected in year one and three were also detected in year two. We assumed that these animals were representative of the population; there were no animals that left the population and later returned.

### **Bayesian Framework**

Below, we briefly outline the key steps and assumption in the use of Bayes' theorem in a mark-recapture framework adapted from Gazey and Staley (1986). This method was initially adapted for mark-recapture estimates with a low number of recaptures (Gazey & Staley, 1986). For a more comprehensive description see Gazey and Staley (1986).

We assumed that the probability of detecting an observed number of recaptures,  $R$ , at time,  $t$ , given some population level,  $N_i$ , could be represented by a simple binomial distribution with replacement:

$$P(R|N_i) = \binom{C_t}{R_t} \left(\frac{M_t}{N_i}\right)^{R_t} \left(1 - \frac{M_t}{N_i}\right)^{C_t - R_t} \quad (1)$$

where the probability that the sample size,  $C_t$ , contains  $R_t$  is conditional on  $N_i$ , given the total number of marked animals in the population,  $M_t$ .

The mark-recapture framework can also be written as a Bayesian algorithm with  $k$  discrete values of  $N_i$ , between  $M_t$  and a realistic ceiling,  $N_k$ , determined from multiple runs of the model.

$$P(N_i|R_1, R_2, \dots, R_T) = \frac{P(N_i)P(R_1, R_2, \dots, R_T|N_i)}{\sum_k^k P(N_i)P(R_1, R_2, \dots, R_T|N_i)} \quad (2)$$

Initially, we used a uniform uninformative prior, except in the condition that  $N_i \geq M_t$ . In other words, population size could not be smaller than the total number of animals marked in the population.

Assuming each sample is independent, we can substitute equation (1) into equation (2) to calculate the posterior distribution:

$$P(N_i|R_1, R_2, \dots, R_T) = \frac{\prod_{t=1}^T \left(\frac{M_t}{N_i}\right)^{R_t} \left(1 - \frac{M_t}{N_i}\right)^{C_t - R_t}}{\sum_{i=1}^k \prod_{t=1}^T \left(\frac{M_t}{N_i}\right)^{R_t} \left(1 - \frac{M_t}{N_i}\right)^{C_t - R_t}} \quad (3)$$

The initial posterior distribution calculated from the uninformative prior was used as the prior for the subsequent calculation. From the final posterior we determined the mode of the distribution, which is equivalent to a maximum likelihood population estimate. In general, the mode is more conservative than estimates of median or mean values.

Similar to a traditional frequentist 95% confidence interval, standardized probability was calculated for fixed bounds  $a$  and  $b$ , such that  $P(a \leq N \leq b)$  is within  $1-\alpha$ . We used two frameworks; the 2.5% and 97.5% quantiles where  $P(N \geq b) = \alpha/2$  and  $P(N \leq a) = \alpha/2$  and the Bayesian posterior interval (credible interval) such that  $b-a$  is a minimum and  $P(a \leq N \leq b) = 1-\alpha$ . We determined the 95% probability of minimum population size.

## RESULTS

During this study we conducted over 1,130 observation hours (304 hrs in 2006, 322 hrs in 2007 and 504 hrs in 2008) attracting white sharks, encompassing 252 days (61 days in 2006, 79 days in 2007 and 112 days in 2008) at sea. During this period, we cataloged a total of 330 useable photographs (62 photos from 2006, 102 photos from 2007 and 166 photos from 2008) comprising 131 individual white sharks. Sharks ranged in estimated size from 259cm to 533cm total length (TL) where  $\mu=437\text{cm}$  and  $\text{s.d.}= 52\text{cm}$ . The sex ratio of males to females was approximately 2:1, however the sex ratio may be biased towards males because it is easier to confirm the presence of claspers than to confirm the absence. If the sex could not be confirmed, the animal was labeled “unknown.” The ratio of known to unknown was 4.26:1.

Analysis of image quality resulted in 131 unique individuals. Matching only those images with quality  $\geq 6$  resulted in a total of 124 individual sharks whereas 129 individuals were identified when images  $\geq 5$  were used. Because many of the low-quality images were duplicates of known sharks and did not represent unique individuals or resights, analyses run including lower quality images only changed the mode of the posterior distribution of  $N$  by  $\pm 2\%$ . We determined that picture quality was high enough to include all 131 individual sharks in the analyses.

