

**LIFE HISTORY OF WHITE STUMPNOSE *RHABDOSARGUS GLOBICEPS*
(PISCES: SPARIDAE) OFF SOUTH AFRICA**

M. H. GRIFFITHS*, C. WILKE*, A. J. PENNEY† and Y. MELO*

Fishery-dependent and fishery-independent distribution analyses together reveal four discrete areas of white stumpnose *Rhabdosargus globiceps* abundance between Port Nolloth and the Kei River off the Cape Province of South Africa: the Western Cape (Saldanha Bay), the South-Western Cape, the Southern Cape and the South-Eastern Cape. On the basis of migratory patterns determined from tagging and catch data, and on differences in growth rate and size-at-maturity, it is concluded that these areas of abundance represent four separate stocks. Each stock apparently disperses offshore in winter (to c. 130 m depth) and concentrates inshore (<60 m depth) in response to oceanographic patterns during summer. Growth rate and size-at-50% maturity (L_{50}) increased clinally from the South-Eastern Cape through to the South-Western Cape, and in all three regions males matured at larger size than females. Sizes at maturity for male and female *R. globiceps* were respectively 18.6 and 15.3 cm (fork length, *FL*) in the South-Eastern Cape, 22.1 and 18.1 cm in the Southern Cape and 24.3 and 23.6 cm in the South-Western Cape. The fitted Von Bertalanffy growth equations for the three regions were: $L_t = 349 (1 - e^{-0.114(t+3.60)})$ mm for the South-Eastern Cape; $L_t = 337 (1 - e^{-0.207(t+1.05)})$ mm for the Southern Cape; and $L_t = 379 (1 - e^{-0.290(t+0.16)})$ mm for the South-Western Cape. Maximum ages recorded in each region were 21 years for the South-Western Cape, 20 years for the Southern Cape and 10 years for the South-Eastern Cape. Lack of older fish in the South-Eastern Cape sample, attributed to inadequate sample size, has probably resulted in overestimates of both L_∞ and *K* in this region. Spawning is from August to February, with a peak in spring (September–November). Early juvenile *R. globiceps* recruit into estuarine and surf-zone marine nursery areas at around 2–5 cm (± 3 months), but move progressively farther offshore with growth; those trawled deeper than 50 m east of Cape Agulhas were predominantly adults (20–35 cm *FL*). Because of cooler water temperatures west of Cape Agulhas, adults there are found from the surf zone to depths of only 20 m in summer.

Key words: age, growth, migration, nurseries, size-at-maturity, spawning, stock discrimination

White stumpnose *Rhabdosargus globiceps* is a medium-sized (attaining 3 kg total weight), endemic, temperate sparid, and is recorded from southern Angola to the Kei River on the east coast of South Africa (Whitfield 1998). It is an important recreational and commercial linefish off the west and south coasts of South Africa (Bennett 1991) and is also taken as a bycatch by inshore trawlers (Japp *et al.* 1994) and beach-seine fishers (Lamberth *et al.* 1994). Estimated annual landings are around 40 tons for shore-anglers, 147 tons for commercial linefishers, 12.5 tons for beach-seine operators and 14 tons for inshore trawlers (Japp *et al.* 1994, Lamberth *et al.* 1994, Lamberth and Joubert 1999).

Knowledge of *R. globiceps* life history, although fundamental to the identification and assessment of stocks as well as to formulation of management strategies for their sustainable utilization, is surprisingly fragmented. From a limited sample of 58 fish, Talbot (1955) tentatively suggested that spawning is between August and February in the South-Western Cape, and that males and females mature at standard lengths of 27 and 23 cm respectively. Spawning apparently occurs inshore in that region (Biden 1930) and eggs and larvae

are pelagic (Gilchrist 1916). Juveniles <15 cm (total length) are found in bays, the surf zone and estuaries, whereas larger fish inhabit the marine environment to depths of 80 m (Barnard 1927, Talbot 1955, Lasiak 1983, Wallace *et al.* 1984, Whitfield and Kok 1992, Lamberth *et al.* 1995). Growth rate of juveniles in estuaries of the South-Western Cape has been described for the first three years of life (Talbot 1955).

The objective of the present study was to provide information on the life history of South African *R. globiceps*, including reproductive seasonality, size-at-maturity, growth, distribution and migration.

MATERIAL AND METHODS

Data collection

Biological (December 1987–January 1995) and length frequency (1987–1996) data were opportunistically collected from *R. globiceps* caught between Cape Columbine and the Kei River (Fig. 1). Three different

* Marine & Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa. E-mail: mgriffit@mcm.wcape.gov.za

† Pisces Research Management Consultants CC, 22 Forest Glade, Tokai Road, Tokai 7945, South Africa

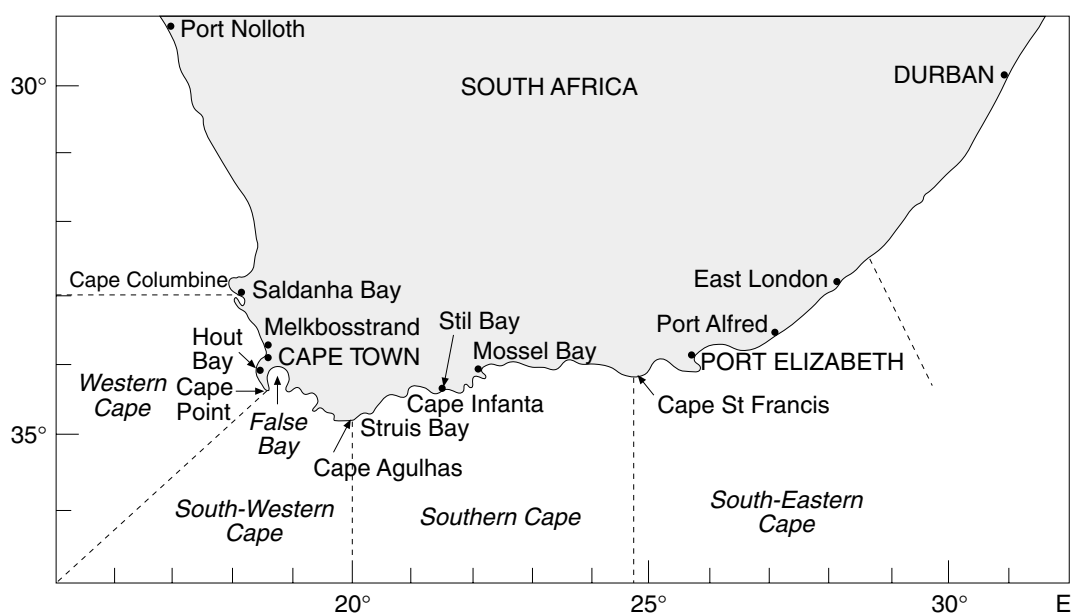


Fig. 1: Map of South Africa showing the four regions and localities mentioned in the text

data sources were used: the commercial linefishery, the inshore trawlfishery and research bottom trawl surveys (South Coast biomass surveys) conducted by Marine & Coastal Management (MCM).

Fish sampled for biological purposes were measured to the nearest 1 mm (fork length), weighed to the nearest gramme, cut open and sexed. Gonads were removed, assigned a visual index of maturity (see Table I) and weighed to the nearest 0.1 g. Gonads collected for histological analysis (1989–1994) were fixed in Bouin's solution for three days and stored in 70% ethanol. They were routinely embedded in paraffin wax, sectioned to 5–7 μm and stained using haematoxylin and eosin. Each histologically prepared gonad was assigned a maturity index based on microscopic criteria (Table I). Otoliths were removed and stored dry in envelopes.

Data were analysed for four regions: Western Cape, South-Western Cape, Southern Cape and South-Eastern Cape (Fig. 1).

Distribution

Areas of *R. globiceps* abundance were delineated using returns from the commercial linefishery and data from South Coast biomass surveys (SCBSs). Annual catch-per-unit-effort (*cpue*) data (catch vessel⁻¹

outing⁻¹) were plotted on a sub-regional basis for the commercial linefishery (an outing did not exceed one day), and the data from 17 SCBSs (Table II) were used to calculate mean numbers of *R. globiceps* per 30-minute trawl, per grid block. SCBS methods are fully described by Badenhorst and Smale (1991), so only a summary is given here. The survey area extended from Cape Agulhas to Port Alfred, and seawards to a depth of 500 m. This area was divided into four depth zones (0–50, 51–100, 101–200 and 201–500 m), which were in turn subdivided into blocks of 5 \times 5 miles. The blocks that were trawled during each survey were selected semi-randomly according to the ratio of blocks per stratum. Bobbins were not used, so trawling was limited to non-reef substrata. The shallowest that the research vessel (*F. R. S. Africana*) could operate was 20 m. A 180-foot German trawl was used with 25 mm mesh (bar) liner attached to the bag. Trawl duration was limited to 30 minutes, and the results of trawls of shorter duration (because of technical reasons or to snagging on reef) were standardized to that time.

Migration

Migration of *R. globiceps* was studied using tagging and catch data. A tagging programme, employing

Table I: Classification and description of macroscopic and microscopic gonad maturity stages of *R. globiceps*

Stage	Description	
	Macroscopic	Microscopic*
1: Inactive	Sexual organs small. Ovaries appear as translucent, yellow to pinkish sacs with no visible eggs. Testis thin and transparent to greyish-white	Ovary consists entirely of primary growth oocytes (i.e. oogonia and perinucleolus stage). Testes contain predominantly spermatogonia
2: Active	Ovary swells and increases in length to 90% of visceral cavity. Colour changes to opaque orange/yellow and eggs are visible to naked eye. Testis become thicker and beige to white in colour. Sperm is present in the main sperm duct, but not in the tissue	Primary growth to tertiary yolked (vitellogenic) oocytes evident in ovary. Atresia evident in some. Testes include all stages of spermatogenesis, but secondary spermatocytes and spermatids most numerous. Central lobes filled with spermatozoa
3: Ripe	Ovary is swollen and amber in colour owing to the presence of a substantial proportion of hydrated/transparent eggs. Testis is swollen and white. It is easily ruptured if lightly pinched, and sperm is present in the sperm duct as well as tissue.	Ovaries contain all stages to tertiary yolk oocytes, but include either hydrated oocytes or post-ovulatory follicles as well. Testes include all stages of sperm development. Spermatozoa found in most lobules and sperm duct
4: Spent	Ovary substantially smaller and flaccid with large lumen. It is reddish orange in colour with few eggs visible. Spent testes were not identifiable	Ovary consists of perinucleolus oocytes with varying proportions of atresia of vitellogenic oocytes. While spermatozoa may be present in some lobules of the testes, most lobules are small, containing only primary and secondary spermatogonia

* Histological terminology according to Hyder (1969) for males and Yamamoto (1956) for females

plastic T-bar tags, was initiated in 1987. *R. globiceps*, captured with hook and line, were tagged in Saldanha Bay, False Bay, off Struis Bay and off Stil Bay. The data for recaptured fish were analysed according to tagging locality, days free and the minimum distance

travelled.

Owners of commercial lineboats and inshore trawlers are required to submit daily catch returns to MCM. Even though linefish catches are under-reported (Sauer et al. 1997), comparison with historical observer data and dealer records reveal that commercial catch returns do reflect seasonal trends in local abundance of migratory species (Griffiths 1988, Griffiths and Hecht 1995). Catches of *R. globiceps* by commercial linefishers in each of the four regions, and the catches by the inshore trawlfishery in the Southern Cape for the period 1986–1996, were totalled on a monthly basis and then expressed as percentages of the combined 11-year catch.

