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AGE AND GROWTH OF TWO POPULATIONS OF WEST COAST STEENBRAS *LITHOGNATHUS AURETI* IN NAMIBIAN WATERS, BASED ON OTOLITH READINGS AND MARK-RECAPTURE DATA

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Age and growth of West Coast steenbras *Lithognathus aureti*, sampled from two separate populations (northern and southern) along Namibia's coast, was determined using sectioned otoliths, and the results were validated using mark-recapture data. For both populations, the special three-parameter Von Bertalanffy growth model described growth adequately. Growth of the southern population was described by the equation $L_t = 73.556(1-e^{-0.065(t+3.92)})$ cm and for the northern population by $L_t = 84.601(1-e^{-0.088(t+2.756)})$ cm. Environmental conditions, such as difference in sea surface temperature, density-dependent competition for food, or biochemical genetic variations between the two populations, are possible reasons for the geographic differences found in the growth rates and length-at-age. Slow growth and longevity are characteristics of West Coast steenbras that make it extremely susceptible to overfishing; careful management of the resource is therefore essential.

Key words: age, growth, mark-recapture, otoliths, West Coast steenbras

The West Coast steenbras *Lithognathus aureti* is a large protandrous sparid inhabiting the surf zone of the Namibian coast (Smith 1968, Lucks 1970). The total annual catch in 1997 was estimated at 245 tons by shore-anglers and 97 tons by commercial linefishing boats; it is therefore the second most important species caught by the former sector and the third most important species landed by the latter. Surprisingly, growth rate, a parameter essential for stock assessment and for understanding the life history of the species, has only recently been determined accurately, by Holtzhausen (1999).

As growth overfishing can easily occur in long-lived species, such as members of the Sparidae, growth information is important for evaluating the status of such fish stocks (Baker *et al*. 1991). Slow growth results in a lower yield per unit stock, an older age at maturity and a slower recovery rate after overexploitation than in fast-growing species (Buxton and Clark 1989). Also, fisheries based on slow-growing species are extremely susceptible to overfishing, so careful management of such fish stocks is essential.

The only previous attempt at age determination of this species was by Lucks (1970), who determined the age of 82 West Coast steenbras from Sandwich Harbour (24°46´S, 14°29´E). Unfortunately, that author did not specify whether scales or otoliths were used in the analysis, or whether fork or total length was measured. A genetic study by Van der Bank and Holtzhausen (1998/99) confirmed the existence of two separate populations in Namibian waters, a closed population in the southern region, and a separate population in the central and northern regions. Beyer *et al*. (1999) estimated the coefficient of variation of length-at-age by analysing age-length data derived from preliminary otolith readings from the southern West Coast steenbras population. In the present study, age-length and mark-recapture data were used to describe growth for both the northern and southern steenbras populations.

MATERIAL AND METHODS

Age determination

Biological data were collected routinely between March 1995 and July 1999 during tag-and-release excursions conducted from Meob Bay (24°40´S, 14°42´E) to the mouth of the Kunene River (17°14´S, 11°45´E).

Samples collected from the northern and central regions were pooled, because West Coast steenbras from these two regions are believed to be from the same population (Van der Bank and Holtzhausen 1998/99). Fish were measured (fork length *FL*) to the nearest 0.5 cm and weighed to the nearest 10 g. The

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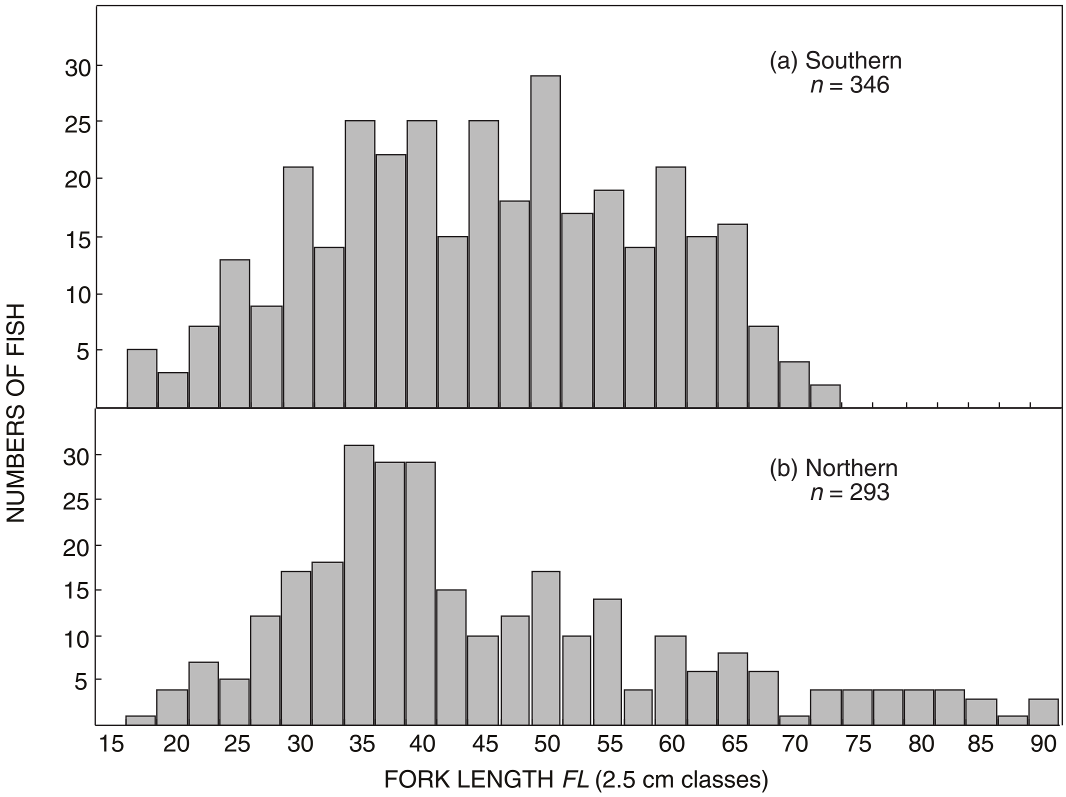

