Life history traits that predispose South African linefishes to overexploitation

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MSc Thesis submitted on 19 February 2018
Word count: 11 728

Thesis submitted for the degree of Master of Science in Marine Biology,
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Acknowledgments

First and foremost I would like to thank my supervisors Sven, Denham and Henning for not only teaching this Vaalie all about fisheries, but doing so with extreme patience and encouragement. I will definitely come out of this master’s degree a better researcher and scientist because of your guidance.

I need to also thank my parents for their unwavering support, even from far away. Matthew Horton needs special thanks for helping me with menial, nitty-gritty work and for allowing me to get my hands dirty in the field.

I am also grateful to the Department of Agriculture, Forestry and Fisheries for allowing me access to data which permitted me to conduct this research.

Table of contents

Abstract

Globally, the status of many fish stocks remains unknown, of which the majority fall under data-limited small-scale fisheries. Management decisions in most of these fisheries are difficult due conflicting objectives and views from fisheries managers and scientists. In South Africa, the traditional boat-based ‘linefishery’ provides such an example of a small-scale, multi-species fishery with a long history. The historical *de facto* open access nature of this fishery resulted in continuous declines in catches of many linefish species, and in 2000 the fishery was declared to be in a state of emergency. This led to a reduction of up to 70% within the fishery, among other measures, such as introductions of size and bag limits. Assessing the status of linefish species is difficult due to a lack of reliable long-term data for the majority of species. The aims of this study were therefore: (1) to quantify the stock status for all linefish species with available life history and size composition information, (2) compare current and historical stock levels to ascertain if the reduction in effort facilitated any recovery in linefish species and (3) correlate the current stock status estimates to life history traits to identify simple indicators of resilience to exploitation. For this purpose, length frequency data from 1988-1990 and 2008-2010 and biological parameters sourced from literature were used to conduct per-recruit analysis to estimate spawner biomass depletion (SBD) for both time periods. The majority of the 26 species analyzed, (68%) showed improvements in spawner biomass between the two time periods, with 12 species undergoing a change in stock status (i.e. improving from collapsed or overexploited). Specifically, increases in length-at-capture (L_c) as well decreases in fishing mortality (F) facilitated recovery for many species. Asymptotic length (L_∞), as well as the ratio between L_c / L_∞ and L_c / L_{opt} (where L_{opt} is the optimum length) were found to be significantly correlated to spawner biomass depletion. Kruskal Wallis analyses revealed that only movement pattern had a significant relationship to SBD, more specifically, migratory species were significantly more depleted than resident ones. This study identifies simple indicators that, in the absence of conventional stock assessments, provide fisheries managers with a fundamental understanding of a species’ susceptibility to overexploitation – offering another decision making tool for use in data poor fisheries such as the South African linefishery.

Keywords: per-recruit, stock assessment, linefish, stock status, life history

Introduction

Overexploitation is a major threat to harvested marine species (Sadovy 2001) and most stocks are overexploited because of misconceptions about the resilience (i.e. the capacity of populations to endure and recover from fishing pressure) of marine fish populations to heavy exploitation (Roberts & Hawkins 1999). Perceptions of vulnerability and the potential for recovery from exploitation differ among fisheries managers and scientists, thus making management decisions challenging (Mace & Hudson 1999, Hutchings 2001). The main goal of fisheries management has shifted from maximizing yields (to avoid growth overfishing) to maintaining sustainable fisheries by ensuring sufficient spawning biomass (to avoid recruitment overfishing) (Rochet 2000, Sadovy 2001), and more recently to include the effect of fishing on ecosystems (Worm *et al.* 2009). Although some stock sizes have increased through governmental control over fishing rights (Trippel 1995, Worm *et al.* 2009), the change in management objectives reveals a poor record of management success and clearly there is something unaccounted for: a large proportion of fisheries are overexploited and recoveries of stocks have often been slower than predicted (Botsford et al. 1997, Sadovy 2001), while declines in some species have been precipitous (Safina 1995, Pauly et al. 1998, Hutchings 2000). Furthermore, conventional management techniques used in large industrial fisheries are not appropriate or enforceable in small-scale fisheries and rebuilding small-scale fisheries is challenging because most fishermen rely so heavily on this resource for income, employment and food (Worm *et al.* 2009) Declines in commercial species have led to concerns about threats of extinction (Denney *et al*. 2002) but many question this because marine fish are assumed to be naturally resilient due to wide distributional ranges, high fecundity and high natural variability in abundance (Matsuda et al. 1997, Musick 1999, Butterworth 2000). Nevertheless, recruitment overfishing can lead to extirpation of species (Musick 1999) and local extirpations of target species (Hughes 1994, Jennings & Kaiser 1998) and the economic extinction of commercially important stocks (Beverton 1990, Hutching & Myers 1994) has already occurred. Local extirpations pose not only a threat to conservation but to coastal communities who rely on fisheries for food and employment. It is therefore important to identify species which are most vulnerable to fishing pressure, so that they may be sustainably managed to avoid compromising the supply of an indispensable protein source and income to these communities (Jennings *et al.* 1999).

In South Africa, Linefishing (the act of fishing with hand-lines or rod and reels, either from the shore or boats) is a small-scale, multi-species and multi-sector fishery the origins of which can be traced back to the 1500s (Griffiths 2000). The fishery was slow to develop due to restrictions implemented by Dutch settlers in the 1700s, but later became a thriving industry when the British captured the Cape Colony in 1795 and removed these restrictions (Griffiths 2000). During the 19th century, fishing effort was between 0.12-0.37 boats per kilometer of coastline and reached a peak in the 1980s, at more than 3 boats per kilometer of coastline (DAFF 2014). This substantial increase led to overfishing of many linefish species (Griffiths 2000). In some parts of South Africa there was an increase in effort but catch rates among anglers decreased, and Catch-Per-Unit-Effort (CPUE) was low in many instances (Bennett 1991, Brouwer *et al.* 1997, Penney *et al.* 1999, Brouwer & Buxton 2002). It has even been reported that catches were so low that anglers rarely reached their daily bag limit (Cowley *et al*. 2002, Parker *et al.* 2016, Parker *et al.* 2017). Furthermore, there has been a temporal change in catch composition along the entire coast of South Africa (Hecht & Tilney 1989, Bennett 1991, Penney *et al.* 1999, Brouwer & Buxton 2002) with the mean length of fish being caught generally decreasing over time (Hecht & Tilney 1989, Yemane *et al.* 2004). The increasing concerns about the decline of many species led to the linefishery being formally recognized in 1985 and the introduction of a management framework, which included mandatory catch reporting together with size and bag limits for selected species (Penney *et al.* 1989, Griffiths 2000, DAFF 2014). Under this framework the level of protection afforded to each species often remained reliant on perceptions of their vulnerability, due mainly to the lack of biological and fisheries data (such as catch and effort or size composition data), which meant formal stock assessments could not be conducted. Despite the introduction of various management measures, pessimistic results of spawning biomass per recruitment assessments and severe declines in catch rates compared to historical levels (Griffiths 2000) provided compelling evidence that stocks had continued to decline and in 2000 the Minister of Environmental Affairs and Tourism declared the linefishery to be in state of emergency (DAFF 2014). This led to the separation of traditional linefish, hake and tuna into separate sectors, the establishment of the Linefish Management Protocol

(LMP), a reduction in nominal effort of up to 70% in the fishery (DAFF 2014) and even moratoria on certain species, such as the seventy-four seabream (*Polysteganus undulosus*).

The South African linefishery, consisting of commercial, recreational and subsistence sectors, targets more than 200 of South Africa's marine fish species. These species belong to more than 38 families and can be broadly divided into (1) resident, demersal species such as hottentot (*Pachymetopon blochii*) and roman (*Chrysoblephus laticeps*), (2) migratory, demersal species such as geelbek (*Atractoscion aequidens*) and elf (*Pomatomus saltatrix*) and (3) pelagic shoaling species such as snoek (*Thyrsites atun*) and yellowtail (*Seriola lalandi*) (Griffiths 2000, Kerwath *et al.* 2012). The combined value of the fishery was more than R2.2 billion per year in 2013 (DAFF 2014) and it employs 27% of all South African fishers; 25 thousand of which are subsistence fishers. Linefishing is an important sector of the South African fishery from a human livelihood point of view and thus its management is of great socio-economic importance.

Currently, the commercial fishery is managed through Total Allowable Effort (TAE) and the recreational fishery by output restrictions, such as size and bag limits in addition to closed areas and seasons (DAFF 2014). A total of 3 450 commercial fishermen and a maximum of 455 vessels operate in three zones along the South African coastline. There are between 450-750 thousand recreational fishermen targeting linefish in South Africa (WWF 2011, Winker *et al*. 2012) and entry into the recreational sector is unlimited (Penney *et al.* 1999). Unfortunately, an increase in recreational fishermen means an increase in fish mortality rates (Attwood & Farquhar 1999), and may thus hinder the recovery of stocks. Surveys conducted among anglers found that although fishermen support regulations, few have knowledge of and comply with the rules set in place (Brouwer *et al.* 1997, Kramer *et al.* 2017). The management of the linefishery is further complicated because many of these species are also targeted or caught as bycatch in other fisheries and there is high levels of illegal fishing as well as unregulated subsistence fishing (DAFF 2014). The fishery has the potential to become one of the most ecologically and economically viable fisheries in South Africa if it can be managed sustainably, mainly due to (a) the fishery being ecologically less destructive than alternative methods, such as trawling, (b) the fishing method being able to be highly selective thus minimizing bycatch and the catch of smaller individuals or unwanted stocks, (c) the fishery providing many employment opportunities due to its labour intensive methods and (d) the potential of a high quality product and the high prices they command on the market (DAFF 2014).

Assessing the status of South African linefish stocks is difficult due to the fishery operating in a range of different areas and targeting multiple species (DAFF 2014) and effort to collect catch statistics has been poor (Attwood & Farquhar 1999), thus resulting in a lack of long-term data needed for sophisticated modeling (Griffiths 2000). Only around a dozen of the 200+ species targeted account for more than 90% of the catch (Mann 2013) and as such, many reports feature data only for these species (for example DAFF 2014, WWF 2015). Linefish stock assessments have relied mostly on CPUE data, age structure production models or per-recruit analysis (Griffiths 1997, WWF 2015). Significant relationships between life history traits and rates of production among fish species have been found (Denney *et al.* 2002) and holds implications for predicting their vulnerability to exploitation (Jennings *et al.* 1998) as well as recovery (Hutchings 2001). It is challenging to measure the intrinsic growth rate of marine species (Denney *et al.* 2002) and therefore life history traits have been used as surrogates for the rate of increase (Musick 1999, Reynolds *et al.* 2001). Past literature reveals that fish species particularly at risk are those that attain larger body sizes, mature later and have slow growth rates (Adams 1980, Jennings *et al.* 1998, Sadovy 2001, Reynolds 2003). Species which have greater habitat specificity are also more vulnerable while those that are less useful to humans are not (Hawkins *et al.* 2000). The use of average fish length of exploited stocks has been shown to be an appropriate indicator of exploitation pressure or fishing mortality (Ehrhardt & Ault 1992, Ault *et al.* 2005b). Some length based assessments also have simple data requirements (Ault *et al.* 2008) and mostly only seek to estimate current levels of fishing mortality (Hillborn 1992).

In this study, length-based per-recruit analysis was applied to obtain depletion estimates for linefish species during 1988-1990 (first period) when the fishery was mostly unregulated and essentially open access. A depletion estimate two decades thereafter for 2008-2010 (second period), eight years after the fishery was declared to be in a state of emergency, was also calculated. Next, linear models were used to correlate the depletion estimates for the second period to a suite of life history and biological traits, as well as species-specific fishery characteristics, to establish which of these contributed most to the exploitation status of the linefish species. Additionally, analyses were conducted to find differences in spawner biomass depletion related to reproduction strategies, distribution and movement patterns. The aims of this study were therefore:(1) to quantify the stock status for all linefish species with available life history and size composition information, (2) compare current and historical stock levels to ascertain if the reduction in effort facilitated any recovery in linefish species and (3) correlate the current stock status estimates to life history traits to identify simple indicators of resilience to exploitation.

Methods

Length frequency data and life history traits

Length frequency data for 26 linefish species were sourced from the National Marine Linefish System (NMLS) for the years 1988-1990 and 2008-2010 (Table 1). The NMLS is a database hosted by the fisheries research division of the Department of Agriculture, Forestry and Fisheries (Kerwath *et al.* 2013a). It is the primary repository for all data related to the linefishery in South Africa and includes recreational and commercial data (Kerwath *et al.* 2013a). The NMLS has over 2.7 million records, making it the largest dataset available within the Ocean Biographic Information System (OBIS) (Kerwath *et al.* 2013a). Fish species were chosen based on availability of length frequency data and length data were grouped into 20mm size classes for analyses. Biological parameters describing growth, longevity and maturity were collected for each fish species from Mann (2013), literature referenced therein and, where available, most recent publications and technical DAFF reports (Appendix A). In the event that multiple values were reported, values were chosen from literature which (1) was the most recently published, (2) obtained values from stocks in South Africa (closest to the Western Cape) or, (3) had the largest sample size, whichever was most applicable. When values were reported separately for females and males, those reported for females were used to approximate the stock's reproductive potential as a function of female spawning biomass. For protogynous species spawning biomass was taken as combined biomass of both sexes to account for reduced fertilization rates in the absence of large old males (Brooks *et al.* 2008).

For consistency in the analysis, species which had length-related parameters reported based on different length measurements were converted to the same length measurement (either total length (TL) or fork length (FL)) by applying the length-length relationships reported in Mann (2013). Species which had parameters reported using a consistent length measurement, were kept as reported. All analyses in this study were conducted using R version 3.5.1.

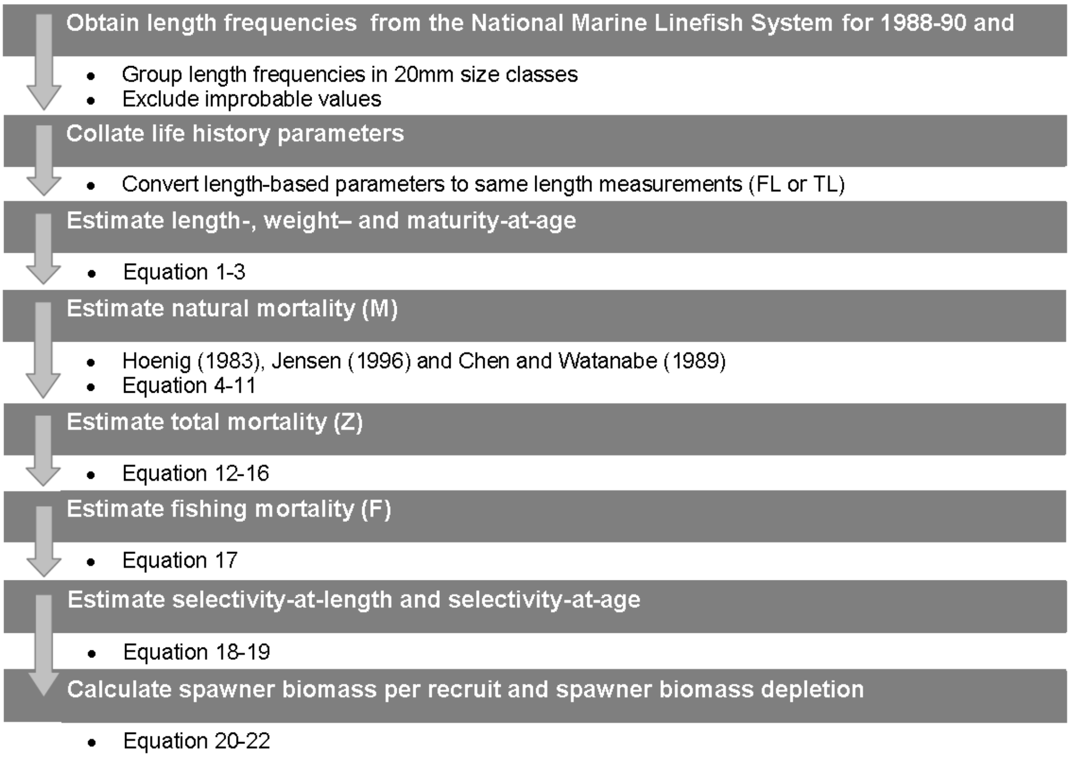

Figure 1. Methodology to estimate spawner biomass depletion of 26 South African linefish species.

Table 1. South African linefish species selected for analysis, with the database identification code (ID) and sample sizes (n) for each time period.

Species	ID	1988-90	2008-10
Carangidae			
Seriola lalandi – yellowtail	YLTL	14628	2783
Coryphaenidae			
Coryphaena hippurus- dolphinfish	DLFS	No data	564
Gempylidae			
Thyrsites atun – snoek	SNOK	6209	37524
Pomatomidae			
Pomatomus saltatrix – elf	ELF	826	402
Sciaenidae			
Argyrosomus inodorus – silver kob	KOB	No data	15634
Atractoscion aequidens – geelbek	GLBK	10894	7744
Scombridae			
Euthynnus affinis - eastern little tuna	ELTN	No data	739
Serranidae			
Epinephelus albomarginatus - white-edged rockcod	WRCD	233	1133
Epinephelus andersoni - catface rockcod	CRCD	264	2387
Epinephelus marginatus - yellowbelly rockcod	YRCD	91	499
Epinephelus rivulatus - halfmoon rockcod	HRCD	378	3738
Sparidae			
Argyrozona argyrozona - carpenter	CRPN	19908	8464
Cheimerius nufar - santer	SNTR	4058	60893
Chrysoblephus anglicus - englishman	ENGL	1409	5696
Chrysoblephus cristiceps - dageraad	DGRD	542	117
Chrysoblephus gibbiceps - red stumpnose	RSTM	1842	431
Chrysoblephus laticeps - roman	ROMN	10101	2132
Chrysoblephus puniceus - slinger	SLNG	9827	214530
Cymatoceps nasutus - black musselcracker	PNSK	63	333
Pachymetopon aeneum - blue hottentot	BLHT	1330	6510
Pachymetopon blochii - hottentot	HTTN	1167	12089
Polysteganus praeorbitalis - scotsman	SCTS	384	1721
Pterogymnus laniarius - panga	PANG	3182	2796
Rhabdosargus globiceps - white stumpnose	WSTM	6553	764
Spondyliosoma emarginatum – steentjie	STNT	1427	400
Triglidae			
Chelidonichthys capensis - cape gurnard	CGRD	No data	538

Growth parameters

Length-at-age was calculated by the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty(1 - e^{-K(t-t_0)}) \qquad \text{Eq. 1}$$

where L_∞ is the predicted asymptotic length, K is the growth coefficient, which describes the rate in that L_∞ is approached, and t_0 is the theoretical age of a fish with a length of zero.

The weight-at-age (W_t) of each species was calculated as:

$$W_t = a{L_t}^b \qquad \text{Eq.2}$$

where a and b are coefficients of the species length-weight relationship and L_t the length-at-age obtained from the VBGF (Eq. 1).

Maturity

The proportion of mature individuals at age t (ψ_t) was expressed as:

$$\psi_t = \frac{1}{1 + e^{-(L_t - L_m)/\delta_\psi}} \qquad \text{Eq. 3}$$

where L_m is the length at which 50% of the individuals attain maturity and δ_ψ describes the width of the logistic maturity ogive function. In the absence of published δ_ψ, an estimate of δ_ψ was taken as 5% of the L_m estimate for consistency to approximate knife-edged maturity.

Natural mortality

The natural mortality (*M*) for each species was estimated as the average of three empirical methods: (1) Hoenig (1983), (2) Jensen (1996) and (3) Chen and Watanabe (1989). Hoenig (1983) assumes that mortality is constant at age and estimates natural mortality by developing a general regression equation using the maximum age of the fish (t_{max}):

$$log(M^H) = 1.44 - 0.982 log(t_{max}) \qquad \text{Eq. 4}$$

Approximating *M* based on the ratio *M* / *K* is derived from life history theory as well as empirical observations (Jensen, 1996; Hordyk *et al.* 2015; Froese *et al.* 2016). As for Hoening (1983)*,* this estimator is based on the assumption of constant mortality at age:

$$M^J = 1.5K \qquad \text{Eq. 5}$$

The Chen and Watanabe (1989) mortality estimation equations assume a convex function of length-at-age, where the mortality shape is that of a "bathtub"; higher mortality at lower ages which stabilises and then increases again at higher ages. Mortality-at-age is estimated as follows:

$$M_t^C = \begin{cases} \dfrac{K}{1 - e^{-K(t-t_0)}} & if\ t \leq t_M \\ \dfrac{K}{a_0 + a_1(t - t_M) + a_2(t - t_M)^2} & if\ t \geq t_M \end{cases} \qquad \text{Eq. 6}$$

where t_M is age at end of reproductive span, i.e. age at the intersection of the stable and senescent growth phases and is calculated as follows:

$$t_M = t_0 - \frac{1}{K}\log(|1 - e^{Kt_0}|) \qquad \text{Eq. 7}$$

and the parameters a_0, a_1 and a_2 are given by:

$$a_0 = 1 - e^{-K(t_M - t_0)} \qquad \text{Eq. 8}$$

$$a_1 = Ke^{-K(t_M - t_0)} \qquad \text{Eq. 9}$$

$$a_2 = -\frac{K^2}{2}e^{-K(t_M - t_0)} \qquad \text{Eq. 10}$$

The final age-specific natural mortality estimate $\bar{M}_t$ for age t used for each species was the mean of M^H, M^J andM_t^C:

$$\bar{M}_t = \frac{\sum M^H + M^J + M_t^C}{3} \qquad \text{Eq. 11}$$

The M_t^C estimates for three species (catface rockcod, red stumpnose and white stumpnose) were excluded as they produced nonsensical, negative values and only the mean between the M^H and M^J estimate was used instead (Appendix B).

Total mortality

The total mortality (*Z*) for each species was estimated by using length converted catch curve analysis (Pauly 1984). This approach compensates for the fact that fish growth slows as they get older, resulting in larger size classes containing more age classes than smaller size classes, which is known as “stack-up” effect (i.e. a larger size class contains a wider range of ages than that of a smaller size class).

The length-converted catch curve was fitted in the form of a linear regression to the right descending limb of the length frequency sample by multiplying the number of fish in each length class by the growth rate of that class, so that:

$$\log\left(\frac{f_i}{dt_i}\right) = a + bt_i \qquad \text{Eq. 12}$$

where f_i is the frequency in length class *i* and dt_i is the time it takes for the fish to grow through a particular length class, which is estimated by:

$$dt_i = -\frac{1}{K}\log\left(1-\frac{L_{i2}}{L_\infty}\right)+\frac{1}{K}\log(1-\frac{L_{i1}}{L_\infty}) \qquad \text{Eq. 13}$$

where L_{i1} and L_{i2} are the lower and upper bounds of length class L_i and t_i is given by:

$$t_i = t_0 - \frac{1}{K}\log(1-\frac{L_i}{L_\infty}) \qquad \text{Eq. 14}$$

The estimate of *Z* was then estimated by taking the negative of the regression slope $Z = -b$ (Eq. 8).

A caveat of the length-converted catch curve approach is that it ignores variation of length-at-age and thus represents a simplified, deterministic approximation for converting length to age based on the von Bertalanffy growth function. A specific property related to this is that cases where $L_i > L_\infty$ are not defined (Eq. 14). However, in this study several length samples comprised a notable proportion of fish in larger size classes than the available L_∞ estimate for the respective species. This can be explained, for example, by large variations in length of older fish or the unaccounted effects of sampling selectivity, resulting in overrepresentation of fast-growing younger fish and slow-growing older fish in length-at-age sample, which could both negatively bias L_∞ (Taylor *et al*. 2005). To include all observed size classes for species where $L_i > L_\infty$, L_∞ and *K* were therefore adjusted prior to length converted catch curve calculations. First, L_∞ was adjusted using the empirical approximation by Froese and Binohlan (2000): $\tilde{L}_\infty = L_{max}/0.95$, where L_{max} is the maximum observed size class for the species. Next, to account the interaction and dependence between $\tilde{L}_\infty$ and *K,* the growth performance index ϕ' (Pauly & Munro 1984) was rearranged to readjust *K,* such that:

$$\phi' = \log_{10}\left(\frac{L_\infty}{10}\right) + \log_{10}(K) \qquad \text{Eq. 15}$$

and

$$\tilde{K} = \left(\phi' - \log_{10}\left(\frac{\tilde{L}_\infty}{10}\right)\right)^{10} \qquad \text{Eq. 16}$$

where $\tilde{L}_\infty$ and $\tilde{K}$ denote the adjusted values of the original values sourced from literature.

Fishing mortality

The rate of fishing mortality (*F*) for each three year time period was estimated by calculating the mean mortality rate across all fully selected age classes:

$$F = \frac{\sum_{t_c}^{t_{max}} Z - \bar{M}_t}{t_{max} - t_c + 1} \qquad \text{Eq. 17}$$

where t_c is the first fully selected age class, t_{max} is the maximum age and *Z* is the instantaneous rate of total mortality obtained from the length-converted catch curve analysis

Selectivity

The selectivity-at-length for each 20mm size class was estimated by fitting a two-parameter nonlinear logistic ogive to the cumulative distribution of the ascending left limb of the length frequency distribution (Eq. 16), with the assumption that the maximum frequency of the length distribution equated to the first fully selected length class. In other words, the first length class frequency was divided by the sum of all the frequencies of length classes up to the maximum frequency. Next, the cumulative sum of the first two length classes were divided by the sum of all the frequencies of length classes up to the maximum frequency, then the cumulative sum of the first three length frequencies, and so forth such that:

$$S_L = \frac{1}{1 + e^{-(L_i - L_{s50})/\delta_{Ls}}} \qquad \text{Eq. 18}$$

where L_{s50} is the length at which 50% of the fish are selected for and δ_{Ls} is the parameter which determines the width of the logistic ogive. The selectivity-at-age was calculated as a function of length-at-age L_t:

$$S_t = \frac{1}{1 + e^{-(L_{t+0.5} - L_{s50})/\delta_{Ls}}} \qquad \text{Eq. 19}$$

Spawner biomass per recruit analysis

Steady-state population numbers per-recruit are calculated as follows:

$$N_t = \begin{cases} 1 & if\ t = t_{min} \\ N_{t-1}e^{-Z_{t-1}} & if\ t_{min} < t < t_{max} \\ N_{t-1}e^{-Z_{t-1}}/1 - e^{-Z_t} & if\ t = t_{max} \end{cases} \qquad \text{Eq. 20}$$

where N_t is the number of individuals at age t, t_{min} is the smallest age class considered (here $t_{min} = 1$), t_{max} is the age class corresponding to maximum reported age, which is treated as a 'plus group' and Z_t is the rate of total mortality of a fish at age t. Z_t is calculated as:

$$Z_t = \bar{M}_t + S_t F \qquad \text{Eq. 21}$$

where $\bar{M}_t$ is the mean natural mortality of the species at age t, S_t is the selectivity at age t and F is the instantaneous fishing mortality rate.

Spawner biomass per recruit was then calculated as the product of number-, weight- and maturity-at-age t, such that

$$SB/R = \sum_{t_{min}}^{t_{max}} N_t W_t \psi_t \qquad \text{Eq. 22}$$

Finally, the depletion of each species was calculated by finding the ratio of spawner biomass at current fishing mortality to spawner biomass at a fishing mortality of zero, SB_0/R (i.e. $Z_t = \bar{M}_t$).

Meta-analysis

The spawner biomass depletion estimates for the 2008-2010 period were regressed to a suite of life history and fishery parameters to find the traits that are significantly related to the depletion status. These were: asymptotic length (L_∞) and growth coefficient (K) from the von Bertalanffy growth function, as well as length at 50% maturity (L_m), maximum age (t_{max}), age at 50% maturity (t_m) and also the ratios between L_m/L_∞, L_c/L_∞, L_c/L_m and L_c/L_{opt} (where L_c is the length at 50% selectivity). L_{opt} is the optimum length where a cohort has reached its maximum growth in biomass (Beverton 1992). It is calculated as:

$$L_{opt} = L_\infty \left(\frac{3}{3 + \bar{M}/K}\right) \qquad \text{Eq. 23}$$

where $\bar{M}$ is the mean natural mortality expressed as the average of all age-specific mortality estimates (i.e. $\bar{M} = \frac{\sum \overline{M_t}}{t_{max}}$). In other words, $\bar{M}$ is the sum of each age-specific mortality mean (the mean between M^H, M^J and M_t^C for each age (Eq. 11)) divided by the maximum age. Species specific input parameters and model outputs can be found in Appendix A.

