

## Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa

M.J. Smale

Port Elizabeth Museum, P.O. Box 13147, Humewood, 6013 Republic of South Africa

Received 10 November 1987; accepted 6 May 1988

The red steenbras (*Petrus rupestris*) is endemic to the south and south-east coasts of South Africa and is the largest member of the family Sparidae. Morphometric relationships between length and mass are given for whole and eviscerated fish. The size distribution of *P. rupestris* is related to locality and water depth. Juveniles and sub-adults are common in shallow (< 50 m) Cape waters between False Bay and East London. Adults are more common offshore, in deep waters (> 50 m), especially off the coast between East London and Coffee Bay, throughout the year. *P. rupestris* were found to be rudimentary hermaphrodites. The development of the functional sexes, and the occurrence of sexual dichromatism, are described. Sexual maturity is attained at about 575 mm fork length in those fishes in the spawning areas. Reproductively ripe fishes were taken from Transkei, East London and a small collection was made from the Agulhas Bank. Peak spawning is between August and October. Current management regulations are discussed and advantages of large marine reserves in conservation of this mobile apex predator are outlined.

Die rooisteenbras (*Petrus rupestris*) is endemies aan die suid- en suidooskus van Suid Afrika en is die grootste lid van die familie Sparidae. Morfometriese verhoudings tussen lengte en massa word gegee vir heel en ontweide vis. Die grootteverspreiding van rooisteenbras hou verband met die streek en die diepte van die water. Jongvisse en half-volwasse visse kom algemeen voor in vlak (< 50 m) Kaapse waters tussen Valsbaai en Oos Londen. Volwassenes kom deur die jaar in dieper (> 50 m) waters voor, veral tussen Oos Londen en Transkei. Rooi steenbras is rudimentêre hermafrodiete en die ontwikkeling van die funksionele geslagte, en seksuele dichromatisme word beskryf. In die broeigebied word seksuele volwassenheid bereik op omtrent 575 mm-vurklengte. Die meeste geslagrype visse was afkomstig van die Transkei en Oos Londen. 'n Kleiner hoeveelheid is ook van die Agulhasbank versamel. Broei-aktiwiteit bereik 'n piek tussen Augustus en Oktober. Die huidige bestuursmaatreëls word bespreek en voordele van groot mariene reserwate vir die bewaring van dié mobiele top-roofvis word beskryf.

The red steenbras, *Petrus rupestris* (Valenciennes, 1830) is the largest member of the family Sparidae in South Africa, attaining 52,2 kg (South African Anglers' Union, 1986). It is, therefore, a highly prized sport and commercial linefish. It is endemic to South Africa, and has been recorded between Natal in the east and False Bay in the south-west (Barnard 1947). Reports dating back to Biden (1930) and Horne (1955) suggest that this fish was more abundant in shallow waters than appears to be the case today. The belief that there has been a decline in abundance of this species is supported by most commercial fishermen who frequently state that catches have declined considerably in the past 30 years. Catch data collected from large linefishing boats fishing off the east coast and landing their catches in Natal support this belief (P.A. Garratt, Oceanographic Research Institute, Durban, pers. comm.).

Despite its importance in the commercial and recreational fisheries, information on its biology is limited. Smale (1986) reported *P. rupestris* to be an apex predator of coastal reefs. Knowledge of its reproduction and breeding biology is limited to three brief notes. Penrith (1972) mentioned that in *P. rupestris* 'normal bisexual development' definitely occurs, although this observation was not substantiated in any way. Robinson (1976) observed the development of a testicular part of the gonad in this species, in a similar way to two protogynous hermaphrodite sparids, *Chrysoblephus cristiceps* and *C. laticeps*. This finding did not support Penrith's observation, and suggested that further

investigation was required. Finally, van der Elst (1981) noted that spawning fish are found off the east coast of South Africa.

The findings of a study on the biology of red steenbras are presented with emphasis on the size composition of catches along the south-eastern coast of South Africa, gonadal development and breeding biology. These findings are discussed in relation to the existing management regulations.

### Materials and Methods

Sampling was initiated in Algoa Bay in 1978 during an investigation of the ski-boat fishery (Smale & Buxton 1985) and a study of feeding inter-relationships of teleost fishes (Smale 1986). Sampling was continued until January 1987 and was concentrated at ski-boat launching sites between Coffee Bay (31°48'S / 25°42'E) and Cape Agulhas (34°50'S / 20°00'E). Spearfishing augmented samples between Algoa Bay and Tsitsikamma Coastal National Park (Figure 1). Fish were measured to the nearest millimetre and weighed. The gonads were removed, weighed, examined macroscopically and staged according to criteria listed in Table 1. A subsample of the gonads was kept to validate staging and to establish sexual development microscopically. This material was preserved in Bouin's solution for about three days then transferred to 50% propanol for storage. The tissues were cut in the desired locality and plane, wax embedded, sectioned at 5–7 µm then stained with

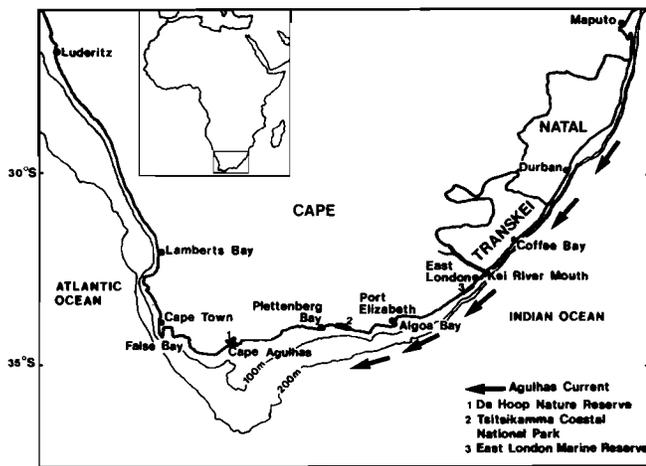


Figure 1 Southern Africa, showing places mentioned in the text.

Table 1 Macroscopic gonad stages recorded in *Petrus rupestris*

	Female	Male
1 Juvenile	Ovotestis with or ovary small, orange, resting ova not visible	Testicular portion not enlarged, no sperm present
2 Active	Ovary enlarged; ova not visible macroscopically	Testis enlarged, may obscure ovary, small amounts of creamy sperm
3 Active/ripe	Ovary enlarged, ova visible macroscopically	Testis large, white, creamy sperm from sectioned tissue
4 Ripe	Ovary turgid with orange ova, many clear, easily seen, may be in oviduct	Testis larger, white, milky sperm from sectioned tissue
5 Ripe running	Eggs released from ovary on pressure to abdomen Ova yellow or clear, easily visible	White testis very large, sperm freely released on applying pressure to abdomen
6 Partially spawned	Ova orange, with clear ones visible amongst them, ovary fairly flaccid	Smaller testis pinky-white sperm milky or creamy Testis more flaccid
7 Spent	Ovary flaccid, often wine red or dirty orange	Testis off white, smaller, creamy sperm in ducts

hematoxylin and eosin Y (Humason 1979). A total of 250 gonads were examined histologically.

Sizes mentioned in the text refer to fork lengths (mm) unless specifically stated otherwise. Gonadosomatic indices (GSI) were determined by the relationship:

$$\text{GSI} = \frac{\text{gonad mass (g)} \times 100}{\text{body mass (g)}}$$

## Results

### Morphometrics

The relationships between body length and mass were determined as follows:

Both sexes:

$$\text{Mass (g)} = 2,7 \times 10^{-5} \times \text{Lcf}^{2,9519} \text{ (mm)} \quad r^2 = 0,997; \quad n = 707$$

Males > 575 mm:

$$\text{Mass (g)} = 2,5 \times 10^{-5} \times \text{Lcf}^{2,96468} \text{ (mm)} \quad r^2 = 0,993; \quad n = 234$$

Females > 575 mm:

$$\text{Mass (g)} = 3,0 \times 10^{-5} \times \text{Lcf}^{2,9372} \text{ (mm)} \quad r^2 = 0,997; \quad n = 220.$$

Using the asymptotic likelihood ratio test (Ratowski 1983) on the parameter a and b for the combined sexes against those calculated for mature males and females separately, showed no significant differences between the sexes ( $F = 1,7$ ;  $P > 0,05$ ;  $d.f. = 452$ ).

$$\text{Total length (mm)} = 2,8579 + 1,0935 \times \text{Lcf (mm)} \quad r^2 = 0,992; \quad n = 615$$

$$\text{Standard length (mm)} = -9,628 + 0,91279 \times \text{Lcf (mm)} \quad r^2 = 0,999; \quad n = 623.$$

The fork length may be calculated from whole body mass:

$$\text{Fork length (mm)} = 37,106791 \times \text{body mass}^{0,33325} \text{ (g)} \quad r^2 = 0,981; \quad n = 707.$$

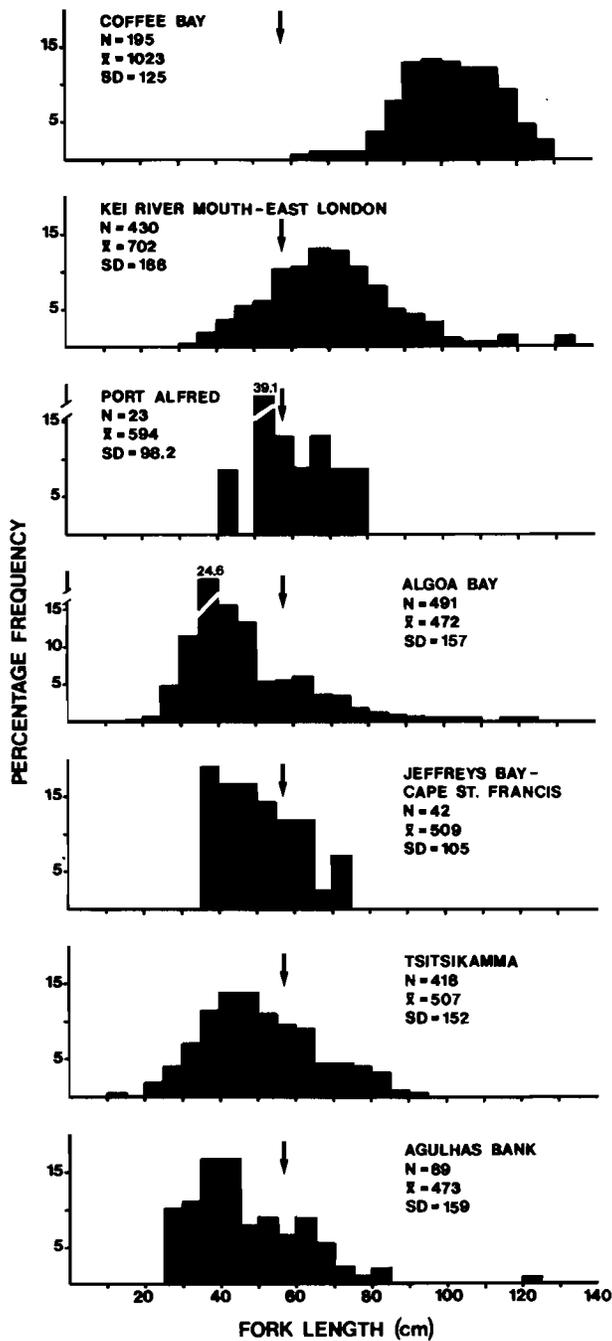
A regression to calculate fork length from fish with guts, gills and gonads removed is:

$$\text{Fork length (mm)} = 37,745 \times \text{mass}^{0,33445} \text{ (g)} \quad r^2 = 0,997; \quad n = 68.$$

### Distribution

The depth at which successful fishing for *P. rupestris* occurs varies considerably between sampling localities. Off Coffee Bay specimens are caught mainly on offshore banks at the edge of the continental shelf. The shelf drops down to about 110 m then rises up to about 87 m and the best fishing areas for *P. rupestris* are at the drop-offs on either side of these reefs. The shallowest depth at which *P. rupestris* is caught in this locality is 55 m, and the reefs between 86–110 m are most productive if the strong but meandering Agulhas current, which closely follows the continental slope (Lutjeharms 1981), does not prevent fishing. Temperatures vary considerably but the best fishing is when bottom temperatures are between 13–16°C on the deep reefs (G.B. Trow, Coffee Bay, pers. comm.).

