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BIOLOGY OF THE REDSPOTTED TONGUESOLE CYNOGLOSSUS ZANZIBARENSIS (PLEURONECTIFORMES: CYNOGLOSSIDAE) ON THE AGULHAS BANK, SOUTH AFRICA

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The biology of the redspotted tonguesole *Cynoglossus zanzibarensis*, a common African cynoglossid inhabiting the Agulhas Bank, South Africa, is described. Growth studies based on sectioned sagittal otoliths revealed that *C. zanzibarensis* is relatively fast-growing and long-lived, attaining ages >8 years. Growth in length was rapid in immature fish, fish attaining 56% of their maximum size within their first year. By sexual maturity, fish had attained 28% of their maximum age and 68% of their maximum length. Total length-at-age was best described by the Von Bertalanffy growth model with combined-sex growth described as $L_t = 354.78(1-e^{-0.43} (t+1.17))$ mm *TL*. Sexually dimorphic growth patterns were evident, females attaining larger lengths, but at a slower growth rate than males. Despite the similar mean size of adult fish, the trawl-sampled adult population was dominated by females, with a sex ratio of 1 male:2.4 females. Female *C. zanzibarensis* mature in their second year of life (275 mm *TL*), after which they spawn small, pelagic eggs throughout the year. Approximations of the rates of total, natural and fishing mortality were estimated to be 0.62, 0.48 and 0.14 year-¹ respectively.

The South African pleuronectiform ichthyofauna is diverse, consisting of six families, 30 genera and 56 species (Smith and Heemstra 1986). Seven species are commercially important and are landed in various trawlfisheries. The most important commercial family is the Soleidae, with Agulhas sole *Austroglossus pectoralis* and West Coast sole *A. microlepis* contributing a large proportion of the economic value of the inshore demersal fisheries on the Cape south and west coasts (Japp *et al.* 1994). The next most important commercial family is the Cynoglossidae, consisting of 13 species. Of these, only *Cynoglossus lida*, *C. atte-nuatus*, *C. capensis* and *C. zanzibarensis* are caught in appreciable amounts as by-catch in either the prawn-, hake- or sole-directed trawlfisheries (Fennessy 1994, Japp *et al.* 1994, Booth and Hecht 1998).

The redspotted tonguesole (also known as sandrat) *C. zanzibarensis* Norman 1939 is the most abundant pleuronectiform and cynoglossid species by mass and number along the Cape south coast (Japp *et al.* 1994). It is common and widely distributed around the African coast, from the South African Cape west coast to the Arabian Sea, on predominantly sandy substrata at depths of 30–430 m (Smith and Heemstra 1986). It is important ecologically on the Agulhas Bank and is preyed on by at least nine teleost and nine elasmobranch species (Smale and Bruton 1985, Payne 1986, Meyer and Smale 1991, Sauer and Smale 1991, Smale 1991, Smale and Cowley 1992, Punt and Leslie 1995, Booth and Buxton 1997). Previous studies have documented its feeding biology (Meyer and Smale 1991),

distribution and abundance (Badenhorst and Smale 1991), but little is known about other aspects of its life history.

Knowledge of the life histories and population dynamics of South African pleuronectiforms is restricted mainly to *A. pectoralis* (Zoutendyk, 1973a, b, 1974, Hecht 1976, Payne 1986, Le Clus *et al.* 1996), *A. microlepis* (Payne 1979) and *Solea bleekeri* (Cyrus 1991). This study investigates major aspects of the life history of *C. zanzibarensis* on the Agulhas Bank, South Africa, including population structure, age and growth rates, mortality rates, sexual maturity and reproductive seasonality.

MATERIAL AND METHODS

Biological data were collected on the Agulhas Bank (Fig. 1) between Cape Agulhas (34°50'S, 20°00'E) and Port Alfred (33°26'S, 26°54'E) between February 1994 and September 1996. Samples were obtained from commercial, inshore trawlers using demersal otter-trawling gear with a stretched mesh of 75 mm, operating from Port Elizabeth and Mossel Bay. Samples were also collected during research demersal trawl surveys conducted twice annually and deploying an otter-trawl with a codend liner of 30-mm stretched mesh (Badenhorst and Smale 1991).