Fig. 1: Length frequencies of West Coast steenbras sampled (excluding fish lengths from rejected otoliths) for growth determination from (a) the southern and (b) the northern population off Namibia

sex of all fish was noted, and both sagittal otoliths were removed. In all, 372 fish were sampled from the southern and 314 from the northern population.

Otoliths were cleaned and dried. The right otolith was lightly heated over a spirit flame until golden brown to enhance definition of growth zones. Care was taken not to char the otoliths, because this tended to obscure growth patterns, particularly near the outer edges. Otoliths were then mounted in rods of clear casting resin and thin-sectioned through the nucleus (to a thickness of about 0.5 mm) by means of a low-speed saw fitted with a single, diamond-tipped blade. Sections were mounted on clear-glass slides.

Sectioned otoliths from fish <30 cm were difficult to read because the hyaline and opaque bands were very close together. A subsample was therefore read whole, while immersed in water, under transmitted light. The results agreed with sectioned otolith readings. Sectioned otoliths were viewed under transmitted light at a magnification of 4.5×. Only the otolith serial number (not *FL*) was known to the reader. Two separate readers read each otolith three times, approximately one week apart. If four of the six readings agreed, the count was accepted as the age. If not, the otolith was rejected.

Annuli were counted starting from the nucleus outwards, assuming that each consecutive hyaline band (dark), separated by an opaque band, accounted for one year. If a reading included half a year, the number was rounded down. Age-length keys were used to transform the length-frequency distributions to age-frequency distributions.

Modelling

Length-at-age was modelled using the three-parameter Schnute (1981) growth model to determine which sub-model (e.g. the normal Von Bertalanffy growth function) could adequately describe the observed data. These data were fitted following the relative error method, which considers that the size of the

Table I: Age-length key for West Coast steenbras from 1 to 32 years old in 2.5 cm length-classes (n = 346) sampled from the southern population off Namibia, 1995–1997

Fork length *FL* interval (cm)	Age (years)																														All ages
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	30	32	
15.0–17.49	3	1																													4
17.5–19.99	2																														2
20.0–22.49		6	2																												8
22.5–24.99		9	3																												12
25.0–27.49		2	8																												10
27.5–29.99		1	8	5	2																										16
30.0–32.49			2	5	9	2	1																								19
32.5–34.99				5	5	9	1																								20
35.0–37.49				2	6	9	8	2	1																						28
37.5–39.99					1	5	2	5	2	2		1																			18
40.0–42.49						1	1	5	6	3	4	2																			22
42.5–44.99						2	2	1	3	3	1	5	1																		18
45.0–47.49								1	1	1	3	6	4	2		1		2													21
47.5–49.99								3	2		1	3	1	2	4	2	1	2		2	1			1							25
50.0–52.49											1	3	2	2	2	5	4	2	1	1	1										24
52.5–54.99												1		4	4	2	3														14
55.0–57.49												1		2	3	3		1		1	2	5	1	1							20
57.5–59.99													1			3	1	2		1	3	1									12
60.0–62.49															3		1		1	2		3	5	4	1				1		21
62.5–64.99																1	1	1	1	1	5	3		2	1	1					17
65.0–67.49																	1				1	1	1		1	1	1	1		1	9
67.5–69.99																							1	1							2
70.0–72.49																		1						1	1					1	4
All lengths	5	19	23	17	23	28	15	17	15	9	10	22	9	12	16	17	12	11	3	8	13	13	8	10	4	2	1	1	1	2	346