Lastly, a Kruskal-Wallis test was performed to find differences in spawner biomass depletion related to reproduction strategies, distribution and movement patterns. Reproductive strategies included gonchoristic and protogynous fish. Distribution was either global, regional (i.e. occurring in southern African waters) or endemic (occurring only in South African waters). Movement patterns were categorized as resident, migratory or nomadic. Migratory movement is deterministic, predictable movement towards spawning grounds or for feeding while nomadic movement is passive. Data were obtained from Mann (2013) or other literature.

Results

Of the 26 species analyzed, length frequency data for four species (dolphinfish, silver kob, eastern little tuna and cape gurnard) were either not available or insufficient for the 1988-1990 period and so comparisons could not be made.

Furthermore, the spawner biomass depletion values for the 2008-2010 period for three species (snoek, geelbek and santer) were in sharp contrast to estimates found in recent, comprehensive, stock assessments conducted by the South African Department of Agriculture, Forestry and Fisheries (DAFF) (Boyd 2017, Kerwath *et al.* 2017, Maggs *et al.* 2017). Consequently, the formal stock assessment estimates were considered more reliable and were used in the evaluation of life history traits instead (Table 2). Red stumpnose was excluded from further analysis due to doubt over the estimates found: 69.2% in 1988 and 89.8% in 2008. This species is listed as endangered on the IUCN Red list and there are reservations regarding the maximum reported age (48 years) found by van Zyl (2013), as this age was estimated from only one specimen.

Table 2. Spawner biomass per recruit depletion estimates from this study and the estimates from recent assessments conducted by the Department of Agriculture Forestry and Fisheries (DAFF).

Species	Per recruit estimate	DAFF estimate	Source
Thyrsites atun	15.2%	60.0%	Kerwath *et al*. 2017
Atractoscion aequidens	4.6%	9.9%	Boyd 2017
Cheimerius nufar	4.0%	25.0%	Maggs *et al.*2017

The depletion estimates for 25 linefish species for the second period show that 10 of these species are underexploited, 9 overexploited and 6 collapsed (Figure 2). Twelve species (out of 21) saw an improvement in their stock status between the two periods (i.e. changed from collapsed to overexploited or underexploited, or from overexploited to underexploited) while only one had a negative status change (yellowbelly rockcod: overexploited to collapsed) (Figure 2, Table 3). Eight had no change in status, but five of those showed increases in spawner biomass (Table 3).

Table 3. Differences in spawner biomass depletion (ΔSBD) between the first (1988-1990) and second (2008-2010) period for 26 South African linefish species. Positive values are indicative of increased spawner biomass, while negative values indicate depletion. An "X" indicates species for which comparisons could not be made. Green shaded values indicate species which underwent a positive change in status (i.e. improved status from collapsed or overexploited), while red shading indicates a negative change in status. No shading indicates no change in overall status. Red stumpnose is not used for comparisons in this study and as such is crossed out.

Species	**ΔSBD (%)**	**Species**	**ΔSBD (%)**
Yellowtail	24.8	Englishman	6.7
Dolphinfish	X	Dageraad	20.1
Snoek	45.4	~~Red stumpnose~~	~~20.6~~
Elf	-8.0	Roman	9.1
Kob	X	Slinger	19.6
Geelbek	3.1	Black musselcracker	30.6
Eastern little tuna	X	Blue hottentot	35.5
White-edged rockcod	-0.7	Hottentot	26.8
Catface rockcod	-12.6	Scotsman	7.7
Yellowbelly rockcod	-16.8	Panga	8.9
Halfmoon rockcod	8.2	White stumpnose	12.9
Carpenter	19.4	Steentjie	7.8
Santer	18.2	Cape gurnard	X

Comparisons between fishery parameters could only be made for 18 species: 11 species showed a decrease in fishing mortality and 16 an increase in their length-at-capture (Table 4). Seventeen out of 21 species showed an increase in spawner biomass from 1988 to 2008 (including the three for which DAFF estimates were used) (Table 2, Figure 2). The four species which showed a decrease in spawner biomass in this period were elf, white-edged-, catface- and yellowbelly rockcod (Table 2, Figure 2). Elf was also one of two species which displayed a decrease in selectivity between the two time periods. The three rockcod's did not show a decrease in selectivity but did show an increase in fishing mortality (Table 4).

Linear regressions showed that only asymptotic length (L_∞), the ratio between length-at-50%-selectivity and asymptotic length (L_c/L_∞) and the ratio between L_c and optimum length (L_c/L_{opt}) had a significant relationship with spawner biomass depletion (Figure 3). The Kruskal-Wallis test revealed no significant relationships between spawner biomass depletion and reproductive strategy (H = 1.305, df = 1, p = 0.25) or species' distribution (H = 2.482, df = 2, p = 0.29) (Figure 4). In contrast, spawner biomass depletion estimates differed significantly among movement pattern categories (H = 7.024, df = 2, $p < 0.05$) (Figure 4). A Kruskal-Wallis multiple comparison post-hoc test revealed that there was only a difference between migratory and resident fish ($p <$ 0.05).

Table 4. Mean natural ($\bar{M}$), total (*Z*) and fishing mortality (*F*) as well as the 50% selectivity for the 1988-1990 and 2008-2010 periods (L_{c1988} and L_{c2008}) for 26 South African linefish species. Mean natural mortality is the average of all age specific mortality estimates (i.e. $\bar{M} = \frac{\sum \overline{M_t}}{t_{max}}$). A (*) denotes the exclusion of the Chen & Watanabe (1989) mortality estimate. Shaded species are those not used in comparisons and an (X) means no estimate could be calculated.

	$\bar{M}$	Z_{1988}	Z_{2008}	F_{1988}	F_{2008}	L_{c1988}	L_{c2008}	L_{opt}
Yellowtail (*S. lalandi*)	0.489	0.914	0.983	0.565	0.535	515.29 mm	687.47 mm	702.28 mm
Dolphinfish (*C. hippurus*)	0.812	X	3.102	X	2.362	X	861.74 mm	972.02 mm
Snoek (*T. atun*)	0.430	1.878	2.235	1.464	1.822	738.37 mm	781.31 mm	775.37 mm
Elf (*P. saltatrix*)	0.264	0.781	1.576	0.523	1.313	284.67 mm	272.62 mm	644.06 mm
Kob (*A. inodorus*)	0.180	X	0.496	X	0.327	X	492.52 mm	901.60 mm
Geelbek (*A. aequidens*)	0.432	1.013	1.541	0.603	1.139	565.97 mm	715.18 mm	733.05 mm
Eastern little tuna (*E. affinis*)	0.863	X	1.847	X	1.018	X	453.73 mm	664.63 mm
White-edged rockcod (*E. albomarginatus*)	0.328	0.530	0.942	0.231	0.654	295.97 mm	476.60 mm	522.20 mm
Catface rockcod (*E. andersoni*)	0.561*	0.998	1.438	0.437	0.877	401.06 mm	557.30 mm	562.37 mm
Yellowbelly rockcod (*E. marginatus*)	0.201	0.319	0.745	0.128	0.563	341.36 mm	604.3 mm	715.99 mm
Halfmoon rockcod (*E. rivulatus*)	0.448	0.729	0.603	0.308	0.180	240.35 mm	224.81 mm	240.75 mm
Carpenter (*A. argyrozona*)	0.113	0.340	0.282	0.232	0.176	258.46 mm	333.12 mm	380.27 mm
Santer (*C. nufar*)	0.153	0.544	0.946	0.398	0.799	272.75 mm	276.95 mm	519.43 mm
Englishman (*C. anglicus*)	0.187	0.357	0.520	0.183	0.351	252.54 mm	363.11 mm	375.00 mm
Dageraad (*C. cristiceps*)	0.157	0.319	0.290	0.171	0.146	248.59 mm	361.66 mm	397.73 mm
Red stumpnose (*C. gibbiceps*)	0.132*	0.170	0.151	0.038	0.019	241.68 mm	328.74 mm	309.38 mm
Roman (*C. laticeps*)	0.177	0.344	0.379	0.182	0.219	221.41 mm	277.03 mm	304.14 mm
Slinger (*C. puniceus*)	0.317	0.731	0.556	0.422	0.247	207.14 mm	227.77 mm	259.48 mm
Black musselcracker (*C. nasutus*)	0.088	0.190	0.139	0.110	0.060	470.15 mm	607.64 mm	687.67 mm
Blue hottentot (*P. aeneum*)	0.314	0.507	0.384	0.256	0.138	245.22 mm	314.94 mm	261.39 mm
Hottentot (*P. blochii*)	0.203	0.538	0.328	0.347	0.139	195.73 mm	215.64 mm	262.26 mm
Scotsman (*P. praeorbitalis*)	0.213	0.454	0.520	0.250	0.323	250.61 mm	367.13 mm	444.97 mm
Panga (*P. laniarius*)	0.227	0.477	0.427	0.268	0.218	234.49 mm	246.21 mm	239.82 mm
White stumpnose (*R. globiceps*)	0.264*	0.678	0.557	0.415	0.293	213.43 mm	237.95 mm	281.17 mm
Steentjie (*S. emarginatum*)	0.411	0.834	0.768	0.420	0.348	176.70 mm	196.93 mm	178.19 mm
Cape gurnard (*C. capensis*)	0.188	X	0.534	X	0361	X	409.98 mm	498.66 mm

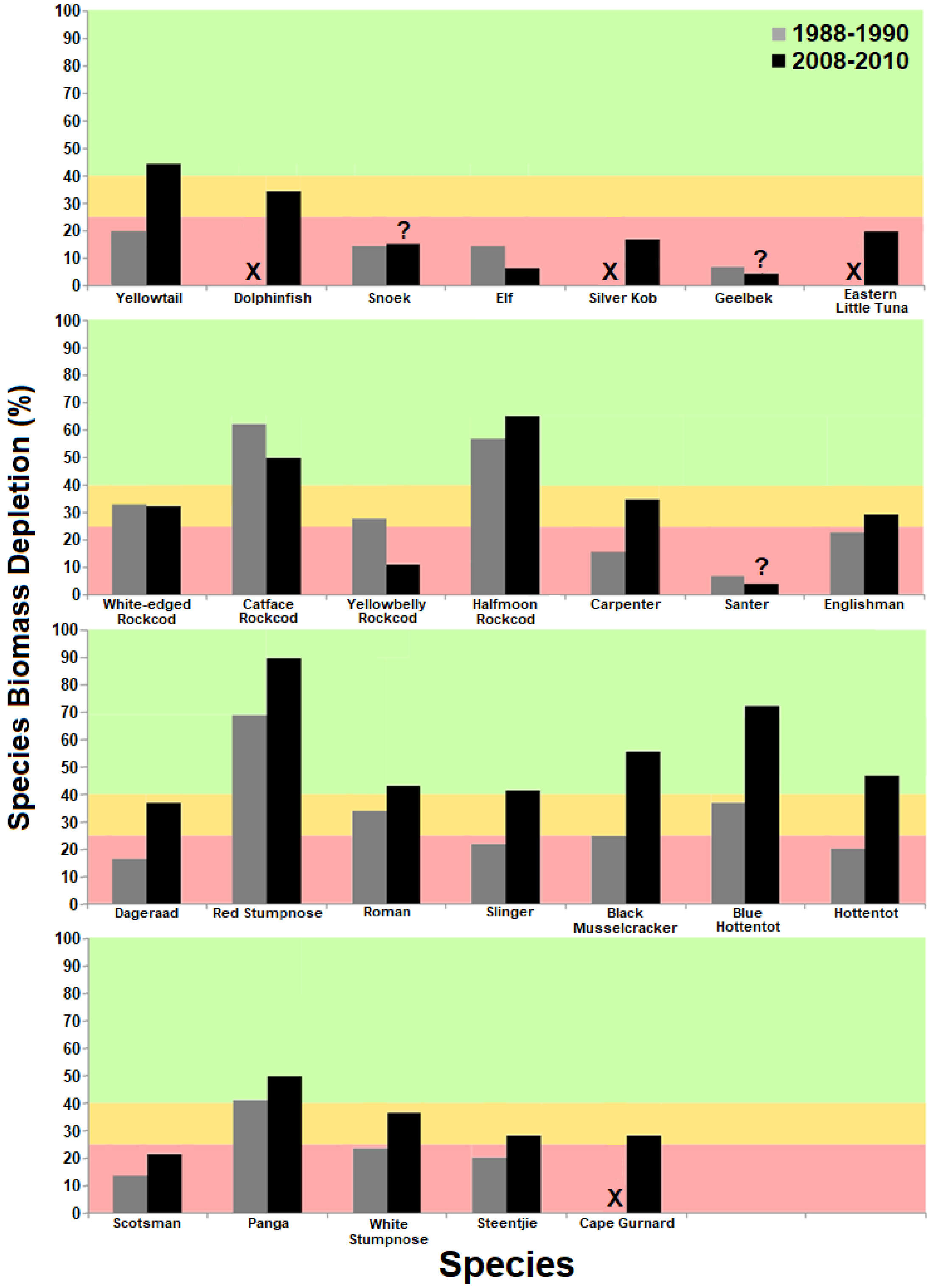

Figure 2. Spawner biomass depletion estimates (%) of 26 South African linefish species for the periods 1988-1990 and 2008-2010. The shaded green area indicates underexploited stocks, yellow shading is overexploited stocks and red shading stocks that are collapsed. A "?" denotes fish which for which recent DAFF estimates were used. An "X" denotes species for which there was no data available.

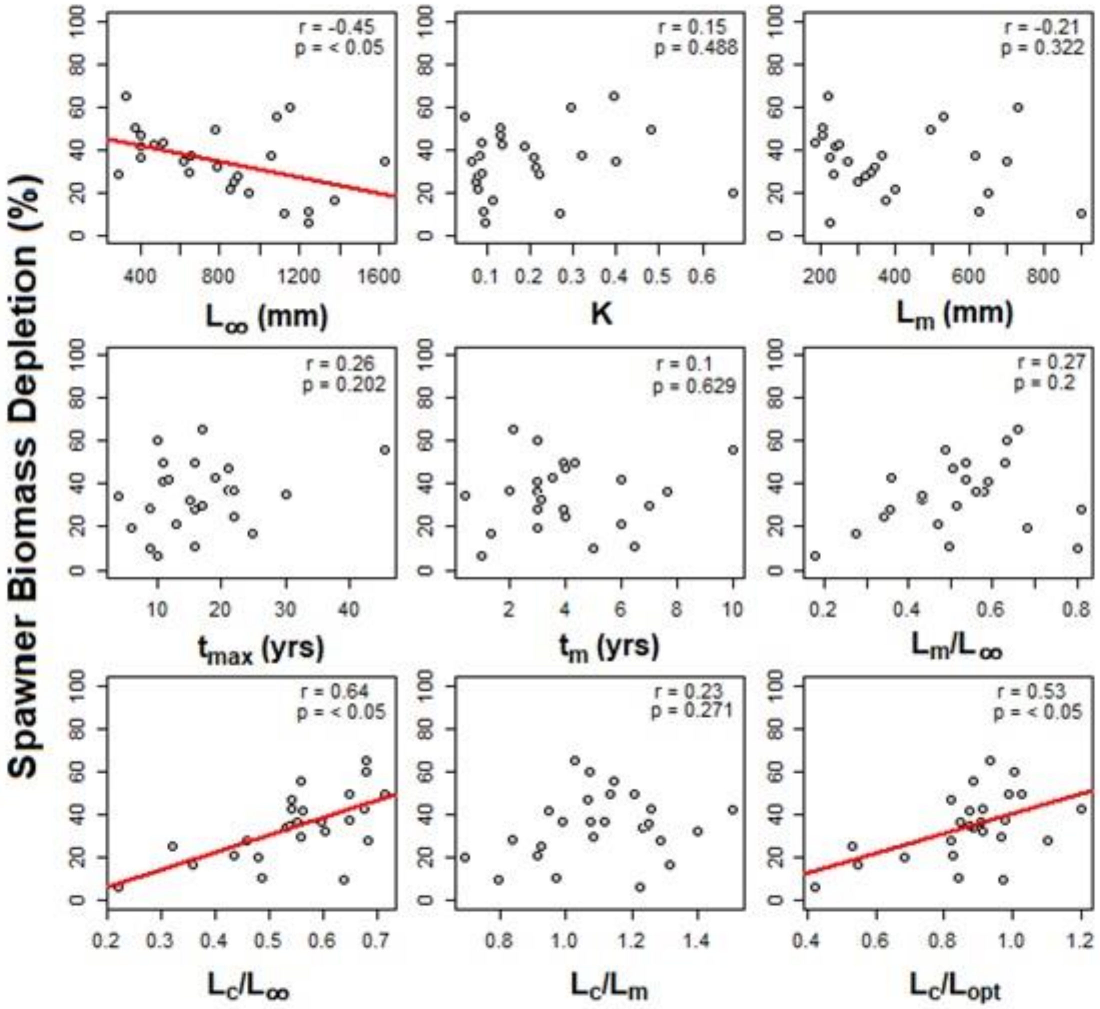

Figure 3. Linear regressions of various life history and fisheries traits to spawner biomass depletion estimates for the period 2008-2010. The correlation coefficient (r) and significance value (p) are reported for each relationship. The various traits analysed were: asymptotic length (L_∞) and growth coefficient (K) from the von Bertalanffy growth function. Length at 50% maturity (L_m), maximum age (t_{max}), age at 50% maturity (t_m) and also the ratios between L_m/L_∞, L_c/L_∞, L_c/L_m and L_c/L_{opt} (where L_c is the length at 50% selectivity).

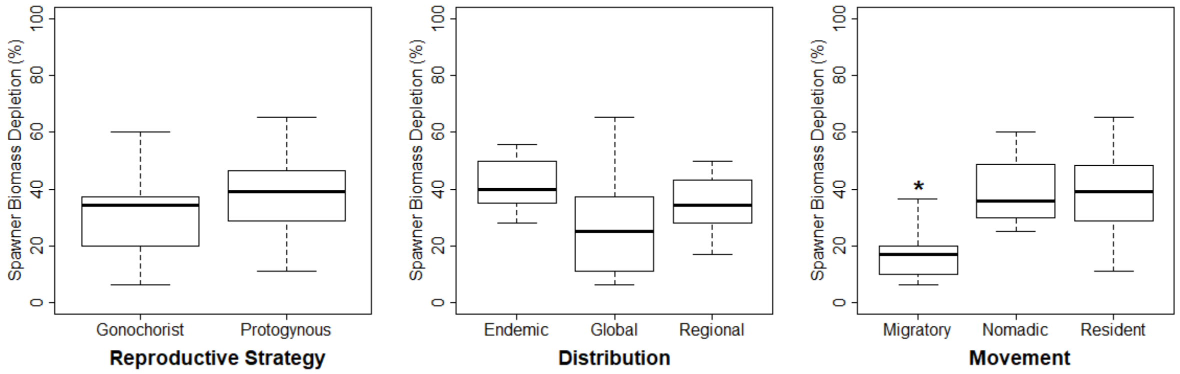

Figure 4. Boxplots showing the median (dark line), upper and lower quartiles as well as maximum and minimum spawner biomass depletion estimates for reproductive strategy, distribution and movement pattern (n = 25) for South African linefish species. An asterisk (*) denotes a significant difference.

Discussion

Per recruit model and life history parameters

The yield per-recruit/spawner-biomass-per-recruit model developed by Beverton and Holt (1957) remains widely used in data poor fisheries stock assessments (Booth & Buxton 1997, Brouwer & Griffiths 2006). It is typically considered the most appropriate stock assessment method when long-term catch data is lacking (Punt 1993, Griffiths 1997). These models incorporate the relationship between mortality and somatic growth in order to predict either the yield or the spawner biomass of a cohort, using different combinations of age/length-at-first-capture and fishing mortality (Griffiths 1997). The per-recruit model depends on a number of assumptions which are susceptible to violations. These include (1) that recruitment is constant and (2) the stock is in an equilibrium state, with natural and fishing mortality being mostly assumed constant from the moment recruits enter the exploited phase. These assumptions may not be representative of true stock dynamics, which may result in inaccurate yield or spawner biomass values (Griffiths 1997). Despite this, the estimated depletion levels for 18 out of 26 South African linefish species either compared reasonably well with results from full age-structured assessments (Winker *et al.* 2012) or were broadly compatible with previous, independent evidence about their stock status (Mann 2013).

Scientists study fish growth in order to perform stock assessments with models such as the per-recruit which rely on various life history input parameters, namely growth function, length-weight relationship, age/length-at-maturity and natural, total and fishing mortality (Punt 1993). Accurate parameter estimations are therefore crucial in the use of per-recruit assessments, but reliable life history data are not always available (Jennings *et al.* 1998, Rochet 2000). In this study, life history parameters were obtained from Mann (2013) and other literature, and the same life history parameters were used in the estimation of spawner biomass depletion for both the first and second periods. Overfishing (excess fishing mortality) has been shown to cause changes in the life history of fish; particularly the length/age-at-maturation and growth rate (Rochet 2000, Sharpe & Hendry 2009). Many of the life history values used in this study, as reported in Mann (2013), were obtained from literature published during the 1980's and 1990's, some even from as early as 1976. Recent stock assessments conducted by DAFF highlighted some conflicts between available life history parameters and the available catch and CPUE time series. (Boyd 2017, Kerwath *et al.* 2017, Maggs *et al.* 2017). As such, there is emphasis on the need for updated, life history parameters to ensure adequate representation of the underlying population dynamics and thus increasing the reliability of stock assessments.

Comparisons between an open access and a regulated fishery

More than 80% of the species in this study showed increases in spawner biomass between the first and the second period of assessment. This indicates that the declaration of emergency in the fishery in 2000 and subsequent reduction in effort (and other management measures) within the linefishery has led to substantial improvements in the status of the majority of linefish stocks. Almost all fishes in this study (apart from elf and halfmoon rockcod) showed increases in length-at-first-capture (L_c) values. Fourteen out of the 18 fish which could be compared had L_c values lower than their length-at-50%-maturity (L_m) values during the first period. These species had individuals being captured before they reached sexual maturity and spawned. The introduction of minimum size limits for some species (most of which are above the L_m value) meant that the L_c values for the second period were mostly higher than L_m (13 species), thus allowing many more individuals to reach sexual maturity and spawn. Froese (2004) presents simple fisheries indicators to deal with overfishing. One on these is to allow all fish to spawn at least once, i.e. 100% of the catch must comprise of mature individuals (Froese 2004). The desirability of only catching fish after they have matured was recognized as early as 1895 (Holt 1895, Myers & Mertz

1998, Vasilakopoulus *et al.* 2011). Allowing fish to spawn at least once will prevent stocks from collapsing regardless of the fishing mortality (Froese *et al.* 2014) and will also prevent recruitment overfishing (Myers & Mertz 1998). It is important, however, to note that this relies on the assumption that recruitment is successful at all times (Froese 2004). In reality this is rarely the case. Recruitment fluctuates drastically with environmental variability, physiological condition and age structure of the spawning population (Vasilakopoulus *et al*. 2011). It has however been shown that higher proportional fishing mortality on immature fish compared to mature fish had significantly negative effects of current stock statuses, thus proving empirical support for this principle (Froese et al. 2008, Vasilakopoulus *et al.* 2011). Size selection is widely used in fisheries and many traditional fishing gears are highly size selective. Consequently, knowledge of methods to develop new, highly selective gear is already established (Cardinale & Hjelm 2012) and can be used to fish only a certain size class (Froese 2004; Froese et al. 2008) something which may be of use in the management of the South African linefishery. It is important to note however that size and bag limits, which are implemented to reduce mortality on exploited stocks, may have the opposite effect. Barotrauma and capture mortality have been recognized as two factors which complicate the management of the South African linefishery (van der Elst 1993, Gotz *et al*. 2007). It is common among many commercial and recreational fisheries to discard or release undesirable catches (Kerwath *et al.* 2013b). Several negative effects of release have been reported (Arlinghaus *et al*. 2007), which are caused by combinations of improper handling, rapid decompression when being caught from depth and injury from fishing gear, among others (Kerwath *et al.* 2013b). Studies of South African linefishes have shown that almost all fish caught and released showed some sign or barotrauma (Gotz *et al.* 2007, Kerwath *et al.* 2013b) and so implementing size limits, with the intent of decreasing mortality, may not be plausible to implement as the *only* management regulation within the fishery.

More than half of the species in this study also showed a decrease in fishing mortality (11 species), emphasizing the success in reduction efforts within the fishery. One of the main focuses of fisheries management is regulating fishing mortality (Froese *et al.* 2008; Froese *et al.* 2014), with meta-analyses showing negative effects of exploitation rate on stock status (Sparholt *et al.* 2007, Worm *et al.* 2009) and a stronger effect on stock status compared to exploitation pattern (i.e. selectivity) (Vasilakopoulus *et al.*

2011). There is a longstanding consensus in fisheries management that fishing mortality should not exceed the mean rate of natural mortality of the exploited phase of the stock ($\bar{M}_{exp}$) (Sheperd 1981, Thompson 1993, Froese *et al.* 2014) but only a third of our species (six species) adhered to this recommendation in the second period (Appendix B). These six species (halfmoon rockcod, slinger, black musslecracker, blue hottentot, hottentot and steentjie) all showed improvements in their spawner biomass estimates. Four of these showed such an improvement that they went from being collapsed in the first period to underexploited in the second period. One species, steentjie, went from collapsed to overexploited and another, halfmoon rockcod, was already underexploited but showed an increase nonetheless. These results suggest that this $\bar{M}_{exp} > F$ "rule of thumb" is highly effective method of fisheries management and would be beneficial as a management reference point in the South African linefishery.

Four species showed a decrease in spawner biomass between the two periods: elf, white-edged-, catface- and yellowbelly rockcod. Elf was only one of two species which showed a decrease in selectivity between the two periods. Not only is elf a migratory species that travels between the Cape and KwaZulu-Natal, it is also a very popular shore angling species: elf catches comprise up to 80% annually in recreational shore-angling records in KwaZulu-Natal (Maggs *et al*. 2012). Furthermore, the development of a large illegal market in KwaZulu-Natal has been reported (Govender 1996). Migratory species (like elf) have significantly lower spawning biomass depletion estimates compared to resident species, as found in this study. This, combined with intensive recreational fishing of this species may explain why elf has not shown any recovery. Additionally, the length-at-maturity value for this species is from literature published in 1976. As mentioned previously, exploitation causes fish to mature earlier and so the L_m used in this study may be outdated. Further investigation is needed, as a variety of reasons are possible for the lack of improvement in this species (Maggs *et al.* 2012). Fennessy (2000) conducted per-recruit assessments and provided relative spawner biomass depletion estimates for four rockcod species. The estimates for white-edged- and catface rockcod were similar to estimates found in this study (±23.0% vs. 32.3% and ±42.0% vs. 49.7% respectively). The difference of approximately 10 years between estimates could potentially have allowed some recovery of these stocks, especially since this is around the time effort reductions were enforced. It is therefore reasonable to assume the estimates derived from this study are an adequate reflection of the current stock status. The current estimate for yellowbelly rockcod of 11% spawner biomass depletion was substantially lower than the ±33.0% estimate by Fennessy (2000). The yellowbelly rockcod is the largest serranid with the lowest growth rate amongst the four in this study. Large fish have been reported as being particularly at risk of over exploitation (Sadovy 2001) (further supported by this study – see below). Furthermore, the size of a fish can affect its value and it is human nature to catch the largest fish possible (Zhou *et al.* 2010). Yellowbelly rockcod is considered a high-quality catch, not only for its "trophy status", but also because it has relatively high market value (Fennessy 2006). These factors may have caused the decline in spawner biomass but further investigation is needed.