Each fish sampled during the study was weighed whole $(\pm 1 \text{ g})$ and measured for standard length (*SL*) and total length (*TL*, $\pm 1 \text{ mm}$). The sexual maturity state

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Fig. 1: Map of the study area showing the position of the Agulhas Bank, South Africa, and places mentioned in the text. The inset map of Africa notes the distributional range of *C. zanzibarensis*

of the gonads was visually assessed (Table I), after they were removed and weighed $(\pm 0.1 \text{ g})$. Eviscerated mass $(\pm 1 \text{ g})$, without removal of the gills, was later recorded. Sagittal otoliths were removed, cleaned and stored for age determination.

Morphometrics, age and growth

Otolith lengths (along the longitudinal axis) and widths (along the transverse axis) were measured (± 0.05 mm) from the left sagittae from a subsample of fish covering all size-classes. The right sagittae

were lightly burned over a methanol flame, until they turned a dark brown colour, to enhance the visibility of growth zones for age determination. The burnt otoliths were embedded in clear casting resin, then sectioned longitudinally through the nucleus using a diamond edged, double-bladed saw. The sections, ranging from 0.2 to 0.5 mm thick, were mounted in DPX on microscope slides and viewed under transmitted light. Otolith readings were made without reference to the length of the fish, each section being read twice by two independent readers on different occasions. If the two readings were not equal, a third was made. An age estimate was accepted as the two most similar

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Table I: Macroscopic appearance of various reproductive stages of C. zanzibarensis

Stage	State	Macroscopic appearance
1 2	Virgin and resting Developing	Ovary long and thin, pink with no visible eggs. Testis visible as a clear strip, tapering posteriorly Ovary larger, becoming orange-red, with a grainy appearance due to visible eggs. Testes whitish and ovoid in cross-section
3	Active	Ovary swollen, orange-red, with large translucent eggs visible in the tissue and lumen. Testis white and triangular in cross-section
4	Post-spawning	Ovary slightly flaccid, with few translucent eggs visible. Brown spots noticeable over most of the gonad. Testis dirty-grey and slightly smaller

readings. If the range of the three readings was not more than two years, a mean age estimate was taken, otherwise the otolith was rejected. The timing of growth check formation was determined by marginal zone analysis, where the optical appearance of the otolith margin was noted and expressed as a percentage of the monthly sample.

Length-at-age was described by the best-fitting model of either the three-parameter specialized Von Bertalanffy growth model:

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

or the four-parameter Schnute growth model:

$$\mathbf{L}_{t} = \left[L_{1}^{b} + (L_{2}^{b} - L_{1}^{b}) \left(\frac{1 - e^{-a(t - t_{1})}}{1 - e^{-a(t_{2} - t_{1})}} \right) \right]^{1/b},$$

where t_1 is the smallest age in the sample, t_2 is the largest age in the sample, t_0 is the age at "zero" length, L_t is the length-at-age, L_{∞} is the predicted asymptotic length, L_1 is the estimated mean length of t_1 year old fish, L_2 is the estimated mean length of t_2 year-old fish and K is the Brody growth constant (Ricker 1975, Schnute 1981). The models were fitted using a downhill simplex search, a non-linear minimization routine to obtain parameter estimates for the selected growth model (Nelder and Mead 1965). Model fits were obtained by minimizing the sum of either the squared absolute or natural log-transformed relative differences between the observed and predicted lengths-at-age. A non-parametric, one-sample runs test was applied to test for residual randomness and a Bartlett's test was used to test for their homoscedasticity. Variance estimates were calculated using (conditioned) parametric bootstrap resampling (Efron 1981) using 1 000 bootstrap resamples. Standard errors and confidence intervals were estimated from the sorted bootstrap output using the percentile method described by Buckland (1984).