In 2006, 39 animals were identified from the 62 photographs. In 2007, we resighted 9 animals (23% resight rate) and identified 45 additional unique animals. We identified 47 new individual animals in 2008 and resighted 12 animals from 2006 and 11 from 2007 (27% recapture rate). Of these 11 animals identified in 2007 and again in 2008, 4 were recorded over all three years of the study.

The total number of animals recorded by their unique fin photograph ( $n=131$ ) was set as the minimum value of  $N_l$ . A ceiling limit ( $N_k$ ) of 500 was determined from the shape of multiple initial calculations of the posterior distribution. The initial posterior distribution determined from the first two sampling periods was used as a prior for the final posterior distribution incorporating the third sampling period (Fig. 3.4). The mode of the posterior probability was  $N=251$  (2.5 and 97.5% quantile [197 360] and 95% credible intervals [191 349]). Our credible intervals were as much as 90% more precise than confidence intervals of previous methods employed at other locations. Figure 3.5 illustrates the 95% probability of minimum population size ( $N_{\min}=206$ ).

## DISCUSSION

Steep rapid declines in large coastal and oceanic shark populations have been reported along the Atlantic (Baum et al., 2003) and Gulf (Baum & Myers, 2004) coasts of North America, but few studies have examined the state of populations along the west coast of North America. The abundance of the white shark population reported here (N=251), which tracking studies indicate extends to the eastern to central Pacific, is strikingly small. Many populations of other large predators, despite having smaller ranges and having been depleted by human interactions, are higher than white sharks. For example, the lion population in the Serengeti, Tanzania was estimated at 2,500 individuals (Bauer & Van Der Merwe, 2004) and grizzly bears in the Greater Yellowstone area alone number at 600 (Haroldson, 2008). Even other large marine predators, such as the Southern Beaufort Sea stock of polar bears (1,526; Regehr et al., 2006), which are listed as threatened under the U.S. Endangered Species Act, and killer whales in the northeastern Pacific from California to the eastern Aleutian Islands (1,145; Secretariat, 2001), which are protected under the U.S. Marine Mammal Protection Act and Appendix II of the U.N. Convention on the Conservation of Migratory Species of Wild Animals, are markedly larger.

Historically, assessment approaches have been geared toward populations with directed fisheries, utilizing fishery data such as total landings, fishery-dependent indices of abundance and age or size-structure. In the case of white sharks, there has been no directed fishery and, though juveniles and adults have interacted incidentally with gill nets, few adults are caught as bycatch. Thus, photographic or tagging studies using mark recapture techniques and models remain the most effective way to derive a census.



Though we cannot definitively determine the reason for the relatively small population size of this apex predator from this estimate, there may be a number of causes. Genetic evidence suggests that the white shark population in the CCA may have recently been founded by a few individuals or experienced a bottleneck (Jorgensen et al., 2009). Alternatively, the population size in the CCA may also be a consequence of a small locally concentrated prey source at the coast. Marine mammals were virtually extirpated from CCA before the Marine Mammal Protection Act of 1972. Following traditional predator-prey dynamics, white shark numbers may be responding to low but increasing numbers of marine mammals (Sydeman & Allen, 1999).

The dorsal fin identification scheme we used here was a highly effective method to identify individual sharks and provides a universal platform to compare individual sharks globally. This method required only one photograph of the dorsal fin from either side. The nature of the trailing edge allowed for some degree of flexibility in the angle the picture was taken. This method has been effective in identifying individuals (Gubili et al., 2009) with less data requirements compared to other methods, such as using pigmentation patterns from six areas on the body of white sharks (Domeier & Nasby-Lucas, 2007). Though a pigmentation pattern identification scheme may be plausible at clear, offshore islands with a constant recreational diver system in place, attempting to gather the same information in very murky water without constant ecotourism effort in CCA is not feasible.