Table II: Number of trawls in which *R. globiceps* were caught during South Coast biomass surveys between Cape Agulhas and Port Alfred during the period 1986–1996

Cruise date	Total number of trawls	Number of trawls with <i>R. globiceps</i>
13 Sep.–Oct. 1986	80	2
9 Sep.–4 Oct. 1987	88	8
11 May–2 Jun. 1988	93	7
11 May–28 May 1989	62	9
24 May–12 Jun. 1990	58	12
8 Sep.–26 Sep. 1990	73	10
8 Jun.–1 Jul. 1991	91	18
14 Sep.–2 Oct. 1991	75	19
1 Apr.–20 Apr. 1992	82	8
3 Sep.–20 Sep. 1992	87	18
19 Apr.–10 May 1993	109	14
2 Sep.–28 Sep. 1993	106	27
8 Jun.–3 Jul. 1994	89	14
22 Sep.–16 Oct. 1994	92	19
23 Apr.–15 May 1995	95	17
30 Sept.–19 Oct. 1995	96	17
11 Apr.–29 Oct. 1996	86	8
All cruises	1 462	227

Reproduction

Size-at-50%-maturity for males and females was estimated by fitting a logistic ogive to the fractions of the mature fish (gonad Stage 2+) per 1 cm length-class, sampled during the breeding season (September–December). The two parameter logistic function is described by

$$P(L) = 1/(1 + \exp^{-(L-L_{50})/\delta})$$

where $P(L)$ is the percentage of mature fish at size L , L_{50} is the length-at-50%-maturity and δ the width of the ogive. L_{50} values were used in conjunction with the fitted Von Bertalanffy growth functions to calculate

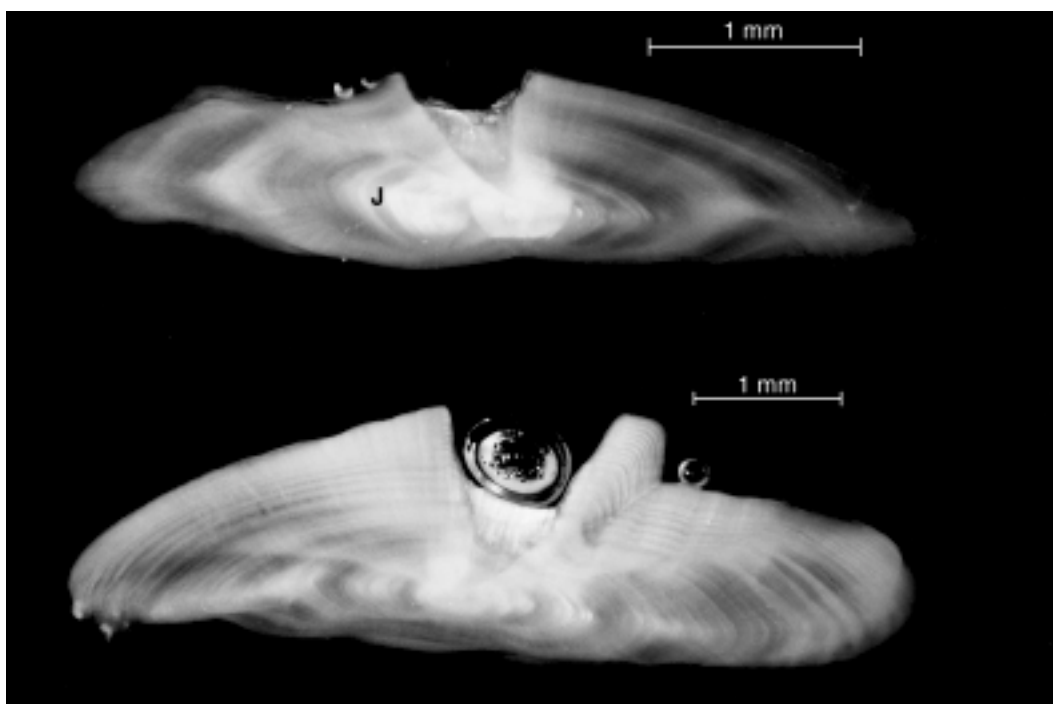


Fig. 2: Transverse otolith sections of a 3-year-old (top) and 18-year-old (bottom) *R. globiceps* from South Africa. J = juvenile ring

ages at 50% maturity in each region.

Reproductive seasonality was established by calculating gonadosomatic indices (*GSI*s) and monthly percentage frequency of each microscopic maturity stage for *R. globiceps* larger than L_{50} .

$GSI = \text{Gonad weight} / (\text{fish weight} - \text{gonad weight}) \times 100$.

Sex ratios were tested for significant deviations from unity with Chi-square tests ($p < 0.05$). Owing to difficulties experienced in sexing some specimens < 20 cm, only *R. globiceps* larger or equal to this length were used in analysis of sex ratios.

Age and growth

Transverse otolith sections have proved to be the most reliable indicators of age for many sparid fish (Buxton and Clarke 1991, Buxton 1993). A total of 641 *R. globiceps* otolith pairs (150–395 *FL*), randomly collected from commercial line catches and SCBSs between Cape Point and Cape Infanta during 1990, was used for ageing. One otolith from each pair was

embedded in a rod of casting resin and then sectioned transversely (~ 0.5 mm) through the core using twin diamond wafering blades and a saw similar to that described by Rauck (1976). Each section was then mounted on a glass slide using DPX mountant and examined on a black background using a dissecting microscope (6 \times magnification) and reflected light. The number of translucent (dark) zones (Fig. 2) was initially counted twice by one reader, at least one week apart, without any reference to fish size. The fine hyaline zone sometimes found within the core (Fig. 2) was assumed to be a juvenile ring. If the readings did not agree, a third reading was done and two coincident readings accepted as the best estimate of age. If none of the readings coincided, the otolith was rejected.

Von Bertalanffy growth curves ($L_t = L_\infty [1 - e^{-K(t-t_0)}]$) were fitted using an iterative least squares procedure (Microsoft Excel solver routine with Newton algorithm option). Growth rates between regions and sexes were compared using likelihood ratio tests (Draper and Smith 1966). To allow for the conversion of fork length-at-age to total length-at-age and to mass-at-age, the relationships between fork length and mass

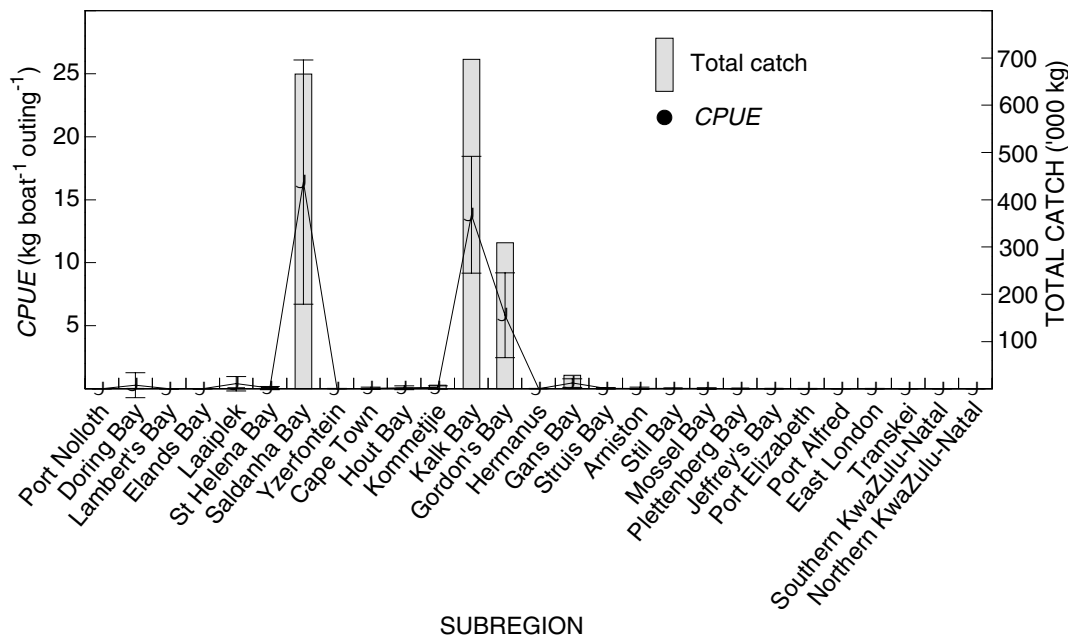


Fig. 3: Mean annual *cpue* ($\pm 1SD$) and total catch for *R. globiceps* caught by commercial linefishers operating between Port Nolloth and the Kei River

and fork length and total length were also derived using the above least squares method.

RESULTS

Distribution and migration

Trawled fish were generally caught over sand/mud substrata and line-caught fish over reef. On account of the high relief rocky nature of the inshore habitat west of Cape Agulhas, *R. globiceps* are trawled in limited quantities off the South-Western Cape. Spatial analysis of linefish catches and *cpue* (Fig. 3) revealed two discrete areas of the abundance of the species on the West Coast, Saldanha Bay (Western Cape) and False Bay (South-Western Cape), whereas data from SCBSs revealed a further two disjunct areas of abundance off the East Coast, one associated with the central Agulhas Bank (Southern Cape) and the other with Algoa Bay off the South-Eastern Cape (Fig. 4). *R. globiceps* were recorded to 130 m in both of these more easterly regions, but were most abundant inshore of the 100-m isobath. According to both density and area of distribution (Fig. 4), the Southern Cape is by far the larger of the two easterly populations.

Of the 982 *R. globiceps* tagged (655 in Saldanha Bay, 191 in False Bay, 61 off Struis Bay and 85 off Stil Bay), only 32 were recaptured. Reported recapture rates were 11.8% from Stil Bay, 8.2% from Struis Bay, 0.5% from False Bay and 2.4% from Saldanha Bay. Tag returns nevertheless suggest that coastal movement is limited (Fig. 5); 94% of recaptures had not moved more than 2 km and the greatest distance travelled was 9 km, in spite of liberty periods of up to 833 days. No movement was recorded between tagging localities or between areas of abundance.

Line catches were highest off the Western Cape from September to March and off the South-Western Cape from December to May (Fig. 6). Although *R. globiceps* were trawled throughout the year off the Southern Cape, there was a clear winter (June–July) peak in catches. Catches reported by the trawl industry for the South-Eastern, South-Western and Western Cape, and for the linefishery off the South-Eastern and Southern Cape each amounted to <5 tons for the study period (1986–1996) and were therefore excluded from the analysis.