Mortality

An age-length key, based on male, female and combined sexes data, was used to transform sex-specific length frequency distributions to sex-specific age frequency distributions. Estimates of total annual mortality (Z) were obtained by means of catch curve analyses using natural log-transformed, age-frequency distribution data. An estimate of total mortality was obtained from the negative of the slope of the straight line fitted to points greater, and including, the age-at-100%-selectivity (represented by the mode of the age



Fig. 2: Length- and age-frequency histograms of male and female *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996

frequency distribution). A second method, described by Cooke and Beddington (1981), was also used to estimate total mortality. This method is considered to be statistically superior to catch curve analysis, particularly when the numbers caught at any age in the catch curve are low, namely

$$Z = \ln \left(1 + \frac{1}{\overline{a} - a_f} \right) \quad .$$

where a_f is the age at full recruitment and \overline{a} is the mean age of all fully recruited fish. Natural mortality (*M*) was estimated using the empirical relationships described by Pauly (1980) as

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Fig. 3: Photomicrograph of a transverse, sagittal otolith section of a 5-year-old *C. zanzibarensis* viewed under transmitted light

$$Log_e M = -0.0152 - 0.279 Log_e L_{\infty} + 0.6543 Log_e K + 0.463 Log_e T$$

and Rikhter and Efanov (1977), which in the present application only considers females:

$$M = \left[\frac{1.521}{t_m^{0.72}}\right] - -0.155$$

where *T* is the mean sea temperature (°C), L_{∞} and K the Von Bertalanffy growth parameters and t_m is the female age-at-50% maturity. The mean annual water temperature along the entire Agulhas Bank is approximately 12°C (M. J. Roberts, Marine & Coastal Management, unpublished data). Fishing mortality (*F*) was obtained by subtraction (F = Z - M).

Reproductive biology

Female length-at-maturity was calculated by determining the proportion of reproductively active fish in each 1cm size-class. Length-at-maturity, also commonly referred to as length (or size)-at-50% maturity, was estimated by fitting a logistic ogive:

$$P_L = \frac{1}{1 + e^{-(L - L_{50})/\delta}}$$

where P_L is the percentage of fish mature at length *L*, L_{50} the length at which 50% of the fish in the size-/ageclass are sexually mature and δ is the steepness of the ogive. The model parameters were estimated by nonlinear minimization of the squared residuals.

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Reproductive seasonality was ascertained using two different methods: first, by a gonadosomatic index, which was calculated by expressing gonad mass as a percentage of eviscerated body mass and second, by calculating the proportion of various maturity stages in visibly mature ovaries (Table I). Adult sex ratio was determined from fish larger than the female length-at-maturity and tested for unity using a χ^2 test.

RESULTS

Morphometrics and population structure

Analysis of the length and age frequencies (Fig. 2) of *C. zanzibarensis* revealed no significant differences between the mean lengths of adult male (303.3 \pm 48.8 mm *TL*) and female fish (304.7 \pm 43.2 mm *TL*, Z = -0.354, p > 0.05, n = 642). The adult population was dominated by females, with a ratio of 1 male:2.43 females, differing significantly from unity in both the

Table II: Morphometric relationships for C. zanzibarensis sampled on the Agulhas Bank between March 1994 and August 1996

Parameter	Parameter Relationship		n
Total mass (g) Eviscerated mass (g) Total length (mm) Total length (mm) Total length (mm)	0.000002 Total length (mm) ^{3.173} 0.000003 Total length (mm) ^{3.093} 1.055 Standard length (mm) + 3.863 79.614 Otolith diameter (mm) – 45.229 71.578 Otolith length (mm) + 63.379	0.91 0.96 0.99 0.81 0.87	506 506 506 50 50 50



Fig. 4: Temporal changes in otolith margin composition for *C. zanzibarensis* sampled on the Agulhas Bank, between March 1994 and August 1996

Table III: Age-length key for combined sexes of *C. zanzi-barensis* sampled on the Agulhas Bank between
March 1994 and August 1996

Total		Ν	umber	of fish	in each	age-cla	ass	
(mm)	1	2	3	4	5	6	7	8
$\begin{array}{c} 13\\ 14\\ 15\\ 16\\ 17\\ 18\\ 19\\ 20\\ 21\\ 22\\ 23\\ 24\\ 25\\ 26\\ 27\\ 28\\ 29\\ 30\\ 31\\ 32\\ 33\\ 34\\ 35\\ 36\\ 37\\ 38\\ 39\\ 40\\ \end{array}$	$ \begin{array}{c} 1 \\ 1 \\ 1 \\ 1 \\ 3 \\ 1 \\ 3 \\ 1 \end{array} $	2 2 1 4 1 1 2 1	$ \begin{array}{c} 1 \\ 4 \\ 1 \\ 2 \\ 1 \\ 1 \\ 2 \\ 7 \\ 4 \\ 5 \\ 4 \\ 1 \\ 3 \\ 3 \\ \end{array} $	$ \begin{array}{c} 1\\ 1\\ 1\\ 2\\ 1\\ 1\\ 2\\ 7\\ 9\\ 9\\ 5\\ 3\\ 4\\ 2\\ \end{array} $	2 1 3 5 5 2 1 1 1	1 1 1 1 1 5 5 3	3 4 1 1	1
n	16	16	41	50	26	20	9	2



