The biology of the bronze bream, *Pachymetopon grande* (Teleostei: Sparidae) from the south-east Cape coast, South Africa

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The biology of the sparid fish, *Pachymetopon grande*, was investigated from data collected on the south-eastern Cape coast between August 1984 and March 1987. Sectioned sagittal otoliths revealed that they are a slow-growing, long-lived species capable of reaching ages in excess of 40 years. Detailed histological examination of gonadal development showed that they are rudimentary hermaphrodites, males and females maturing after a non-functional intersexual stage. The breeding season is restricted to between January and June, and observations suggest that they are group spawners with pelagic eggs. Maturity was reached at 300 mm fork length or approximately 5,5 years old. *P. grande* is primarily herbivorous, feeding selectively on rhodophytes found on inshore reefs down to approximately 20 m. Minor dietary components included hydrozoans, octocorals and other small invertebrates. Macroalgal degradation by gut endosymbionts or the utilization of macroalgal epibionts was not evident, suggesting that storage and extracellular carbohydrates of the macroalgae were utilized in the diet. The importance of *P. grande* to the inshore recreational angling fishery, together with certain aspects of its biology, underline the need for conservation measures aimed at ensuring the sustainability of this resource.

Die lewenswyse van die spariede vis *Pachymetopon grande* is ondersoek. Inligting is tussen Augustus 1984 en Maart 1987 aan die kus van die Oos-Kaap ingesamel. Ondersoek van snitte van sagittale otoliete het bewys dat die visse lanklewend is met 'n stadige groeitempo, en 'n ouderdom van tot 40 jaar kan bereik. Uitvoerige histologiese studie van die geslagsklier het bewys dat die visse rudimentêr hermafrodities is en dat mannetjies en wyfies, na 'n nie-funksionele inter-seksuele stadium, differensieer. Die broeityd is beperk tot tussen Januarie en Junie en dit blyk dat hulle in groepe kuitskiet en dat die eiers in die waterkolom bly. Geslagsrypheid word bereik teen 300 mm vurklengte of ongeveer 5,5 jaar oud. *P. grande* is hoofsaaklik 'n plantvreter, en wei selektief op rhodofiete (rooi-alge), wat op rotsriwwe naby die kus voorkom, tot dieptes van ongeveer 20 m. Voedselitems van mindere belang sluit hidrosoë, oktokorale en klein invertebrate in. Daar was geen bewyse dat alge deur ingewand-simbionte afgebreek word of dat die epibionte van die alge benut word nie. Dit dui daarop dat opgegaarde en buite-sellulêre koolhidraat van groot alge in die dieet verbruik word. Die belangrikheid van *P. grande* in kus-sporthengel sowel as sekere aspekte van sy biologie ondersteep die noodsaaklikheid om beskermings-maatreëls in te stel om die oorlewing van dié natuurlike hulpbron te verseker.

The bronze bream, *Pachymetopon grande* (Gunther 1859), is a sparid species endemic to southern Africa, although the full extent of its distribution is uncertain. Smith & Heemstra (1986) and Bauchot & Smith (1984) both give the northern limit as southern Madagascar, while van der Elst (1981) indicates that the species is found around the entire Madagascan coast. The southern limit of its distribution is given as Knysna on the Cape south coast. The bronze bream is an inshore species and is found on rocky shores down to approximately 25 m (Buxton & Smale 1984; Beckley & Buxton 1989). Reports on the biology of this species are mainly anecdotal. Van der Elst (1981) notes that it is almost excusively herbivorous, although Bauchot & Smith (1984) include ascidians and crustaceans in its diet. Van der Elst (1981) also states that *P. grande* attains sexual maturity between 40–45 cm caudal-fork length and breeds during late winter and spring on the Natal coast. Penrith (1972) suggested that *P. grande* was a gonochoristic species.

The bronze bream is an important recreational shore-angling fish, particularly along the south-eastern Cape coast (Clarke & Buxton 1989), but does not occur in sufficient numbers to be of any commercial significance. Despite this, a need has been recognized to provide a biological basis for the management of recreational angling species (Wallace & van der Elst 1983). In this study information on the diet, age, growth and reproductive biology of *P. grande* is presented, and the conservation status of the species is discussed.

Methods

Data were collected from August 1984 to March 1987 in the area between Knysna and East London, although most of the sampling was done in the Port Elizabeth and Tsitsikamma regions (Figure 1). Large fish were obtained mostly from recreational anglers and spearfishermen, but to obtain fish in the size classes not represented in their catches, specimens were speared by research divers using SCUBA. This sampling was limited to inshore reefs (< 20 m) in the Tsitsikamma National Park and off the rocky coastline west of Port Elizabeth.

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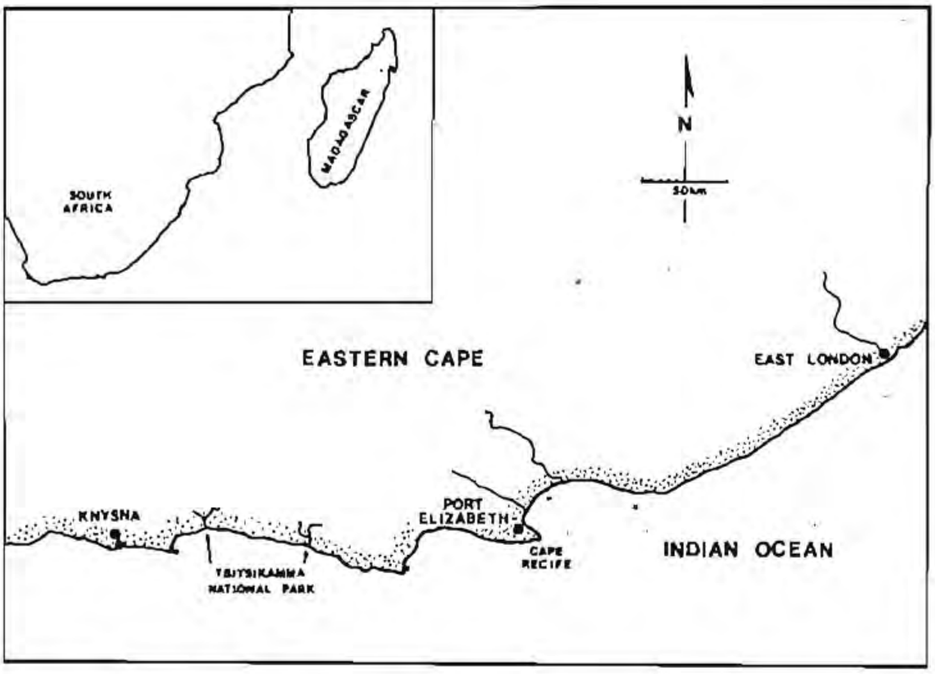

Figure 1 Map of the study area showing places mentioned in the text.