R. globiceps landed by the linefishery ranged from 15 to 49 cm *FL*, adults of 23–35 cm constituting the bulk of the catch (Fig. 7). Although the modes of line-caught size frequency distributions off the South-Western and Western Cape were essentially the same

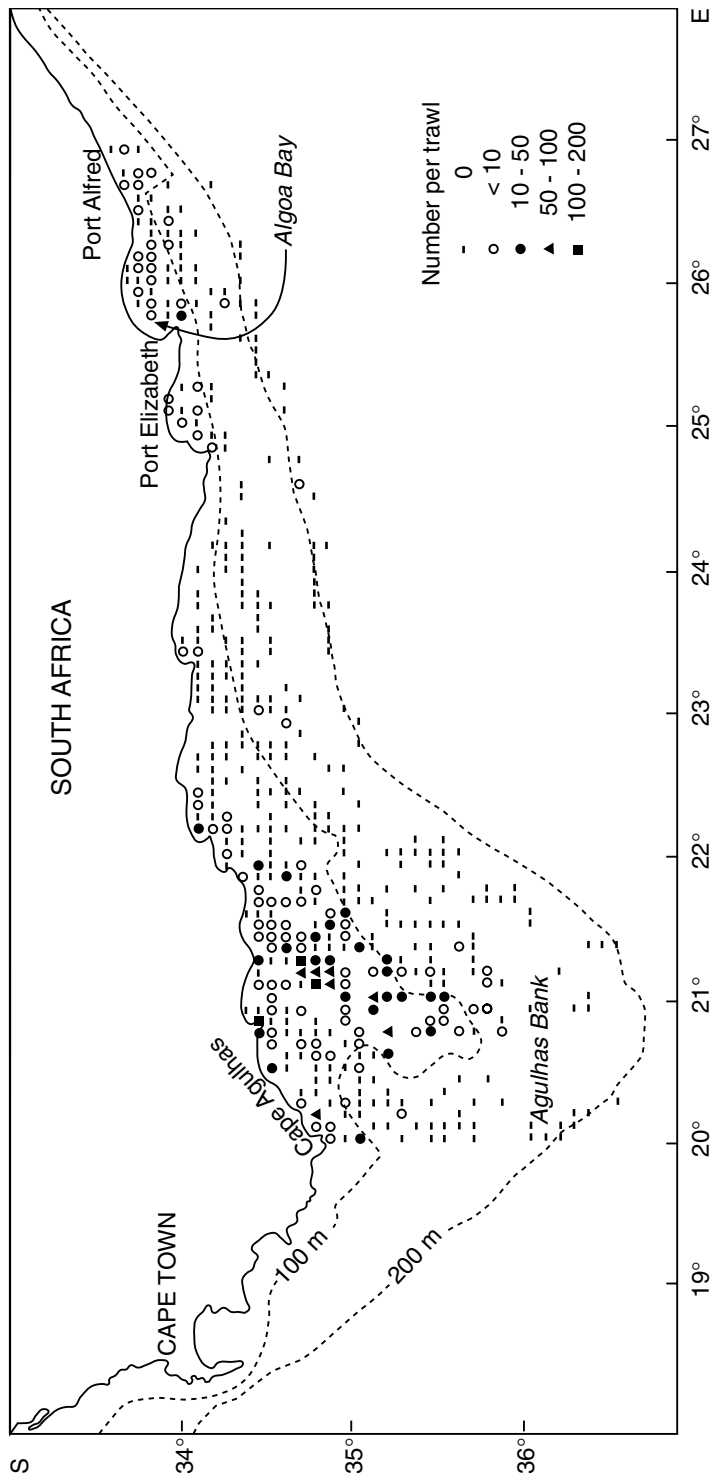


Fig. 4: Mean number of *R. globiceps* per 30-minute trawl per grid block for 17 South Coast biomass surveys, 1986-1996 (n = 1 462 trawls)

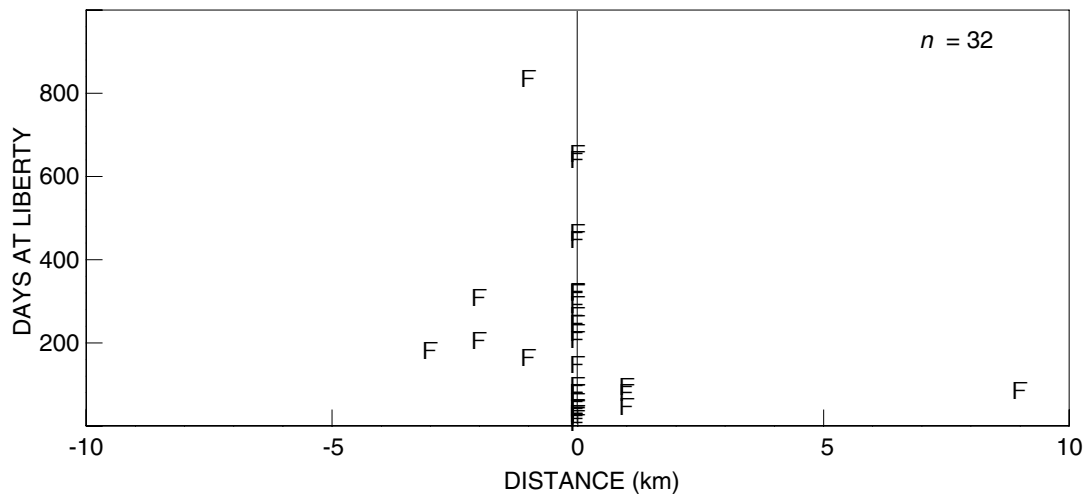


Fig. 5: Minimum distance travelled v. days at liberty for *R. globiceps* tagged off Saldanha Bay, False Bay, Struis Bay and Stil Bay. Negative values designate coastwise movement to the west and positive values movement to the east

(24 cm), the catches from the latter region included a larger proportion of fish 30–40 cm and a lower proportion of fish <22 cm. The Southern Cape line catch had a larger mode (28 cm), but with similar proportions of larger fish to those of the South-Western Cape. The low proportion of fish <25 cm off the Southern Cape is presumably because *R. globiceps*

are no longer targeted there, but are rather caught as a bycatch when fishers target species such as silver kob *A. inodorus*, which have larger mouths (and therefore require larger hook sizes).

Size composition of *R. globiceps* trawled off the South-Eastern and Southern Cape during SCBSs increased markedly with depth (Fig. 8). The bulk of the

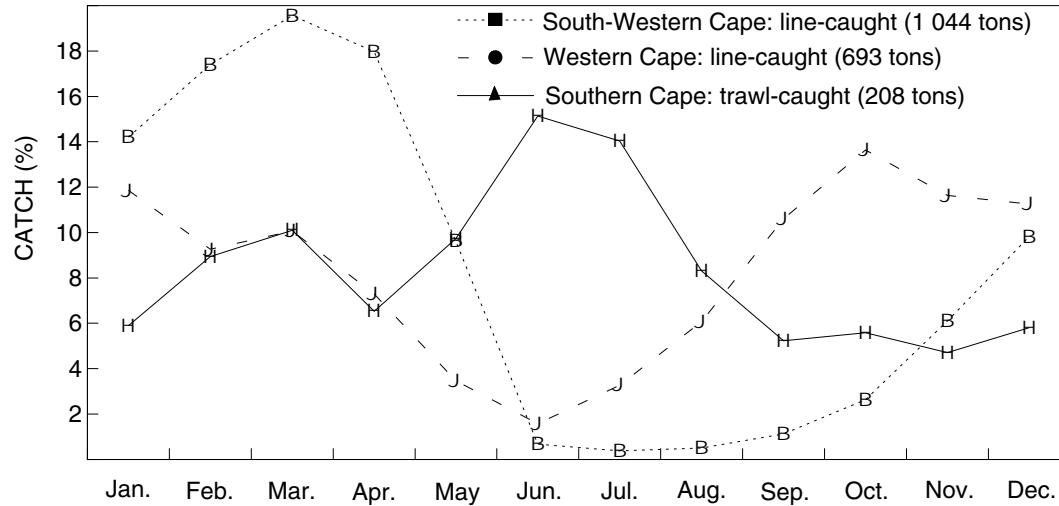


Fig. 6: Catches of *R. globiceps* made by commercial linefishers off the Western and South-Western Cape and by inshore trawlers off the Southern Cape, combined on a monthly basis and expressed as a percentage of the total catch for the period 1986–1996. Total catches for the 11-year period are given

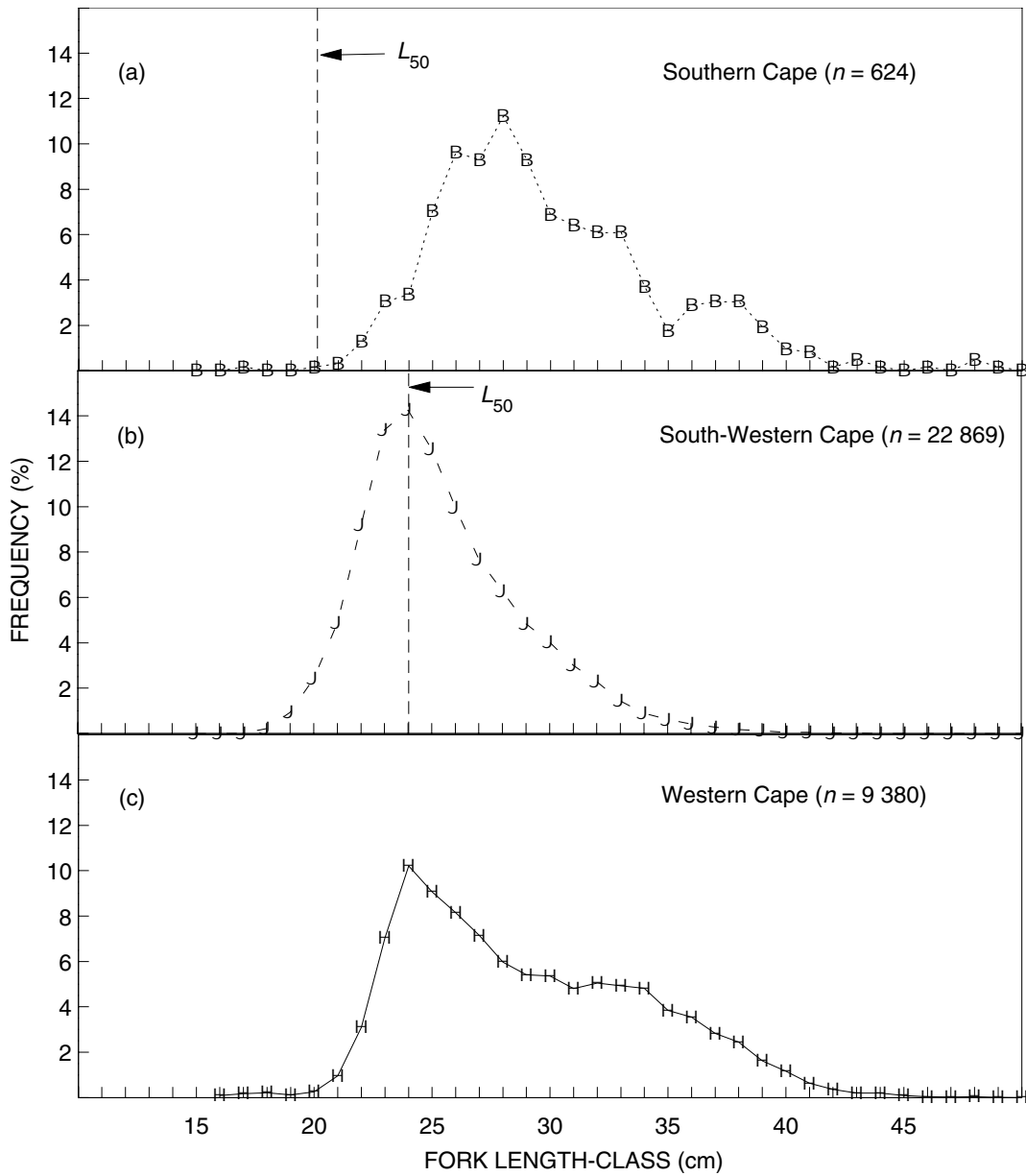


Fig. 7: Length distributions for *R. globiceps* caught by commercial linefishers off (a) the Southern Cape (b) the South-Western Cape and (c) the Western Cape. The average size at maturity (L_{50}) for males and females combined for (a) and (b) are shown

R. globiceps trawled between 25 and 50 m were 14–22 cm long (predominantly immature fish), whereas those trawled deeper than 50 m were generally adults

of 20–35 cm. Catches deeper than 100 m constituted a lesser proportion of fish 20–24 cm than those trawled between 50 and 100 m.