Life history and fishery parameters related to exploitation

The linear regression analysis indicated that only asymptotic length (L_∞), the ratio between length-at-capture and asymptotic length (L_c/L_∞) and the ratio between length-at-capture and optimal length (L_c/ L_{opt}) was significantly correlated to spawner biomass depletion. Large body sizes have been shown to be correlated with population declines (Jennings *et al.* 1999, Reynolds 2003, Hutchings *et al.* 2012, Comeros-Raynal 2016). This may be due to large body sizes being highly correlated to other "vulnerable" life history traits such as lower intrinsic rates of population increase and late maturity (Reynolds *et al.* 2005). In other words, although body size is significantly correlated to spawner biomass depletion, it is probably not the main cause of depletion but rather other life history traits associated with large body sizes. In this study for example, yellowtail, snoek and black musselcracker can all reach body lengths of more than one meter but all three these species are currently underexploited. However, species which have larger body sizes are disproportionately valued and targeted by humans and so size may still be an important factor determining if a species will be exploited. Neither growth rate nor length at maturity was significantly correlated to spawner biomass in this study. Late maturity has been shown to be correlated with population declines (Reynolds 2003) but growth rate has not (Jennings *et al.* 1998). As mentioned before, overfishing leads to changes in life history traits. Although length-at-maturity was not shown to be significantly correlated to spawner biomass depletion in this study, it may be due to outdated maturity values used in these analyses.

There was a significant relationship between L_c/L_∞. A ratio of L_c/L_∞ close to one indicates that fish are being caught close to the end of their lifespan while a value close to zero indicates that small fish are being caught. This seems to be an uninformative relationship, as the length-at-maturity of each fish would determine whether growth- or recruitment overfishing is occurring. For example, in this study steentjie has a relatively high L_c/L_∞ ratio (0.68), which one could easily assume would indicate better stock status due to later capture (because juveniles are left to grow and spawn). Steentjie has been shown to be overexploited (28.1%) however and this may be due to the fact that it matures late relative to its body size (L_m = 235mm and L_∞ = 289.15mm).

The optimum length (L_{opt}) is the length at which a cohort has reached its maximum growth in biomass. This length is larger than length at maturity and capture at this length would allow fish to spawn more than once (Froese 2004; Cardinale & Hjelm 2012). Hence, an L_c/L_{opt} ratio of larger than one would allow multiple spawnings as fish are caught on or over the optimum value. In this study only three species had ratios larger than one (blue hottentot, panga and steentjie), and three (yellowtail, catface rockcod and englishman) were very near to one (i.e. >0.95). Four of these species were underexploited and the other two, steentjie and englishman, had improved from being collapsed to overexploited. Fishing closer to L_{opt} may increase resilience to overfishing while still producing pretty good yields (Froese *et al.* 2008, Cardinale & Hjelm 2012; Froese *et al.* 2016), and may be of interest for size limit consideration for the South African linefishery.

In terms of categorical life history traits, only movement behavior (migratory vs. resident) of fish was found to be significantly correlated spawner biomass depletion estimates. Migratory fish in this study were significantly more depleted than resident ones. Studies have shown that resident species (or species with small home ranges) are more readily protected by marine protected areas (MPA) than their more mobile counterparts (Kramer & Chapman 1999, Gell & Roberts 2003). It is understandable then that there would be a significant difference between migratory and resident species depletions in South Africa, a country which has 22 MPA's. MPA's have restricted applicability for protecting species which migrate such as silver kob and geelbek, unless they are positioned strategically and enforced at particular places or times, for example during spawning seasons (Griffiths 2000). In contrast, resident species such as roman have been shown to improve when protected (Kerwath *et al*. 2013c)

This study is the first of its kind in South Africa to assess the status of such a large number linefish species simultaneously, encompassing nine families of bony fishes distributed across four biogeographic regions. The general increase in spawner stock biomass between the 1980's, when the fishery was essentially open access, and the 2000's, after the fishery was declared to be in a state of emergency is encouraging. This study shows that several improvements have occurred within the fishery, namely many reductions in fishing mortality and increases in the size at first capture. Although fisheries recommendations are mostly developed through complex modeling systems, these types of assessments are expensive as well as being data and time intensive. They are also sometimes poorly understood by fisheries managers and fishermen and are unlikely to be used in a small-scale fishery such as the South African linefishery. This study has shown that simple indicators, such as catching fish at optimum length or at least above length-at-maturity, or limiting fishing mortality to be lower than natural mortality, succeeds in increasing stock status in most fish. Put simply, lowering effort will cause species to recover. These indicators are not the panacea for the management of the South African linefishery however, as some fish have not shown improvements and may need more complex management strategies to improve their status. Furthermore, implementing newer size limits may not work in practice, and may lead to increased discarding and mortality due to barotrauma. Additionally, they may be difficult to enforce due to not only the scope of the fishery, but because of the cost to do so. Rebuilding of small-scale fisheries in developing countries is difficult due to the heavy reliance fishermen have on the fisheries for food and employment, but a combination of management methods (such as community management and more selective gear) hold promise for reestablishing marine fisheries (Worm *et al.* 2009).

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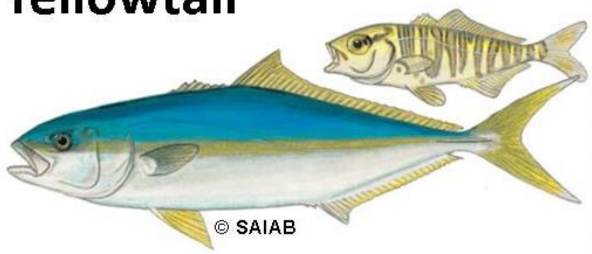
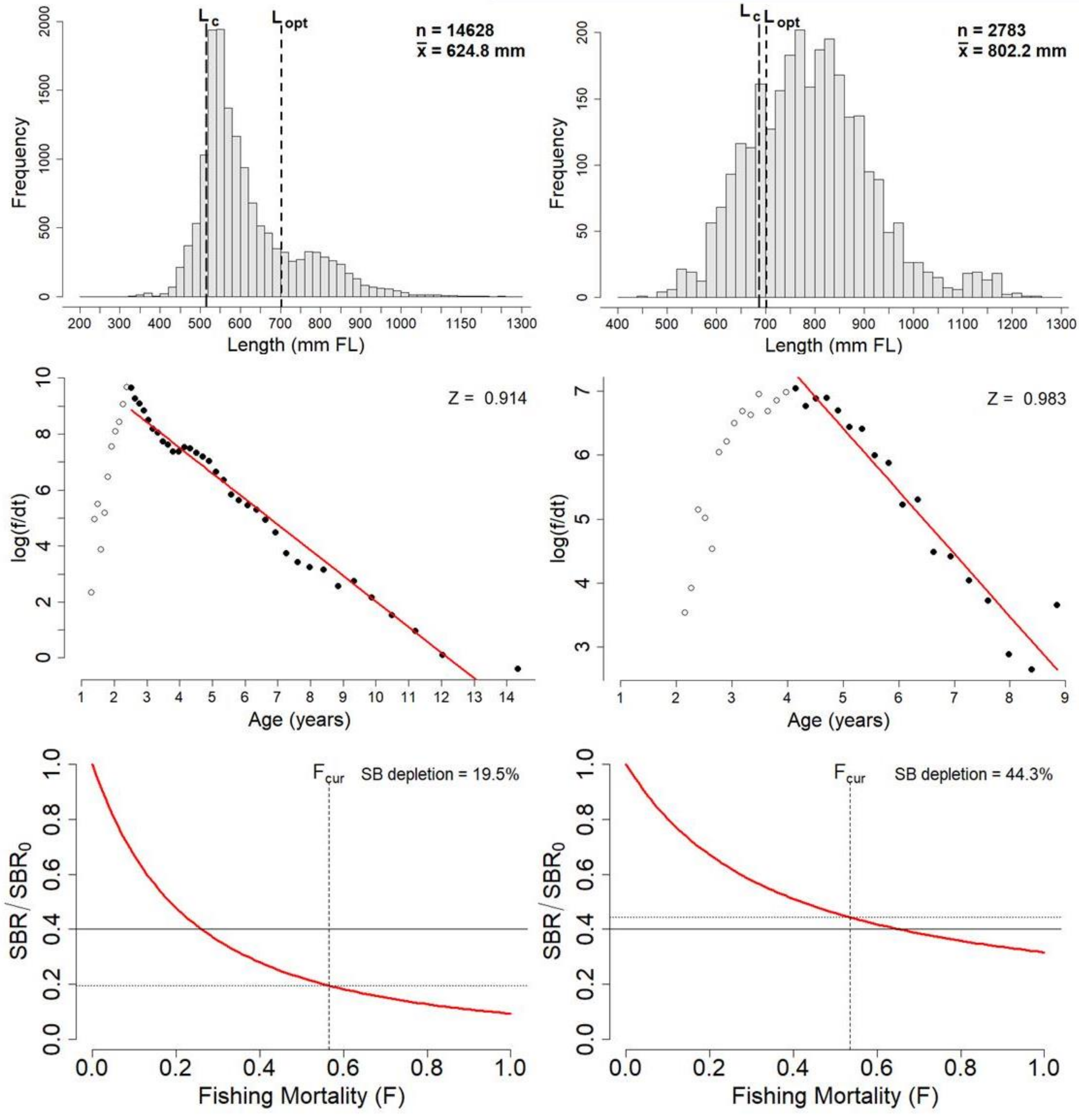
Appendix A – Species profiles

Each species analyzed in this study has a species profile consisting of: scientific and common name, figure and life history parameters (table). There are also six graphs (three pairs, 1988-1990 as the left column and 2008-2010 as the right), as follows: Top row: length frequency data with length-at-capture (L_c) and optimum length (L_{opt}), with number of fish caught during that period (n) and mean length ($\overline{x}$). Middle: catch curves showing the estimated total mortality (Z). Bottom row: depletion estimates (SB Depletion).

Seriola lalandi
Yellowtail

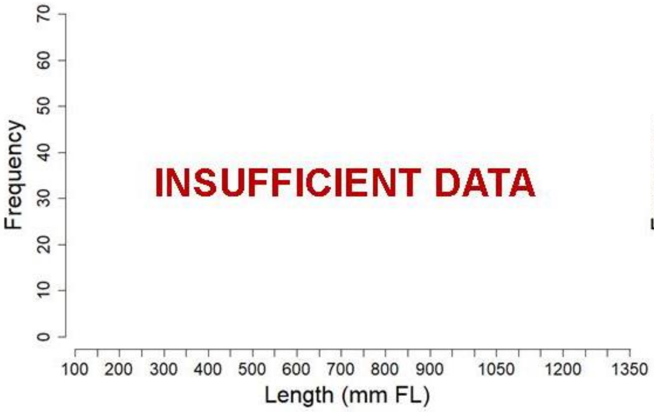


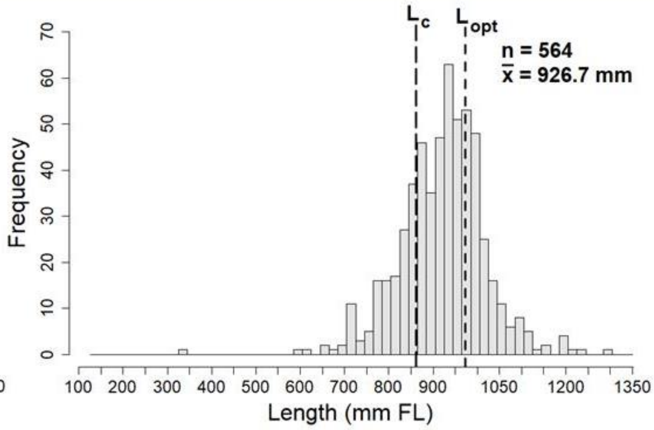
Parameters	Value	Unit	Reference
L_∞	1060	mm	Parker *et al.* 2017
K	0.32	yr^{-1}	Parker *et al.* 2017
t_0	-0.09	yrs	Parker *et al.* 2017
a	$6x10^{-5}$	g/mm	Parker *et al.* 2017
b	2.75		Parker *et al.* 2017
L_m	615	mm	Mann 2013
δ	30.75	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	21	yrs	Mann 2013
L_{opt}	702.28	mm	This study

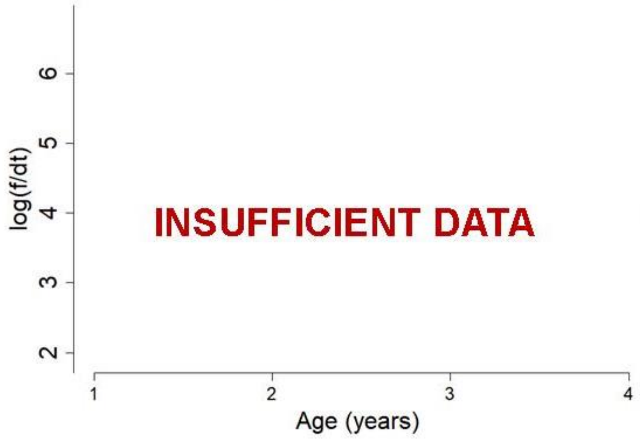


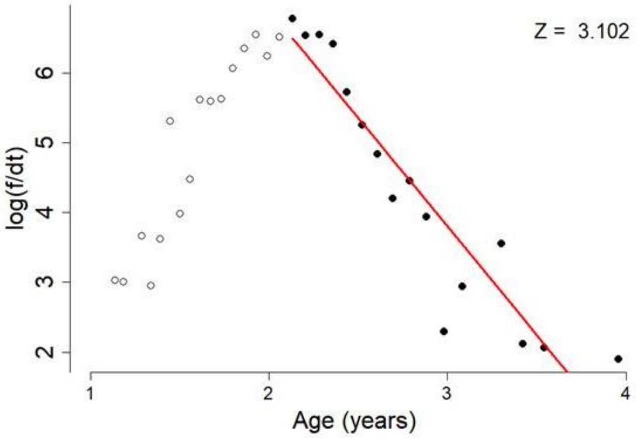
Coryphaena hippurus
Dolphinfish

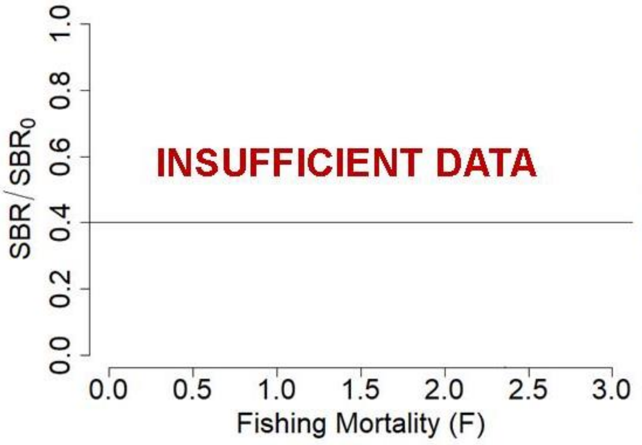
Parameters	Value	Unit	Reference
L_∞	1629.76	mm	Mann 2013
K	0.4	yr^{-1}	Mann 2013
t_0	0	yrs	Mann 2013
a	$4.4x10^{-5}$	g/mm	Mann 2013
b	2.602		Mann 2013
L_m	700	mm	Mann 2013
δ	35.00	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	4	yrs	Mann 2013
L_{opt}	972.02	mm	This study

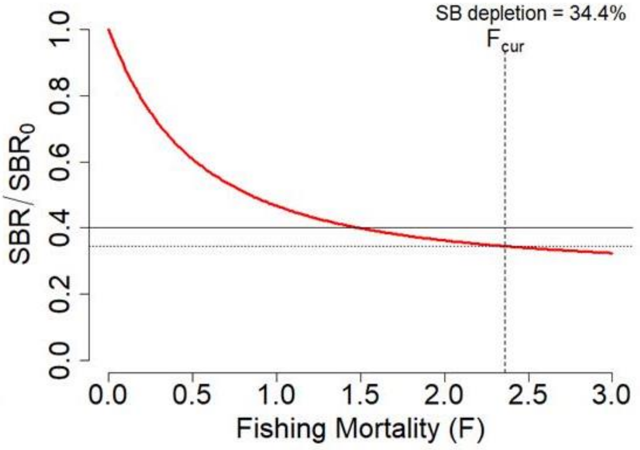








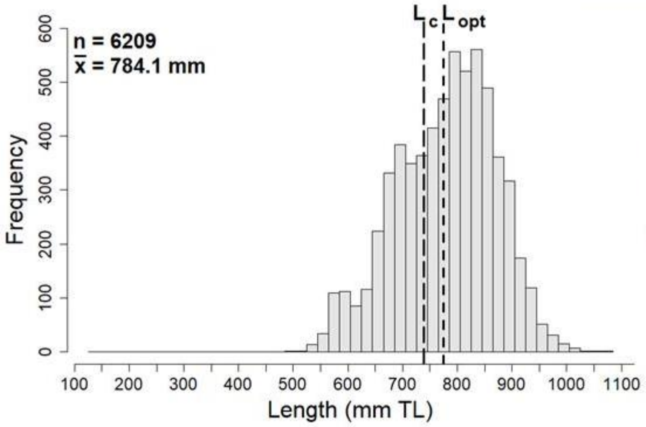


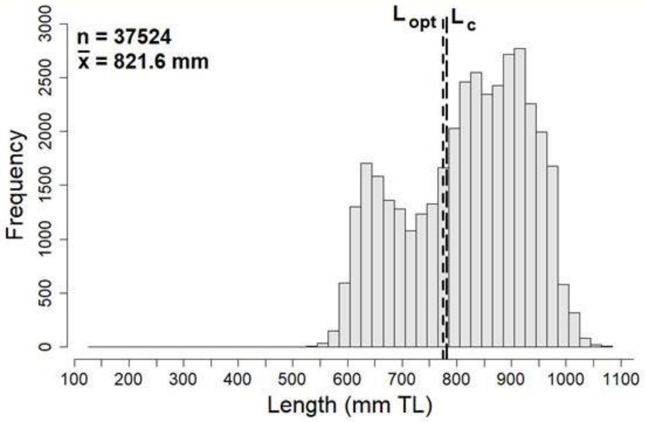


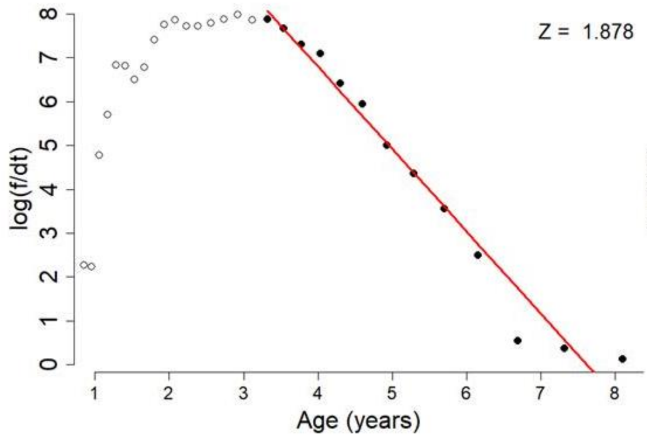
Thyrsites atun

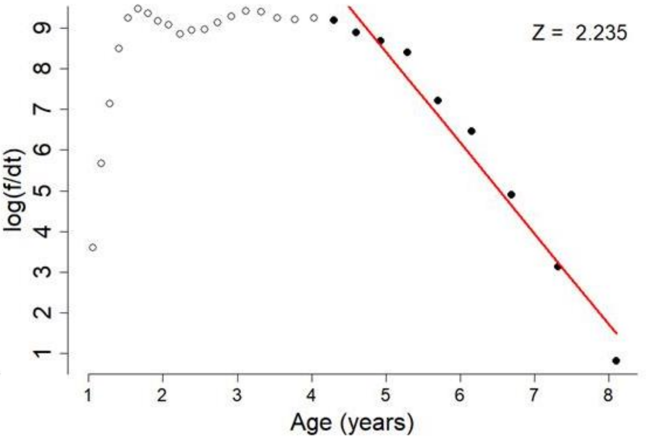
Snoek

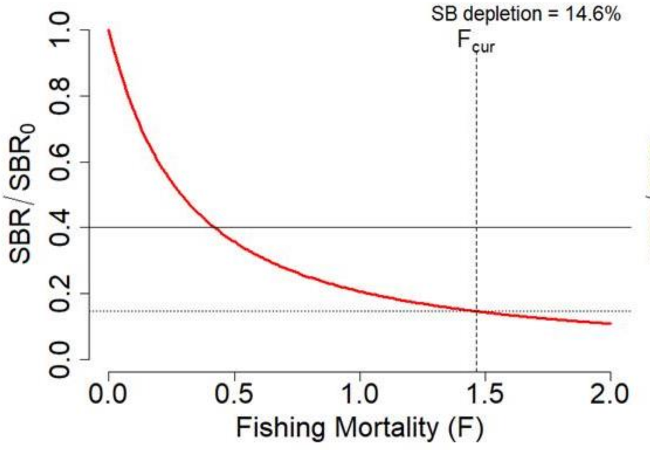
Parameters	Value	Unit	Reference
L_∞	1153	mm	Mann 2013
K	0.2943	yr^{-1}	Mann 2013
t_0	-1.056	yrs	Mann 2013
a	$6x10^{-6}$	g/mm	Mann 2013
b	3.07		Mann 2013
L_m	730	mm	Mann 2013
δ	36.5	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	10	yrs	Mann 2013
L_{opt}	775.37	mm	This study

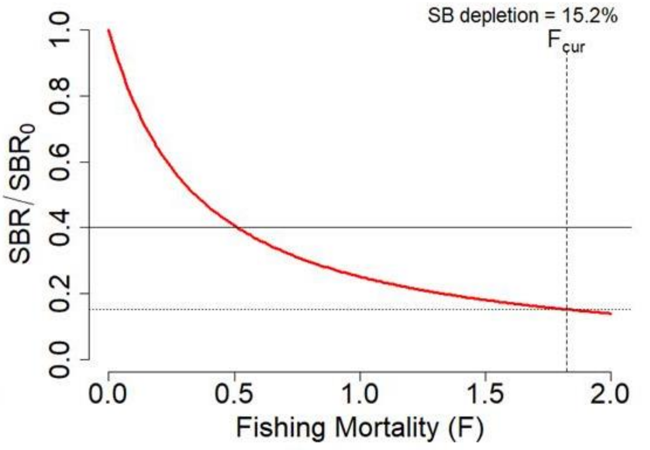




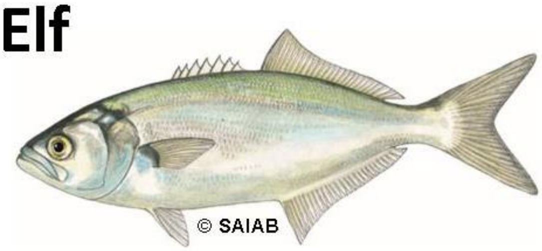




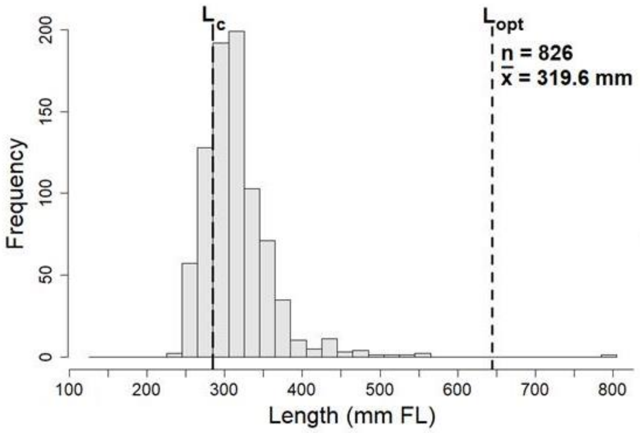


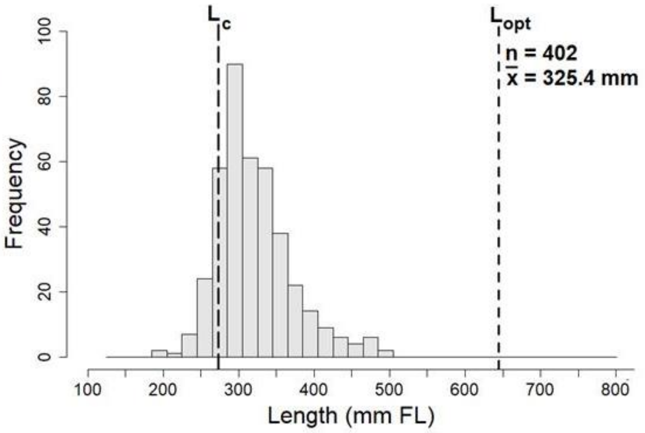


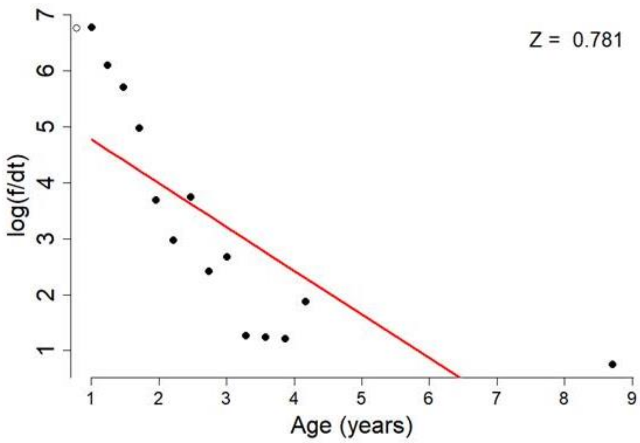
Pomatomus saltatrix
Elf

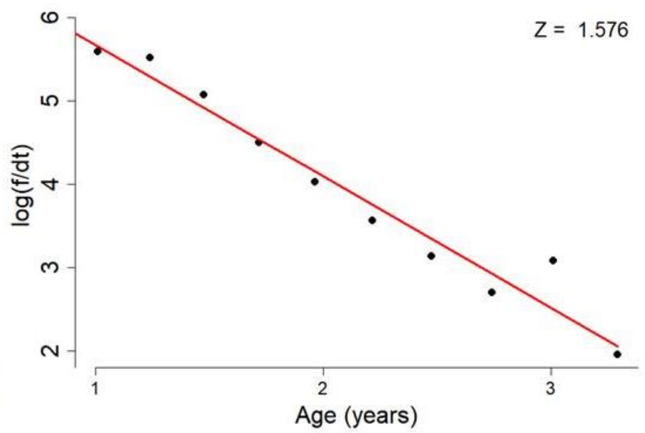


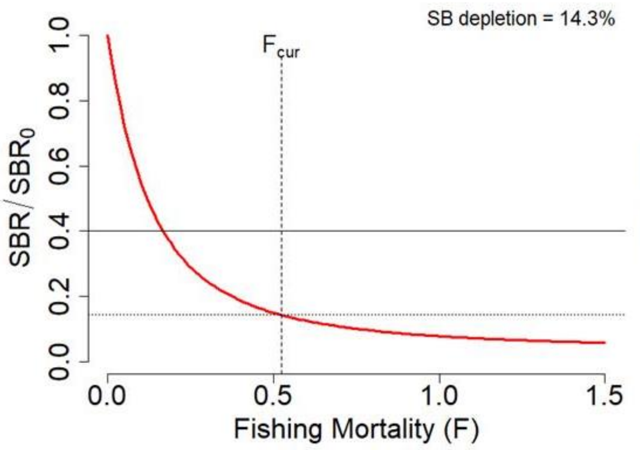
Parameters	Value	Unit	Reference
L_∞	1247	mm	Mann 2013
K	0.094	yr^{-1}	Mann 2013
t_0	-2.09	yrs	Mann 2013
a	$1.5x10^{-5}$	g/mm	Mann 2013
b	2.98		Mann 2013
L_m	222.44	mm	Mann 2013
δ	11.12	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	10	yrs	Mann 2013
L_{opt}	644.06	mm	This study

