# The feeding biology of four predatory reef fishes off the south-eastern Cape coast, South Africa

M.J. Smale
Port Elizabeth Museum, Port Elizabeth

The feeding of three sparid reef fish, *Cheimerius nufar, Petrus rupestris, Polysteganus praeorbitalis* and one serranid, *Epinephelus guaza*, is described. Examination of stomach contents revealed that *C. nufar* takes both demersal and pelagic prey. Although reef fish dominate the diets of small *C. nufar*, larger individuals take pelagic prey frequently. *P. rupestris* takes reef prey almost exclusively and is an important top predator on hard substrata in the south-eastern Cape. *P. praeorbitalis* preys mainly on reef fishes and is found mainly in shallow water in this region. Hunting behaviour for both solitary and grouped prey by these sparids has been recorded from underwater observations in the wild, and in tanks. *E. guaza* is a solitary ambush predator of small fish, crabs and octopods. All four species show clear ontogenetic changes in diet and overlaps in their resource use are discussed.

*S. Afr. J. Zool.* 1986, 21: 111 – 130

Die voeding van drie rifvisse van die Sparidae, naamlik *Cheimerius nufar, Petrus rupestris, Polysteganus praeorbitalis* en een van die Serranidae, *Epinephelus guaza*, word beskryf. Maaginhoudanalises onthul dat *C. nufar* bodembewonende sowel as pelagiese prooi vreet. Alhoewel rifvisse oorheers in die dieet van klein *C. nufar*, neem groter enkelinge dikwels pelagiese prooi. *P. rupestris* neem byna uitsluitend rifprooi en is 'n belangrike boonste roofvis van riwwe in die suidoostelike Kaap. *P. praeorbitalis* jag veral rifvisse en word meestal in vlak water in die streek gevind. Jaggewoontes van hierdie Sparidae vir beide individuele en groeplewende prooi, is opgeteken deur middel van onderwaterwaarnemings in die natuur en in tenks. *E. guaza* is 'n alleenlewende hinderlaag-roofvis van kleiner visse, krappe en agtpotiges. Al vier spesies wys ontogenetiese veranderings in hul diëte en die oorvleueling van hul hulpbronbenutting word bespreek.

*S.-Afr. Tydskr. Dierk.* 1986, 21: 111 – 130

**M.J. Smale**
Port Elizabeth Museum, P.O. Box 13147, Humewood,
6013 Republic of South Africa

Received 5 July 1985; accepted 30 October 1985

Trophic relationships and behaviour of tropical reef fishes have been studied extensively (Starck & Davis 1966; Randall 1967; Starck 1970; Harmelin-Vivien & Bouchon 1976; Harmelin-Vivien 1981). The feeding relationships of South African reef fishes are less well known, although recent studies have provided information on several species (Nepgen 1977; Joubert & Hanekom 1980; Coetzee & Baird 1981a; Nepgen 1982; Buxton 1984). Detailed studies of co-existing temperate reef predators have not previously been attempted because of the difficulty of identifying well-digested prey, which results in a large proportion of the prey being grouped as unidentified fishes. Consequently, the few prey identified need not necessarily be the most dominant food items. In the present study it was possible to identify the majority of prey from digestion-resistant parts (fish otoliths and cephalopod beaks) which were then measured and related to prey size.

The feeding biology of the following three sparid, and one serranid reef fish is described in this paper: *Cheimerius nufar* (santer), which is widely distributed along the east coast of Africa, in the northern Indian Ocean and parts of the north-eastern Pacific Ocean; *Petrus rupestris* (red steenbras), which is endemic to the south and east coast of South Africa between Durban and the Agulhas Bank; *Polysteganus praeorbitalis* (scotsman), which is endemic between Mozambique and Algoa Bay, and *Epinephelus guaza* (yellowbelly rockcod), which is found in the Mediterranean, the north-west coast of Africa, north-east coast of South America, South West Africa, and on the west, south and east coasts of South Africa (Smith 1938; van der Elst 1981).

