



## On the life history of the lesser gurnard (Scorpaeniformes: Triglidae) inhabiting the Agulhas Bank, South Africa

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Growth analysis based on sectioned sagittal otoliths revealed the lesser gurnard *Chelidonichthys queketti* on the Agulhas Bank to be relatively fast growing and long lived, with ages of up to 7 years being recorded. Total length at age (mm) was described best by the specialized von Bertalanffy growth model as  $L_T = 306 \cdot 1 (1 - e^{0.53(t+0.18)})$ . First approximations of total, natural and fishing mortality rates were determined at 0.73, 0.38 and 0.35 year<sup>-1</sup> respectively. The adult population was male dominated with a sex ratio of 1 female : 1.2 males with the mean size of males and females being similar. The lesser gurnard is an iteroparous species with females maturing by the end of the first year of life (195 mm  $L_T$ ), thereafter spawning throughout the year with reproductive activity peaking over spring and late summer. The lesser gurnard appears to exhibit similar life-history patterns to other triglid species in that it can be classified as a generalist. Generalistic life-history characteristics such as a fast growth rate, early sexual maturity at a relatively large size, a non-seasonal spawning pattern, feeding on a variety of prey organisms and the ability to inhabit various substrata could all contribute to it maintaining a high biomass on the Agulhas Bank.

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Key words: age and growth; reproduction; maturity; mortality; by-catch management.

### INTRODUCTION

The lesser or quekett's gurnard *Chelidonichthys queketti* (Regan, 1904) is an endemic South African triglid species found between Cape Town and Durban (Smith & Heemstra, 1986). Little is known about the biology of this species with Meyer & Smale (1991) describing its feeding biology and Badenhorst & Smale (1991) and Smale *et al.* (1993), describing aspects of its distribution and abundance. These authors found that it was widely distributed over various sediment types between 28–228 m in depth with the bulk of its biomass being found between 50–150 m. Throughout its distributional range it was shown to be an epibenthic predator feeding predominantly on gammarid amphipods, small brachyurans and small teleosts.

The lesser gurnard is the most abundant triglid species by mass and number inhabiting the Agulhas Bank area where large quantities are caught in the hake-directed inshore and deep-sea trawl fisheries (Japp *et al.*, 1994). Despite being caught in appreciable numbers, this small fish is discarded at sea with only the large individuals landed commercially with the larger, sympatric Cape gurnard *C. capensis* (Cuvier). The need for a biologically based bycatch/discard management strategy and the paucity of data available on the biology of this species prompted an investigation into aspects of its life history including population structure, age and growth rates using sectioned otoliths, mortality rates, sexual maturity and reproductive seasonality on the Agulhas Bank.

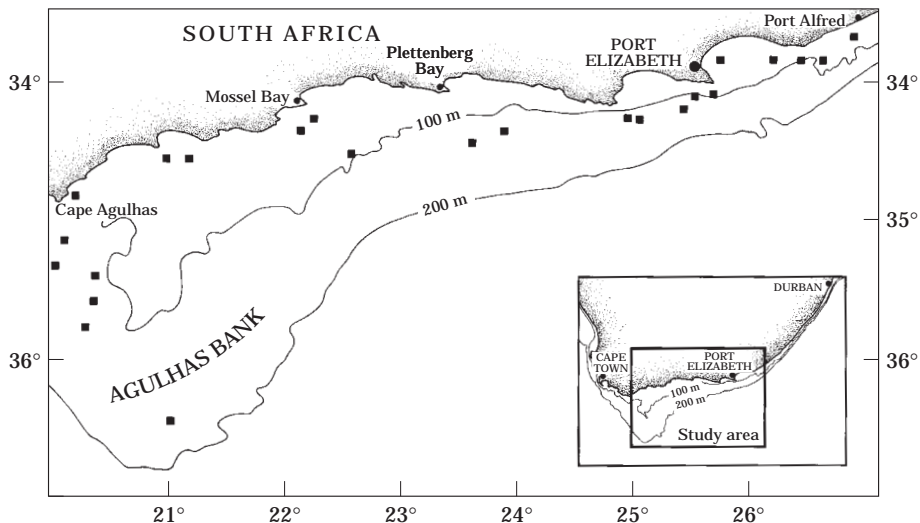


FIG. 1. Map of the study area showing the position of the Agulhas Bank, South Africa and sampling areas (■). The distribution range of *Chelidonichthys queketti* extends from Cape Town to Durban from 28 to 228 m in depth.

## MATERIALS AND METHODS

Data were collected between February 1994 and September 1996 on the Agulhas Bank area between Port Alfred and Cape Agulhas using research (stretched mesh liner 25 mm) and commercial (stretched mesh 75 mm) demersal otter trawling gear (Fig. 1). Each fish was weighed (1 g), measured (1 mm) (standard, fork and total lengths) and sexual maturity state assessed visually (Table I) before the gonads were removed and weighed to the nearest 0.1 g. Commercially trawled fish are landed headless, and it was for this reason headed mass (g), headed length (mm) (distance from the base of the first dorsal spine to the tip of the tail) and longest pectoral ray length (mm) were taken to aid future fisheries research in later collection of length frequency data.

Sagittal otoliths were removed, cleaned and stored dry in manilla envelopes for later age determination. Otolith length (along the longitudinal axis), width (along the transverse axis), thickness (across the nucleus) (0.01 mm) and mass (0.0001 g) were taken from the left sagittae from a subsample of fish covering all size classes. Right sagittae were burned lightly over a methanol flame to enhance annuli with care taken not to char the otoliths which were small and burnt rapidly. The otoliths were embedded in clear casting resin, sectioned to 0.2–0.5 mm through the nucleus using a diamond-edged, double-bladed saw, and mounted on microscope slides with DPX mountant. Alternating opaque and hyaline zones were clearly visible with each otolith being read twice under transmitted light. Readings were undertaken without reference to their lengths at weekly intervals. If the two readings did not agree, a third was taken. The age estimate was accepted as the two similar readings. If the three readings differed by 2 years the mean age estimate was taken, otherwise the otolith was rejected. The timing of growth check formation was determined by noting the visual appearance of the otolith margin and expressing it as a percentage of the monthly sample.