The length distribution of fishes collected by line and spear-fishing in all areas is given in Figure 2. The Coffee Bay sample comprised large *P. rupestris* exclusively and these were all taken by hook and line at depths of about 55–160 m. Despite a depth range of 10–160 m being fished by anglers, and the use of small hooks to capture other linefishes (such as the sparids *Chrysolephus cristiceps* and *Polysteganus undulosus*), the smallest *Petrus rupestris* recorded off Coffee Bay measured 622 mm.



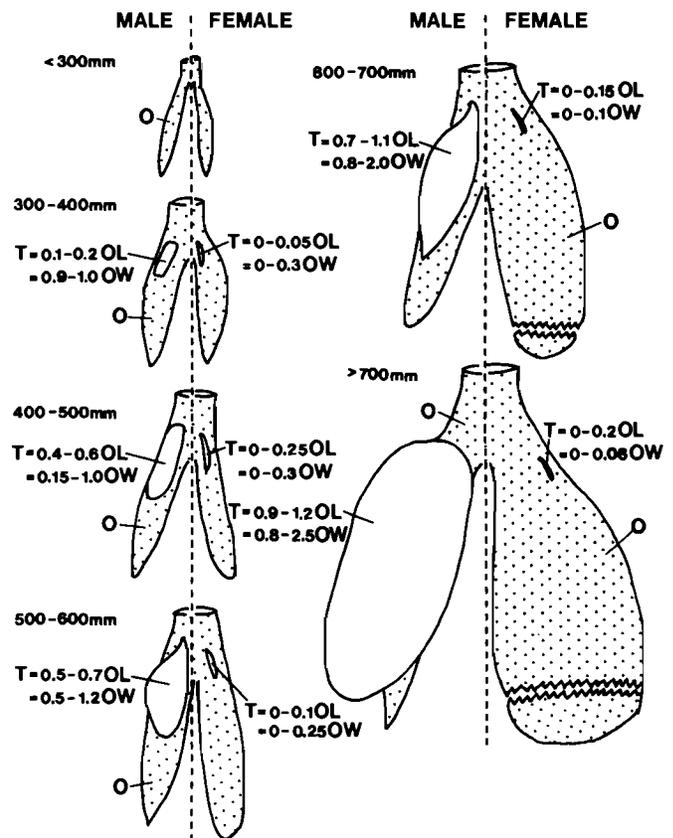
**Figure 2** Length frequency distribution of *Petrus rupestris* taken at different sampling localities between 1978 and 1987. The arrow indicates the size at 50% maturity. Means and standard deviations in mm.

A wider size range was encountered in samples taken between East London and Kei River Mouth. The largest fish were caught mainly in depths of 90–100 m while smaller size classes were more common in water shallower than 50 m. On the Cape south coast between Algoa Bay and the Agulhas Bank, *P. rupestris* of 152 – > 1000 mm are caught from about 15 m to at least 50 m. Diving observations have shown that fish smaller than 600 mm are most common in waters down to 30 m (Buxton & Smale 1984). These observations were confirmed by linefishing in shallow water. Large fish are not, however, confined to deep water and individuals

larger than 1 m are occasionally encountered in shallow waters (12 m) in areas such as Tsitsikamma Coastal National Park (TCNP) and elsewhere on the Cape south coast.

*P. rupestris* have been captured from the shore in False Bay (Biden 1930) where individuals of 74lb (33,6kg,  $\pm$  1225 mm FL) and 93lb (36,1kg  $\pm$  1290 mm FL) were reported by Horne 1955. Large fish were also reported from the shallows at Robberg (Plettenberg Bay) and at Tsitsikamma. These fish were most often caught in summer and autumn, through to May. Horne (1955) noted that they migrated away from these areas in autumn and they were not taken in winter by shore anglers.

Considering the distribution of *P. rupestris* and the apparently improved fishing at temperatures between 13–16°C, it appears that this species is strongly influenced by temperature. This may explain the absence of small red steenbras in warm inshore waters of the Transkei, where the monthly mean inshore water temperature may reach 24,5°C (Table 2), which may be outside their preferred temperature range.



**Figure 3** Schematic diagram of macroscopic appearance of sexual development of *P. rupestris*. The left side illustrates development of a male and the right side a female fish. The processes occur in different individuals, but are illustrated together for convenience. T is testis, O is ovary, OL is ovary length, OW is ovary width. The relative proportions of the testis to the ovary width and length are shown for different sized fish from measurements made of fresh material. Values of zero indicate that the testis may not be visible macroscopically.

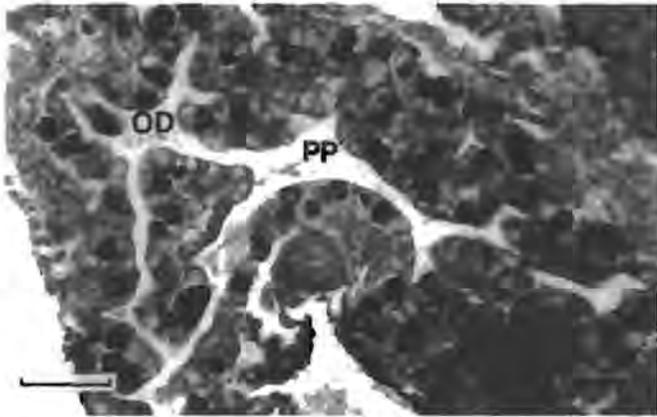
**Table 2** The mean, standard deviation and number of readings of monthly temperature recordings at five depth ranges in four coastal localities. The data were calculated from the degree square closest to the locality mentioned, using data in the SADCO data base. Cape Agulhas = 20–21°E / 34–35°S. Cape Recife = 26–27°E / 34–35°S. East London = 28–29°E / 32–33°S. Coffee Bay = 29–30°E / 31–32°S.

Depth (m)	Jan			Feb			March			April			May			June			July			Aug			Sep			Oct			Nov			Dec		
	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n	$\bar{T}$	SD	n			
<b>Cape Agulhas</b>																																				
0–10	21,2	0,9	86	21,6	1,1	119	20,8	1,6	84	19,0	1,6	139	17,1	1,0	110	16,0	0,7	94	15,4	0,6	81	15,2	0,6	101	15,6	0,7	111	16,8	1,2	141	18,3	1,0	87	20,2	0,9	112
11–25	20,3	1,7	35	20,7	2,0	46	20,1	2,8	22	18,5	2,3	45	16,7	1,5	34	16,0	0,6	30	15,4	0,6	33	15,0	0,8	30	15,4	0,6	33	16,3	0,7	43	17,1	1,4	43	19,1	1,3	33
26–50	17,4	3,7	55	16,9	3,9	67	17,4	4,3	32	15,4	3,7	74	14,1	2,8	60	15,3	1,2	59	15,3	1,0	53	15,1	0,5	48	15,5	0,6	58	16,2	0,6	75	16,5	1,8	40	17,7	2,0	61
51–100	12,0	1,2	20	12,5	1,9	33	10,9	0,9	19	11,0	1,5	27	12,5	2,6	24	11,8	1,4	22	14,2	1,6	12	13,2	2,7	32	15,4	0,6	18	15,1	1,0	32	13,7	1,4	33	14,3	1,7	17
101–200	9,7	0,5	8	9,2	0,3	4	9,2	0,4	20	9,1	0,3	17	9,5	0,7	6	10,4	1,3	7	10,1	0,5	6	10,9	1,4	7	11,0	1,7	14	10,6	1,1	26	9,7	0,8	11	9,7	0,6	14
<b>Cape Recife</b>																																				
0–10	20,8	2,1	20	20,8	1,5	51	22,0	2,2	16	20,1	1,6	32	19,2	1,9	15	18,5	2,1	18	18,4	1,7	41	17,0	1,6	16	18,3	3,1	14	19,9	1,6	37	18,4	2,9	17	22,3	1,3	16
11–25	19,7	3,2	15	19,6	2,4	34	22,5	3,2	7	18,4	1,7	27	18,3	2,3	13	18,2	1,6	10	17,4	1,7	25	16,9	2,0	5	21,0	4,0	2	19,3	1,7	17	17,3	2,4	17	21,7	1,8	11
26–50	15,9	4,0	22	15,2	2,6	54	19,1	3,6	20	13,8	2,8	49	16,3	2,7	19	17,4	3,1	23	16,9	2,6	41	16,2	2,9	14	18,9	3,2	14	16,6	2,3	38	15,4	3,7	26	17,8	3,3	22
51–100	12,6	3,3	27	11,3	1,8	66	15,2	3,9	23	10,6	2,6	60	15,4	3,8	22	14,4	3,2	22	14,0	2,9	36	15,2	3,2	12	16,8	3,2	26	14,7	3,4	59	12,8	3,6	26	15,0	2,5	19
101–200	12,7	2,9	14	10,1	2,1	45	12,0	3,7	17	11,6	2,7	16	13,3	2,0	15	11,5	2,0	10	13,1	3,7	8	15,3	2,2	3	16,4	2,3	14	13,3	2,4	33	12,3	3,1	13	11,8	2,5	11
<b>East London</b>																																				
0–10	20,9	3,2	17	23,9	2,3	9	19,4	2,4	8	18,7	2,8	15	21,7	3,0	25	21,6	1,7	39	19,3	1,8	8	16,9	2,5	19	18,7	1,8	9	19,5	2,2	9	19,5	1,5	6	23,9	–	1
11–25	18,2	3,6	12	22,9	1,1	6	16,1	1,7	2	18,0	0,9	11	20,6	2,6	12	20,4	1,1	8	16,5	0,6	2	18,0	2,3	3	18,2	1,7	4	20,6	2,0	5	18,7	1,2	6	23,6	0,4	4
26–50	15,7	2,7	14	21,1	3,5	20	13,7	1,0	4	17,8	1,8	18	19,8	3,7	19	19,2	3,1	28	17,2	3,0	12	18,2	3,1	5	17,3	1,5	6	20,7	0,6	10	17,4	0,6	6	20,0	0,5	3
51–100	18,4	3,7	9	18,1	1,9	14	ND	ND	ND	17,2	1,1	15	19,4	2,4	22	19,0	3,5	44	19,1	2,5	7	19,2	1,4	10	ND	ND	17,1	1,0	14	15,8	1,0	13	18,9	0,3	2	
101–200	17,4	1,7	5	17,2	1,2	10	ND	ND	ND	14,6	0,2	5	15,7	1,7	20	16,3	2,5	19	18,2	1,7	4	15,1	1,4	13	21,6	–	1	15,8	–	1	13,0	0,6	6	ND	ND	ND
<b>Coffee Bay</b>																																				
0–10	20,7	0,1	2	24,5	2,7	17	20,7	2,0	7	23,8	1,7	23	23,7	0,7	25	22,1	1,4	95	20,9	1,5	13	20,5	1,6	12	20,9	1,2	7	23,7	3,5	9	ND	ND	22,8	2,3	4	
11–25	18,9	0	1	23,8	2,2	5	15,9	0,2	3	21,0	2,0	21	23,5	1,6	3	22,4	0,8	10	20,7	1,3	6	20,0	2,3	5	21,3	1,3	10	21,1	3,8	8	ND	ND	23,9	–	1	
26–50	ND	ND	ND	23,6	2,4	23	15,5	3,8	6	18,6	2,7	34	23,7	1,5	7	21,3	2,0	33	20,1	2,1	18	20,0	1,9	9	19,7	2,0	11	19,6	2,9	11	ND	ND	19,7	2,3	8	
51–100	ND	ND	ND	20,9	1,2	20	ND	ND	ND	15,8	1,2	54	20,7	2,1	7	18,0	2,0	54	18,9	2,8	16	20,3	1,7	17	18,2	1,6	6	21,9	3,3	28	ND	ND	16,6	1,4	4	
101–200	ND	ND	ND	17,3	1,5	20	ND	ND	ND	15,0	0,7	8	17,0	0,9	7	15,2	1,5	23	16,4	2,5	13	17,7	1,4	17	17,8	–	1	21,1	3,1	15	ND	ND	16,4	0,3	2	