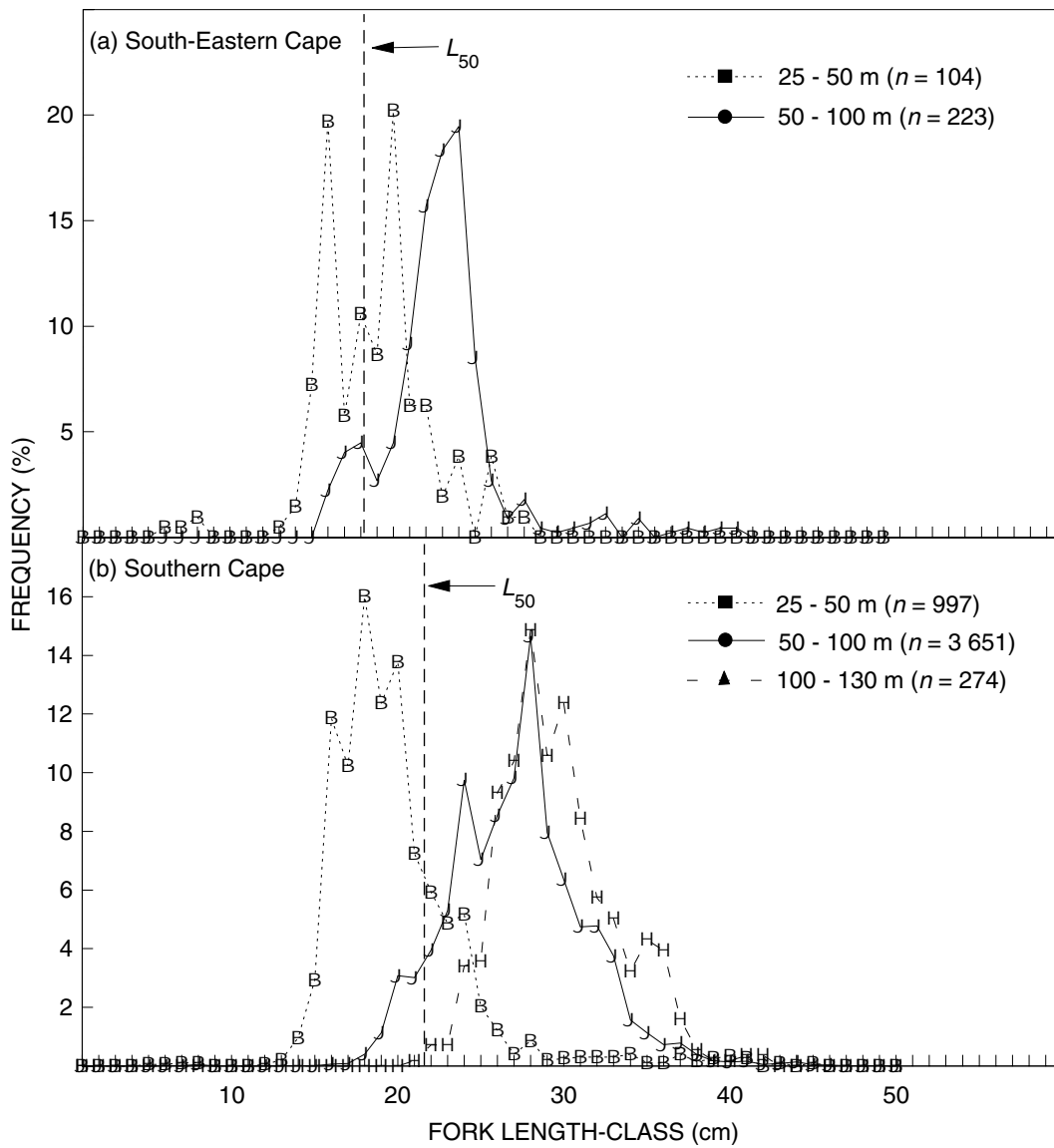


Fig. 8: Length distributions per depth range of *R. globiceps* trawled off the South-Eastern and Southern Cape during South Coast biomass surveys, 1986–1996. The average size at maturity (L_{50}) for males and females combined are shown

Reproduction

Size-at-maturity, based on macroscopic criteria, increased progressively from the South-Eastern Cape through to the South-Western Cape (no juveniles were sampled off the Western Cape, so size-at-maturity

could not be calculated for that region). This cline was evident for both sexes, but in each region males matured at a larger size than females (Fig. 9). Respective sizes-at-50%-maturity (FL) for males and females were 18.6 and 15.3 cm off the South-Eastern Cape, 22.1 and 18.1 cm off the Southern Cape and 24.3 and 23.6 cm

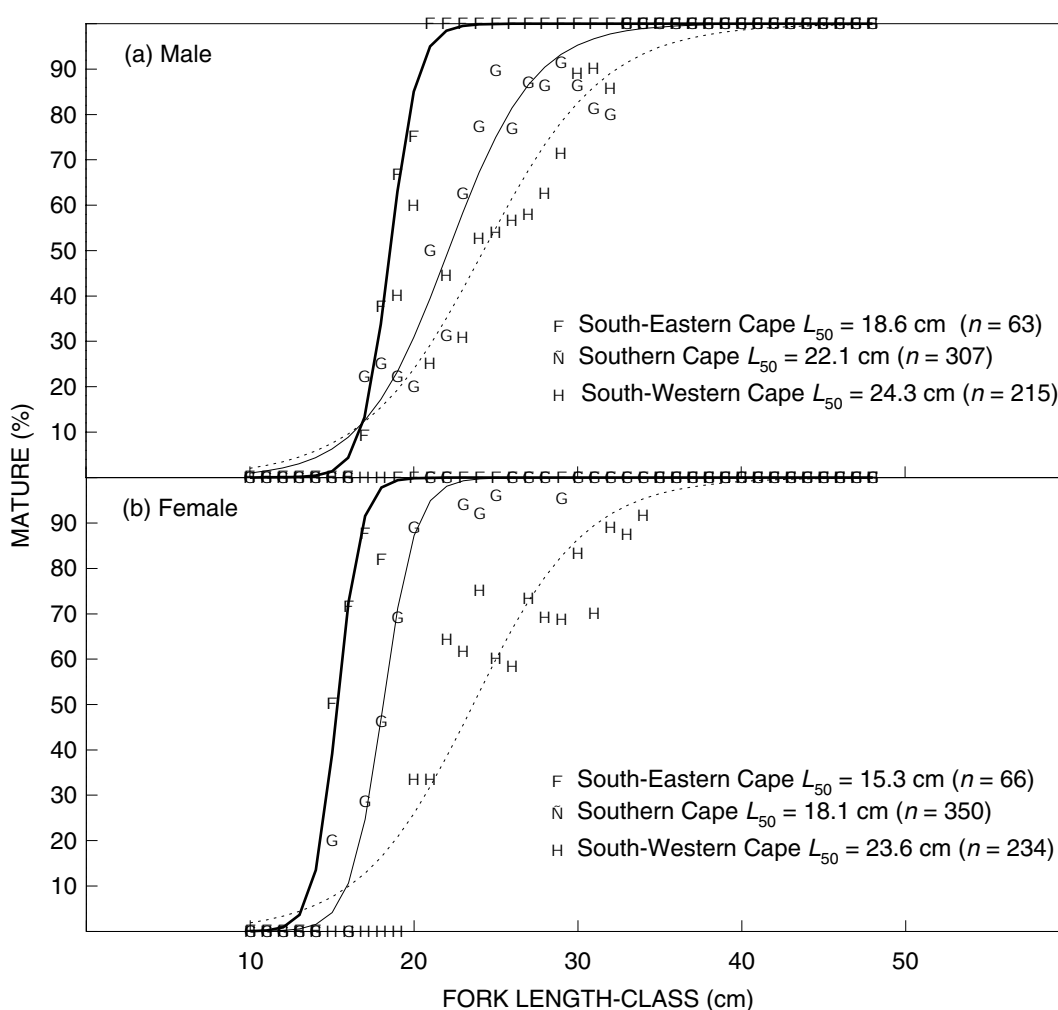


Fig. 9: Relationship between size and percentage maturity of (a) male and (b) female *R. globiceps* for three regions. Solid lines describe the fitted logistic function

off the South-Western Cape. The sizes-at-maturity estimated for the Southern Cape¹, based on histological criteria, were 22.1 and 19.1 cm for males and females respectively, and were therefore similar to those derived for this region from the macroscopic analyses. The 1 cm difference observed for females is more likely to be a function of the smaller histological sample (141 v. 350) than to misclassification owing to the use of macroscopic stages.

¹ Size ranges and the number of gonads preserved were insufficient to calculate sizes at maturity, based on microscopic criteria, for the other regions

Male and female *GSI*s were highest from August to November and from August to December respectively (Fig. 10). Thereafter, the *GSI* values of both sexes declined, attaining their lowest level in March. These data suggest a protracted spawning season from late winter to early summer. Female *GSI*, generally regarded as a better indicator of spawning season than male *GSI*, peaked between September and November (i.e. spring). Monthly proportions of histologically ripe ovaries (with hydrated oocytes or post-ovulatory follicles) support a protracted spawning season from August to February (Fig. 11) and confirmed the spring spawning peak (September–October).

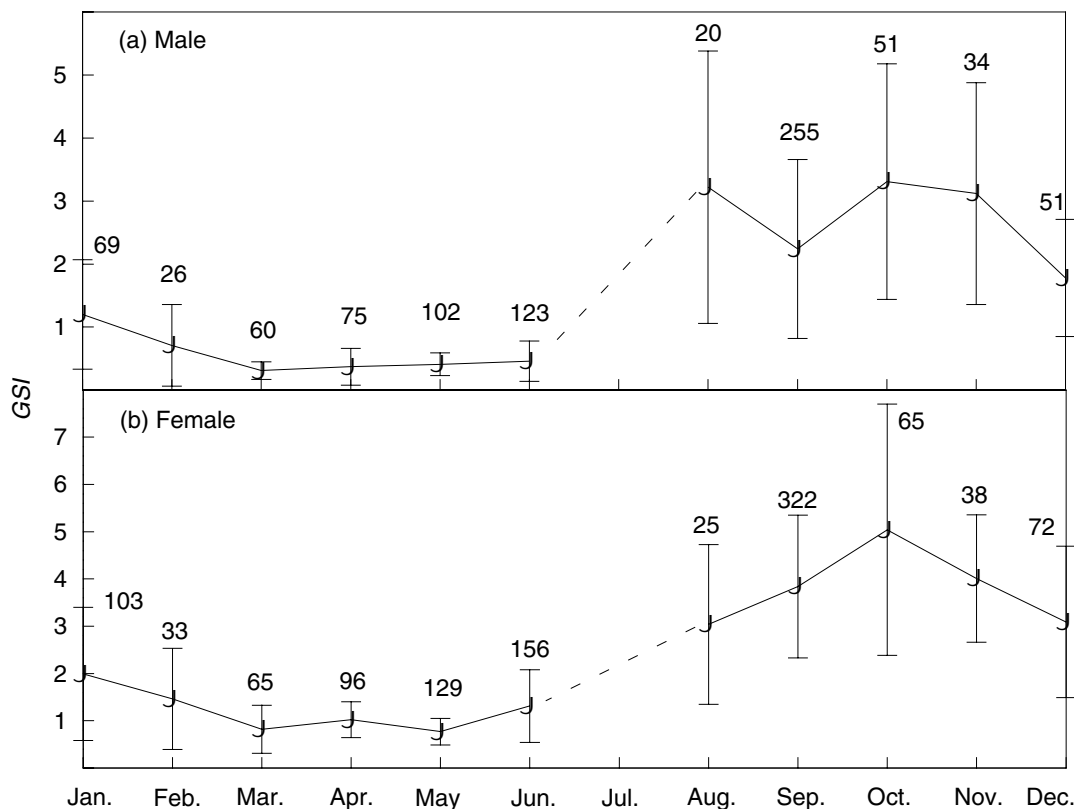


Fig. 10: Mean monthly gonadosomatic indices ($\pm 1SD$) for mature (a) male and (b) female *R. globiceps*, 1985–1995. Although data were pooled across regions, the regional size-at-50%-maturity was used to select mature fish in each case. Monthly sample numbers are also shown

Sex ratios for *R. globiceps* off the South-Eastern and Western Cape approximated unity, whereas there was one male for every 1.2 females off the Southern and South-Western Cape (Table III). It is nevertheless possible that the sex ratios calculated for the former two regions were biased by small sample sizes ($n = 151$ and 34 v. $1\ 886$ and 525 respectively), and hence may not be representative of the populations there. Owing to the dependency of the Chi-squared test on sample size, only the sex ratio for the Southern Cape was significant. For example, a sex ratio of 1:1.2 requires a sample size of at least 550 to be statistically significant.