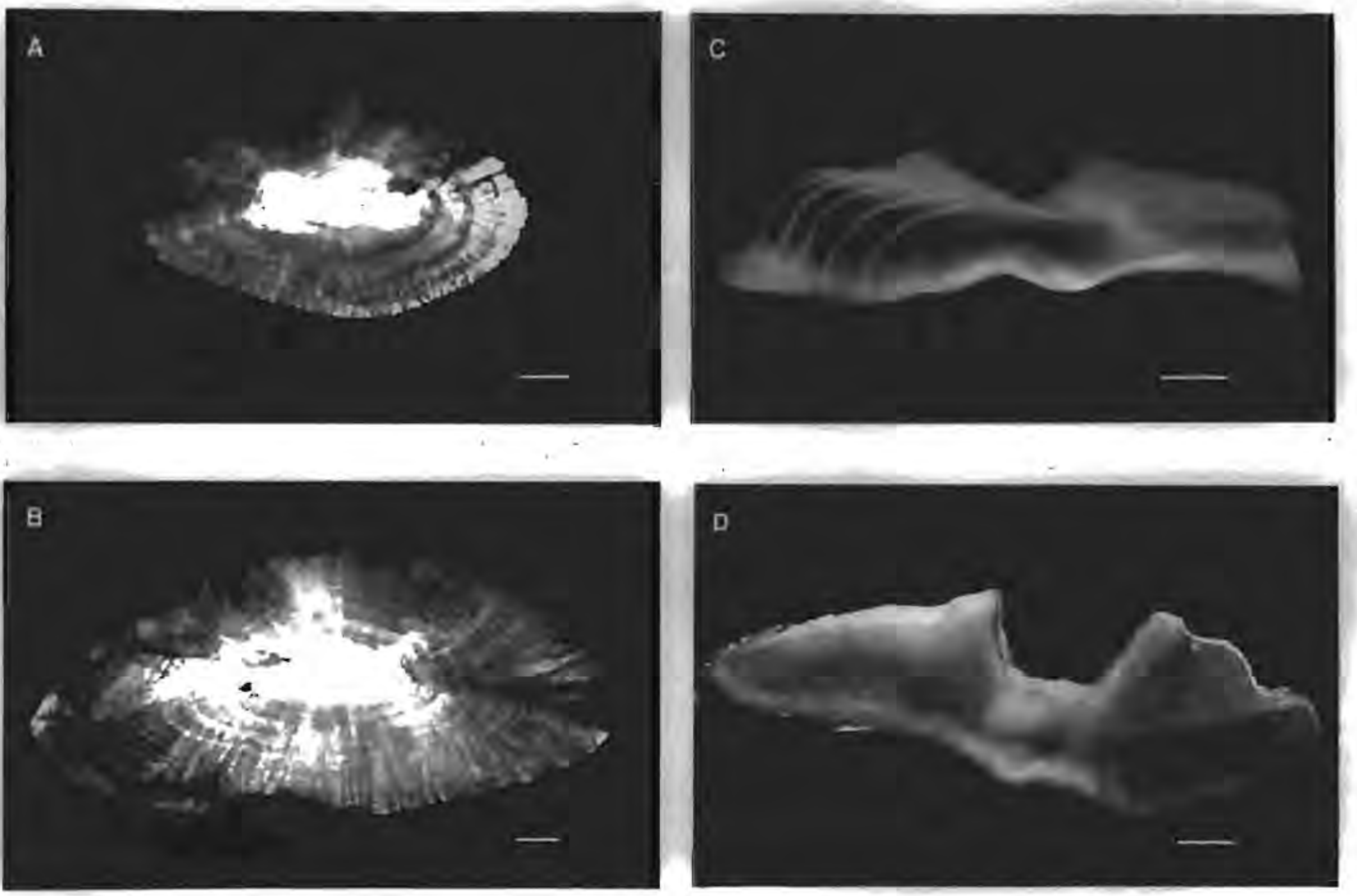

Figure 2 Photomicrographs of the sagittal otoliths of *Pachymetopon grande* viewed under reflected light. (a) Whole otolith from a small fish (FL = 244 mm) showing well defined growth zones. Age was determined as three years. Scale bar = 1 mm. (b) Whole otolith from a larger fish (FL = 441 mm) showing less well defined growth zones, particularly at the margin of the otolith. Scale bar = 1 mm. (c) Transverse section through the otolith of a small fish (FL = 290 mm). Alternating opaque (narrow) and hyaline (wide) zones are clearly visible. Age determined as six years. Scale bar = 0,5 mm. (d) Transverse section through the otolith of a fish of 449 mm FL, showing a stacking of growth zones. Age was determined as 24 years. Scale bar = 0,5 mm.

Each fish was weighed (g) and measured (total, caudal-fork and standard lengths in mm). Sex and the developmental stages of the gonads were determined using the visual criteria described by Buxton & Clarke (1986). Subsamples of the gonads were fixed in Bouin's solution for histological description of gonadal development and gametogenesis. Gonad samples were transferred from Bouin's after 3–4 days, routinely embedded, sectioned at 7 μm and stained using Harris' haematoxylin and eosin. The contents of the stomach and hindgut were removed, weighed and preserved separately in buffered 10% formalin. The total content of the stomach and hindgut was shown to comprise as much as 12,05% of the body mass, and for this reason eviscerated body mass was used in morphometric relationships. Sagittal otoliths were removed, cleaned and stored dry in manila envelopes for later age determination. The lengths, widths and weights of a sample of otoliths were determined.

Dorsal fin spine and pectoral fin ray sections, vertebrae, operculae, scales and both whole and sectioned otoliths from 15 fish were examined to determine the structure most suitable for age and growth assessment. Of these, growth patterns were most visible in sectioned sagittal otoliths. Left sagittal otoliths were lightly burned over an open spirit flame to enhance the annuli. Care was taken not to char the otolith as this obscured the growth patterns particularly on the margin of the otolith. The otoliths were mounted in resin, sectioned through the nucleus to 0,5 mm and mounted on a glass slide with DPX mountant. Otoliths were examined under transmitted light using a low power dissecting microscope. Alternating opaque and hyaline zones were easily visible (Figure 2), and were counted by each author up to five times. If less than three readings coincided the otolith was rejected. The percentage frequency of occurrence of opaque and hyaline zones on the otolith margin was plotted on a monthly basis to determine the number of growth zones deposited annually. Length-at-age was described using the von Bertalanffy model, fitted using the iterative technique described by Butterworth, Punt, Borchers, Pugh & Hughes (1989) and Punt & Hughes (1989).

A gonado-somatic index was calculated by relating gonad mass to eviscerated body mass, expressed as a percentage. Size at sexual maturity was determined by recording the proportion of reproductively active fish (developing, ripe, ripe-running and partially spawned), during the breeding season. Adult sex ratio was determined using fish larger than the length at 50% maturity.

Stomach contents were washed into a 0,2-mm mesh sieve before sorting. The high bulk and fragmented nature of most of the dietary items made it necessary to sub-sample the contents for further analysis (Chan & Chau 1979), using a modified Folsom splitter (James & Worner 1978). Contents were analysed in terms of frequency of occurrence and wet mass, and ranked by multiplying the frequency of occurrence by the mean percentage volume. In small fish gravimetric determination of bulk contribution was not suitable for analysing stomach contents because of the small stomach capacities. Consequently, a subjective visual estimate of volumetric contribution was used to calculate the ranking index.

Macroscopically, the algal component of the diet appeared undigested throughout the alimentary tract, evidenced by the ability to easily identify macrophytes in rectal samples. For this reason a number of techniques were used to assess the importance of algae to the diet of *P. grande*. The presence of microbial gut endosymbionts, and consequently the potential to degrade complex algal polysaccharides, was investigated by high power microscopic examination of the gut lining as well as the intestinal contents (Fishelson, Montgomery & Myrberg 1985). The mucous coating on the algae was examined in fresh and ingested material using freeze microtomy and lastly the epibiont populations on the algae were examined using SEM. Samples of *Plocamium corallorhiza* taken from the reef were compared to samples taken from the oesophagus, stomach and hindgut of *P. grande*. They were fixed in a 2,5% solution of gluteraldehyde in a phosphate buffer, rinsed in phosphate buffer, air dried and coated with gold before viewing under SEM.

Qualitative information on the distribution and abundance of *P. grande* was obtained by SCUBA diving in the inshore waters (< 38 m depth) of the Port Elizabeth and the Tsitsikamma National Park areas.