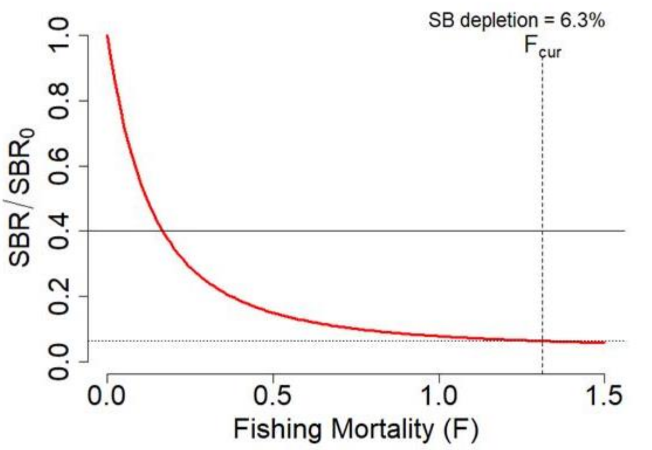




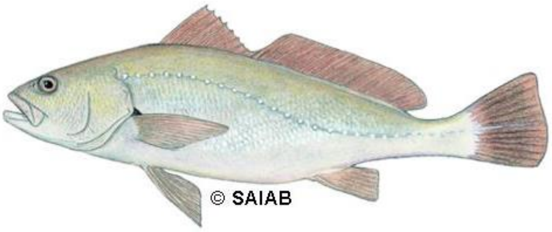




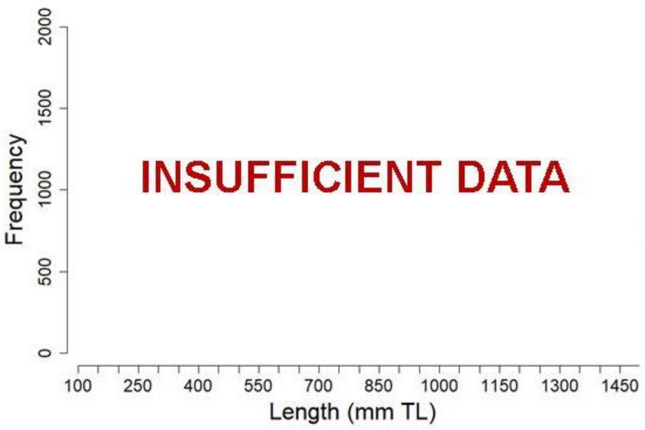


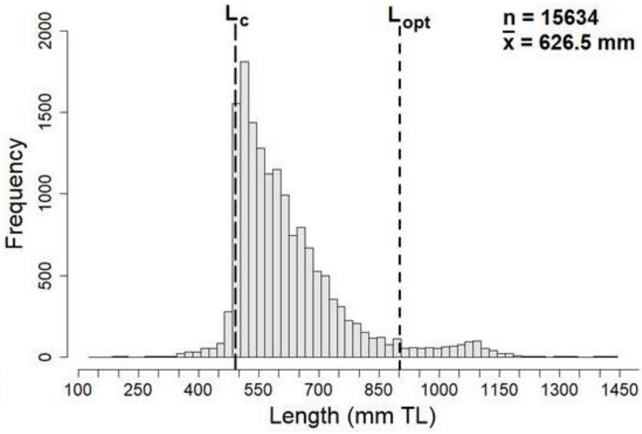


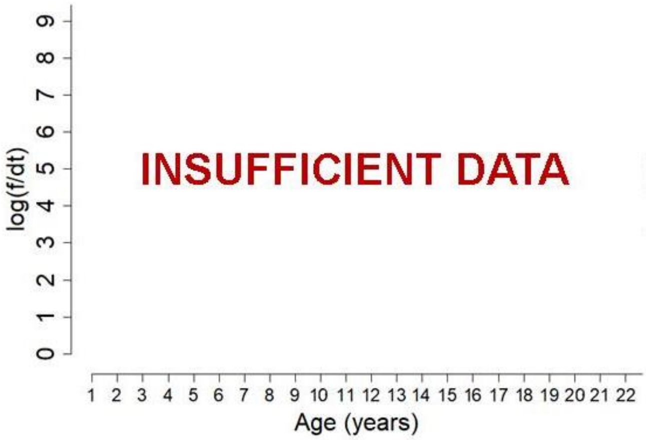
Argyrosomus inodorus
Silver Kob

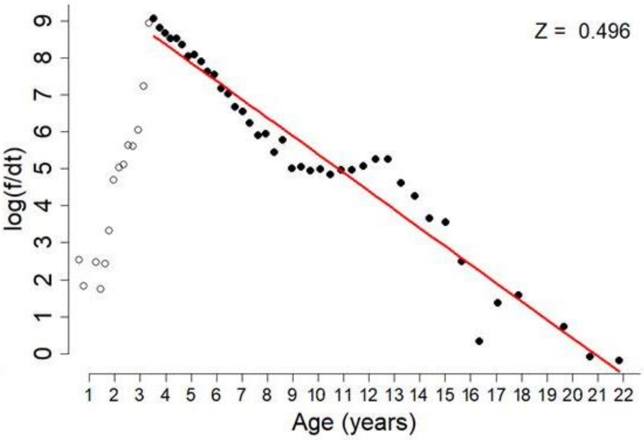


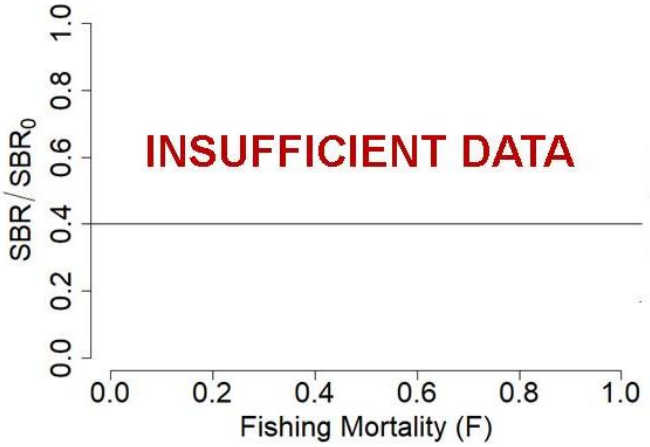
Parameters	Value	Unit	Reference
L_∞	1372	mm	Winker *et al.* 2017
K	0.115	yr^{-1}	Winker *et al.* 2017
t_0	-0.85	yrs	Winker *et al.* 2017
a	$6x10^{-6}$	g/mm	Mann 2013
b	3.07		Mann 2013
L_m	375	mm	Winker *et al.* 2017
δ	18.75	mm^{-1}	Assumed: 0.05*L_m
t_{max}	25	yrs	Mann 2013
L_{opt}	901.60	mm	This study

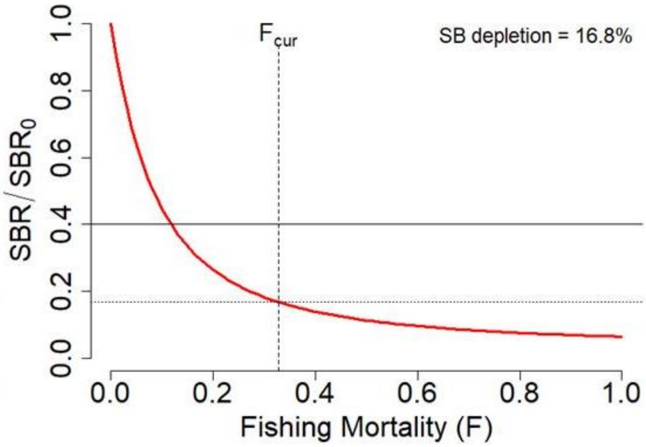




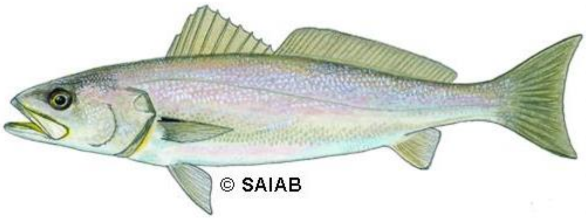




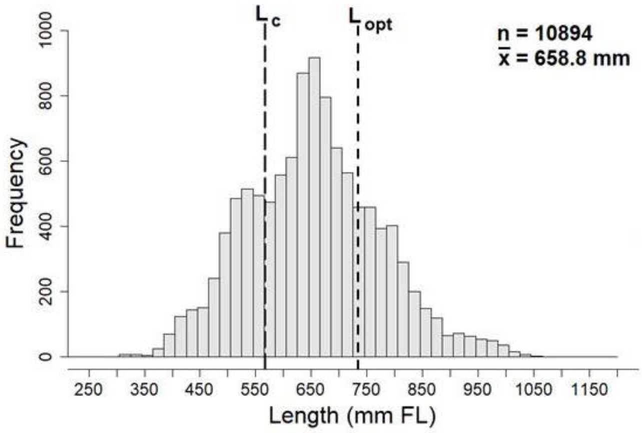


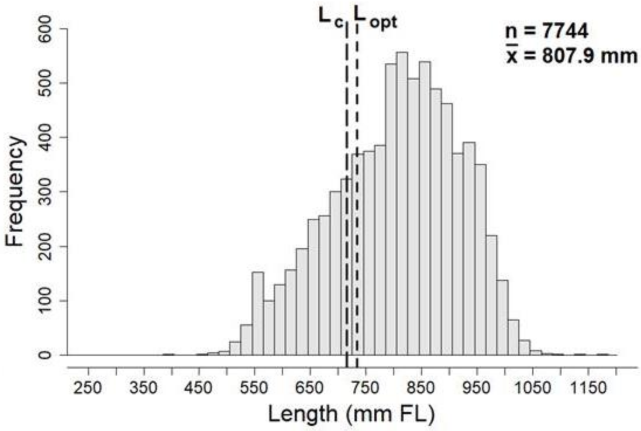


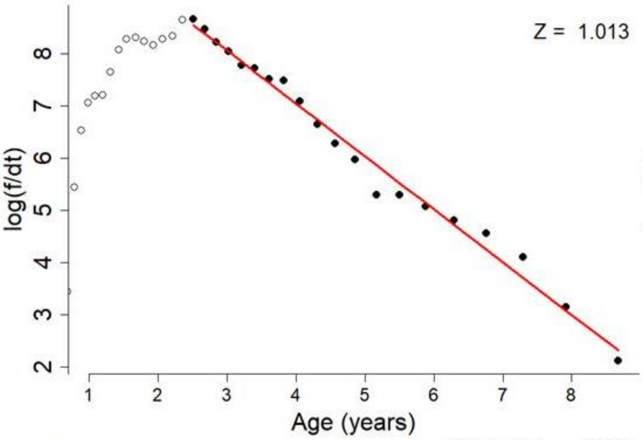
Atractoscion aequidens
Geelbek

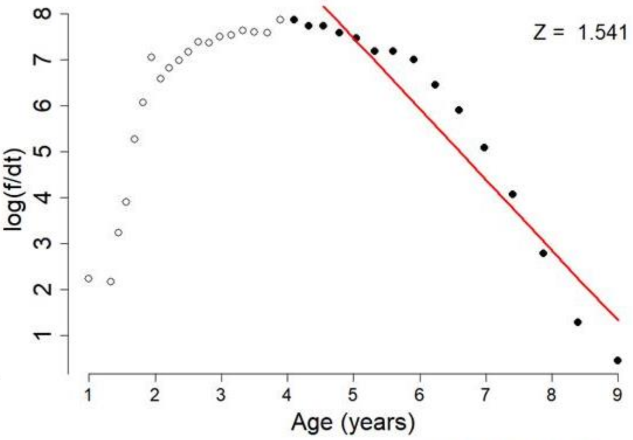


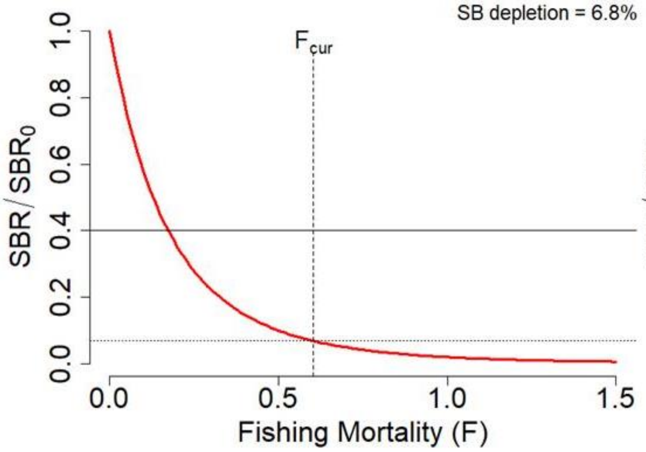
Parameters	Value	Unit	Reference
L_∞	1124.01	mm	Boyd 2017
K	0.27	yr^{-1}	Boyd 2017
t_0	-0.723	yrs	Boyd 2017
a	8.42×10^{-6}	g/mm	Mann 2013
b	3.01		Mann 2013
L_m	900	mm	Mann 2013
δ	45.00	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	9	yrs	Mann 2013
L_{opt}	733.05	mm	This study

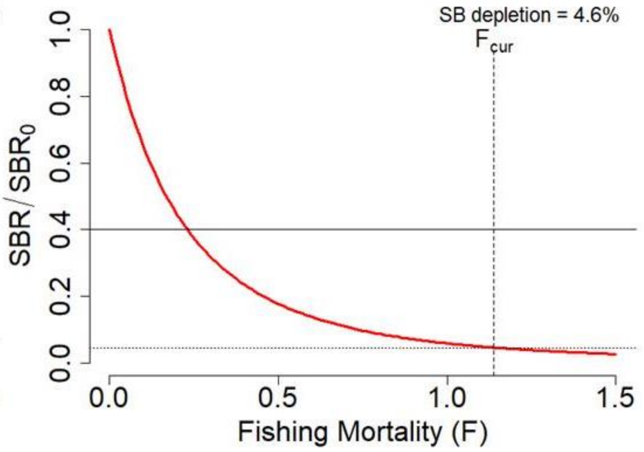




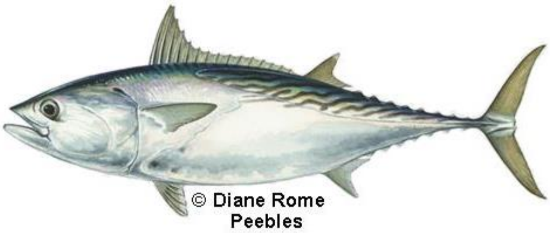






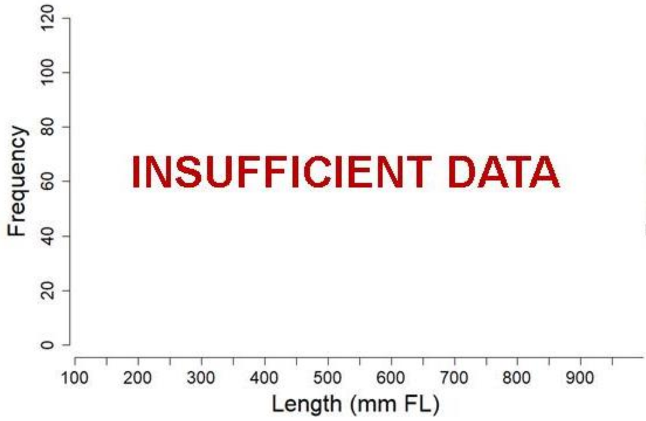


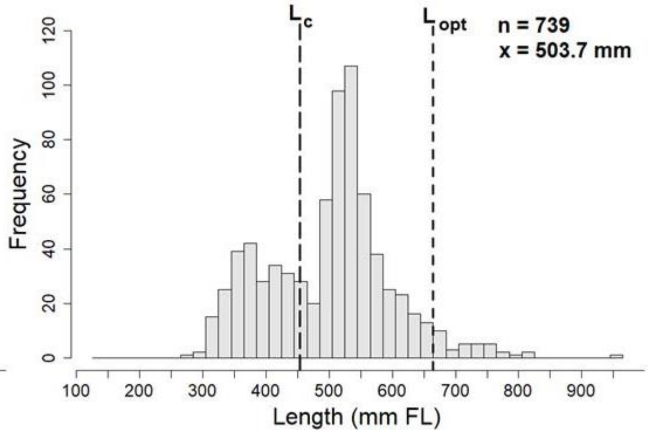
Euthynnus affinis
Eastern Little Tuna

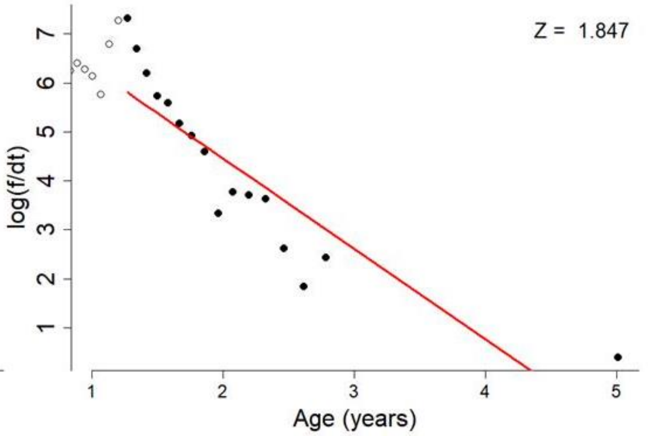


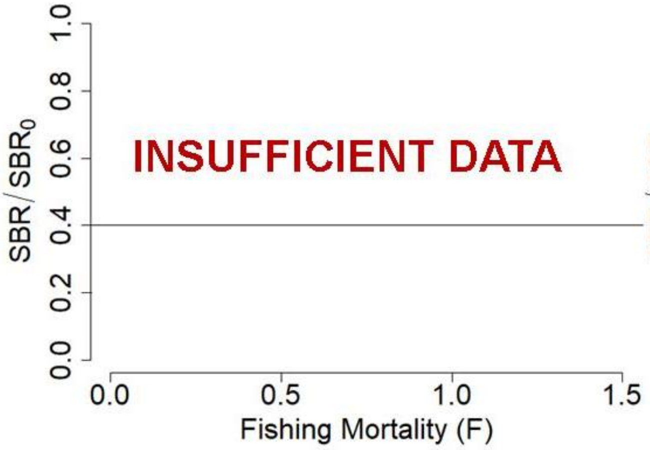
© Diane Rome Peebles

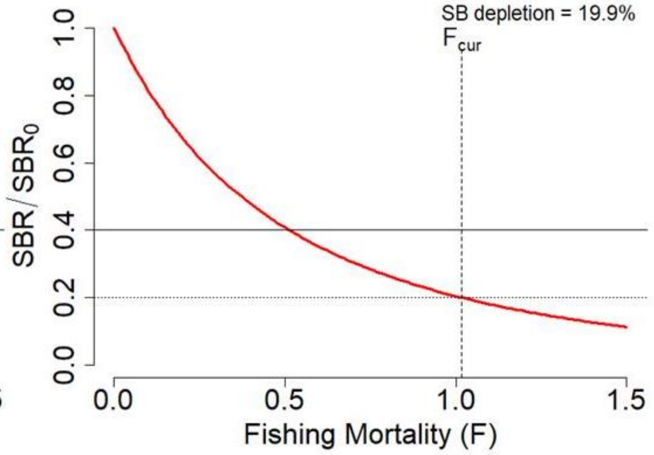
Parameters	Value	Unit	Reference
L_∞	950	mm	Mann 2013
K	0.67	yr^{-1}	Mann 2013
t_0	0	yrs	Mann 2013
a	$3x10^{-5}$	g/mm	Mann 2013
b	2.908		Mann 2013
L_m	650	mm	Mann 2013
δ	32.5	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	6	yrs	Mann 2013
L_{opt}	664.63	mm	This study





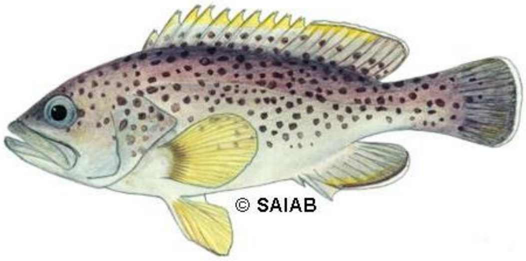


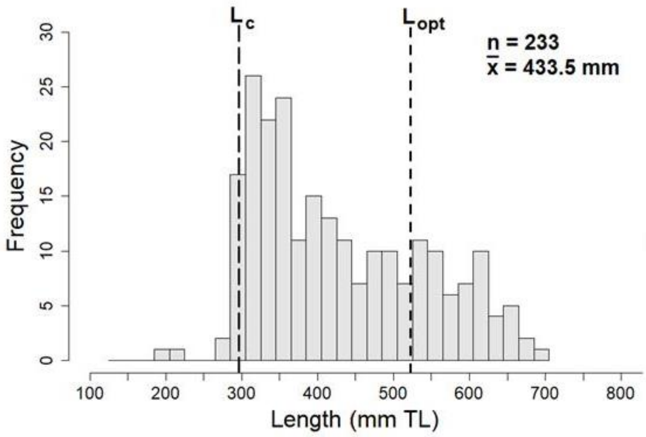


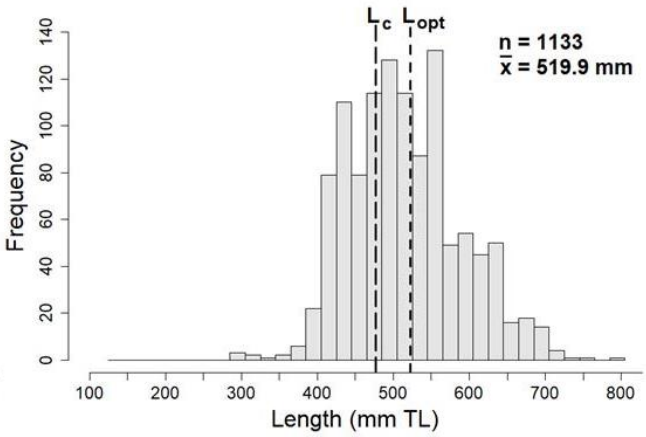


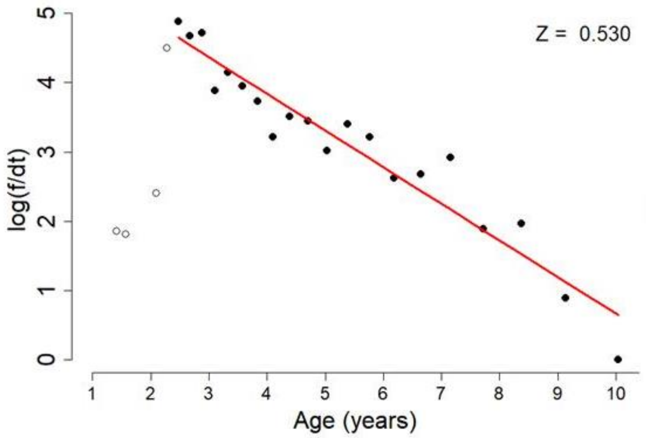
Epinephelus albomarginatus
White-edged Rockcod

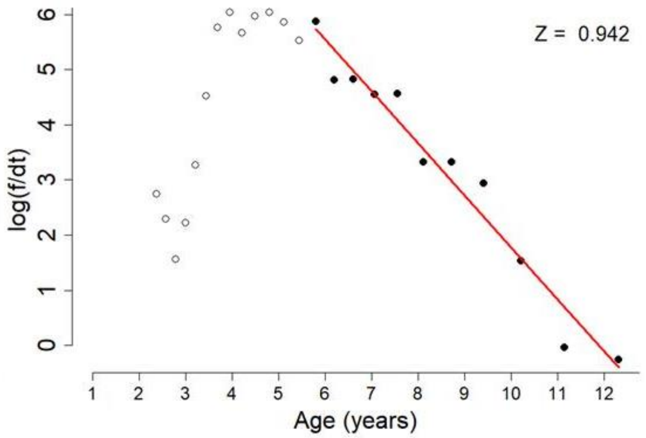
Parameters	Value	Unit	Reference
L_∞	789	mm	Mann 2013
K	0.214	yr^{-1}	Mann 2013
t_0	0.09	yrs	Mann 2013
a	8.76×10^{-6}	g/mm	Mann 2013
b	3.085		Mann 2013
L_m	341	mm	Mann 2013
δ	17.05	mm^{-1}	Assumed: $0.05 * L_m$
t_{max}	15	yrs	Mann 2013
L_{opt}	522.20	mm	This study

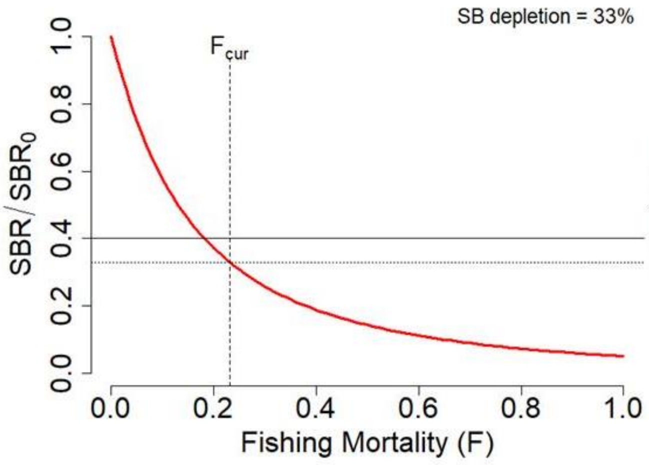


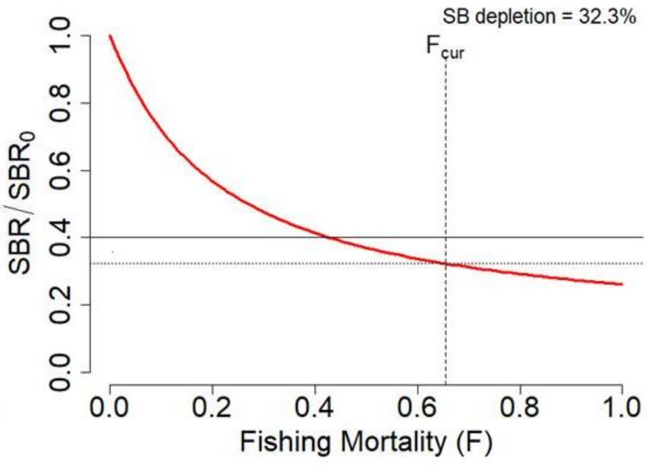






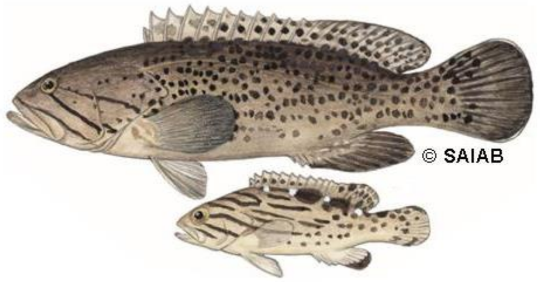




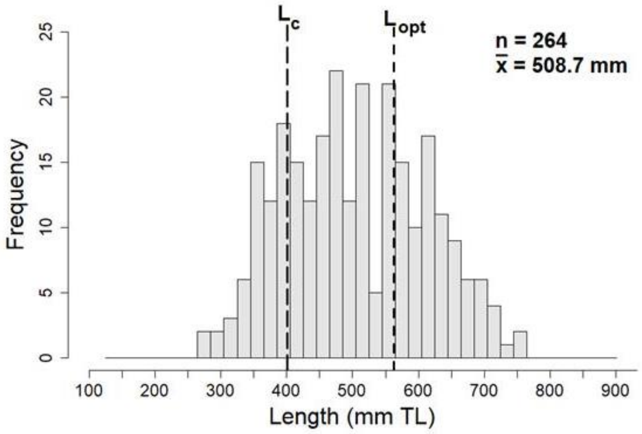


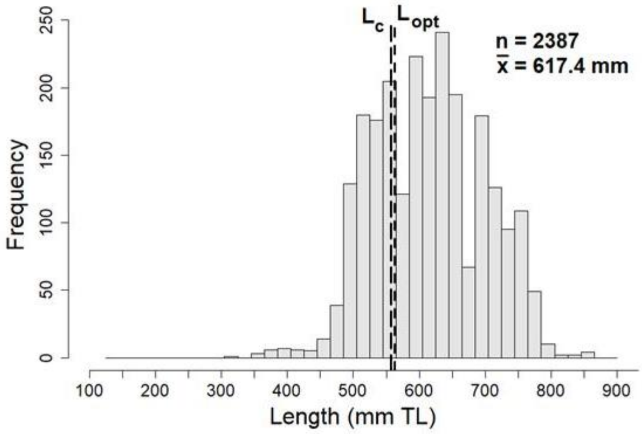
Epinephelus andersoni

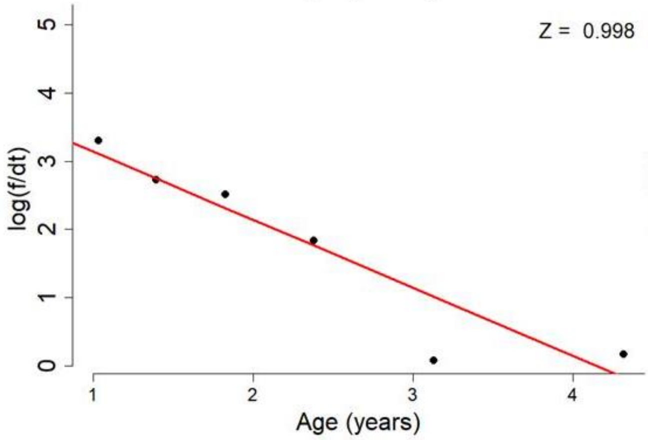
Catface Rockcod

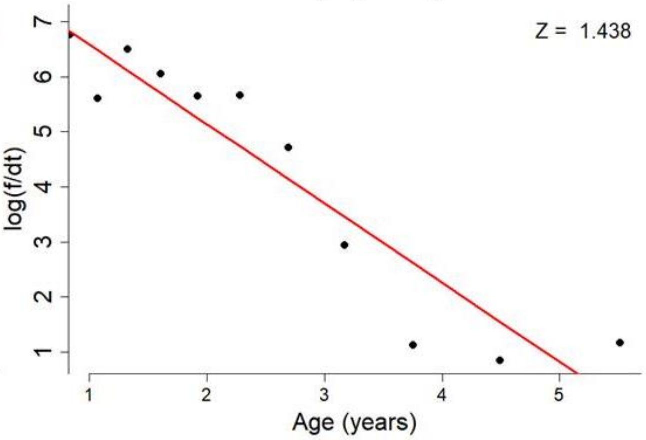


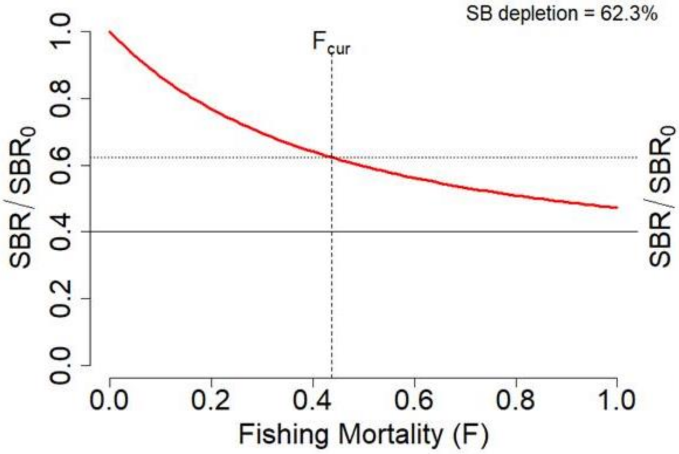
Parameters	Value	Unit	Reference
L_∞	781	mm	Mann 2013
K	0.481	yr^{-1}	Mann 2013
t_0	-2.76	yrs	Mann 2013
a	$2.26x10^{-5}$	g/mm	Mann 2013
b	2.905		Mann 2013
L_m	492	mm	Mann 2013
δ	24.6	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	11	yrs	Mann 2013
L_{opt}	562.37	mm	This study