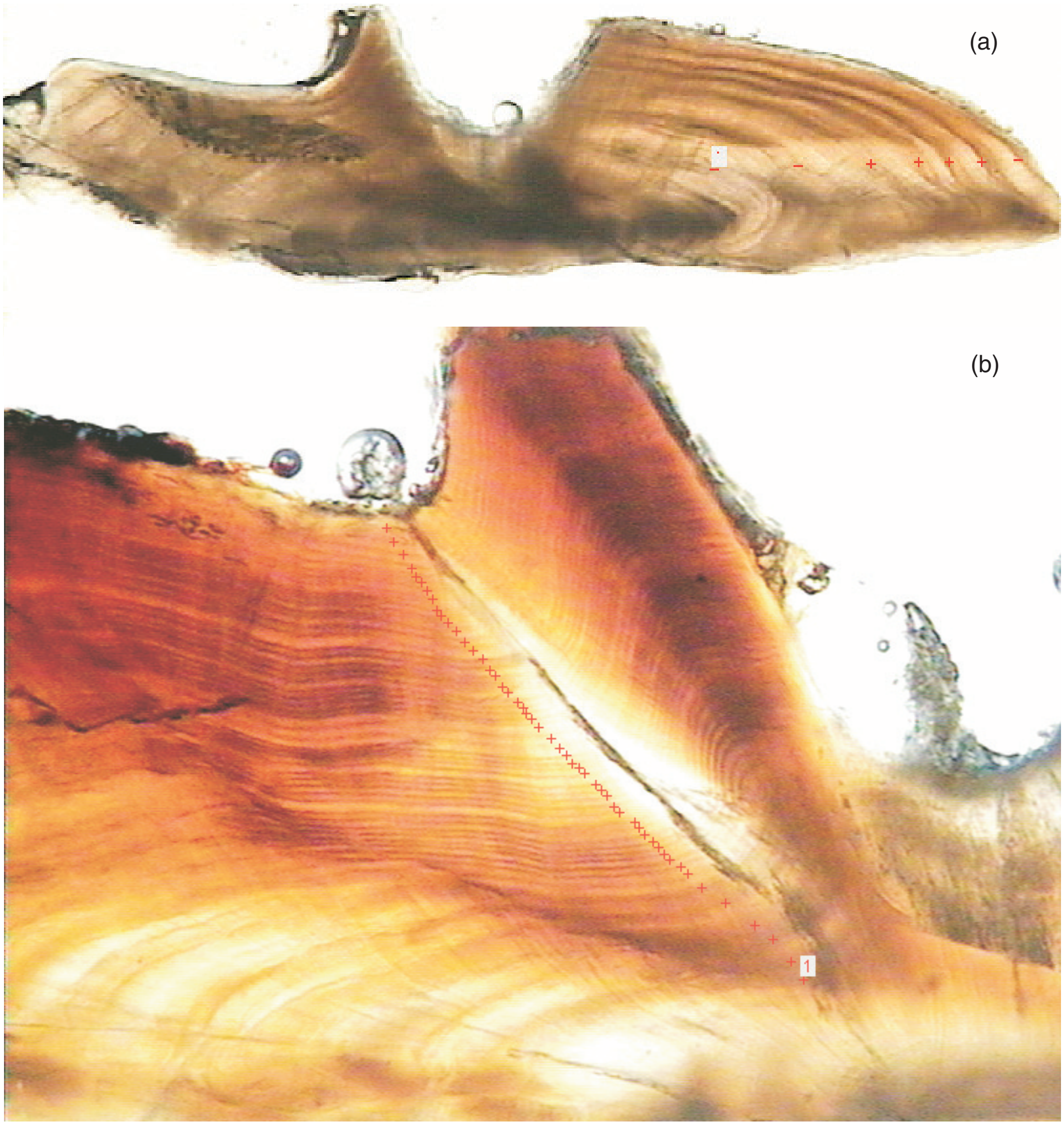

Fig. 2: Photomicrographs of sectioned saggital otoliths of West Coast steenbras viewed under transmitted light – (a) a 7-year-old from the southern and (b) a 50-year-old from the northern population. Growth zone stacking in the otolith of the older fish is clear

residual increases with age.

Confidence limits (95%) and standard errors (*SE*s) for each parameter of the model were calculated using the percentile method (500 bootstraps, Efron 1981). The models were fitted using PC-Yield 2.2 (Punt 1992) to obtain parameter estimates for the selected growth model. Some of the criteria followed during the analysis were randomness, no systematic trends in the lowest sum-of-squared residuals, and credible L_∞ values that were close to but lower than the observed maximum length. The differences in growth rate between the two populations were compared by means of a likelihood-ratio test, as described by Draper and Smith (1966).

Validating age estimates using mark-recapture data

A total of 33 410 West Coast steenbras was tagged and released along the Namibian coast. Of these, 615 were recaptured, of which 328 were measured accurately enough to calculate growth rate. In all, 188 of these recaptures were from the southern and 140 from the northern population. To avoid possible bias on estimating mean annual growth rate as a result of, for example, seasonality in growth, recaptured fish that were at liberty for less than one year were excluded from the analysis. Consequently, 82 recaptures from the southern and 28 from the northern population were used in the analysis.