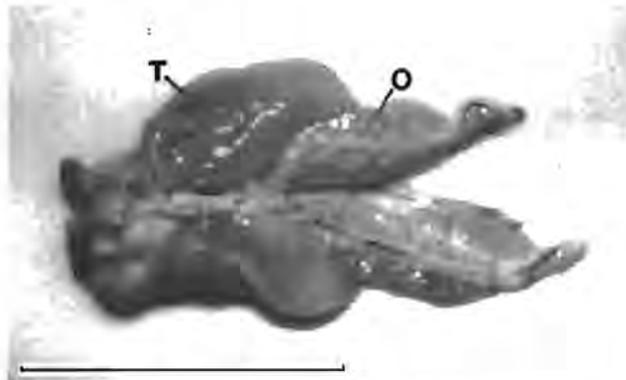
### Gonad differentiation

The gonads of *P. rupestris* are paired structures which are attached to the dorsal surface of the abdominal cavity by a mesorchium and extend about one-third to a half of its length when inactive. The ovaries join in a common duct before entering the cloaca. Macro- and microscopic examination of the gonads revealed ovotestes which develop differently in males and females (Figure 3). In juvenile fish the gonad structure appears female macroscopically and microscopically (Figures 3 & 4). Small haemophilic-staining ova are visible but the oogonia and spermatogonia were indistinguishable from each other in the slide. The ovary remains the largest and most obvious component of developing and reproductively inactive males until about 700 mm (Figures 3 & 5). The testicular tissue may be either barely or not visible macroscopically in young fish and large functional females (Figures 3 & 6). It may be found as a slight ridge at posterior, ventrolateral surface of the gonad, and is white in colour, compared to the pinkish orange ovarian part. Fat cells are associated with the anterior part of the mesorchium in front of the gonad and appear similar to the gonad in colour.

In developing and functional females, the testicular



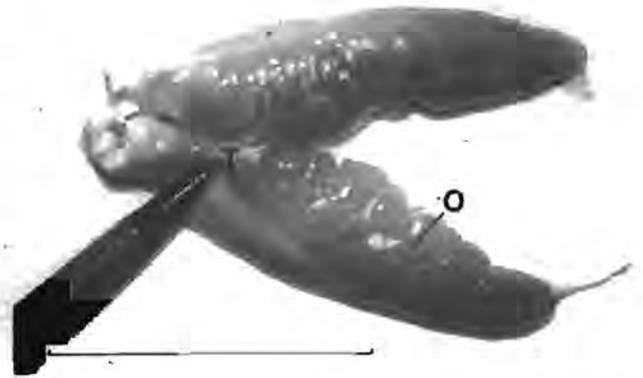
**Figure 4** Cross section of the gonad of a juvenile *P. rupestris* measuring 215 mm. PP = pre-perinuclear oocyte. OD = oviduct. The bar is 100  $\mu$ m.



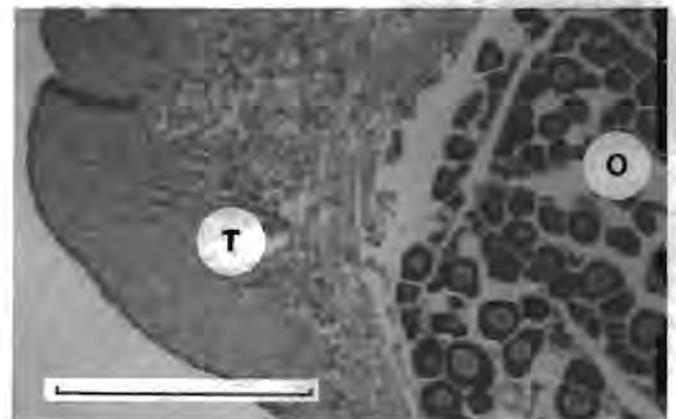
**Figure 5** Ovotestis of a functional male measuring 861 mm taken from TCNP in April. T = testis, O = ovary. The scale bar is 50 mm.

portion of the ovotestis consists of a ridge of primary sex cells which lies in the posterior ventrolateral area the ovary (Figures 3 & 7). This tissue shows little sign of spermatogenesis and sperm ducts are usually not visible (Figure 8). Testicular tissue was evident in gonads sectioned in the appropriate area and plane of functional females up to a size of about 800 mm. During the breeding season it was difficult to locate the testicular tissue, because the ovaries were distended with ripening eggs (Figure 9).

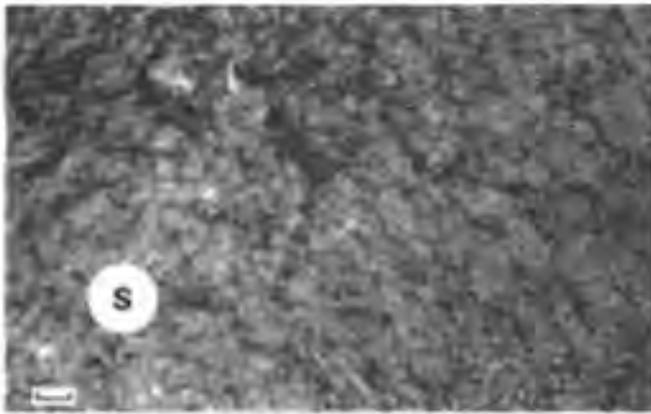
In developing males the testicular tissue grows both laterally and anteriorly. The ovarian tissue still dominates the gonad in size in early stages and the male tissue appears kidney shaped (Figures 3 & 5). The appearance of sperm ducts begins at about 400–450 mm with corresponding testicular growth, development of sex cells and spermiogenesis. Atresia of the previtellogenic oocytes may be observed and a few oocytes remain while the testis develops (Figure 10). By 500–550 mm sperm may be found in developed sperm ducts in the reproductive season. With the growth of testicular tissue the ovary is obscured macroscopically, especially in



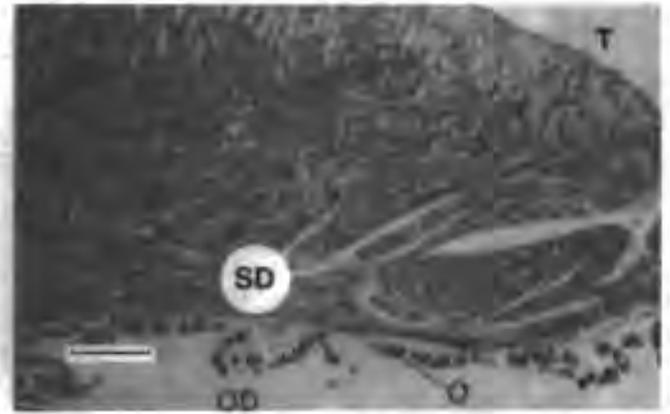
**Figure 6** Ovotestis of a functional female of 700 mm taken from TCNP in April illustrating the ridge of testicular tissue. T = testis, O = ovary. The scale bar is 50 mm.



**Figure 7** Transverse section of an ovotestis of a developing female of 552 mm taken in February, illustrating a ridge of undifferentiated spermatogonia. T = testis, O = ovary. The scale bar is 500  $\mu$ m.



**Figure 8** Undifferentiated spermatogonia of the female ovotestis illustrated in Figure 7. S = spermatogonia. The bar is 20  $\mu$ m.



**Figure 10** A functional male ovotestis illustrating sperm ducts and oogonia in a fish of 620 mm taken from Tsitsikamma in October. SD = sperm duct, O = oogonia, T = testis, OD = oviduct. The scale bar is 500  $\mu$ m.



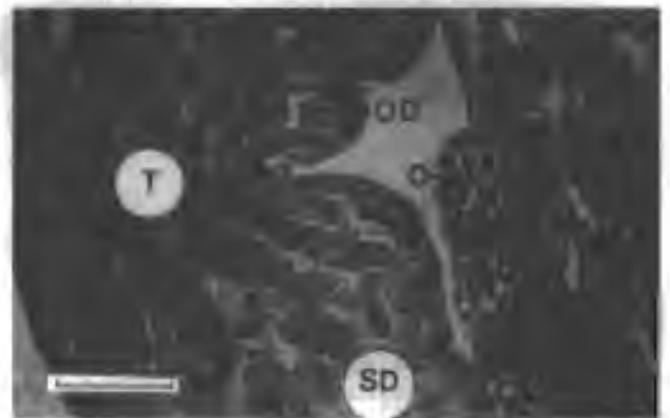
**Figure 9** A ripe ovary from a female of 788 mm taken from off East London in late August illustrating the turgid nature of the tissue at this stage. Clear, ripe ova are visible inside the ovary. The scale bar is 50 mm.



**Figure 11** Reproductively active ovotestis of a male measuring 972 mm taken from off East London in August, illustrating the dominance of testicular tissue. The scale bar is 50 mm.

reproductively active males with large gonads in the breeding season (Figure 11). The ovarian lamellae become progressively reduced and, when the male is fully mature, the ovarian part has the appearance of an empty sac. Oocytes could be seen in this area of the gonad when examined microscopically (Figure 12). The sperm ducts and oviduct are separated and sperm was never found within the ovarian part of the gonad.