Though this estimate represents the population of white sharks in CCA that feed on marine mammals (juveniles lack serrated teeth to feed on marine mammals) it does not include sharks from GI nor juvenile and YOY sharks occurring in the California

Current ecosystem. Domeier and Nasby-Lucas (2007) have similar photo-ID records from white sharks at GI. The Bayesian model developed here could easily be utilized to derive a total white shark population in the entire NEP. To date, the satellite tag and acoustic tag data sets, which currently represent 167-tagged individuals (Jorgensen et al., 2009), indicate little interchange between CCA and GI. Thus, the total population abundance in the NEP will likely be larger.

Currently it is uncertain whether photo-ID methods would be applicable or feasible on YOY or juvenile white sharks. Satellite tagging data indicate white sharks have vertical and horizontal diving behaviors that bring them to the surface for long durations (Boustany et al., 2002; Weng et al., 2007a, 2007b; Domeier & Nasby-Lucas, 2008; Jorgensen et al., 2009) making a dorsal fin identification approach possible. The availability of captive specimens at the Monterey Bay Aquarium also provides a means for testing this methodology for the short-term on animals in a captive environment. Additional data from GI sharks and, if mark-recapture data is available, YOY and juvenile sharks, can be incorporated into the Bayesian framework used here, expanding the population estimate to the entire NEP.

The assumptions of a closed population mark recapture framework were approximately met. Tagging studies showed philopatry of these sharks over the duration of our study (Jorgensen et al., 2009). No animals were found to leave the population and/or return (Jorgensen et al., 2009). In addition, no animals appeared to lose their marks (i.e. major fin damage, see Fig. 3.3) or were affected by the marking process. Further studies across longer-time series or other geographic locations will further reassess whether these assumptions are met.

This population estimate provides a baseline to further assess and monitor white sharks' status. We can begin to assess quantitatively the effects of anthropogenic disturbances such as fishing mortality and ecotourism on population size. Though fully protected in US waters since 2003 and in California waters since 1997, white sharks continue to be illegally exploited for commercial purposes (e.g. shark fin soup) or incidentally caught in other fisheries. For example, halibut gillnet fisheries along the California coast have had high interactions with tagged YOY white sharks (Weng et al., 2007b). Shivji et al. (2005) used genetic markers to determine that white shark fins, mostly from individuals 1.2–2.0 m total length, were being illegally harvested and sold in US markets. The authors further suggested, because white shark fins were labeled and stored separately from other fins, that there may be a specific economic incentive for their fins. Illegal trade of these animals in the US, where regulations are the strictest, suggests that current enforcement and management strategies are not effective. Establishing a baseline for their population size and status allows quantitative determination of the threat imposed by illegal fishing.

In addition to illegal fishing practices, other anthropogenic factors may have population effects. At FAR, normally prime feeding grounds for white sharks, increased levels of human use for ecotourism and cage diving have the potential to alter foraging strategies and population levels (Orams, 2002). A population estimate from this study can aid in monitoring the population level in the entire CCA, but with further effort, can allow a comparison of population trends between high ecotourism areas (FAR) and low-use areas (TOM).

This study establishes a quantitative measure for white shark population size in the CCA. It is currently unknown if this reflects recent population declines or not, but it is clear that white sharks, among the largest predators in the oceans, exist in unexpectedly low numbers. The sequential Bayesian framework used here allows the use of time series and additional data (i.e. photo-ID data from Guadalupe Island and juvenile data) to provide a more informed estimate and insight into the direction of population changes as well as a comparison between trends in locations. It also provides a framework for developing a long-term monitoring strategy to measure changes in the CCA white shark population. In addition, a longer time series can more accurately determine parameters for an open population (e.g. survival, natural mortality) as well as the effect of movement rates on population estimates.

## ACKNOWLEDGEMENTS

I thank J. Cornelius, J. Barlow, K & C Chapple, K. Neff, C. Logan, J. Schaefer, R. Elliot, B. Cornapple, M. Peterson, D Nothhelfer and T. Kuhn for assistance with fieldwork, lab work, data processing and editing. I am grateful to S. McAfee, J. Fitzgerald, S. Neil, B. Becker, R. Theiss, T. O'Leary, E. Homer and crew of the R.S.V. Derek M. Bayliss for vessel and logistical support. This project was funded by PEMREM, NOAA-Seagrant, the Sloan, Moore and Packard Foundations as a part of the Tagging of Pacific Pelagics (TOPP) program of the Census of Marine Life. The Monterey Bay Aquarium Foundation, Pacific Coast Science and Learning Center, Patricia King and Bodega Marine Laboratory inter-campus travel grants also provided financial support.