## Materials and Methods

Initiated in February 1978 and continued to May 1982, this study was run concurrently with an investigation of the biology of the fishes caught by ski-boat anglers in the south-eastern Cape (Figure 1). For logistical reasons most material was collected from Algoa Bay and environs on most weekends that fishing was possible. As many ski-boat catches as possible were examined on each sampling day. Sparids were measured using fork length (FL), and total length (TL) was used for the serranid. A subsample of the fish caught was weighed. Stomachs which had not been everted were labelled and kept on ice until they were processed in the laboratory, later that day. The fishing locality, depth and bait used were recorded. Neither formalin nor alcohol was used to preserve stomach contents as otoliths are etched or made brittle, making identification difficult and measurements inaccurate.

Stomachs were opened and the contents sorted, counted, drained and weighed to the nearest 0,1 g. Bait was easily

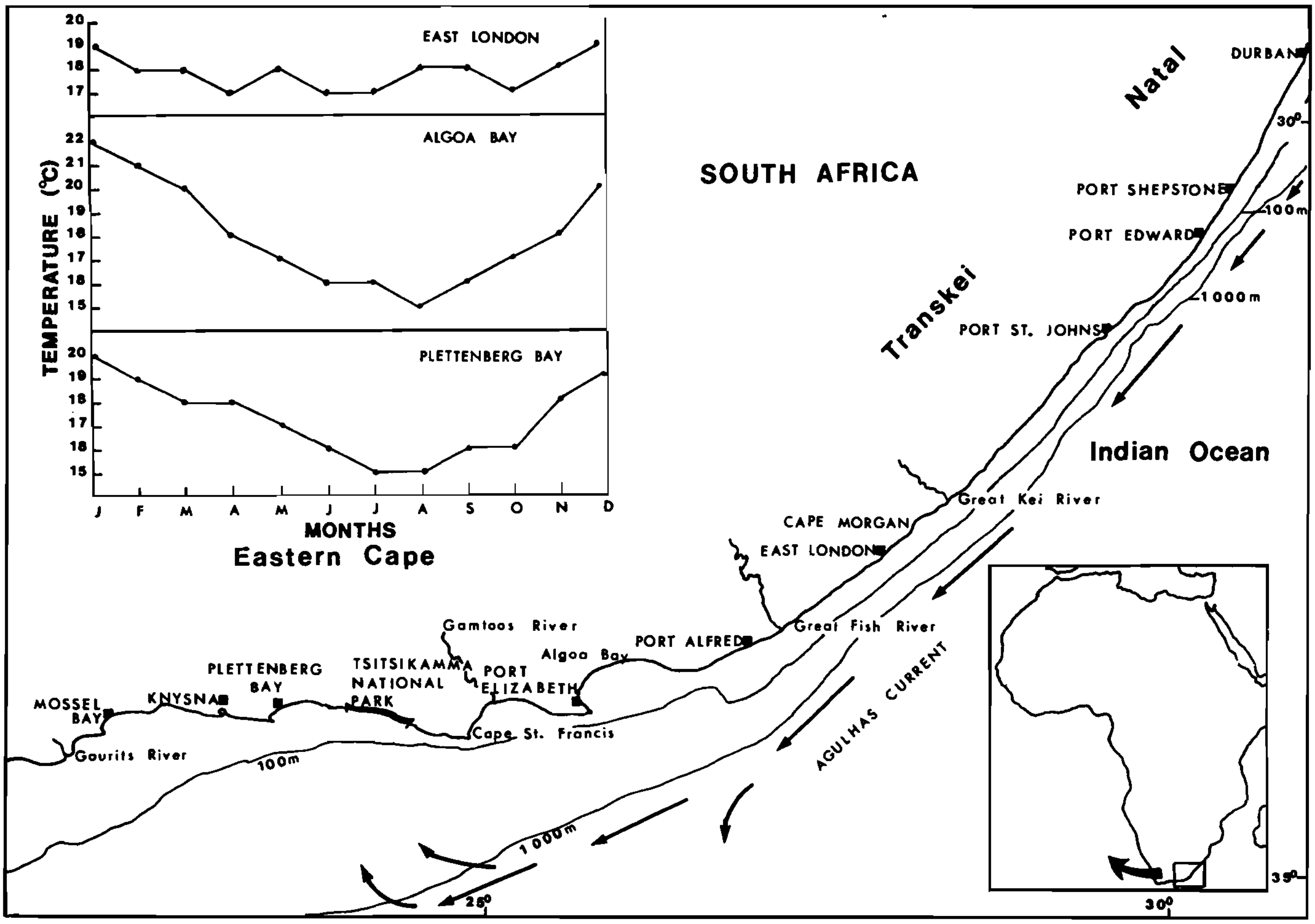

Figure 1 The south-eastern coast of South Africa showing places mentioned in the text.

recognized and discarded. Otoliths were collected from fish skulls, and beaks were removed from the buccal masses of cephalopods. Food remains and stomach walls were rinsed with water and any additional beaks and otoliths found were kept. Otoliths were stored dry in labelled vials; cephalopod beaks and other invertebrates were preserved in 10% formalin.

