ESTIMATES OF THE NUMBERS OF WHITE SHARKS (*Carcharodon carcharias*) IN EASTERN AND SOUTHERN SOUTH AFRICA: A POST-MORATORIUM ASSESSMENT

By

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Abstract

A moratorium was placed on fishing for white sharks (*Carcharodon carcharias*) in South Africa in 1991 prior to knowing the population status of this species. A mathematical model was developed to estimate the total numbers of white sharks from 1950 to 2050 in the presence of fishing (F = 0.055 year^{-1}) and without fishing (moratorium). The total number of white sharks from Richard's Bay to Struis Bay, South Africa was estimated to be 1,954 (range=1,855-2,050) for the year 2004. If the moratorium was to be lifted and fishing was to resume, the results of the model indicate that the instantaneous fishing mortality rate F of 0.035 year^{-1} or less allows the population to increase in numbers from 2004 to 2050. A sensitivity analysis determined that the instantaneous natural mortality rate M (tested range=0.070-0.190 year^{-1}) and the average number of pups per mature pupping female (tested range=4-14 pups) were highly sensitive parameters of the model. The maturity age span (maturity minimum age=13 and 16 years; longevity=23, 36, and 60 years) and timeframe of the female reproductive cycle (two or three years) were the least sensitive parameters of the model.

Introduction

White shark biology

The great white shark (*Carcharodon carcharias*) belongs to the Family Lamnidae, within the Order Lamniformes (Helfman *et al.* 1997). Other species within Lamnidae, known as the mackerel sharks, include the shortfin mako (*Isurus oxyrinchus)*, salmon (*Lamna ditropus*), and porbeagle (*Lamna nasus*). Sharing the broader category within the order of Lamniformes are the spotted ragged-tooth shark (*Carcharias taurus*), goblin (*Mitsukurina owstoni*), common thresher (*Alopias vulpinus*), megamouth (*Megachasma pelagios*), and basking sharks (*Cetorhinus maximus*). White sharks may be considered coastal or oceanic epi-pelagic fish and are found in all temperate and marginal tropic waters (Tricas *et al.* 1997). It has not been found to swim in brackish or fresh water (Compagno *et al.* 1997).

White sharks are seldom prey, with killer whales (*Orcinus orca*), large pinnipeds, and other large sharks suspected to be the only natural threats (Compagno 2001), not including humans. As opportunistic feeders, white sharks will not only eat their preferred prey of marine mammals, bony fish, and other chondrichthyans but will also consume marine birds and benthic invertebrates (Compagno *et al.* 1997). White sharks can catch large and highly mobile prey such as mako sharks, tuna, swordfish, and dolphins (Compagno *et al.* 1997). Klimley *et al.* (2001) found that white sharks off the California coast were most likely solitary hunters, but also remain in the vicinity of other sharks and may take part in feeding when others kill. There is also evidence of agonistic behaviour such as tail slapping when more than one shark is near available prey (Klimley *et al.* 1996a). Studies by Strong (1996) and Klimley *et al.* (1996b) dispute the previous notion that white sharks attack prey from behind in a more horizontal position and instead use a variety of tactics, including vertical anterior attacks. White sharks have also been found to breach, or jump out of the water to attack prey (Compagno 2001).

Tricas and McCosker (1984) described the mechanics of the jaw during attacks, in which the protrusion of the upper jaw and depression of the lower jaw may help to increase the force of the bite. The serrated teeth are mainly used for the initial bites, and make up most of the calcified parts of the white shark. Teeth have aided in the evolutionary and taxonomic placement of white sharks (Hubbell 1996, Applegate and Espinosa-Arrubarrena 1996, Long and Waggoner 1996), as well as giving clues to distribution (Barrull 1994).

Radio acoustic positioning buoys (RAPs), ultrasonic telemetry receivers, and stomach transmitters with temperature and depth sensors have all added to the knowledge base of swimming patterns of white sharks. Klimley *et al.* (2001) tagged five adult white sharks in October of 1997, and found that there were no differences among the time of day or night in the amount of time spent in the RAP range and type of activity. McCosker (1987), Klimley *et al.* (2001) and Goldman *et al.* (1996) are among those that have reported white sharks to keep stomach temperature above that of the surrounding sea temperature, and an overall elevated body temperature has been reported by Carey and Teal (1969), Carey *et al.* (1981, 1982), and Smith and Rhodes (1983). The metabolism of the white shark is such that feeding on a seal could sustain the shark's need for food for many weeks (Klimley *et al.* 2001).

Although these aspects of the white shark pertaining to habitat, diet, swimming and feeding behaviour are known there is still much more to be researched in each field. Up until the 1980's, few researchers focused on the white shark, and despite the increased research from the 1980's to the present, little is known on mating, natality, or even lifespan. Because sharks lack the typical age indicators of bony fishes, such as large calcified otoliths, researchers have instead used vertebrae. Wintner and Cliff (1999) determined the ages of white sharks from vertebral growth rings, estimating the age of mature males to be between eight and ten years and mature females no younger than 12 to 13 years. Previously, Compagno (1991b) stated the age of maturity to be around 14 years for females based on preliminary research carried out by Cailliet *et al.* (1985), which coincides with the results of Wintner and Cliff (1999). The Florida Museum of Natural History (FMNH) lists the oldest white shark caught to be 14 years of age, but states that the lifespan is most likely much longer. Porbeagles are listed to live to a maximum of thirty years, with at least one specimen found to be 26 years old (Campana *et al.* 2002). The FMNH also lists the maximum age of salmon sharks to be 20 years for females and 27 years for males, while the shortfin mako lives to about 20 years. Campana *et al.* (2002), in confirming the use of vertebral bands to indicate age in the porbeagle, also applied the technique to a shortfin mako specimen and found it to be 21 years of age. Compagno *et al.* (1997) state that females may live to 23 years of age, but do not give an age for males. Cailliet *et al.* (1985) estimated from a von Bertalanffy growth model a maximum age of 27 years for white sharks, while Smith *et al.* (1998) estimated from a von Bertalanffy growth equation a maximum age of 36 years. In their study of population demography, Mollet and Cailliet (2002) used a longevity for white sharks of both 36 and 60 years of age.

The male white shark's reproductive system is similar to that of the blue shark (*Prionace glauca*) (Pratt 1996). Sperm from the male is transferred to the female by modified pelvic fins, or claspers, and fertilization occurs internally (Pratt 1996). White sharks reproduce ovoviviparously, and the embryos developing in the uterus are thought to be nourished by oophagy (Francis 1996). Compagno (1991b) found that litters containing seven to 11 embryos were common, but can range from four to an unconfirmed maximum of 14 embryos found in a female in Australian waters (Uchida *et al.* 1996). Because of large litter size it is unlikely the white shark practices embryophagy like that documented in *Carcharias taurus* (Francis 1996; Gilmore *et al.* 1983; Gilmore 1993). Tricas *et al.* (1997) state that seven to nine pups are actually born per litter and that over a lifetime females are thought to give birth to four to six litters.

It is possible that gestation exceeds one year (Francis 1996, Compagno 2001). Mollet *et al.* (2000) estimates gestation to be 18 months, similar to the 15- to 18-month gestation period found for the shortfin mako. Therefore, the estimated reproductive cycle may be two or three years, depending on the resting period (Mollet *et al.* 2000).

Male to female ratios have been investigated in South Africa, with Cliff *et al.* (1989) finding a male to female ratio of 1:1.4 in KwaZulu-Natal. A much greater difference at Struis Bay was reported where 85 percent of the observed population was female (Ferreira and Ferreira 1996). More recently, Cliff *et al.* (1996) found a ratio closer to 1:1, where females comprised 54 percent of the population.

White shark status

Japp (1999) provided a detailed review of the shark fisheries history in South Africa, with the general facts highlighted here. Shark fisheries activities were not reported in South Africa until 1934 by Von Bonde, in which the economic potential for exploitation would have been high. The first fishery to start directly targeting many shark species was in Durban in the early 1930's, with simple gill nets. At the start of the decade, catches were estimated to be about 136 tons, whereas over 1,000 tons were reportedly caught by 1940. With the coming of the Second World War, vitamin A, found in fish liver oil, was in high demand. The cod liver oil industry in the United States was in a sharp decline. Fishers therefore turned towards shark populations to fulfil the demand. Soupfin sharks were the main target, but other species were caught as well, using not only gill nets but also handlines and short longlines. Although catch records were few and somewhat unreliable, catches by 1951 were said to reach as much as 1,500 tons per trip. Concern for shark populations brought about the formation of the Sea Fisheries Shark Advisory Committee in 1948, which placed the first regulations on shark fisheries in South Africa, setting a minimum net mesh size of 9". An increase in interest for the hake (*Merluccius capensis and M. paradoxus*) and sole (*Austroglossus pectoralis*) fisheries coupled with the decrease of vitamin A necessity and increase of utilizing sharks as fish food lured many foreign trawlers into South African waters. The depletion of hake and sole led to the setting in 1978 of the first total allowable catches (TACs) for these species. Catch reports of sharks have improved since then.