Fig. 5: Observed mean length-at-age (\pm *SD*) of male and female *C. zanzibarensis* using sectioned sagittal otoliths from fish sampled on the Agulhas Bank between March 1994 and August 1996. The growth curve was fitted using the specialized Von Bertalanffy growth model with an absolute-error structure fitted to the combined sex data

length frequency ($\chi^2 = 20.63$, df = 11, p < 0.05) and age frequency data ($\chi^2 = 70.76$, df = 8, p < 0.01).

Morphometric relationships between length, total and eviscerated mass, otolith length and otolith width are summarized in Table II. Analysis of Covariance revealed no significant differences between males and females using slopes of the linear regression of the log-transformed total length and eviscerated mass data (F = 1.21, df = 2, 488, p > 0.05) and total lengthstandard length data (F = 2.35, df = 2, 488, p > 0.05). Male and female morphometric data were consequently pooled to reflect a combined sex population.

Age and growth

Alternating opaque and hyaline zones were visible in the sectioned otoliths, with zones most easily discernible along the dorsal axis (Fig. 3). Marginal zone analysis confirmed that one opaque and one translucent zone were formed each year, between April and July (Fig. 4). It was assumed that each opaque zone represented an annulus, with one year's growth represented by a pair of optically opaque and adjacent translucent zones. Of the 217 otoliths analysed, 35 (16 %) were rejected as unreadable. The age estimates of the other 182 fish were used to construct an age-length key (Table III) and for the estimation of growth parameters.

					Length-at-age (mm)				
Age (years)	Females				Males		Both sexes		
	n	Observed (±SE)	Expected	п	Observed (±SE)	Expected	п	Observed $(\pm SE)$	Expected
1 2 3 4 5 6 7 8	9 124 28 32 13 10 7 1	227.9 (36.3) 233.0 (32.9) 298.3 (46.2) 314.6 (37.4) 343.5 (33.3) 349.1 (15.9) 349.3 (21.4) 400.0	223.4 263.3 293.9 317.5 335.6 349.5 360.2 368.4	7 12 13 18 15 10 2 1	191.3 (40.3) 275.4 (45.3) 299.2 (48.2) 304.4 (32.7) 322.9 (37.9) 312.9 (38.6) 344.0 (7.1) 365.0	193.5 270.0 300.4 312.5 317.3 319.2 319.9 320.3	16 16 41 50 28 20 9 2	$\begin{array}{c} 228.9 \ (50.9) \\ 304.4 \ (44.7) \\ 310.8 \ (35.7) \\ 280.9 \ (55.0) \\ 325.6 \ (23.9) \\ 343.2 \ (27.6) \\ 349.6 \ (13.9) \\ 396.5 \ (4.9) \end{array}$	214.0 262.8 294.7 315.5 329.0 337.9 343.7 347.5

Table IV: Observed ($\pm SE$) and expected lengths-at-age for male, female and combined sexes of *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996. Expected length-at-age is estimated from the threeparameter specialized Von Bertalanffy model points

Length-at-age was adequately described by both growth models using the statistically suitable absolute (as opposed to the relative) error structure, because it provided both residual randomness and homoscedasticity. No significant differences were found between the two growth models fitted using a *F* test (*F* = 0.35, *df* = 1, 178, *p* > 0.05). The Von Bertalanffy model was chosen to represent growth in *C. zanziba-rensis*, because it has fewer parameters and is therefore statistically more robust (Fig. 5). However, a significant difference was found between the growth models applied to the male and female datasets (*F* = 3.39, *df* = 3, 176, *p* < 0.05), with females ($L_{\infty} = 354.8 \text{ mm } TL$, K = 0.43·year⁻¹) attaining a larger maximum size at a lower growth rate than males ($L_{\infty} = 320.6 \text{ mm } TL$, K = 0.92·year⁻¹). Estimated growth of parameters and their associated variance for males, females and the combined sexes data are summarized in Tables IV and V.