Length at age was described by the three-parameter specialized von Bertalanffy growth model of the form

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

TABLE I. Classification and description of the macroscopic maturity stages of *Chelidonichthys queketti* gonads

Stage	Macroscopic appearance
Virgin and resting	The visually unsexable gonad is translucent and threadlike.
Developing	Ovary increases slightly in size becoming darker orange-red with a grainy appearance due to small visible eggs. Testis becomes opaque and ovoid in cross section.
Active	Ovary becomes orange and swollen filling most of the abdominal cavity. Large translucent hydrated eggs are visible through the tunica and in the lumen. Testis is white and triangular in cross section.
Post-spawning	Ovary is red and becomes flaccid with few translucent eggs visible. Brown spots are noticeable over most of the gonad. Testis becomes dirty-grey in colour and decreases marginally in size.

and the four-parameter Schnute growth model of the form

$$L_t = \left[ L_1^b + (L_2^b - L_1^b) \left( \frac{1 - e^{a(t-t_1)}}{1 - e^{-a(t_2-t_1)}} \right) \right]^{1/b}$$

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  $t$ ;  $L_\infty$  is the predicted asymptotic length;  $L_1$  the estimated mean length of  $t_1$ -year-old fish;  $L_2$  the estimated mean length of  $t_2$ -year-old fish;  $K$  is the Brody growth coefficient; and  $a$  and  $b$  are the Schnute growth parameters (Ricker, 1975; Schnute, 1981). The models were fitted using a downhill simplex search, a nonlinear minimization routine to obtain parameter estimates for the selected growth model (Punt, 1992). Model fits were obtained by minimizing the sum of either the squared absolute or relative differences between the observed and predicted lengths at age. A non-parametric one-sample runs test was used applied to test for randomness of the residuals and a Bartlett's test was used to test for their homoscedasticity. Variance estimates were calculated by using (conditioned) parametric bootstrap resampling (Efron, 1982) with 500 bootstrap iterations. Standard errors and 95% confidence intervals were constructed from the bootstrap data using the percentile method described by Buckland (1984).

An age-length key was used to transform the length-frequency distributions from commercial and research trawls to age frequency distributions (Butterworth *et al.*, 1989). Estimates of total annual mortality ( $Z$ ) were obtained by means of catch curve analyses using the 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 than the age at full recruitment. A second method to estimate total mortality was used as it 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

$$Z = \ln \left[ 1 + \frac{1}{(\bar{a} - a_f)} \right]$$

where  $a_r$  is the age at full recruitment and  $\bar{a}$  is the mean age of all fully recruited fish (Butterworth *et al.*, 1989). Natural mortality ( $M$ ) was estimated using the empirical relationship described by Pauly (1980) as

$$\log_{10}M = -0.0066 - 0.279 \log_{10}L_{\infty} + 0.6543 \log_{10}K + 0.4634 \log_{10}T$$

where  $T$  is the mean sea temperature ( $^{\circ}\text{C}$ ), and  $L_{\infty}$  (mm) and  $K$  are the von Bertalanffy growth parameters described above. The mean annual water temperature along the entire Bank was  $12^{\circ}\text{C}$  (M. J. Roberts, Sea Fisheries Research Institute, unpublished data). Fishing mortality was obtained by subtraction ( $F = Z - M$ ).

Female length at maturity was calculated by determining the proportion of reproductively active fish (active and postspawning) in each cm size class. Length at maturity also commonly referred to as length (or size) at 50% maturity, is defined as that length at which 50% of the sample is sexually mature. This was estimated by fitting a logistic ogive of the form

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

where  $P_L$  is the percentage of fish mature at length  $L$  and  $L_{50}$  the length at maturity and  $\delta$  the steepness of the ogive. The model parameters were estimated by minimizing the squared difference between the observed and predicted maturity values. Reproductive seasonality was ascertained using different methods; by a gonadosomatic index which was calculated by expressing gonad mass as a percentage of eviscerated body mass, calculating the proportion of various maturity stages in mature ovaries and by calculating the percentage of mature ovaries with hydrated eggs clearly visible macroscopically through the tunica. Adult sex ratio was determined using fish larger than the length at maturity.

## RESULTS

### POPULATION STRUCTURE AND MORPHOMETRICS

Whilst the mean length of adult male and female lesser gurnard was found to be similar ( $Z = 0.33$ ;  $P > 0.05$ ), the adult population was male dominated with an adult sex ratio of 1 female: 1.16 males, differing significantly from unity using both length ( $\chi^2 = 34.7$ ; d.f. 7,  $P < 0.05$ ) (Fig. 2) and age ( $\chi^2 = 46.1$ ; d.f. 4,  $P < 0.05$ ) (Fig. 3) frequency data.

Morphometric relationships between length and weight, otolith length, otolith diameter, otolith mass and otolith width are summarized in Table II. Using a likelihood ratio test (Draper & Smith, 1966), no significant differences between males or females were found for both the total length-eviscerated mass ( $F = 1.60$ ; d.f. 1, 340,  $P > 0.05$ ) and total length-otolith length ( $F = 2.71$ ; d.f. 1, 108,  $P > 0.05$ ) relationships. Therefore, all morphometric analyses were pooled.