Japp (1999) also provided a comprehensive summary of fishing fleets, gear types, and shark restrictions. In more recent years, the heaviest exploitation of sharks lies within the large-scale bottom-trawl fisheries, followed by the longline fisheries and recreational hook and line fisheries. The offshore trawl fishery consists of smaller stern trawlers ranging from 30 to 50 meters long up to larger factory freezer vessels exceeding 50 meters in length. Otter trawls are primarily used with a minimum stretched mesh size of 110 mm. The inshore trawl fishery consists of both stern trawlers and side trawlers, with a minimum stretched mesh size of 75 mm. Catches of several species of sharks within the trawl fisheries are due to bycatch. The longline fishery does directly target large pelagic species of sharks, which requires a permit as does any commercial fishery targeting sharks. Both recreational and commercial line fisheries, consisting of shore anglers, skiboats, estuarine fishermen and spearfishermen target shark species. Gear is usually rod and line as well as spears. Surface drift nets, anchored set-nets, and beach-seine nets comprise the commercial net fisheries. Most net catches of sharks are bycatch, but there is a targeted gill net fishery for the St. Joseph (*Callorhinchus capensis*) using 75 meter-long nets with a stretched mesh size of 17.6 cm. The protective gill nets along the KwaZulu-Natal Coast also play a factor in shark mortality. The nets catch a variety of shark species including white sharks, with the majority being juveniles or young adults and few large adults.

From a global standpoint, the late 1980's and early 1990's was a turning point for shark awareness, with the white shark being no exception. Publicity on Dangerous Reef's decline of white sharks in Australia alerted not just the scientific community but also the general public, and resulted in a collaborative program focusing on research and managerial strategies (Bruce 1989). The United States National Marine Fisheries Service (NMFS), faced with an increasing fishing effort for sharks on the east coast, devised a national fisheries management plan in 1990 (Compagno 1991c). Support for NMFS grew when the American Elasmobranch Society formed a committee for conservation (Compagno 1991c). A newsletter, *Chondros*, also increased awareness of the status of sharks in association with the International Working Group on Chondrichthyan Fishes (Compagno 1991c).

In South Africa, it was not known if the trading of shark fins and jaws was significantly affecting white sharks, let alone the unknown impact of bycatch through gillnetting, longlining, and catches in the KwaZulu-Natal protective nets (Compagno 1991c). However, it was known that white shark parts and products were sold at a high price (Compagno 1991a). Also, the then director of the Sea Fisheries Institute, now Marine and Coastal Management, was aware of the white shark status globally (Compagno 1991d). As a pre-emptive management plan, a moratorium was passed prohibiting the catching or killing of white sharks in South African waters in April of 1991 (Compagno 1991a). The United States, Australia, Namibia, and Malta followed in banning the catching or killing of white sharks. By 1997, the IUCN listed the white shark in category K of its Red List, which meant that it was "suspected but not definitely known to be threatened" (Compagno *et al.* 1997, p.61). In November of 2003 the IUCN listed the white shark as "vulnerable", but perhaps will soon be listed as "endangered" (Fergusson *et al.* 2000). As of September 24, 2002 the Convention on Migratory Species, a UN treaty, was passed. All 80 nations under the treaty were banned from catching or harming white sharks (J.R. 2002). A recent stock assessment in the Northwest Atlantic found a 79% decline in the number of white sharks from 1986 to 2000 (Baum *et al.* 2003), which confirmed earlier concerns.

With regards to the South African white shark population, the effects of the moratorium are still undetermined. Dudley (2002) examined catch data recorded for 14 species of sharks caught in the KwaZulu-Natal nets from 1978 to 1999. Catches of white sharks did not represent a significant decreasing trend, however, catch per unit effort (CPUE) when including all months of each year did significantly decrease (Dudley 2002). Catch and CPUE were also examined when the months of the sardine (*Sardinops sagax*) run (June and July) were omitted. The ability to predict the movements of the sardine shoals increased over the study period, allowing time for retraction of the nets before the run and downwardly biasing the catch. When the months of the sardine abundance were not included, both white shark catch and CPUE did not show significant trends, although the catch trend did switch from an overall decline to an overall increase of the number of animals (Dudley 2002). Dudley (2002) also discussed the results of a previous study, in which no significant trend in catch or CPUE trends were found. Even with mixed results, Dudley (2002) states "the data do tend to support the suggestion that protection of the white shark should continue".

The need for modelling

Data collected from the natural environment is critical when assessing the size of a population but since time, money, and capacity are limited, it is impractical to count every individual of a population. Thus theoretical methods must be used. Population models have been found to be useful not only in assessing many different fisheries, but aiding scientists and policy-makers in developing management strategies. Such models involve data that can be collected to serve as input into mathematical equations, which produce a theoretical management output. The mathematical equations used to link input and output contain variables, parameters, and operators (Sparre and Venema 1997). Two basic types of models exist: holistic and analytical. Analytical models are used when more data can be obtained and involve parameters such as growth of individuals and mortality rates (Sparre and Venema 1997). Life history traits are used mainly in analytical models. Holistic models are used when data is lacking and involve relationships between fishing effort and total catch, like that discussed by Dudley (2002). Since the designed model in this study uses the analytical approach, more emphasis will be placed on analytical models. With regard to fisheries, the earliest analytical model was developed by Baranov (1918), in which different levels of fishing were linked to the mass and numbers of fish (Beverton and Holt 1957). Since then a number of deterministic, and/or stochastic models using a variety of equations have been developed, perhaps the most noteworthy being von Bertalanffy's work. In 1938 von Bertalanffy determined that the rate of growth in length of a fish species is related to the difference of its maximum length and length at time t. As in Baranov's equations, growth in terms of weight can also be accounted for in von Bertalanffy's equations. With the additions and alterations on these early fisheries equations, it became more accepted that it was possible to manage fisheries based on natural and fishing mortality, recruitment, and growth (Beverton and Holt 1957).

The basic concept behind the purpose of fisheries models is that with increasing fishing effort, there is an initial increase in catch until a point is reached in which the fishing pressure becomes too great for the population to remain stable (Sparre and Venema 1997). The maximum sustainable yield (MSY) is the point at which the maximum number of fish can be caught at a rate in which the population can still sustain itself (Sparre and Venema 1997). In order to obtain MSY most models require estimates of variables such as mass, length and age as in Baranov's or von Bertalanffy's equations.

South Africa currently uses population models to determine maximum sustainable yields or total allowable catches (TACs) for the country's populations of hake (*Merluccius capensis and M. paradoxus*), sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*), amongst other species. Fisheries models have been used on sharks as well. Smith *et al.* (1998) incorporated life history traits into a modified demographic model in order to estimate intrinsic rebound potentials of 26 species of Pacific sharks. The white shark and other large oceanic species were found to be able to withstand fishing pressure better than large coastal species (Smith *et al.* 1998). Bruce *et al.* (2001) developed abundance indices to assess the status of white sharks in Australia, and also found that bycatch of white sharks is the leading cause of mortality in the area. Using pelagic longline data from the Northwest Atlantic, Baum *et al.* (2003) constructed generalized linear models (GLMs) to establish trends of several shark populations, including the white shark. Baum *et al.* (2003), utilizing simple models, also determined which conservation plans would work best for the species examined. As previously mentioned, Dudley (2002) utilized catch and CPUE trends to assess 14 species of sharks off the eastern coast of South Africa. In the previous study reviewed by Dudley (2002), it was suggested by the researchers "that catch trends in the shark nets may not be useful in the study of local shark population dynamics" (Dudley 2002). Musick *et al.* (2000) states that the use of traditional stock models for assessing equilibrium strategists such as sharks may not be applicable and instead "age-based demographic matrix or Bayesian stock production" methods are most likely more applicable. Whatever the case may be with sharks, the little data that is available can be used in a scientific manner to produce results that are more scientifically sound than guesswork alone.

White shark population assessment in South Africa

Cliff *et al.* (1996) performed a five-year mark-recapture study based in eastern and southern South Africa, from Richard's Bay to Struis Bay. A total of 73 white sharks were tagged between 1989 and 1993, with captures, recaptures, releases, and re-releases recorded. With this data, a modified Petersen estimate was used to determine population size, while Baranov's catch equation was used to determine mortality rates. Over the five-year span, the population was estimated to consist of 1,279 individuals with an instantaneous mortality rate (Z) of 0.53 year^{-1} and an instantaneous fishing mortality rate (F) of 0.055 year^{-1}. Instantaneous natural mortality rate M was estimated to be likely no higher than that of the familial relative, the porbeagle (M = 0.18 year^{-1}). Cliff *et al.* (1996) concluded that the real fishing mortality rate F "may be lower than 0.055 year^{-1} and, in our opinion, does not represent overfishing of white shark stocks". Even so, it was advised that more research is needed before the moratorium should be lifted.

In this study an age-structured population model is developed and uses the results of Cliff *et al.* (1996) as a foundation and the corresponding information on the white shark's biological and ecological features as input parameters. The model is aimed to estimate the number of white sharks from Richard's Bay to Struis Bay in South Africa from 1993 to the present. It will be run to omit fishing mortality as the moratorium is still in place and include fishing mortality as if the moratorium would cease in 2004. Fishing mortality, as in Cliff *et al.*

(1996), will represent all targeted and bycatch fisheries. Results will be assessed to determine the effect of the moratorium on white sharks. Parameters having the most influence on population size will be determined by performing a sensitivity analysis on the model. Finally, limitations and impacts of using such a model will be discussed.