Results

Age and growth

Morphometric relationships are summarized in Table 1. Linear measurements of the otolith were power functions of fish length, reflecting a decreasing increment in the width and length of the otolith with size. In contrast, otolith mass was proportional to fish length, reflecting an increase in the relative thickness of the otolith with age. The thickening was due to a stacking of growth zones (*sensu* Blacker 1974), making the estimation of age from whole otoliths difficult in the larger fish (see Figure 2). There was also an apparent anomaly in the optical properties of whole and sectioned otoliths. In whole otoliths the wide growth zones were opaque, whereas in sectioned otoliths they were translucent.

Table 1a Relationships between length and mass in *Pachymetopon grande*, sampled between Knysna and East London from August 1984 to March 1987

Equation	r^2	n
TL (mm) = $1{,}140417^{0{,}997}$ FL (mm)	0,999	622
SL (mm) = $0{,}7985^{1{,}016}$ FL (mm)	0,998	622
Mass(g) = $0{,}000022^{3{,}046}$ FL (mm)	0,987	622
Ev. Mass (g) = $0{,}000022^{3{,}007}$ FL (mm)	0,991	622

Ev.Mass = Eviscerated mass

Table 1b Relationships between otolith measurements (length, width and mass) and fork length in *Pachymetopon grande*, sampled between the Tsitsikamma National Park and Bird Island from August 1984 to September 1986

Equation	r^2	n
FL (mm) = $11{,}092^{1{,}455}$ OL (mm)	0,964	200
FL (mm) = $16{,}92779^{1{,}722}$ OW (mm)	0,924	231
OM (g) = $0{,}008e^{0{,}007}$ FL (mm)	0,942	200

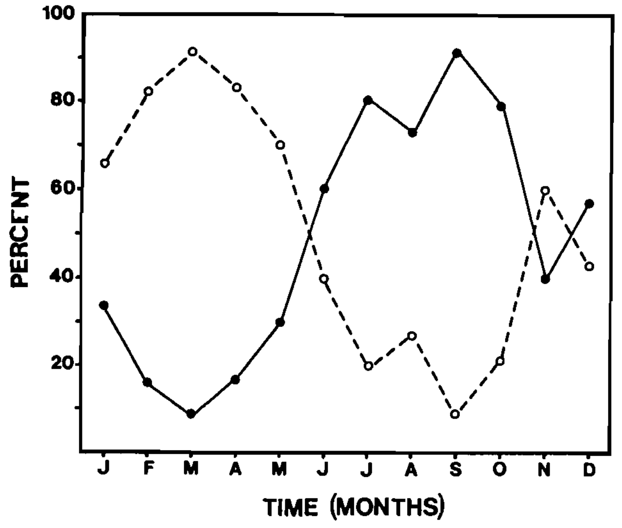

Figure 3 Temporal changes in the composition of the margin in *Pachymetopon grande* otoliths sampled between the Tsitsikamma and Bird Island from August 1984 to September 1986. Opaque and hyaline margins are represented by solid and dashed lines respectively. (n = 350).

Buxton & Clarke (1989) reviewed this problem, stating that care should be exercised in the interpretation of the relative growth rate of opaque and hyaline zones in the otolith.

A total of 423 otoliths were read of which 73 (17%) were rejected. The frequency of opaque and hyaline zones on the otolith margin, showed that one opaque and one hyaline zone were deposited each year (Figure 3). The opaque zone, deposited between June and November was considered as the annulus.

Mean length-at-age data is given in Table 2. A test of the randomness and homoscedasticity of the residuals (difference between the data and the fitted curve) (Draper & Smith 1966), showed that the absolute error model was the most appropriate fit to the data. Von Bertalanffy parameter estimates for males, females and both sexes combined are summarized in Table 3. Attempts to fit the von Bertalanffy model to the full data set (350 points) failed. Successive removal of age classes showed that while the relative error model would fit the data after removal of the 0-year-olds, it placed considerable emphasis on the lower aged fish and on the associated larger errors for older aged fish. Consequently L_∞ was low (see Table 3). Omitting both 0- and 1-year-old

Table 2 Observed and expected length-at-age for male, female and all *Pachymetopon grande* sampled between the Tsitsikamma and Bird Island between August 1964 and September 1987. (Obs — observed mean length ± standard error, Exp — length predicted from the von Bertalanffy model, (n) — number of data points)

Age class	Males			Females			All data		
(years)	Obs.	(n)	Exp.	Obs.	(n)	Exp.	Obs.	(n)	Exp.
0	–		206	–		155	95,8 ± 2,0	(12)	102
1	–		231	–		190	137,8 ± 1,8	(12)	153
2	–		254	–		222	182,6 ± 3,8	(21)	197
3	–		274	233,7 ± 8,3	(6)	250	231,5 ± 5,2	(27)	234
4	291,0 ± 11,3	(6)	293	275,5 ± 7,9	(6)	275	283,8 ± 6,3	(18)	266
5	314,7 ± 7,2	(9)	311	313,9 ± 7,5	(18)	298	310,0 ± 13,4	(30)	294
6	328,5 ± 5,0	(13)	326	307,4 ± 4,3	(16)	318	319,0 ± 3,6	(37)	318
7	334,0 ± 5,4	(16)	341	338,0 ± 4,6	(22)	336	337,3 ± 3,5	(42)	338
8	358,0 ± 5,5	(20)	354	354,4 ± 5,5	(19)	351	355,8 ± 3,7	(41)	355
9	353,7 ± 6,4	(9)	366	369,4 ± 4,6	(30)	366	365,0 ± 4,0	(40)	370
10	383,3 ± 13,5	(10)	377	372,5 ± 5,0	(15)	379	376,0 ± 6,3	(27)	383
11	360,4 ± 8,6	(5)	387	354,7 ± 5,2	(3)	390	358,3 ± 5,5	(8)	394
12	421,0 ± 11,0	(2)	396	–		400	419,7 ± 6,5	(3)	404
13	–		405	417,0	(1)	409	417,0	(1)	412
14	448,0	(1)	412	–		417	448,0	(1)	419
15	434,0 ± 15,0	(2)	419	–		425	434,0 ± 14,0	(2)	425
16	436,5 ± 14,4	(4)	425	–		431	436,5 ± 14,4	(4)	430
17	452,3 ± 9,0	(3)	431	492,0	(1)	438	450,8 ± 14,6	(5)	434
18	449,0	(1)	437	410,0	(1)	442	429,5 ± 19,5	(2)	438
19	–		441	473,0	(1)	446	473,0	(1)	441
20	–		446	438,0	(1)	451	438,0	(1)	444
21	437,0	(1)	450	–		454	437,0	(1)	447
22	–		453	442,5 ± 12,5	(2)	457	440,0 ± 7,6	(3)	448
23	–		457	441,0	(1)	460	464,0 ± 23,0	(2)	450
24	455,0	(1)	460	460,5 ± 11,5	(2)	463	458,7 ± 7,0	(3)	452
25	–		462	505,0	(1)	465	505,0	(1)	453
26	–		465	–		467	479,0	(1)	455
28	432,0	(1)	470	–		470	432,0	(1)	456
38	–		483	486,0	(1)	480	486,0	(1)	460