Age and growth

Transverse sections of the saggital otoliths of *R. globiceps* consist of an opaque core followed by alternating

translucent and opaque zones (Fig. 2). Although the annual nature of these zones was not validated, because samples were not available for each month of the year, Talbot (1955) established that, based on cohort analysis, fish of one year displayed one translucent zone. Furthermore, given that similar zones are deposited annually in the otoliths of other Cape sparids, e.g. blue hottentot *Pachymetopon aeneum*, mussel-cracker *Sparodon durbanensis*, poenskop *Cymatoceps nasutus*, bronze bream *Pachymetopon grande* (Buxton and Clarke 1986, 1991, 1992), Roman *Chrysolephus laticeps* and daggeraad *C. cristiceps* (Buxton 1993), it is reasonable to assume that each translucent zone of *R. globiceps* older than one year also represented one year of growth. Of the 641 otoliths prepared for growth analysis, only 13 (2%) were rejected because counts did not agree.

Observed lengths varied widely within age-groups (Fig. 12). The observed values were evenly distributed

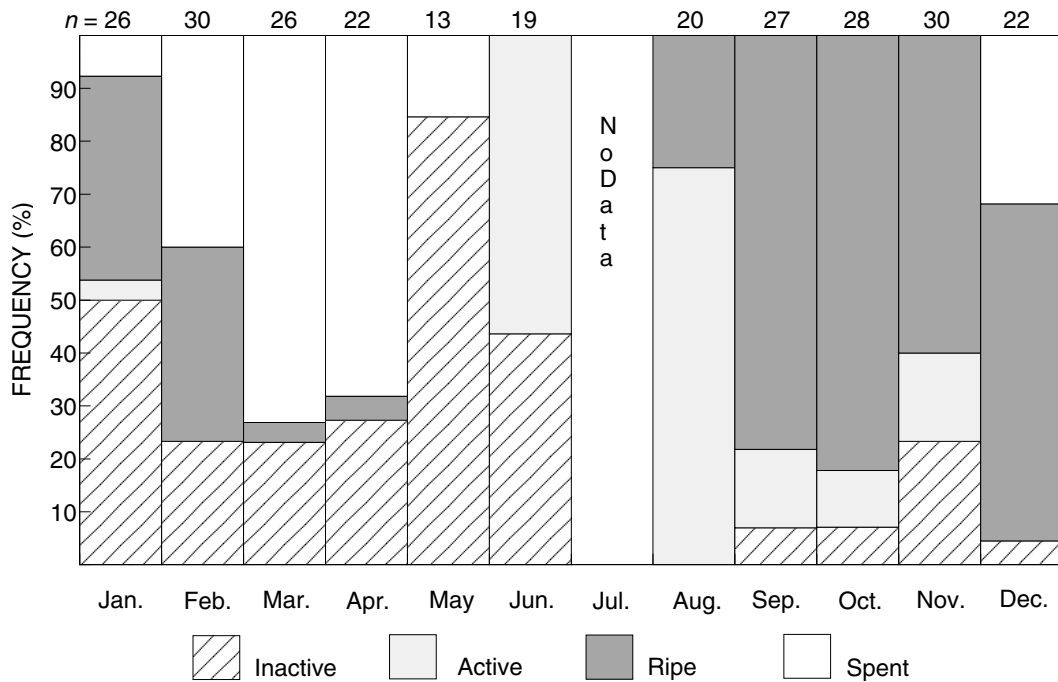


Fig. 11: Monthly percentage of microscopic ovarian stages for *R. globiceps* sampled east of Cape Point, 1989–1994. Sample numbers (*n*) are provided

about fitted growth models (Fig. 12), indicating that the von Bertalanffy growth function adequately described the growth of *R. globiceps* in each region (Fig. 12); the derived parameters of the model are given in Table IV. Likelihood ratio tests showed that growth rates between regions ($F = 69.8$, $df = 6$ and 624 , $p = 0.05$) and between sexes ($F = 4.7$, $df = 3$ and 568 , $p = 0.05$) were significantly different. Growth rate increased clinally from the South-Eastern Cape through to the South-Western Cape (Fig. 13a). The absence of fish >10 years of age from the South-Eastern Cape possibly resulted in an overestimate of L_{∞} and therefore K could have been underestimated for that region. Growth in both sexes was rapid for the first six years, after which it slowed, but more so in males than in females (Fig. 13b), growth divergence occurring after maturity. Although the oldest fish aged was a male of 21 years (oldest female was 18 years), ages were generally distributed evenly among the sexes, indicating similar patterns of longevity (Fig. 13b).

Morphometric relationships

The relationships between fork length (*FL*) and total

length (*TL*) and *FL* and weight in *R. globiceps* are described by the functions

$$FL = 0.8916 TL + 1.3716 \text{ mm}; n = 2\ 660, r^2 = 0.998, \text{ range} = 25\text{--}483 \text{ mm } FL$$

$$W = 1.3799 \times 10^{-5} FL^{3.078} \text{ g}; n = 2\ 710, r^2 = 0.990, \text{ range} = 25\text{--}483 \text{ mm } FL$$

Morphometric measurements for fish <150 mm were obtained from fish caught by the beach-seine fishery in False Bay.

DISCUSSION

Spatial analysis of linefish catch and *cpue* revealed two discrete areas of inshore abundance of *R. globiceps*, Saldanha Bay (Western Cape) and False Bay (South-Western Cape). Data from SCBSs show a further two disjunct areas of abundance east of Cape Agulhas; one associated with the central Agulhas Bank (Southern Cape) and the other with Algoa Bay in the South-Eastern Cape. *A. inodorus*, which has a similar distri-

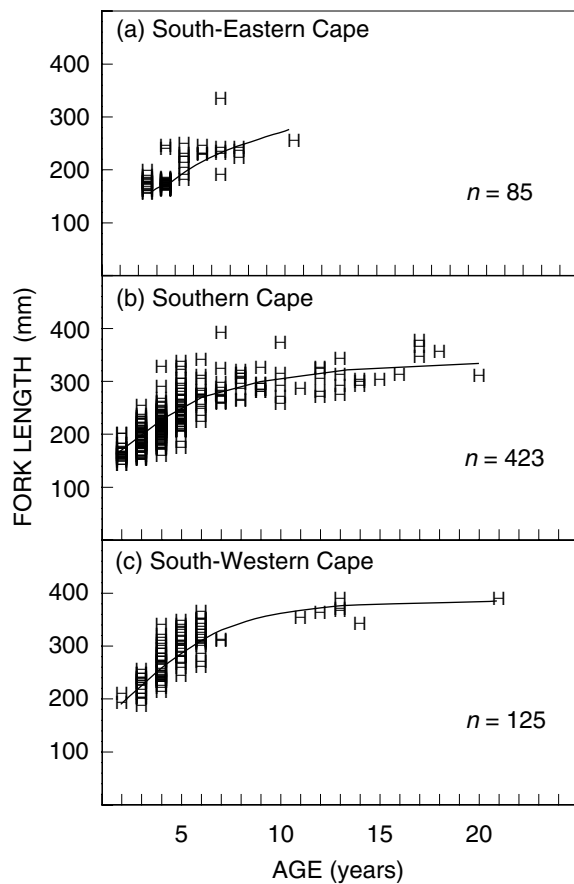


Fig. 12: Calculated Von Bertalanffy growth curves and observed lengths-at-age for *R. globiceps* sampled in the three regions during 1990 (sexes combined)

bution along the eastern seaboard (i.e. east of Cape Point), was demonstrated by Griffiths (1997a), using tagging, biological and morphometric data, to consist of three discrete stocks. These were separated by the cold,

bottom mixed layer (<12°C) close to the coast between Cape Hangklip and Cape Agulhas, and between Knysna and Cape St Francis (Griffiths 1997a). In the present study, differences in growth rate and size at maturity and the lack of movement of tagged fish between regions suggest that areas of *R. globiceps* abundance also represent separate stocks. Historical records of large beach-seine catches along the West Coast between Hout Bay and Melkbosstrand during the early 20th century (Biden 1930) suggest that overlap/exchange between False Bay and Saldanha Bay stocks may have been greater in the past. The present low catch rates in this area by the netfishery (Hutchings and Lamberth 2002) are attributed to range contractions concomitant with population declines associated with exploitation (Griffiths 2000).

R. globiceps is generally caught by hook and line in water depths <50 m (<20 m west and <50 m east of Cape Agulhas), whereas commercial trawlers operate seawards of this depth. Line catches off the Western and South-Western Cape are lowest during winter, whereas trawl catches off the Southern Cape are highest during that season. Catch data therefore suggest that, even though longshore coastal migration is limited (based on tagging data), seasonal onshore/offshore movement does take place. Inverse relationships in line and trawl catches of *A. inodorus* in both the Southern and South-Eastern Cape were shown, by mark-recapture, to reflect offshore winter dispersal in response to seasonal retreat of the bottom mixed layer (Griffiths 1997a). Offshore movement of *R. globiceps* is expected to be less pronounced off the South-Western and Western Cape, because the cold, bottom mixed layer is generally much closer to the coast there (Atkins 1970, Boyd et al. 1985, Greenwood and Taunton-Clark 1992, Largier et al. 1992). The capture of *R. globiceps* at a depth of 130 m east of Cape Agulhas represents a substantial increase over the previously published depth limit of 80 m.