Methods

Population estimates were determined using an age-structured model with the following constants: instantaneous total mortality Z, consisting of natural mortality M and fishing mortality F; the age of maturity and lifespan; the number of pups per female; the timespan of the female reproductive cycle. The timeframe was divided into three periods. First, a pre-moratorium period was established covering the years 1950 to 1993 to include instantaneous fishing mortality rate F. It was important to include a time period before 1993 in order to determine the population status prior to the moratorium. The second, or moratorium period, spans from 1993 to 2004. Although the moratorium was officially in place in mid-1991, the data used from Cliff *et al.*'s study (1996) includes the years 1992 and 1993. Therefore, the starting year of 1993 was used assuming that the numbers of sharks during the five-year collecting period was not significantly affected by the moratorium at such an early stage. Lastly, the third period for future projected estimates spanned from the present (2004) to 2050.

Baseline

With the estimate of F=0.055 year^{-1} by Cliff *et al.* (1996) it was assumed that such an instantaneous fishing mortality rate existed and remained constant from 1950 to 1993. Natural mortality M was set at 0.125 year^{-1}, taken from Smith *et al.* (1998), and is the median amongst Mollet and Cailliet (2002), Smith *et al.* (1998), and Cliff *et al.* (1996). Therefore the total instantaneous mortality rate from 1950-1993 was Z=0.180 year^{-1}. For the period 1993-2004, Z equalled M because the moratorium was in place, with F=0. The period 2004-2050 also had F=0 for the baseline, but the input value could be changed after 2004 to account for fishing if the moratorium were removed, or set at zero if the moratorium were to continue. Changing F for the years 2004 and later would not change F for earlier years.

It was assumed that each mature female produced seven pups, which was the median calculated from Francis (1996) when the unconfirmed litters of two and 14 were omitted and the same value used by Smith *et al.* (1998). A reproductive cycle of two years assumed that each mature female reproduced every two years, or the equivalent of one-half of all mature females reproducing every year. Therefore, a reproductive cycle of three years averaged into one-third of all mature females giving birth each year. A two-year reproductive cycle was used for the baseline setting.

Calculation of initial age distribution (1950)

The number of survivors per age was calculated as follows:

(1) $$\text{survivors at age}_t = 100 \times (e^{-Mt})$$

where the instantaneous natural mortality rate M equalled 0.125 year^{-1}, and e represented the mathematical constant. Time t ranged from 0 to 23 years, the maximum age found by Compagno *et al.* (1997), for the baseline setting. The survivor total for each age was divided by the sum of all survivors to find the fraction of the total population in each age. The fraction calculated in each age from 0 to 23 years was multiplied to an arbitrary starting population of 1,000 animals, equalling the starting number of animals in each age.

Calculating 1951-2050

(2) $$\gamma_\psi = \alpha \times \beta \times \mu \times \lambda$$

$\gamma_\psi =$ number of pups born ($\text{age}_t = 0$) for year ψ
$\alpha =$ fraction of females
$\beta =$ fraction of mature females giving birth (reproductive cycle)
$\mu =$ fraction of mature sharks
$\lambda =$ number of pups per female

In order to calculate the number of pups born for 1951 and successive years (Equation 2), the number of mature animals first had to be calculated. Assuming that maturity occurs at age 12 (Wintner and Cliff 1999), and the reproductive cycle is two years, then the youngest possible age for a female shark to give birth would be 13 years. Summing of the total number of survivors between the ages of 13 to 23 equals the total number of mature animals. The number of mature animals (x) was then multiplied by the constant fraction of females (0.5), assuming that there is a 1:1 ratio between males and females, and the reproductive cycle (0.5 of all capable birthing females per year) to estimate the number of mature females giving birth in 1951 (n=57.9). The number of pups per female (seven) was multiplied by the number of mature females giving birth (n=57.9) to estimate the number of pups born (n=405). Survivors were calculated by multiplying the total number of pups by e^{-Z}.

(3) $$x_{\psi+1} \text{ at age}_{t+1} = x_{\psi} \text{ at age}_{t} \times e^{-Z}$$

$x_{\psi+1}$ = number of survivors in year $\psi + 1$
t = year of age
x_{ψ} = number of survivors in year ψ
e = mathematical constant
Z = total instantaneous mortality

Total survivors in each age class from 1 to 23 years is shown in Equation 3. The number of survivors in year ψ+1 for age class t+1 is the number of survivors in the previous year of the previous age multiplied by e^{-Z}. Therefore, the number of survivors in 1951 three years of age would equal the number of survivors that were two years of age the previous year (1950) multiplied by e^{-Z}. The total number of survivors for each year was the sum of the survivors in each age group.

Calculation readjustment (1950)

The final step after completing the model through 2050 was to readjust the starting population in 1950. Initially the population was set arbitrarily at 1,000. However, this initial population was reset to mathematically make it possible in the model to have a population of 1,279 animals by 1993 (Cliff *et al.* 1996).

Sensitivity Analysis

Each of the model parameters was tested for sensitivity (F, M, maturity age span, reproductive cycle timeframe, and number of pups per female). The calculation readjustment for 1950 had to be performed for every tested input value in each parameter except for fishing mortality since the analysis did not change the fishing rate pre-1993.

Fishing mortality

Fishing was kept constant prior to 1993 and was tested for sensitivity from 2004 to 2050. The F input values tested followed the 95% confidence limits determined by Cliff *et al.* (1996), from 0.015 year^{-1} to 0.100 year^{-1} at 0.005 intervals.

Natural mortality

Input values for M ranged from 0.070 year^{-1} to include the values published by Mollet and Cailliet (2002) at intervals of 0.010 up to 0.190 year^{-1} since Cliff *et al.* (1996) stated it is unlikely to exceed that of the porbeagle.

Number of pups

The parameter for the number of pups born per female was tested for the known range of 4 to the unconfirmed number of 14 pups per litter at intervals of 1 pup.

Maturity age span

The ranges for mature white sharks in the population were calculated using varying input values for maximum age and minimum age of females able to give birth. Recall that the baseline used a maximum age of 23 years, and a minimum age of females able to give birth at 13 years. The estimates found by Smith *et al.* (1998) of 36 years maximum age and Mollet and Cailliet (2002) of 60 years maximum age were tested in the analysis. The baseline fraction of mature sharks was altered to include a later maturity of 16 years. All combinations of minimum age of maturity and maximum age were used in the sensitivity analysis.

Reproductive cycle

The timeframe of the reproductive cycle was tested for two years in the baseline as well as three years during the sensitivity analysis.

Results

Baseline

All estimates of the number of animals are presented as the model output followed by ranges that take into consideration five percent error above and below the predicted output. With the initial input values for the parameters (Table I) and disregarding fishing, the population of white sharks increases from a surviving 1,330 (range=1,263-1,396) individuals in 1994 to 1,953 (range=1,855-2,050) individuals in 2004. The calculated number of sharks in 1950 was 2,754 (range=2,616-2,891) with a steady decrease until 1993 followed by an increase to 10,900 (range=10,355-11,445) animals by 2050 (Figure 1).

Sensitivity Analysis

The ranges of outputs, including an error factor of five percent above and below the predicted outputs, are given for each analysis performed.

Fishing mortality

The results of running the sensitivity analysis for the instantaneous fishing mortality rate *F* are given in Figures 2 and 3. Tested *F* input values of 0.035 year^{-1} or less produced increases in the model population to 2050, with a range of outputs of 1,998-5,655 animals. Those *F* input values tested at 0.040 year^{-1} and greater produced decreases in the model population to 2050, with a range of outputs of 94-1,746 animals. All outputs prior to 2004 are equal since fishing mortality was kept constant prior to 1993 and no fishing was present from 1993 to 2004.

Natural mortality

Figures 4 and 5 display the results of the model with changing *M* values. The total number of sharks for the year 2004 ranged from 951 to 3,631. Tested *M* input values of 0.170 year^{-1} and greater produced a decrease in the population while all others tested below 0.170 year^{-1} produced an increase in the model population from 1993-2050. The highest *M* value of 0.190 year^{-1} produced a population of 277 (range=263-291) animals by 2050, whereas the lowest *M* value of 0.070 year^{-1} produced numbers exceeding 200,000 animals. The predicted population size from 1950 to 1993 increases with tested *M* inputs of 0.100 year^{-1} and less, while the opposite occurs with tested *M* inputs of 0.110 year^{-1} and greater. Calculated starting populations in 1950 ranged from 199 to over 59,000 animals.

Number of pups

The analysis of the number of pups is shown in Figure 6. All tested values of pups produced increases in the model population from 1993 to 2050. Four to nine pups per female produced decreases in the population from 1950 until 1993, while 10 to 14 pups per female produced increases in the population for the whole timeframe. For the year 2004, the number of predicted sharks ranged from 1,338 to 3,127. Starting populations in 1950 ranged from 394 to 12,301 animals, while populations in 2050 ranged from 1,710 to over 100,000.

