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## A method to determine size-specific natural mortality applied to westcoast steenbras (*Lithognathus aureti*) in Namibia

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### Abstract

In traditional single-species fish stock assessment natural mortality is considered constant, independent of age or size. It is argued that predation mortality is generally related to prey size, that it decreases with increasing size and that such size-specific signals can best be detected in stocks that are close to a virgin state. Size-specific natural mortality rates of westcoast steenbras (*Lithognathus aureti*) were determined by using length frequencies of rod-caught fish from a lightly exploited and closed population at Meob Bay, Namibia. It was assumed that natural mortality is inversely proportional to (body) length and approaching a constant minimum rate ( $M_{\infty}$ ) as the fish grow bigger. Simple and new length-based catch curve methods were developed using the traditional simplification of neglecting variations in length at age. The von Bertalanffy growth parameters for annual mean growth as well as the coefficient of variation of length at age were estimated from analyzing age-length data. A simple deterministic simulation model was developed to examine the robustness of the methods and the impact of variability in individual growth. The model assumes that fish grow with a constant coefficient of variation in length at age. The simple method works within 10% precision criteria in most real cases. It is shown that overestimating mean length at old age ( $\bar{L}_{\infty}$ ) counteracts the effects of overlapping lengths for consecutive age groups. This fact can be used to estimate the fundamental mortality-to-growth ratio ( $M_{\infty}/K$ ) without any prior knowledge on growth. The application of  $M_{\infty}$  for steenbras to obtain size-specific natural mortality rate for silver kob (*Argyrosomus inodorus*), as an input parameter for virtual population analysis, is also proposed. © 1999 Elsevier Science B.V. All rights reserved.

**Keywords:** Natural mortality; Size specific rates; Length-based methods; Individual growth variation; Simulation; *Lithognathus aureti*

### 1. Introduction

Although the instantaneous rate of natural mortality ( $M$ ) is a key factor in fish population dynamics, this is difficult to estimate accurately, particularly if little information is available on the biology of the fish.

Natural mortality accounts for decreasing fish stock abundance potentially due to numerous other causes apart from fishing, including e.g. predation, cannibalism, disease, spawning stress, starvation and senescence.

As direct measurements are usually impossible to obtain, measurable quantities that are assumed proportional to  $M$  are often used for the estimation of natural mortality. A number of methods to determine

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an instantaneous rate of size-independent natural mortality have been suggested in the literature, most using life-history parameters (e.g. Beverton and Holt, 1959; Rikhter and Efanov, 1976; Pauly, 1980; Gunderson and Dygert, 1988; Jensen, 1996; Lorenzen, 1996). In a review on the estimation of size-independent natural mortality rate in fish stocks, Vetter (1988) concluded that  $M$  is far from constant for many fish stocks and this within-stock variability should not be ignored as the standard fishery models can be sensitive to the variations in  $M$ . Changes in natural mortality rate with body size of fish within single fish stocks have been discussed by e.g. Ricker (1969), Ware (1975) and Peterson and Wroblewski (1984). Beyer (1989); Example 10, simply considered mass balance in the predation-food-consumption process and deduced that fish growing according to the von Bertalanffy growth equation (VBGE) was consistent with predation mortality being inversely proportional to length,  $L$ , i.e.

$$M(L) = M_{\infty} \frac{L_{\infty}}{L}, \quad (1)$$

where  $L_{\infty}$  as usual, denotes the mean length of infinitely old fish and  $M(L_{\infty})=M_{\infty}$  similarly denotes the mortality (predation) of infinitely old fish – a notation we retain in the present study.

Particularly in slow growing long-lived species the usual assumption in single-species fish stock assessment that natural mortality remains constant for all age (size) groups appears to be unreasonable. The simple assumption that natural mortality rate is inversely proportional to body length was adopted as an attractive and promising hypothesis. This study is an approach to quantify size-specific natural mortality for westcoast steenbras (*Lithognathus aureti*) and further apply it to silver kob (*Argyrosomus inodorus*).

In situations of zero fishing mortality, new linearized length-based catch curves are derived from first principles to estimate  $M/K$  in the case of size-independent natural mortality and  $M_{\infty}/K$  in the case of size dependent mortality according to Eq. (1), where  $K$  as usual denotes the curvature parameter in VBGE. These simple methods require knowledge of  $L_{\infty}$ . The VBGE parameters for mature steenbras are obtained from age-length data and further discussed in the light of mark-recapture data. It is of note that our mortality analysis is developed from the fundamental

basis of traditional fish population dynamics, i.e. a year-class is considered to comprise identical fish. This is generally a fallacy because it is well-known that fish of the same age may differ considerably in size. It is therefore not clear how the length-based methods perform as the coefficient of variation in length at age (CV) increases thereby creating a considerable amount of overlap in the size-range of consecutive age groups. This and related issues of robustness and bias are examined using a deterministic simulation model assuming that the individual fish of a cohort grow according to VBGE with the same  $K$  and with the same specific growth rate (in length), i.e. the constant CV-growth model of Beyer and Lassen (1994). The model is also used to demonstrate the important role of the mortality-to-growth ratio for length-based population dynamics.

## 2. Materials and methods

This study was undertaken in the Meob Bay area (24°31'S, 14°36'E) (Namibia, south-western Africa), situated in the Namib Naukluft Park which falls under the jurisdiction of the Ministry of Environment and Tourism. The Namibian Sea Fisheries Act (no. 29 of 1992) prohibits recreational fishing in restricted areas and only fishing for scientific purposes is allowed. The Meob Bay area was therefore a unique study area as no fishing effort and hence zero fishing mortality ( $F$ ) (except for some biological sampling) occur. In the years 1995–1997, regular surveys were undertaken at Meob Bay by the Linefish section as part of the Namibian Fish Tagging Project (NAFTAP). Of the approximately 16 400 steenbras that were marked and released at Meob Bay during the period 1992–1997, 146 were recaptured within this area and only eight ranging from 35.5 to 70 cm fork length (FL) were recaptured south of Walvis Bay in the Sandwich area (23°08'S, 14°26'E) (which lies approximately 160 km from Meob Bay). As only 5.5% of westcoast steenbras were recaptured outside the Meob Bay area, the population under investigation was treated as being closed and unexploited. Note that this 5.5% is most certainly an overestimate as the fishing pressure in the Sandwich area is much higher than in the Meob Bay area because this is open to angling for the general public.

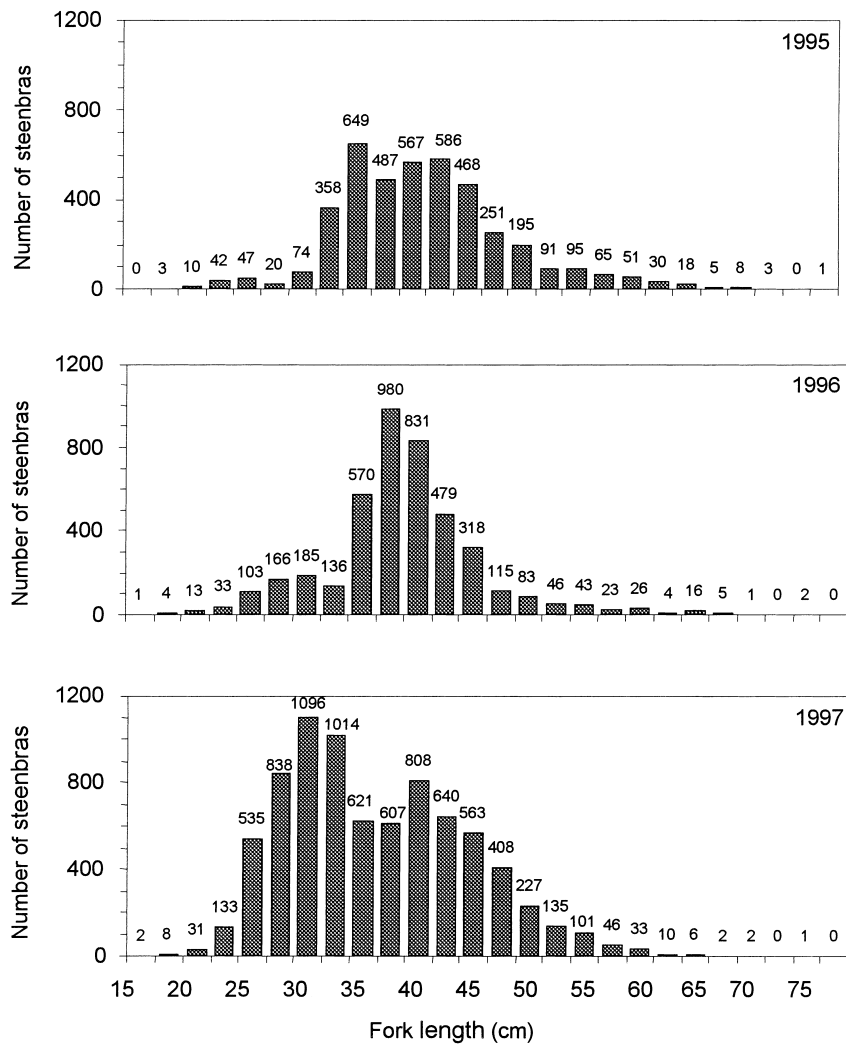


Fig. 1. Length frequency distributions of *L. aureti* sampled at Meob bay, Namibia, with rod and reel from the shore throughout 1995 ( $n_{95}=4124$ ), 1996 ( $n_{96}=4183$ ) and 1997 ( $n_{97}=7867$ ). (Shown lengths refer to lower class limits; 2.5 cm classes).

Westcoast steenbras were caught from the shore with rod and reel and measured to the nearest 0.5 cm FL. Length frequency distributions in 2.5 cm classes are shown in Fig. 1. Preliminary experimentation with hook-size selectivity was also carried out (Fig. 2).