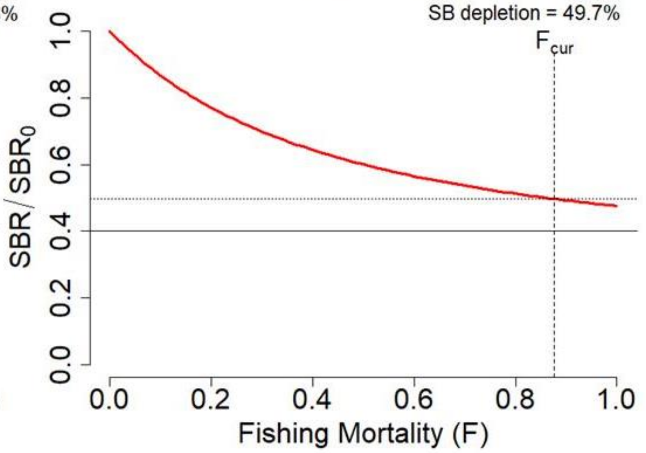




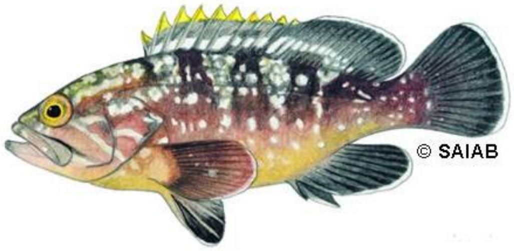




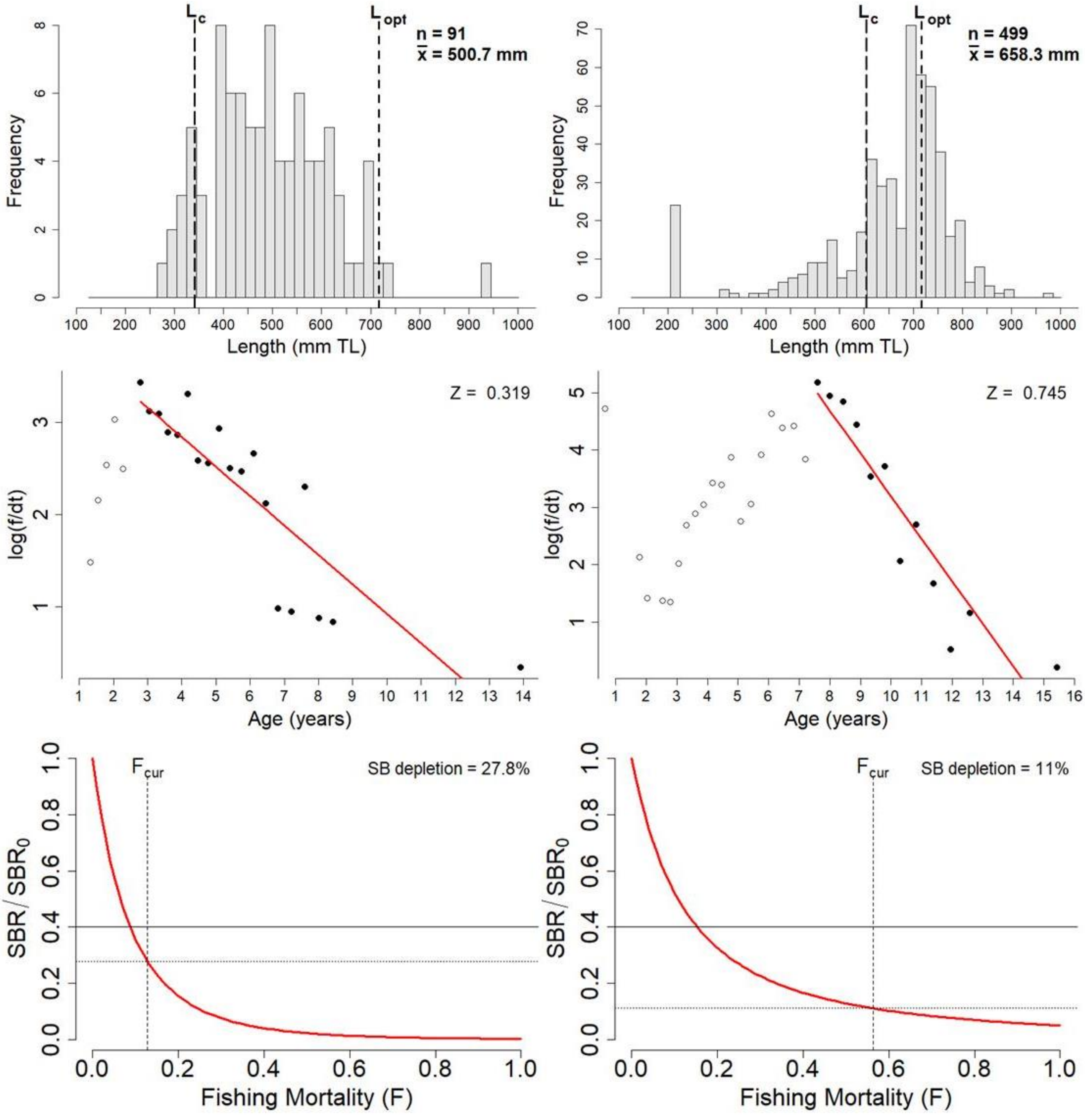




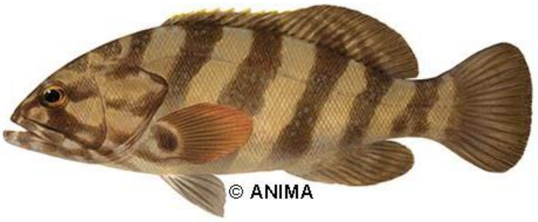
Epinephelus marginatus
Yellowbelly Rockcod



Parameters	Value	Unit	Reference
L_∞	1249	mm	Mann 2013
K	0.09	yr^{-1}	Mann 2013
t_0	-1.43	yrs	Mann 2013
a	$1.25x10^{-5}$	g/mm	Mann 2013
b	3.055		Mann 2013
L_m	622	mm	Mann 2013
δ	31.1	mm^{-1}	Assumed: 0.05*L_m
t_{max}	16	yrs	Mann 2013
L_{opt}	715.99	mm	This study



Epinephelus rivulatus
Halfmoon Rockcod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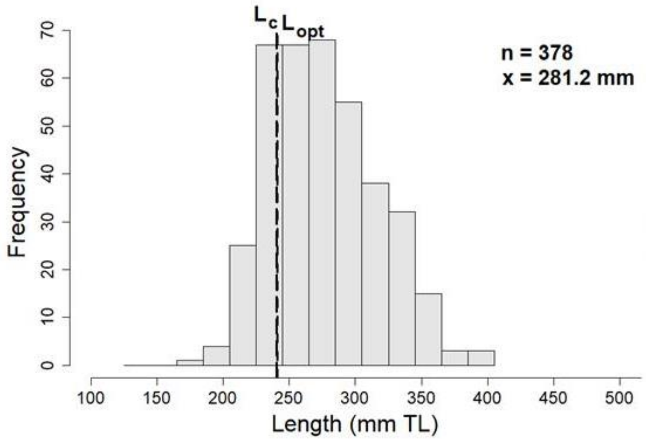
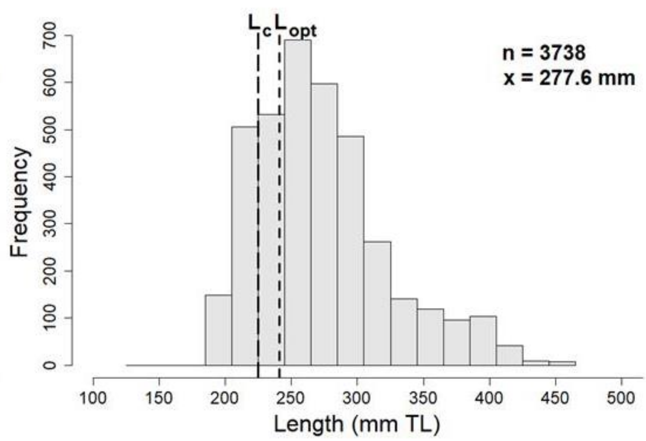
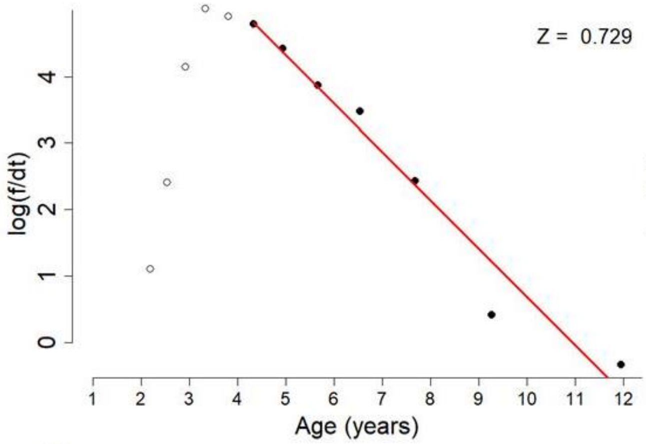
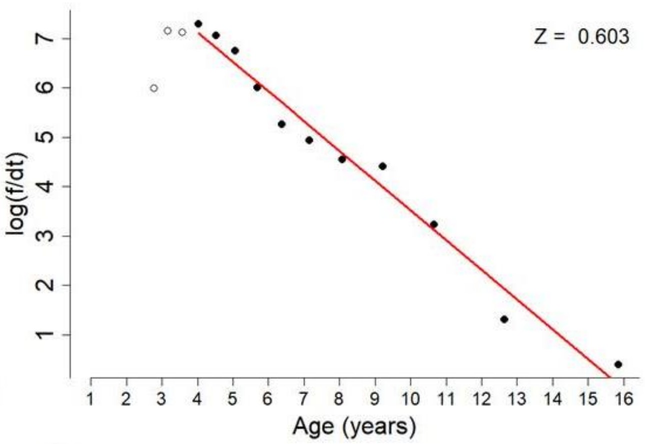
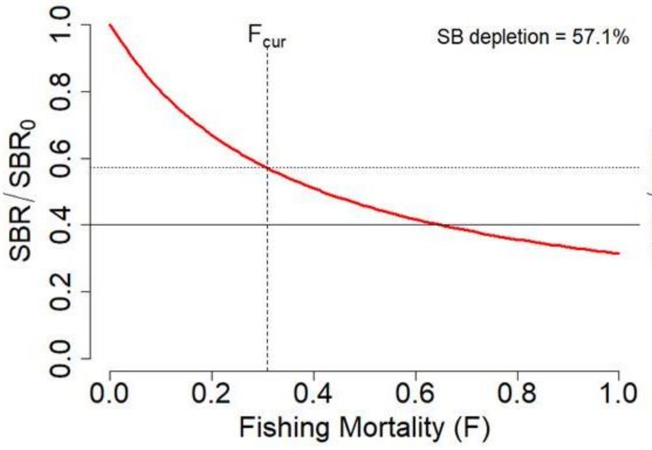
Parameters	Value	Unit	Reference
L_∞	332	mm	Mann 2013
K	0.394	yr^{-1}	Mann 2013
t_0	0.02	yrs	Mann 2013
a	1.96×10^{-5}	g/mm	Mann 2013
b	2.968		Mann 2013
L_m	219	mm	Mann 2013
δ	10.95	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	17	yrs	Mann 2013
L_{opt}	240.75	mm	This study

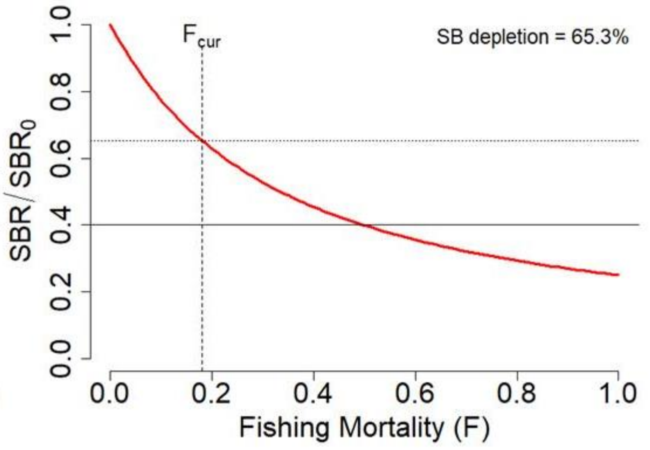




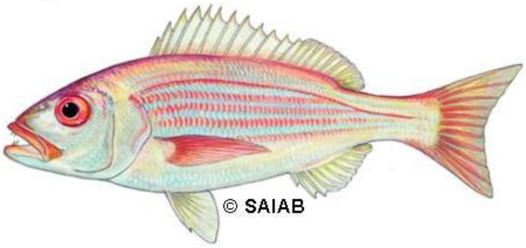




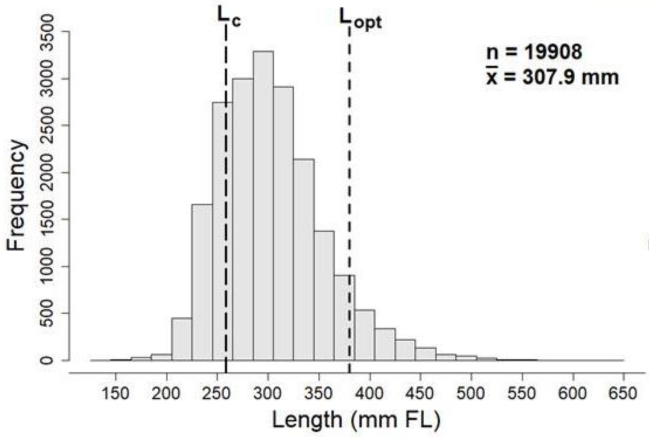


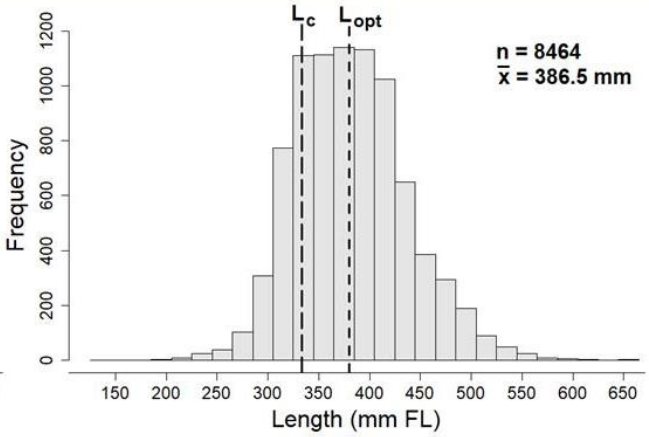


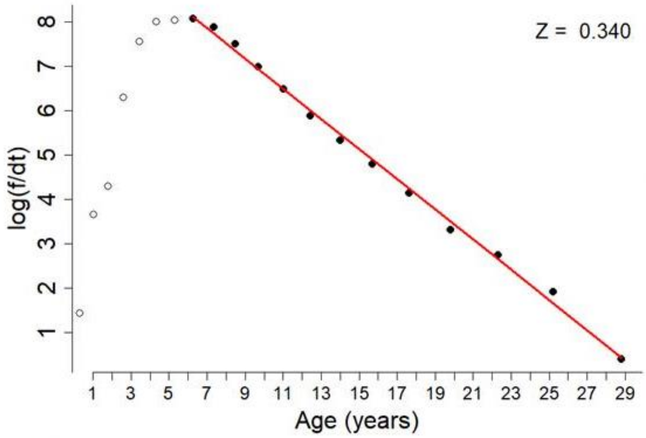
Argyrozona argyrozona
Carpenter

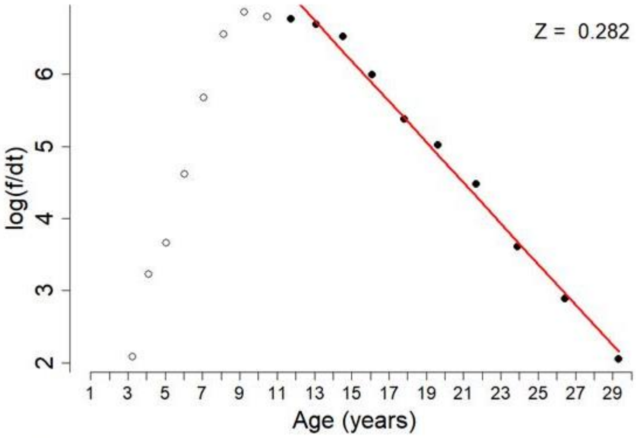


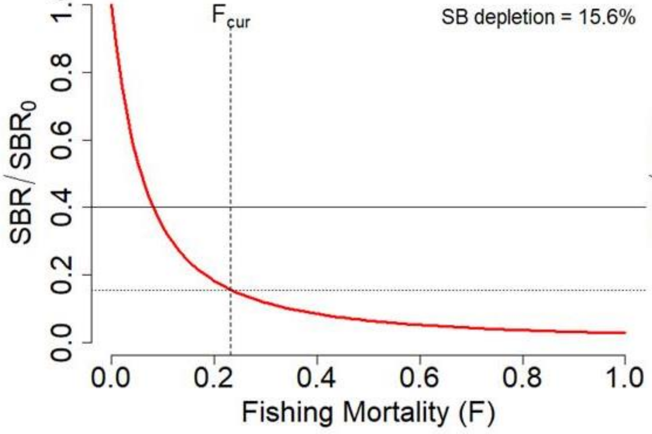
Parameters	Value	Unit	Reference
L_∞	619	mm	Mann 2013
K	0.06	yr^{-1}	Mann 2013
t_0	-4.5	yrs	Mann 2013
a	$4x10^{-5}$	g/mm	Mann 2013
b	2.8553		Mann 2013
L_m	267	mm	Mann 2013
δ	13.35	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	30	yrs	Mann 2013
L_{opt}	380.27	mm	This study

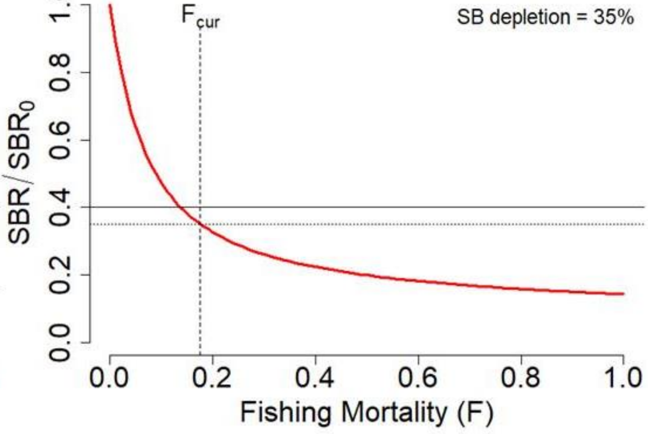




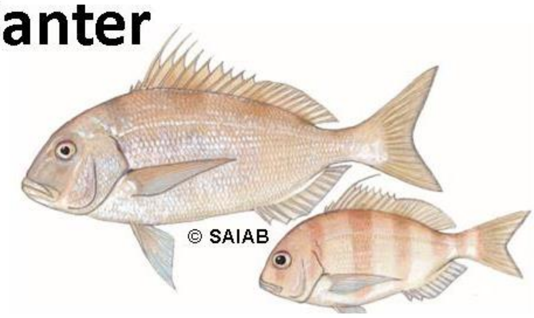




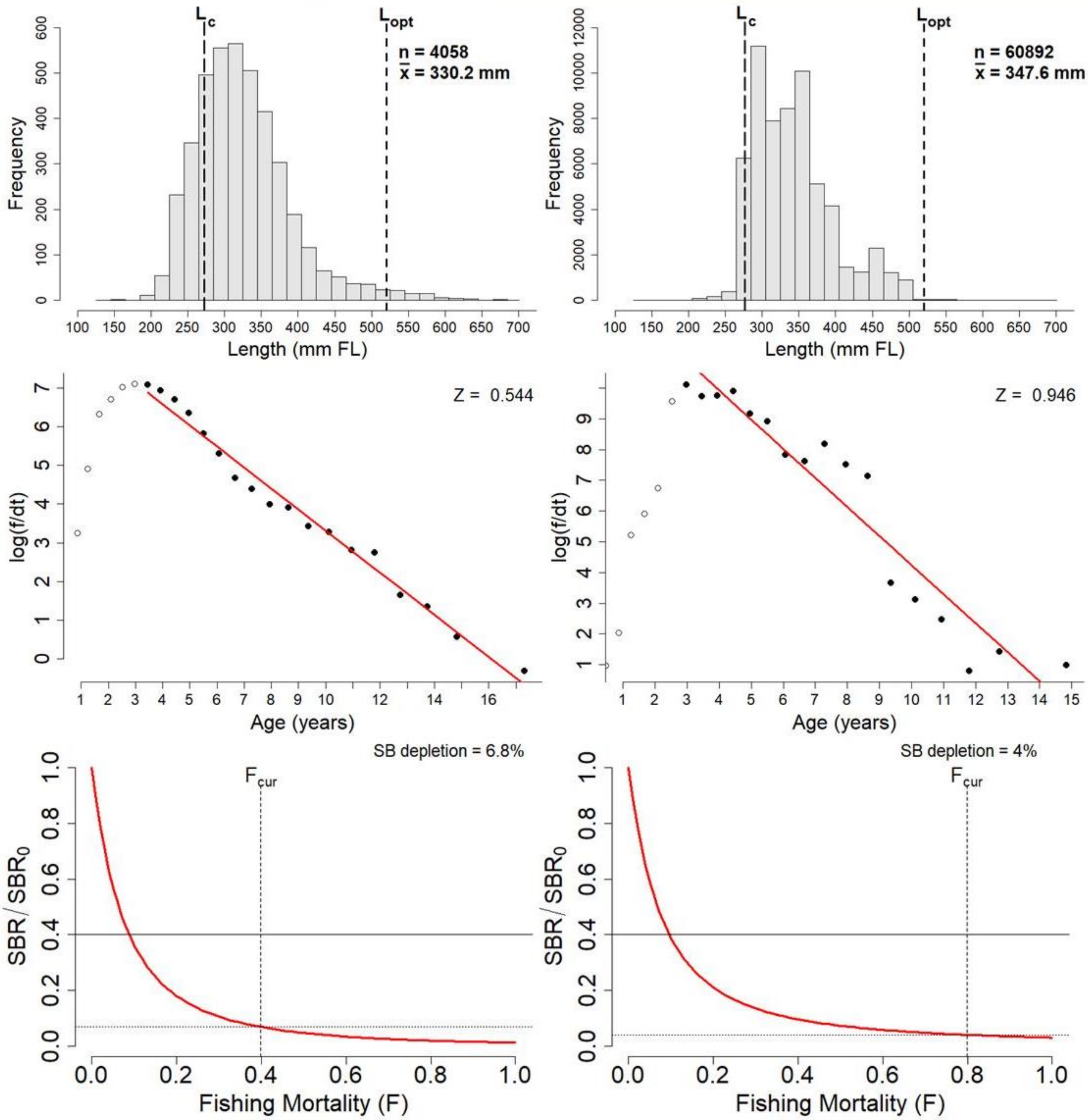




Cheimerius nufar
Santer

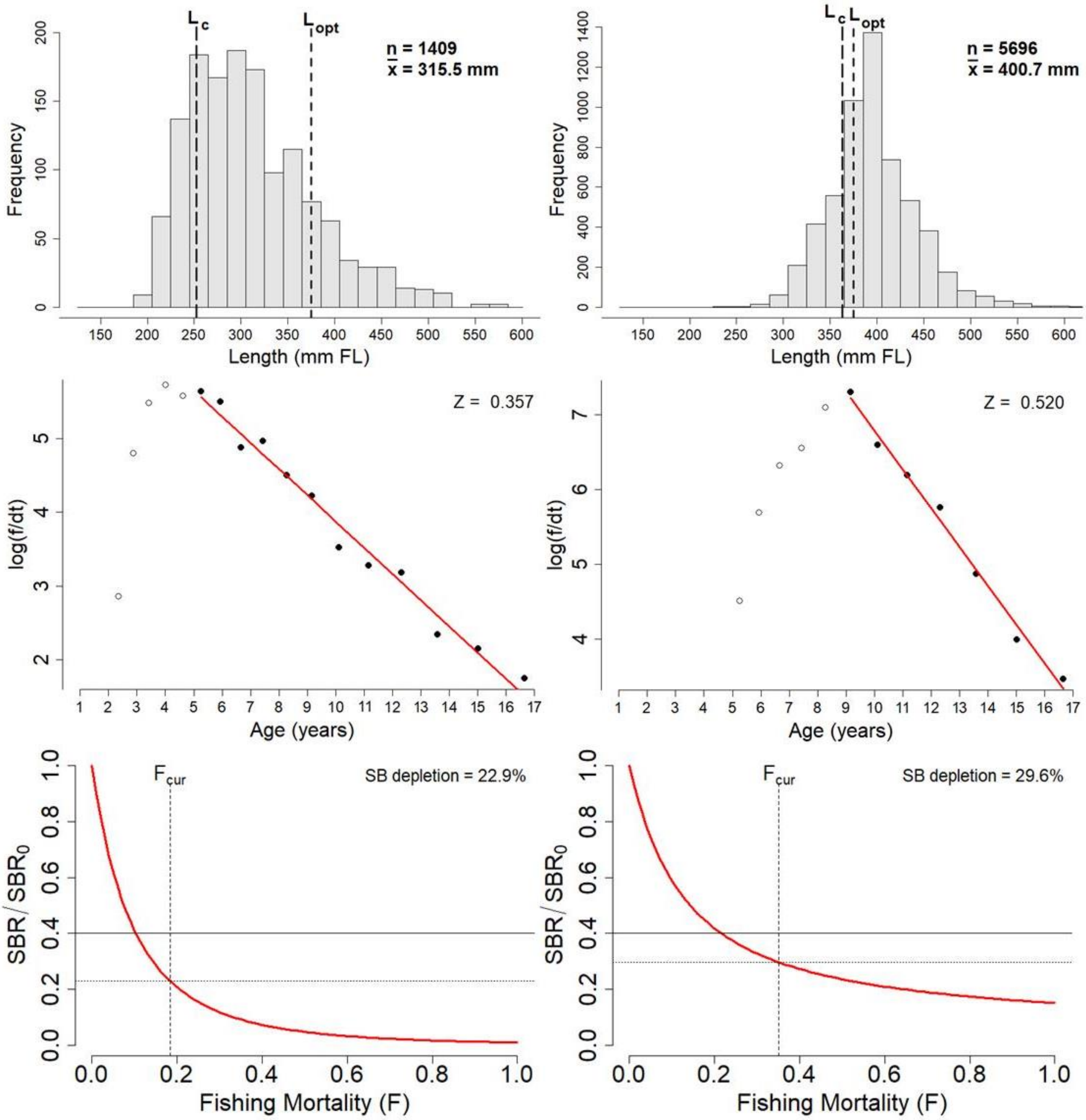


Parameters	Value	Unit	Reference
L_∞	868	mm	Maggs *et al*.2017
K	0.076	yr^{-1}	Maggs *et al*.2017
t_0	-2.48	yrs	Maggs *et al*.2017
a	$2.4x10^{-4}$	g/mm	Mann 2013
b	2.571		Mann 2013
L_m	298.2	mm	Mann 2013
δ	14.9	mm^{-1}	Assumed: 0.05*L_m
t_{max}	22	yrs	Mann 2013
L_{opt}	519.43	mm	This study