### AGE AND GROWTH

Alternating opaque and hyaline zones were visible in the otolith sections with zones most easily discernible on the dorsal area of the otolith (Fig. 4). Marginal zone analysis confirmed that one opaque and one hyaline zone was formed each year, between April and July (Fig. 5). It was assumed that each opaque zone represented an annulus with a year's growth represented by an opaque and its adjacent hyaline zone. Of the 259 otoliths analysed, 24 (9.3%) were rejected as unreadable with the remainder of the otoliths used to construct an age-length key and for the estimation of growth parameters. Whilst length at age was described adequately using both growth models, with an absolute (as opposed to

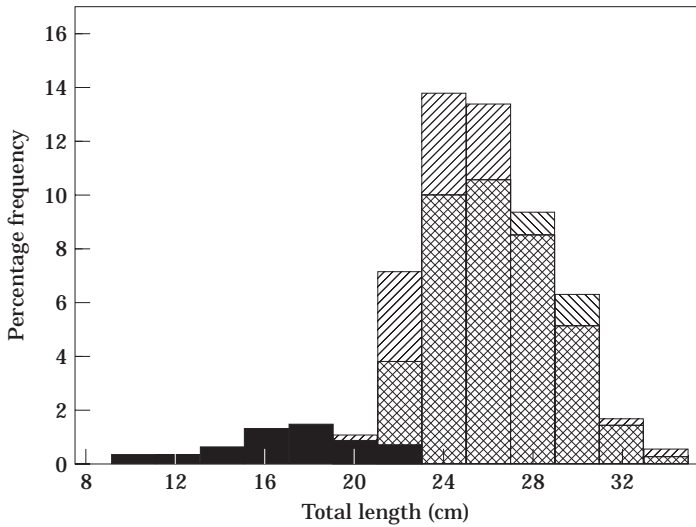


FIG. 2. Length-frequency histograms of male (▨), female (▩) and immature (■) *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa.  $n=1598$ .

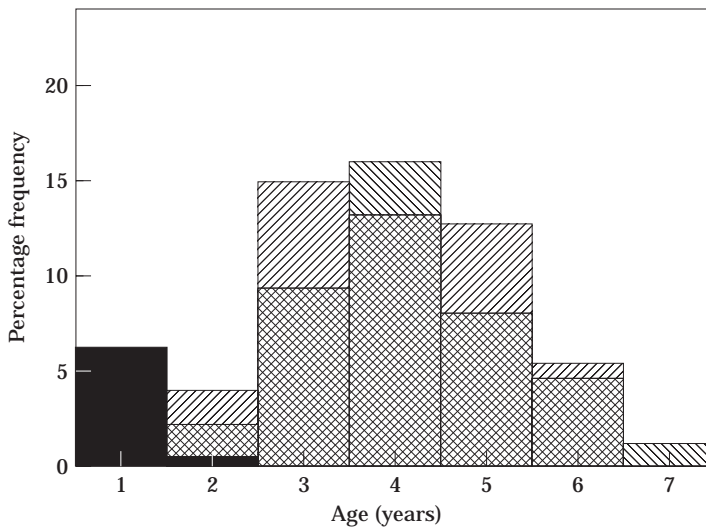


FIG. 3. Age-frequency histograms of male (▨), female (▩) and immature (■) *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa.  $n=1598$ .

the relative) error structure providing residual homoscedasticity, no significant difference was found between them using a likelihood ratio test ( $F=0.35$ ; d.f. 2, 231,  $P>0.05$ ). Therefore, the von Bertalanffy model was chosen, as it has fewer parameters making it statistically more robust, its parameters are commonly used in mortality estimates (Pauly, 1980) and per recruit modelling (Ricker, 1975) and for ease of comparison between growth studies conducted on other triglid species. No significant differences were found between mean lengths at age of males and females using a Student's  $t$ -test ( $P>0.05$ ) or between the

TABLE II. Morphometric relationships for *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa

Relationship	$n$	$r^2$
Total mass (g)	=0.00004 total length (mm) <sup>3.12</sup>	649 0.99
Eviscerated mass (g)	=0.00004 total length (mm) <sup>3.09</sup>	649 0.99
Headed and eviscerated mass (g)	=0.00003 total length (mm) <sup>3.12</sup>	592 0.99
Total length (mm)	=1.21 fork length (mm)+5.53	649 0.99
Total length (mm)	=1.06 standard length (mm) - 3.22	649 0.99
Total length (mm)	=0.77 headed length (mm)+0.75	100 0.98
Total length (mm)	=4.38 pectoral length (mm) - 1.96	579 0.92
Total length (mm)	=80.39 otolith length (mm) - 44.85	120 0.89
Total length (mm)	=101.40 otolith width (mm) - 41.00	120 0.89
Total length (mm)	=233.53 ln (otolith thickness, mm)+681.25	120 0.86
Total length (mm)	=90.22 ln (otolith mass (g))+681.25	120 0.93

modelled length-at-age using a likelihood ratio test ( $F=3.39$ ; d.f. 2, 222,  $P>0.05$ ). The data were pooled and a single growth model estimated (Fig. 6; Table III). Point estimates and estimates of associated variance for males, females and the combined data are summarized in Table IV. A summary of previous age and growth studies on triglid species using whole and sectioned otoliths is presented in Table V.

#### MORTALITY

Age frequencies derived from transformed length-frequency data collected from research and commercial gear provided estimates of total mortality (Fig. 7). Fish were first recruited at 1 year into the research and commercial trawls and were fully recruited by 2 and 4 years, respectively. Total mortality estimates obtained both from catch curve analysis and from the Butterworth *et al.* (1989) method were considerably different, with the commercial trawl data in particular, producing higher estimates (Table VI). All four estimates were averaged to obtain a first approximation of total mortality at 0.73 year<sup>-1</sup>. Pauly's (1980) empirical estimate of 0.38 year<sup>-1</sup> was taken as a first approximation of natural mortality and by substitution fishing mortality was calculated as 0.35 year<sup>-1</sup>.

#### REPRODUCTIVE BIOLOGY

Gonads were suspended by the dorsal mesentery in the posterior region of the visceral cavity with both gonadal lobes equally developed. All macroscopic stages of gonadal development were easily discernible. Female sexual maturity proceeded rapidly ( $\delta=0.33$  year<sup>-1</sup>), first being evidenced in fish measuring 19 cm  $L_T$  (1.6 years) with all females sampled being sexually mature by 21 cm  $L_T$  (2.1 years). Size at maturity was estimated from the logistic ogive at 19.5 cm  $L_T$  (1.7 years) (Fig. 8). Individual gonadosomatic indices showed that reproductive activity extended throughout the year, peaking in spring (July–October) and late summer/autumn (January–May) (Fig. 9). A similar trend was evident using the



FIG. 4. Photomicrograph of a transverse, sagittal otolith section of a 7-year-old *Chelidonichthys queketti* viewed with transmitted light. Bar=1 mm.