In two individuals measuring 705 mm and 970 mm, considerably larger than the size at 50% maturity, ovotestes with well developed ovarian and testicular elements were found. This raises the possibility of protogynous hermaphroditism, but was more probably the result of abnormal development since it was observed so rarely. Microscopic examination revealed that although relatively small, the testicular section was fully mature with all stages of spermatogenesis occurring in the tissue (Figure 13). In the ovarian section large-scale atresia was evident and the largest eggs measured about 200  $\mu$ m, and had been at the primary yolk vesicle stage prior to atresia. The largest eggs are not shown in



**Figure 12** Ovotestis of a ripe functional male cross-sectioned near the vent. Turgid sperm ducts full of spermatozoa and a few ova are evident in the oviduct of a functional male of 752 mm from East London. SD = sperm duct, OD = oviduct, O = ova, T = testis, scale bar = 600  $\mu$ m.

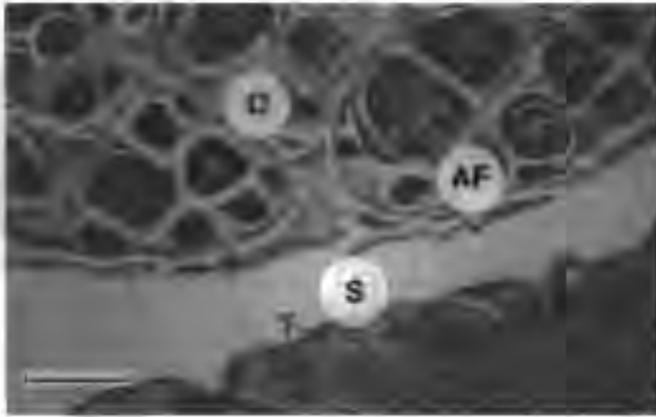


Figure 13 Atrophy of advanced oocytes (up to primary yolk stage) in a functional male of 970 mm taken from Coffee Bay in August. T = testis, S = spermatozoa, AF = atretic follicle, O = ovary. The scale bar is 100  $\mu$ m.

Figure 13. The testicular tissue was much smaller than normal for a large functional male while the ovarian section was unusually large. The growth of testicular tissue and reduction in the size of ovarian tissue therefore appeared to be abnormally delayed in both specimens. No evidence of a prior functional female phase was evident from the slides. Although these were probably abnormal developments, they illustrate the bipotential nature of the gonads. This bipotentiality results in difficulty in the identification of the sex of some individuals, especially prior to maturation. In the field, sex determination was decided on the macroscopic appearance of the ovotestis, as outlined in Figure 3. Beyond the size of about 500 mm identification of the functional sex was generally not difficult, especially when mature adults were sampled during the breeding season in spawning areas. Apparent hermaphrodites, according to macroscopic identification of the relatively well developed testicular part of the ovotestis, were established to be males on the basis of spermatogenesis, well developed sperm ducts and atrophy of ova.

An investigation of the size distribution of males and females is often used to infer the reproductive pattern of fishes which are sequential hermaphrodites. In protogynous hermaphrodites, functional females are generally smaller than males, whereas in protandrous species the reverse may be true (Atz 1964; Penrith 1972). Data from Coffee Bay, where only large, sexually mature individuals were sampled, shows that males and females are of a similar size range, had similar means and the same maximum size (Figure 14). There was no significant difference in the size distribution of males and females ( $t(2) = 1,129$ ;  $p > 0,05$ ;  $d.f. = 193$ ). This supports the evidence above that *P. rupestris* function as secondary gonochorists (*sensu* Atz 1964).

#### Colouration

A difference in colour is found between juvenile, adult male and female *P. rupestris*. Juveniles are initially red

or orange anteriorly and dorsally with a yellow caudal peduncle and belly. There is a dark red spot, which is larger than the eye, on the caudal peduncle behind the dorsal fin (Figure 15). Adult females are generally a uniform copper colour, whilst males develop a black-coloured back and upper lip with variously black mottled operculae. This colour is most obvious in reproductively active males in the breeding season. Some functional males and females larger than about 600 mm have grey

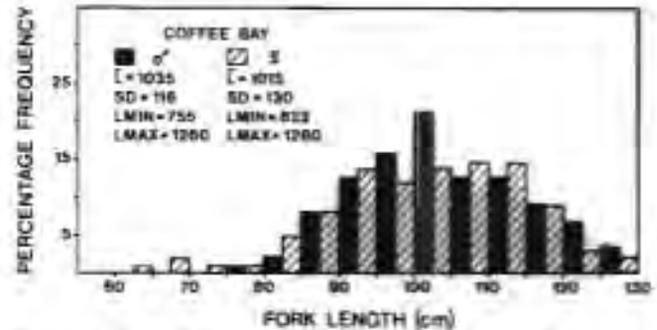


Figure 14 Length frequencies of male and female *P. rupestris* taken from Coffee Bay between 1984 and 1986. Means, standard deviations and measurements in mm.

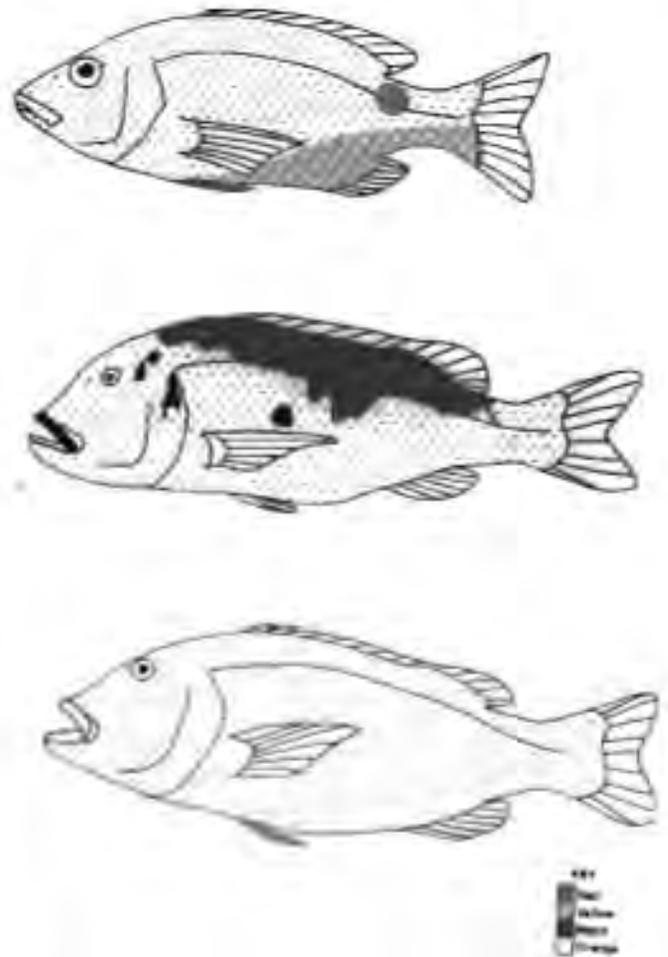


Figure 15 Diagrams of colour patterns of juvenile and adult male and female *P. rupestris*. The drawings are from slides of fish measuring about 180, 1200 and 1180 mm, respectively.

backs. Examination of the gonads of males in this colour phase shows that although they contain sperm, the testes are not enlarged, suggesting that these individuals are not reproductively active either in that season or in the locality in which they were taken. The females similarly appeared reproductively inactive.

#### Size at sexual maturity

The size at sexual maturity was estimated during peak spawning period (July to September), using fishes from East London and Transkei. This area was chosen because fishes over a wide size range were found to exhibit clear signs of spawning. Material collected from the Cape south coast had a relatively high incidence of large, sexually inactive fishes, suggesting that most of the areas sampled in this region (< 30 m) were not part of the spawning grounds.

Figure 16 shows that fishes smaller than 500 mm showed little evidence of sexual activity. Both sexes showed 100% maturation in the 700–750 mm size class. The 50% level of maturity is attained in the 550–600 mm class and may be assumed to occur at about 575 mm fork length and 630 mm total length.

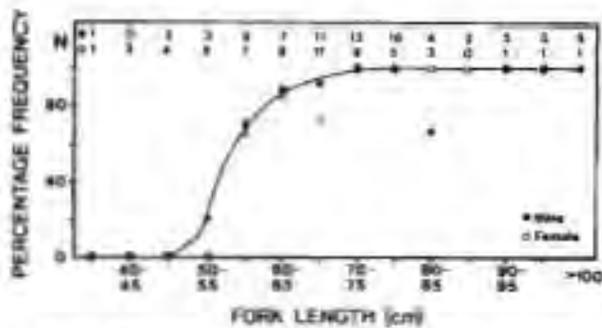


Figure 16 Percentage maturity and number of male and female red steenbras taken between East London and Coffee Bay in July–September exhibiting gonads in ripe to partially spawned stages of maturity.

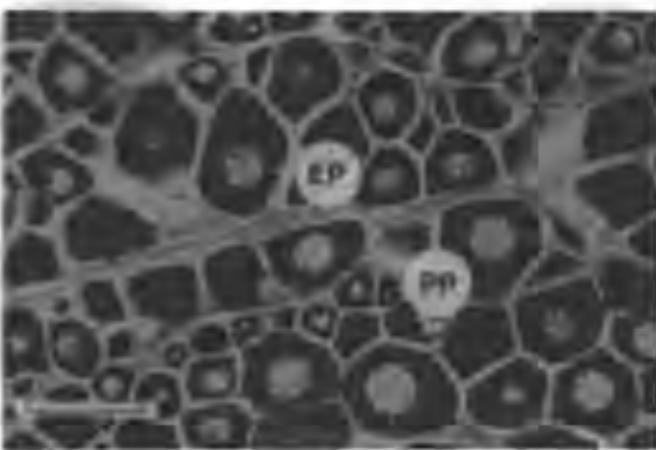


Figure 17 Previtellogenic oocytes. EP = early perinuclear oocytes, in a resting female ovary. PP = preperinuclear oocytes. The scale bar is 100 µm.

#### Histology of the gonads and gametogenesis

Coetzee (1983) described in detail the gametogenesis of the sparid *Cheimereus nufar*. Since *P. rupestris* exhibited similar stages and development of the sex cells, the cycle will only briefly be described and illustrated. Previtellogenic oocytes were found in resting ovaries of females collected from East London, mainly between January and April (Figure 17). Vitellogenesis appeared to begin in June and by July secondary yolk vesicles were evident (Figure 18). Samples collected just prior to and during the spawning season (July–October) contained both ripe ova and atretic follicles (Figures 19–21). From September to November the proportion of atretic follicles increased while the proportion of ripe ova decreased in tissue sections. The sizes of *P. rupestris* ova were larger at equivalent stages compared to *C. nufar* (Coetzee 1983).