Otoliths of all fish prey were identified by comparing them with material held in the Port Elizabeth Museum collections. Otoliths were paired when possible and the highest number of either left or right otoliths counted. Measurements of undigested otoliths were to the nearest 0,01 mm. Digested otoliths were obvious because of their chalky eroded appearance and these were not measured. Cephalopod beaks were paired and the highest number of either upper or lower beaks were counted. These were identified by comparison with reference material and descriptions and drawings in the literature (Clarke 1962; Pinkas, Oliphant & Iverson 1971). Beaks were measured according to Clarke (1962) using measuring calipers for those larger than 2 mm and a binocular microscope for smaller specimens. Crustaceans were counted and weighed.

Total length (TL) was used for all fish prey. Dorsal mantle length was used for all cephalopods except *Loligo reynaudi*, for which ventral mantle length was used. Stomach contents were analysed using percentage frequency (%F), percentage number (%N) and percentage wet mass (%M) of prey, which overcomes the disadvantage of using only one of these methods (Hynes 1950; Windell 1968; Hyslop 1980). Combinations of these measures were not used as they may compound sources of error (Hyslop 1980).

Ontogenetic changes in prey taken by each predator were investigated by separating the material into arbitrary size groupings after a preliminary examination of the stomach data. The number of groups used depended on the sample size and length range of material. An index of food similarity was calculated for each size group of predator, using the method of Field, Clarke & Warwick (1982).

Stomach fullness was calculated by dividing stomach mass by predator mass and expressing the result as a percentage.

Underwater observations of the behaviour of the predators and prey were made during more than 45 h of SCUBA diving around Algoa Bay and in the Tsitsikamma Coastal National Park from 1978 to 1982. Limited logistical support and unsuitable diving conditions restricted the time available for observations. Additional observations were made on fishes held in the 20-m diameter main fish tank of the Port Elizabeth Oceanarium where more than 15 species of local fishes are held for public viewing. Interactions between predators and prey were noted during 10 h of observation. No special experiments were set up but interactions between *C. nufar* and schools of juvenile (< 100 mm) *Sarpa salpa, Trachurus trachurus* and *Pomadasys olivaceum* were studied.

## Results

### *Cheimerius nufar* (Ehrenberg 1830) — santer

A total of 3235 *C. nufar* were sampled between 1978 and 1982 (Figure 2a). Of these 92,6% had either everted their stomachs during capture, had empty stomachs or had been gutted. Two hundred and forty stomachs contained prey (Figure 2b). Of these, eight were shot by speargun, three were netted during

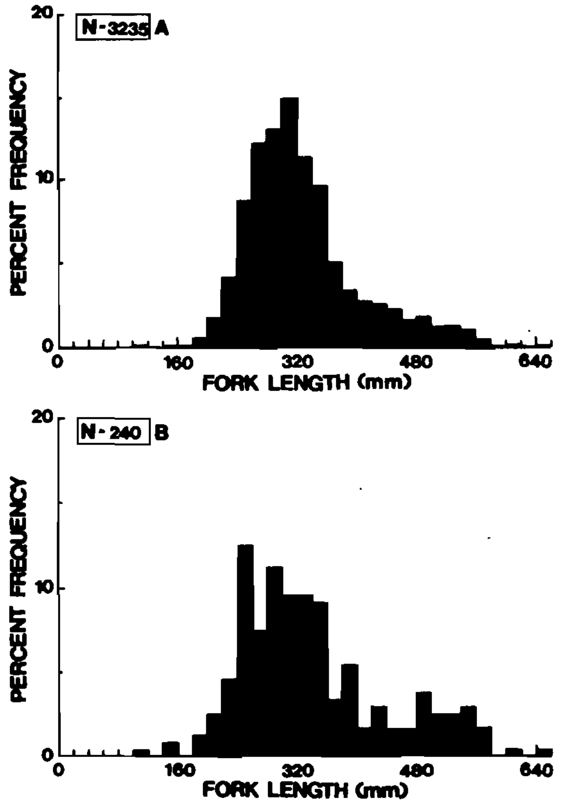

**Figure 2** Histograms of the length frequencies of the entire sample of *Cheimerius nufar* (A) and those with stomach contents (B).

gill-net trials and the rest, 229, were caught by hook and line. The stomach contents were similar, irrespective of fishing method, when predator size was taken into account. The smallest fish collected with stomach contents was 103 mm, the largest 641 mm FL. The highest stomach fullness was 7,9% of body mass.