2.1. Determination of growth parameters for westcoast steenbras

Estimated values for the von Bertalanffy growth parameters are needed for the length-based mortality

analysis, however, no useful information has been reported in the literature on the growth of the westcoast steenbras. A preliminary growth analysis was carried out by reading ring structures on otoliths following the method used by Buxton and Clarke (1989) and Benneth (1993) (Fig. 3). VBGE parameters for mean annual growth were estimated from these age-length data by non-linear least square ( $L_{\infty}=70$  cm,  $K=0.083$  yr<sup>-1</sup> and  $t_0=-2.4$  yr; Fig. 3(a)). The coefficient of variation of length at age,  $\gamma=CV(L_{\text{age}})$ , was estimated from the relative

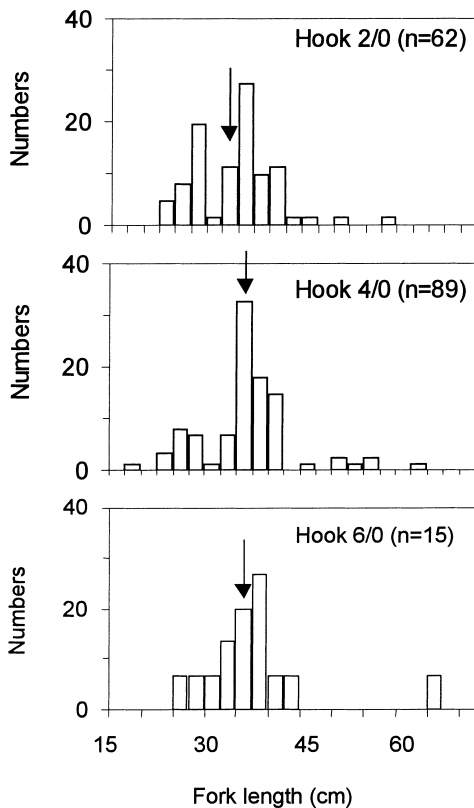


Fig. 2. Results of pilot hook selectivity experiment. An equal number of randomly selected fishermen (six per hook-size), with approximately the same fishing experience, were fishing for two sessions of 5 h each in the same area using the same bait. Catch in numbers of steenbras with the various hook-sizes used in the experiment are shown; arrows indicate mean lengths. (Shown lengths refer to lower class limits; 2.5 cm classes).

residuals ( $\gamma=0.116$ ; Fig. 3(b)). Assuming  $L_\infty$  to be known, the mark-recapture data were also used to obtain estimates of  $K$  independently of  $t_0$ , the apparent age of zero length. This analysis is included only as a preliminary investigation as more detailed considerations and estimation of growth are outside the scope of this paper. The data included length when first caught ( $L_1$ ), length at recapture ( $L_2$ ) and days free ( $\Delta t$ ). To avoid considerable bias on the estimation of the mean annual  $K$  due to e.g. seasonality in growth, fish which had spent less than one year in freedom were excluded from the analysis. Of the 89 recaptures recorded, 40 provided such accurate lengths at mark-recapture with  $\Delta t \geq 1$  yr, and this data was used to estimate individual

$K$ 's from VBGE, i.e. in the present application,

$$K = \frac{1}{\Delta t} \ln \left[ \frac{L_\infty - L_1}{L_\infty - L_2} \right]. \quad (2)$$

Fig. 4 shows  $K$ -values obtained in this way by assuming that the (unknown) growth trajectories of the individual fish could adequately be described by the same  $L_\infty=70$  cm and produced a mean value of  $\bar{K} = 0.072 \pm 0.006(\text{SE}) \text{ yr}^{-1}$ , ( $n=40$ ). Omitting three possible outliers (exceeding the 99.5% probability level estimated by  $\bar{K} + 2.576 \text{ SD}$ , ( $n=37$ )) resulted in  $\bar{K} = 0.064 \pm 0.004(\text{SE}) \text{ yr}^{-1}$  ( $n=37$ ). Repeating the procedure for  $L_\infty$  values in the range 60–80 cm resulted in mean  $K$  values that can be approximately described by  $\bar{K} = 334 L_\infty^{-2}$ , ( $n=40$ ). When individual  $L_\infty$ 's instead were chosen at random from a normal distribution with mean 70 cm and  $\gamma=0.1$ , we obtained  $\bar{K} = 0.070$  and a mean standard deviation of 0.043 based on 200 simulations. It should be noted that the maximum length of steenbras recorded in 1995–1997 was  $L_{\text{max}}=80$  cm ( $n=16\ 174$ ).

## 2.2. Estimating size-independent natural mortality ( $M$ )

In establishing the general basis, the impact of a constant instantaneous rate of total mortality,  $Z=F+M$ , was first considered ( $F$ =fishing mortality). The traditional cohort assumption of a one-to-one relationship between size and age (i.e.  $\gamma=0$ ) furthermore implies that the number of fish alive may be considered a function of length,  $N(L)$ , instead of age (or of time). Dividing the rate of change in numbers,  $dN/dt=-ZN$ , by the rate of growth,  $dL/dt=K(L_\infty-L)$ , gives the length-based starting point,

$$\frac{dN(L)}{dL} = -\frac{Z}{K} \frac{N(L)}{L_\infty - L}. \quad (3)$$

Integrating this (physiological) rate of population decline over the length interval from  $L_0$  to  $L$ , assuming constant parameters  $Z$ ,  $K$  and  $L_\infty$ , yields the length-based survivorship (Beyer, 1989),

$$N(L) = N(L_0) \left[ \frac{L_\infty - L}{L_\infty - L_0} \right]^{Z/K},$$

$$Z = F + M, \quad L_0 \leq L \leq L_\infty. \quad (4)$$

Thus in the case of constant mortalities independent of length, the fraction of fish surviving, while growing

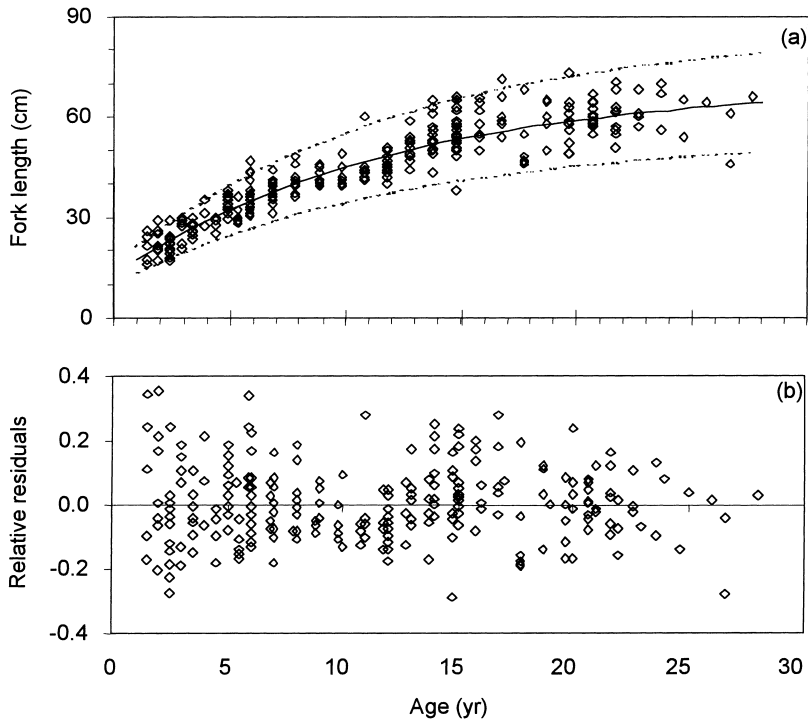


Fig. 3. Otolith readings of steenbras (*L. aureti*) caught in Meob bay, Namibia, in 1996 ( $n=282$ ). (a) Plot with estimated von Bertalanffy mean growth curve. Stipled curves indicate approximate 95% confidence intervals for length at age estimated as mean length multiplied by  $(1 \pm 2 \times \gamma)$ . (b) Residuals relative to mean length vs. age. The constant coefficient of variation in length at age,  $\gamma$ , is estimated as the standard deviation of these relative residuals.

from a (constant) length  $L_0$  to some length  $L$ , is obtained as the length-ratio of potential growth span in the square bracket to the power of  $Z/K$  and equals the usual exponential survivorship,  $\exp(-Z\Delta t)$ , if  $\Delta t$

represents the time required to grow from  $L_0$  to  $L$  (according to VBGE).  $L_0$  was obtained at the length at full recruitment to the fishery. The length-based beginning point for deriving the linearized catch curve is

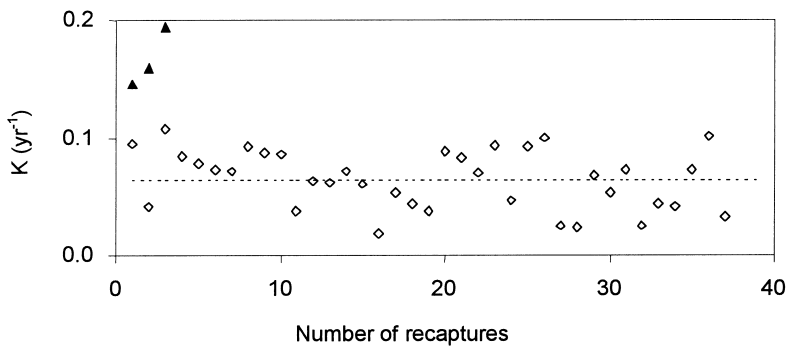


Fig. 4. Single fish estimates of  $K$  from mark-recapture data of steenbras (*L. aureti*) with one year or more in freedom and assuming  $L_\infty=70$  cm for all fish ( $n=40$ ). The stipled line shows the average omitting the three possible outliers (which are denoted by triangles).

similarly derived from dividing the catch rate,  $dC/dt = FN$ , by the growth rate, i.e.

$$\frac{dC}{dL} = \frac{F}{K} \frac{N(L)}{L_\infty - L}. \quad (5)$$

Considering this (physiological) catch rate at the mid-point,  $\bar{L} = (L_1 + L_2)/2$ , of a length class to equal  $C(L_1, L_2)/\Delta L$ , the catch from that length class divided by the class length ( $\Delta L$ ), and inserting the survivorship, Eq. (4), gives in a first approximation that

$$C(L_1, L_2)/\Delta L \propto (L_\infty - \bar{L})^{Z/K-1}.$$

This proportionality captures the essence of Eq. (5) when recruitment,  $N_0 = N(L_0)$ , to size  $L_0$ , and all parameters of growth and mortalities can be considered constant implying a steady-state situation. In the present application to the closed and unexploited population of westcoast steenbras inhabiting Meob Bay,  $C$  and  $F$  are referred to as the catch and fishing mortality ( $F=f$ , which is very small compared to  $M$ ) for all the surveys. Hence, considering  $\Delta L$  constant and taking logarithms gives the length-based catch curve (Beyer, 1989),

$$\ln C_i = \text{constant} + (M/K - 1) \ln(L_\infty - \bar{L}_i), \quad (6)$$

where index  $i$  refers to length class no  $i$ . Thus, provided that the mean annual growth parameters,  $K$  and  $L_\infty$ , are known, an estimate of size-independent natural mortality for steenbras could be obtained from linear regression with log to catch per length class as dependent variable and log potential growth span as explanatory variable.

### 2.3. Estimating natural mortality of infinitely old fish ( $M_\infty$ )

In more realistic natural mortality scenarios where smaller fish are gradually exposed to higher predation mortalities than bigger fish, the decline of numbers of fish as they increase in length is no longer described by Eq. (3), which is only valid for constant mortality. It is, however, possible to relate  $M$  as obtained from the estimation procedure in Eq. (6) to  $M_\infty$  for old and big fish (Section 3.2 and Appendix A). To establish a correct basis for estimating  $M_\infty$  in the case of natural mortality being inversely proportional to length, the first step taken was to modify total mortality according

to Eq. (1):

$$Z = F + M_\infty L_\infty / L. \quad (7)$$

Inserting this expression for  $Z$  in Eq. (3), the new length-based survivorship is again derived from simple integration (Beyer, 1989),

$$N(L) = N(L_0) \left[ \frac{L_\infty - L}{L_\infty - L_0} \right]^{Z_\infty/K} \left[ \frac{L_0}{L} \right]^{M_\infty/K},$$

$$Z_\infty = F + M_\infty, \quad L_0 \leq L \leq L_\infty. \quad (8)$$

Thus the impact of natural mortality being inversely proportional to length is that the number of fish attaining length  $L$  is reduced by the survival factor  $(L_0/L)^{M_\infty/K}$  compared to the situation of a constant  $Z$  equal to the minimum mortality level,  $Z_\infty$ . Note again that  $Z_\infty$  in Eq. (8) can be replaced by  $M_\infty$  as presently there is almost no fishing on the population. Eq. (5) for the physiological catch rate with constant (size-independent) fishing mortality is still valid for this or any other case of size-dependent natural mortality as long as the appropriate survivorship is used for the survivors  $N(L)$ . A similar expression of proportionality for steady-state situations could, therefore, be obtained but modified according to the additional survival factor, i.e.

$$C(L_1, L_2)/\Delta L \propto \bar{L}^{-M_\infty/K} (L_\infty - \bar{L})^{M_\infty/K-1}$$

$$= \bar{L}^{-1} (L_\infty/\bar{L} - 1)^{M_\infty/K-1}.$$

Multiplying with  $\bar{L}$ , taking logarithms and assuming constant class length, a new linear regression was obtained,

$$\ln(C_i \bar{L}_i) = \text{constant} + (M_\infty/K - 1) \ln(L_\infty/\bar{L}_i - 1). \quad (9)$$

This constitutes a very simple basis for estimating the natural mortality of (infinitely) old fish,  $M_\infty$ , when natural mortality increases for the younger and smaller fish in inverse proportion to decreasing length (Eq. (1)). Assuming again the mean annual growth parameters,  $K$  and  $L_\infty$ , are known,  $M_\infty$  for westcoast steenbras could therefore be obtained from linear regression using log to catch  $\times$  midlength as dependent variable and log to the relative potential growth span as explanatory variable, i.e.  $\log(\text{max mean length}/\text{midlength} - 1) = \log(\text{potential growth span}/\text{midlength})$ .