Samples from Coffee Bay were generally in a more advanced state of the reproductive cycle than off East London at the same time of year. In Coffee Bay maturing oocytes were found in some of the sectioned tissues as early as May. This pattern of earlier development in gonads obtained in Transkei was

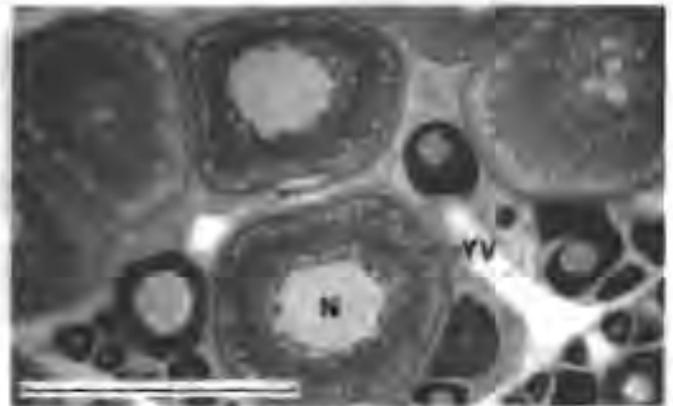


Figure 18 Vitellogenic oocytes in a maturing ovary. YV = yolk vesicles, N = nucleus. The scale bar is 250 µm.

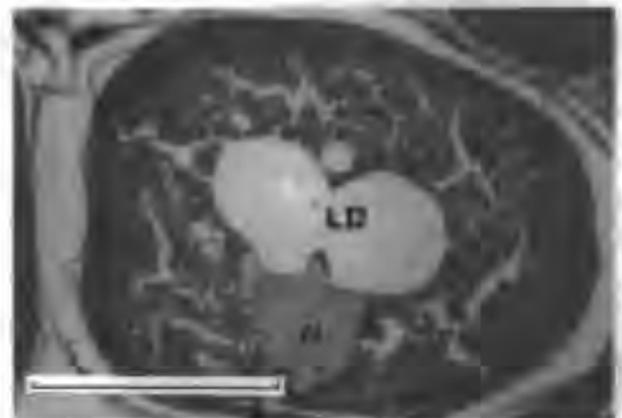
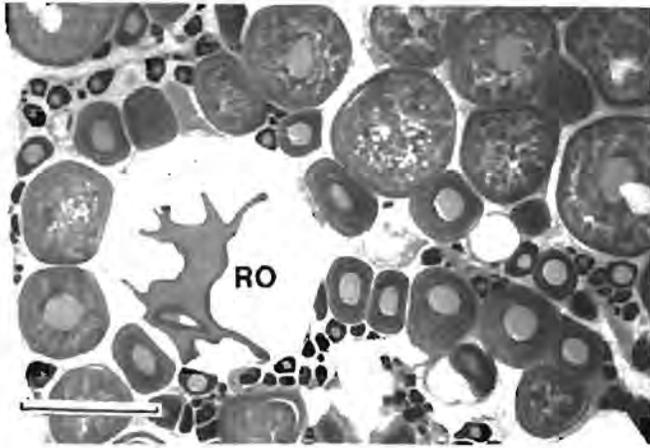
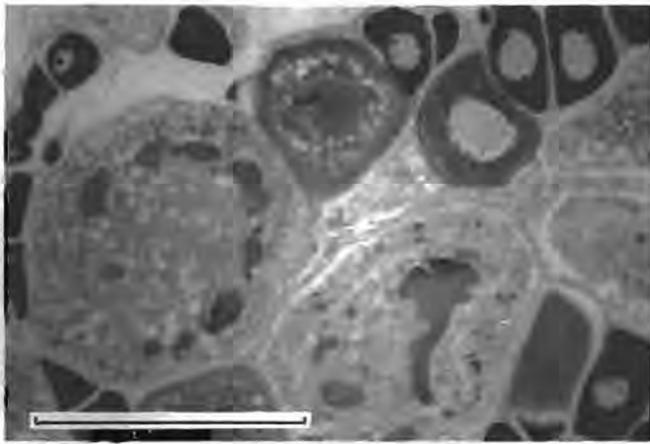


Figure 19 Migratory nucleus stage. LD = lipid droplet, N = nucleus. The scale bar is 250 µm.



**Figure 20** Cross section of a ripe ovary showing a burst ripe oocyte and other ova in earlier stages of maturation. RO = ripe oocyte. The scale bar is 500  $\mu\text{m}$ .



**Figure 21** Aretic oocytes. The scale bar is 300  $\mu\text{m}$ .

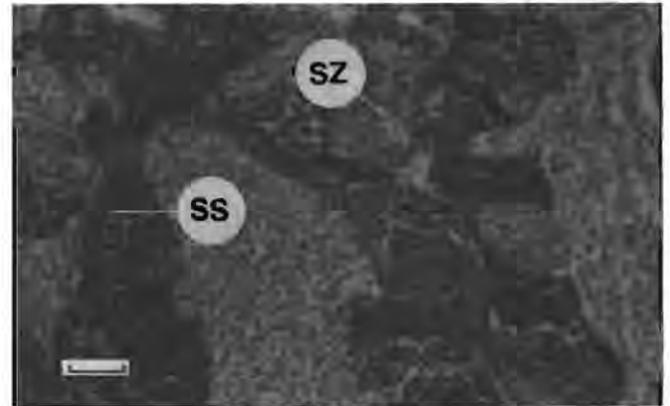
similarly reflected in the GSI values (see below).

Testicular recrudescence is less obvious than ovarian cycling because there may be sperm in the testis throughout the year. Spermatogenesis was most obvious from about May, whereafter mature males exhibited ducts full of sperm until about November or December. Spermatogenesis appeared to cease for the season in November or December (Figures 22–24).

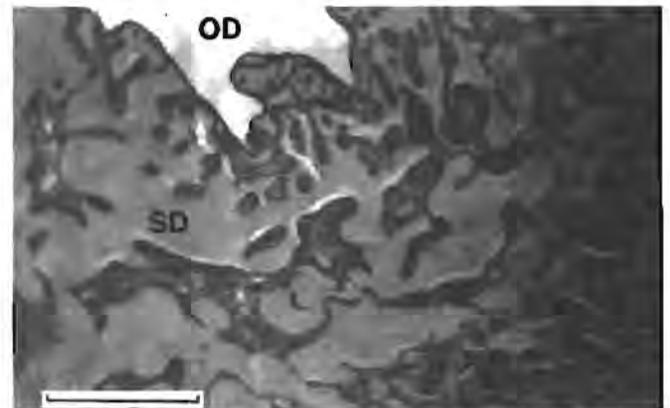
Nonfunctional ova were found occasionally in functional testicular tissue (Figure 25). Brown bodies were also found in both male and female gonads infrequently. They were more common in old fishes (Figure 26). Brown bodies have been reported in other studies (Reinboth 1970; Buxton 1987), and they may be associated with atresia.

Examination of gonads occasionally revealed abnormal structures which were different to the majority of fish sampled. Large, flattened leathery structures were observed in the gonads of large females (1175 and 1190 mm) which were caught from Transkei and East London. They were amorphous in structure when sectioned and appeared to be composed of clotted blood. One male of 1035 mm was found with unusual

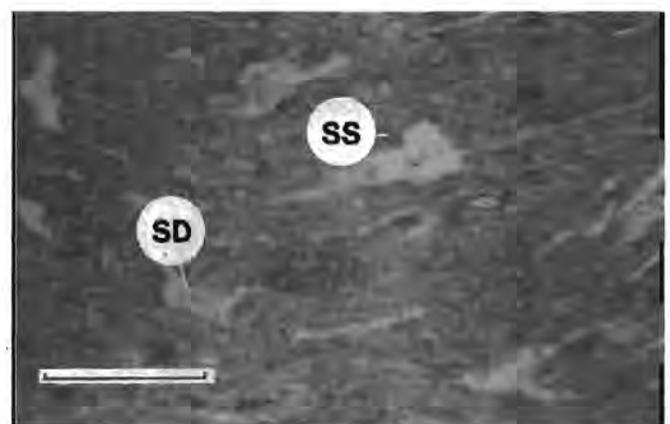
spherical structures associated with the gonad (Figure 27). The cause of these abnormalities was not determined, but in all cases the breeding potential of the fish concerned would have been reduced because, in the case of the females they filled about one quarter of the gonad volume, while the male's testes were considerably smaller than normal for a fish of that size. These



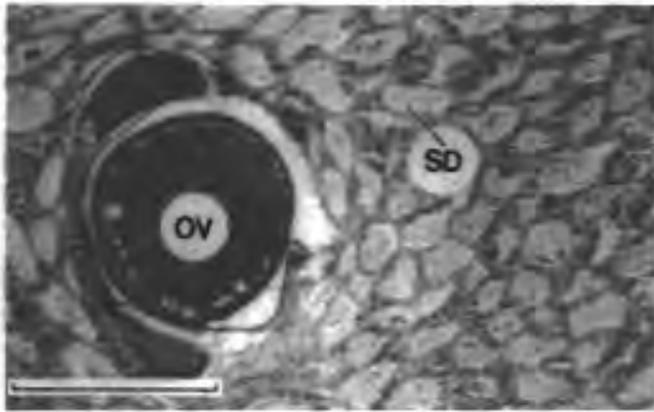
**Figure 22** Spermatogenesis in a male of 1018 mm showing cysts of spermatids (SS) and spermatozoa (SZ). The scale bar is 20  $\mu\text{m}$ .



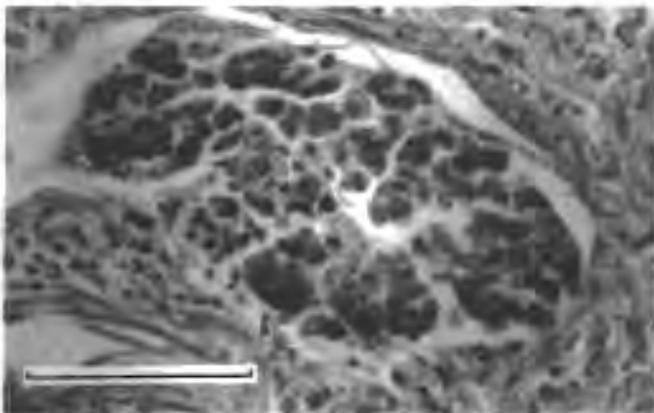
**Figure 23** Sperm ducts full of spermatozoa. SD = sperm duct, OD = rudimentary oviduct. The scale bar is 500  $\mu\text{m}$ .



**Figure 24** Resting testis of a mature male of 755 mm at the end of spawning season (December) taken at Coffee Bay. SD = sperm duct, SS = spermatids. The scale bar is 100  $\mu\text{m}$ .



**Figure 25** Oocytes in testicular tissue of a functional male of 810 mm. Ov = oocyte, SD = sperm duct. The scale bar is 200  $\mu$ m.



**Figure 26** A brown body in the testis of a mature male of 1246 mm, taken from Coffee Bay in June 1986. The scale bar is 200  $\mu$ m.



**Figure 27** Abnormal structures associated with the testes of a male of 1035 mm taken in December 1987 from Coffee Bay. The label is 77 mm wide.

conditions were found in large fish and may have been part of normal ageing and senescence, or disease.