The general size composition of *R. globiceps* trawled off the South-Eastern and Southern Cape during SCBSs (non-reef substrata) increased from 14–22 cm at

Table III: Male (M) to female (F) ratios of *R. globiceps* from the South-East (SE), Southern (S), South-Western (SW) and Western (W) Cape

Length-class (FL, cm)	SE Cape			S Cape			SW Cape			W Cape		
	M:F	n	χ^2	M:F	n	χ^2	M:F	n	χ^2	M:F	n	χ^2
20–29	1:1	123	0.00	1:1.3	634	11.67*	1:1.1	82	0.05	1:1.3	7	0.14
30–39	1:1.3	25	0.36	1:1.2	823	7.97*	1:1.2	242	1.65	1:0.8	16	0.25
40–49	1:2	3	0.33	1:1.1	429	0.52	1:1.2	201	1.80	1:1.2	11	0.09
Total	1:1	151	0.06	1:1.2	1 886	17.56*	1:1.2	525	3.20	1:1	34	0

* $p < 0.05$

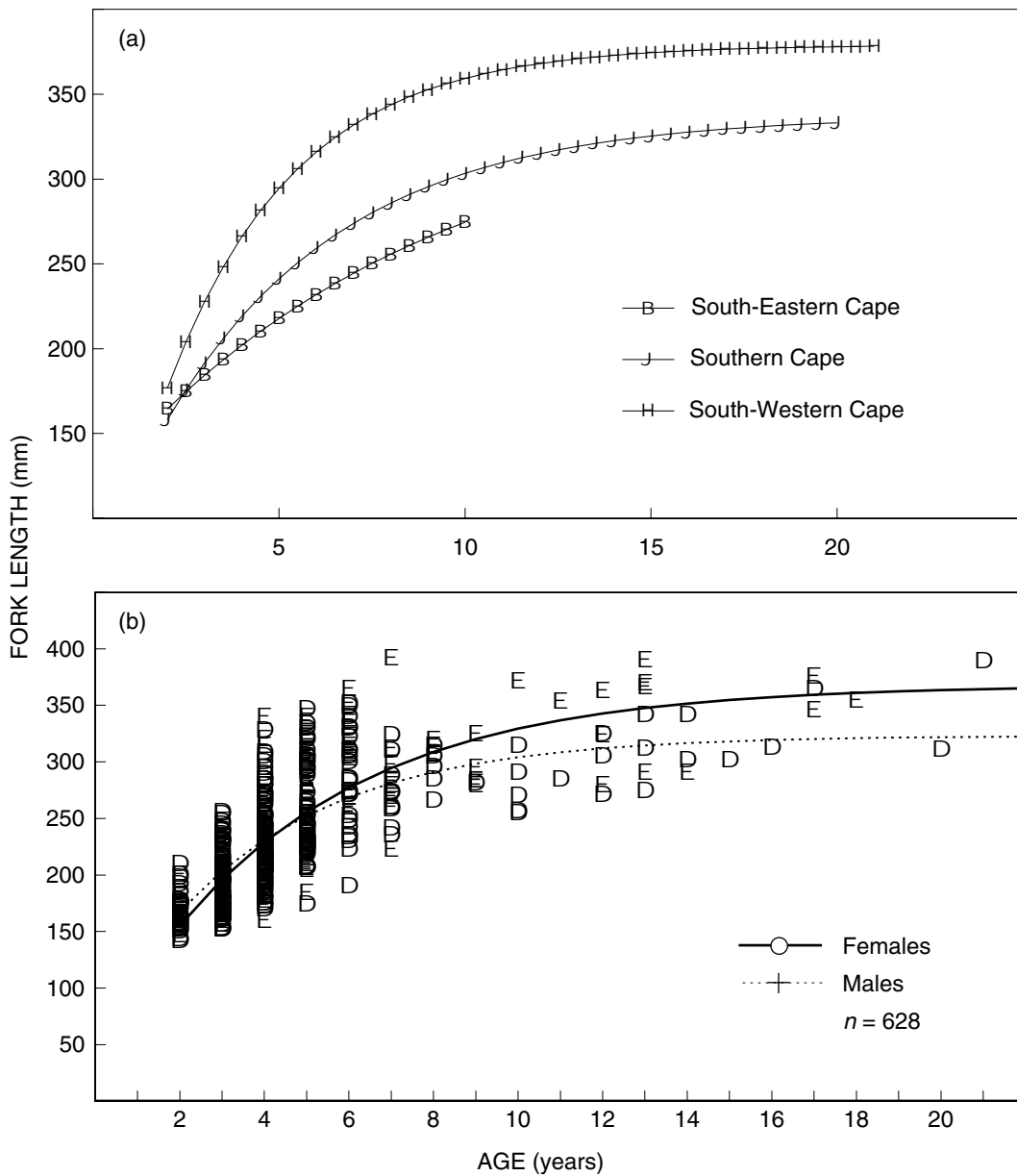


Fig. 13: (a) Comparison of growth rates (fitted Von Bertalanffy curves) of *R. globiceps* sampled in each region (sexes combined), and (b) calculated Von Bertalanffy growth curves and observed lengths-at-age for male and female *R. globiceps* (regions combined) sampled during 1990

depths of 25–50 m to 19–32 cm at 50–100 m and to 23–35 cm at 100–130 m. Previous studies have established the occurrence of early juveniles 2–15 cm long in estuaries (Talbot 1955, Beckley 1983, 1984a,

Bennett 1989a, Whitfield and Kok 1992, Clark *et al.* 1994) and in the surf zone (Lasiak 1983, Lamberth *et al.* 1995), and juveniles of 5–15 cm on soft substrata 5–30 m deep (Beckley 1984b, Wallace *et al.*

Table IV: Parameter estimates for the Von Bertalanffy model fitted to observed length-at-age data collected for *R. globiceps* off South Africa during 1990

Region/sex	Parameter			
	K	L_{∞}	t_0	n
South-Eastern Cape	0.114	349	-3.60	85
Southern Cape	0.207	337	-1.05	423
South-Western Cape	0.290	379	-0.16	125
Combined regions	0.242	342	-0.55	633
Males (all regions)	0.262	323	-0.786	320
Females (all regions)	0.213	368	-0.559	291

1984). *R. globiceps* appear therefore to recruit into estuarine and surf-zone nursery areas at around 2–5 cm (c. 3 months; Talbot 1955), moving progressively farther offshore with growth. Although recruitment takes place from December through June, there is a clear peak during January and February (Talbot 1955, Lasiak 1983, Bennett 1989a, 1989b, Lamberth *et al.* 1995), which corresponds with the September–October spawning peak. Maximum size occurring in estuaries and the surf zone increased from 11 cm off the South-Eastern Cape (Beckley 1983, 1984a, Lasiak 1983) to >20 cm off the South-Western Cape (Talbot 1955, Lamberth *et al.* 1994), suggesting that juveniles move beyond the surf zone at an earlier stage where water temperatures are higher. Similarly, adult *A. inodorus* are found within the cool surf zone west of Cape Agulhas, but remain farther offshore to the east of this area, where the inshore water is warmer (Griffiths 1997a).

Sparid reproductive styles may be broadly divided into two categories: sequential hermaphrodites and rudimentary hermaphrodites, also termed “late” gonochorists (Buxton and Garratt 1990). In the former, individuals function first as one sex and then change to the other (protogyny or protandry), whereas in the latter, they undergo a juvenile intersex stage, functioning as only one sex during their lives. Although there has been some confusion surrounding the reproductive style of *R. globiceps* (Talbot 1955, Penrith 1972), Melo *et al.* (in prep.) clearly demonstrate, based on histological criteria, that the species is a serial-spawning rudimentary hermaphrodite. The sex ratios calculated during the present study for *R. globiceps* (1 male: 1.2 female – all data) were also typical of those observed for other rudimentary hermaphrodites, generally 1:1.1–1:1.4 (Table IV). In contrast, sex ratios of sparids that are protogynous hermaphrodites are typically skewed towards females in the order of 1:2.0–1:4.0 in unexploited populations and 1:2.0–1:19.0 in exploited ones (Garratt 1985, Buxton 1993, Pajuelo and Lorenzo 1996, 1998).

Size-at-maturity and growth rate of *R. globiceps* increased clinally from the South-Eastern Cape through to the South-Western Cape. Because age-at-maturity also increased over this range (Table IV), the previous observation is not a simple function of growth rate. Given that marine fish evolve life-history strategies that maximize life-time reproductive success, within environmental and genetic constraints, optimal size (and age) at maturity is determined by trade-offs between the following interrelated/co-dependent parameters: fecundity (increases with size), growth rate (declines after maturity) and mortality (dependent on size and therefore growth rate – Roff 1984, 1988, 1992). It therefore follows that any factor (environmental or anthropogenic) that alters one of the above parameters could shift the optimal size-at-maturity. Empirically, changes in life-history traits, such as growth rate and size at maturity, have been observed for many species and have been attributed to both environmental factors as well as fishing (*inter alia* Borisov 1978, Rijnsdorp *et al.* 1991, Trippel 1995, Law 2000). Therefore, while the positive correlation between *R. globiceps* growth rate and size-at-maturity is consistent with both life-history theory and empirical observations of stocks of other species, the selective pressure driving the spatial trend is worthy of further discussion.

R. globiceps have been exploited for more than a century and, despite technological advances, the catch rates of commercial linefishers declined over the last 70 years by as much as 68% off the Western Cape, 52% off the South-Western Cape and 99.8% off the Southern Cape (Griffiths 2000). The large decline in catch rate in the last region is probably because they are also trawled there (albeit as a bycatch). Even though historical catch-and-effort data were not available for the South-Eastern Cape, fishing mortality associated with trawling is also anticipated to be high there. In terms of the trade-off scenario, high fishing mortality would decrease the average reproductive lifespan of individuals within a population and would therefore indirectly favour earlier maturity. In addition to this, fishing is also directly selective with respect to heritable life history traits, such as growth rate², with the result that exploited populations are expected to evolve in response to harvesting (Policansky 1993, Law 2000). *C. cristiceps* (Buxton 1993) and red porgy *Pagrus pagrus* (Harris and McGovern 1997) are two examples of sparids in which size-at-maturity, size-

² For example, faster growing individuals of a given year-class either recruit to adult fishing grounds or attain the minimum size limit at a younger age than those that grew slower, and in both cases would be exposed to fishing for longer and therefore be selected against



Fig. 14: Photograph of male and female *R. globiceps* of equal size illustrating sexual dichromatism

at-sex-change and growth rate are inversely related to fishing mortality. It is therefore probable that higher fishing mortality east of Cape Agulhas (as a result of trawling) has selected for earlier maturity and slower growth in the *R. globiceps* populations there. It is also possible that life history traits of *R. globiceps* from the South-Western Cape may have changed, but without baseline information a firm conclusion is not possible at this stage. It is important to note that, although changes in life history traits may reflect genetic shifts, it is extremely difficult to separate genetic alterations from the phenotypic responses of wild populations to exploitation (Jennings and Kaiser 1998, Law 2000).