Maturity age span

The predicted totals from the sensitivity analysis of the minimum ages of maturity and ages of longevity are shown in Figure 7. All combinations of ages produced decreases in the population from 1950 to 1993 followed by increases from 1993 to 2050. Estimates of the number of animals in 2004 ranged from 1,525 to 2,251. Tested maturity ranges of 13-36 and 13-60 years of age produced similar estimates, while 16-36 and 16-60 years of age also had similar results. The highest increase post-1993 of all ranges tested occurred with the longest timeframe of 13-60 years of age. The shortest timeframe of 16-23 years of age produced the slowest increase of animals post-1993.

Reproductive cycle

Both of the reproductive cycles tested display decreases in the population from 1950 to 1993 with increases in the population from 1993 to 2050, but with a great difference in rates (Figure 8). A three-year reproductive cycle causes the population to decline quicker and recover more slowly than a two year cycle. In a three-year cycle the starting population in 1950 is 7,925 (range=7,529-8,321) animals, or approximately three times that of a two-year cycle. The population following a three-year cycle is predicted to be 2,950 (range=2,803-3,098) animals by 2050, almost one-fourth of that predicted for a two-year cycle. The three-year cycle also produces a population of 1,541 (range=1,464-1,618) survivors for 2004, which is similar to the two-year cycle output of 1,953 (range=1,855-2,050) animals.

Discussion

Outcome of the baseline and sensitivity analysis

Baseline

The estimated range for the population of white sharks in southeastern South Africa of 1,855-2,050 animals is higher than the 95% confidence limit range of the mean (839-1,843) from the five-year study by Cliff *et al.* (1996). Carrying capacity was not factored into the model, mainly to keep the model as simple as possible and also because an estimate of carrying capacity for southeastern South Africa would be very crude. Because it is not known, it is possible that the carrying capacity for the region examined would not be high enough to allow the predicted model population for 2004 and beyond to be present in reality. It is also possible that white sharks grow faster than previously thought, supporting Smith *et al.*'s (1998) conclusion that large oceanic sharks can rebound relatively quickly compared to large coastal sharks. Even so, it is important to focus on the results for the years 1993-2004, since carrying capacity would become more of a factor the further the model is projected into the future.

Natural mortality

The estimate of *M* by Cliff *et al.* (1996) to be no more than 0.18 year^{-1} is partially supported by the outcome of the sensitivity analysis for *M*, since input values of 0.17 year^{-1} and greater produced a declining population in the model through 2050 even without fishing pressure. Looking at the model in a short-term manner (from 1993 to 2004), the predicted highest and lowest estimate of animals for 2004 holds the largest difference of all sensitivity analyses. It is not possible to say whether one estimated *M* is correct and another is not, however, it can be said that the difference between the predicted maximum *M* stated by Cliff *et al.* (1996) and that of Mollet and Cailliet (2002) is large enough to have the heaviest effect on the model's outcome.

Number of pups

When fishing is present prior to 1993, the model displays a decline in the population when an input of four to nine pups per female birthing is used. All estimated populations recover when the moratorium is in place. This suggests at least two possibilities: one, that a fishing rate of 0.055 year^{-1} may indeed have been too high for the population of white sharks; or two, that an average litter size of nine pups per female birthing or less may be too low. The outcome of the analysis for the number of pups displayed the second largest difference in population estimates for 2004. According to the model, the average number of pups holds a great effect on population size and therefore would be crucial in determining a sustainable fishing rate if one were to exist in the future.

Maturity age span

It was expected that the shortest time period of maturity to death (16-23 years of age) would produce the lowest population size outcome in the model while the longest time period (13-60 years of age) would produce the largest population size outcome. However, it is evident according to the outcome of the analysis that longevity does not hold as much influence on the model population as does the minimum age of maturity. Similar population sizes were estimated with maturity of 13 years of age and longevity of both 36 and 60 years. Also, the population sizes estimated with maturity of 16 years and longevity of both 36 and 60 years were similar. Although there is a large difference between each minimum maturity age living 23 years compared to 36 and 60 years, it is not as large as the difference of 13-23 and 16-23 years of age. The importance of knowing the average age of maturity is highly important and more so than longevity according to the model. Overall though the maturity age span analysis resulted in the second smallest difference in the range of estimates for 2004, emphasizing that the rate of instantaneous mortality *M* and the average number of pups is more crucial in estimating the population according to the model.

Reproductive cycle

Reproductive cycles of two and three years have results following the same general trend. A three-year reproductive cycle would have a slower rebound potential from fishing effects and would decline more rapidly during fishing than a two-year reproductive cycle. In general it would be essential to know how often females reproduce in order to form any viable management plan, but according to the model the effect of every two or three years is not as heavy on the outcome as is the number of offspring. The population estimates for 2004 hold the smallest difference, but it should be noted that having only two reproductive cycle timeframes tested could be a factor.

Assumptions and method consideration

This age-structured model was designed in order to obtain estimates of a population in which no large data set or time series is currently available. The model represents a hypothetical situation in which the individual influences of biological factors can be examined on a population's size. In order to limit complexity, certain assumptions had to be made. Although a female to male ratio of 1:1 is realistically possible (Cliff *et al.* 1996), what may not be realistic is for the ratio to remain constant over a 100-year period. It may be possible that females and males have different longevities, mortality rates, or affinities for being observed by researchers. For instance, if a study area covers a nursery ground then most likely females will be overestimated in the population. The model also assumes that the mortality rate is the same for all ages. It may be more realistic for the mortality rate to be higher for that of juveniles, or that animals within a size range are more prone to be caught as bycatch on longlines or nets.

The female reproductive cycle timeframe, *F*, *M* and the number of pups per mature female remain constant throughout the timeframe. Therefore, no analyses were performed to see how the estimates would change if for instance the average number of pups remained at seven over the 100 years but each year held different averages. Because the number of pups and mortality were the two most sensitive variables of the model, yearly fluctuations could have a drastic effect on the final outcome. However, it may be unlikely in reality that *M* and the average number of pups change easily with fluctuating natural or human pressures, but *F* and possibly the reproductive timeframe could change significantly at any time. Factors such as food resources and habitat destruction, especially with nursing areas, may affect how often a female will mate but cannot be said with certainty. It may not be found in reality that all females reproduce every two years and do so consistently throughout a lifetime. With regards to the maturity age span variable, it was assumed that females could give birth until death, so that no maximum age of birthing was used. It is also assumed that during the moratorium, no deaths due to fishing occur. In reality, as discussed previously, white sharks make up part of the bycatch of different fisheries, as well as deaths due to the KwaZulu-Natal nets. Unfortunately it is difficult to separate *F* into a targeted fisheries rate and a bycatch rate. Although making such assumptions affects the outcome, the sensitivity analysis examines ranges over 100 years time so that the effects of changing values over the years could be summarized more appropriately than using a shorter timeframe. As more data is made available, more of such variability could be added to the basic model outlined here.

Effects of the moratorium and fishing pressure

The sensitivity analysis displayed that instantaneous fishing mortality rates of 0.035 year^{-1} and less would not result in population declines in the model. It was expected that the fishing rate for white sharks would be between that of the gummy shark (*Mustelus antarcticus)* at five to six percent with a lifespan of 16 years and that of the soupfin shark (*Galeorhinus galeus*) at two to three percent with a lifespan of 50 years (Tricas *et al.* 1997). Indeed a fishing rate of 0.035 year^{-1} for the white shark falls within that range (3.44%). This conclusion from the model however does not support the statement made by Cliff *et al.* (1996) that the instantaneous fishing rate of 0.055 year^{-1} most likely would not represent overfishing.

Management considerations

If the moratorium was lifted and fishing were permitted, enforcement of the total catch allowed would have to be strict. From the results of the model, an instantaneous fishing mortality rate no greater than 0.035 year^{-1} would be low enough to sustain the white shark population. This needs to be interpreted with respect to the limitations of the model, such that natural and human pressures in reality would need to be factored in. Even so, an annual fishing rate of 3.44% (64-70 sharks predicted from the model for 2004) falls within the established fishing rates for the gummy and soupfin sharks.

There is a strong need for accurate reporting of bycatch and net deaths. Because *F* in the model represented the summation of targeted and bycatch fishing pressures, it would be difficult to establish a targeted fishing rate without having accurate reports of bycatch. Fishing in the model also did not discriminate by sex or size (and correspondingly age). Applying all fishing pressure to one size group or sex would alter the sustainable fishing rate predicted by the model. It would have to be determined what size class (and/or sex) to target if any to maximize catch but continue sustaining the population at an optimal size class (or sex) balance. A cost/benefit analysis would also be of importance to establish whether it would be more economically beneficial to fish for white sharks and take them to market, or keep more white sharks alive for industries such as tourism (cage diving, sightseeing). Another aspect that has not been discussed is the impact white sharks have on their prey populations, and depending on the intricate balance, it could be beneficial to keep the population low or high to control the prey populations.