#### 2.4. Simulation model of mortality regimes with individual growth variation

A deterministic simulation programme was developed using simple (EXCEL) spreadsheets. Input parameters for growth are first  $L_{\infty}$ ,  $K$  and  $t_0$  for specifying mean annual VBGE, and secondly the constant coefficient of variation in length at age,  $\gamma$ , for quantifying the combined effect of individual growth variation and an extended spawning season. The mortality regime considered is one of constant (size-independent) mortality,  $M$ , or one of mortality decreasing in inverse proportion to increasing length according to Eq. (1) and specified by  $M_{\infty}$ . Selection is quantified by a standard S-shaped logistic curve (e.g. Sparre and Venema, 1998) specified by the length at 50% selection,  $L_{50}$ , and the parameter  $r$  of selection range:

$$S(L) = 1 / (1 + \exp(-r(L - L_{50}))), \quad r = 2 \ln 3 / \text{SR}, \quad (10)$$

where SR is the selection range.

Starting with the first midlength,  $\bar{L}_1$ , and using the class interval,  $\Delta L$ , the basic idea is to calculate the average length composition of the population of steenbras in a specific year by adding the contributions from individual age groups. The historical series of annual recruitment,  $R_i$ , ( $i=0,1,2,\dots$ ), to age zero constitutes the remaining input parameters. Suppose, as an example, 1996 is the year considered. If  $R_0=10\,000$  in the model then  $R_{1996 \text{ age } 0}=10\,000$  fish of age zero are recruited to the population at the beginning of 1996. The individual lengths of these fish are considered normally distributed with mean length  $L_{\text{age } 0}=L_{\infty}(1-\exp(Kt_0))$  and standard deviation  $\gamma \times L_{\text{age } 0}$ . At the end of 1996 the survivors of these fish have grown to mean length  $L_{\text{age } 1}=L_{\infty}(1-\exp(-K(1-t_0)))$  and their standard deviation in length has similarly increased to  $\gamma \times L_{\text{age } 1}$  (thereby maintaining the constant  $\text{CV}=\gamma$ ). To simplify the mortality calculations under the size-specific regime, the fish are considered exposed to a constant rate of natural mortality throughout 1996 which equals the rate, Eq. (1), using the mean length of the fish in the middle of the year. In the present application the model is used only to simulate steady-state conditions so all  $R_i$ 's are basically considered equal. For example,  $R_{36}=10\,000$  implies that also 10 000 fish were recruited at age zero in 1960 of which only  $R_{1996 \text{ age } 36}=10\,000$

$\exp(-\text{CUM}_{36})$  survive to age 36 years and are recruited to the population at the beginning of 1996. Here  $\text{CUM}_{36}$  denotes the cumulative mortality over the past 36 years calculated as the sum of the 36 annual levels (the first of which is described above). The recruits,  $R_{1996 \text{ age } 36}$ , are normally distributed with mean length  $L_{\text{age } 36}=L_{\infty}(1-\exp(-K(36-t_0)))$  and standard deviation  $\gamma \times L_{\text{age } 36}$ . During 1996 these big fish will grow less than one length class, i.e. such old cohorts will spread out over a number of length classes which is determined entirely by the individual variability in size specified by  $\gamma$ .

The calculations are done on a monthly basis. For each age group the mean annual number of live fish in a month is derived and these fish are considered normally distributed according to the common CV ( $=\gamma$ ) and the mean length attained at the midpoint of that month. Using this normal distribution (for each age group and month in the year considered), the exact proportion of fish which belongs to each length class is calculated as the difference between the cumulative normal distribution function at the upper and lower class limits of each class. Multiplying with the mean annual number of fish (per age group and month) and adding up (over months and age groups) then gives the complete (annual) length composition for the population. The simulated length frequencies for the sample are obtained by multiplying these population frequencies with the selectivities, Eq. (10), calculated at the class midpoints. These sample frequencies represent the  $C_i$ 's in the linearized length-based catch curves, Eqs. (6) and (9), and the programme was finalized by using the simulated sample for these regressions. Fifty age groups were used and the programme has been tested in various ways to ensure sufficient precision and accuracy for the present application.

### 3. Results

#### 3.1. Quantification of growth

The mean growth curve for the individuals comprising a cohort of steenbras,  $\bar{L}$  as a function of age  $t$ , is considered described by VBGE with parameters estimated from the (non-linear) least square fit to the age-length data (Fig. 3(a)), i.e.

$\bar{L}_\infty = 70$  cm,  $K = 0.083 \text{ yr}^{-1}$  and  $t_0 = -2.4$  yr, so

$$\bar{L} = 70(1 - \exp(-0.083(t + 2.4))). \quad (11)$$

This mean growth curve did not change if estimation instead was done by minimizing the relative residuals squared. It could not be rejected that the relative residuals were normally distributed ( $P=0.05$ ,  $\chi^2$ -test) with standard deviation  $\gamma=0.116$  (Fig. 3(b)).

Assuming  $L_\infty=70$  cm resulted in  $\bar{K} = 0.072 \text{ yr}^{-1}$  using all 40 mark-recapture data for one year or longer in freedom. One or two of the three possible outliers (found outside the estimated 0.5% and 99.5% probability levels; Section 2.1 and Fig. 4), however, represent outlier values in the present data. This is because the Poisson probability,  $P(X \geq 3 | \lambda = 0.4) = 0.8\%$ , of getting three or more values when the expected value is  $\lambda = 40 \times 0.01 = 0.4$ , is considerably smaller than 5%. Omitting one outlier yielded  $\bar{K} = 0.069 \pm 0.005 \text{ yr}^{-1}$  (SE), ( $n=39$ ). This estimate includes fish which had spent an uneven number of seasons in freedom. Considering data for two or more years in freedom the most reliable, assuming a seasonal  $K$ -change of  $\pm 30\%$  and, applying 10% precision criteria resulted in  $1\frac{1}{2}$  yr as the minimum accepted time spent in freedom. Of the 40 recaptures previously considered ( $\Delta t \geq 1$  yr), 19 met this criterion ( $\Delta t \geq 1\frac{1}{2}$  yr; Table 1), including the three outliers, and omitting one outlier yielded  $\bar{K} = 0.083 \pm 0.007 \text{ yr}^{-1}$  (SE), ( $n=18$ ).

### 3.2. Estimation of natural mortality

Adding numbers at length from Fig. 1, the maximum frequency of the total number of westcoast steenbras caught in 1995–1997 occurs at the (2.5 cm) length class starting at 40 cm. This pooled data from the next class onwards (i.e.  $L \geq 42.5$  cm) was considered representative for the length frequencies in the population (i.e. virtually 100% selection) and used for the estimation of natural mortality assuming all fish grow with  $L_\infty=70$  cm and  $K=0.083 \text{ yr}^{-1}$ . Using the linearized catch curve in Eq. (6) the estimate of the (maximum) size-independent natural mortality yielded  $M=0.41 \text{ yr}^{-1}$  (Fig. 5(a)). Assuming size-dependent mortality we obtained  $M_\infty=0.285 \text{ yr}^{-1}$  (Fig. 5(b)) using the linearized catch curve in Eq. (9). These estimates increased slightly if the length frequencies for  $L \geq 42.5$  cm alternatively were

Table 1  
Mark-recapture data for steenbras with  $\Delta t \geq 548$  days free

$L_1$	$L_2$	$\Delta L$	$\Delta t$	$K$
27	35	8	704	0.107
27	35	8	900	0.083
28.5	35.5	7	929	0.073
28.5	35.5	7	940	0.072
31	38	7	848	0.085
31.5	37.2	5.7	936	0.062
32.5	38	5.5	937	0.062
33	40.5	7.5	1159	0.071
33	37	4	691	0.060
33.5	38	4.5	912	0.053
34.5	40.5	6	772	0.088
35	39.5	4.5	603	0.083
35	42	7	1162	0.070
35	41.8	6.8	847	0.093
35	42	7	891	0.091
38	41	3	888	0.040
45	53	8	968	0.145
32	40.5	8.5	581	0.159
36	46	10	658	0.193

Length when first caught ( $L_1$ ), length at recapture ( $L_2$ ) and growth ( $\Delta L$ ) are given in cm. Single fish estimates of the VBGE parameter  $K$  ( $\text{yr}^{-1}$ ) are all based on  $L_\infty=70$  cm. Possible outliers at the bottom.

pooled on a percentage basis (i.e.  $M=0.42$  and  $M_\infty=0.294 \text{ yr}^{-1}$  from equivalent plots (not shown) to Fig. 5 by giving the tails ( $L \geq 42.5$  cm) of the annual length frequencies equal weight). Note that only five points were used for the regressions. This is mainly because the larger the fish the more deviation from a straight line is anticipated due to a considerable variation in length at age (Section 3.4). The usual uncertainty, however, due to low catches of large fish also plays a role. This can easily be illustrated. Of the total catch of  $n=16174$  fish, 272 represent the last of the five points included (i.e. length class starting at 52.5 cm). The number of fish in such a length class ( $L$ ) can be considered binomially distributed,  $\text{Bin}(n, p_L)$ , with mean  $np_L$  and variance  $np_L(1-p_L)$ . We estimate  $p_L=272/16174$ , so the standard deviation of the number of fish in the length class becomes ca. 16. Thus a 95% confidence interval for this number is approximately (240, 304). Introducing just one change due to random chance by replacing the observed catch (272) for the last point by the outer limit (304) will cause a slight reduction in the slope of the regression line in Fig. 5(b) and the new estimate,  $M_\infty=0.274$ , represents