Despite the cline in size-at-maturity, males in each region matured at a greater size and age than females. Notwithstanding an inadequate sample size, Talbot (1955) reached a similar conclusion for the South-Western Cape. This feature is unusual for gonochoristic fish, including sparids (Smale 1988, Bennett 1993), because females generally mature at an equivalent or greater size/age than males (Roff 1984, Grimes 1987). *R. globiceps* are sexually dichromatic, suggesting mate selection by females and paired spawning

(Anderson 1994). The head of the male is darker than that of the female, resulting in a prominent white lower jaw in the male; there are also black patches, in a roughly vertical band, immediately posterior to the head of the male, with the one ventrally and anterior to the pelvic fins being the most prominent (Fig. 14). Studies on mate selection in fish, including the dichromatic sparid *Cheimarius nufar* (Garratt 1991), indicate that larger males secure more matings than smaller ones (see review by Roff 1992). Although *R. globiceps* spawning behaviour has not yet been documented, the males of other South African sparids that display sexual dichromatism, e.g. soldier *Crysolephus nufar* and slinger *C. puniceus*, both of which develop a pale saddle on each flank, aggressively defend temporary territories and contest for ripe females (Garratt 1991, 1993). Slower growth after maturity in male than in female *R. globiceps* could therefore be a function of higher energy demands associated with male spawning behaviour. Most other sparids demonstrating sexual dimorphism and paired spawning are sequential protogynous hermaphrodites, so males are consequently also larger than females (Buxton 1990, Buxton and Garratt 1990). The size of the testis (rela-

Table V: Life history parameters and dimensionless ratios for *R. globiceps* and 14 other South African sparids. Protogynous (PG) and protandrous (PA) hermaphrodites are indicated; all other species were rudimentary hermaphrodites

Species	L_{50}	L_{∞}	t_{50}	t_{max}	L_{50}/L_{∞}	t_{50}/t_{max}	Male:Female ratio	Source
<i>Rhabdosargus globiceps</i>								
South-Eastern Cape*	153	349?	1.5	10?	-	-	1:1	Present study
Southern Cape	181	337	2.6	20	54%	13%	1:1.2	Present study
South-Western Cape	236	379	3.2	21	62%	15%	1:1.2	Present study
<i>Rhabdosargus sarba</i> ^{PA}	260	745	2.5	13	35%	19%	1:1	Mann & Radebe (2000)
<i>Pachymetopon blochii</i>	220	538	5	12	41%	42%	1:1.4	Pulfrich & Griffiths (1988)
<i>Pachymetopon aeneum</i>	225	467	5	12	48%	42%		Buxton & Clarke (1986)
<i>Pachymetopon grande</i>	300	461	5.5	38	65%	15%	1:1.2	Buxton & Clarke (1992)
<i>Chrysoblephus laticeps</i> ^{PG}	180	425	2	17	42%	12%	1:1-1:3.9	Buxton (1993)
<i>Chrysoblephus cristiceps</i> ^{PG}	365	655	7.7	21	56%	37%	1:2.3-1:13.0	Buxton (1993)
<i>Chrysoblephus puniceus</i> ^{PG}	240	406	2.5	17	59%	15%	1:2.3-1:18.0	Garratt (1985), Garratt <i>et al.</i> (1993)
<i>Cymatoceps nasutus</i> ^{PG}	425	1 090	7	45	40%	16%	1:3.9	Buxton & Clarke (1986)
<i>Sparodon durbanensis</i>	350	1 021	5.4	31	34%	17%	1:1.1	Buxton & Clarke (1991)
<i>Petrus rupestris</i>	575	1 383	7.2	33	42%	22%	1:1.2	Smale & Punt (1991)
<i>Polysteganus undulosus</i>	650 ^{TL}	942 ^{TL}	7.7	20	69%	39%	1:1.1	Ahrens 1964, Chale-Matsau (1996)
<i>Lithognathus lithognathus</i>	650	998	6	21	65%	29%	1:1	Bennett (1993)
<i>Pterogymnus lanarius</i>	200	380	4	16	53%	25%	1:1.8	Booth & Buxton (1997)
<i>Sarpa salpa</i> ^{PA}	145	224	1.9	6	65%	32%	1.6:1	Van der Walt & Beckley (1997), Van der Walt & Mann (1998)

* The low maximum age for *R. globiceps* in the South-Eastern Cape is believed to be an underestimate resulting from inadequate sample size. The absence of data for the post 10-year slow-growth phase has also likely resulted in an overestimate of L_{∞} . Dimensionless ratios were therefore not calculated for *R. globiceps* there

L_{50} = fork-length-at-50%-female maturity (mm)

L_{∞} = theoretical asymptotic length (mm)

t_{50} = age (years) at L_{50}

t_{max} = maximum age (years) recorded

TL = total length

tive to body size) of broadcast paired-spawners, including sparids (Buxton 1990), is often much smaller than the ovary (Sadovy 1996). However, where the relative size of ovaries and testes is as similar as in *R. globiceps*, sperm competition is anticipated (Stockley *et al.* 1997), and the presence of satellite/sneaker males or "streaking" activity (*sensu* Garratt 1991) may be predicted. Mean monthly *GSI* for male *R. globiceps* ranged from 60 to 106% of that for females during the period August–November. Because life history strategies evolve to maximize the lifetime breeding success of individuals (Roff 1992), the early losses in breeding success associated with delayed maturity in male *R. globiceps* would theoretically be offset by higher mating frequency at a larger size once maturity is attained.

In reviewing reproductive styles in sparids, Buxton and Garratt (1990) concluded that the life history characteristics of rudimentary hermaphrodites favoured the selection of mating behaviour such as random mating between pairs or group spawning, both within spawning aggregations. In this regard, male selection by female *R. globiceps*, as implied by sexual dichromatism and larger male size at maturity, must be

considered to be the exception rather than the rule.

Of a total of 41 sparid species found in South African waters, 29 are endemic (Smith and Heemstra 1986). The great diversity in life-history strategy of South African sparids is reflected in maximum sizes (L_{∞}) and ages (T_{max}) attained: L_{∞} varied from 224 to 1 383 mm *FL* and T_{max} from 6 to 45 years (Table V). *R. globiceps* may therefore be regarded as a medium-sized representative ($L_{\infty} = 337-379$ mm) of intermediate longevity ($T_{max} = 21$ years). Dimensionless ratios provide a useful means for further comparing the life histories of animals that grow to different sizes (see Beverton 1992 for review). The life history strategy of *R. globiceps* was compared with those of 14 other South African sparids, based on the relationships between length-at-maturity and asymptotic length and between age-at-maturity and maximum observed age. Sexual maturity within the family was attained at lengths of 34–69% of L_{∞} , and ages of 12–42% of T_{max} (Table IV). In terms of these values, *R. globiceps* mature at a relatively large size (54–62% of L_{∞}) but at an early age (13–15% of T_{max}), a reflection of the growth rate slowing dramatically after maturity. Although three other congeneric species are found in

South African waters (*R. thorpei*, *R. holubi* and *R. sarba*), the life history of only *R. sarba* has been studied in any detail. This subtropical, protandrous hermaphrodite species grows to over twice the length of *R. globiceps*, but it lives to little more than half the age (Table V), demonstrating considerable life history variation within the genera of this family, despite morphological similarities.

Based on their slow growth, a maximum age of more than 20 years and high residency, *R. globiceps* are predicted to be particularly vulnerable to overfishing (Parrish 1998, Griffiths 2000). The current minimum size limit of 22.4 cm *FL* (25 cm *TL*) is larger than the female *L*₅₀ value for east of Cape Agulhas and marginally smaller than that for the South-Western Cape (23.6 cm), thereby providing some protection against recruitment overfishing. Nevertheless, per-recruit studies have shown that optimal sizes at first capture (in terms of both yield and spawner stock reference points) are often larger than the size at maturity (Griffiths 1997b). Stock assessment and evaluation of the current regulations, based on the biological parameters presented in this paper, is therefore imperative to the wise/sustainable management of the *R. globiceps* resource. Biological investigation of the Western Cape stock is recommended in this regard.

ACKNOWLEDGEMENTS

We thank our colleagues in the Demersal Section at MCM for providing data summaries for South Coast biomass surveys, and numerous technicians who assisted over the years by participating in field trips or preparing summaries of size composition and catch-and-effort data. Prof. C. D. Buxton (Tasmanian Aquaculture and Fisheries Institutes) and an anonymous referee commented constructively on an early draft of the manuscript.

LITERATURE CITED

- AHRENS, R. L. 1964 — A preliminary report on the biology of the seventy four *Polysteganus undulosus* (Regan) in Natal waters. M.Sc. thesis, University of Natal, Durban: 77 pp.
- ANDERSON, M. 1994 — *Sexual Selection*. Princeton Press, Princeton.
- ATKINS, G. R. 1970 — Thermal structure and salinity of False Bay. *Trans. R. Soc. S. Afr.* **39**(2): 117–128.
- BADENHORST, A. and M. J. SMALE 1991 — The distribution and abundance of seven commercial trawlfish from the Cape south coast of South Africa, 1986–1990. *S. Afr. J. mar. Sci.* **11**: 377–393.
- BARNARD, K. H. 1927 — A monograph of the marine fishes of southern Africa. *Ann. S. Afr. Mus.* **21**: 419 pp.
- BECKLEY, L. E. 1983 — The ichthyofauna associated with *Zostera capensis* Setchell in the Swartkops Estuary, South Africa. *S. Afr. J. Zool.* **18**(1): 15–24.
- BECKLEY, L. E. 1984a — The ichthyofauna of the Sundays Estuary, South Africa, with particular reference to the juvenile marine component. *Estuaries* **7**(3): 248–258.
- BECKLEY, L. E. 1984b — Shallow-water trawling off the Swartkops Estuary, Algoa Bay. *S. Afr. J. Zool.* **19**(3): 248–250.
- BENNETT, B. A. 1989a — A comparison of the fish communities in nearby permanently open, seasonally open and normally closed estuaries in the South-Western Cape, South Africa. *S. Afr. J. mar. Sci.* **8**: 43–55.
- BENNETT, B. A. 1989b — The fish community of a moderately exposed beach on the Southwestern Cape coast of South Africa and an assessment of this habitat as a nursery for juvenile fish. *Estuar. coast. Shelf Sci.* **28**(3): 293–305.
- BENNETT, B. A. 1991 — Long-term trends in the catches by shore anglers in False Bay. *Trans. R. Soc. Afr.* **47**(4&5): 683–690.
- BENNETT, B. A. 1993 — Aspects of the biology and life history of white steenbras *Lithognathus lithognathus* in southern Africa. *S. Afr. J. mar. Sci.* **13**: 83–96.
- BEVERTON, R. J. H. 1992 — Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.* **41**(Suppl. B): 137–160.
- BIDEN, C. L. 1930 — *Sea-Angling Fishes of the Cape*. London: Oxford University Press: xii + 304 pp.
- BOOTH, A. J. and C. D. BUXTON 1997 — The biology of the panga, *Pterogymnus laniarius* (Teleostei: Sparidae) on the Agulhas Bank, South Africa. *Environ. Biol. Fishes* **49**: 207–226.
- BORISOV, V. M. 1978 — The selective effect of fishing on the population structure of species with a long life cycle. *J. Ichthyol.* **18**(6): 896–904.
- BOYD, A. J., TROMP, B. B. S. and D. A. HORSTMAN 1985 — The hydrology off the South African south-western coast between Cape Point and Danger Point in 1975. *S. Afr. J. mar. Sci.* **3**: 145–168.
- BUXTON, C. D. 1990 — The reproductive biology of *Chrysoblephus laticeps* and *C. cristiceps* (Teleostei: Sparidae). *J. Zool., Lond.* **220**: 497–511.
- BUXTON, C. D. 1993 — Life-history changes in exploited reef fishes on the east coast of South Africa. *Environ. Biol. Fishes* **36**: 47–63.
- BUXTON, C. D. and J. R. CLARKE 1986 — Age, growth and feeding of the blue hottentot *Pachymetopon aeneum* (Pisces: Sparidae) with notes on reproductive biology. *S. Afr. J. Zool.* **21**(1): 33–38.
- BUXTON, C. D. and J. R. CLARKE 1989 — The growth of *Cymatoceps nasutus* (Teleostei: Sparidae), with comments on diet and reproduction. *S. Afr. J. mar. Sci.* **8**: 57–65.
- BUXTON, C. D. and J. R. CLARKE 1991 — The biology of the white musselcracker *Sparodon durbanensis* (Pisces: Sparidae) on the Eastern Cape coast, South Africa. *S. Afr. J. mar. Sci.* **10**: 285–296.
- BUXTON, C. D. and J. R. CLARKE 1992 — The biology of the bronze bream, *Pachymetopon grande* (Teleostei: Sparidae) from the south-east Cape coast, South Africa. *S. Afr. J. Zool.* **27**(1): 21–32.
- BUXTON, C. D. and P. A. GARRATT 1990 — Alternative reproductive styles in seabreams (Pisces: Sparidae). *Environ. Biol. Fishes* **28**: 113–124.
- CHALE-MATSAU, B., 1996 — Age and growth of the queen mackerel (*Scomberomorus plurilineatus*), and seventy-four (*Polysteganus undulosus*) off KwaZulu-Natal, South Africa. M.Sc. thesis, University of Natal (Durban): 110 pp.
- CLARK, B. M., BENNETT, B. A. and S. J. LAMBERTH 1994 —