Forming management regulations would be difficult due to the many factors involved, but enforcing such regulations could be more difficult. A study performed by Boustany *et al.* (2002) tracked six adult white sharks from central California. The tracking period lasted from about two weeks to six months, with the furthest distance covered by one animal to be 3,800 kilometres (Boustany *et al.* 2002). A recent genetics study by Pardini *et al.* (2001) suggests that white shark populations off Australia and New Zealand are one mixed population, whereas the South Africa population genetically differs significantly enough from both to constitute a separate population (Pardini *et al.* 2001). It is also suggested that males are rovers whereas females are non-roving animals, although field evidence has not yet been published to confirm this (Pardini *et al.* 2001). Both studies may have serious implications in the management of white sharks—that management is not just a local issue but also a global issue. If females are indeed coastal and stay within a specified region to occupy nursing grounds, then management and enforcement is needed at the local scale. Likewise, if males are indeed rovers that can travel great distances and are possibly mating with a specific population of females, they must not only be protected where the females are located, but must also be protected in all areas in which they roam. Enforcement of such protection seems impractical and unattainable, but the 2002 UN Treaty does provide a start in the right direction.

Conclusion

According to the model, the total number of white sharks at present in eastern and southern South African waters is 1,953 (range=1,855-2,050). No fishing due to the moratorium caused the declining population to increase in numbers after 1993. The fishing rate estimated by Cliff *et al.* (1996) did represent overfishing in the model. With fishing pressure included, instantaneous fishing mortality rates of 0.035 year^{-1} or less produced increasing populations from 2004 to 2050. Instantaneous natural mortality M and the number of pups per birthing female were highly sensitive parameters to the model, whereas the maturity age span and reproductive cycle both held less sensitivity to the model. Although not present in the model, carrying capacity should be considered as well as other behavioural and biological factors in the management and conservation of white sharks.

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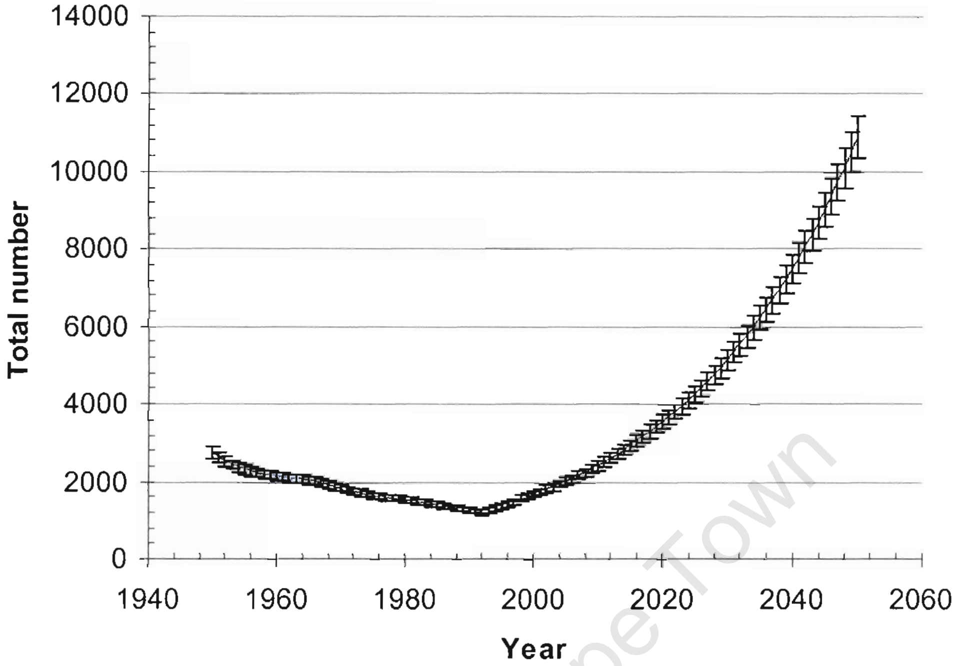

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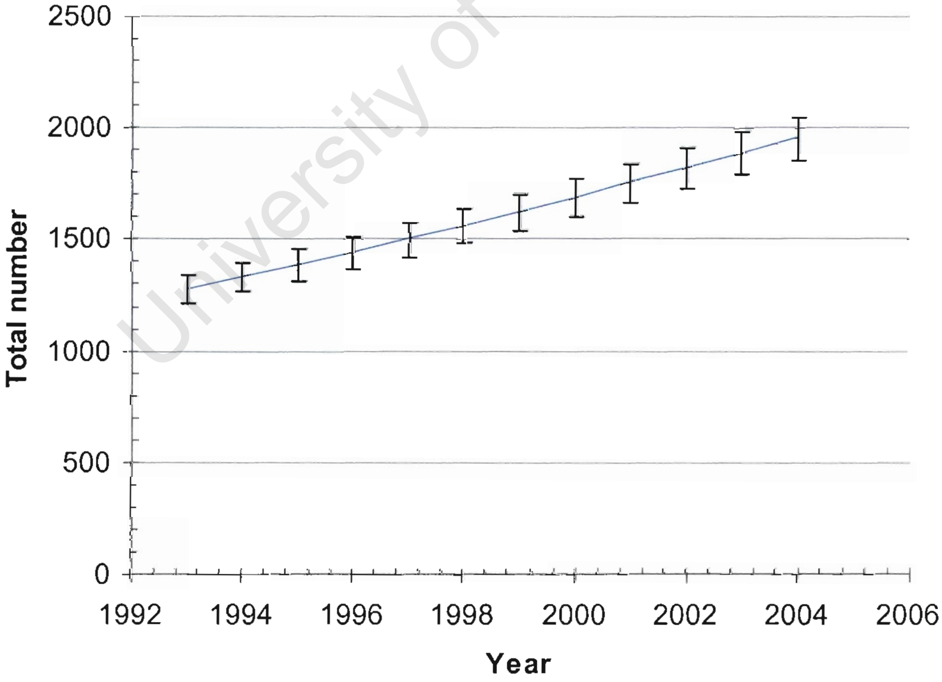


Figure 1. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 1950 to 2050 (a) and 1993 to 2004 (b). All input values of the parameters are at the baseline setting. No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output.

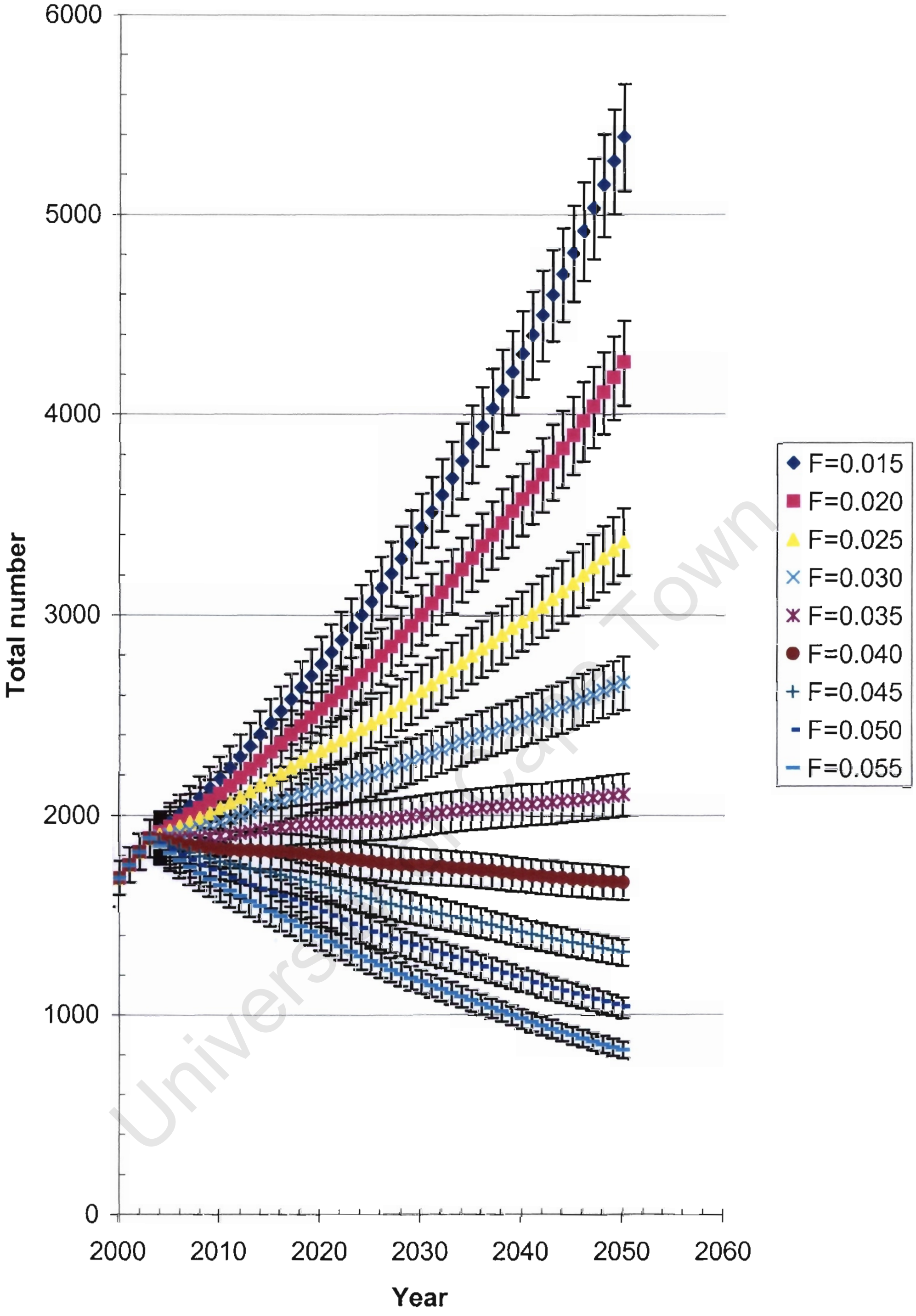


Figure 2. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 2004 to 2050, with varying *F* input values ranging from 0.015 year^{-1} to 0.055 year^{-1}. All input values of the remaining parameters are at the baseline setting. Error bars indicate 5% error above and below model output.