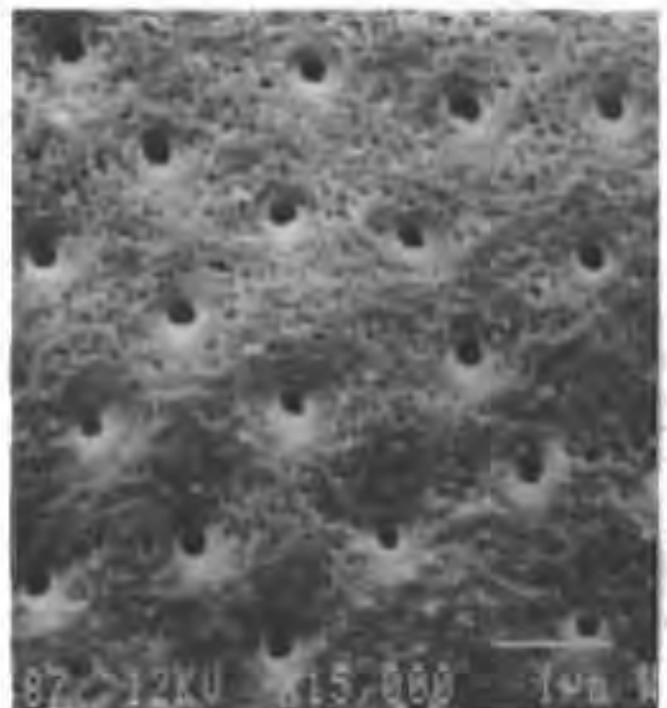
**Mature oocytes**

Clear eggs were obtained from ripe females on one

occasion and released into a bowl of seawater and mixed with sperm from a ripe male. The eggs were spherical and floated in the sea water. Electron micrographs show them to be smooth but with numerous pores of about 250 nm at a density of about 47 per 100  $\mu$ m<sup>2</sup> over the entire surface (Figures 28, 29). Similar structures were



**Figure 28** Electron micrograph of a ripe ovum of *P. rupestris*. The scale bar is 100  $\mu$ m.



**Figure 29** Electron micrograph of an ovum showing the regular patterns of pores in the membrane. The scale bar is 1  $\mu$ m.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

reported by Olivar (1987) in several fishes from the south-eastern Atlantic. Boehlert (1984) described similar pores in *Lactoria diaphana* as pits, as he found no evidence that they penetrate the chorion. The mean diameter ( $\pm$  standard deviation) of 10 red steenbras eggs was  $1,02 \pm 0,8$  mm. Most of the eggs had a single yolk droplet which measured  $0,25 \pm 0,05$  mm. These measurements are within the normal range of sparid pelagic eggs (Brownell 1979). Although traditional views have emphasized the importance of oil droplets in buoyancy of eggs, Craik & Harvey (1987) reported that the high aqueous content of the egg may provide 90% of the buoyancy while the lipid fraction may only generate 10% of it.

Breeding cycle

Figure 30 shows GSI values for 3 localities: Coffee Bay, East London and areas south-west of Algoa Bay. On the basis of gonadosomatic indices and the occurrence of clear ova in ovaries, spawning appears to occur in the vicinity of Coffee Bay between May and October, the peak being recorded in July to September. Macroscopic observations were confirmed microscopically. In the East London sample spawning appears to be delayed by about a month and peaks in August. The low sample numbers collected there between September and November result from adverse weather conditions for ski-boating at that time of the year, and the proclamation of the closed season during these months since December 1984.

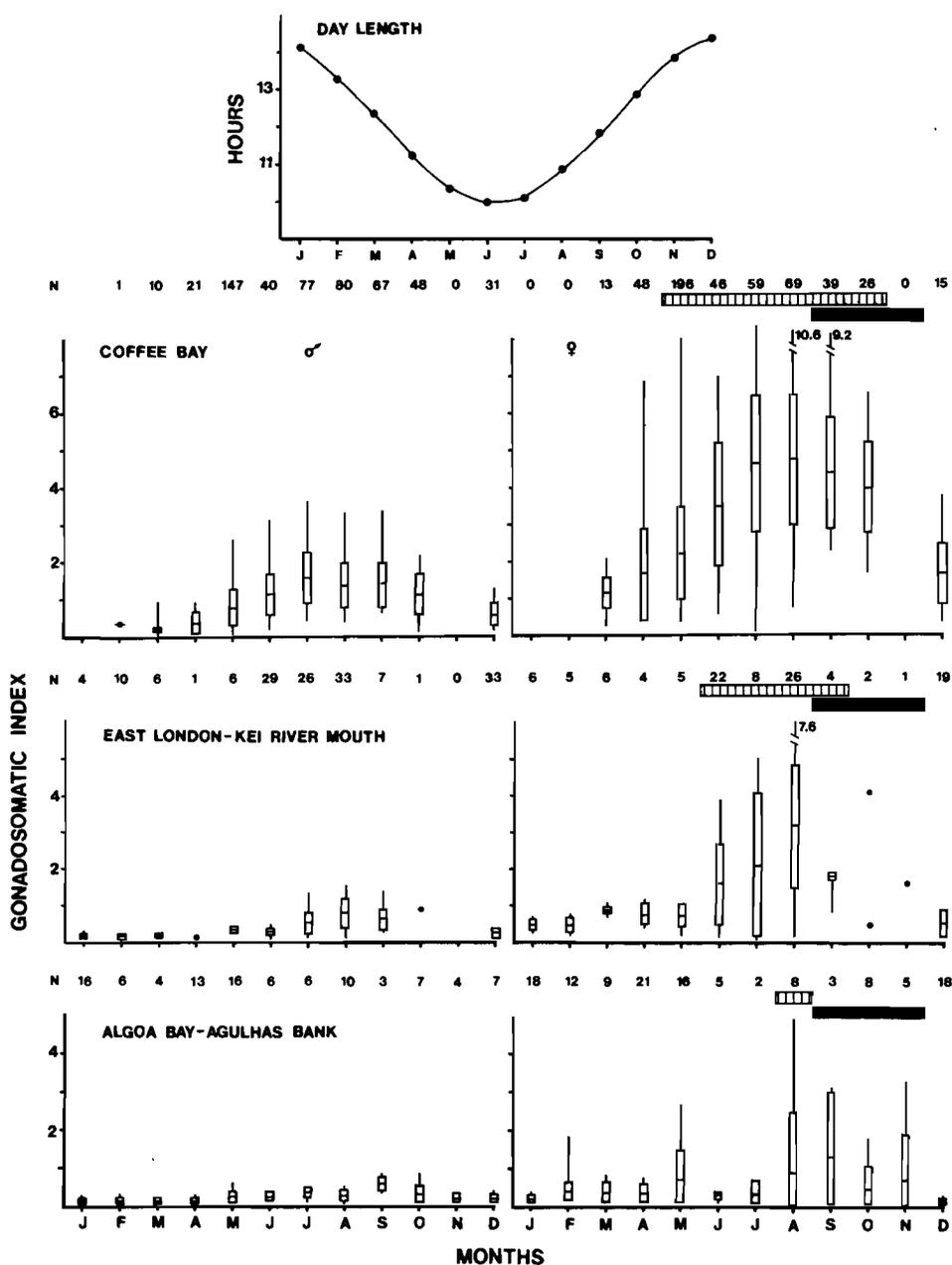
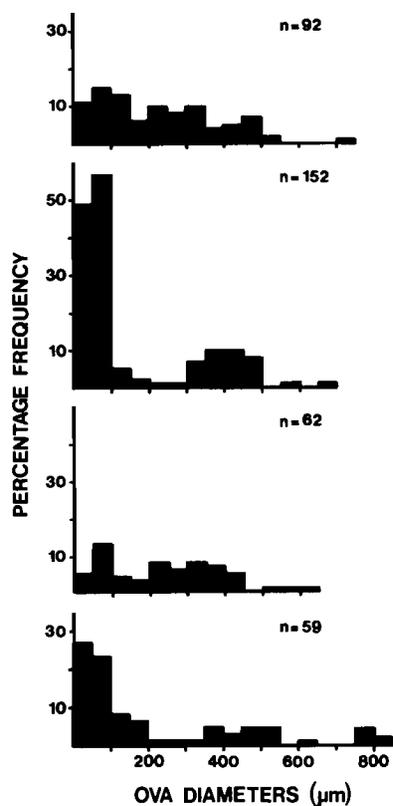


Figure 30 Gonadosomatic indices of sexually mature *P. rupestris* males and females (> 575 mm) from three areas. The mean monthly day length is also illustrated. The mean, one standard deviation and range are shown. The number of samples (N), closed season (solid line) and months in which clear ova were found in the ovaries (hatched bar) are shown.

Reproduced by Sabinet Gateway under licence granted by the Publisher (dated 2010).

Although the spawning season lasts about four months, individuals do not necessarily spawn over such a prolonged period. Examination of ovaries revealed that both previtellogenic ova and maturing oocytes in two major stages of vitellogenesis were found in gonads of fish ready to spawn (Figure 20). Although it was not possible to determine the length of time over which an individual spawned without studying live specimens, *P. rupestris* appear to exhibit group-synchronous maturation, as has been recorded in other members of this family (de Vlaming 1983). This is also reflected in the size frequency of ova in the ovarian lamellae (Figure 31). Furthermore, many ripe ova are found in the oviduct and these are not shown in the figure as the ovaries of the large, ripe individuals could not be mounted whole on slides. Group-synchronous development is not necessarily associated with simultaneous spawning of the entire stock of eggs *in toto* (de Vlaming 1983), and the appearance of the ovary of *P. rupestris* both macro- and microscopically suggests that it is a multiple spawner. Spawning may take place over a period of several weeks or possibly months.

In contrast to the areas of East London and Transkei, relatively little reproductive activity was recorded from the Cape south coast samples, which were caught mainly inshore (Figure 30). Females taken on shallow inshore reefs (< 30 m) showed either early stages of development of the ovaries, or occasionally appeared to have spawned some time previously, possibly elsewhere.



**Figure 31** Histograms of ova diameters in ripe ovaries of four mature females, showing group synchronous maturation. N is the number of eggs counted along a randomly drawn line across ovarian lamellae of a sectioned and mounted ovary.

Males had spermatozoa in the testes, but their gonads were considerably less well developed than their counterparts further north at the same time of year. Three mature fish obtained from Agulhas bank offshore reefs (68–100 m) during the breeding season showed the same stages of development as those collected from East London at the same time of year. Males larger than 600 mm had black backs and well-developed testes, and the single female captured had clear eggs in her ovaries. Five *P. rupestris* smaller than 500 mm, which were collected in the same sample, were immature.

### Sex ratio

The sex ratio of mature (> 575 mm) *P. rupestris* was calculated for the following localities: TCNP, Algoa Bay, East London and Coffee Bay (Table 3). Although the values varied between localities, there was no significant difference from a ratio of 1:1 at all localities except East London. This difference was attributable to a large sample of males collected in one month, which may have had undue influence on the small sample size. There was a significant monthly difference in the sex ratio of samples taken from Coffee Bay (Table 4).