The prey of *C. nufar* are shown in Table 1, grouped according to predator size. The principal prey (> 4% of any two methods of analysis) are illustrated in Figure 3. The smallest group comprises eight fish between 100 and 200 mm. Invertebrates comprise the bulk of the sample both numerically (97%) and by mass (86%). Crustaceans made up the bulk of the numbers (96%) but only made up 23% by mass. Mysids were the single most important prey group. A single *Octopus vulgaris* made up 63% of the prey mass. Fish prey (3%N, 14%M) were all demersal reef or ubiquitous species.

The 201 – 400 mm group took large numbers of crustaceans (81%N) which constituted 5% of prey mass. Mysids made up 80% of the number but 1% of the mass, whereas cephalopods made up 2% by number and 43% by mass. *Loligo reynaudi* was the single most important species by mass (33%) although numerically minor (1%), and *Octopus vulgaris* was also an important prey (10%M, 0,4%N). Thirty-one fish taxa made up 18% by number and 52% by mass of the prey taken. These included schooling pelagic species (6%N, 13%M) and demersal and benthic fishes (9%N, 31%M). *Engraulis capensis* and the clinids were the two most important taxa by mass.

Large *C. nufar* (401 – 700 mm) took few invertebrates (10%N, 6%M). Crustaceans made up 6% of the number and 1% of prey mass, whereas cephalopods made up 5% by number and 4% by mass. Fish made up the bulk of the prey taken (90%N, 95%M). Pelagic schooling species, (66%N, 81%M) and demersal species (19%N, 13%M) were also found. It is important to note that the majority of stomachs of this size group were obtained in 1978 when *Sardinops ocellata* was particularly abundant in Algoa Bay and consequently the overall importance of *S. ocellata* may be overemphasized.

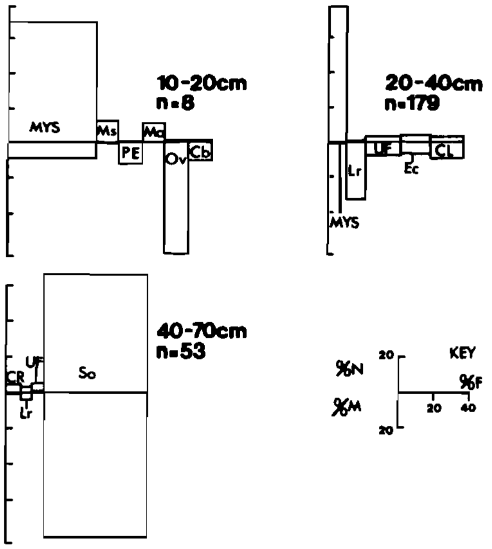

**Figure 3** The principal prey of *Cheimerius nufar*. The size range of each group and the number of stomachs is shown. Cb: *Chirodactylus brachydactylus*, CL: Clinidae, CR: Crustacea, Ec: *Engraulis capensis*, Lr: *Loligo reynaudi*, Ma: *Macropatasma africanum*, Ms: *Mysidopsis* sp., MYS: Mysidacea, Ov: *Octopus vulgaris*, PE: Penaeidae, So: *Sardinops ocellata*, UF: Unidentified fish.

The percentage similarity of the prey taken by these predator size groups is shown in Figure 4 according to prey mass. The low similarities result from different prey species being major components of the diet of each group.