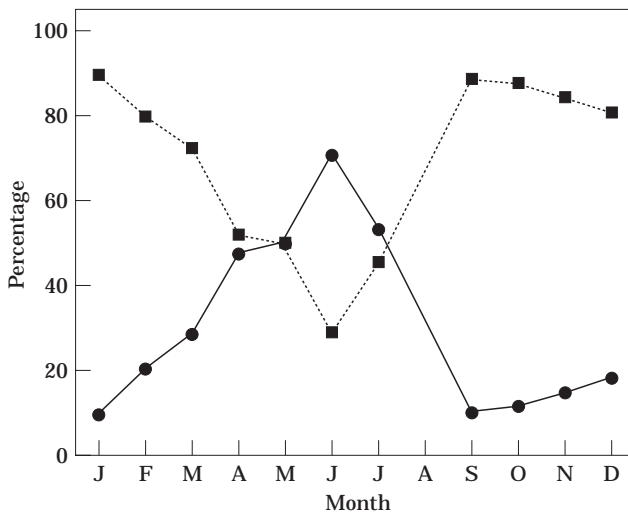


FIG. 5. Temporal changes in otolith margin composition (—, opaque; ---, hyaline) for *Chelidonichthys queketti* sampled monthly on the Agulhas Bank, South Africa.

macroscopical maturity indices and the proportion of ovaries with hydrated eggs (Fig. 10). A summary of size and age at sexual maturity for different triglid species is presented in Table VII.

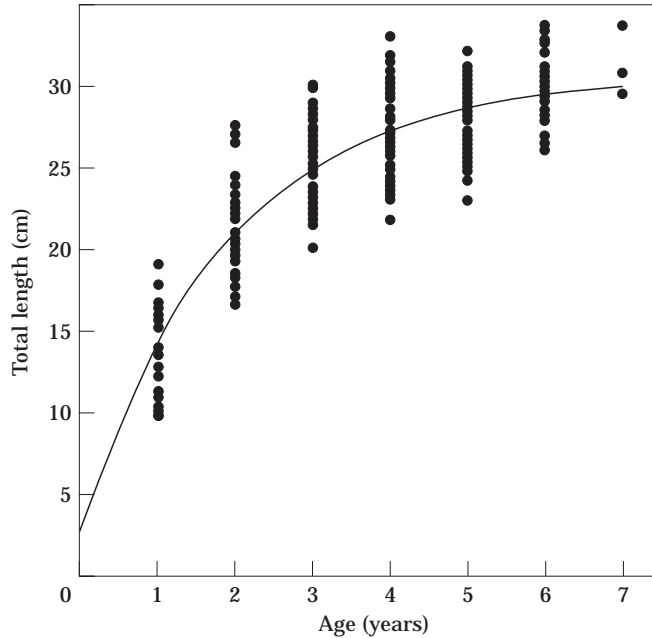


FIG. 6. Observed individual mean lengths at age of *Chelidonichthys queketti* using sectioned sagittal otoliths sampled on the Agulhas Bank, South Africa. The growth curve was fitted to both sexes using the von Bertalanffy growth model with an absolute error structure.  $L_T = 306.11 (1 - e^{-0.53(t+0.18)})$ ,  $n=235$ .

TABLE III. Observed mean length at age ( $\pm$  S.D.) for male, female and all *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa

Age (years)	Females		Males		Unsexed + females + males	
	Mean $\pm$ S.D.	<i>n</i>	Mean $\pm$ S.D.	<i>n</i>	Mean $\pm$ S.D.	<i>n</i>
1	149.6 $\pm$ 20.1	13	155.7 $\pm$ 22.3	6	142.0 $\pm$ 25.4	26
2	202.9 $\pm$ 20.1	18	215.9 $\pm$ 26.9	16	209.2 $\pm$ 27.1	35
3	249.0 $\pm$ 23.2	23	255.5 $\pm$ 22.3	28	255.0 $\pm$ 21.9	51
4	272.8 $\pm$ 23.2	32	271.6 $\pm$ 25.6	26	272.3 $\pm$ 24.5	58
5	278.7 $\pm$ 23.3	16	281.3 $\pm$ 23.2	23	280.3 $\pm$ 22.6	39
6	303.3 $\pm$ 21.6	9	292.4 $\pm$ 17.6	12	297.1 $\pm$ 19.7	21
7	320.6 $\pm$ 18.4	5	—	—	320.6 $\pm$ 18.4	5

## DISCUSSION

The length at age estimates revealed that the lesser gurnard is a relatively fast-growing and long-lived species with a life span in excess of 7 years. The maximum known length (350 mm  $L_T$ ; Smith & Heemstra, 1986) was similar to the largest sampled (354 mm  $L_T$ ) and aged (338 mm  $L_T$ ) in this study. The maximum theoretical length predicted from the growth model was, however, lower at 306 mm  $L_T$ . Female lesser gurnards appeared to have a slower growth rate and a larger maximum length and age than the males. Whilst this difference



TABLE IV. Point estimates, associated standard errors and 95% confidence intervals for male, female and combined data fitted using the von Bertalanffy model for *Chelidonichthys queketti* from samples collected on the Agulhas Bank, South Africa

	Point estimate	S.E.	95% CI
Females ( $n=116$ )			
$L_{\infty}$	327.9 mm $L_{T_1}$	15.4	306.9, 366.0
$K$	0.38 year <sup>-1</sup>	0.07	0.25, 0.52
$t_0$	-0.59	0.28	-1.29, -0.16
Males ( $n=112$ )			
$L_{\infty}$	296.8 mm $L_{T_1}$	7.98	285.6, 317.3
$K$	0.59 year <sup>-1</sup>	0.09	0.39, 0.77
$t_0$	-0.24	0.29	-1.06, 0.15
Unsexed + males + females ( $n=235$ )			
$L_{\infty}$	306.1 mm $L_{T_1}$	6.41	295.4, 320.2
$K$	0.53 year <sup>-1</sup>	0.05	0.43, 0.63
$t_0$	-0.18	0.13	-0.46, 0.04

was not found to be significant, similar to *Trigla lyra* (L.) (Papaconstantinou, 1981), it is the most common pattern found in other triglid species, particularly those with significant sexual morphometric differences (Elder, 1976; Hecht, 1977; Papaconstantinou, 1982, 1983, 1984; Baron, 1985).