It was assumed that the Von Bertalanffy growth function would adequately describe the growth of these recaptured fish and that the growth rate (K) could be determined from the equation

$$K = 1/t \times \ell n([L_\infty - L_1] / [L_\infty - L_2]) \quad , \qquad (1)$$

where t denotes days at liberty, L_1 is fish length at first capture and L_2 is fish length at recapture. The asymptotic length (L_∞) was set at 73 cm for the southern population and at 84 cm for the northern population; these values were estimated from the otolith-based method. The value of K (the rate at which the asymptote is approached) was estimated for each recaptured fish and the mean was calculated for each population. To test the sensitivity of these estimates, the 95% confidence intervals of L_∞ for each population were estimated. The differences in K between the two populations were compared by likelihood ratio tests (Draper and Smith 1966). Von Bertalanffy growth curves $L_t = L_\infty(1 - e^{-K(t-t_0)})$ were fitted using an iterative least squares procedure.

The median monthly sea surface temperatures recorded by satellite data (Ministry of Fisheries and Marine Resources, unpublished) for the Meob Bay area in the south and the Rocky Point (18°59´S, 12°28´E) area in the north were plotted and applied in searching for possible reasons for differences in growth rate between southern and northern populations, should they occur.

RESULTS

Of the otoliths examined, 26 (7%) were rejected from the southern population of West Coast steenbras and 21 (6.7%) from the northern population. During the study period, only 14 fish ≥70 cm *FL* were caught from the southern population (Fig. 1a). Of these, nine were analysed for age and five had no discernible male or female gonads. However, large steenbras were more frequently encountered in the northern population; of the total of 2 201 caught, 35 were ≥70 cm (Fig. 1b).

After the otoliths had been heated and sectioned, a broad opaque nucleus surrounded by alternating narrow opaque and broader hyaline zones became clear (Fig. 2). Otoliths from the southern population were more difficult to read than those from the northern population, because the opaque and hyaline bands were narrower and less obviously differentiated.

No specimens older than 32 years (length-class 70–72.49 cm – Table I) were found in the southern population, whereas the oldest fish in the northern population was estimated to be 50 years (length-class 82.5–84.99 cm – Table II). One-year-old fish were found in only the 15–19.99 cm length-class in the southern population, whereas such fish were from 15 to 29.99 cm in the northern population. Fish 35–37.49 cm long from the southern population were between 4 and 9 years old, whereas this length-class was represented by fish 2–5 years old in the northern population. The greatest age spread in the southern population was in the 47.5–49.99 cm length-class, ages ranging between 8 and 24 years. Ages in the same length-class in the northern population ranged between 5 and 8 years. In the northern population, the greatest age spread was in the 75.0–77.5 cm length-class, ages ranging between 18 and 33 years. Fish of that age range were in the 70–72.49 cm length-class in the southern population.

West Coast steenbras are protandric (Holtzhausen 1999), so length-age data for the sexes were pooled. Growth was best described by the three-parameter Von Bertalanffy model for both the southern (Fig. 3a: $F = 1.644$, $p < 0.05$) and northern populations (Fig. 3b: $F = 12.178$, $p < 0.05$). 95% confidence intervals were then estimated by multiplying mean length by ($1 \pm 2\gamma$), where γ is the coefficient of variation in length-at-age. Following Beyer *et al.* (1999), the constant coefficient of variation in length-at-age ($\gamma = 0.091$ and 0.110 for the southern and northern population respectively) was derived from the standard deviation of relative residuals.

The value of K using mark-recapture data and an L_∞ of 73 cm ranged between 0.016 and 0.128 (mean 0.0671; $SE = 0.005$) for the southern population, when omitting two outliers (Fig. 4a). For the northern population, K ranged between 0.039 and 0.173 (mean 0.102; $SE = 0.005$) at an $L_\infty = 84$ cm, when omitting three outliers (Fig. 4b). These results suggest a considerable difference between the growth rates of West Coast steenbras from the southern and northern populations off Namibia. This was confirmed by the results of a likelihood ratio test ($F_{(3;\ 633)} = 311.8$,