## LITERATURE CITED

- Ainley, D. G., Strong, C. S., Huber, H. R., Lewis, T. J., & Morrell, S. H. 1980. Predation by Sharks on Pinnipeds at the Farallon Islands. *Fishery Bulletin* **78**: 941–945.
- Anderson, S. D., & Pyle, P. 2003. A temporal, sex-specific occurrence pattern among white sharks at the South Farallon Islands, California. *California Fish and Game* **89**: 96–101.
- Bascompte, J., Melián, C. J., & Sala, E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences* **102**: 5443.
- Bauer, H., & Van Der Merwe, S. 2004. Inventory of Free-Ranging Lions Panthera Leo in Africa. *Oryx* **38**: 26-31.
- Baum, J. K., & Myers, R. A. 2004. Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecology Letters* **7**: 135–145.
- Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J., & Doherty, P. A. 2003. Collapse and conservation of shark populations in the Northwest Atlantic. *Science* **299**: 389.
- Boustany, A., Davis, S., Pyle, P., Anderson, S., Le Boeuf, B., & Block, B. 2002. Satellite tagging - Expanded niche for white sharks. *Nature* **415**: 35-36.
- Cailliet, G. M., Natanson, L. J., Welden, B. A., & Ebert, D. A. 1985. Preliminary studies on the age and growth of the white shark, *Carcharodon carcharias*, using vertebral bands. *Memoirs of the Southern California Academy of Sciences* **9**: 49–60.
- Castro, A. L., & Rosa, R. S. 2005. Use of natural marks on population estimates of the nurse shark, *Ginglymostoma cirratum*, at Atol das Rocas Biological Reserve, Brazil. *Environmental Biology of Fishes* **72**: 213–221.
- Cliff, G., van der Elst, R. P., Govender, A., Witthuhn, T. K., & Bullen, E. M. 1996. First estimates of mortality and population size of white sharks on the South African coast. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 393-400).
- Currey, R. J., Rowe, L. E., Dawson, S. M., & Sloaten, E. 2008. Abundance and demography of bottlenose dolphins in Dusky Sound, New Zealand, inferred from dorsal fin photographs. *New Zealand Journal of Marine and Freshwater Research* **42**: 439–449.
- Domeier, M., & Nasby-Lucas, N. 2007. Annual re-sightings of photographically

- identified white sharks (*Carcharodon carcharias*) at an eastern Pacific aggregation site (Guadalupe Island, Mexico). *Marine Biology* **150**: 977-984.
- Domeier, M., & Nasby-Lucas, N. 2008. Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Marine Ecology Progress Series* **370**: 221-237.
- Gazey, W. J., & Staley, M. J. 1986. Population estimation from mark-recapture experiments using a sequential Bayes algorithm. *Ecology* **67**: 941-951.
- Goldman, K. J., An, S. D., McCosker, J. E., & Klimley, A. P. 1996. Temperature, swimming depth, and movements of a white shark at the South Farallon Islands, California. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 110-120).
- Gubili, C., Johnson, R., Gennari, E., Oosthuizen, W., Kotze, D., Meyer, M., Sims, D., Jones, C., & Noble, L. 2009. Concordance of genetic and fin photo identification in the great white shark, *Carcharodon carcharias*, off Mossel Bay, South Africa. *Marine Biology* **156**: 2199-2207.
- Haroldson, M. 2008. Assessing Trend and Estimating Population Size from Counts of Unduplicated Females, 2008. In C. C. Schwartz, M. A. Haroldson, & K. West, (Eds.), *Yellowstone grizzly bear investigations: annual report of the Interagency Grizzly Bear Study Team*. Montana: U.S. Geological Survey (pp. 9-14).
- Heilbrun, R. D., Silvy, N. J., Tewes, M. E., & Peterson, M. J. 2003. Using automatically triggered cameras to individually identify bobcats. *Wildlife Society Bulletin* **31**: 748-755.
- Heupel, M. R., & Bennett, M. B. 1997. Histology of dart tag insertion sites in the epaulette shark (jb960370). *Journal of Fish Biology* **50**: 1034-1041.
- IUCN. 2009. IUCN Red List of Threatened Species. Retrieved November 16, 2009, from <http://www.iucnredlist.org>
- Jorgensen, S. J., Reeb, C. A., Chapple, T. K., Anderson, S., Perle, C., Van Sommeran, S. R., Fritz-Cope, C., Brown, A. C., Klimley, A. P., & Block, B. A. 2009. Philopatry and migration of Pacific white sharks. *Proceedings of the Royal Society B: Biological Sciences*. Retrieved November 4, 2009, from <http://rspb.royalsocietypublishing.org/content/early/2009/10/29/rspb.2009.1155.abstract>
- Klimley, A. P., & Anderson, S. D. 1996. Residency Patterns of white sharks at the south Farallon Islands, California. In A. P. Klimley & D. G. Ainley (Eds.), *Great*