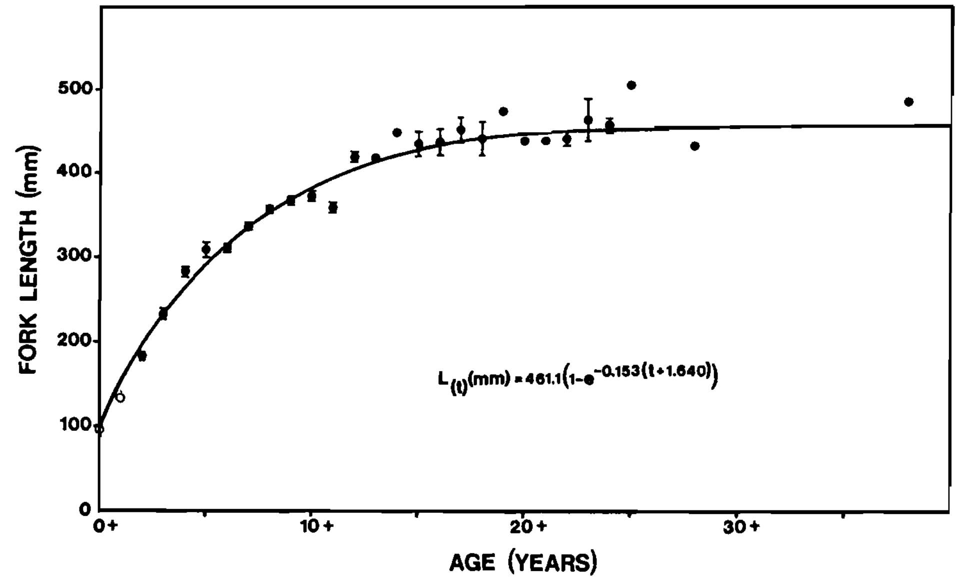

Figure 4 Mean length-at-age in *Pachymetopon grande* sampled between Tsitsikamma and Bird Island from August 1984 to September 1986. Ages 0+ and 1+ were excluded during the fitting of the von Bertalanffy model to the data. T-bars indicate standard errors.

Table 3 Von Bertalanffy parameter estimates of length-at-age data for males, females and all data, and after succesive removal of the early age classes

Data	Model	L_∞	K	t_0	n
Males	Absolute error	492,2	0,091	–5,96	102
Females	Absolute error	484,2	0,114	–3,38	148
Males + Females	Absolute error	484,3	0,108	–4,06	250
Total data set	No appropriate fit				
Total less 0+	Relative error	445,9	0,173	–1,108	338
Total less 0+ & 1+	Absolute error	461,1	0,153	–1,640	326

fish provided a good fit using the absolute error model (see Table 3). These results indicated that the growth rate of very young fish was substantially different to that of older fish, and should therefore be modelled separately. Mean length-at-age for males, females and both sexes combined is shown in Figure 4. No significant difference was found between the mean length-at-age of males and females (t test, $p < 0,05$), except for age 6 ($t = 3,26$; $df = 27$), and for this reason the sexes were combined in further analyses.

The relative growth rate was initially quite fast, tapering off after approximately 10 years with a maximum recorded age of 38 years.

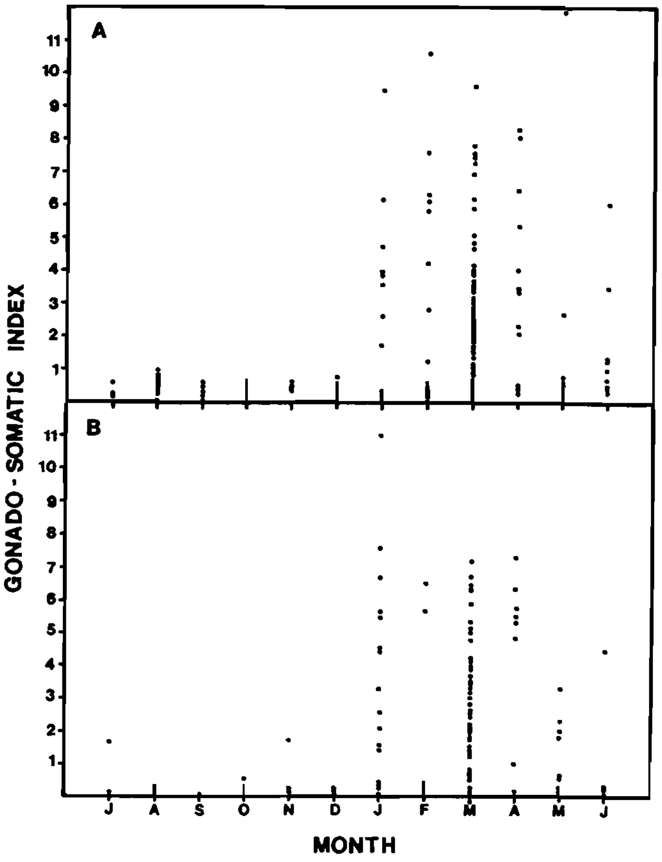

Figure 5 Seasonal variation in individual gonado-somatic indices for 209 female (a) and 268 male (b) *Pachymetopon grande*, sampled between Knysna and East London from August 1984 to March 1987.

Reproduction

Seasonal variation in individual gonado-somatic indices indicated that reproductive activity extended from January to June (Figure 5). During this period ripe-running fish were only sampled between January and April. The frequency distribution of the sexes in the sample is shown in Figure 6. Adult male to female sex ratio was 1 : 1,16, not significantly different from unity ($\chi^2 = 3,04$; $p < 0,05$). The proportion of mature fish in the different size classes is shown in Figure 7. The size at 50% maturity, which is commonly used to determine the minimum size at which fish should be exploited in a linefishery, was estimated at approximately 300 mm FL, equal to a 5,5-year-old fish.

In *P. grande* the gonads were suspended by the dorsal mesentery in the posterior region of the visceral cavity. Both gonads were equally developed although occasionally either one was reduced. Intersexual gonads were recognized macroscopically in the smaller size classes and histological examination showed that the ovarian and testicular parts were spatially separated by connective tissue (Figure 8c). Posteriorly, the tunica albuginea of the ovarian elements

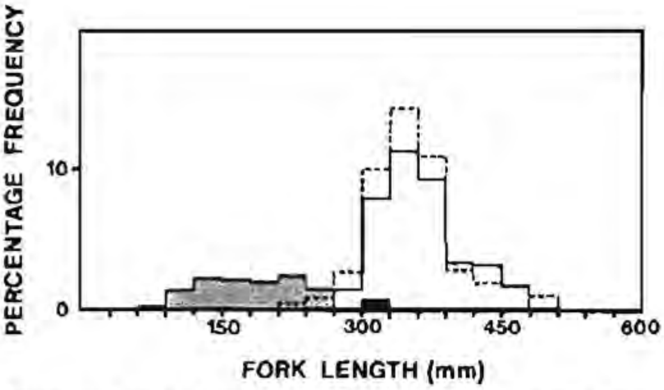

Figure 6 Length frequency distributions of male (solid line), female (dashed line), juvenile (shaded) and intersexual (solid) *Pachymetopon grande* sampled between Knysna and East London from August 1984 and March 1987 (n = 656).

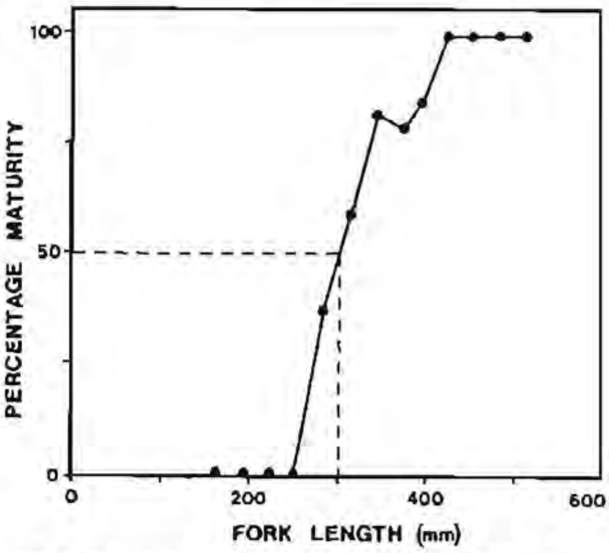

Figure 7 Percentage frequency of mature individuals in different length classes of *Pachymetopon grande*, sampled between Knysna and East London from August 1984 to March 1987.