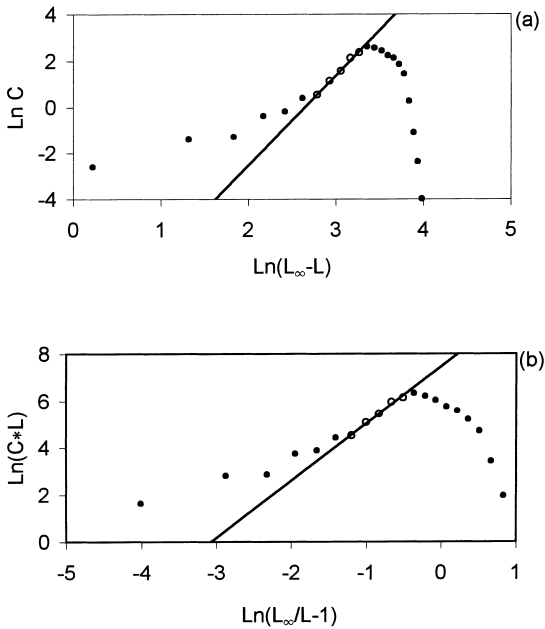


Fig. 5. Length-based catch curve analyses for the estimation of natural mortality for steenbras (*L. aureti*) in Meob Bay, Namibia, using pooled length frequencies of rod-caught fish in 1995–1997 (*C* in %) and assuming  $L_{\infty}=70$  cm. The (open circle) points used for regression analyses represent the length range 42.5–55 cm. Note small fish are to the right and big fish to the left in the plots: (a) constant (size-independent) mortality analysis, Eq. (6):  $y=3.9043x-10.338$  ( $n=5$ ,  $R^2=0.99$ ), i.e.  $M=0.407$  yr<sup>-1</sup> for  $K=0.083$  yr<sup>-1</sup>; (b) size-dependent mortality analysis, Eq. (9):  $y=2.4296x+7.4696$  ( $n=5$ ,  $R^2=0.99$ ), i.e.  $M_{\infty}=0.285$  yr<sup>-1</sup> for  $K=0.083$  yr<sup>-1</sup>.

a reduction of 4%. Similarly the confidence interval for the number of fish representing the first point (i.e. length class starting at 42.5 cm) becomes (1627, 1783) due to random chance. It is likely, however, that the catch in this length class, which would truly reflect the population in the sea, should be even higher due to selection (Section 3.3). With  $L_{50}=38$  cm and  $r=0.5$  cm<sup>-1</sup>, Eq. (10) yields  $1/S(43.75)=1.056$  and raising the catch by this factor gives 1800 fish for the first point included in the analysis. Introducing instead this change causes a slight increase in the slope of the regression line in Fig. 5(b) and the new estimate,  $M_{\infty}=0.290$ , represents an increase of 2%.

It is of note that the estimates of  $M$  and  $M_{\infty}$  from Fig. 5 are consistent with each other in the following sense. If the method of constant  $M$  is (incorrectly) used in a size-dependent mortality scenario, which is truly

specified by  $M_{\infty}$ , then

$$M_{\infty} = M\bar{L}_{repr}/L_{\infty}, \quad (12)$$

where  $M=0.41$  yr<sup>-1</sup> is the estimate of a constant mortality obtained by the regression in Eq. (6) using a length range which is represented by  $\bar{L}_{repr} = 48.75$  cm, the midlength of that length range (Appendix A).

The results suggest the size-specific mortality model, Eq. (1),

$$M(L) = 20/L, \quad L_{\infty} = 70 \text{ cm}, \quad M_{\infty} = 0.29 \text{ yr}^{-1}, \quad (13)$$

where  $M(L)$  is the instantaneous rate of natural mortality (yr<sup>-1</sup>) for steenbras of length  $L$  (cm).

### 3.3. Estimation of the resultant ogive from length-based catch curve

The result of applying the Pauly (1984a) method to length-based catch curves for a size-dependent mortality regime is a new method for estimating the resultant selection ogive,  $S_{res}(L)$ . The idea is that the difference between the predicted catch (determined by the extension of the regression line towards the smaller fish (i.e. to the right on Fig. 5(b)) and the actual numbers should represent the ogive resulting from the combined effect of recruitment and gear (hook) selectivity (Pauly, op.cit.). Denoting the intercept in the regression, Eq. (9), by ‘a’ the predicted catch in length class no.  $i$  (assuming 100% selection under steady-state conditions),  $C_{pred, i}$  is determined from

$$C_{pred, i}\bar{L}_i = \exp(a)(L_{\infty}/\bar{L}_i - 1)^{M_{\infty}/K-1}.$$

Hence, from the condition that the actual catch  $C_i=C_{pred, i}S_{res, i}$  the resultant ogive in the size-dependent mortality scenario is obtained as

$$S_{res, i} = C_i \exp(-a)\bar{L}_i(L_{\infty}/\bar{L}_i - 1)^{1-M_{\infty}/K}. \quad (14)$$

Fitting the logistic curve in Eq. (10),  $S_{res}(L)$ , to these class points for the resultant ogive (using standard non-linear least square) yields  $L_{50}=38.5$  cm and  $r=0.4$  cm<sup>-1</sup> for all 1995–1997 data (Fig. 6). If catch data for 1997 is omitted  $L_{50}$  decreases slightly but  $r$  increases to  $0.55$  cm<sup>-1</sup> (Fig. 6 top). Both sets of estimates are based on  $M_{\infty}=0.285$  yr<sup>-1</sup>,  $K=0.083$  yr<sup>-1</sup> and  $L_{\infty}=70$  cm.

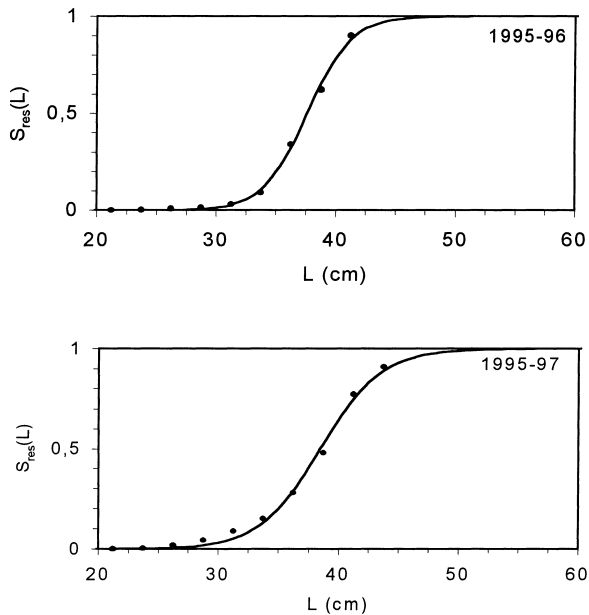


Fig. 6. Estimation of the resultant selection ogive,  $S_{res}(L)$ , for the rod-and-reel fishery of steenbras (*L. aureti*) in Meob Bay, Namibia, from length-based catch curve analysis in a size-dependent mortality regime ( $M_{\infty}=0.285 \text{ yr}^{-1}$ ,  $K=0.083 \text{ yr}^{-1}$ ,  $L_{\infty}=70 \text{ cm}$ ). Points represent (resultant) selection by length obtained as the ratio of number of fish caught to the predicted number had the selection been 100% (see text). The parameters of the fitted logistic curve are  $L_{50}=37.6 \text{ cm}$  and  $r=0.55$  for 1995–1996 catch data, and  $L_{50}=38.5 \text{ cm}$  and  $r=0.4$  for all (1995–1997) catch data.

### 3.4. Robustness and bias of mortality estimation methods

If not specified otherwise results in this section refer to steady-state calculations with the simulation model based on the steenbras related parameter set  $L_{\infty}=70 \text{ cm}$ ,  $K=0.083 \text{ yr}^{-1}$ ,  $r=0.5 \text{ cm}^{-1}$ ,  $L_{50}=38 \text{ cm}$ ,  $M_{\infty}=0.30 \text{ yr}^{-1}$  for the size-specific mortality regime and  $M=0.4 \text{ yr}^{-1}$  for the constant (size-independent) mortality regime. The mortality considerations are independent of the constant annual recruitment level since catches in numbers at length (2.5 cm classes) are calculated in percentages. Note also that the mortality estimates are independent of whether  $t_0=-2.4 \text{ yr}$  or say,  $t_0=0 \text{ yr}$ . The variation in length at age as expressed by the constant coefficient of variation,  $\gamma=CV(L_{age})$ , constitutes a key parameter for method performance and population dynamics.

#### 3.4.1. Method performance in the steenbras case

The methods are producing precise and accurate estimates of mortality,  $M_{\infty}=0.30 \text{ yr}^{-1}$  (Fig. 7(a)) and  $M=0.40 \text{ yr}^{-1}$  (Fig. 7(c)), when the underlying assumption of negligible variation in length at age is fulfilled. The first (low) point on these graphs is somewhat to the left of the regression lines because of too large class interval. These points represent highly left-skewed distributions within the length class starting at 67.5 cm and ending at  $L_{\infty}=70 \text{ cm}$ , which simply are poorly represented by the class midpoint (68.75 cm) because no fish grow beyond  $L_{\infty}$  when  $\gamma=0$ . Moving the points ca. 0.25 cm down (to  $L=68.5 \text{ cm}$ ) place them on the lines in the figures.

Using the wrong estimation method transforms the line into a convex curve (Fig. 7(b)) or a concave curve (Fig. 7(d)) depending on whether the true mortality regime is governed by the  $M_{\infty}$ -scenario or the constant  $M$ -scenario (Appendix A). This results in an overestimate (39%;  $M=0.42$ , Fig. 7(b)) or an underestimate (29%;  $M_{\infty}=0.28$ , Fig. 7(d)) of the mortality for large fish. Unbiased estimates, however, can be obtained by using Eq. (12) and  $L_{repr}=50 \text{ cm}$  (Appendix A). Note that the concave shape of the points in Fig. 7(d) is not very apparent because the first point should be moved somewhat to the right.

In the steenbras case, the coefficient of variation in length at age is not zero ( $\gamma=0$ ; Fig. 7) but almost 12% ( $\gamma=0.116$ ; Fig. 8). Catches in numbers at age are spread out over several length classes with a considerable overlap for consecutive age groups and fish grow beyond  $L_{\infty}$ . The first points (for large fish) deviate the most from a straight line and convex catch curves are formed in all cases (Fig. 8). Both methods underestimate mortality (ca. 10%,  $M_{\infty}=0.27$ , Fig. 8(a); vs. 15%,  $M=0.34$ , Fig. 8(c)). Applying the wrong method gives results ( $M=0.37$ , Fig. 8(b);  $M_{\infty}=0.24$ , Fig. 8(d)) that are consistent with these biased mortality estimates (according to Eq. (12)).