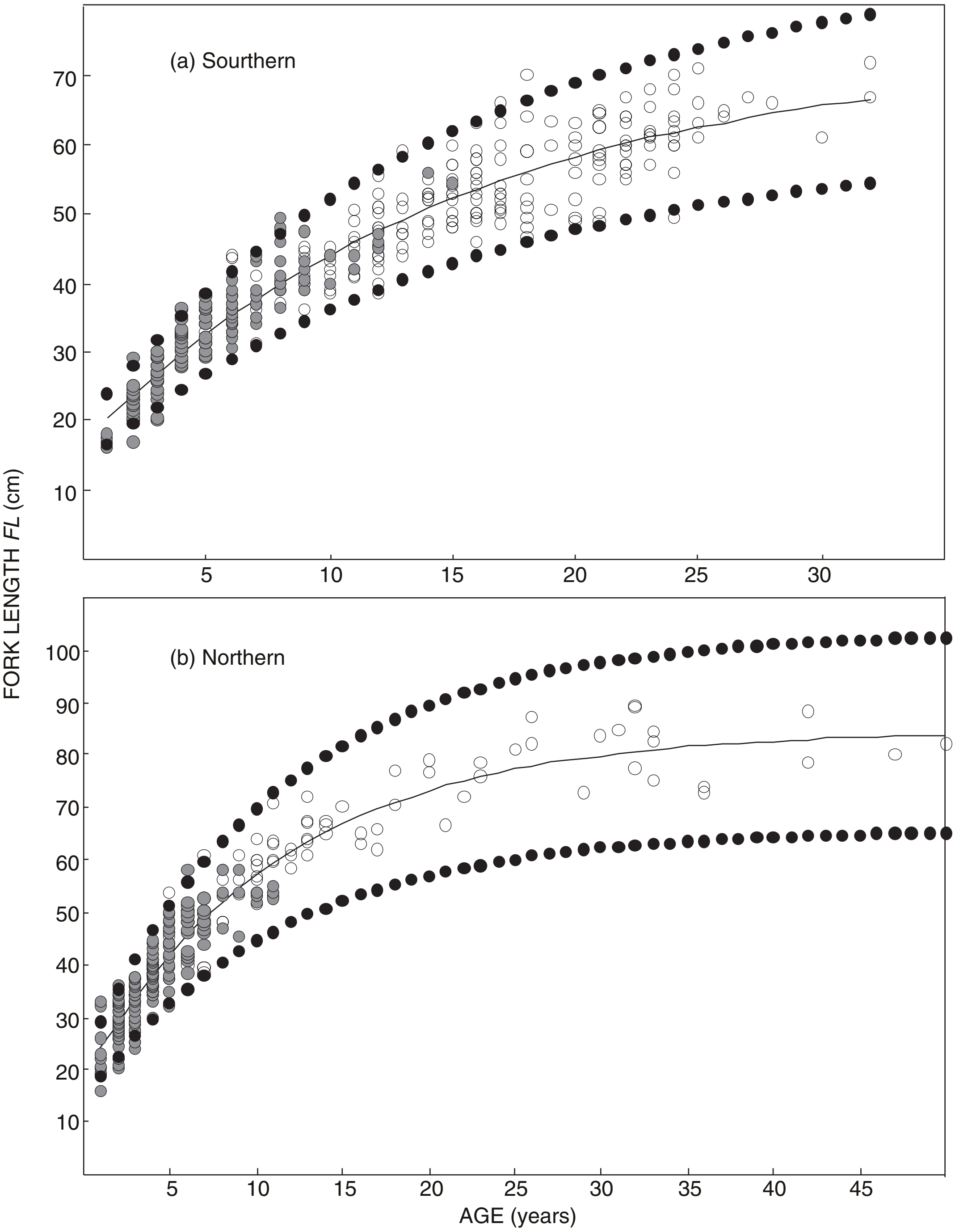

Fig. 3: Observed age-length data (open circles), fitted Von Bertalanffy growth curves (solid line) and approximate 95% confidence intervals for length-at-age (dotted curves) for West Coast steenbras sampled from (a) the southern and (b) the northern population. The constant coefficient of variation in length-at-age is estimated as the standard deviation of these relative residuals

Table II: Age-length key for West Coast steenbras from 1 to 50 years old in 2.5 cm length-classes ($n = 293$) sampled from the northern population off Namibia, 1996–1998

Fork length *FL* interval (cm)	Age (years)																																	All ages
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	20	21	22	23	25	26	29	30	31	32	33	36	42	47	50	
15.0–17.49	1																																	1
17.5–19.99	2																																	2
20.0–22.49	3	5																																8
22.5–24.99	1	2	1																															4
25.0–27.49	1	8	3																															12
27.5–29.99		11	3																															14
30.0–32.49	1	12	4	1	1																													19
32.5–34.99	1	12	11	3																														27
35.0–37.49		2	10	17	4																													33
37.5–39.99			3	17	2	1	4																											27
40.0–42.49				11	3	6																												20
42.5–44.99				4	5	1	1																											11
45.0–47.49					5	2	2	1	1																									11
47.5–49.99					3	5	6	2																										16
50.0–52.49					1	4	2			2																								9
52.5–54.99					1		2	2	2	5	4																							16
55.0–57.49								1	1	2	1																							5
57.5–59.99						1		2	1	1	1	1																						7
60.0–62.49							1		1	2	1	2	1				1																	9
62.5–64.99										1	2		2			1																		6
65.0–67.49													1	2		1	1			1														6
67.5–69.99													1	1																				2
70.0–72.49											1		1		1			1			1													5
72.5–74.99																									1					2				3
75.0–77.49																		1	1			1							1					4
77.5–79.99																			1			1						1			1			4
80.0–82.49																							1	1								1	1	4
82.5–84.99																										1				2				3
85.0–87.49																								1			1							2
87.5–89.99																												2			1			3
All lengths	10	52	35	53	25	20	18	8	6	13	10	3	6	3	1	2	2	2	2	1	1	2	1	2	1	1	1	3	3	2	2	1	1	293