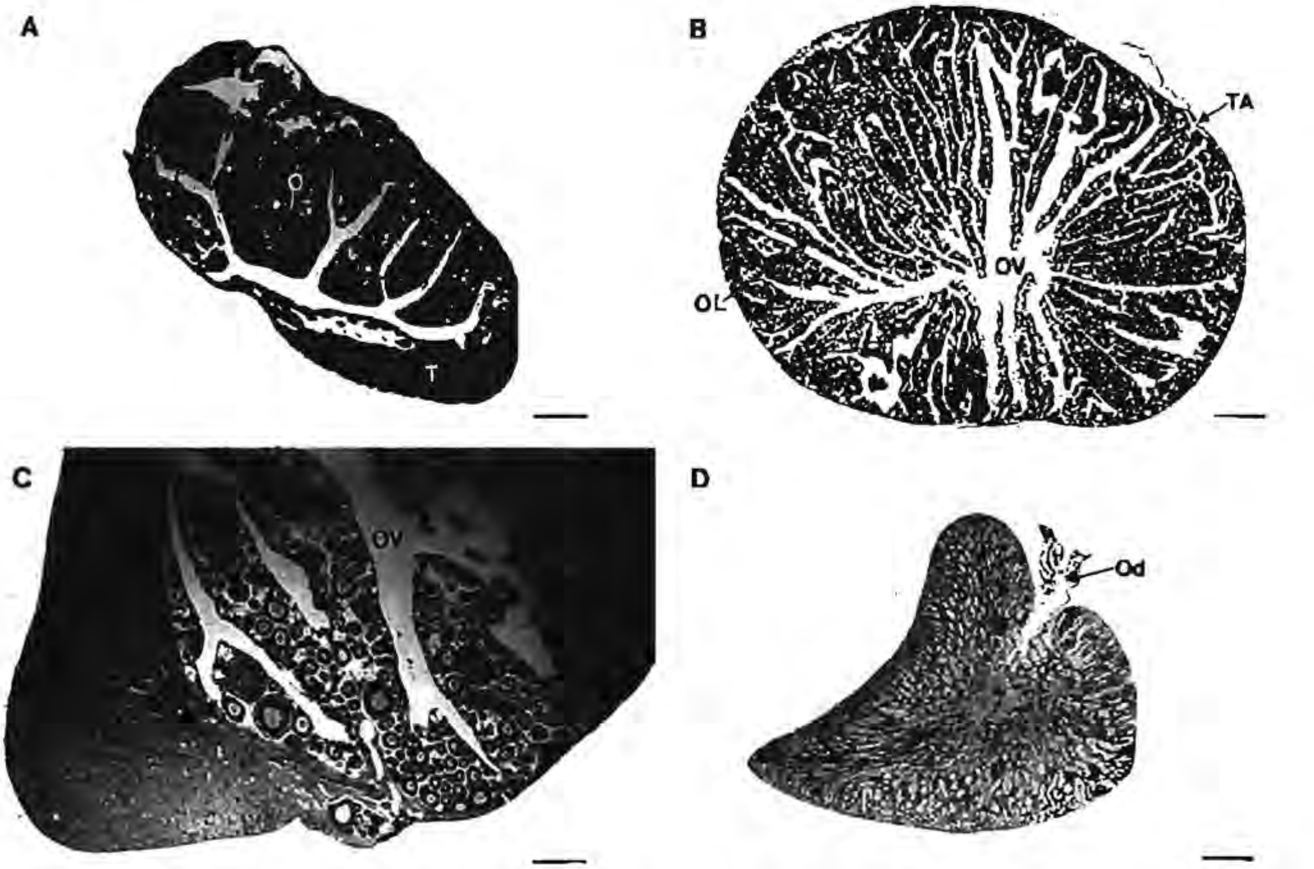

Figure 8 Transverse sections through the gonads of *Pachymetopon grande* illustrating ovarian and testicular development. (a) The ovotestis of a juvenile fish (FL = 288 mm), showing the testis (T) and the ovary (O) separated by connective tissue. Scale bar 0,25 mm. (b) The ovary of a functional female showing the ovigerous lamellae (OL) protruding into the ovocoel (OV). Oocytes are in the pre-vitellogenic stages of development. TA — tunica albuginea. Scale bar = 1,0 mm. (c) The ovotestis of a developing male (FL = 269 mm) showing the simultaneous increase in the size of the testis and the degeneration of the ovary. Note that spermatogenesis is evident in the testis and that the oocytes had reached the cortical alveolar stage of development prior to the onset of atresia. Scale bar = 0,25 mm. (d) The testis of a functional male in which the lobules are filled with sperm. The previous intersexual history is evident from the oocytes surrounding the rudimentary oviduct (Od). Scale bar = 1,0 mm.

fused to form a common oviduct and sperm ducts were located in the connective tissue surrounding the oviduct, a pattern typical of the Sparidae (Atz 1964). Histological examination showed that the early ontogeny of the immature gonad was dominated by ovarian tissue, testicular elements being present only as a small ridge of spermatogonia on the ventral surface of the ovary. Continued development of the ovarian tissue resulted in a functional female. Alternatively, the testicular element increased in size and enveloped the ovary and, after ovarian atresia, the previous immature intersexual stage was only evident from a few isolated pre-vitellogenic oocytes surrounding a rudimentary oviduct in the adult testis. In some cases oocyte development in the intersexual fish had progressed as far as the cortical alveolar stage before oogonial atresia and testicular maturation took place.

Gametogenesis in *P. grande* was similar to that of other sparids (Coetzee 1983; Buxton 1990), and is typical of the pattern found in most teleosts (Figure 9). Unfertilized eggs from a ripe-running female sampled in the Tsitsikamma area were 0,85 mm in diameter, and had a single large lipid droplet approximately 0,08 mm in diameter. These eggs were also neutrally buoyant in seawater. As in many other sparids, sperm was present in the testis throughout the year, but spermatogenesis peaked during the breeding season.

Feeding

Stomach content analysis showed that adult *P. grande* were omnivorous browsers, feeding on a variety of reef organisms found in shallow water (Table 4). Algae were the dominant dietary category, being present in all the stomachs examined and comprising 62% in terms of bulk. Twenty species of algae were recorded, of which the majority (68%) were fleshy rhodophytes. Red algae of the genus *Plocamium* were most important, comprising 71% of the macroalgal component. Six species of coralline algae (*Cheilosporum sagittatum*, *Arthrocardia corymbosa*, *Amphiroa bowerbankii*, *Amphiroa ephedraea*, *Arthrocardia* sp. and *Corallina* sp.) were recorded, but these were of minor importance, accounting for only 1,07% of the total mass of macroalgae. One species of brown algae (*Dictyota liturata*) was frequently