*White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 365-374).

- Myers, R. A., & Worm, B. 2005. Extinction, survival or recovery of large predatory fishes. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **360**: 13–20.
- Myers, R. A., & Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* **423**: 280–283.
- Orams, M. B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management* **23**: 281–293.
- Pacific Fisheries Management Council. 2003. Fishery Management Plan and Environmental Impact Statement for U.S. West Coast Fisheries for Highly Migratory Species. Portland, Oregon.
- Pyle, P., Anderson, S. D., & Ainley, D. G. 1996. Trends in white shark predation at the South Farallon Islands, 1968-1993. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 375-380).
- Regehr, E. V., Amstrup, S. C., & Stirling, I. 2006. Polar bear population status in the southern Beaufort Sea. *US Geological Survey Open-File Report* **1337**: 20.
- Schindler, D. E., Essington, T. E., Kitchell, J. F., Boggs, C., & Hilborn, R. 2002. Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecological Applications* **12**: 735–748.
- Seber, G. A. F. 1973. *The Estimation of Animal Abundance and Related Parameters*. London: Griffin.
- Secretariat, C. S. A. 2001. *Population Structure and Genetic Variability in Northeastern Pacific Killer Whales: Towards an Assessment of Population Viability/LG Barrett-Lennard and GM Ellis*. Canadian Science Advisory Secretariat.
- Shivji, M. S., Chapman, D. D., Pikitch, E. K., & Raymond, P. W. 2005. Genetic profiling reveals illegal international trade in fins of the great white shark, *Carcharodon carcharias*. *Conservation Genetics* **6**: 1035–1039.
- Smith, S. E., Au, D. W., & Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine & Freshwater Research* **49**: 663–678.
- Stevens, J., Bonfil, R., Dulvy, N., & Walker, P. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* **57**: 476-494.



- Strong, W. R., Bruce, B. D., Nelson, D. R., & Murphy, R. D. 1996. Population dynamics of white sharks in Spencer Gulf, South Australia. In A. P. Klimley & D. G. Ainley (Eds.), *Great White Sharks: The Biology of Carcharodon carcharias*. San Diego: Academic Press (pp. 401-414).
- Sydeman, W. J., & Allen, S. G. 1999. Pinniped population dynamics in central California: correlations with sea surface temperature and upwelling indices. *Marine Mammal Science* **15**: 446–461.
- Weng, K. C., Boustany, A. M., Pyle, P., Anderson, S. D., Brown, A., & Block, B. 2007a. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* **152**: 877-894.
- Weng, K. C., O'Sullivan, J. B., Lowe, C. G., Winkler, C. E., Dewar, H., & Block, B. A. 2007b. Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series* **338**: 211–224.
- Würsig, B., & Jefferson, T. A. 1990. Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission* **12**: 43–52.