Note that when  $\gamma$  increases (as from Fig. 7 to Fig. 8), the fact that the mortality analyses are restricted to fish  $< L_{\infty}$  will cause catch at length to decrease rather than to increase. The development of the convex catch curves (Fig. 8) must therefore be caused by an interplay between mortality and growth (including individual variability). In the present cases of high mortality-to-growth ratios,  $M_{\infty}/K=3.6$  and  $M/K=4.8$ , occurring simultaneously with a large

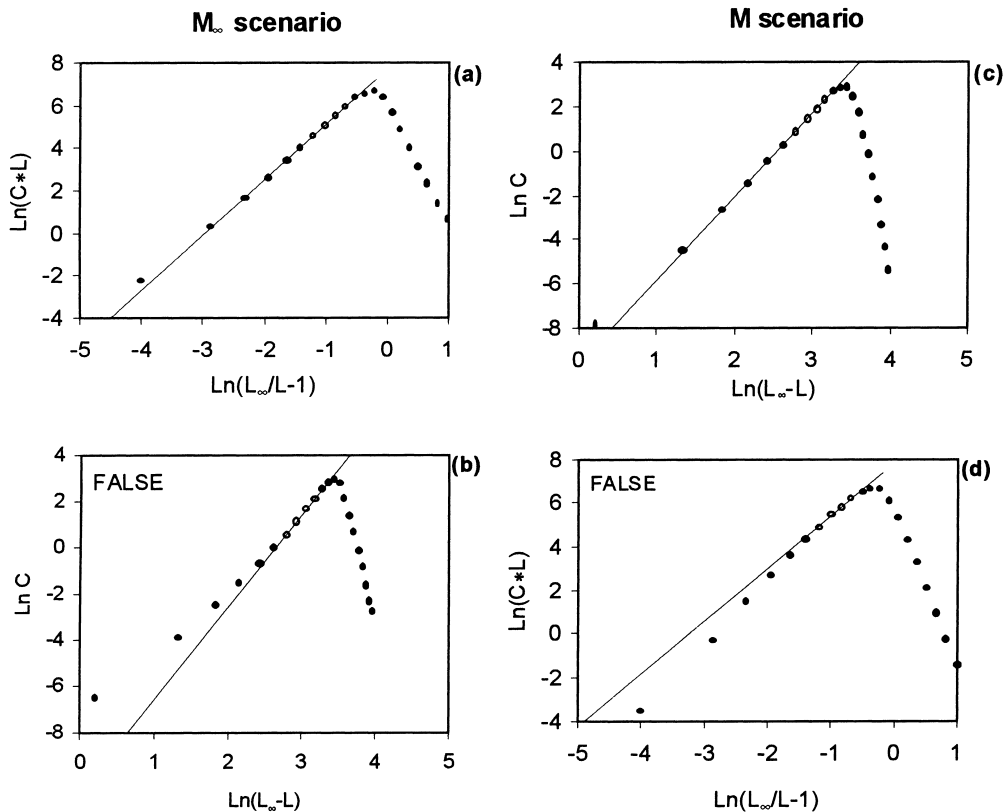


Fig. 7. Performance of the mortality estimation methods in steady state with no variation in length at age ( $\gamma=0$ ) but otherwise based on simulations of the steenbras case. Left panel shows results in the size-dependent mortality scenario  $M_{\infty}=0.3 \text{ yr}^{-1}$  whereas the right panel refers to the constant mortality scenario of  $M=0.4 \text{ yr}^{-1}$ . The four points (open circle) used for regression analyses represent the length range 45–55 cm: (a)  $M_{\infty}$ -method:  $y=2.59x+7.66$ ; (b)  $M$ -method:  $y=4.01x-10.6$ ; (c)  $M$ -method:  $3.78x-8.91$ ; (d)  $M_{\infty}$ -method:  $y=2.42x+7.83$ .

variation in length at age, the decrease in numbers at mean length (from one cohort to the next) is much faster than the decrease in numbers, within a specific cohort, from the mean length to neighboring classes (as described by the rather flat-top of a normal distribution with a CV of 12%). The increase in the catch of large fish in such cases (e.g. the first points in Fig. 8(a) compared to Fig. 7(a)) is therefore mainly due to a ‘new’ catch of big fish of later year-classes, i.e. younger fish of which only the bigger ones have grown to the size considered.

The model with size-dependent mortality does provide a good fit to the tail of big steenbras in the catch distribution (Fig. 9). In this model  $P[L \geq 77.5 \text{ cm}] = 0.00010$ , so on average, the catch of  $n=16\,174$  steenbras should comprise 1.6 fish of  $L \geq 77.5 \text{ cm}$ . In the actual sample  $L_{\max} = \text{ca. } 80 \text{ cm}$ . The number ( $X$ ) of

fish  $\geq 80 \text{ cm}$  in such samples is binomially distributed,  $\text{Bin}(n, p_{80+})$ ;  $p_{80+} = P[L \geq 80] = 0.00004$ , so the probability of catching one or more of these large steenbras is  $P[X \geq 1] = 1 - P[X = 0] = 1 - (1 - 0.00004)^{16174}$  or ca. 50%. Similarly the catch of fish  $\geq L_{\infty}$  is binomially distributed with  $p_{70+} = 0.0011$ , i.e. with mean  $np_{70+} = 18$  and standard deviation  $(np_{70+}(1-p_{70+}))^{1/2} = 4.2$ . Thus, according to the model, relating to a total catch of 16 174 steenbras, (9, 25) is an approximate 95% confidence interval for the number of fish, which will be caught with a length greater or equal to  $L_{\infty}$ . We caught 18 (Fig. 1).

### 3.4.2. Sensitivity to changes and errors in the growth parameters

In steady state, with constant  $L_{\infty}$  and no variation in length at age ( $\gamma=0$ ), the size structure of the popula-

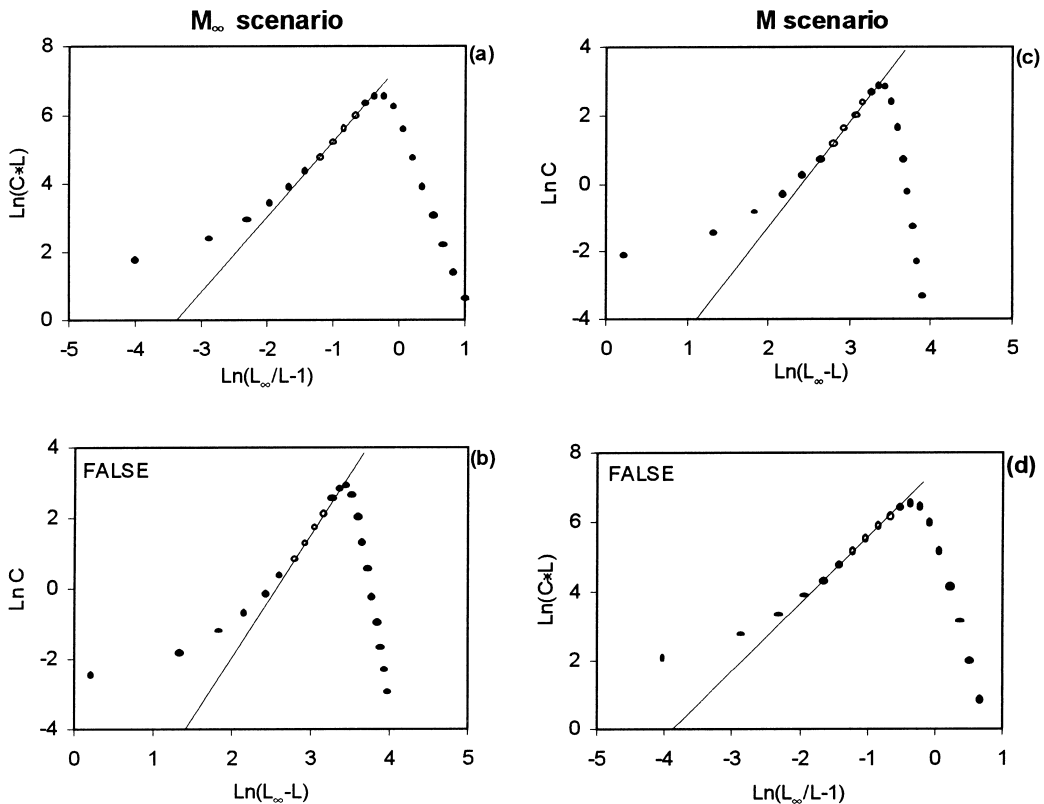


Fig. 8. Performance of the mortality estimation methods in steady state with a considerable variation in length at age simulating the steenbras case ( $\gamma=0.116$ ). Left panel shows results in the size-dependent mortality scenario  $M_\infty=0.3 \text{ yr}^{-1}$  and right panel refers to the constant mortality scenario of  $M=0.4 \text{ yr}^{-1}$ . The four points (open circle) used for regression analyses represent the length range 45–55 cm: (a)  $M_\infty$ -method:  $y=2.21x+7.45$ ; (b)  $M$ -method:  $y=3.48x-8.89$ ; (c)  $M$ -method:  $3.08x-7.40$ ; (d)  $M_\infty$ -method:  $y=1.93x+7.49$ .

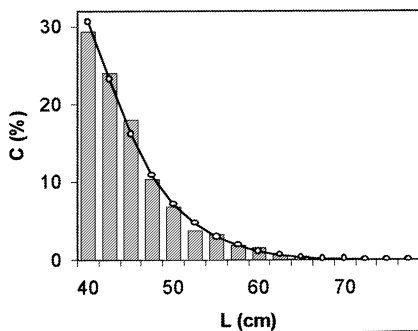


Fig. 9. Catch at length of steenbras (*L. aureti*)  $\geq 40$  cm sampled in Meob Bay, Namibia, throughout 1995–1997 (bars). Equivalent catch percentages (curve) are obtained with the model under steady-state conditions in the size-dependent mortality regime ( $M_\infty=0.285$ ,  $K=0.083$ ,  $L_\infty=70$ ,  $\gamma=0.116$ ,  $r=0.5$ ,  $L_{50}=38$ ). Lengths in 2.5 cm classes (numbers refer to lower class limits).

tion is exclusively determined by  $M/K$  and  $M_\infty/K$  in the constant and size-specific mortality regimes, respectively. For all practical purposes simulations show that this result is also true with a considerable variation in length at age. For example, with  $\gamma=0.1$ , catch length frequencies and, hence, the regression line Eq. (9), remain unaltered when a situation of  $M_\infty=0.3 \text{ yr}^{-1}$  and  $K=0.1 \text{ yr}^{-1}$  is changed into the extreme situation of  $M_\infty=1.2$  and  $K=0.4$  or  $M_\infty=0.15$  and  $K=0.05$  (e.g. the deviations in estimated slopes are less than 1% (not shown)). All such cases of  $M_\infty/K=3$  produce the same length-based population dynamics. If only  $K$  is doubled, however,  $K=0.2 \text{ yr}^{-1}$  and  $M_\infty=0.3 \text{ yr}^{-1}$ , the mortality-to-growth rate ratio is halved,  $M_\infty/K=1.5$ , which drastically changes the length frequency distribution of the sample (Fig. 10). The fish grow twice as fast (as in the

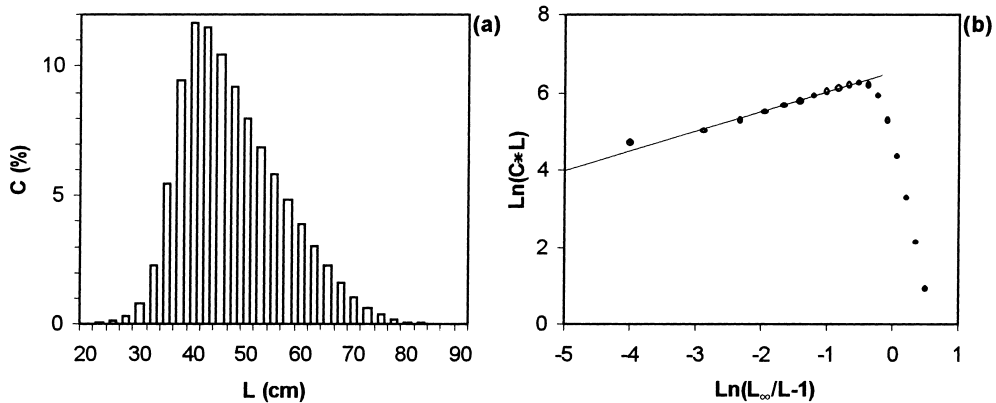


Fig. 10. Steady-state catch representation with  $K=0.2 \text{ yr}^{-1}$  and considerable variation in length at age ( $\gamma=0.1$ ) but otherwise simulating the size-dependent mortality scenario  $M_\infty=0.3 \text{ yr}^{-1}$  in the steenbras case (Fig. 8(a) and (b)): (a) percentage catches at length in 2.5 cm classes (numbers refer to lower class limits); (b) linearized catch curve:  $y=0.508x+6.52$ .