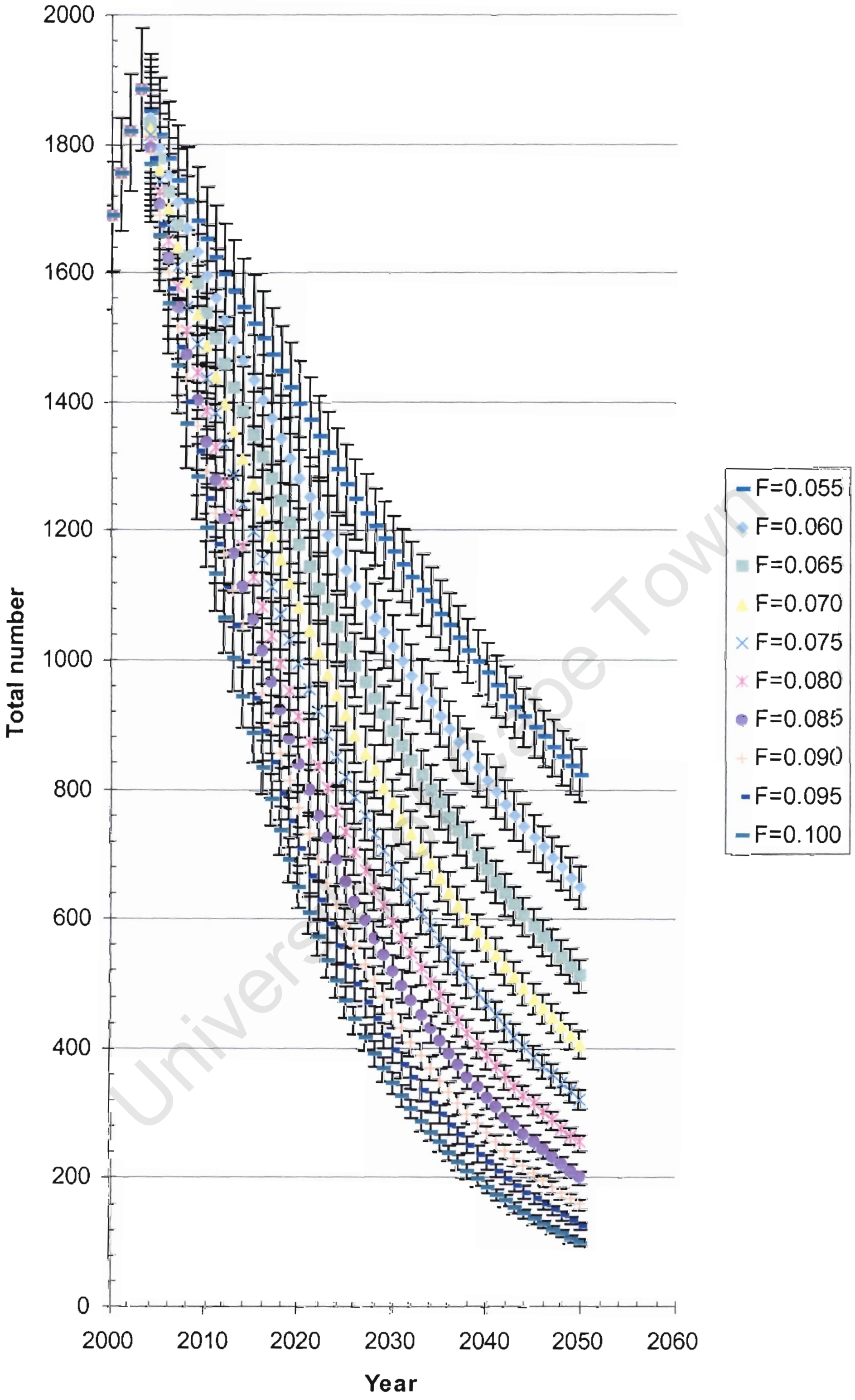


Figure 3. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 2004 to 2050, with varying *F* input values ranging from 0.055 year^{-1} to 0.100 year^{-1}. All input values of the remaining parameters are at the baseline setting. Error bars indicate 5% error above and below model output.

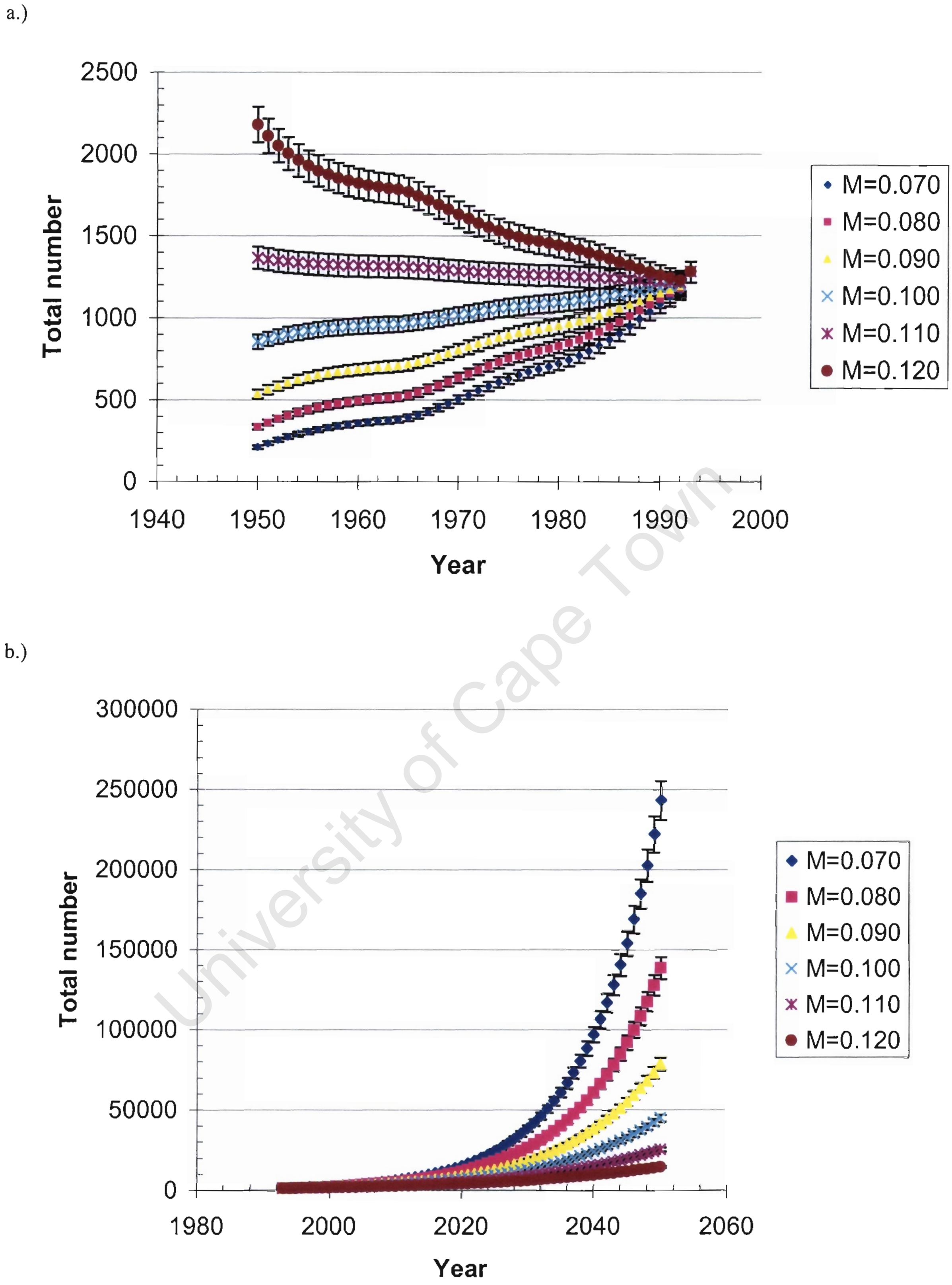
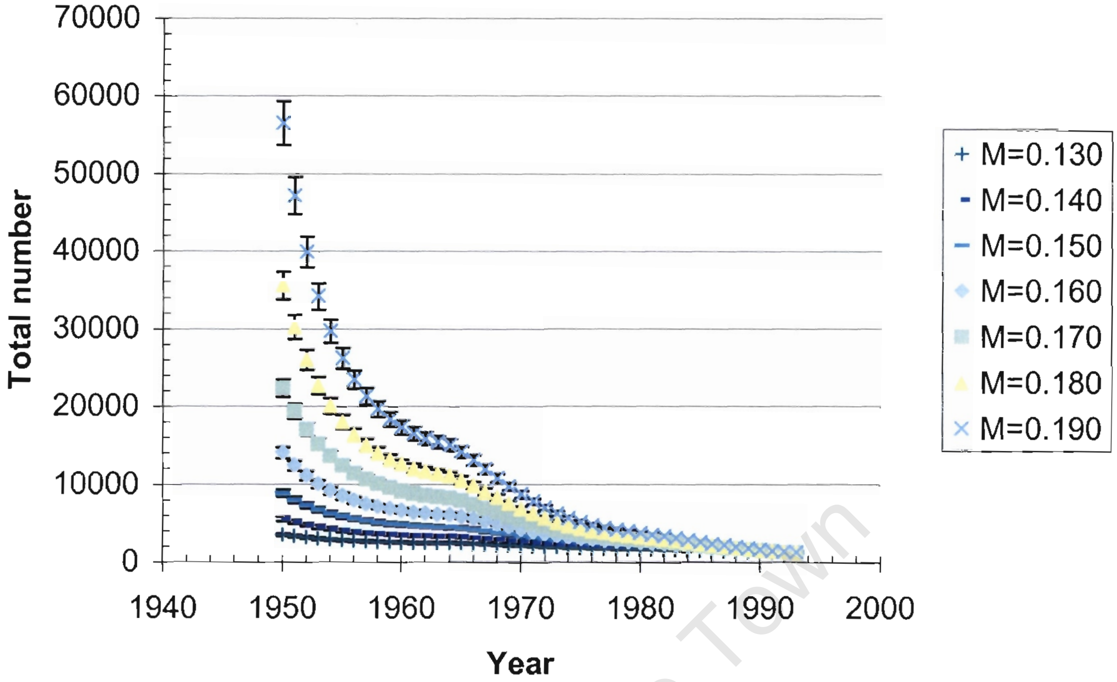