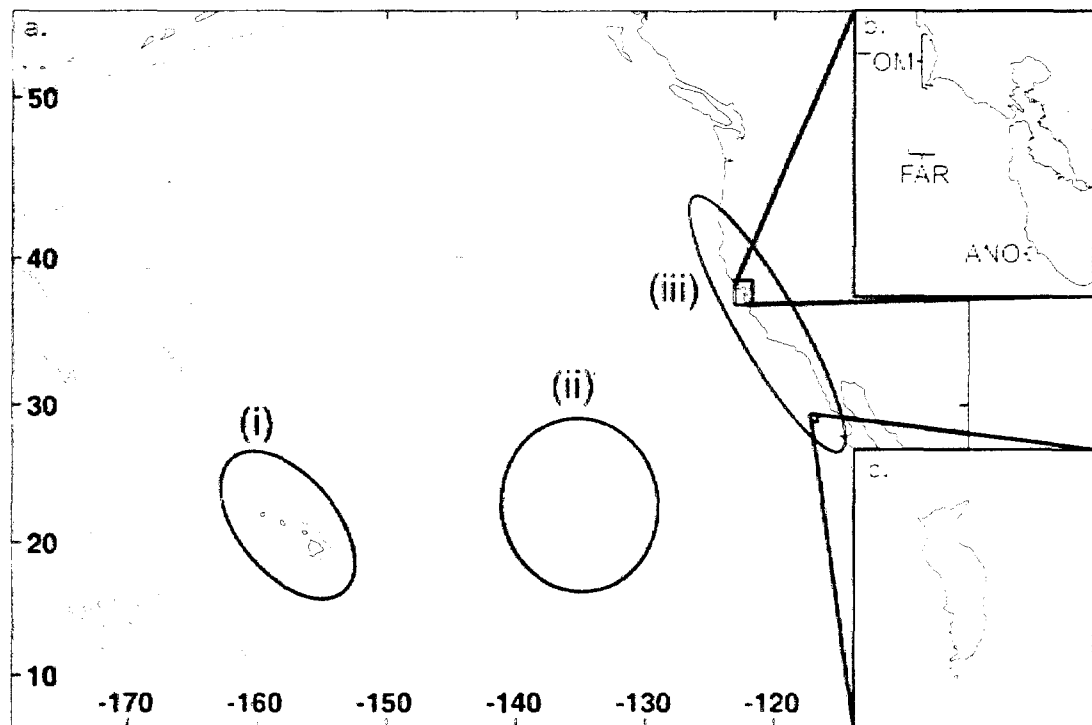


Figure 3.1 (a) The focal use areas in the NEP examined in this study. Coastlines and landmasses are designated by dark grey (i) slope and offshore waters around Hawaii (ii) the 'White Shark Café' and (iii) North American shelf or coastal waters. (b) Describes the three main aggregation sites in CCA. (c) Highlights the coastal known aggregation site at Guadalupe Island, Mexico.