$K=0.1$  case) and succeed in becoming bigger because the mortality regime has not changed. If steenbras were growing at this rate, we would expect  $L_{\text{max}}=88 \text{ cm}$  and  $375 \text{ fish} \geq L_\infty$  in the 1995–1997 sample. Despite this faster growth rate, a considerable overlap in the length ranges of consecutive age groups still exists. The performance of the linearized catch curve method, however, improves considerably (Fig. 10(b)) mainly because of the impact of the low mortality-to-growth ratio.

Another issue concerns the impact of possible errors in the growth parameters used for the linear regressions, Eqs. (6) and (9), on the estimation of mortality. The growth parameter  $K$  only appears in the slopes of these lines which implies that any relative error in  $K$  produces exactly the same error on the mortality estimate,  $(\text{slope}+1)K$ . For example, using a 20% underestimate of  $K$  in interpreting the slope of the line in Fig. 10(b) results also in a 20% underestimate of  $M_\infty$ . The equivalent situation for  $K=0.1 \text{ yr}^{-1}$  results in a 25% underestimate of  $M_\infty$  because the effect of the  $M_\infty/K=3$  (and  $\gamma=0.1$ ) scenario is already an underestimate of  $M_\infty/K$  by 6.4% (not shown). The other growth parameter,  $L_\infty$ , appears only in the log-calculation of the explanatory variables. An overestimate of  $L_\infty$  causes therefore horizontal movements of the points (to the right). The points will move towards creating a concave curve with such increasing  $L_\infty$ -errors because the impact is largest on the biggest fish close to the true  $L_\infty$  (e.g. the first points in Fig. 8(a)

and (c)). Suppose, for example,  $L_\infty=80 \text{ cm}$  is (incorrectly) used for the mortality estimation in the  $M_\infty$ -scenario of Fig. 8(a) (which is truly generated with  $L_\infty=70 \text{ cm}$ ) then a perfectly straight line appears (Fig. 11(a)). The convex shaped (caused by  $\gamma=0.116$ ) is in this case balanced out by the 14% overestimation of  $L_\infty$ . The equivalent straight-line-situation to the  $M$ -scenario of Fig. 8(c) occurs when  $L_\infty=85 \text{ cm}$  is (incorrectly) used (Fig. 11(b)). Both situations turn the ( $\gamma$ -contaminated) underestimates of mortality (Fig. 8(a) and (c)) into overestimates (8.5%,  $M_\infty=0.33$ , Fig. 11(a); 34%,  $M=0.53$ , Fig. 11(b)). In general the  $\gamma$ -effect can be counteracted by an appropriate  $L_\infty$ -error. Simulations show that using the (incorrect) value of  $L_\infty$ , which produces a straight line, improves the estimate of  $M_\infty$  (but not the estimation of a constant  $M$ ). When  $1 < M_\infty/K < 3$  the  $\gamma$ -effect is small (not exceeding a few percent), so only a slight adjustment of  $L_\infty$  is needed for obtaining a straight line. Note that for  $M_\infty/K < \text{ca. } 1.5$ , the  $\gamma$ -effect is a slight overestimate of  $M_\infty/K$  so the adjustment involves an underestimate of  $L_\infty$ . When  $M_\infty/K > 3$ , the bias (underestimate) of  $M_\infty/K$  caused by high  $\gamma$ -values is considerably reduced by this concept of a straight-line- $L_\infty$ . For example, in case of a CV of 15%, the underestimates (due to this  $\gamma=0.15$ ) increase from  $-11\%$  to  $-25\%$  when  $M_\infty/K$  doubles from 3 to 6. However, the overestimates by using straight-line- $L_\infty$ 's (81 and 93 cm, respectively) increase only from 8% to 11%. In these examinations, a straight-line- $L_\infty$

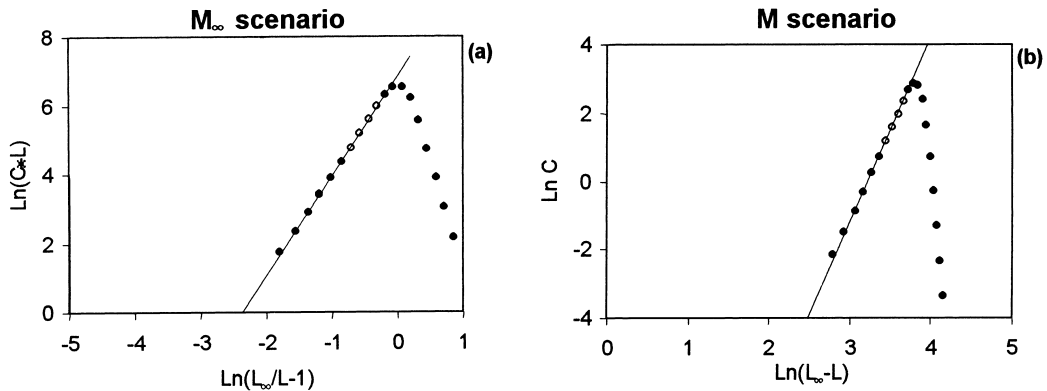


Fig. 11. Apparent excellent performance of the mortality estimation methods in steady state when  $L_\infty$  is overestimated. The scenarios refer to the steenbras case as in Fig. 8(a) and (c) ( $L_\infty=70$  cm,  $K=0.083$  yr $^{-1}$ ,  $\gamma=0.116$ ,  $L_{50}=38$  cm,  $r=0.5$  cm $^{-1}$ ) with (a)  $M_\infty=0.3$  yr $^{-1}$  and (b)  $M=0.4$  yr $^{-1}$ . The four points (open circle) used for regression analyses represent the length range 45–55 cm: (a)  $L_\infty=80$  cm incorrectly used in  $M_\infty$ -method:  $y=2.92x+6.90$ ; (b)  $L_\infty=85$  cm incorrectly used in  $M$ -method:  $y=5.44x+17.5$ .

was obtained as the (incorrect) value of  $L_\infty$  which made the four-points-regression line (i.e. based on range 45–55 cm; e.g. Figs. 7 and 8) coincide with the eight-points-regression line (i.e. based on range 45–65 cm). Using all 10 points (45–70 cm) in the steenbras case (Fig. 5(b)) gives the best straight-line-fit for  $L_\infty=80$  cm resulting in  $M_\infty=0.304$  (not shown). The equivalent case in the simulation model ( $M_\infty=0.285$ ,  $K=0.083$ ,  $L_\infty=70$ ,  $\gamma=0.116$ ) yields  $M_\infty=0.307$ .

Simultaneous errors of opposite direction in the estimation of  $K$  and  $L_\infty$  tend to cancel out in their combined effect on the mortality estimate (Table 2). In extremes situations, however, the errors may give an additive effect. If the slope of the unbiased linearized catch curve, Eq. (9), is negative (i.e. when  $M_\infty/K < 1$ ) then the effect of overestimating  $L_\infty$ , (which always creates a steeper line), becomes one of underestimating  $M_\infty/K$  that will add to the effect of underestimating  $K$ . An example of such a situation is  $M_\infty/K=0.75$ ; the additive error effect pertains for all reasonable values of  $\gamma$  (Table 2), but a sufficiently high  $\gamma$ -value can turn the line down to horizontal level which neutralizes the impact of  $L_\infty$ -errors (e.g. in the  $M_\infty/K=0.75$  case, independently of  $L_\infty$ -errors,  $\gamma=0.25$  implies virtually an unbiased estimate of  $M_\infty$  when  $K$  is 20% underestimated (but creates a 56% overestimate when  $K$  is 20% overestimated)). At the other extreme shown in Table 2,  $M_\infty/K=6$ , more than a 10% overestimate of  $L_\infty$  is

required to counterbalance the impact of  $\gamma$  when  $\gamma > 0.05$ .

### 3.4.3. Sensitivity to recruitment variations

The issue concerning the impact of recruitment variability on the performance of the  $M_\infty$ -estimation method is addressed with reference to a situation of high  $M_\infty/K$  ratio (the steenbras case; Fig. 7(a), Fig. 8(a)) and to a situation of low  $M_\infty/K$  ratio (Fig. 10(b)). Annual recruitment to age zero (Section 2.4) is considered log-normally distributed with a CV of 50%. In the model, each realization of the recruitment process therefore consists of a series of 51 recruitment numbers which represent values of identical and independently distributed (IID) random variables. Using each of such recruitment series as input, the model delivers length-based catch sample and related linearized catch curve analysis for the size-dependent mortality regime considered ( $M_\infty=0.3$ ). Assuming the catch sample refers to 1996, the recruitment series refer to year-class strength for the years 1946–1996. Results are independent of the (constant) level of mean annual recruitment. Results in terms of which year-classes are important for estimating  $M_\infty$ , however, are not independent of  $t_0$ .

For clarification the (unrealistic) situation of no variation in length at age ( $\gamma=0$ ) is first considered. In the steenbras case ( $K=0.083$ ,  $L_\infty=70$ ,  $t_0=-2.4$ ) the length range 45–55 cm was used for obtaining the regression line (Fig. 7(a)). These size limits are

Table 2  
Bias in  $M_\infty$ -estimation due to 10% error in the estimate of  $L_\infty$  and an opposite 20% error in the estimate of  $K$

$M_\infty$ -scenario <sup>a</sup>			Bias in estimation			
			+10% ( $L_\infty$ )	-20% ( $K$ )	-10% ( $L_\infty$ )	+20% ( $K$ )
$\gamma$	$M_\infty/K$	$K$ (yr <sup>-1</sup> )	$M_\infty/K^b$ (%)	$M_\infty$ (%)	$M_\infty/K^b$ (%)	$M_\infty$ (%)
0.025	6.0	0.05	16	-7.1	-23 <sup>c</sup>	-7.2 <sup>c</sup>
0.025	3.0	0.10	8.5 <sup>d</sup>	-13 <sup>d</sup>	-19 <sup>d</sup>	-2.7 <sup>d</sup>
0.025	1.5	0.20	5.7	-15	-11	7.1
0.025	0.75	0.40	-12	-30	7.2	29
0.05	6.0	0.05	11	-11	-25 <sup>c</sup>	-10 <sup>c</sup>
0.05	3.0	0.10	7.5 <sup>d</sup>	-14 <sup>d</sup>	-20 <sup>d</sup>	-3.4 <sup>d</sup>
0.05	1.5	0.20	6.1	-15	-11	7.4
0.05	0.75	0.40	-13	-30	6.7	28
0.1	6.0	0.05	-1.9	-22	-31 <sup>c</sup>	-17 <sup>c</sup>
0.1	3.0	0.10	7.6	-14	-22 <sup>d</sup>	-6.2 <sup>d</sup>
0.1	1.5	0.20	8.4	-13	-9.2	8.9
0.1	0.75	0.40	-15	-32	5.3	26
0.125	6.0	0.05	-7.3	-26	-34 <sup>c</sup>	-20 <sup>c</sup>
0.125	3.0	0.10	4.6	-16	-23 <sup>d</sup>	-8.0 <sup>d</sup>
0.125	1.5	0.20	9.9	-12	-8.3	10
0.125	0.75	0.40	-9.8	-28	8.6	30

Results are based on catch curve analyses with a size-dependent mortality regime (40–55 cm length range used for regressions). Underlying catches at length are produced by the simulation model in steady state.