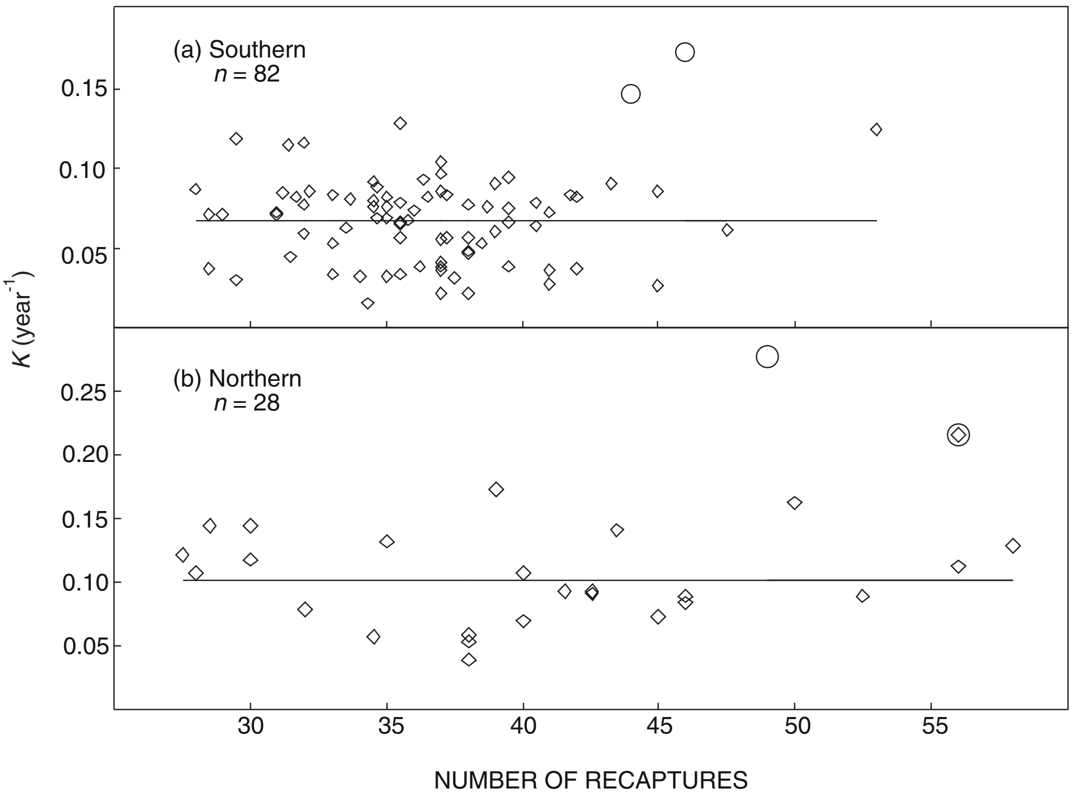

Fig. 4: Single fish estimates of *K* from mark-recapture data of West Coast steenbras with one year or more of freedom from Namibia's (a) southern population, assuming L_∞ = 73 cm for all fish and with the line showing the average when two outliers are excluded (large circles), and (b) northern population, assuming L_∞ = 84 cm for all fish and with the line showing the average when three outliers are excluded (two circles, one with open diamond inside)

$p < 0.001$).

Figure 5 shows that the curvature of the fitted Von Bertalanffy growth curves for the otolith and mark-recapture data for the southern population are almost identical, suggesting that the rings observed in the otoliths are annuli. For the northern population, mark-recapture data indicate fractionally faster growth than length-at-age data, whereas the curvature does not differ substantially. This agreement between growth curves estimated from growth-ring analysis and those from mark-recapture observations gives confidence in assuming that growth rings are formed annually. It also supports the current estimates of the parameters *K* and L_∞. The growth of West Coast steenbras from the southern population was described by the equation

$$L_\infty = 73.556(1 - e^{-0.065(t+3.92)}) \text{ cm} \quad ,$$

and those from the northern population by

$$L_\infty = 84.601(1 - e^{-0.088(t+2.756)}) \text{ cm} \quad .$$

The resultant L_∞ for each population is smaller than the largest fish measured during the whole study period (80 and 94 cm for southern and northern populations respectively, neither of which was included in the analyses of age). According to Pulfrich and Griffiths (1988), if early growth does not conform to a Von Bertalanffy type equation, and if such data are included, the outcome would be a lower value of L_∞. When those authors omitted data from one-year-old fish in their analysis of growth of the hottentot *Pachymeton blochii*, L_∞ values increased from 41.1 to 53.8 cm.