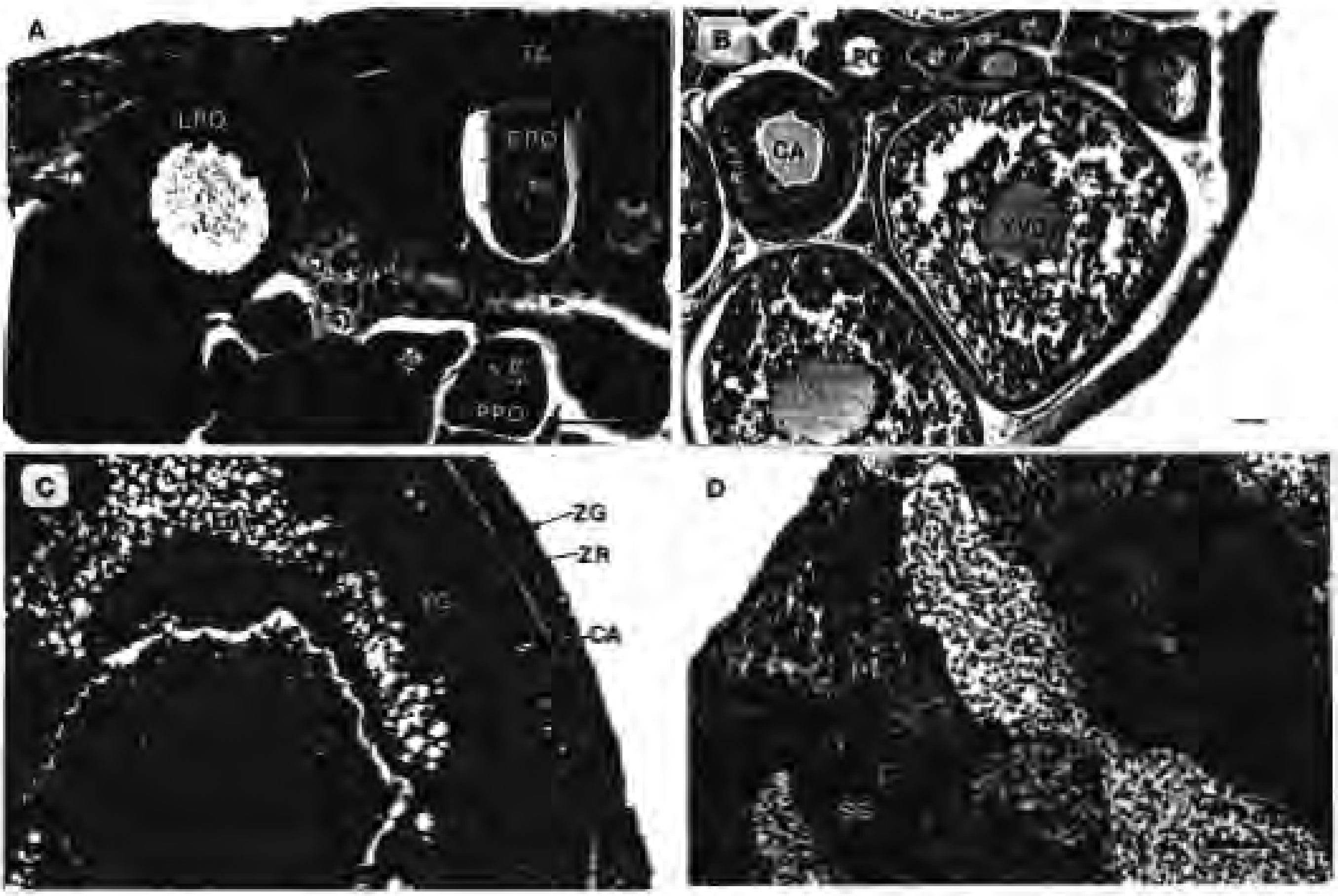

Figure 9 Photomicrographs illustrating gametogenesis in *Pachymetopon grande*. (a) Pre-vitellogenic oocytes in various stages of development including oogonia (ON)) pre-perinuclear (PPO), early-perinuclear (EPO) and late-perinuclear (LPO) oocytes. TA — tunica albuginea. Scale bar = 50 µm. (b) Vitellogenic stages of development include the cortical alveolar stage (CA) which marks the onset of vitellogenesis and yolk vesicle oocytes (YVO) in which yolk platelets fill the cytoplasm. Scale bar = 150 µm. (c) Higher magnification of an oocyte showing the accumulation of yolk in the cytoplasm (YG), cortical alveoli (CA) in the peripheral regions of the cell and the accumulation of lipid droplets (LD) around the nucleus. LC — lampbrush chromosomes, ZR — zona radiata and ZG — follicular layer. Scale bar = 50 µm. (d) Section through the testis showing the various stages of spermatogenesis including spermatogonia (SG), spermatids (ST) and a lobule filled with sperm (S). Scale bar = 50 µm.

Table 4 Stomach content analysis of adult *Pachymetopon grande,* larger than 330 mm fork length, sampled between Knysna and Port Elizabeth from January 1985 to March 1987 (n = 46, T(trace) = < 0,01%)

Species	% Frequency occurrence	Mean % mass	Rank
Algae	**100,00**	**62,56**	**6256,00**
Plocamium corallorhiza	43,48	21,49	
Plocamium suhrii	65,22	21,42	
Champia compressa	47,83	3,49	
Laurencia flexuosa	17,39	3,49	
Plocamium rigida	43,48	2,06	
Dictyota liturata	30,43	0,84	
Arthrocardia spp.	13,04	0,40	
Hypnea rosea	10,87	0,38	
Chondrococcus spp.	28,26	0,24	
Calliblepharis fimbriata	4,35	0,21	
Cheilosporum sagittatum	6,52	0,10	
Gelideum cartilagineum	4,35	0,10	
Gelideum pristoides	2,17	0,10	
Arthrocardia conpulosa	2,17	0,10	
Amphiroa bowerbankii	4,35	0,06	
Ceramium spp.	8,70	0,03	
Acrosorium spp.	2,17	0,01	
Amphiroa ephedraea	2,17	0,01	
Laurencia natalensis	2,17	0,01	
Corallina spp.	2,17	T	
Unidentified remains	54,35	8,02	
Hydrozoa	**78,26**	**13,76**	**1076,86**
Lytocarpus filamentosus	34,78	3,40	
Sertulariidae	19,57	3,03	
Thecocarpus formosus	28,26	0,48	
Lafoeidae	15,22	0,44	
Plumulariidae	26,09	0,35	
Thyroscyphus spp.	10,87	0,34	
Halopterinae	4,35	0,06	
Solanderiidae	2,17	0,06	
Plumulariinae	4,35	0,05	
Aglaophenia pluma	13,04	0,03	
Sertularella goliathus	4,35	0,02	
Pycnotheca spp.	4,35	0,01	
Thecocarpus flexuosus	2,17	0,01	
Unidentified remains	73,91	5,48	
Octocorallia	**52,17**	**14,05**	**732,99**
Eunicella papillosa	26,09	5,09	
Xenia spp.	23,91	4,35	
Lophogorgia flammea	10,87	1,48	
Homophyton spp.	2,17	0,32	
Unidentified Octocorallia	36,96	2,81	
Colonial Ascidiacea	**34,78**	**3,79**	**131,82**
Polyclinum spp.	6,52	1,14	
Didemnidae	2,17	T	
Unidentified remains	28,26	2,65	
Crustacea	**78,26**	**0,99**	**77,48**
Amphipoda	52,17	0,32	
Caprellidea	65,22	0,44	
Tanaidacea	6,52	0,13	
Isopoda	15,22	0,05	
Unidentified remains	2,17	0,05	
Mollusca	**28,26**	**0,26**	**7,35**
Gastropoda	21,74	0,21	
Pelecypoda	15,22	0,05	
Shell fragments	2,17	T	
Unidentified remains	2,17	T	
Porifera	**6,52**	**2,02**	**13,17**
Bryozoa	**17,39**	**0,34**	**5,91**
Polychaeta	**8,70**	**0,05**	**0,44**
Ophiuroidea	**2,17**	**T**	**T**
Unidentified	**28,26**	**0,05**	**1,41**
Amorphous	**10,87**	**0,18**	**1,96**

present in the stomach contents (30,43%) but was unimportant in terms of percentage mass contributions (0,84%). Numerous invertebrates were also consumed, of which hydroids, octocorals, colonial ascidians and small crustaceans were most important. Many of the smaller mobile prey items were probably ingested incidentally by fish browsing on attached macroalgae, hydrozoans and octocorals.