Discrepancies in maximum age estimates have occurred with the use of whole and sectioned otoliths in triglid species with studies using unsectioned otoliths recording maximum ages less than those from sectioned otoliths. Although these studies might reflect changes due in population characteristics, the differences are marked and emphasize the problem with the former method of age determination. The problem of under ageing long-lived species such as groupers, snappers and seabreams is common to scale- and unsectioned-otolith-based ageing techniques (Withell & Wankowski, 1988; Milton *et al.*, 1995; Booth & Buxton, 1997), often leading to an overestimation of mean length at age and growth rate. The longevity of triglids and the rapid decrease in growth rate leading to an asymptotic maximum length early in life, results in little change in the von Bertalanffy growth model parameters, allowing for comparison of growth performance between species and/or populations using the different ageing methods. Due to the interaction and dependence between the von Bertalanffy growth parameters,  $K$  and  $L_{\infty}$ , an index taking this into consideration needs to be used to compare overall growth performance. The parameter  $\phi' = \ln K + 2 \ln L_{\infty}$  (Pauly & Munro, 1984) can be used as it has been found that similar species, stocks or families with different growth parameters can have similar  $\phi'$  estimates. A wide range of  $\phi'$  values (5.12–7.01) were found for triglids with the population and sexes with the fastest growth rates and largest maximum sizes attaining the largest  $\phi'$  values. Whilst the  $\phi'$  values for male lesser gurnards were higher than those for females, overall growth performance was not found to differ significantly from values from other species (Student's  $t$ -test,  $P > 0.05$ ).

TABLE V. A summary of triglid age and growth estimates using whole or sectioned otoliths. Overall growth performance is calculated using  $\phi' = \ln K + 2 \ln L_{\infty}$

Species	Sex	Method	Max age	$L_{\infty}$	K	$\phi'$	Source
Aspitrigla cuculus	Male	Whole	5	20.4	0.51	5.36	Papaconstantinou (1983)
Aspitrigla cuculus	Female	Whole	7	27.6	0.22	5.12	Papaconstantinou (1983)
Aspitrigla cuculus	Male	Sectioned	13	37.1	0.52	6.57	Baron (1985)
Aspitrigla cuculus	Female	Sectioned	21	41.7	0.46	6.68	Baron (1985)
Chelidonichthys capensis	Male	Whole	11	58.6	0.19	6.48	Hecht (1977)
Chelidonichthys capensis	Female	Whole	12	71.4	0.17	6.76	Hecht (1977)
Chelidonichthys capensis	All	Whole	12	70.2	0.15	6.61	Hecht (1977)
Chelidonichthys capensis	Male	Sectioned	12	75.5	0.08	6.12	Wood-McPhail (1997)
Chelidonichthys capensis	Female	Sectioned	16	80.3	0.10	6.46	Wood-McPhail (1997)
Chelidonichthys capensis	All	Sectioned	16	89.4	0.08	6.46	Wood-McPhail (1997)
Chelidonichthys kumu	All	Whole	10	52.0	0.41	7.01	Staples (1972)
Chelidonichthys kumu	Male	Whole	10	28.8	0.64	6.27	Elder (1976)
Chelidonichthys kumu	Male	Whole	10	36.4	0.57	6.63	Elder (1976)
Chelidonichthys queketti	Male	Sectioned	6	29.7	0.59	6.25	This study
Chelidonichthys queketti	Female	Sectioned	7	32.8	0.38	6.01	This study
Chelidonichthys queketti	All	Sectioned	7	30.6	0.53	6.21	This study
Eutrigla gurnardus	Male	Whole	5	26.4	0.22	5.03	Papaconstantinou (1982)
Eutrigla gurnardus	Female	Whole	8	—*	—*	—	Papaconstantinou (1982)
Eutrigla gurnardus	Male	Sectioned	15	34.4	0.77	6.81	Baron (1985)
Eutrigla gurnardus	Female	Sectioned	16	38.0	0.86	6.12	Baron (1985)
Prionotus evolvans	All	Sectioned	7	—†	—†	—	McEachran & Davis (1970)
Trigla lucerna	Male	Whole	4	—†	—†	—	Papaconstantinou (1984)
Trigla lucerna	Female	Whole	10	—†	—†	—	Papaconstantinou (1984)
Trigla lucerna	Male	Sectioned	14	48.4	0.46	6.98	Baron (1985)
Trigla lucerna	Female	Sectioned	15	48.4	0.33	6.65	Baron (1985)
Trigla lyra	All	Whole	7	74.1	0.11	6.40	Papaconstantinou (1981)
Trigloporus lastovista	Male	Sectioned	18	36.9	0.65	6.79	Baron (1985)
Trigloporus lastovista	Female	Sectioned	17	39.5	0.58	6.81	Baron (1985)

\*Growth parameters were not estimated as the Ford-Walford plot predicted an infinite  $L_{\infty}$ ; †growth parameters were not estimated.