### Discussion

The family Sparidae exhibits five forms of reproduction

**Table 3** Sex ratios of sexually mature (> 575 mm fork length) *Petrus rupestris* taken at different localities. The significance of the difference from a ratio of 1 : 1 is shown

Locality	Ratio M:F	Number	$\chi^2$	Significance
TCNP	1 : 1,3	127	1,77	NS
Algoa Bay	1 : 1,4	92	2,1	NS
East London	1 : 0,65	49	12,67	$p < 0,001$
Coffee Bay	1 : 0,98	137	0,05	NS

**Table 4** Monthly male and female numbers from Coffee Bay. The  $\chi^2$  value and significance level for a deviation from an equal sex ratio is given

Month	Male	Female	Dominant		$\chi^2$	Significance
			Sex			
January			No data			
February	1	0	M			
March	10	13	F		1,0	NS
April	21	48	F		10,56	$p < 0,005$
May	147	198	F		7,56	$p < 0,01$
June	40	46	F		0,42	NS
July	77	59	M		2,38	NS
August	80	69	M		0,8	NS
September	67	39	M		7,4	$p < 0,01$
October	48	28	M		5,26	$p < 0,025$
November			No data			
December	31	15	M		19,56	$p < 0,001$

according to a recent review by Garratt (1986). In fact this may be an overestimate of reproductive styles caused in part by a lack of attention to detail, inadequate sampling over a wide size range, the lack of thorough microscopic examination and the use of poorly defined terms, as has also been observed by Buxton & Garratt (1988). An example of this is *P. rupestris*, previously reported as a gonochorist by Penrith (1972). There are other examples such as *Diplodus sargus* and *Pterogymnus laniarius*, where different reproductive styles have been attributed to these species by different authors (Garratt 1986). It seems likely that when more comprehensive and careful studies of the family are completed, rudimentary hermaphroditism, protandry and protogyny will be the three recognized reproductive styles in the family, as has also been suggested by Buxton & Garratt (1988). In all three there appears to be a complex interaction between the environment and the ambosexually developing reproductive tissues. The control of these processes, and the factors which determine which sex will become functional are unknown. Hormones may play a role, but even in well-studied species, interacting factors are poorly understood (de Vlaming 1983). Environmental cues may have an influence, as has been found with sequential hermaphrodites (Shapiro 1984), but the genetic mechanisms of sex determination are not well understood (Price 1984). The abnormal development recorded above in two male fish with unusually large and developed ovarian parts of the gonad may have been caused by the inadequate suppression of the non-functional sex.

Studies on South African sparids have yet to proceed beyond the descriptive stage, although Atz (1964) noted that sparids offer rich opportunities to study the evolution of hermaphroditism. The pattern of sexual development described above for *P. rupestris* conforms with previous descriptions of rudimentary hermaphroditism in the Sparidae (Atz 1964; Reinboth 1970; Mehl 1973; Coetzee 1983). Both macroscopic and microscopic examination of the gonads showed that development of either male or female tissue of the ovo-testis occurs prior to sexual maturity and that inversion from one functional sex to the other does not occur after maturity. Yamamoto (1969) calls this type of sexual development 'undifferentiated' gonochorism while Alekseev (1982) suggests that the term 'juvenile protogyny' is more appropriate on the basis of the development of the gonadal tissues without invoking evolutionary implications. Given the presence of rudiments of tissues of both sexes in juveniles, the more widespread term 'rudimentary hermaphroditism' (Atz 1964) is adopted here.

Daylength is widely recognized to have an influence on hormones and reproduction (de Vlaming 1972). Onset of gonad development of *P. rupestris* appears to be correlated with short daylength during winter. Wallace & Selman (1981) note that primary growth of oocytes, during which the nucleus enlarges and multiple nucleoli form, is gonadotropin independent. Later development, in which yolk vesicles form, followed by vitellogenesis and maturation is gonadotropin

dependent. These developments occurred from about June in the East London samples, but slightly earlier in material from Transkei. Spawning was found to occur between August and October, and from May to October off the Cape and Transkei, respectively. The effects of temperature on the reproductive cycle could not be excluded, because of the limited data available. Although reproduction appears to occur in cooler, deep waters, water temperature appears to fluctuate considerably on deeper continental shelf areas (Table 2). This may be related in part to the movement of the Agulhas current and other less well documented water movement such as pulsed movement and Ekman veering (Schumann 1986). How *P. rupestris* respond to hydrographic changes during the breeding season is unknown but temperature is unlikely to trigger hormonal changes and reproduction when fluctuations appear to occur unpredictably through the year, although there probably is an optimal temperature range for reproduction. Furthermore, it is likely that a large fish like *P. rupestris* would be able to move to more suitable spawning sites if temperatures were to change from optimal. De Vlaming (1972) noted that both temperature and photoperiod may interact to control sexual cycling but that few studies have been performed to adequately separate these factors.

It appears that red steenbras spawn both at the north-east end of their range and the offshore areas to the south. It is not possible at present to determine the relative importance of the stock in different areas, as targeted catch and effort are not presently quantifiable in different areas. Judging from the well-known and long-exploited stock of large adults in the Transkei, this presently seems to be a large or principal part of the reproductively active adult stock. Considering the paucity of records of spawning fish from the eastern Cape, the possibility of a spawning migration for at least part of the stock cannot be excluded. This appears to happen off Natal (van der Elst 1981), but it is noteworthy that fish may be caught in areas such as Coffee Bay throughout the year. This does not support the concept of a typical spawning migration (Harden Jones 1970). Adults probably move inshore into the shallows of the Cape south and east coasts when not spawning, explaining the presence of large fish inshore in the summer months, such as those recorded by Horne (1955). The absence of these fish in present day shore-based fishing is probably a result of exploitation and stock size reduction.

The marked dichromatism observed in reproductively active fishes in the breeding season is probably associated with courtship and mating, as is commonly found with many other species of reef fish (Thresher 1984). An equally marked breeding colouration change has been noted in male *Spondylisoma emarginatum*, a nest-building sparid (van Bruggen 1965) which develop distinctive black patterns in the breeding season, compared to their normal silvery brown during the rest of the year. This nest-building behaviour has been noted in the British congeneric *S. cantharus*, where colour

change was also observed (Potts 1984). Unlike this nest-building fish which has demersal eggs (Potts 1984) *P. rupestris* has eggs which float in seawater, suggesting that it is a pelagic spawner and not a demersally spawning nest builder. The colouration may be related to displays, mate recognition and possibly sexual competition. Observations of reproductive behaviour and spawning were not possible because spawning occurred in deep water not accessible to SCUBA diving, and did not occur in aquarium maintained individuals in the Port Elizabeth Oceanarium. The distinctive differences suggest that pair spawning may occur, as has been found in other sexually dichromic fishes (Brawn 1961a & b; Thresher 1984; Choat & Robertson 1975). Furthermore, it is likely that spawning is associated with the Agulhas current, as pelagic spawners usually leave the reef with a characteristic twilight dash, to reduce egg predation (Thresher 1984). The apparent locality of spawning sites adjacent to the Agulhas current may be important for egg dispersal.

The overall range of sex ratios calculated for sexually mature *P. rupestris* (1 : 1,4–1 : 0,98 male to female) were not significantly different from the theoretically expected ratio of 1 : 1 (Krebs & Davies 1985), except a small sample from East London (1 : 0,65). In other South African sparids which appear to function as secondary gonochorists, the following values have been recorded: Coetzee (1983) calculated a ratio of 1:2 for *Cheimerius nufar* and Garratt (1985) found a ratio of 1 : 2,5 in Natal; Nepgen (1977) observed a ratio of 1 : 1,2 in *Argyrozona argyrozona*. The sex ratios of protogynous sparids may be more skewed towards the females and values such as 1 : 2 in *Chrysolephus laticeps* (Penrith 1972), and 1 : 2,3 to 1 : 18,8 in *C. puniceus* at different localities (Garratt 1985). Buxton (1987) found male : hermaphrodite : female ratios of 1 : 0,58 : 1,11 and 1 : 1 : 4,22 in *C. laticeps* and *C. cristiceps*, respectively. Both Garratt (1985) and Buxton (1987) observed changes in the sex ratio of protogynous hermaphrodites, with females becoming more dominant in exploited areas. Although the sex ratio of rudimentary hermaphrodites is unlikely to be as obviously affected by exploitation, a bias towards 'females' may be expected if immature fishes which are hard to sex are included in the female data. Both Coetzee's (1983) and Garratt's (1985) data show apparent females dominating the sample prior to maturation. Juveniles were excluded from the calculation of sex ratios in the present study to avoid this. The sex ratio of fishes caught by line will also be influenced by gear size selectivity and behaviour, such as schooling and reproduction. Until more is known about schooling and reproductive behaviour, mating systems (Warner 1984) and sexual development, the biological significance of sex ratios sampled by linefishing is likely to remain difficult to interpret.

Macroscopic visual gonad staging methods are widely used in fisheries work. The need to substantiate them with microscopic examination was confirmed during this study. For example, wine-red ovaries were occasionally found out of the major spawning period, although indicative of postspawning. These were usually found to

have been incorrectly staged when checked microscopically. The use of the macroscopic staging system is largely a field shorthand whereby descriptions of the gonad are coded onto data sheets. They are most reliable as indicators of either non-breeding, imminent spawning (when clear eggs are visible) or post spawning. Difficulty was experienced when trying to determine whether a gonad was partially spawned and would spawn again, or whether it had finally finished spawning in a particular season. The importance of adequate microscopic confirmation of spawning stages cannot be over-emphasized.

The reported trends of decreased abundance of *P. rupestris* were not confirmed during this study owing to the absence of reliable long-term data on trends in catch and effort in the study area. Until this becomes available, management will have to rely on information gathered on the life history of the species. This study has revealed that inshore areas (< 30 m) of the southern Cape coast between East London and the Agulhas bank are important nursery areas of juveniles and subadults. Adults appear to move offshore and an important part of the adult stock is found off Transkei and East London throughout the year. The adults off the Transkei coast are all large and this could infer that the stock is healthy. A major problem, however, is determining how large this part of the population is and how vulnerable it is to over-exploitation. If adults migrate and concentrate on these grounds, it could represent an important and vulnerable concentration of large fish which may be vital to stock recruitment. It is clearly important to monitor accurately catches of this part of the stock in particular. These offshore reefs have a degree of natural protection from fishing in the form of frequent bad weather and the powerful Agulhas current, which often prevents fishing. These factors, the ever increasing cost of fuel and apparently smaller and unprofitable catches appear to have reduced the incursions of Natal-based line boats to the Transkei and Cape. Long-term conservation of the adult stock cannot rely on physical factors alone. The steady improvement of echo sounders and other fishing gear will probably offset any protection afforded by their habitat, resulting in increased fishing pressure on this prized fish, which appears to show signs of heavy exploitation.

Management of *P. rupestris* is presently undertaken using four different strategies. Firstly, a closed season between 1 September and 30 November for this species has been introduced since December 1984 along the entire coast. Transkei, which has its own conservation legislation, had not implemented a closed season during the study or at the time of writing. Secondly, there is a minimum size limit (250 mm TL). Thirdly, it is one of a group of reef fishes of which no more than five in total may be taken by fishermen, other than full-time professionals. Finally, some protection is afforded by three marine reserves; the Tsitsikamma Coastal National Park (TCNP) (Buxton & Smale 1984), the de Hoop reserve (DHR) (A. Penney, Sea Fisheries Research Institute, pers. comm.) and probably the East London marine reserve areas.

Of these four management strategies, the closed season is one which probably has considerable benefit, reducing fishing effort directed at *P. rupestris*, thereby lowering catches, and allowing apparently aggregated ripe adults to spawn. This measure applies to both professional and amateur fishermen throughout the country, except those in Transkei. Considering that *P. rupestris* begins spawning earlier in Transkei than in the Cape, a closed season in Transkei earlier in the year appears to be advisable. In practice, however, the benefit of a country-wide closed season over the same months with the greater ease of control would suggest that the current closed season should also be introduced in Transkei, even though early spawners would not be protected.