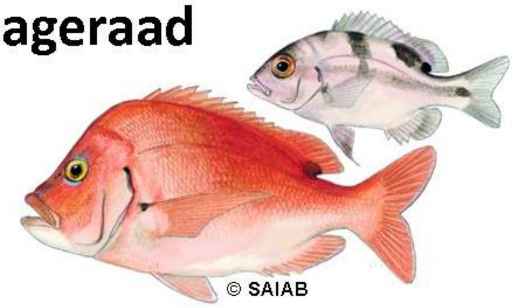


Chrysoblephus anglicus
Englishman

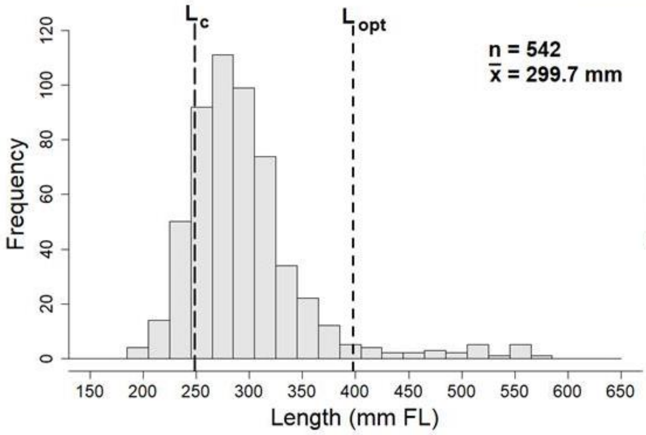
Parameters	Value	Unit	Reference
L_∞	650	mm	Mann 2013
K	0.085	yr^{-1}	Mann 2013
t_0	-1.85	yrs	Mann 2013
a	$1.27x10^{-4}$	g/mm	Mann 2013
b	2.74		Mann 2013
L_m	335.20	mm	Mann 2013
δ	16.76	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	17	yrs	Mann 2013
L_{opt}	375	mm	This study

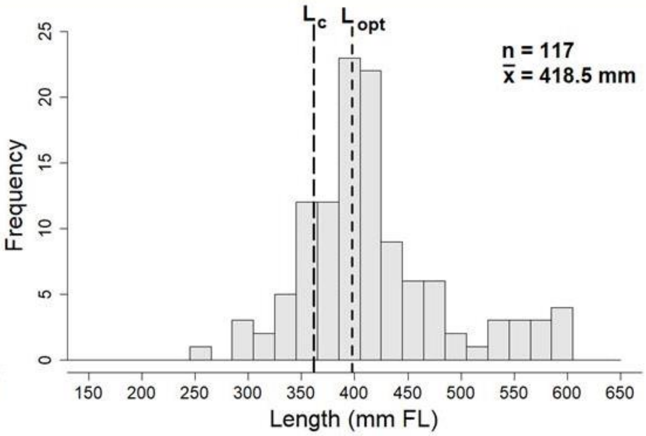


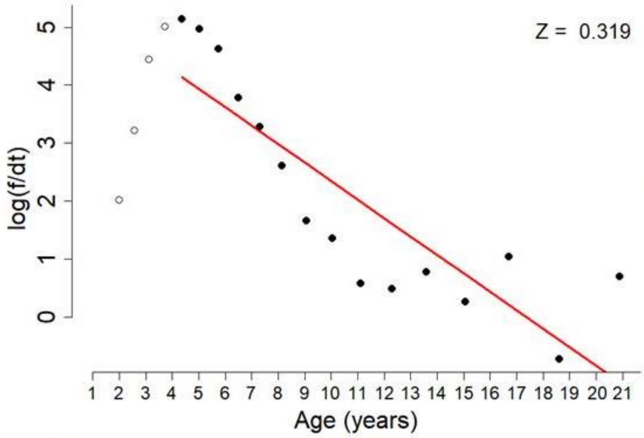
Chrysoblephus cristiceps
Dageraad

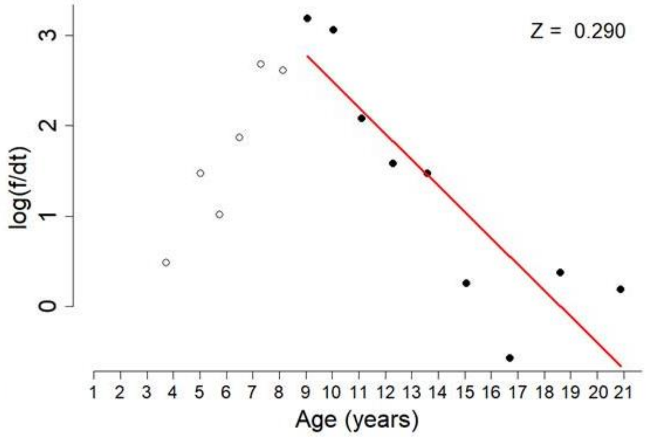


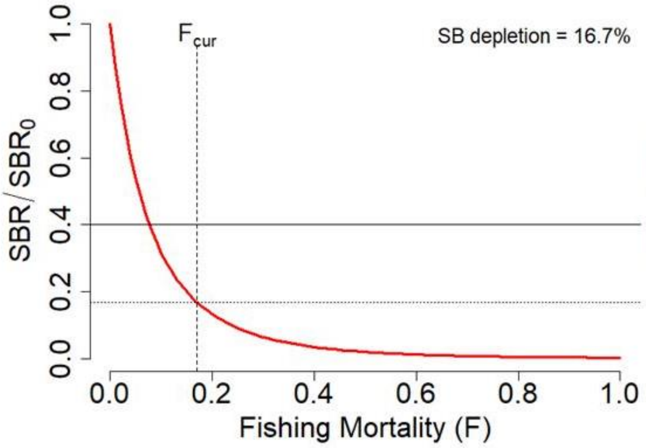
Parameters	Value	Unit	Reference
L_{∞}	654.7	mm	Mann 2013
K	0.081	yr^{-1}	Mann 2013
t_0	-2.35	yrs	Mann 2013
a	$1.3x10^{-4}$	g/mm	Mann 2013
b	3.151		Mann 2013
L_m	365	mm	Mann 2013
δ	18.25	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	22	yrs	Mann 2013
L_{opt}	397.73	mm	This study

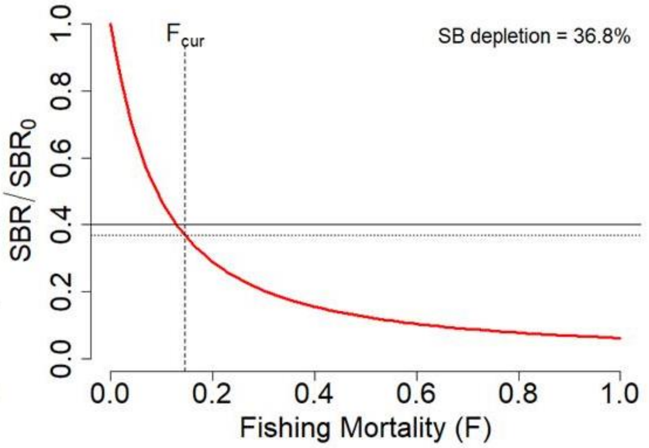






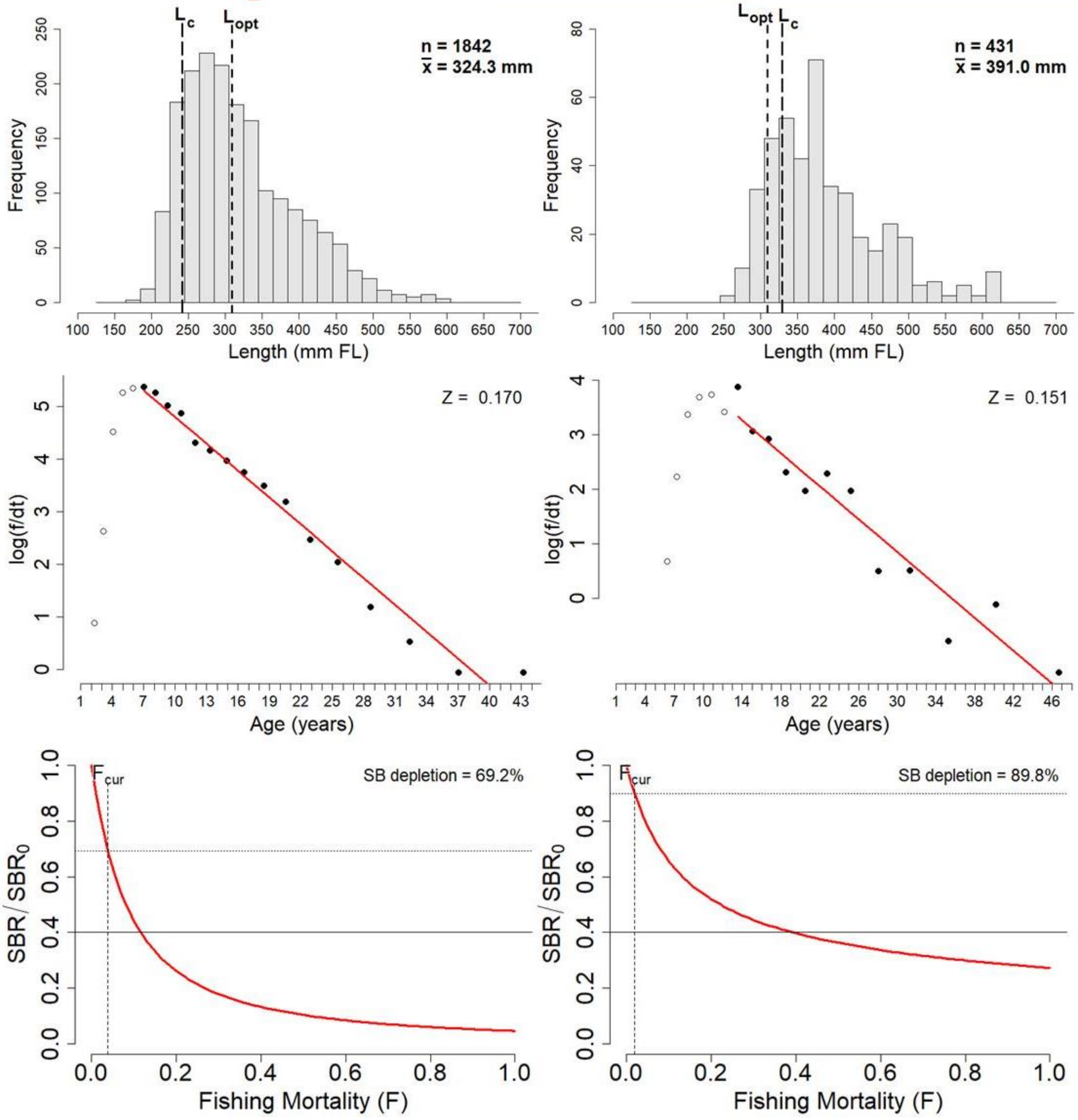




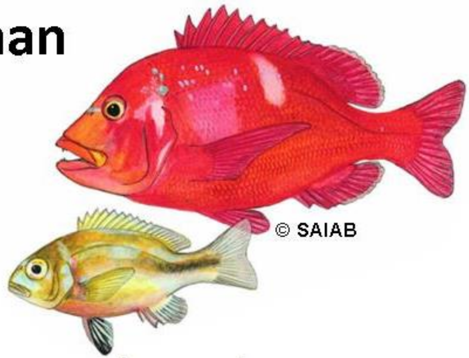


Chrysoblephus gibbiceps
Red Stumpnose

Parameters	Value	Unit	Reference
L_∞	429.85	mm	Mann 2013
K	0.113	yr^{-1}	Mann 2013
t_0	-3.799	yrs	Mann 2013
a	9.49×10^{-5}	g/mm	Mann 2013
b	2.802		Mann 2013
L_m	249	mm	Mann 2013
δ	12.45	mm^{-1}	Assumed: $0.05 \cdot L_m$
t_{max}	48	yrs	Mann 2013
L_{opt}	309.38	mm	This study



Chrysoblephus laticeps
Roman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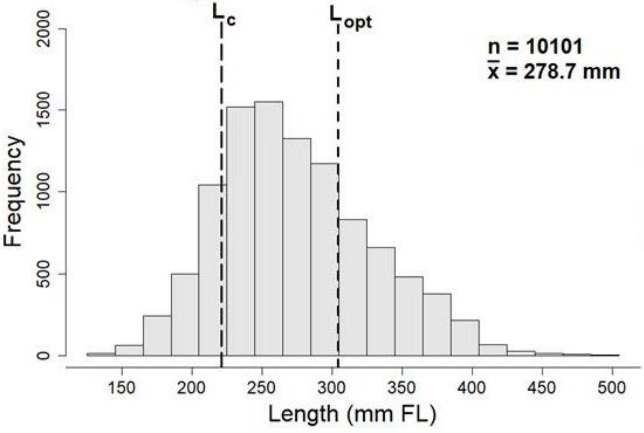
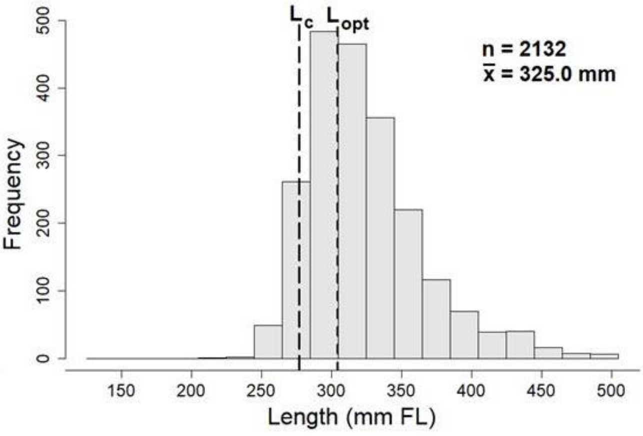
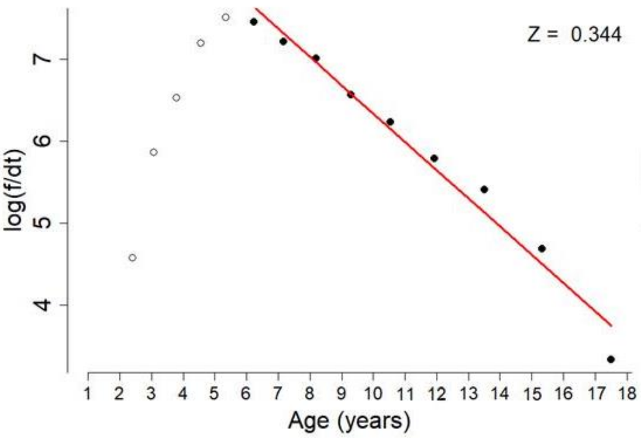
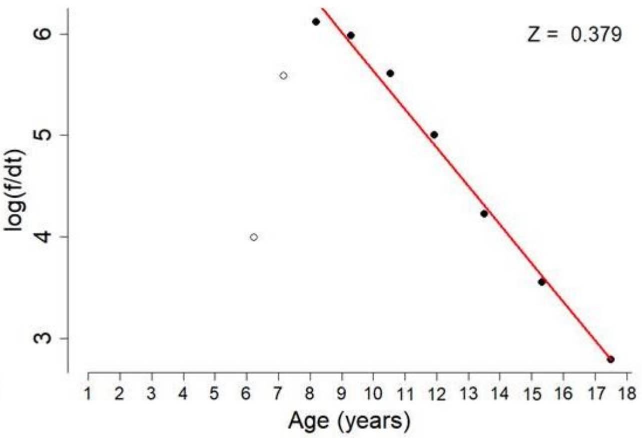
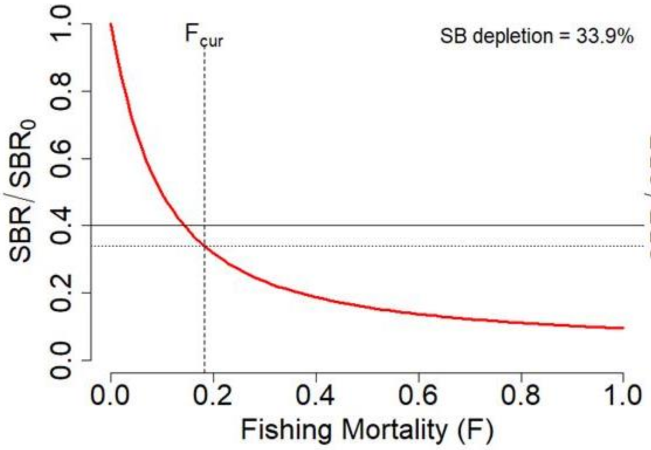
Parameters	Value	Unit	Reference
L_∞	512.8	mm	Mann 2013
K	0.086	yr^{-1}	Mann 2013
t_0	-1.77	yrs	Mann 2013
a	$1.2x10^{-3}$	g/mm	Mann 2013
b	3.0743		Mann 2013
L_m	184	mm	Mann 2013
δ	9.2	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	19	yrs	Mann 2013
L_{opt}	304.14	mm	This study

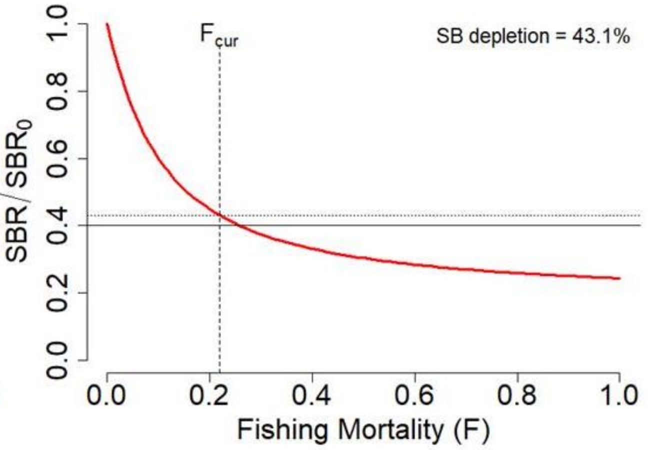






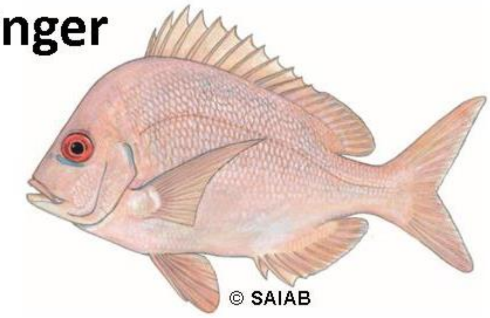




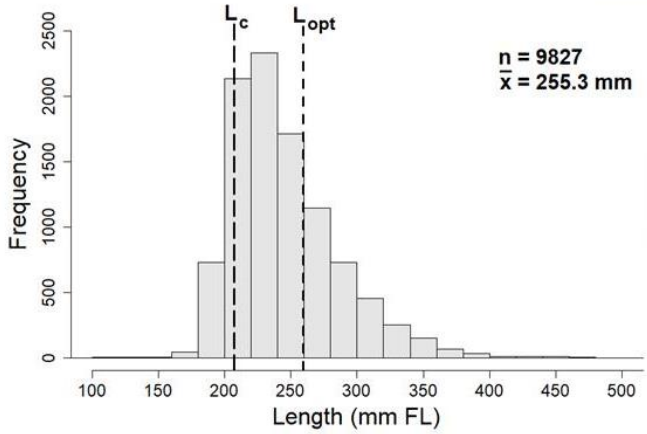


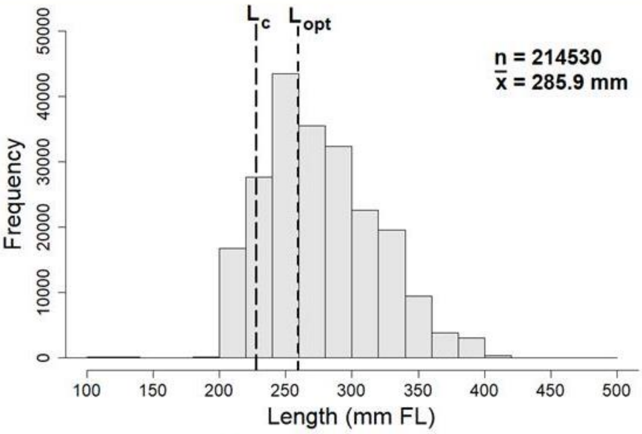
Chrysoblephus puniceus

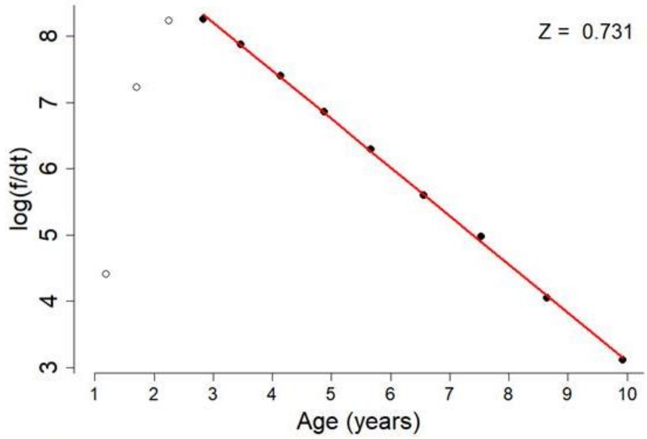
Slinger

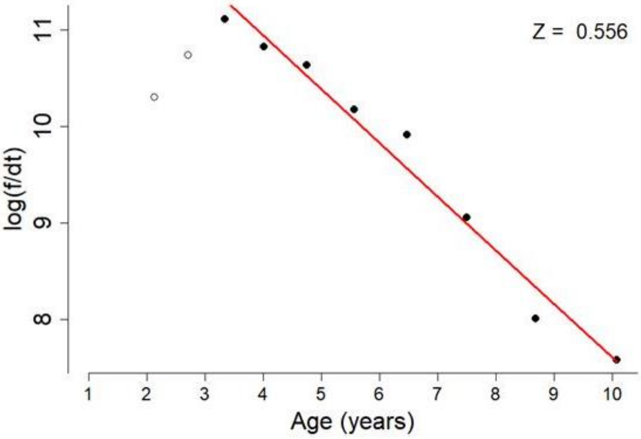


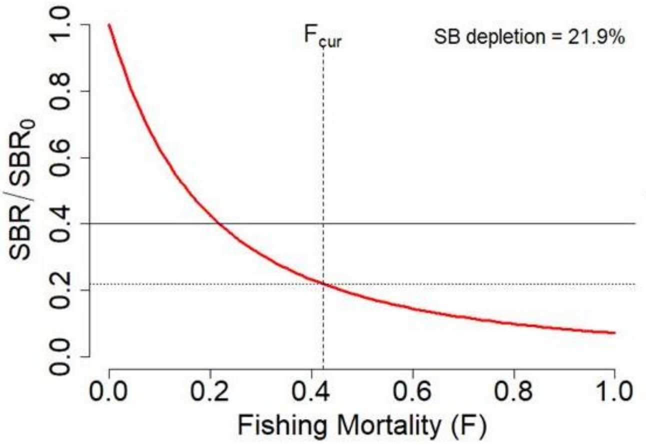
Parameters	Value	Unit	Reference
L_∞	406.1	mm	Mann 2013
K	0.187	yr^{-1}	Mann 2013
t_0	-2.253	yrs	Mann 2013
a	$7.2x10^{-5}$	g/mm	Mann 2013
b	2.82		Mann 2013
L_m	240	mm	Mann 2013
δ	12	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	11	yrs	Mann 2013
L_{opt}	259.48	mm	This study