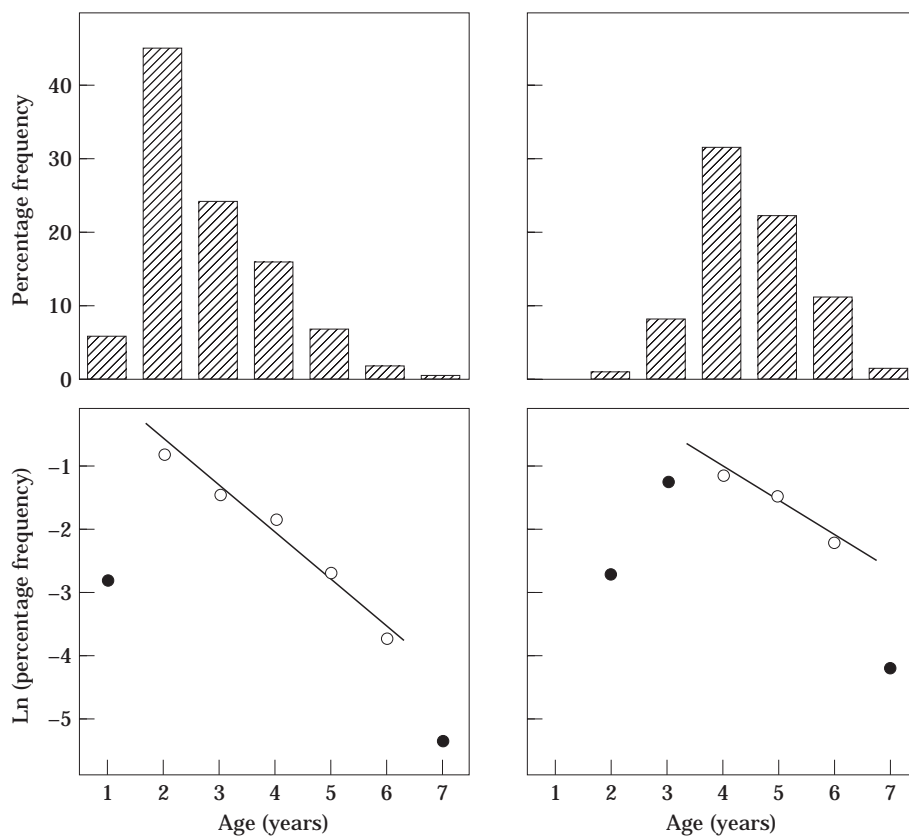


FIG. 7. Age-frequency distributions and catch-curves of *Chelidonichthys queketti* sampled using research (left) and commercial (right) trawling gear on the Agulhas Bank, South Africa. The negative of the slope from a least squares regression equation fitted to the natural log of the age frequency values gives an estimate of total mortality. Only open dots were used in the least squares regression. Research:  $b = -0.71 \pm 0.07$ ;  $Z = 0.71 \text{ year}^{-1}$ ,  $n = 46\ 141$ ; commercial:  $b = -0.53 \pm 0.11$ ,  $Z = 0.53 \text{ year}^{-1}$ ,  $n = 1502$ .

TABLE VI. Total ( $Z$ ), natural ( $M$ ) and fishing ( $F$ ) mortality estimates obtained for *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa using both research and commercial trawl gear

	$Z$ (catch curve)	$Z$ (Butterworth <i>et al.</i> , 1980)	$Z$ average	$M$ Pauly (1980)	$F$
Research trawl	0.71	0.80	0.76	0.38	0.38
Commercial trawl	0.53	0.86	0.70	0.38	0.32
Averaged estimate	0.62	0.83	0.73	0.38	0.35

Despite differences in ageing methodology, an overview of growth patterns in triglids reveals that fast growth and longevity are common triglid characteristics with many species reaching at least 50% of their maximum size before

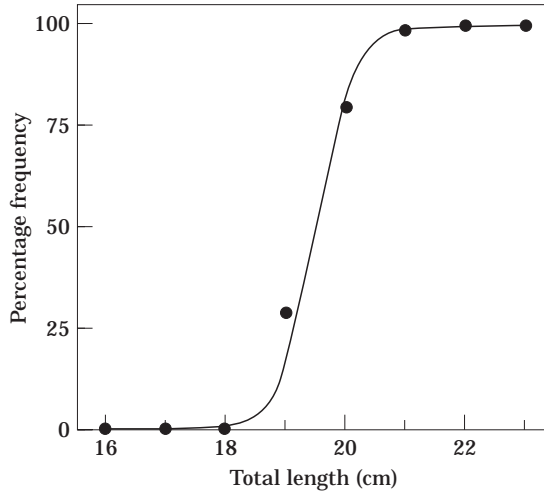


FIG. 8. Percentage frequency of mature female *Chelidonichthys queketti* in different length classes sampled on the Agulhas Bank, South Africa. The curve was fitted using a logistic ogive.

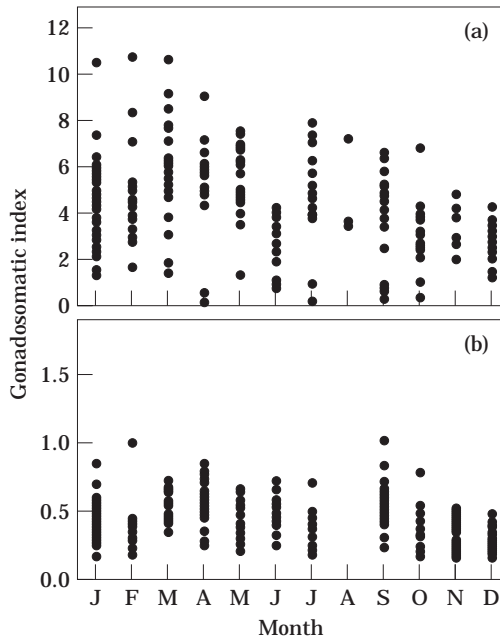


FIG. 9. Seasonal variation of individual gonadosomatic indices for (a) female ( $n=252$ ) and (b) male ( $n=326$ ) *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa.

sexual maturation (McEachran & Davis, 1970; Elder, 1976; Hecht, 1977; Papaconstantinou, 1982, 1983, 1984). Growth in the lesser gurnard was rapid with *c.* 60% of the maximum size attained before sexual maturity which occurred at the end of the first year of life. This decrease in growth rate appears to be as a result of a shift in somatic to reproductive growth which would probably be expensive energetically as spawning extends throughout the year. Fast growth,