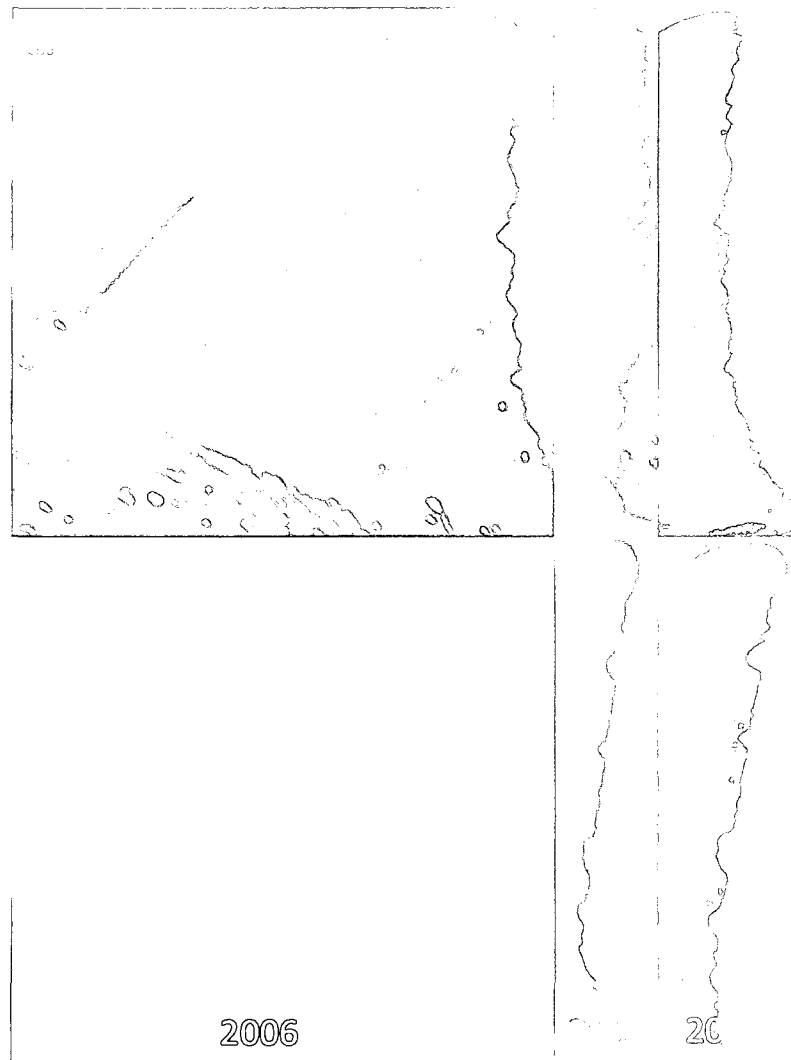


Figure 3.2 Photographs show the dorsal fin of (a) a 3.0m male and (b) a 3.5m male. Both sharks were identified in consecutive years as being present at the TOM site where the photos were taken in 2006, 2007 and 2008. The trailing edge of the fin, similar to a fingerprint, conserves the unique notches throughout the study period and allows them to be individually identified.



Figure 3.3 (a) This animal was seen in 2004 with a unique trailing edge, but no apparent damage. (b) In 2005, this fin was obviously damaged, as evident by the fresh tissue on the fin, but the trailing edge is still recognizable. (c) By 2008, the fin healed with a new large notch, but the fin still retained previous notches to be identified.