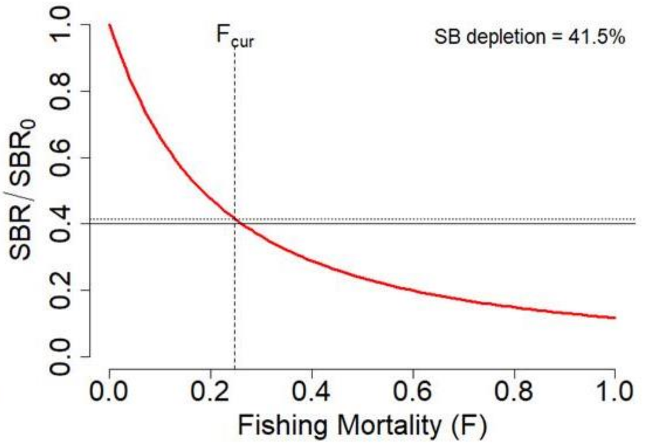




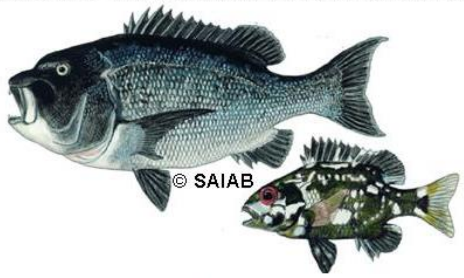




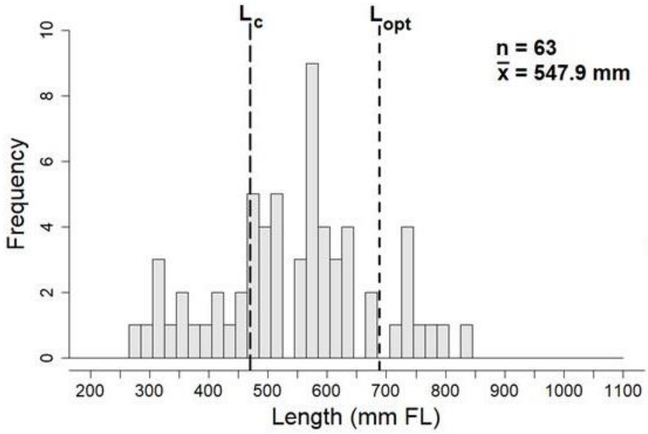


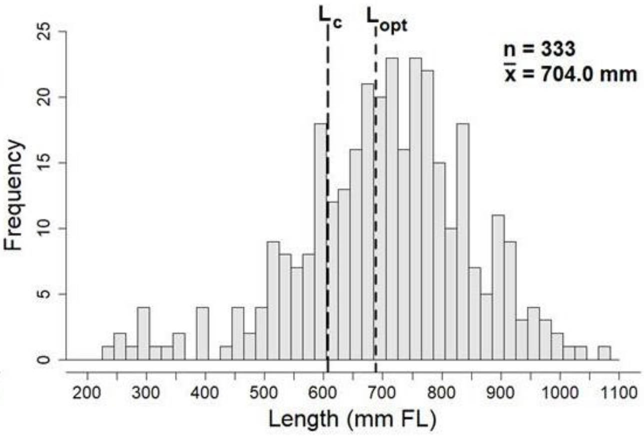


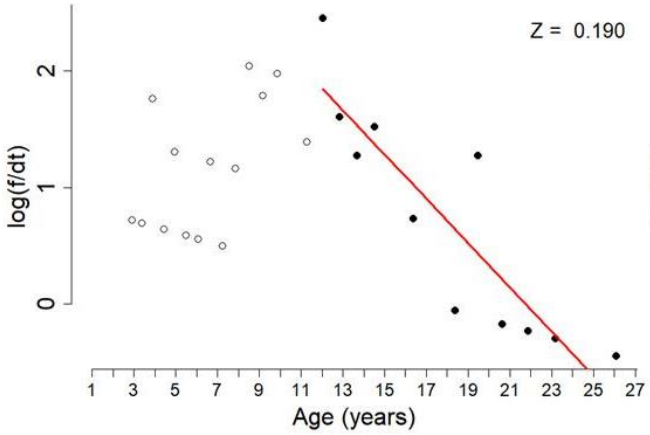
Cymatoceps nasutus
Black Musselcracker

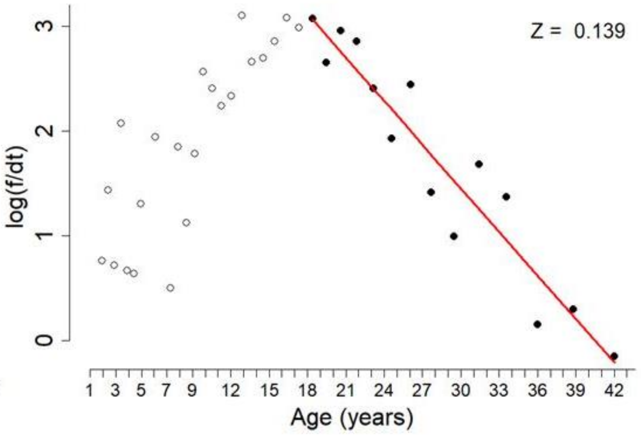


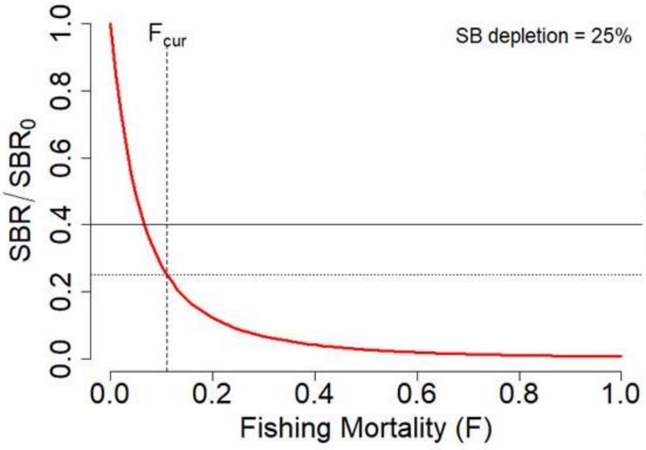
Parameters	Value	Unit	Reference
L_{∞}	1089.5	mm	Mann 2013
K	0.0502	yr^{-1}	Mann 2013
t_0	-2.885	yrs	Mann 2013
a	$2.24x10^{-5}$	g/mm	Mann 2013
b	3.0355		Mann 2013
L_m	530	mm	Mann 2013
δ	26.5	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	45.5	yrs	Mann 2013
L_{opt}	687.67	mm	This study

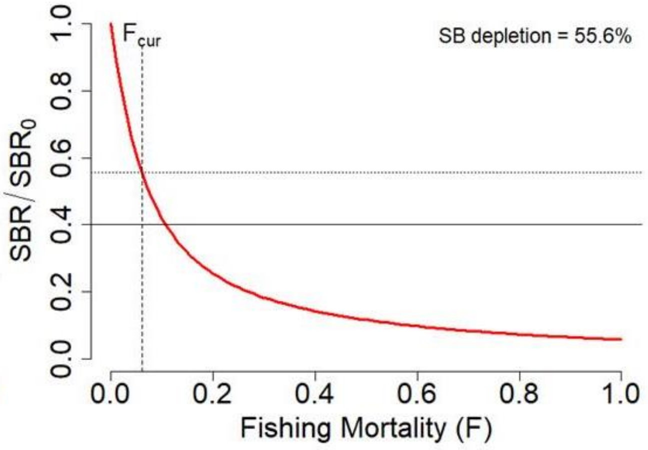




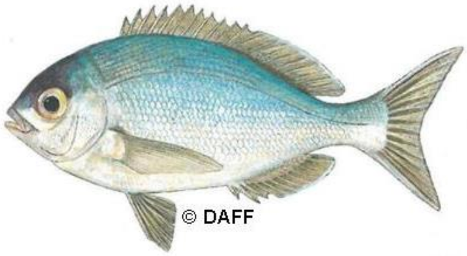




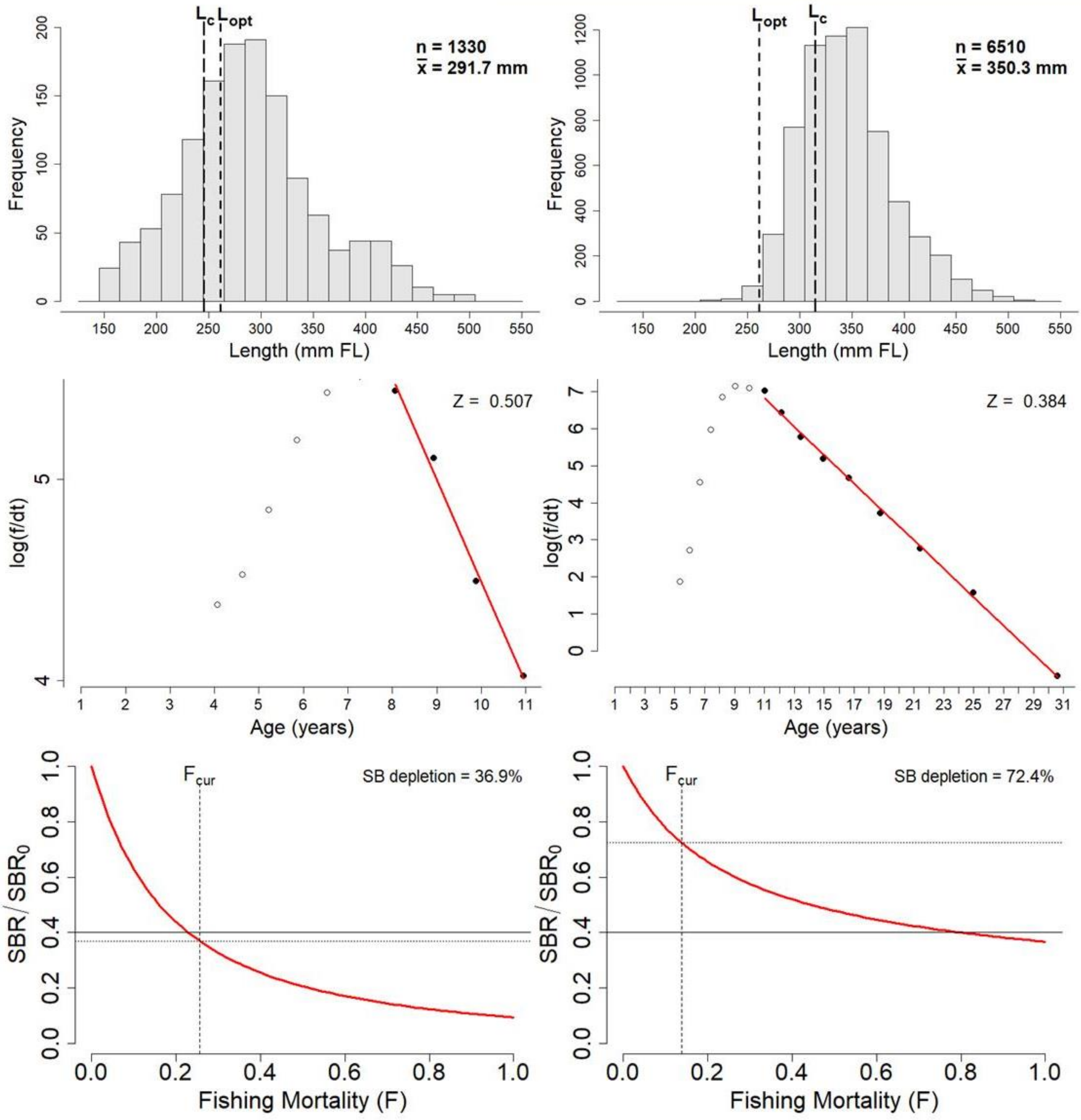




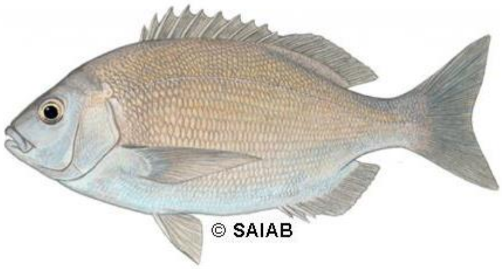
Pachymetopon aeneum
Blue Hottentot



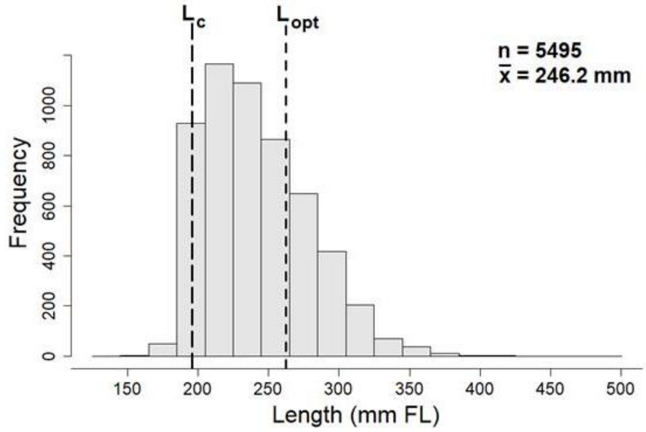
Parameters	Value	Unit	Reference
L_∞	467.1	mm	Mann 2013
K	0.133	yr^{-1}	Mann 2013
t_0	0.247	yrs	Mann 2013
a	$1x10^{-5}$	g/mm	Mann 2013
b	3.149		Mann 2013
L_m	250	mm	Mann 2013
δ	12.5	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	12	yrs	Mann 2013
L_{opt}	261.39	mm	This study

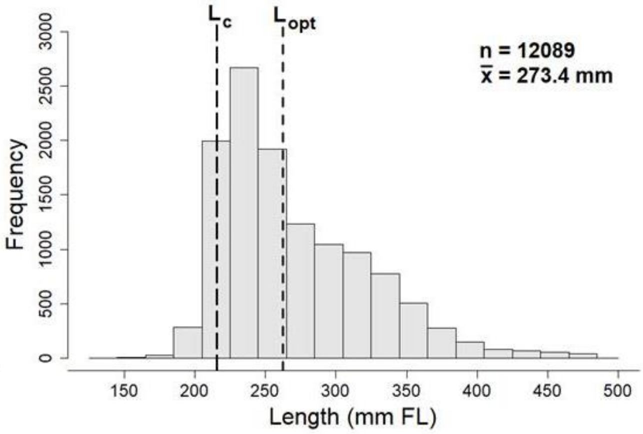


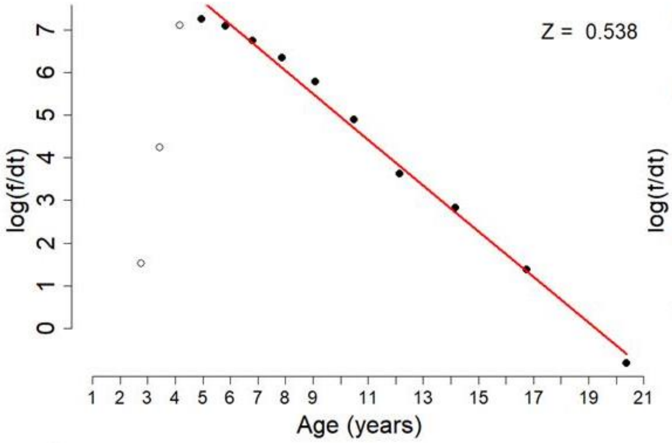
Pachymetopon blochii
Hottentot

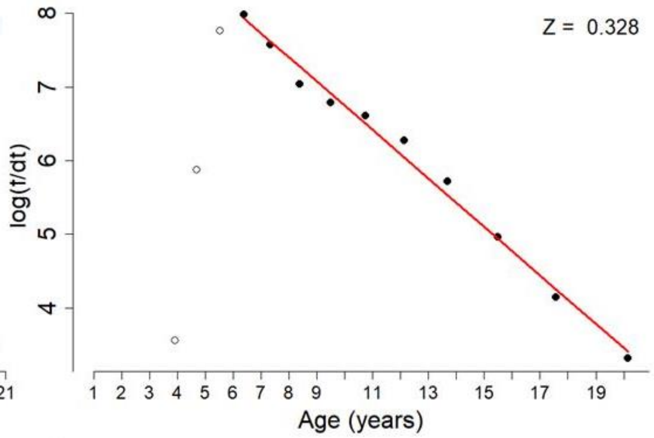


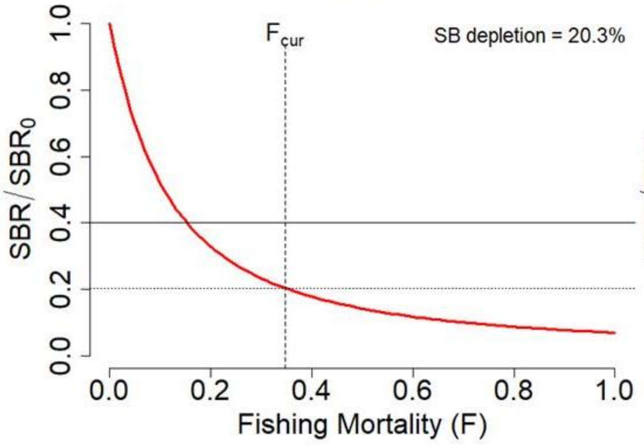
Parameters	Value	Unit	Reference
L_∞	398.77	mm	Mann 2013
K	0.13	yr^{-1}	Mann 2013
t_0	-1.29	yrs	Mann 2013
a	$3.31\text{x}10^{-5}$	g/mm	Mann 2013
b	2.9467		Mann 2013
L_m	202	mm	Mann 2013
δ	10.1	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	21	yrs	Mann 2013
L_{opt}	262.26	mm	This study

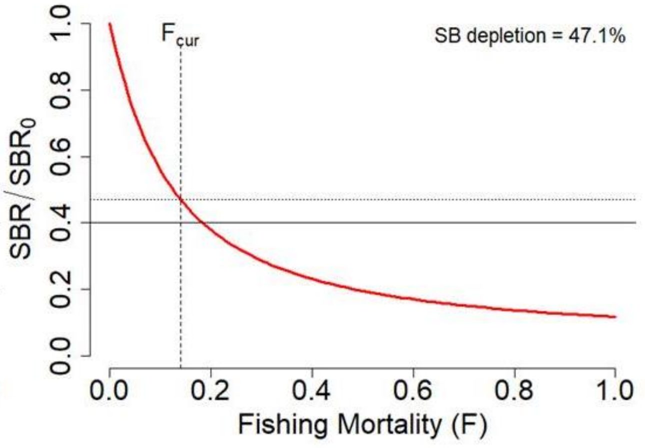




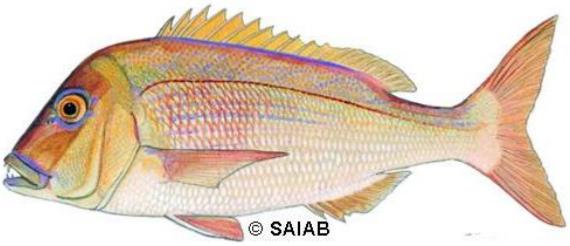




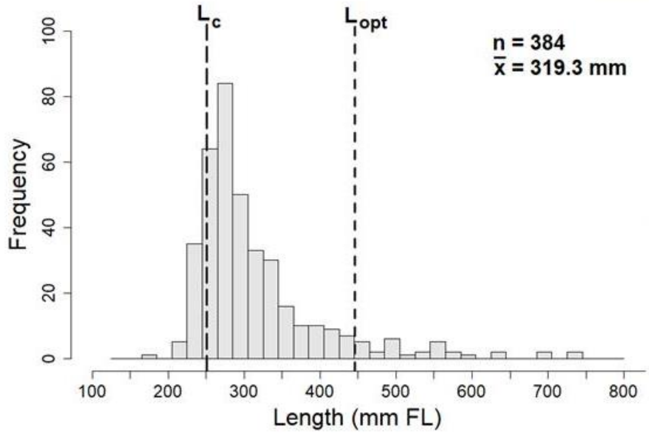


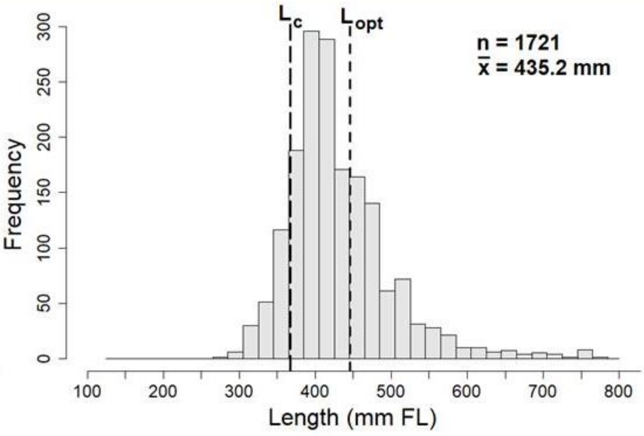


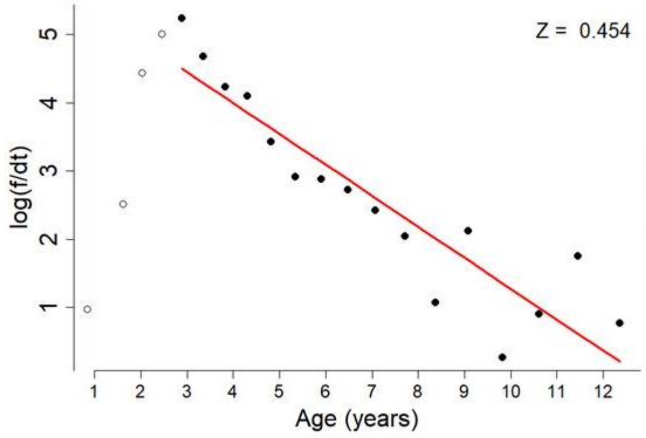
Polysteganus praeorbitalis
Scotsman

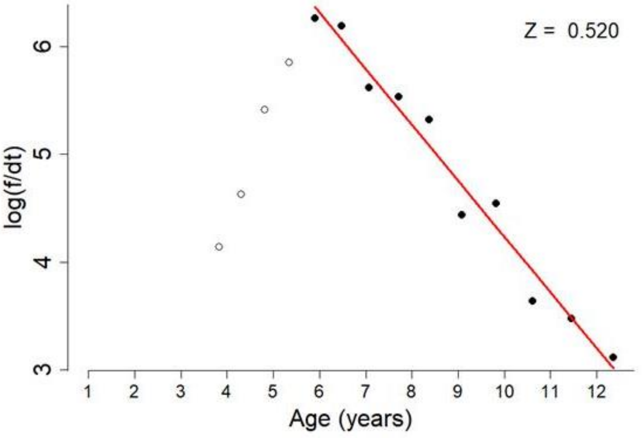

© SAIAB

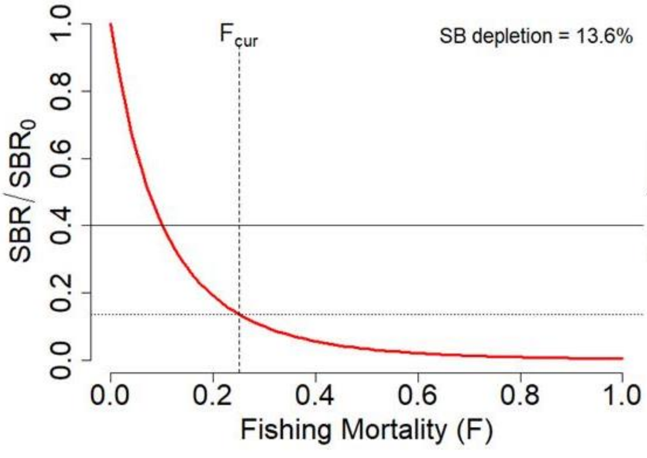
Parameters	Value	Unit	Reference
L_∞	850	mm	Mann 2013
K	0.078	yr^{-1}	Mann 2013
t_0	-2.115	yrs	Mann 2013
a	$5.89x10^{-5}$	g/mm	Mann 2013
b	2.81		Mann 2013
L_m	400	mm	Mann 2013
δ	20.0	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	13	yrs	Mann 2013
L_{opt}	444.97	mm	This study

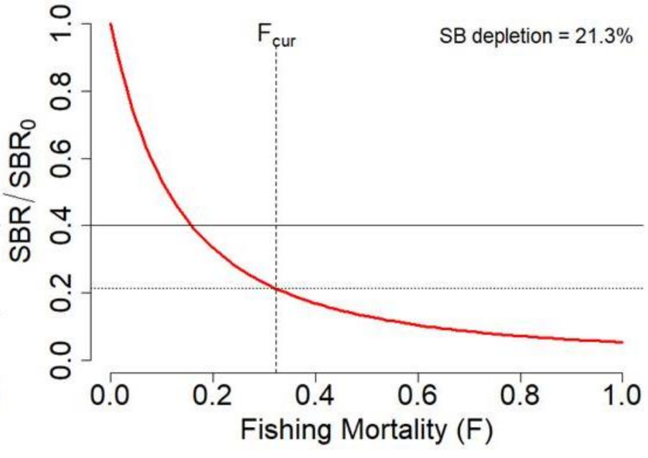




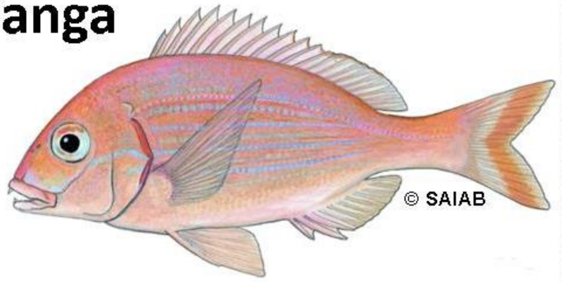




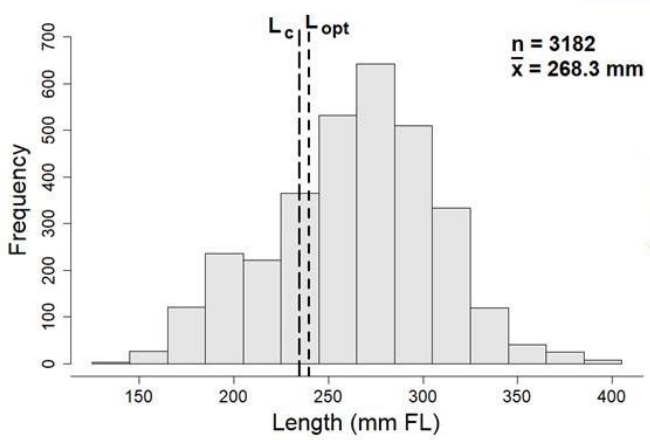


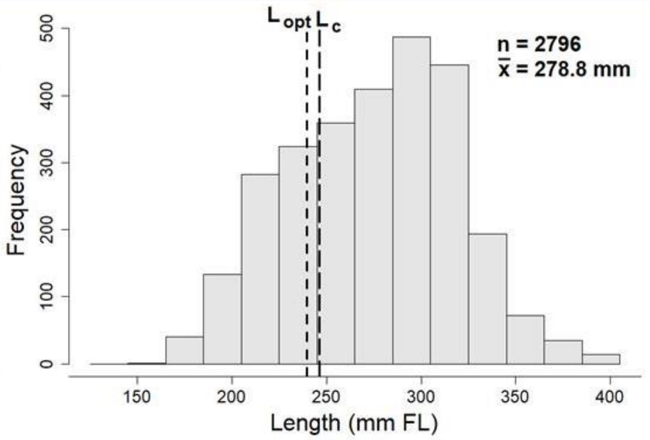


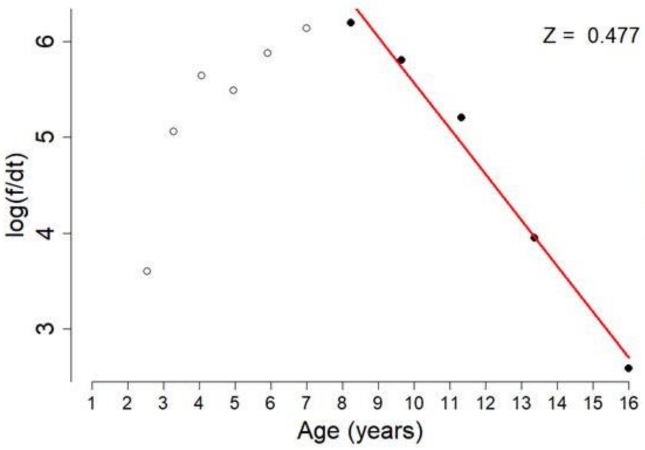
Pterogymnus laniarius
Panga

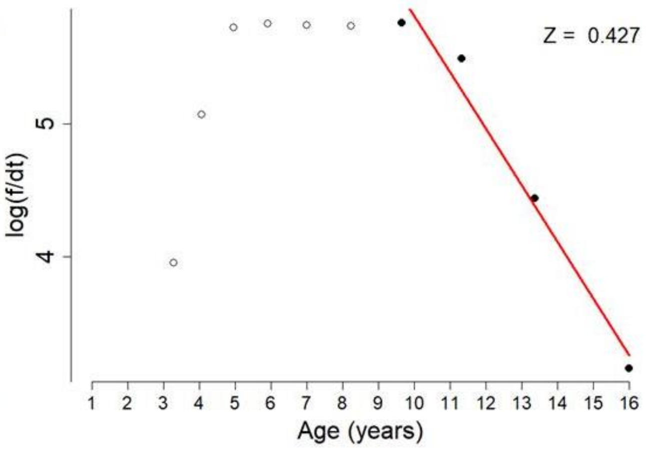


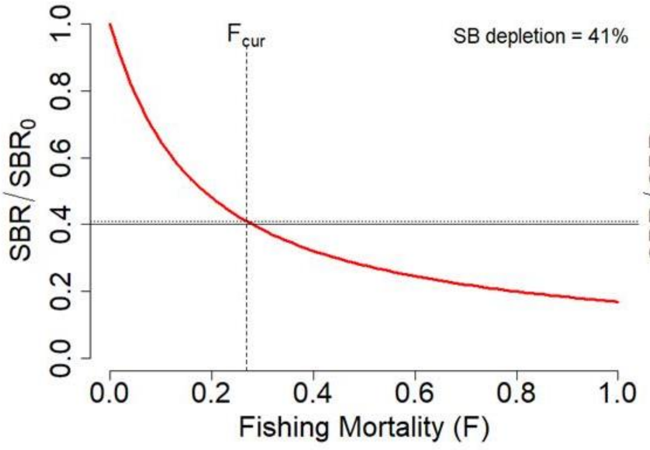
Parameters	Value	Unit	Reference
L_∞	379.4	mm	Mann 2013
K	0.13	yr^{-1}	Mann 2013
t_0	-1.78	yrs	Mann 2013
a	$2x10^{-5}$	g/mm	Mann 2013
b	3.031		Mann 2013
L_m	204	mm	Mann 2013
δ	10.2	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	16	yrs	Mann 2013
L_{opt}	239.82	mm	This study