<sup>a</sup>  $L_\infty=70$  cm,  $M_\infty=0.3$  yr<sup>-1</sup>,  $r=0.5$  cm<sup>-1</sup>,  $L_{50}=38$  cm.

<sup>b</sup> This dimensionless mortality-to-growth ratio is obtained as slope+1 from regressions using (incorrectly) either 77 or 63 cm for  $L_\infty$  (as specified above). Multiplying with the biased estimate of  $K$  gives  $M_\infty$ -estimate in the next column. Only percentage deviations from true values are shown.

<sup>c</sup> Length range 40–50 cm used for regressions (due to shift in the mode).

<sup>d</sup> Length range 42.5–52.5 cm used for regressions.

reached at age 10 and 16 yr, so 1980–1986 are the seven recruitment years of real importance. This was confirmed by simulation (the slope of the line in Fig. 7(a) did not change when recruitment varied in the years 1946–1979 and 1987–96). Simulations with recruitment variations for 1980–1986 yielded  $M_\infty$ -estimates (using the same four points as in Fig. 7(a)) with a CV of 24% and mean  $\bar{M}_\infty = 0.29$ . Extending the length range for the regressions to 10 classes, 40–65 cm, and performing simulations with recruitment variations in all years, 1946–1996, increased the precision (CV( $M_\infty$ )=4.7%, ( $\bar{M}_\infty = 0.293$ ;  $n=50$  realizations)).

With the considerable variation in length at age for steenbras,  $\gamma=0.116$ , later (>1986) as well as earlier (<1980) year-classes may contribute to the four-points  $M_\infty$ -estimation in Fig. 8(a). Considering 95%-confidence limits to determine these contributions gives the

criteria  $L_{lower}(1+2\gamma)=45$  and  $L_{upper}(1-2\gamma)=55$  or  $L_{lower}=36.5$  cm and  $L_{upper}=71.6$  cm. Since on an average fish attains 36.5 cm at age 6.5 yr, year-classes 1987–1989 will contribute to the catch of 45 cm or bigger fish (right-tail effect) and since  $L_{upper} > \bar{L}_\infty$ , all year-classes before 1980 may potentially contribute to the catch of 55 cm or smaller fish (left-tail effect). It was confirmed by simulation that the slope of the line in Fig. 8(a) did not change when recruitment varied in the years 1990–1996. Neither did recruitment variations for 1946–1979 affect the results (CV( $M_\infty$ )=0.5%) because of the high mortality-to-growth ratio,  $M_\infty/K=3.6$ , i.e. negligible catches of smaller but older fish in the 45–55 cm domain. The performance of the  $M_\infty$ -estimation method in Fig. 8(a) is therefore determined by recruitment variations in 1980–1989. Simulations show reasonable precision, CV( $M_\infty$ )=8.6%, and high accuracy,  $\bar{M}_\infty = 0.267 \pm 0.0023$ (SE),

( $n=100$ ). Note that 0.267 is the  $\gamma$ -affected  $M_\infty$ - (under)estimate obtained with constant recruitment (Fig. 8(a)). If the length range for the regressions is doubled the precision improves at the cost of less accuracy ( $CV(M_\infty)=6.4\%$ ,  $\bar{M}_\infty = 0.253 \pm 0.0023(SE)$ , ( $n=50$ ), eight points (40–60 cm)).

Considering the situation of low mortality growth ratio,  $M_\infty/K=1.5$ , in Fig. 10 to represent 1996, the basic catch contribution to length range 45–55 cm comes from only three year-classes, 1989–1991, i.e. ages 5–7 yr due to the higher growth rate ( $K=0.2$ ,  $t_0=0$ ). With  $\gamma=0.1$  (Fig. 10(a)), however, fish bigger than the average for ages 3–4 (1992–1993) and also fish smaller than the average for ages 8–9 (1987–1988) are present in the population in sufficient numbers to contribute to the catches of 45–55 cm fish. The (usual four-points) estimates of  $M_\infty$  change only slightly when recruitment varies for the years 1994–1996 and 1946–1986 ( $CV(M_\infty)=2.0\%$ ,  $n=40$ ). Only the seven years, 1987–1993 (ages 3–9 yr), are important with respect to the impact of recruitment variability on  $M_\infty$ -estimation. The precision of the mortality estimates ( $CV(M_\infty)=29\%$ ,  $\bar{M}_\infty = 0.29 \pm 0.012(SE)$ , ( $n=50$ ), four points (45–55 cm)) increases when the length range for regression is doubled ( $CV(M_\infty)=17\%$ ,  $\bar{M}_\infty = 0.301 \pm 0.0073(SE)$ , ( $n=50$ ), eight points (45–65 cm)).

### 3.5. Application of steenbras mortality analysis to silver kob

The silver kob (*A. inodorus*) stock in Namibia is currently being assessed using cohort analysis (e.g.

Sparre and Venema, 1998). One of the input parameters required for a VPA is an estimate of the rate of instantaneous natural mortality. This fishery model is very sensitive to changes in  $M$  when fishing mortality ( $F$ ) is relatively small, such as for silver kob in Namibian waters. For this application it is assumed that westcoast steenbras and silver kob, of the *same size*, die at approximately the same natural mortality rate. This seems to be a reasonable assumption, as the study of Lorenzen (1996) showed a good correlation between mean weight and the natural mortality rate for fish living in a natural ecosystem i.e. any fish with a certain weight will have approximately the same natural mortality rate. Although westcoast steenbras and silver kob are two different fish species which have different growth rates and might differ in their susceptibility to disease and senescence, this assumption might be feasible since, as implied by Cushing (1974) and Carpenter et al. (1985), the highest contribution to natural mortality is predation. Westcoast steenbras and silver kob basically share the same habitat (viz. the surfzone from Meob Bay north to Cape Frio ( $18^\circ 26'S$ ,  $12^\circ 00'E$ )) and are therefore exposed to the same predators such as sharks and fur seals.

Assuming that kob's natural mortality is governed by a similar natural mortality pattern to that of westcoast steenbras of approximately the same length, the natural mortality of infinite old kob ( $M_\infty \text{ kob}$ ) was calculated as  $0.2 \text{ yr}^{-1}$  by using the following equation:

$$M_\infty \text{ kob} = M_\infty \text{ steenbras} \times L_\infty \text{ Steenbras} / L_\infty \text{ kob},$$

where  $M_\infty$  of westcoast steenbras is  $0.29 \text{ yr}^{-1}$  and

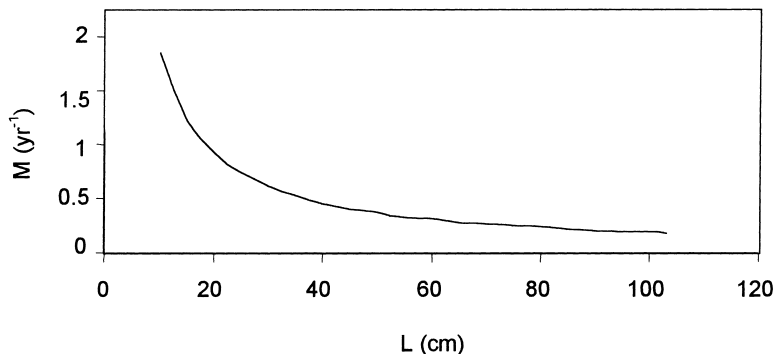


Fig. 12. Natural mortality at length for steenbras (*L. aureti*) and silver kob (*A. inodorus*) assuming these species are exposed to the same size-specific predation mortality,  $M(L)=20/L$ , due to predation from e.g. sharks and fur seals, which is believed to constitute the main component of natural mortality.



$L_{\infty}=70$  cm while  $L_{\infty}$  of kob is 103 cm (own data). Fig. 12 shows size-specific natural mortality of kob obtained in this way (i.e. Eq. (13)).

#### 4. Conclusion and general discussion

An extremely simple size-specific model of natural mortality is considered as an alternative to the usual assumption of a constant value of natural mortality for all sizes,  $M$ . Mortality is considered inversely proportional to length and the model is completely specified by  $M_{\infty}$ , the mortality at  $\bar{L}_{\infty}$ , the mean length at old age. This model can explain in detail the tailing-off in the length frequencies of samples of mature fish from an unexploited population of westcoast steenbras. It accounts for high numbers of smaller fish in the population and thus provides good descriptions of the apparent selection ogive using the Pauly (1984a) concept of resultant curve. In general the model can explain the one in a million survival which governs recruitment to most fish stocks (Beyer, 1989: Example 1).

Simple, linearized and length-based catch curve methods are presented to estimate the mortality-to-growth ratios,  $M/K$  and  $M_{\infty}/K$ , which determine the length structure of the population in the constant and size-specific mortality regimes, respectively. The methods are developed under the traditional assumptions of steady-state conditions and no variations in length at age,  $CV(L_{age})=\gamma=0$ , and furthermore require that  $\bar{L}_{\infty}$  is known. Under these conditions the methods result in precise and accurate ratio-estimates. In general, however, lengths of individual fish of the same age are characterized by a considerable CV, probably around 10%, and the straight lines turn into convex curves. Considering 10% precision criteria and applying the methods with the insight gained from simulations, the bias caused by this CV-effect is not serious when  $1 < M_{\infty}/K < 3$ . Higher values of  $M_{\infty}/K$  lead to serious underestimates when CV exceeds 10%. In general the bias can be reduced to acceptable limits by applying the straight-line –  $\bar{L}_{\infty}$  method, i.e. using the value of  $\bar{L}_{\infty}$  which counteracts the CV-effect thereby producing a straight line catch curve. This is important because it allows for the estimation of the fundamental length-based mortality concept,  $M_{\infty}/K$ , without prior knowledge on growth. Straightforward

modifications of “the Jones length-based (pseudo)cohort analysis” (Jones, 1976; Jones and van Zalinge, 1981; reviewed in Jones, 1984; Pauly, 1984b; and Sparre and Venema, 1998) show that knowledge of  $M_{\infty}/K$  alone is sufficient for carrying out length-based VPA (steady state) for exploited stocks under various  $L_{\infty}$ -scenarios with size-specific natural mortality. Thus total annual catch by length and an estimate of  $M_{\infty}/K$  constitute the minimum data requirement for performing complete fish stock assessments and yield predictions. Work on this important issue for tropical fish stock assessment and related CV-effects is in progress.