Although sample sizes were low, some indication of the variability in diet with area is presented in Figure 10. Algae were clearly the most important dietary item in all areas sampled, but the proportion of other prey items appeared to reflect the area in which the fish were sampled. Off Port Elizabeth, in the area around Cape Recife, sample sites were in shallow water (< 15 m) where the reef was dominated by algae, relief was low and few filter-feeding organisms were visible. By comparison, the two sites in the Tsitsikamma National Park were characterized by high relief and an abundance of filter-feeding organisms. However, the Knoll was generally a shallower site than Rheeders, thus macroalgae were more abundant (Buxton & Smale 1984). In Knysna, samples were obtained from recreational spearfishermen operating in water down to approximately 25 m.

Separate analyses of the stomach contents of juvenile and adult fish sampled in shallow water (< 15 m) off Port Elizabeth are shown in Table 5. The diet was similar in both size classes, macroalgae being the most important dietary category, of which rhodophytes were predominant. Other prey consumed included hydrozoans, crustaceans and octocorals. Although only a minor component, crustaceans were more important in the diet of juveniles than in adults, suggesting some feeding selectivity on the part of juveniles.

Microscopic examination of the gut lining and the intestinal contents did not reveal microbial populations. This, and the low level of macroalgal digestion, indicated that gut endosymbionts were not involved in primary or secondary digestion of macrophytes, or in the supply of micronutrients to *P. grande* (*cf.* Fishelson *et al.* 1985). Thin sections of fresh *Plocamium corallorhiza* showed that the mucous layer coating the weed was very thin and unlikely to play a significant role in the diet of the fish. Finally, SEM examination of algal samples taken from the reef and from the alimentary tract revealed low numbers of epibionts on both fresh and ingested material. No trends, either in number or state of digestion of epibionts, were observed in the samples taken from the different regions of the alimentary tract (Figure 11). Epibionts in significant numbers were only found in places where the weed appeared to have been damaged (Figure 11c).

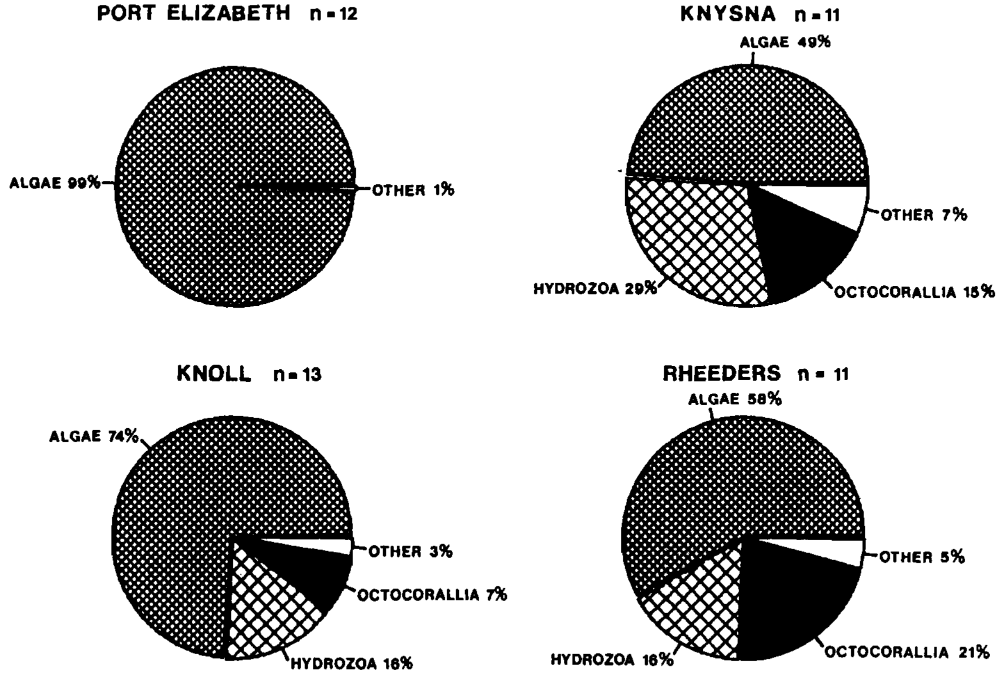

Figure 10 A comparison of the diet of adult *Pachymetopon grande* (> 330 mm FL) sampled from four different localities on the East Cape coast between February 1985 and March 1987. Prey are represented in terms of their percentage ranked importance.

Table 5 Stomach content analysis of 12 adult (> 330 mm FL) and 11 juvenile (88–232 mm FL), *Pachymetopon grande* sampled off Port Elizabeth between February 1985 and May 1986. (T(trace) = < 0,01%)

	% Frequency of occurrence		Mean % volume		Rank	
Species	Adult	Juv.	Adult	Juv.	Adult	Juv.
Algae	**100,0**	**100,0**	**94,1**	**86,8**	**9410,0**	**8681,0**
Plocamium corallorhiza	100,0	100,0	66,7	49,9		
Champia compressa	95,0	36,4	11,8	6,2		
Laurencia flexuosa	25,0	–	8,0	–		
Hypnea rosea	16,7	–	1,4	–		
Plocamium rigida	50,0	–	1,2	–		
Gelidium cartilagineum	8,3	–	0,1	–		
Plocamium suhrii	16,7	9,1	0,03	0,02		
Laurencia natalensis	8,3	–	0,03	–		
Dictyota liturata	8,3	–	0,03	–		
Amphiroa bowerbankii	8,3	–	T	–		
Ceramium spp.	8,3	72,7	T	22,2		
Chondrococcus spp.	–	18,2	–	2,8		
Unidentified remains	75,0	72,7	4,8	5,8		
Colonial Ascidiacea	**16,7**	**–**	**3,8**	**–**	**63,0**	**–**
Hydrozoa	**41,7**	**81,8**	**0,1**	**9,3**	**3,8**	**760,8**
Pycnotheca spp.	8,3	–	0,01	–		
Octocorallia	**8,3**	**27,3**	**0,4**	**1,3**	**3,4**	**36,3**
Crustacea	**25,0**	**100,0**	**0,01**	**2,4**	**0,3**	**239,0**
Isopoda	8,3	45,5	0,01	0,3		
Amphipoda	16,7	100,0	T	1,2		
Caprellidea	8,3	54,6	T	0,5		
Mysidacea	–	18,2	–	0,1		
Copepoda	–	9,1	–	0,1		
Crustacean remains	–	27,3	–	0,3		
Pycnogonida	**–**	**9,1**	**–**	**0,1**	**–**	**0,8**
Gastropoda	**–**	**9,1**	**–**	**0,1**	**–**	**0,1**
Unidentified	**75,0**	**18,2**	**0,1**	**0,1**	**6,0**	**2,0**
Amorphous	**8,3**	**9,1**	**0,5**	**0,3**	**4,1**	**2,5**

Distribution

SCUBA observations revealed that juvenile *P. grande* were common over shallow subtidal reefs (< 10 m) that were covered in seaweeds such as the rhodophyte *Plocamium corallorhiza*. Adult and subadult fish were also common in shallow water, often occurring in large shoals around high profile reefs (see also Buxton & Smale 1984). They were only occasionally observed in water deeper than 20 m.