Considering the increasing trend in the ski-boat fishery in this area (Smale & Buxton 1985), a bag limit for amateur fishermen is probably of limited benefit, especially as it does not apply to professionals. The minimum size regulation is of limited benefit because 50% sexual maturity is only attained at 630 mm TL, more than twice the minimum size which may be legally kept. The practical problem in the case of minimum sizes is that *P. rupestris* is only one component of the exploited multi-species reef fish community, and it matures at a much larger size than the others. It is therefore susceptible to exploitation at a size when many other co-existing reef species are mature. Release of these fishes once captured is of dubious benefit as they often suffer from barotrauma when brought to the surface from more than 20 m and will often not survive when released.

Marine reserves are an attractive conservation option. In both TCNP and DHR *P. rupestris* receive some measure of protection. This protection appears to cover only the earlier stages of the life cycle because, as far as is known, breeding areas are not included in any of the existing marine reserves. At present they encompass only limited areas of water deeper than 50 m as they do not extend more than three nautical miles offshore. In addition to the possibility of immature fish moving out of the park and being subject to exploitation, adults must move out of the park to breed. Extension of the seaward boundaries to include areas of the shelf to depths of at least 100 m would be beneficial and provide a multi-species and ecosystem approach to conservation. If sited carefully, part of the *P. rupestris* spawning ground could be protected.

*P. rupestris* have large ovaries of up to at least 1,8 kg in large individuals during the spawning season, suggesting that they are highly fecund and that large numbers of eggs are released during the spawning season. As a result, they may be less sensitive to heavy exploitation than species exhibiting a lower reproductive output (Adams 1980). Measures in addition to the closed season to safeguard part of the adult spawning stock, are nevertheless desirable, especially if the apparent stock decline continues. With the careful location of a marine reserve which encompasses part of the adult stock, recruitment to the fishery would probably be ensured.

## Acknowledgements

This project would not have been possible without the willing co-operation of numerous ski-boat anglers along the coast. Mr G. Winch kindly saved material and provided a base at East London. Mr G. B. Trow assisted with collecting material, recorded temperature data for catches with a thermometer supplied by the author, and provided a base at which to work when away from the laboratory. The National Parks Board gave permission to work in TCNP, and Messers J. Allen, P. Joubert, D. Bower and their assistants provided logistical support there. Staff of the Sea Fisheries Research Institute, including the Master and crew of RV *Africana* are thanked for helping to obtain fish from the Agulhas Bank. The project benefitted from the assistance given by colleagues at the Port Elizabeth Museum and the Department of Ichthyology and Fisheries Science, Rhodes University (RU), who assisted with some of the field collecting. Mr R. Cross of the Electron Microscope Unit (RU) took the electron micrographs. Mr A. Punt of Applied Mathematics Department, University of Cape Town assisted with regression analyses. Dr P. Price kindly assisted with sectioning some of the reproductive tissues. Miss M. du Plessis did the final drawings. In particular I thank Dr C.D. Buxton and Mr J.R. Clarke for field assistance, discussions and critical reviews of this paper. Two anonymous referees critically reviewed and improved the paper. This project was financed by the Linefish Programme of the South African National Committee for Oceanographic Research.

## References

- ADAMS, P.B. 1980. Life history patterns in marine fishes and their consequences for fisheries management. *Fish. Bull.* 78: 1-12.
- ALEKSEEV, F.E. 1982. Hermaphroditism in sparid fishes (Perciformes, Sparidae). 1. Protogyny in porgies, *Pagrus pagrus*, *P. orphus*, *P. ehrenbergi* and *P. auriga* from West Africa. *J. Ichthyol.* 22: 85-94.
- ATZ, J.W. 1964. Intersexuality in fishes. In: Intersexuality in vertebrates including man. (Eds) Armstrong, C.N. & Marshall, A.J. Academic Press, London. pp. 145-232.
- BARNARD, K.H. 1947. South African fishes. Standard Press, Cape Town.
- BOEHLERT, G.W. 1984. Scanning electron microscopy. In: Ontogeny and systematics of fishes. *Spec. Publ. (1) Am. Soc. Ichthys & Herps.* pp. 43-48.
- BIDEN, C.L. 1930. Sea-angling fishes of the Cape (South Africa). Oxford University Press, London.
- BRAWN, V.M. 1961a. Aggressive behaviour in cod (*Gadus callarias* L.). *Behaviour* 18: 107-147.
- BRAWN, V.M. 1961b. Reproductive behavior of the cod (*Gadus callarias* L.) *Behaviour* 18: 177-198.
- BROWNELL, C.L. 1979. Stages in the early development of 40 marine fish species with pelagic eggs from the Cape of Good Hope. *Ichthyol. Bull. J.L.B. Smith Inst. Ichthyol.* 40: 1-84.
- BUXTON, C.D. 1987. Life history changes of two reef fish species in exploited and unexploited marine environments in South Africa. Ph.D. thesis, Rhodes University, South Africa. 220 pp.

- BUXTON, C.D. & GARRATT, P.S. 1988. Alternative reproductive styles in seabreams (Teleostei: Sparidae). In: *Alternative Life History Styles of Fishes*. (Ed.) Bruton, M.N. *Environ. Biol. Fish.* (in press).
- BUXTON, C.D. & SMALE, M.J. 1984. A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park. *Koedoe* 27: 13–24.
- CHOAT, J.H. & ROBERTSON, D.R. 1975. Protogynous hermaphroditism in fishes of the family Scaridae. In: *Intersexuality in the animal kingdom*. (Ed.) Reinboth, R. Springer-Verlag, Berlin. pp. 263–283.
- COETZEE, P.S. 1983. Seasonal histological and macroscopic changes in the gonads of *Cheimerius nufar* (Ehrenberg, 1820) (Sparidae, Pisces). *S. Afr. J. Zool.* 18: 76–88.
- CRAIK, J.C.A. & HARVEY, S.M. 1987. The causes of buoyancy in eggs of marine teleosts. *J. mar. biol. Ass. U.K.* 67: 169–182.
- DE VLAMING, V. 1972. Environmental control of teleost reproductive cycles: a brief review. *J. Fish Biol.* 4: 131–140.
- DE VLAMING, V. 1983. Oocyte development patterns and hormonal involvements among teleosts. In: *Control processes in fish physiology*. (Eds) Rankin, J.C., Pitcher, R.T. & Duggan, R.T. Croom Helm, London. pp. 176–199.
- GARRATT, P.A. 1985. The offshore linefishery of Natal: I: Exploited population structures of the Sparids *Chrysoblephus puniceus* and *Cheimerius nufar*. *Invest. Rep. Oceanogr. Res. Inst.* 62: 1–18.
- GARRATT, P.A. 1986. Protogynous hermaphroditism in the slinger, *Chrysoblephus puniceus* (Gilchrist & Thompson, 1908) (Teleostei: Sparidae). *J. Fish Biol.* 28: 297–306.
- HARDEN JONES, F.R. 1970. *Fish Migration*. Camelot Press, London.
- HORNE, C. 1955. *Fisherman's Eldorado*. Timmins, Cape Town.
- HUMASON, G.L. 1979. *Animal tissue techniques*. 4th edition. W.H. Freeman, New York.
- KREBS, J.R. & DAVIES, N.B. 1985. *An introduction to behavioural ecology*. Blackwell Scientific Publications, Oxford.
- LUTJEHARMS, J.R.E. 1981. Features of the Agulhas Current circulation from satellite remote sensing. *S. Afr. J. Sci.* 77: 231–236.
- MEHL, J.A.P. 1973. Ecology, osmoregulation and reproductive biology of the white steenbras *Lithognathus lithognathus* (Teleostei: Sparidae). *Zool. Afr.* 8: 157–230.
- NEPGEN C.S. de V. 1977. The biology of the hottentot *Pachymetopon blochii* (Val.) and the silverfish *Argyrozona argyrozona* (Val.) along the Cape south-west coast. *Invest. Rep. Sea Fish. Branch (S. Afr.)* 105: 1–35.
- OLIVAR, M.-P. 1987. Chorion ultrastructure of some fish eggs from the south-east Atlantic. In: *The Benguela and Comparable Ecosystems*. (Eds) Payne, A.I.L., Gulland, J.A. & Brink, K.H. *S. Afr. J. Mar. Sci.* 5: 659–671.
- PENRITH, M.J. 1972. Sex reversal in the sparid fish *Chrysoblephus laticeps*. *Koedoe* 15: 135–139.
- POTTS, G.W. 1984. Parental behaviour in temperate marine teleosts with special reference to the development of nest structures. In: *Fish Reproduction — strategies and tactics*. (Eds) Potts, G.W. & Wootton, R.J. Academic Press, London. pp. 223–244.
- PRICE, D.J. 1984. Genetics of sex determination in fishes — a brief review. In: *Fish Reproduction — strategies and tactics*. (Eds) Potts, G.W. & Wootton, R.J. Academic Press, London. pp. 77–89.
- RATOWSKI, D.A. 1983. *Non-linear regression modelling*. Marcel Dekker, New York.
- REINBOTH, R. 1970. Intersexuality in fishes. *Mem. Soc. Endocr.* 18: 515–543.
- ROBINSON, G.A. 1976. Sex reversal in the dageraad *Chrysoblephus cristiceps* (Pisces: Sparidae). *Koedoe* 19: 43–48.
- SCHUMANN, E. 1986. The bottom boundary layer inshore of the Agulhas Current off Natal in August 1975. *S. Afr. J. mar. Sci.* 4: 93–102.
- SHAPIRO, D.Y. 1984. Sex reversal and sociodemographic processes in coral reef fishes. In: *Fish Reproduction — strategies and tactics*. (Eds) Potts, G.W. & Wootton, R. Academic Press, London. pp. 103–118.
- SMALE, M.J. 1986. The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa. *S. Afr. J. Zool.* 21: 111–130.
- SMALE, M.J. & BUXTON, C.D. 1985. Aspects of the recreational ski-boat fishery off the eastern Cape waters of South Africa. *S. Afr. J. mar. Sci.* 3: 131–144.
- SOUTH AFRICAN ANGLERS UNION. 1986. Records: 1985. *sl. SAAU*: 1–80.
- THRESHER, R.E. 1984. *Reproduction in reef fish*. T.F.H. Publ., U.S.A.
- VAN DER ELST, R.P. 1981. *A guide to the common sea fishes of southern Africa*. Struik, Cape Town.
- VAN BRUGGEN, A.C. 1965. Records and observations in the Port Elizabeth Oceanarium in 1960. *Der Zoologische Garten, Leipzig*. 31: 184–202.
- WALLACE, R.A. & SELMAN, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *Am. Zool.* 21: 325–343.
- WARNER, R.R. 1984. Mating behavior and hermaphroditism in coral reef fishes. *Am. Sci.* 72: 128–136.
- YAMAMOTO, T. 1969. Sex differentiation. In: *Fish physiology*, Vol. III. (Eds) Hoar, W.S. & Randall, D.J. Academic Press, New York. pp. 117–177.