Beyer *et al.* (1999) derived a higher average value of *K* and a lower value of t_0 (the hypothetical age at which fish would have been zero length) for the southern population than was estimated during the

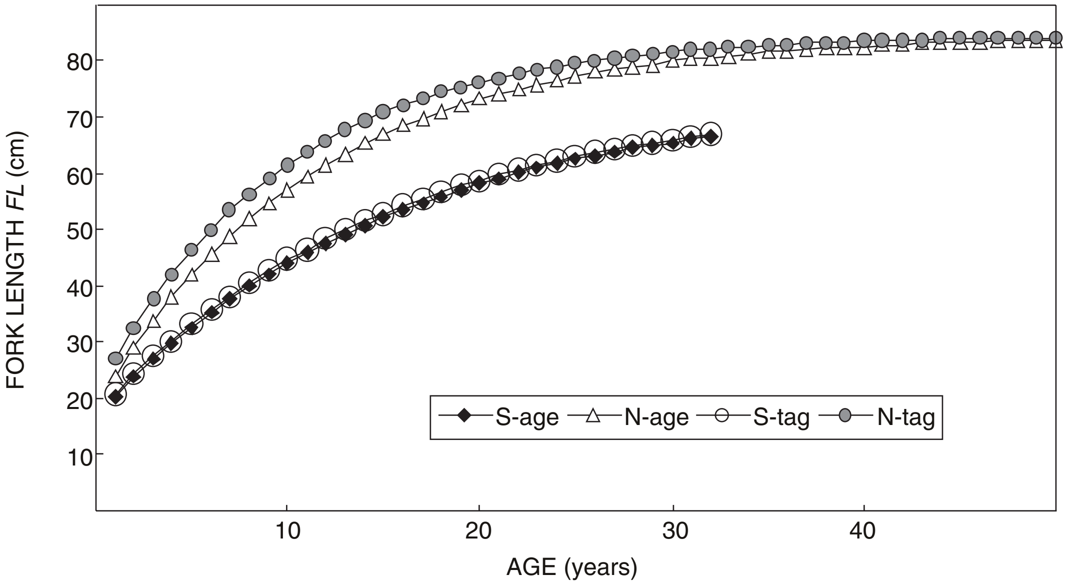

Fig. 5: Calculated length-at-age using Von Bertalanffy growth parameters derived from otolith readings and from mark-recapture data for West Coast steenbras from the southern and northern populations off Namibia. For the southern population the Von Bertalanffy growth parameters t_0 = -3.92 and L_∞ = 73 derived from analysis of southern population otolith data, and for the northern population the parameters t_0 = -2.756 and L_∞ = 84 cm derived from analysis of northern otoliths, were used for mark-recapture data analysis. S-age and N-age = lengths-at-age estimated from otolith readings for the southern and northern populations respectively, S-tag and N-tag = lengths-at-ages respectively estimated from mark-recapture results from the southern and northern populations respectuively

current study (Table III). Although their results were preliminary, their value of K based on 37 recaptured fish was marginally lower than the results from the present study, during which 82 recaptures were analysed (Table IV).

DISCUSSION

West Coast steenbras are long-lived, attaining ages of more than 50 years in the northern population and at least 32 years in the southern population. The northern population therefore appears to attain greater lengths and ages-at-length than the southern. Southern African sparids that attain similar longevity are musselcracker *Sparodon durbanensis*, that can live to 31 years (Buxton and Clarke 1991), and poenskop *Cymatoceps nasutus*, which has been reported to attain 45 years (Buxton and Clarke 1989). The red steenbras *Petrus rupestris*, the largest sparid in southern Africa, can live for at least 33 years (Smale and Punt 1991) and white steenbras *Lithognathus lithognathus* for at least 22 years (Bennett 1993).

It appears that the southern population of West Coast steenbras is relatively older, in other words that they grow more slowly, than their northern counterparts. Further, their length-at-age also varies considerably between individual fish, e.g. the 17 age-classes between fish 47.5–50 cm long. These differences might be ascribed to environmental factors, such as higher average sea surface temperature in the north than in the south. Kirchner and Voges (1999) hypothesized that differences in temperature and food availability could be responsible for the slower growth rate of silver kob *Argyrosomus inodorus* caught in the southern area compared to that of those caught in the central and northern areas of the Namibian coast.

The genetic variations that seem to exist between these two West Coast steenbras populations (Van der Bank and Holtzhausen 1998/99) may explain the differences in their growth rates. Agenbag and Shannon (1988) suggested that the Benguela upwelling cell in the vicinity of Lüderitz could provide a barrier to interchange of biota between the northern and southern parts of the system. Although surface distributions of