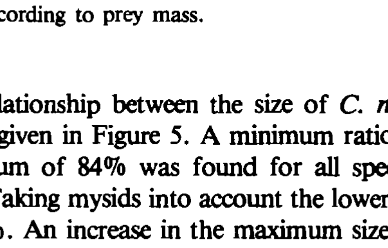

**Figure 4** Similarity dendrogram of diets of *Cheimerius nufar* size groups, according to prey mass.

The relationship between the size of *C. nufar* and prey length is given in Figure 5. A minimum ratio of 6,3% and a maximum of 84% was found for all species, excluding mysids. Taking mysids into account the lower limit drops to about 1%. An increase in the maximum size of prey eaten and the increase in minimum size of prey taken is seen in Figure 5. The increase in maximum prey size taken by predators up to 330 mm is much greater than the increase thereafter.

The histograms in Figure 6 show considerable overlap in the size of prey taken by *C. nufar* smaller or larger than 400 mm, except for *Sardinops ocellata*. The length range of other prey taken by *C. nufar* but not shown in Figure 6 are: *Argyrosomus hololepidotus* (158 – 315 mm); *Pomadasys olivaceum* (54 – 146 mm); clinids (20 – 116 mm); Engraulidae

**Table 1** The prey of *Cheimerius nufar*, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g. The habitat of fish prey is indicated by the letters: (P) pelagic, (S) soft substrata, (R) reef and (U) ubiquitous

| | 100 – 200 mm | | | 201 – 400 mm | | | 401 – 700 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Polychaeta | | | | 0,6 | 0,1 | < 0,1 | | | |
| Crustacea | | | | | | | | | |
| Unidentified crustaceans | | | | 0,6 | 0,1 | < 0,1 | 7,5 | 4,5 | 1,0 |
| Mysidacea | 50,0 | 69,6 | 8,6 | 10,1 | 78,9 | 1,3 | | | |
| *Mesopedopsis slabberi* | | | | 0,6 | 0,8 | < 0,1 | | | |
| *Mysidopsis* sp. | 12,5 | 13,0 | 1,1 | | | | | | |
| Caridea | | | | 0,6 | 0,2 | 0,3 | | | |
| Penaeidea | 12,5 | 0,7 | 12,0 | 1,1 | 0,1 | 0,2 | | | |
| *Macropatasma africanum* | 12,5 | 12,3 | 0,6 | | | | | | |
| Brachyura | 12,5 | 0,7 | 0,9 | 7,8 | 0,8 | 2,3 | 1,9 | 1,1 | 0,2 |
| *Plagusia chabrus* | | | | 2,8 | 0,2 | 1,2 | | | |
| Mollusca | | | | | | | | | |
| Sepiidae | | | | 1,1 | 0,1 | 0,1 | 1,9 | 1,1 | 0,1 |
| Loliginidae | | | | 0,6 | 0,1 | < 0,1 | | | |
| *Loligo reynaudi* | | | | 10,1 | 1,0 | 32,6 | 5,7 | 3,4 | 4,3 |
| Octopoda (Benthic) | | | | 1,1 | 0,1 | 0,4 | | | |
| *Octopus vulgaris* | 12,5 | 0,7 | 62,7 | 3,9 | 0,4 | 9,9 | | | |
| Ophiuroidea | | | | 0,6 | 0,1 | < 0,1 | | | |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | 12,5 | 0,7 | 1,5 | 19,0 | 2,8 | 7,2 | 7,5 | 4,5 | 0,4 |
| *Gonorynchus gonorynchus* (S) | | | | 1,1 | 0,1 | 0,4 | | | |
| *Etrumeus teres* (P) | | | | 5,0 | 1,1 | 0,9 | | | |
| *Sardinops ocellata* (P) | | | | 2,8 | 0,5 | 4,7 | 56,6 | 65,9 | 81,3 |
| *Engraulis capensis* (P) | | | | 16,2 | 4,3 | 6,5 | | | |
| *Galeichthys* sp. (S) | | | | 2,8 | 0,5 | 0,9 | | | |
| *Halidesmus scapularis* (R) | | | | 1,1 | 0,1 | 0,3 | | | |
| Bothidae (S) | | | | 0,6 | 0,1 | <0,1 | | | |
| *Cynoglossus capensis* (S) | | | | 1,1 | 0,1 | 0,8 | | | |
| *Cynoglossus zanzibarensis* (S) | | | | 0,6 | 0,1 | 0,4 | | | |
| *Cheilodactylus fasciatus* (R) | | | | 1,1 | 0,1 | 1,5 | | | |
| *Cheilodactylus pixi* (R) | | | | 2,8 | 0,3 | 1,9 | 1,9 | 1,1 | 0,5 |
| *Chirodactylus brachydactylus* (R) | 12,5 | 0,7 | 9,7 | 2,2 | 0,3 | 0,9 | | | |
| *Acanthistius sebastoides* (R) | | | | 0,6 | 0,1 | 0,5 | | | |
| *Trachurus trachurus* (P) | | | | 1,7 | 0,2 | 0,9 | | | |
| *Argyrosomus hololepidotus* (S) | | | | 0,6 | 0,1 | 2,4 | 5,7 | 3,4 | 3,8 |
| *Pomadasys olivaceum* (S) | | | | 0,6 | 0,1 | 0,3 | 5,7 | 3,4 | 4,9 |
| Sparidae (U) | | | | 1,1 | 0,2 | 0,1 | | | |
| *Boopsoidea inornata* (R) | | | | 0,6 | 0,1 | 0,1 | | | |
| *Diplodus sargus* (R) | | | | 1,1 | 0,1 | 0,1 | | | |
| *Sarpa salpa* (R) | | | | | | | 3,8 | 2,3 | 2,3 |
| *Spondyliosoma emarginatum* (R) | | | | 0,6 | 0,1 | 4,5 | 1,9 | 4,5 | 1,1 |
| *Sphyraena africanum* (P) | | | | 0,6 | 0,1 | 0,1 | | | |
| Gobiidae (U) | 12,5 | 0,7 | 1,2 | 9,5 | 1,2 | 2,1 | | | |
| Clinidae (R) | | | | 18,4 | 3,7 | 9,3 | 1,9 | 1,1 | < 0,1 |
| *Pavoclinus* spp. (R) | | | | 1,1 | 0,1 | 0,3 | | | |
| *Pavoclinus laurentii* (R) | | | | 0,6 | 0,1 | 0,3 | | | |
| *Cremnochorites capensis* (U) | | | | 1,7 | 0,6 | 1,3 | 1,9 | 3,4 | 0,2 |
| *Coccotropsis gymnoderma* (R) | | | | 1,1 | 0,1 | 0,1 | | | |
| Triglidae (S) | | | | 0,6 | 0,1 | 2,3 | | | |
| Gobiesocidae (R) | 12,5 | 0,7 | 1,7 | 1,1 | 0,1 | < 0,1 | | | |
| *Chatrabus melanurus* (R) | | | | 0,6 | 0,1 | 0,3 | | | |
| Totals | 8 | 138 | 10,8 | 179 | 1907 | 909,5 | 53 | 88 | 2208,4 |