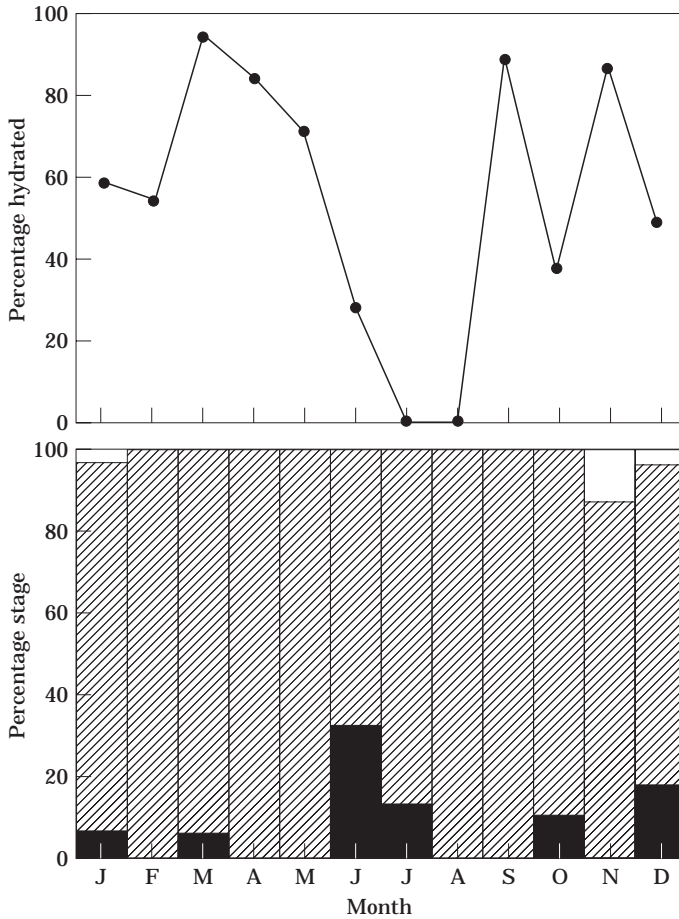


FIG. 10. Seasonal variation of the percentage of ovaries with hydrated eggs visible macroscopically through the tunica and the percentage of macroscopic gonad stages in ovaries of *Chelidonichthys queketti* sampled on the Agulhas Bank, South Africa. ■, Developing; ▨, active; □, postspawning.

reaching a large proportion of maximum length, could allow for a maximization of reproductive capacity which coupled with continual spawning through life could enable a high lifelong fecundity without much additional somatic growth. Alternatively, differential age-specific mortality rates could select for rapid growth to a size large enough to reproduce and where reduced mortality would be an advantage. As no information regarding age-specific rates is available and few predators are known to prey on lesser gurnard to any large extent (Meyer & Smale, 1991; Smale & Cowley, 1992), either one or both of these scenarios could provide a mechanism to select for fast growth and an early asymptotic length in this species.

The catch curve total mortality estimate from the commercial trawls was slightly lower than that obtained from the research trawl data. Furthermore, the few data points in the catch curve regression for the commercial trawl data set make the regression slope insignificant ( $P > 0.1$ ) and therefore this needs to be viewed with caution. The use of the method described by Butterworth *et al.*

TABLE VII. A summary of triglid reproductive parameters as a function of age and length

Species	$T_m$ (years)	$T_{max}$ (years)	$L_m$ (cm)	$L_{\infty}$ (cm)	$T_m/T_{max}$	$L_m/L_{\infty}$	Source
<i>Aspitrigla cuculus</i>	2	7	—	27.6	0.29	—	Papaconstantinou (1983)
<i>Chelidonichthys capensis</i>	3	12	30.5	71.4	0.25	0.43	Hecht (1977)
<i>Chelidonichthys capensis</i>	4	16	35.0	80.3	0.25	0.44	Wood-McPhail (1997)
<i>Chelidonichthys kumu</i>	2	10	24	36.4	0.20	0.66	Elder (1976)
<i>Chelidonichthys queketti</i>	1.7	7	19.5	32.8	0.24	0.59	This study
<i>Trigla lucerna</i>	4	10	—	—	0.40	—	Papaconstantinou (1984)
<i>Trigloporus lastovista</i>	3	8	16.0	35.6	0.38	0.45	Papaconstantinou (1986)

$T_m$ , Age at (50%) maturity;  $T_{max}$ , maximum known age;  $L_m$ , length at (50%) maturity;  $L_{\infty}$ , maximum asymptotic length.

(1989) possibly provides a more accurate estimate of mortality yielding the most similar estimates for both the research and commercial data sets. Using this method, the estimate of total mortality for the commercial data set was slightly higher than that estimated from the research trawls in the area, possibly reflecting localized depletion of lesser gurnard on commercial trawling grounds. The averaged estimate of fishing mortality was high, almost equal to the natural mortality estimate, albeit highly dependent on the value of natural mortality assumed from the empirical relationship. This suggests that the lesser gurnard population on the Agulhas Bank might be subjected to heavy fishing pressure. Generally, little is known about triglid mortality rates with most studies concentrating on the estimation of total mortality using catch curve analysis. The highest published estimate of total mortality was estimated by Papaconstantinou (1986) for *Trigloporus lastoviza* Brännich in the Saronikos Gulf at  $1.04 \text{ year}^{-1}$ . Other estimates have been restricted to the genus *Chelidonichthys* with Elder (1976) estimating total mortality for *C. kumu* (Lesson & Garnot) in New Zealand, with  $Z=0.60 \text{ year}^{-1}$  for males and  $0.65 \text{ year}^{-1}$  for females. Both sexes were recruited into the fishery at 2 years of age. A recent study conducted on *C. capensis* in South Africa by Wood-McPhail (1997) estimated  $Z$  at  $0.60 \text{ year}^{-1}$  for pooled male and female data. Both sexes were recruited into commercial trawl fishery at approximately 5 years of age. The lesser gurnard was intermediate with the estimate of  $Z=0.73 \text{ year}^{-1}$  and recruiting into the trawlfishery at 4 years of age. The differences between ages at recruitment reflect the size of the mesh used in the different studies with a maximum stretched mesh-size of 10.2 cm used by Elder (1976) and 75 cm used both commercial vessels in both this study and that of Wood-McPhail (1997). The retention of small lesser gurnards was a consequence of net clogging during the long trawl hauls of 2–3 h. Few estimates of natural mortality are available (Papaconstantinou, 1986; Wood-McPhail, 1997), all of which are based on Pauly's (1980) empirical relationship. These estimates range between  $0.09$  and  $0.18 \text{ year}^{-1}$ . In contrast the estimate obtained for *C. queketti* was substantially higher at  $0.38 \text{ year}^{-1}$  which is possibly related to its smaller size and faster growth rate than those in the other two species.