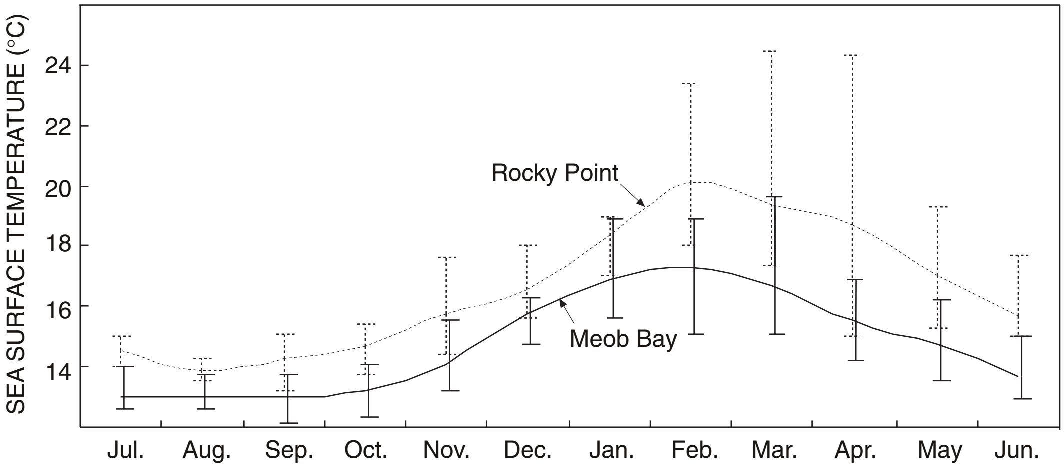

Fig. 6: Median monthly sea surface temperatures at Meob Bay and Rocky Point (data range January 1987 – December 1998). Bars indicate the upper and lower temperature ranges for each area

temperature, salinity and chlorophyll-*a* revealed no significant longshore gradients to explain this boundary, the distribution of shoals, commercial catches and larvae of pelagic fish in the Benguela ecosystem pointed to a well-defined biological boundary near 24°30´S in the vicinity of Meob Bay. Upwelling in the Lüderitz cell produces one or more cold-water filaments, of which the larger appears to be semi-permanently positioned with its northern edge approximately off Meob Bay. Agenbag and Shannon (1988) suggest that it is the combined effect of changes of circulation and turbulence/stratification that causes the biological discontinuity.

Kirchner and Voges (1999) demonstrated differences in growth rate of silver kob between the same two areas, although they were from the same stock (Van der Bank and Kirchner 1997). Bennett (1993) found no difference in the growth rate of white steenbras sampled from different geographical areas off southern Africa. That sparid, however, grew exceptionally fast (K = 0.44) by sparid standards in both warm (East Coast) and cold (West Coast) waters. West Coast steenbras from the southern region grew very slowly (K = 0.065), even slower than its relatives in the north (K = 0.088). However, the geographical differences in growth rates may be explained by differences in sea temperature and the food environment, or by density-dependent competition for food. With sea surface temperature some 4°C higher in the north around Rocky Point than in the south around Meob Bay (Fig. 6), it may be possible to ascribe the differences in growth rate between the two West Coast

Table III: Growth parameter values obtained from age-length data using the special three-parameter Von Bertalanffy growth model (VBGF) and also estimates of K and t_0 obtained by mark-recapture calculations. Preliminary results obtained by Beyer *et al.* (1999) for the southern population are included

Population and study	Value		
	L_∞	K	t_0
Southern			
Special VBGF (this study, n = 346)	73.6	0.065	-3.92
Beyer *et al*. (preliminary study, n = 282)	70.0	0.083	-2.4
Northern			
Special VBGF (this study, n = 293)	84.6	0.088	-2.756

Table IV: Estimates of K obtained by mark-recapture analysis. Preliminary results obtained by Beyer *et al.* (1999) for the southern population are included

Population and study	Value of K	
	Including outliers	Excluding outliers
Southern		
Special VBGF (this study, n = 82)	0.069	0.067
Beyer *et al*. (preliminary study, n = 40)	0.072	0.064
Northern		
Special VBGF (this study, n = 28)	0.117	0.102

steenbras populations to this environmental factor. However, for now this possibility must remain conjecture.

Stomach content analysis of 3 339 West Coast steenbras from the southern population showed black mussels *Choromytilus meridionalus* and brown mussels *Perna perna* to be the preferred food. The fact that 61.3% of West Coast steenbras stomachs examined from the southern population were empty, suggests that food availability may be responsible for the slower growth in that region; only 31.2% of those examined from the northern population had empty stomachs.

According to Landa (1999) an inverse relationship between growth and population density exists in some fish species. This phenomenon may be the result of growth being negatively influenced by total stock density (the more common cause) or by the density of a year-class (less frequent cause), or another density-dependent mechanism.

West Coast steenbras have all the characteristics of fish that can easily be overexploited, i.e. slow growth and longevity. Therefore, fisheries based on such species are extremely susceptible to overfishing and careful management is essential.

Estimates of mean individual growth rates are crucial to age-based stock assessment (Schirripa and Burns 1997). Those authors stated also that growth rates should be used to determine levels of maximum yield and ultimately to formulate stock conservation strategies. The results of the current paper were also used in assessment of the northern stock of West Coast steenbras (Holtzhausen and Kirchner 2001); from that work, management measures aimed at rational exploitation of the stock have been proposed.

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