Figure 4. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters with varying *M* input values ranging from 0.070 year^{-1} to 0.120 year^{-1} at intervals of 0.010 year^{-1} for the years 1950 to 1993 (a) and 1993 to 2050 (b). All input values of the remaining parameters are at the baseline setting. No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output. Note the different scale between (a) and (b).

a.)



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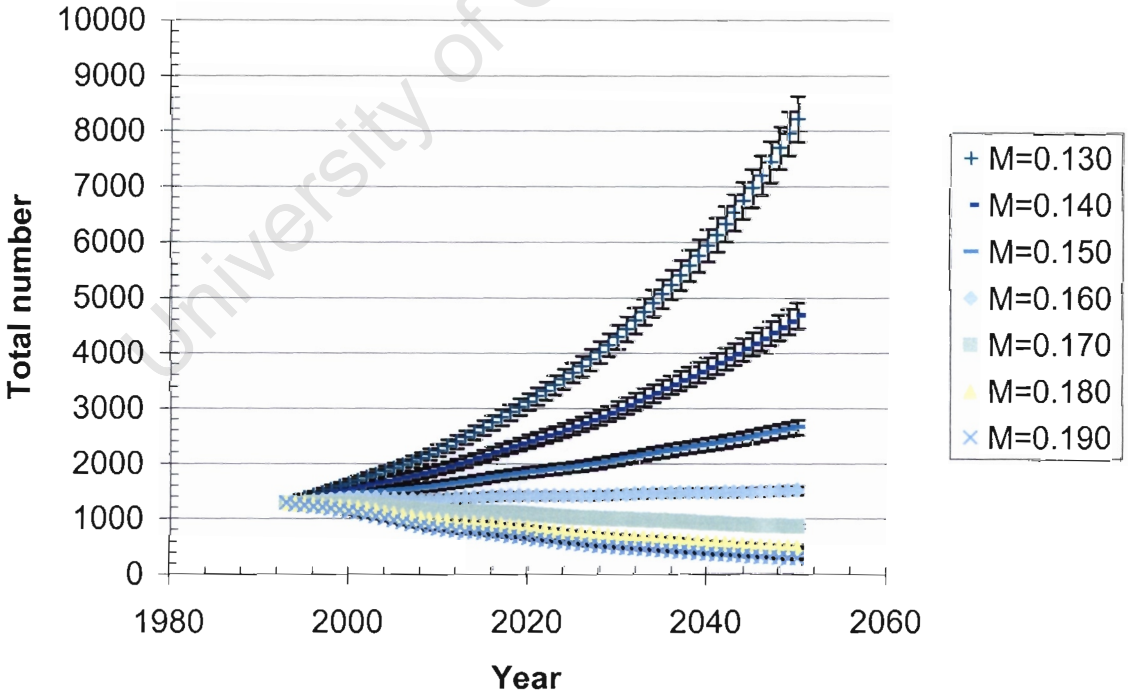
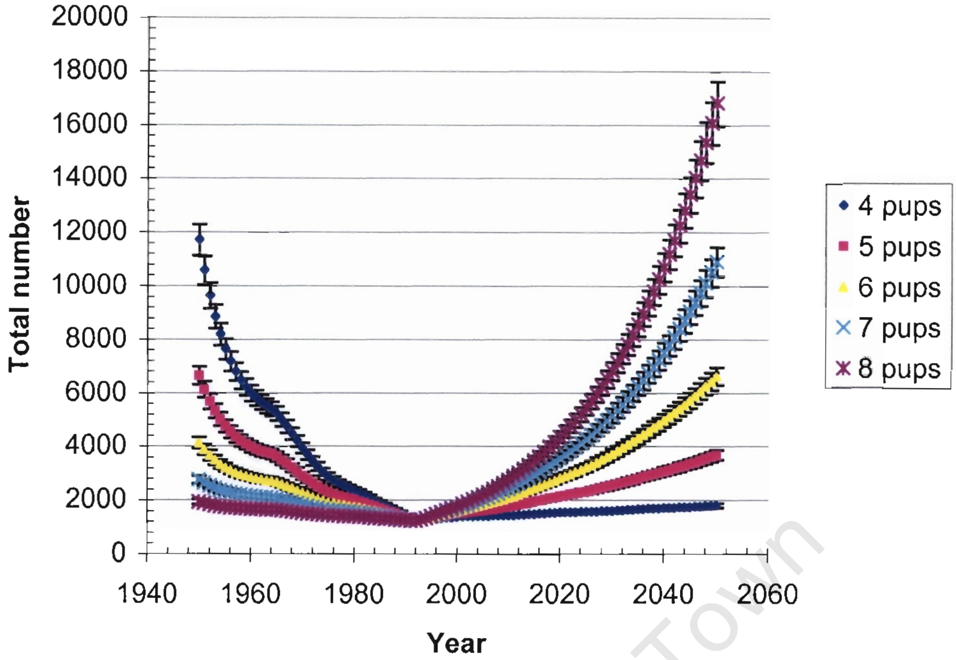


Figure 5. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters with varying *M* input values ranging from 0.130 $year^{-1}$ to 0.190 $year^{-1}$ at intervals of 0.010 $year^{-1}$ for the years 1950 to 1993 (a) and 1993 to 2050 (b). All input values of the remaining parameters are at the baseline setting. No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output. Note the different scale between (a) and (b).

a.)



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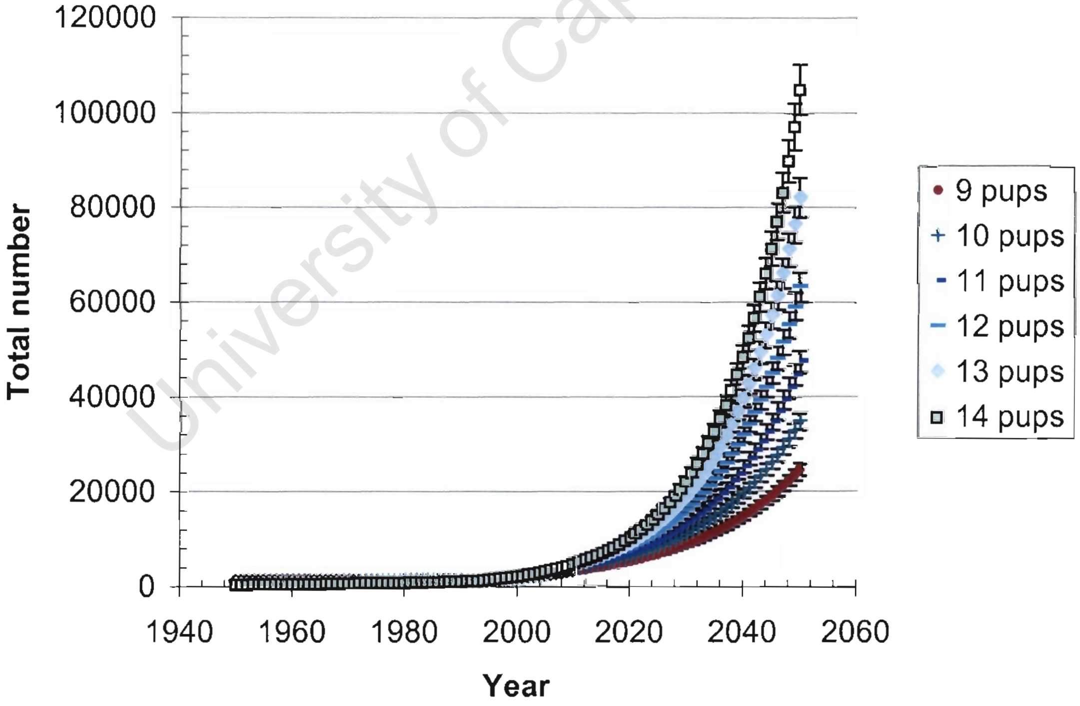

Figure 6. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 1950 to 2050 with four to eight pups (a) and nine to fourteen pups (b) per mature female birthing at intervals of one pup. All input values of the remaining parameters are at the baseline setting. No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output. Note the different scale between (a) and (b).