##### 4.1. Methods

The constant CV-growth model (Beyer and Lassen, 1994) provides in a first approximation a description of the combined effects of an extended spawning season and individual variability in growth. CV ( $=\gamma$ ) constitutes an important parameter of population dynamics. Unfortunately, values of CV are seldom reported in the literature although such values are readily obtained (and available) for most stocks either by analyzing length at age (Fig. 3) or from Bhattacharya analyses and related methods for splitting a composite length distribution into separate normal distributions (Sparre and Venema, 1998, and references herein). Myers (1989) found an average CV of ca. 12% for cod but also that CV tends to increase with older age; a phenomenon which may have general validity as e.g. individual-based stochastic simulation models of growth often reveals this feature (e.g. Beyer and Laurence, 1980). This may imply an even greater CV-effect than demonstrated in this study. Although the constant CV-growth model is not intended to consider individual growth trajectories as smooth VBGE-curves, the implication of the model is that an individual of length  $L_{0i}$  at age 0 attains length  $L_i(t) = L_{0i} \times \bar{L}(t)/\bar{L}_0$  at age  $t$  where  $\bar{L}(t)$  is the mean length at age  $t$  in the cohort (Eq. (11)) and  $\bar{L}_0$  similarly denotes the mean length at age 0. Thus, in the constant CV model, individuals are considered to grow with the same  $K$  but with individual values of  $L_{\infty}$  and they all grow with the same specific growth rate (because the relationship above implies  $L_i^{-1}dL_i/dt = \bar{L}^{-1}d\bar{L}/dt$ ). Disregarding very small fish it should be mentioned that mean size at age for all practical purposes is not

affected by the size-selective mortality used in this study.

An important aim of this paper has been to use and apply simple methods and deterministic models rather than to optimize the various statistical estimation procedures. It is clear that under more realistic assumptions concerning the variation of individual growth rates, estimation procedures for the growth parameters can be improved (Sainsbury, 1980; Francis, 1988). The linearized catch curve, Eq. (9), also possesses simplicity at the cost of introducing some interdependency between  $x$  and  $y$  (created through the dependency in both  $x$  and  $y$  on the class midlengths). The effect of this type of  $x$ - $y$ -interdependence (which also occurs in many of the traditional methods of fish stock assessment) can be neglected in most applications.

The (length-based) mortality estimation methods are based on fewer approximations than the traditional length-converted catch curve (Sparre and Venema, 1998). Our methods appear robust for most species as Beverton and Holt (1959) found that the ratio  $M/K$  mostly lies in the range of 1.5–2.5. The sensitivity of  $M_\infty$ -estimates to opposite errors in the estimates of  $K$  and  $\bar{L}_\infty$  is relatively small (Table 2). This analysis is based on “the Pauly empirical phi-prime formula” (e.g. Pauly and Munro, 1984), which can be expressed as  $K \propto L_\infty^{-2}$  (where the coefficient of proportionality is almost constant within closely related fish species). Applying this formula to independent trials of estimating the growth parameters based on different length frequency samples for the same species (had these been available) implies that e.g. a 10% overestimate of  $L_\infty$  is likely to be accompanied by a 20% underestimate of  $K$ . The considerable recruitment variations obtained with a CV of 50% is likely to represent the right order of magnitude for most species (Mertz and Myers, 1996). The mortality estimates are relatively insensitive to this variation unless  $M_\infty/K$  attains low values in which case it is important to stabilize the estimation procedure by including the points representing the large fish (but  $<L_\infty$ ) in the regression although these points are based on fewer fish. For large values of  $M_\infty/K$  the estimation procedure can instead be sensitive to the CV- or  $\gamma$ -effect but then the straight-line- $L_\infty$  method is recommended. Note that this method does not work for the estimation of  $M/K$  in case of constant mortality.

## 4.2. Case study

This study provides the first estimates of growth and mortality of westcoast steenbras reported in the literature. The only scientific ageing and growth study done on westcoast steenbras in the past comprised 82 otolith readings by Lucks (1970). Unfortunately, the underlying method of ageing was not documented clearly and neither did Lucks (op.cit.) attempt to obtain estimates of the growth parameters based on his tentative age-length key. With fish attaining lengths of 40 cm and more at age 1 and ca. 75 cm at age 6 yr, his results indicate a growth rate which is at least three times faster than we have estimated for Meob Bay steenbras. It is understandable, however, that the results by Lucks (op.cit.) would be somewhat different from ours because he collected his steenbras samples from a different population (Van der Bank and Holtzhausen, unpublished genetic data). Considering mortality, it is not possible to make a clear differentiation between the two regimes considered (Fig. 5) although the  $M_\infty$ -scenario appears slightly more convincing than the  $M$ -scenario (i.e. by comparing Figs. 5 and 8). This is because the differences between applying true and false methods happen to be very small for *both* scenarios in this case (Fig. 8(a) vs. Fig. 8(d); Fig. 8(c) vs. Fig. 8(b)). Our present knowledge of  $M_\infty$ ,  $K$ ,  $\bar{L}_\infty$  and  $\gamma$  conforms to the constant CV-growth model, explains the observed  $L_{\max}$  and provides an adequate description of the length structure for 40+ cm in the 1995–1997 total sample of more than 16 000 steenbras. The independent results from tagging are also in agreement with these growth estimates. As we, in the model, are considering  $K$  constant but  $L_\infty$  to vary at the individual level, the mark-recapture data in Table 1 could alternatively be used to estimate  $\gamma$  and  $\bar{L}_\infty$  assuming  $K$  fixed (i.e. solving Eq. (2) with respect to  $L_\infty$ ). This gives results in good agreement with the age-length data, e.g.  $\gamma=0.12$  and  $\bar{L}_\infty = 69$  ( $n=18$ ) with  $K=0.08$ .

Several issues need further clarification. This includes the relatively high (negative) value of  $t_0$  (–2.4 yr for a long-lived species), seasonality in growth as well as the bimodality in the length frequencies for 1995 and 1997 (Fig. 1). The bimodality can be explained by recruitment variations using the simulation model (not shown). However, westcoast steenbras is a protandrous species and it is likely that

this complicated life history adds to the natural variations, in particular during immature growth and the transient stages. The controversial issue of hook selectivity also needs further experimentation and studying in continuation of the present pilot experiment (Fig. 2) although many authors do use the trawl-type of selection curves (e.g. Booth and Buxton, 1997; Griffiths, 1997) as also suggested by the results from this study. Work on these and related issues of the population dynamics of westcoast steenbras is in progress.

The application of the steenbras mortality analysis to other species sharing the same habitat (Section 3.5) appears promising. Griffiths (1997) determined instantaneous natural mortality for the two South African *A. inodorus* stocks by using relationships among life history parameters (viz. Gunderson and Dygert, 1988; Boudreau and Dickie, 1989; Hoening, 1983). He assumed that  $M$  is between 0.1 and 0.2 yr<sup>-1</sup>, which seems to be a reasonable estimate as an input parameter for the yield-per-recruit model, as fishing mortalities for the South African silver kob stocks are high (e.g. ranging between 0.37 and 0.47). One of the future objectives of the assessment of the Namibian kob stock would be to investigate the effect that the protection of young fish would have on the total biomass. Therefore it is the value of  $M$  at the time of recruitment that would be important, and currently no information on the value of  $M$ , and in particular on size-specific  $M$ , is available for silver kob off the Namibian coast.

While e.g. the mark-recapture results indicate that the Meob Bay area has a closed population of west-coast steenbras, the same assumptions cannot be made of the kob population. Recaptures recorded elsewhere of kob marked-and-released in the Meob Bay area suggest that part of (if not all) kob move out of the area for at least a certain time of the year. Mark-and-release surveys indicate that kob move out of the area with the onset of winter in May/June, only to return with the onset of summer in November/December. Therefore, using “catch curve analysis” to estimate  $M$ , could not be applied, as the estimate of  $Z$  would contain an unknown migration coefficient.

In conclusion, it can be said that traditionally in most stock assessment models, only a “guesstimate” of average natural mortality is used currently in single-species assessments. Such an assumption of size-independent  $M$  is probably sufficient where only the

adult stock is considered (in particular for smaller species), but, being able to estimate natural mortality for a certain size class, will improve the accuracy of the assessment, in particular when dealing with a large range of body-sizes for larger species (i.e. slow-growing and long-lived species).

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## Appendix A

### *Relationships between mortality estimates*

The linearized length-based catch curves, Eq. (6) for  $M$  and Eq. (9) for  $M_\infty$ , were derived as approximations under the assumption that the impact of variation in length at age can be neglected. In this appendix these curves are considered to represent exact relationships between catch at length ( $C$ ) and length ( $L$ ) for the respective mortality regimes. First, assuming that mortality is size-dependent as specified by Eq. (1), Eq. (9) states

$$\ln(CL) = \text{constant} + (M_\infty/K - 1) \ln(L_\infty/L - 1)$$

or by taking the logarithms,

$$\begin{aligned} \ln C = \text{constant} + (M_\infty/K - 1) \ln(L_\infty - L) \\ - M_\infty/K \ln L, \end{aligned}$$

where  $y = \ln C$  is the dependent variable and  $x = \ln(L_\infty - L)$  is the explanatory variable if the method of constant  $M$ , Eq. (6), is (incorrectly) used. Hence  $L = L_\infty - e^x$ , so

$$y = \text{constant} + (M_\infty/K - 1)x - M_\infty/K \ln(L_\infty - e^x).$$

The change in the slope of this curve is given by

$$\frac{dy}{dx} = \frac{M_{\infty} L_{\infty}}{K L} - 1, \quad L = L_{\infty} - e^x.$$

The minimum slope is  $M_{\infty}/K-1$  and occurs when  $L=L_{\infty}$ . Thus, when the traditional constant  $M$ -method expressed as

$$\ln C = \text{constant} + (M/K - 1) \ln(L_{\infty} - L)$$

is used in the size-dependent mortality regime, the result becomes a convex curve with slope that reflects this increase in mortality for the smaller fish, i.e. the slope of the curve starts by producing the minimum,  $M=M_{\infty}$  for the very large fish, but then increases,  $M=M_{\infty}L_{\infty}/L$ , as  $L$  decreases (Fig. 7(b)). In practice, however, it is not feasible to use the minimum slope for estimating  $M_{\infty}$  because of the impact of  $CV>0$  (for length at age) (Fig. 8(b)) and the uncertainty in the catch representation of the larger fish in the population. Instead it is better to consider the other extreme where the impact of the unavoidable variation in length at age (i.e.  $\gamma>0$ ) is minimum and use the maximum slope (occurring for small but fully recruited fish), i.e.  $M_{\infty} = K(1 + \text{maximum slope})\bar{L}_{\text{repr}}/L_{\infty}$  where  $\bar{L}_{\text{repr}}$  denotes the representative mid-length for the small fish used in the  $M$ -regression.

Similar considerations apply to a constant mortality regime if the size-dependent  $M_{\infty}$ -regression is (incorrectly) used. In this case,  $y=\ln(CL)$  and  $x=\ln(L_{\infty}/L-1)$ , the slope becomes

$$\frac{dy}{dx} = \frac{M L}{K L_{\infty}} - 1, \quad L = L_{\infty}/(1 + \exp(x)),$$

which produces a concave curve (Fig. 7(d)). The maximum slope (occurring for very large fish) represents the correct mortality,  $M_{\infty}=M$ , but as  $L$  decreases the slope must also decrease to produce smaller  $M_{\infty}=ML/L_{\infty}$  which reflects the constant (size-independent) mortality.

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