Discussion

As with other members of the Sparidae (Buxton & Clarke 1989), *P. grande* was found to be a long-lived species. Growth in length was slow (K = 0,153), reaching an asymptote at approximately 15 years old. Beyond this age, growth in length was insignificant although the fish were capable of attaining ages in excess of 30 years. The theoretical maximum length ($L\infty$ = 461 mm) was less than the observed maximum in the study (532 mm FL) and the known maximum length (572 mm, S.Afr. record, JLB Smith Institute of Ichthyology, Grahamstown, pers. comm.). The otoliths of large fish were very difficult to read because the annuli were very close together, but a single positively aged fish of 38 years, together with the above, suggest that *P. grande* may reach ages in excess of 40 years old. Such longevity has important implications for management and conservation of the species, which are discussed below.

Maturation of either the testis or the ovary followed an intersexual sub-adult phase in which non-functional elements of both sexes were present. In some individuals, pre-vitelline oocytes were present in the rudimentary ovary at the same time as spermatogenesis in the testis, but no evidence of functional hermaphroditism was found. Gonadal ontogeny was similar to that described by Coetzee (1986) for *Dilpodus sargus capensis*. He suggested that active

Figure 11 Scanning electron micrographs of *Plocamium corallorhiza* sampled from the stomach (a) and hindgut (b) of *Pachymetopon grande*, showing the low number of epibionts on the weed in both areas of the gut. Fresh weed was similar in appearance to these (c), and significant numbers of epibionts were only found in places where the weed appeared to be damaged.

spermatogenesis in the ovotestis of *D. s. capensis* was evidence of a special type of protandric development, in which the individual still had the capacity to develop into either sex. However, to be consistent with the definition of protandry, such an interpretation is dependent on the demonstration that the individual had a functional male history prior to becoming a female. The observation that sperm maturation occurs at a smaller size than egg maturation, did not necessarily indicate protandry, special case or otherwise. For this reason we believe that *P. grande* is a rudimentary hermaphrodite or late gonochorist (*sensu* Buxton & Garratt 1990).

As with other rudimentary hermaphrodites that have been studied (Coetzee 1983; Garratt 1985; Smale 1988; Buxton & Clarke 1991), the gonado-somatic index was found to be equitable in both sexes and, relative to sex-changing species (Buxton 1990), the testis was large. The correlation between the size of the testis and spawning behaviour is often stated (Choat & Robertson 1975), a large testis being favoured under conditions of intense sperm competition in a group-spawning situation. Other correlates of group spawning include monomorphism between the sexes and an equal sex ratio in adults, both of which are characteristic of *P. grande*. According to Warner (1984), under such conditions the potential for sex change is reduced and suggests that spawning may be either in pairs matched by size or in groups where males compete.

Unlike other sparid examples in the literature, peak reproductive activity in *P. grande* did not coincide with peak summer water temperatures and maximum photoperiod (Garratt 1985; Coetzee 1986; Buxton 1990). Instead peak spawning lagged behind temperature and photoperiod, occurring between late summer and early winter. The reason for this difference is not apparent, but could relate to the herbivorous diet of these fish (all other sparids examined so far being carnivorous). For example, the breeding season may be timed to ensure that the settlement of juveniles on subtidal reefs coincides with the annual macroalgal cycle. Although macroalgal productivity cycles are less marked in subtidal waters, biomass estimates are lowest in April in the Port Elizabeth area (W. du Preez, University of Port Elizabeth, pers. comm.).

Macroalgae were the principal dietary component in both juvenile and adult *P. grande*, yet they did not masticate their food, were not feeding on epibionts and did not seem to harbour a microbial population capable of degrading the cellulose component of seaweeds. Although not tested for *P. grande*, cellulose activity appears to be uncommon in herbivorous fish (Gerking 1984). The results suggested that *P. grande* were capable of digesting major fractions of algal nutrients without the mechanical destruction of algal cells (*cf.* Conacher, Lanzing & Larkin 1979; Montgomery & Gerking 1980; Gerking 1984). In herbivorous marine fish which are not capable of cellulose digestion, either through endogenous enzymes or gut endosymbionts, dietary composition is frequently consistent with predictions based purely on the macroalgal biochemistry (Montgomery & Gerking 1980). Fleshy algae are generally superior to calcareous (coralline) algae as a food resource on the basis of ash, calories, total protein and total lipid content. In addition, on the basis of nutrient and energy content, chlorophytes are superior to phaeophytes and both are superior to rhodophytes. However, when the digestibility of storage and extracellular carbohydrates is taken into account, chlorophytes and rhodophytes may be superior to phaeophytes (Montgomery & Gerking 1980). Edwards & Horn (1982) indicated that rhodophytes may be taken in preference to chlorophytes because the variable composition of extracellular polysaccharides, the acid-labile bonds linking the polysaccharide subunits, and the broad substrate specificity of many glucosidases may combine to make the extracellular carbohydrates of this group more susceptible to digestion than those of the chlorophytes (Montgomery & Gerking 1980; Horn, Murray & Edwards 1982).

The macroalgal composition of the diet of *P. grande* is not inconsistent with the above argument. The absence of chlorophytes, for example, indicated that rhodophytes were preferred algae because both are abundant on the reef, especially in water shallower than 9 m. Selectivity in the diet was also evident from the frequency of other algae in the diet, corallines being of minor importance despite their abundance on the reef. Although largely speculative, the results suggest that bronze bream are selective browsers, feeding principally on fleshy rhodophytes because of their comparatively high nutritive value and readily digestible extracellular carbohydrate component. The invertebrate component of the diet is thought to supply the essential proteins necessary for growth (Montgomery & Gerking 1980). Clearly an investigation of the biochemistry of local algal species, including studies on the role of secondary defensive compounds, is desirable. This, combined with a study of the feeding selectivity and assimilation efficiency of the predators (Gerking 1984), would contribute significantly to the understanding of herbivory in southern African marine reef fishes.

Observations made during this study show that *P. grande* is a temperate marine species, found on relatively shallow reefs down to approximately 20 m. The feeding preferences and reproductive biology are consistent with this interpretation. Despite contradictory statements in the literature it is unlikely that these fish are found in the sub-tropical waters of northern Natal and Madagascar.

In its distributional range the bronze bream is a sought-after angling species, especially in the southern and eastern Cape areas. The conservation status of *P. grande*, like so many reef fishes is dependent on whether one views it in economic or biological terms. While it may be true to say that it is unlikely that a species can be fished to extinction, the sustainability of the resource in both economic and recreational terms is threatened. A number of factors contribute to this view. Like other sparids and temperate reef fishes in general, bronze bream are slow-growing, long-lived species that mature late in life. Because such fishes have a low production–biomass ratio and a low yield per unit stock they are susceptible to growth overfishing and under heavy exploitation are likely to experience considerable depletion in the older age classes (Ricker 1963). Although not threatened by commercial exploitation, recreational angling is becoming increasingly popular in South Africa (van der Elst 1989), hence there is an ever-increasing pressure on the stock. In addition, Clarke & Buxton (1989) showed that peak catches of these fish occur during the breeding season. Lastly, there have been no specific catch regulations such as a minimum size, aimed at protecting these fish. For these reasons it is important that attention be given to establishing specific measures to protect the resource. Such measures should at least include a size limit (350 mm FL, based on age at maturity) and bag limits similar to those for other co-existing threatened reef species. Consideration may also be given to decommercialization of *P. grande* because of their insignificance in commercial catches (*cf.* Buxton & Clarke 1989; 1991), a measure that appears to have been beneficial to *Coracinus capensis*, another inshore recreational angling species (Bennett 1988).

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