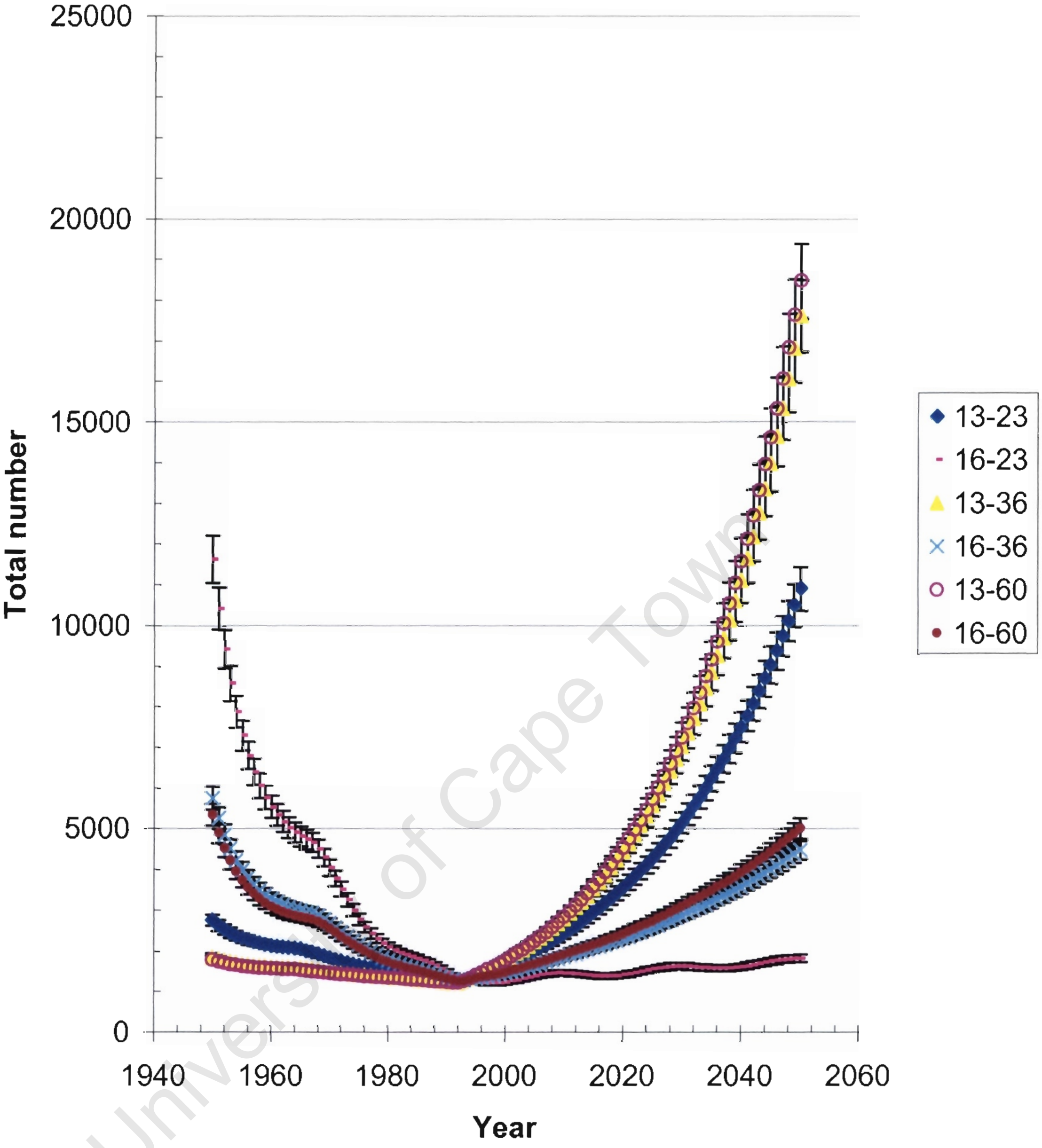

Figure 7. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 1950 to 2050 with input values for the age range of minimum maturity (13 and 16 years) to maximum age (23, 36, and 60 years). No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output.

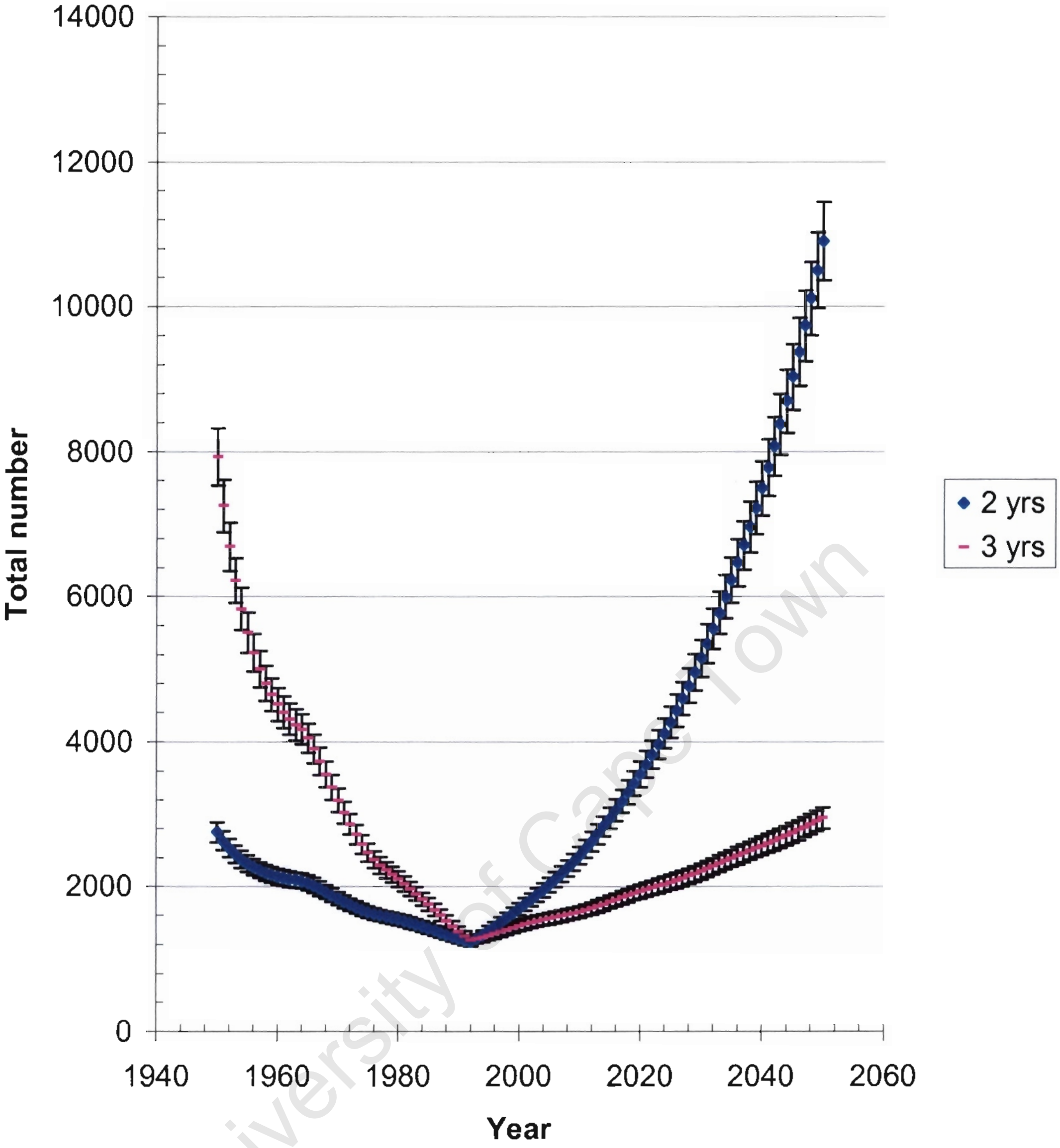

Figure 8. Predicted numbers of white sharks from Struis Bay to Richard's Bay in South African waters for the years 1950 to 2050, with females reproducing every two years and every three years. All input values of the remaining parameters are at the baseline setting. No fishing is accounted for post-1993. Error bars indicate 5% error above and below model output.

Table I. The baseline input values of all parameters in the model, with the respective ranges and interval steps of the sensitivity analyses.

Parameter	*Baseline input value*	*Sensitivity analysis range*	*Sensitivity analysis interval step*
F	0.055 year^{-1}	0.015-0.100 year^{-1}	0.005
M	0.125 year^{-1}	0.070-0.190 year^{-1}	0.010
Number of pups	7	4-14 pups	1
Mature age span	Minimum maturity:13 yrs; Maximum age:23 yrs	13-60 years	13-23, 16-23 13-36, 16-36 13-60, 16-60
Reproductive cycle	2 years	2 and 3 years	1 year