Mortality

Age frequencies obtained from transformed lengthfrequency data provided first approximations of estimates of total mortality (Fig. 6, Table VI). Males and females were represented in both the commercial and research trawl samples at 1 year of age, and fish were fully selected by age 4 years. Total mortality estimates obtained using the catch-curve analysis and the Cooke and Beddington (1981) method were similar,

Table V: Point estimates, associated standard errors (*SE*) and 95% confidence intervals (*Cl*) for male, female and combined sex data for the three-parameter specialized Von Bertalanffy model fitted to *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996

Parameter	Point estimate	SE	95% CI (left and right)							
Females (n = 104)										
$egin{array}{c} L_{\infty} \ K \ t_0 \end{array}$	395.08 mm <i>TL</i> 0.27·year ⁻¹ -2.14·year	6 841.27 0.11 1.44	348.39, 675.98 0.06, 0.49 -6.14, -0.82							
Males (n = 78)										
$egin{array}{c} L_{\infty} \ \mathbf{K} \ t_0 \end{array}$	320.57 mm <i>TL</i> 0.92·year ⁻¹ -0.01·year	9.79 0.29 0.41	306.98, 346.29 0.46, 1.69 -1.15, 0.49							
Both sexes $(n = 182)$										
$egin{array}{c} L_{\infty} \ K \ t_0 \end{array}$	354.78 mm <i>TL</i> 0.43·year ⁻¹ -1.17·year	15.83 0.11 0.57	353.43, 396.64 0.23, 0.64 -0.26, -0.42							



Fig. 6: Age frequency distributions and catch curves of male, female and combined sexes of *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996. The estimate of total mortality is calculated as the negative of the slope from a least-squares regression equation fitted to the natural logarithm of the age frequency values of fully recruited fish

but with slightly lower estimates (8–19%) using the catch-curve analysis (Table VI). An averaged estimate of total mortality using the catch curve and Cooke and Beddington (1981) methods for males and females was estimated at 0.62 year 1. However, estimates of natural mortality using the two empirical models were dissimilar. The estimate derived from Pauly's (1980) model for females was lower than that obtained using Rikhter and Evanov (1977) model, which was also higher than the estimate for total mortality. Considering that the latter model only applies to female fish and the former model is statistically more accurate, an average of the different estimates positively biasing Pauly's (1980) estimates was considered appropriate. All estimates were averaged, using one (female data) Rikhter and Evanov (1977) method and three (male, female and combined sexes data) Pauly (1980) estimates to derive an approximation of natural mortality for C. zanziba*rensis.* That value was 0.48 year⁻¹, and by a process of simple subtraction, fishing mortality was therefore equal to 0.14·year⁻¹.

Reproductive biology

In *C. zanzibarensis*, the gonads were situated posteriorly of the urogenital pore, in a secondary extension of the visceral cavity. Both dorsal and ventral gonads were equally developed, with no significant differences between the size of ovaries (Mann-Whitney U-test; T = 7 695.5, p = 0.433, n = 89) or testes (T = 2 151, p = 0.196, n = 48). The ovaries were approximately 30 times larger than the testes in reproductively active fish.

Sexual maturity in males was more difficult to quantify than in females. The macroscopically distinct changes in females reflected the larger histological changes (such as vitellogenesis) in the ovaries at matu-

Table VI: Instantaneous total (*Z*) and natural mortality rates (*M*) estimated for *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996. Instantaneous total mortality was estimated directly from an age-converted, linearized catch curve, whereas natural mortality estimates were derived from various indirect, empirical models

Ζ	М	Method						
Females								
0.58 0.63	0.25 0.71	Pauly (1980) Rihkter and Evanov (1977) Catch curve Cooke and Beddington (1981)						
Males								
0.58 0.67	0.59	Pauly (1980) Catch curve Cooke and Beddington (1981)						
	Be	oth sexes						
0.62 0.75	0.35	Pauly (1980) Catch curve Cooke and Beddington (1981)						
Averaged estimates for both sexes								
0.62	0.48							

ration. In males, the microscopic changes associated with spermatogenesis were smaller, resulting in macroscopic differences that were marginally distinct. Sexual maturation in female fish was initiated at approximately 1.3 years of age (240 mm *TL*), with all fish being fully mature after 4 years of age (>320 mm *TL*, Fig. 7). Age- and length-at-maturity were determined from the fitted logistic ogive at 2.2 years of age and 275 mm *TL* respectively.