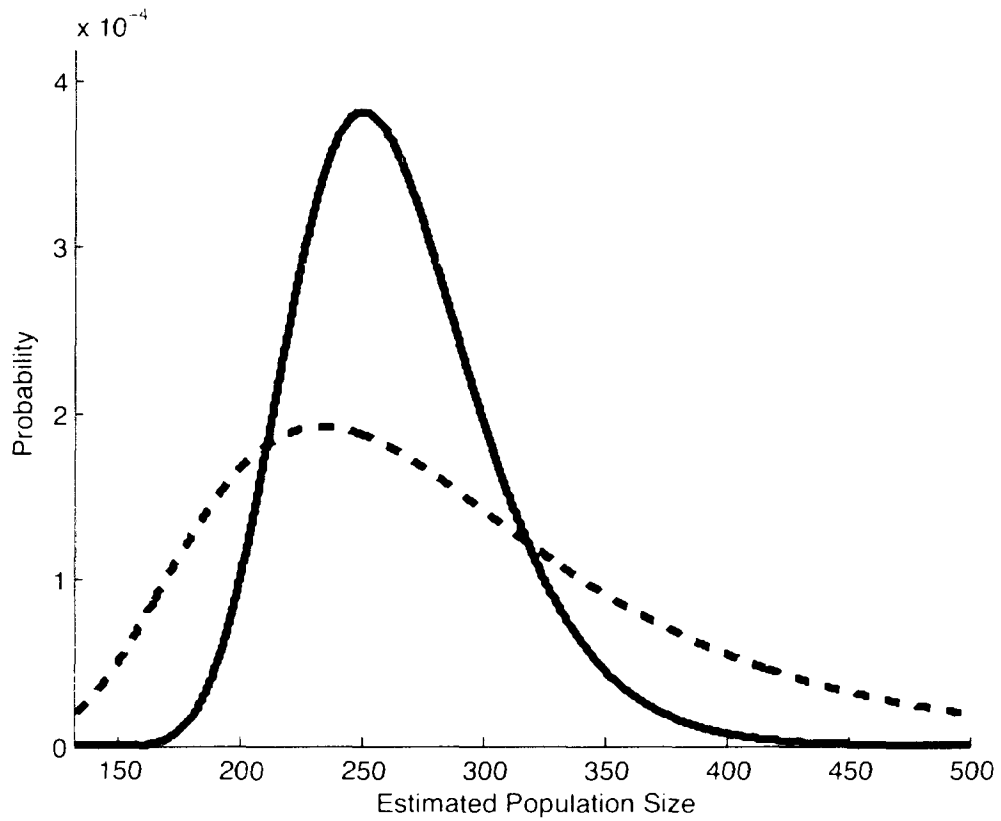


Figure 3.4 The initial posterior (--) calculated from the first recapture period (2007) is used as a prior for future calculations. The solid line represents the final frequency distribution (2008) with all data ( $N=251$  and  $N_k=500$ ).

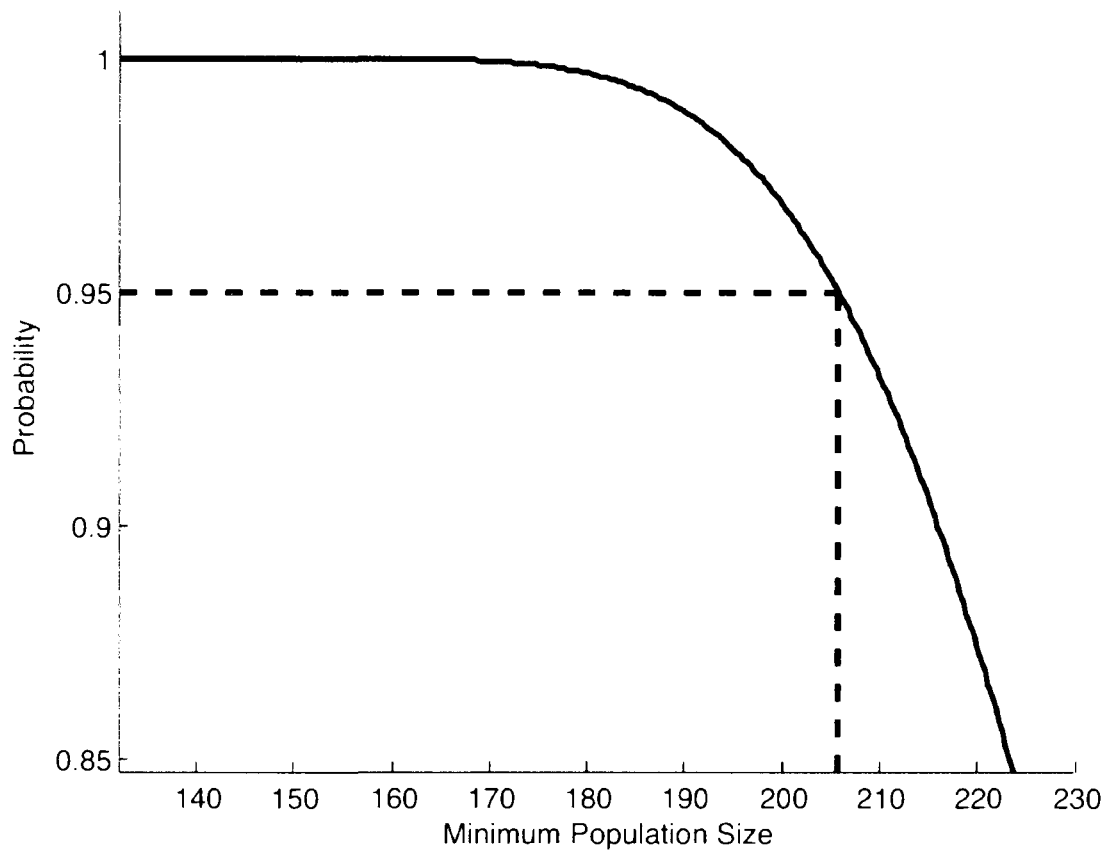


Figure 3.5 A cumulative posterior distribution illustrates the 95% probability that the population is a minimum of  $N_{\min}=206$ . Life is good.