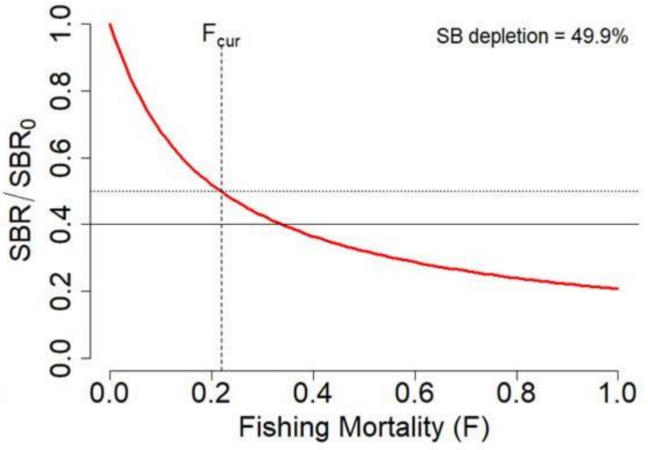












Rhabdosargus globiceps

White Stumpnose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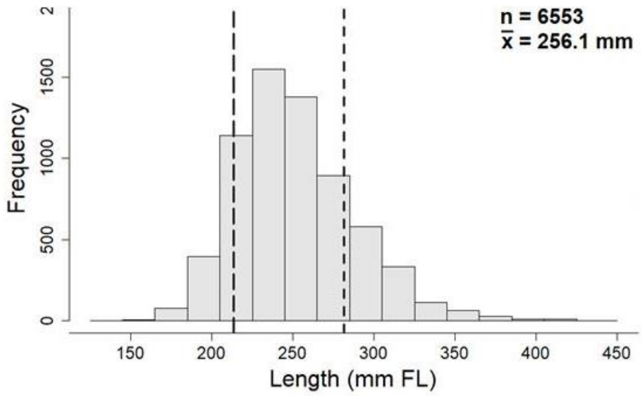
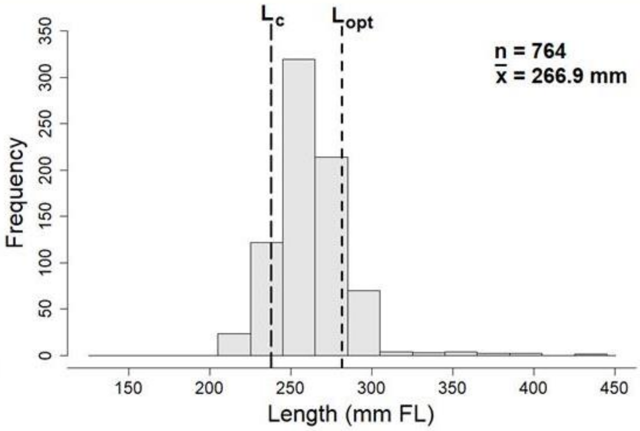
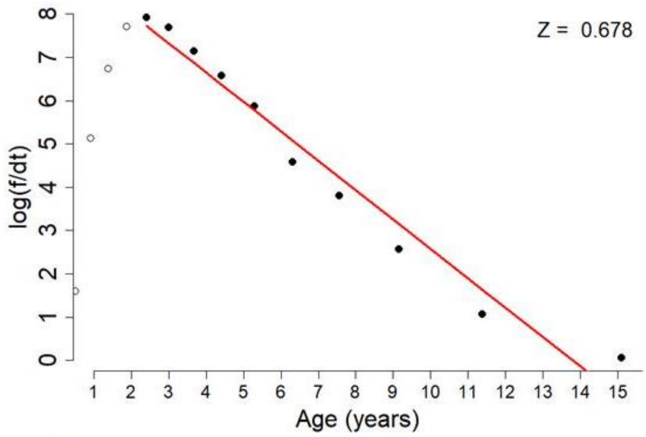
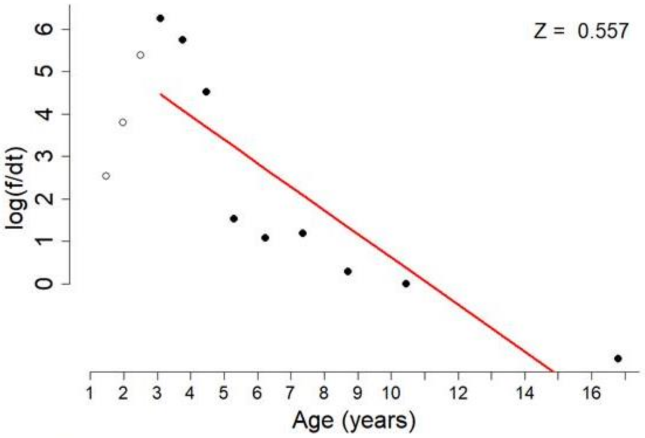
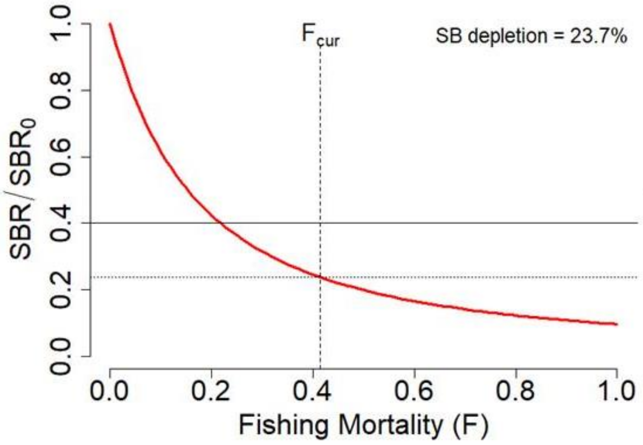
Parameters	Value	Unit	Reference
L_∞	399	mm	Mann 2013
K	0.21	yr^{-1}	Mann 2013
t_0	-2.0	yrs	Mann 2013
a	$2.02x10^{-5}$	g/mm	Mann 2013
b	3.011		Mann 2013
L_m	222	mm	Mann 2013
δ	11.1	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	21	yrs	Mann 2013
L_{opt}	281.17	mm	This study

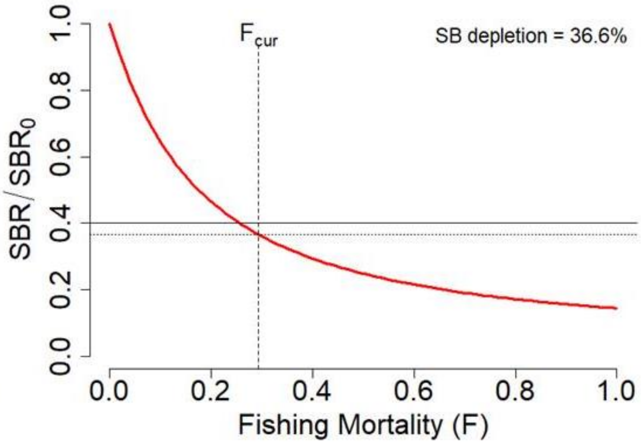




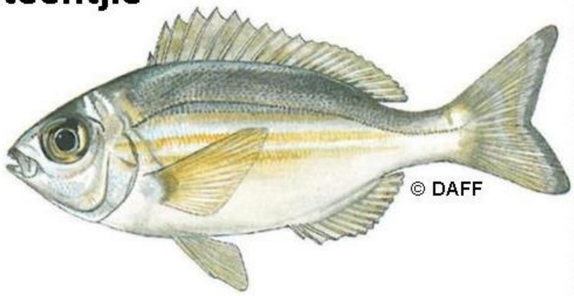




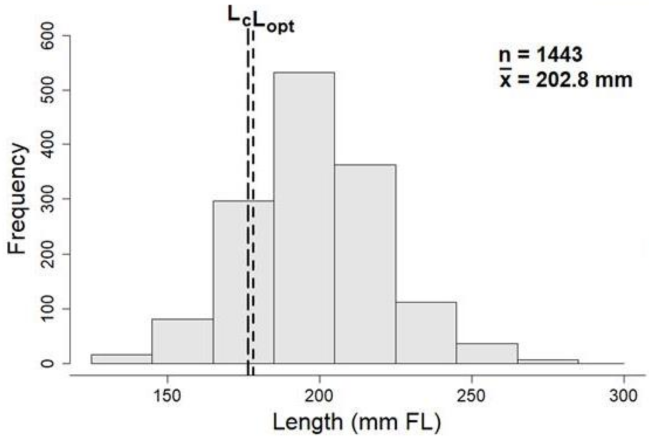


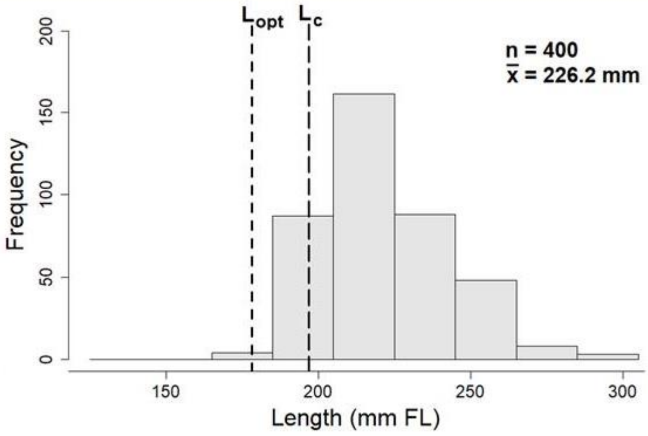


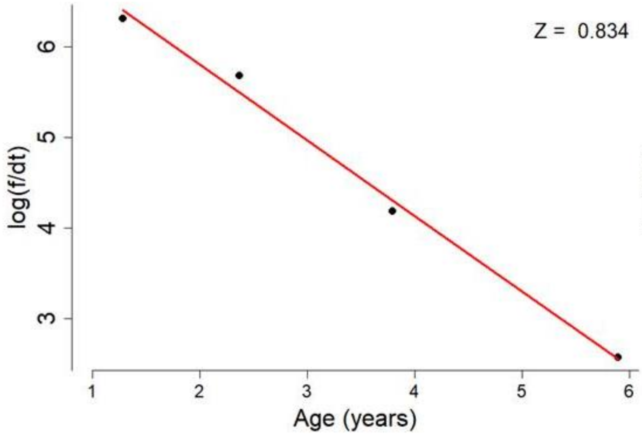
Spondyliosoma emarginatum
Steentjie

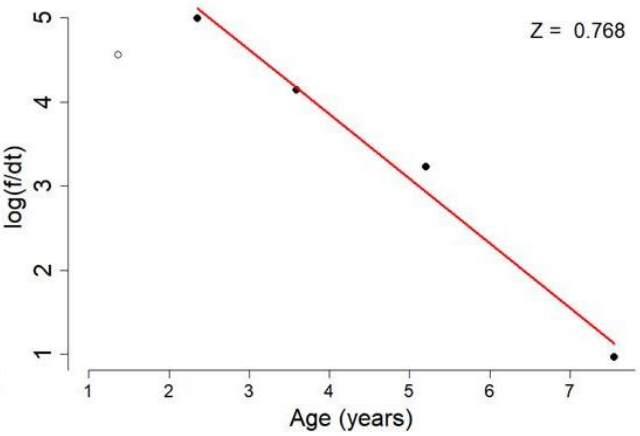

© DAFF

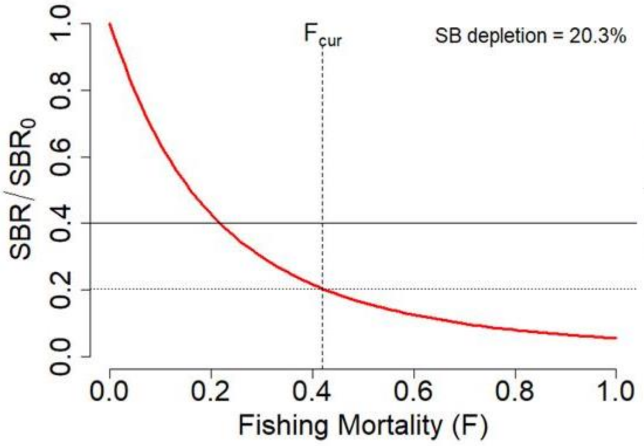
Parameters	Value	Unit	Reference
L_∞	289.15	mm	Mann 2013
K	0.22	yr^{-1}	Mann 2013
t_0	-3.82	yrs	Mann 2013
a	$3x10^{-5}$	g/mm	Mann 2013
b	2.9625		Mann 2013
L_m	235	mm	Mann 2013
δ	11.75	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	9	yrs	Mann 2013
L_{opt}	178.19	mm	This study

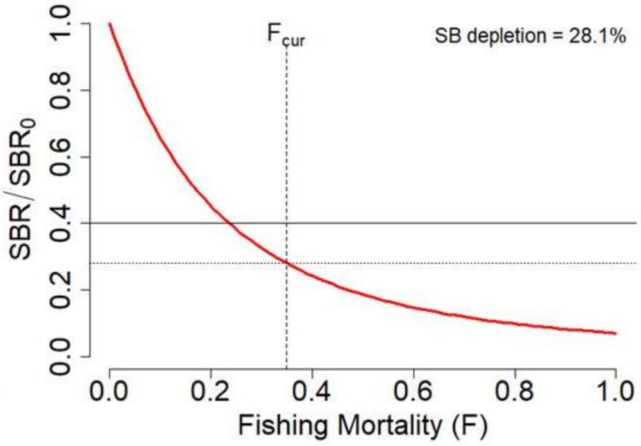






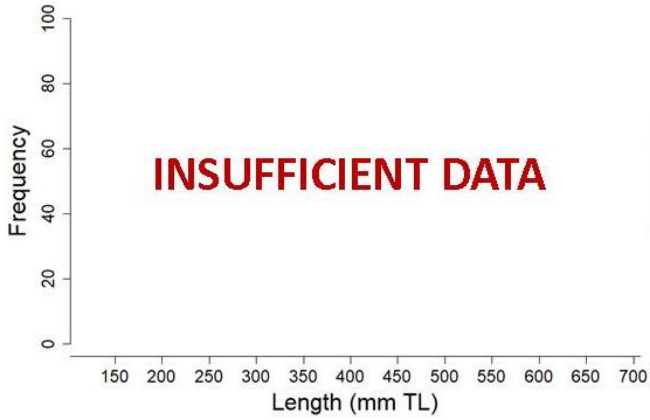


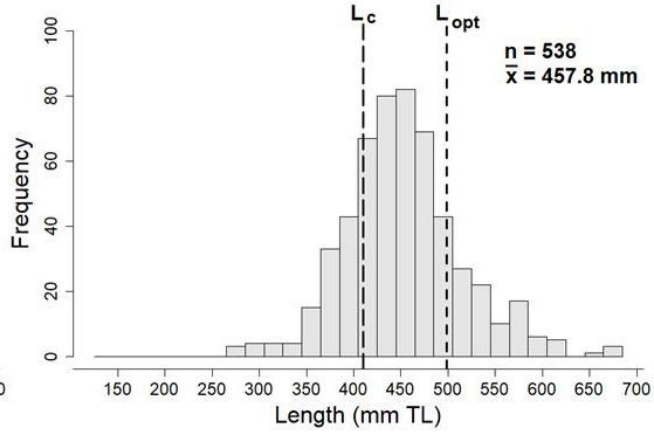


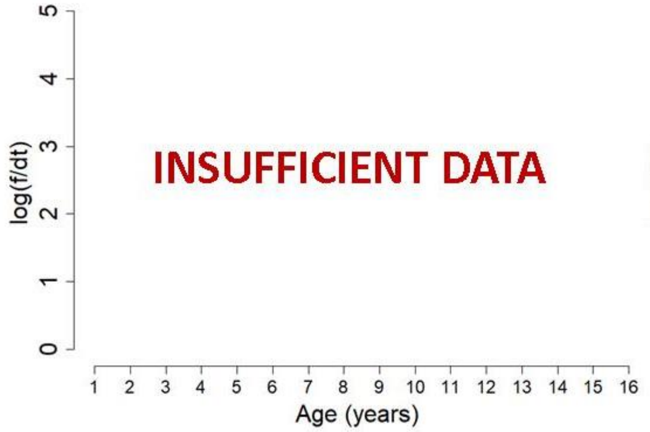


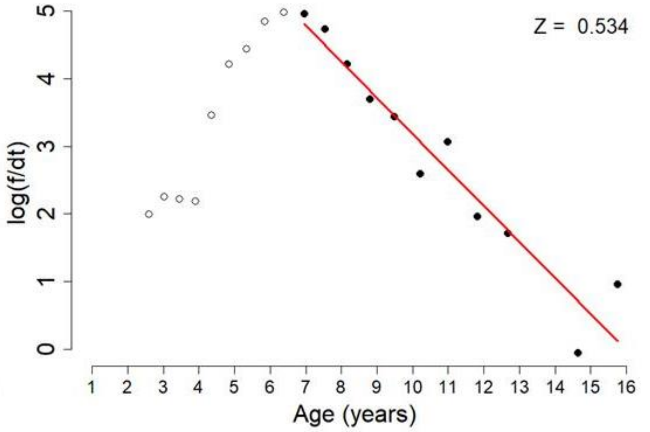
Chelidonichthys capensis
Cape Gurnard

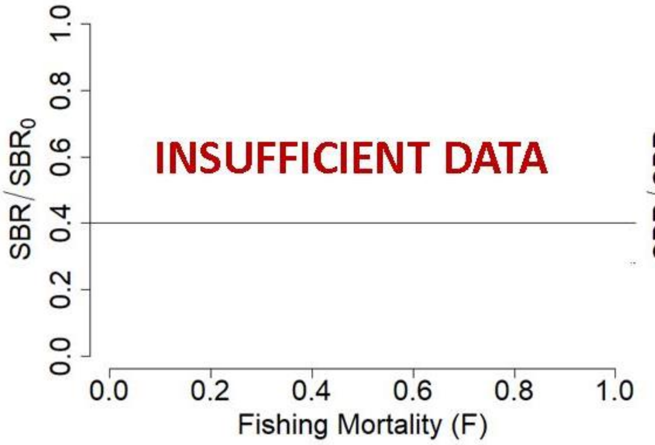
Parameters	Value	Unit	Reference
L_∞	894.23	mm	McPhail 1998
K	0.0.79	yr^{-1}	McPhail 1998
t_0	-2.043	yrs	McPhail 1998
a	$8.6x10^{-3}$	g/mm	McPhail 1998
b	3.02		McPhail 1998
L_m	319	mm	McPhail 1998
δ	15.95	mm^{-1}	Assumed: $0.05*L_m$
t_{max}	16	yrs	Mann 2013
L_{opt}	498.66	mm	This study

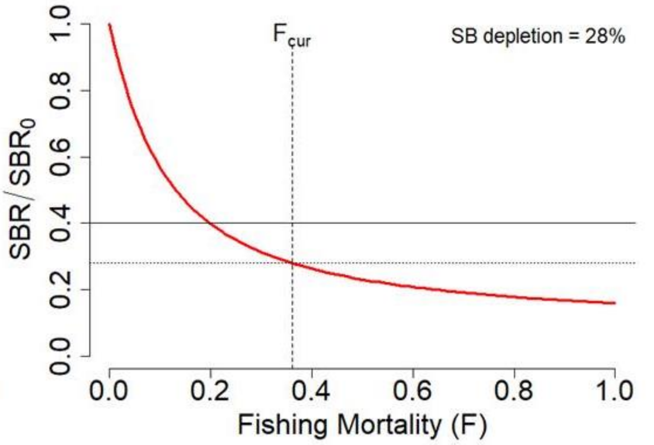












Appendix B – Natural mortality estimates

The natural mortality estimates from Hoenig (1983) – M^H, Jensen (1996) – M^J, and Chen & Watanabe (1989) – M^C for 26 South African linefish species. The M^C estimates are for individual years, starting from 1 year old fish to individual species maximum age (t_{max}). Bold M^C estimates are those for age classes which are fully selected. The mean natural mortality for the exploited phase (M_{exp}) (i.e. age classes that are fully selected) is the average of the mean of bold M^C estimates, summed with M^H and M^J, i.e. $M_{exp} = (M^H + M^J + \overline{\overline{M^C_{bold}}})/3$. The M_{exp} estimate for species marked with an asterisk (*) is the average between M^H and M^J, as their M^C estimates were nonsensical.

Species	M^H	M^J	M^C										$\bar{M}_{exp}$
Yellowtail	0.488	0.480	1.087	0.656	0.510	**0.438**	**0.398**	**0.373**	**0.357**	**0.346**	**0.338**		0.448
Dolphinfish	1.082	0.600	1.213	0.726	**0.572**	**0.501**							0.740
Snoek	0.440	0.442	0.648	0.496	0.422	0.380	**0.356**	**0.343**	**0.340**	**0.346**	**0.363**	**0.392**	0.413
Elf	0.440	0.141	**0.373**	**0.295**	**0.247**	**0.216**	**0.193**	**0.177**	**0.164**	**0.153**	**0.145**	**0.138**	0.264
Kob	0.179	0.173	0.600	0.412	0.321	**0.269**	**0.235**	**0.211**	**0.193**	**0.180**	**0.170**	**0.161**	0.169
			0.155	**0.149**	**0.144**	**0.140**	**0.137**	**0.134**	**0.132**	**0.130**	**0.128**	**0.127**	
			0.125	**0.124**	**0.123**	**0.122**	**0.122**						
Geelbek	0.488	0.405	0.726	0.519	0.426	0.375	**0.343**	**0.323**	**0.309**	**0.300**	**0.297**		0.402
Eastern little tuna	0.727	1.005	1.372	**0.908**	**0.774**	**0.719**	**0.694**	**0.682**					0.829

White-edged rockcod	0.295	0.321	1.209 0.638 0.462 0.378 0.329 **0.298** **0.277** **0.262** **0.251** **0.243** **0.237** **0.232** **0.228** **0.225** **0.223**	0.288
Catface rockcod*	0.401	0.722	0.890 1.727 -3.136 -0.637 -0.315 -0.195 -0.134 -0.099 -0.076 -0.061 -0.049	0.561
Yellowbelly rockcod	0.277	0.135	0.458 0.339 0.274 0.233 0.205 0.185 0.169 **0.157** **0.148** **0.140** **0.134** **0.128** **0.124** **0.120** **0.117** **0.114**	0.181
Halfmoon rockcod	0.261	0.591	1.230 0.727 0.570 **0.498** **0.458** **0.435** **0.421** **0.412** **0.406** **0.402** **0.399** **0.398** **0.396** **0.396** **0.396** **0.396** **0.397**	0.422
Carpenter	0.150	0.090	0.213 0.186 0.166 0.150 0.138 0.128 0.120 0.114 0.108 0.103 0.099 **0.095** **0.092** **0.089** **0.087** **0.085** **0.083** **0.081** **0.079** **0.078** **0.077** **0.075** **0.074** **0.073** **0.072** **0.072** **0.071** **0.070** **0.070** **0.069**	0.106
Santer	0.203	0.114	0.327 0.263 **0.223** **0.195** **0.175** **0.160** **0.148** **0.138** **0.131** **0.124** **0.119** **0.114** **0.110** **0.106** **0.103** **0.101** **0.098** **0.096** **0.094** **0.093** **0.091** **0.090**	0.147
Englishman	0.261	0.128	0.395 0.305 0.252 0.217 0.193 0.175 0.161 0.150 0.141 **0.134** **0.128** **0.123** **0.119** **0.115** **0.112** **0.109** **0.106**	0.169
Dageraad	0.203	0.122	0.341 0.273 0.230 0.201 0.181 0.165 0.153 0.143 0.135 **0.128** **0.123** **0.118** **0.114** **0.110** **0.107** **0.105** **0.102** **0.100** **0.098** **0.097**	0.144

			0.095	**0.094**									
Red stumpnose*	0.094	0.170	0.270	0.235	0.211	0.193	0.179	0.169	0.160	0.154	0.148	0.144	0.132
			0.141	0.139	0.138	0.137	0.137	0.138	0.140	0.142	0.145	0.150	
			0.155	0.162	0.171	0.183	0.197	0.216	0.241	0.275	0.324	0.402	
			0.541	0.853	2.185	-3.367	-0.916	-0.520	-0.357	-0.270	-0.215	-0.177	
			-0.150	-0.129	-0.113	-0.100	-0.089	-0.080	-0.073	-0.067			
Roman	0.234	0.129	0.406	0.311	0.256	0.220	0.195	0.176	0.162	0.151	**0.142**	**0.135**	0.161
			0.129	**0.124**	**0.120**	**0.116**	**0.113**	**0.110**	**0.107**	**0.105**	**0.103**		
Slinger	0.401	0.281	0.410	0.341	**0.299**	**0.271**	**0.252**	**0.239**	**0.231**	**0.227**	**0.226**	**0.228**	0.309
			0.234										
Black musselcracker	0.099	0.075	0.283	0.231	0.196	0.172	0.154	0.140	0.128	0.119	0.112	0.105	0.079
			0.100	0.095	0.091	0.088	0.085	0.082	0.079	**0.077**	**0.075**	**0.074**	
			0.072	**0.070**	**0.069**	**0.068**	**0.067**	**0.066**	**0.065**	**0.064**	**0.063**	**0.062**	
			0.061	**0.061**	**0.060**	**0.060**	**0.059**	**0.059**	**0.058**	**0.058**	**0.057**	**0.057**	
			0.056	**0.056**	**0.056**	**0.055**							
Blue hottentot	0.368	0.200	1.396	0.640	0.434	0.338	0.284	0.249	0.224	0.207	0.193	0.183	0.246
			0.175	**0.168**									
Hottentot	0.212	0.195	0.505	0.374	0.304	0.261	0.233	**0.212**	**0.197**	**0.185**	**0.176**	**0.169**	0.189
			0.163	**0.158**	**0.154**	**0.151**	**0.148**	**0.146**	**0.144**	**0.142**	**0.142**	**0.141**	
			0.141										

Scotsman	0.340	0.117	0.362 **0.122**	0.284 **0.117**	0.237 **0.113**	0.206	0.183	**0.166**	**0.153**	**0.143**	**0.135**	**0.128**	0.197
Panga	0.277	0.195	0.429 **0.160**	0.335 **0.156**	0.281 **0.153**	0.246 **0.150**	0.222 **0.148**	0.204 **0.146**	0.191	0.181	0.172	**0.166**	0.209
White stumpnose*	0.212	0.315	0.449 0.279 -0.440	0.370 0.301	0.323 0.334	0.293 0.387	0.274 0.474	0.262 0.642	0.255 1.069	0.254 4.145	0.257 -1.904	0.265 -0.733	0.264
Steentjie	0.489	0.330	0.342	0.318	**0.308**	**0.310**	**0.326**	**0.358**	**0.418**	**0.535**	**0.822**		0.419
Cape gurnard	0.277	0.119	0.370 **0.123**	0.289 **0.118**	0.240 **0.114**	0.208 **0.110**	0.185 **0.107**	0.168 **0.104**	**0.155**	**0.144**	**0.136**	**0.129**	0.173