Analysis of the mean gonadosomatic indices in mature fish (Fig. 8) and the macroscopic maturity indices (Fig. 9) showed that reproductive activity extended throughout the year. Fish with ovaries in a "ripe" condition dominated throughout the year, with a larger proportion in a "developing" state in April, July and August.

DISCUSSION

The ages obtained from the otolith data and growth model estimates indicated that *C. zanzibarensis* is a relatively fast-growing species with a lifespan of more than 8 years. The mean maximum theoretical length (355 mm *TL*) predicted from the Von Bertalanffy growth model was slightly lower than the maximum



Fig. 7: Percentage frequency of mature female *C. zanziba-rensis* in different length-classes of fish sampled on the Agulhas Bank between March 1994 and August 1996. The curve was fitted using a logistic ogive

observed length of 405 mm TL recorded during the study. The maximum theoretical length is possibly a fair reflection of the mean maximum size of the population because few fish were >400 mm TL and the 95% confidence interval (for L_{∞}) includes fish up to 397 mm TL. Male C. zanziberensis reached a smaller size and had a faster growth rate than female fish, a growth pattern similar to many teleost species (Pauly 1994). These growth patterns were also similar to those of other cynoglossids (Rajaguru 1992, Terwilliger and Munroe 1999) and soleids (Zoutendyk 1974, Hecht 1976, Ramos 1982, Payne 1986), in which fish exhibit a faster growth rate before sexual maturity, after which growth in length (but not mass) tends to become asymptotic. This change in growth rate after the onset of sexual maturation is attributable to the utilization of available energy for reproduction instead of somatic growth and is possibly energetically expensive, as in the case of C. zanzibarensis that spawn throughout the year. Female C. zanzibarensis matured at a large proportion (68%) of their maximum length, yet at a small proportion (28%) of their maximum age. Similar ratios have been documented for Cynoglossus arel (48 and 33% respectively - Rajaguru 1992), Symphurus plagiusa (50 and 32% respectively - Terwilliger and Munroe 1999) and A. pectoralis (47 and 32% respectively – Zoutendyk 1974). This growth pattern would enable fish to attain a size large enough to escape predators, compete with conspecifics to spawn, and to ensure a reasonably high fecundity at first spawning,



Fig. 8: Seasonal variation of individual gonadosomatic indices for (a) female and (b) male *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996

because the relative investment of energy into future gonad-free total mass is reduced in reproductively active adults (Roff 1982).

The relative size of the ovaries compared to the testes was of interest, because pair spawners tend to have relatively small testes compared to the ovaries. Relatively large testes are indicative of group spawners (Choat and Robertson 1975), testis size being selected under conditions of intense sperm competition. The ovary/testes size ratio of *C. zanzibarensis* is therefore indicative of pair spawning, as is the case in other flatfish. Observations on spawning behaviour in other flatfish species suggest that pair spawning takes place in a manner in which the male swims under the female and lifts her off the substratum into the water column to spawn (Konstantinou and Shen 1995). Close contact during the spawning process would

therefore ensure little sperm wastage and increased fertilization rate. Despite Buxton and Garratt's (1990) observation that there is often sexual dimorphism in fish that exhibit pair spawning, there was no evidence for sexual dimorphism in *C. zanzibarensis*.

C. zanzibarensis appears to spawn throughout the year, with final egg maturation and hydration taking place rapidly and in small batches. In the present study, no fish was sampled with "ripe-running" gonads and only a few female fish with hydrated eggs visible in the ovaries were found each month. Wood (1998) noted continuous reproductive activity in C. zanzibarensis, deduced from the year-round presence of eggs, pre-flexion, post-flexion and fully metamorphosed larvae in monthly plankton collections along the south-east coast of South Africa. Considering that the time taken from hatching to metamorphosis and subsequent settlement is more than 30 days, these data confirm that the reproductive condition of the gonads are a reasonable proxy for the assessment of reproductive seasonality in this species.