The lesser gurnard, as with many sympatric species on the Agulhas Bank, exhibits an extended spawning period with peaks in intensity over late summer and spring. This is supported by the presence of triglid larvae throughout the year sampled during monthly plankton surveys in the Tsitsikamma National Park (A. D. Wood, Rhodes University, unpublished data). Agulhas Bank species have been shown to have either a discrete spawning season such as *Genypterus capensis* (Smith) (Japp, 1989) or more commonly, a protracted spawning season with one or more peaks in reproductive activity as in *Merluccius capensis* Castelman, *Austroglossus pectoralis* Kamp (Payne, 1986), *Chelidonichthys capensis* (Hecht, 1976, 1977; Wood-McPhail, 1997), *Pterogymnus lanarius* Cuvier (Booth & Buxton, 1997) and *Cynoglossus zanzibarensis* Norman (Booth, unpublished data). These two types of spawning seasonality, either protracted and continuous or short and intense are noticeable in the Southern and Northern hemisphere triglid species respectively. Protracted spawning is also common in *C. kumu* with some level of spawning occurring throughout the year peaking in late spring and early summer (Elder, 1976; Clearwater & Pankhurst, 1994) and both *Trigla lyra* and *C. capensis* off Namibia (Trunov & Malevanyy, 1974). The North American triglid *Prionotus evolans* (L.) (McEachran & Davis, 1970) and the Mediterranean species *Eutrigla gurnardus* (L.) (Papaconstantinou, 1982) and *Trigla lucerna* L. (Papaconstantinou, 1984) exhibit a seasonal spawning pattern over the warmer spring–summer period. Non-seasonal spawning with an increase in activity over spring and autumn was common in insular lutjanid populations inhabiting areas with low amplitude oceanographic cycles (Grimes, 1987) with spawning seasonality appearing to be correlated to production and food availability. If production is low and continuous and food scarce and patchy, then spawning will be continuous, bet-hedging against starvation and predation (Grimes, 1987). Alternatively, if food production for larvae and juveniles was continuous then there would be no pressure towards selecting those individuals which exhibit a seasonal spawning pattern. Non-seasonal spawning by triglids on the Agulhas Bank is probably due to the environment's reduced seasonality with little offshore wind-driven upwelling which is common in the littoral areas and reduced intra-annual localized temperature fluctuations (Schumann *et al.*, 1982). Similarly, if food was abundant and seasonal such as in the northern hemisphere, this would provide a mechanism for selecting individuals with a seasonal spawning strategy which is common in the North American and Mediterranean triglid species.

Species inhabiting different environments exhibit different patterns of life-history characteristics, an effect of morphological and reproductive characteristics, population sizes and their genetic frequencies being adjusted through natural selection. As a result, different names have been given to the phenotype pairs which arise from these life-history dichotomies such as *r* selected and *K* selected, generalists and specialists or altricial and precocial (MacArthur & Wilson, 1967; Adams, 1980; Bruton, 1989). A generalist (*r* selected/altricial) species will have a life-history strategy which will tend towards high productivity. Typical life-history characteristics include a small body size, low age at sexual maturity, high rate of mortality and a short life span. In contrast a specialist (*K* selected/precocial) will have a life-history strategy which tends towards the efficient use of a specific limiting resource. Therefore, specialists exhibit delayed

maturity, have low growth rates, large body sizes, increased life spans and lower natural mortality rates. To understand where triglids fit into this life-history classification continuum, various life-history parameters for which a reasonable level of certainty are known such as dietary preferences, maximum length, maximum age, growth rate, size at maturity and age at maturity can be investigated. Several parameters that are poorly understood such as habitat preferences and natural mortality rates can be utilized, albeit to a limited extent.

Aspects of the biology of triglids suggest that they have a generalistic and opportunistic life-history style. Limited data available regarding habitat preferences suggest that they are found over a variety of substrata, particularly those containing soft sediments and unconsolidated substrates such as mud, sand and low-profile reef with interspersed mud and sand depressions (Ross, 1977; Papaconstantinou, 1982; Badenhorst & Smale, 1991; Smale *et al.*, 1993; Booth, unpublished data). Several studies on feeding biology and resource partitioning in the family, reveal an opportunistic feeding pattern, feeding on a wide variety of available prey organisms. Triglid diets consist predominantly of epibenthic crustaceans, polychaetes and fishes (Marshall, 1946; Ross, 1977; Caragitsou & Papaconstantinou, 1990; Meyer & Smale, 1991). Whilst there was little evidence of resource partitioning within sympatric South African species (Meyer & Smale, 1991), limited depth-zone-related resource partitioning was reported in eight triglid species off the west coast of Florida (Ross, 1977). Triglid growth patterns reveal longevity in most species, many of which exhibit extremely rapid growth before sexual maturity (Tables V and VII). In the species reviewed, at least 43% of their maximum size was attained before sexual maturity and sexual maturity was attained early in life, at approximately 25% of the maximum possible age. Early maturity in a long-lived species with reproduction initiated at a large size therefore will ensure high individual reproductive output. Reproductive potential can be maximized, as in the lesser gurnard, by spawning throughout the year or seasonally, depending on when oceanographic conditions are suitable for larval survival. Therefore, it appears that a combination of these life-history characteristics which would maximize reproduction directly could be a strategy to enable triglids to exploit effectively the predominantly temperate soft substratum environments which they inhabit.

The large numbers and relatively high biomass of lesser gurnard on the Agulhas Bank suggest that it plays an important role as an epibenthic predator. High fishing pressures could result in a large reduction in lesser gurnard numbers, impacting on the epibenthic faunae. Fortunately its recruitment into the commercial fisheries occurs after size at maturity providing a refuge of spawner biomass which is not accessible using current fishing gears. This, together with its high natural mortality and growth rates, should provide sufficient surplus production and yield per recruit to offer a certain degree of resilience to high fishing pressure. Future work should focus on the distribution and abundance of different age classes in order to isolate possible nursery areas and/or migrations and to ascertain whether or not there is resource partitioning with *C. capensis* on a spatial and temporal scale. The biological information presented in this study will add to the database of information on by-catch species inhabiting the Agulhas Bank and will contribute to a scientific basis for future management.



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