- A comparison of the ichthyofauna of two estuaries and their adjacent surf zones, with an assessment of the effects of beach-seining on the nursery function of estuaries for fish. *S. Afr. J. mar. Sci.* **14**: 121-131.
- DRAPER, N. R. and H. SMITH 1966 — *Applied Regression Analysis*, 2nd ed. New York; Wiley: 709 pp.
- GARRATT, P. A. 1985 — The offshore linefishery of Natal. 2. Reproductive biology of the sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. *Investl Rep. oceanogr. Res. Inst. S. Afr.* **63**: 21 pp.
- GARRATT, P. A. 1991 — Spawning behaviour of *Cheimerius nufar* in captivity. *Environ. Biol. Fishes* **31**: 345-353.
- GARRATT, P. A. 1993 — Comparative aspects of the reproductive biology of seabreams (Pisces: Sparidae), Ph.D. thesis, Vol. 1. Rhodes University: vii +175 pp.
- GARRATT, P. A., GOVENDER, A. and A. E. PUNT 1993 — Growth acceleration at sex change in the protogynous hermaphrodite *Chrysoblephus puniceus* (Pisces: Sparidae). *S. Afr. J. mar. Sci.* **13**: 187-193.
- GILCHRIST, J. D. F. 1916 — Eggs and larvae of Cape fishes. *Mar. Biol. Rep., Cape Tn* **3**: 1-26.
- GREENWOOD, C. and J. TAUNTON-CLARK 1992 — An atlas of mean monthly and yearly average sea surface temperatures around the southern African coast. *Internal Rep. Sea Fish. Res. Inst. S. Afr.* **124**: 112 pp.
- GRIFFITHS, M. H. 1988 — Aspects of the biology and population dynamics of the geelbeck *Atractoscion aequidens* (Cuvier) (Pisces: Sciaenidae) off the South African coast. M.Sc. thesis, Rhodes University, South Africa: 149 pp.
- GRIFFITHS, M. H. 1997a — The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters. *Fishery Bull., Wash.* **95**(1): 47-67.
- GRIFFITHS, M. H. 1997b — The application of per-recruit models to *Argyrosomus inodorus*, an important South African sciaenid fish. *Fish. Res.* **30**: 103-115.
- GRIFFITHS, M. H. 2000 — Long-term trends in catch and effort of commercial linefish off South Africa's Cape Province: snapshots of the 20th century. *S. Afr. J. mar. Sci.* **22**: 81-110.
- GRIFFITHS, M. H. and T. HECHT 1995 — On the life-history of *Atractoscion aequidens*, a migratory sciaenid off the east coast of southern Africa. *J. Fish Biol.* **47**: 962-985.
- GRIMES, C. B. 1987 — Reproductive biology of the Lutjanidae: a review. In *Tropical Snappers and Groupers*. Polovina, J. J. and S. Ralston (Eds). London; Westview Press: 239-294.
- HARRIS, P. J. and J. C. MCGOVERN 1997 — Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972-1994. *Fishery Bull., Wash.* **95**: 732-747.
- HUTCHINGS, K. and S. J. LAMBERTH 2002 — Catch-and-effort estimates for the gillnet and beach-seine fisheries in the Western Cape, South Africa. *S. Afr. J. mar. Sci.* **24**: 205-225.
- HYDER, M. 1969 — Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia* (Pisces: Teleostei). *Trans. Am. microscop. Soc.* **88**: 211-231.
- JAPP, D. W., SIMS, P. F. and M. J. SMALE 1994 — A review of the fish resources of the Agulhas Bank. *S. Afr. J. Sci.* **90**(3): 123-134.
- JENNINGS, S. and M. J. KAISER 1998 — The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* **34**: 201-252.
- LAMBERTH, S. J., BENNETT, B. A. and B. M. CLARK 1994 — Catch composition of the commercial beach-seine fishery in False Bay, South Africa. *S. Afr. J. mar. Sci.* **14**: 69-78.
- LAMBERTH, S. J., BENNETT, B. A. and B. M. CLARK 1995 — The vulnerability of fish to capture by commercial beach-seine nets in False Bay, South Africa. *S. Afr. J. mar. Sci.* **15**: 25-31.
- LAMBERTH, S. J. and A. JOUBERT 1999 — Prioritizing linefish species for research and management: a first attempt. In *Proceedings of the Third Southern African Marine Linefish Symposium, Arniston, April-May 1999*. Mann, B. Q. (Ed.). *Occ. Rep. S. Afr. Network coast. oceanogr. Res.* **5**: 130-137.
- LARGIER, J. L., CHAPMAN, P., PETERSON, W. T. and V. P. SWART 1992 — The western Agulhas Bank: circulation, stratification and ecology. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 319-339.
- LASIAK, T. A. 1983 — Recruitment and growth patterns of juvenile marine teleosts caught at King's Beach, Algoa Bay. *S. Afr. J. Zool.* **18**(1): 25-30.
- LAW, R. 2000 — Fishing, selection, and phenotypic evolution. *ICES J. mar. Sci.* **57**: 659-668.
- MANN, B. Q. and P. V. RADEBE 2000 — *Rhabdosargus sarba*. In *Southern African Marine Linefish Status Reports*. Mann, B. Q. (Ed.). *Spec. Publ. oceanogr. Res. Inst. S. Afr.* **7**: 77-78.
- MELO, Y. C., BOSCH, S. L. and W. J. VEITH (in preparation) — Rudimentary hermaphroditism in white stumpnose, *Rhabdosargus globiceps*.
- PAJUELO, J. G. and J. M. LORENZO 1996 — Life history of the red porgy *Pagrus pagrus* (Teleostei: Sparidae) off the Canary Islands, central east Atlantic. *Fish. Res.* **28**: 163-177.
- PAJUELO, J. G. and J. M. LORENZO 1998 — Population biology of the common pandora *Pagellus erythrinus* (Pisces: Sparidae) off the Canary Islands. *Fish. Res.* **36**: 75-86.
- PARRISH, R. H. 1998 — Life history strategies for marine fishes in the late holocene. In *Global versus Local Changes in Upwelling Systems*. Durand, M. H., Cury, P., Mendelssohn, R., Roy, C., Bakun, A. and D. Pauly (Eds). Paris; ORSTOM: 525-535.
- PENRITH, M. J. 1972 — Sex reversal in the sparid fish *Chrysoblephus laticeps*. *Koedoe* **15**: 135-139.
- POLICANSKY, D. 1993 — Evolution and management of exploited fish populations. In *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, October 1992*. Kruse, G., Eggers, D. M., Marasco, R. J. Pautzke, C. and T. J. Quinn (Eds). Anchorage; University of Alaska: 651-664.
- PULFRICH, A. and C. L. GRIFFITHS 1988 — Growth, sexual maturity and reproduction in the hottentot *Pachymetopon blochii* (Val.). *S. Afr. J. mar. Sci.* **7**: 25-36.
- RAUCK, G. 1976 — A technique of sawing thin slices out of otoliths. *Ber. dt. wiss. Kommn Meeresforsch.* **24**(4): 339-341.
- RIJNSDORP, A. D., DAAN, N., VAN BEEK, F. A. and H. J. L. HESSEN 1991 — Reproductive variability in North Sea plaice, sole and cod. *ICES J. mar. Sci.* **47**: 352-375.
- ROFF, D. A. 1984 — The evolution of life history parameters in teleosts. *Can. J. Fish. aquat. Sci.* **41**(6): 989-1000.
- ROFF, D. A. 1988 — The evolution of migration and some life history parameters in marine fishes. *Environ. Biol. Fishes* **22**: 133-146.
- ROFF, D. A. 1992 — *The Evolution of Life Histories, Theory and Analysis*. New York; Chapman & Hall: 535 pp.
- SADOVY, Y. J. 1996 — Reproduction of reef fishery species. In *Reef Fisheries*. Polunin, N. V. C. and C. M. Roberts (Eds). London; Chapman & Hall: 15-59.
- SAUER, W. H. H., PENNEY, A. J., ERASMUS, C., MANN, B. Q., BROUWER, S. L., LAMBERTH, S. J. and T. J. STEWART 1997 — An evaluation of attitudes and responses to monitoring and management measures for the South African boat-based linefishery. *S. Afr. J. mar. Sci.* **18**: 147-163.
- SMALE, M. J. 1988 — Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. *S. Afr. J. Zool.* **23**(4): 272-287.
- SMALE, M. J. and A. E. PUNT 1991 — Age and growth of the red steenbras *Petrus rupestris* (Pisces: Sparidae) on the south-east coast of South Africa. *S. Afr. J. mar. Sci.* **10**: 131-139.
- SMITH, M. M. and P. C. HEEMSTRA (Eds) 1986 — *Smiths' Sea Fishes*. Johannesburg; Macmillan: xx + 1047 pp.

- STOCKLEY, P., GAGE, M. J. G., PARKER, G. A. and A. P. MØLLER 1997 — Sperm competition in fishes: the evolution of testis size and ejaculate characteristics. *Am. Naturalist* **149**: 933–954.
- TALBOT, F. H. 1955 — Notes on the biology of the white stumpnose, *Rhabdosargus globiceps* (Cuvier), and on the fish fauna of the Klein River estuary. *Trans. R. Soc. S. Afr.* **34**(3): 387–407.
- TRIPPEL, E. A. 1995 — Age at maturity as a stress indicator in fisheries. *Bioscience* **45**: 759–771.
- VAN DER WALT, B. A. and L. E. BECKLEY 1997 — Age and growth of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa. *Fish. Res.* **31**: 241–248.
- VAN DER WALT, B. A. and B. Q. MANN 1998 — Aspects of the reproductive biology of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa. *Fish. Res.* **33**: 241–248.
- WALLACE, J. H., KOK, H. M., BUXTON, C. D. and B. [A.] BENNETT 1984 — Inshore small-mesh trawling survey of the Cape south coast. 1. Introduction, methods, stations and catches. *S. Afr. J. Zool.* **19**(3): 154–164.
- WHITFIELD, A. K. 1998 — Biology and ecology of fishes in southern African estuaries. *Ichthyol. Monogr. J. L. B. Smith Inst. Ichthyol.* **2**: 223 pp.
- WHITFIELD, A. K. and H. M. KOK 1992 — Recruitment of juvenile marine fishes into permanently open and seasonally open estuarine systems on the southern coast of South Africa. *Ichthyol. Bull. J. L. B. Smith Inst. Ichthyol.* **57**: 1–39.
- YAMAMOTO, K. 1956 — Studies on the formation of fish eggs. 1. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. *J. Fac. Sci. Hokkaido Univ., Ser. 6, Zool.* **12**(3): 362–376.