Most teleost species investigated on the Agulhas Bank exhibit an extended spawning period through-out the year. This is likely a response to proximate oceanographic conditions rather than taxonomic differences. There is a protracted spawning season, with one or more peaks in reproductive activity, for Cape hake Merluccius capensis, Agulhas sole Austroglossus pectoralis (Zoutendyk 1974, Payne 1986), Cape gurnard Chelidonichthys capensis (Hecht 1976, McPhail 1998), panga Pterogymnus laniarius (Booth and Buxton 1997) and lesser gurnard Chelidonichthys queketti (Booth 1997). Worldwide, spawning seasonality in the Lutjanidae has been correlated to both the productivity of the environment and food availability (Grimes 1987). If the expectations of production, and hence food availability, is continuous (even if patchy), then continuous spawning can be favoured. A continuous supply of suitable food for larvae and juveniles would therefore provide no selective pressure against individuals that exhibit a non-seasonal spawning pattern. The Agulhas Bank is a relatively stable and moderately productive system (Largier et al. 1992), with reduced offshore, winddriven upwelling and relatively stable temperatures throughout the year (Schumann et al. 1982). In contrast, the Benguela system on the west coast of southern Africa is unstable and highly productive, with spawning patterns more seasonal (Payne 1986) than on the Agulhas Bank.

The catch-curve total mortality estimates for males, females and combined sexes/age-frequency data were slightly lower than that obtained using the Cooke and Beddington (1981) method. The regression for the male catch-curve data was not significantly different



Fig. 9: Seasonal variation in the percentage of macroscopic gonad stages in the ovaries of *C. zanzibarensis* sampled on the Agulhas Bank between March 1994 and August 1996

(p > 0.05), whereas both the female and combined sexes linear regression models were significant (p < 0.05). The averaged estimate of fishing mortality was relatively low at 0.14·year⁻¹, less than the averaged natural mortality estimate of 0.48·year⁻¹, albeit highly dependent on the value of natural mortality assumed from the empirical relationships. This suggests that *C. zanzibarensis* on the Agulhas Bank is not too heavily impacted by fishing pressure, not being a targeted species, in contrast to *A. pectoralis* on the Cape south coast.

Little information is available on natural mortality rates in other cynoglossid species, particularly those inhabiting temperate environments. The only data available for comparison are from the sympatric A. pectoralis, whose natural mortality rate ranges between 0.35 and 0.47 year⁻¹ (Payne 1986) and for blackcheek tonguefish Symphurus plagiusa from Chesapeake Bay, which range between 0.73 and 0.77 year⁻¹ (Terwilliger and Munroe 1999). The estimates of natural mortality for Agulhas sole are most similar to those for C. zanzibarensis, possibly reflecting their similar habitats on the Agulhas Bank, and the limited migration in both species. Terwilliger and Munroe (1999) suggested that the high natural mortality rate observed for S. plagiusa reflects offshore emigration from the Chesapeake Bay, which results in the low abundance of older individuals in the bay population.

Studies on the feeding biology of sympatric fish on the Agulhas Bank identified at least nine teleost and nine elasmobranch species that prey on C. zanzibarensis (Smale and Bruton 1985, Payne 1986, Meyer and Smale 1991, Sauer and Smale 1991, Smale 1991, Smale and Cowley 1992, Punt and Leslie 1995, Booth and Buxton 1997). Considering that C. zanzibarensis is shorter-lived, has a higher growth rate, attains a smaller maximum size than A. pectoralis, and is preyed on by more sympatric fish, its natural mortality rate would be expected to faster than that of A. pectoralis. However, C. zanzibarensis is more abundant than A. pectoralis on the Agulhas Bank (Badenhorst and Smale 1991), suggesting that similar relative proportions of individuals would die naturally (as a result of predation, senescence and disease) from both populations, resulting in a similar rate of natural mortality.

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C. zanzibarensis appear to inhabit areas of coarse, unconsolidated sediments. They are mainly found >100 m deep on sandy substrata (Meyer and Smale 1991, Smale *et al.* 1993, Japp *et al.* 1994). Surficial sediments that are dominated by sand constitute a large area of the Agulhas Bank, as opposed to small areas clay and silt, the favoured habitat of *A. pectoralis* (Le Clus *et al.* 1996). As a consequence, *C. zanzibarensis* is more widely distributed than *A. pectoralis* over the

Table VII: Summary of prey consumed by *C. zanzibarensis* on the Agulhas Bank in two size-classes corresponding to fish that were immature and mature. The importance of prey items to the diet is calculated by noting the percentage of stomachs that contained each prey item (%*F*), the numerical importance of each prey item to the total diet (%*N*) and the percentage mass of each prey item to the total diet (%*M*). An index of relative importance (*IRI*) was calculated as $IRI = (\%N + \%M) \times \%F$ (modified from Meyer and Smale 1991)

Drov	Immature 153–260 mm				Mature 261–379 mm			
Ticy	%F	%N	%M	IRI	%F	%N	%M	IRI
Polychaeta	22	8.8	7.6	359.9	22.11	5.9	9.4	338.7
Crustacea Unidentified Amphipoda Isopoda Mysidacea Euphausiacea Stomatopoda Macrura Anomura Brachyura	27 28 22 3 1 5 10 2 40	$ \begin{array}{c} 14.1 \\ 16.2 \\ 19.0 \\ 1.1 \\ 0.4 \\ 2.8 \\ 3.9 \\ 1.4 \\ 21.5 \\ \end{array} $	4.4 1.9 23.6 0.2 0.1 8.4 2.3 0.8 30.6	497.9 508.5 936.9 3.6 0.5 56.3 61.2 4.4 2084.4	61.1 44.2 5.3 2.1 4.21 9.5 25.3 33.7	$28.1 \\ 25.9 \\ 1.5 \\ 0.4 \\ - \\ 0.9 \\ 2.2 \\ 14.0 \\ 10.9$	$ \begin{array}{c} 10.6 \\ 4.0 \\ 0.8 \\ 0.5 \\ - \\ 3.3 \\ 3.0 \\ 22.1 \\ 18.3 \end{array} $	2 358.8 1 323.5 12.3 - 17.8 49.7 914.4 986.2
Mollusca	9	2.8	2.3	45.9	10.5	2.2	1.8	43.4
Osteichthyes	21	8.1	12.1	423.2	24.2	7.2	18.9	632.4
Sand	28	-	5.8	_	34.7	-	6.8	-
Unidentified matter	_	_	_	_	3.2	0.88	0.5	
Total	218	284.0	26.6		95.0	456.0	34.2	

Bank (Badenhorst and Smale 1991). Meyer and Smale (1991) commented on the possible sandy habitat preference of *C. zanzibarensis* from the occurrence of sand in the stomachs of the fish. Those authors suggested two origins for the sand in the stomachs: either *C. zanzi-barensis* pounces on prey and sand is incidentally ingested, or the sand is from the guts of ingested polychaetes. *C. zanzibarensis* has a weakly developed terminal mouth that enables it to feed on a range of small, sedentary invertebrates such as polychaetes, isopods, amphipods and crabs. Larger individuals also consume small fish (Table VII). Overall, it has been described it as a deep, demersal predator on small epibenthic invertebrates (Smale 1992).

With the exception of *C. macrostomus* on the west coast of India, cynoglossids are classed worldwide as bycatch species (Rajaguru 1992, Fennessy 1994, Terwilliger and Munroe 1999). This is partly a consequence of their being generally small and commercially unimportant, as well as their low densities. The group has been lumped with other small pleuronectiforms in the "sole" category within FAO statistical bulletins, which has impeded the collation of data suitable for individual stock assessments. Off South Africa, the present rate of fishing mortality exerted on *C. zanzibarensis* appears to be fairly low, indicating that a large portion of the stock is not caught by the trawlfishery. With the relatively low biomass of *C.*

zanzibarensis on the Agulhas Bank and the species not being targeted by the trawlfishery, directed fishing appears to be economically unfeasible. They will certainly continue to constitute a portion of future trawlfish bycatch, because of their wide distribution (Japp et al. 1994, Booth et al. 1999). Current fishing practices are also problematic. Commercial demand for C. zanzibarensis is low, resulting in their frequently being discarded and only landed if catches of the highpriced A. pectoralis are low. C. zanzibarensis is marketed on the East Coast (particularly in Port Elizabeth) as "lemon sole", instead of the less-appealing common name "sandrat". The flesh is highly edible and is often used as a substitute for Agulhas sole. Therefore, there is potential only for improved utilization rather than increased harvesting or bycatch reduction for this species. Improvement of market stability should therefore be investigated as a suitable option to improve their utilization in the future.

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