20 – 160 mm; *Galeichthys* species (51 – 72 mm) and *Octopus* species (20 – 60 mm).

Temporal variation of important prey (> 4% mass) is shown in Figure 7. Prey varied considerably through the year, schooling fishes and squid becoming sporadically important at the beginning and end of the year, while demersal reef fish such as clinids and gobies occurred almost throughout the year. From this it would appear that *C. nufar* is an opportunistic top predator which switches prey according to the relative abundance of suitable organisms. When schooling species become available, especially in summer, *C. nufar* switch from benthic and demersal prey to the schooling pelagic species.

There was considerable variation in prey taken by *C. nufar*

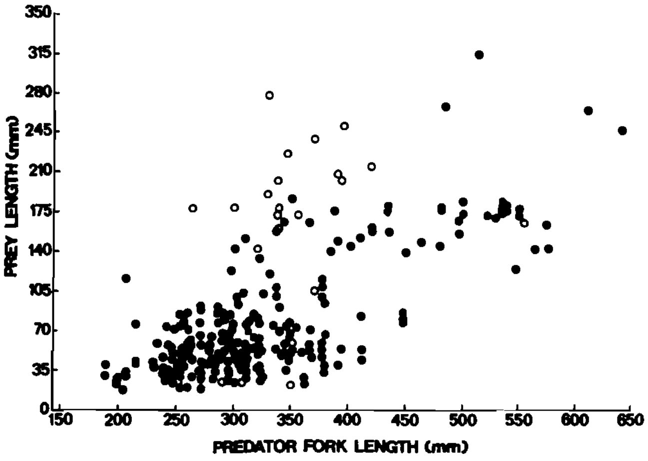

Figure 5 Scatter diagram of prey length against fork length of *Cheimerius nufar*. Cephalopods are shown by open circles and fishes by closed circles.

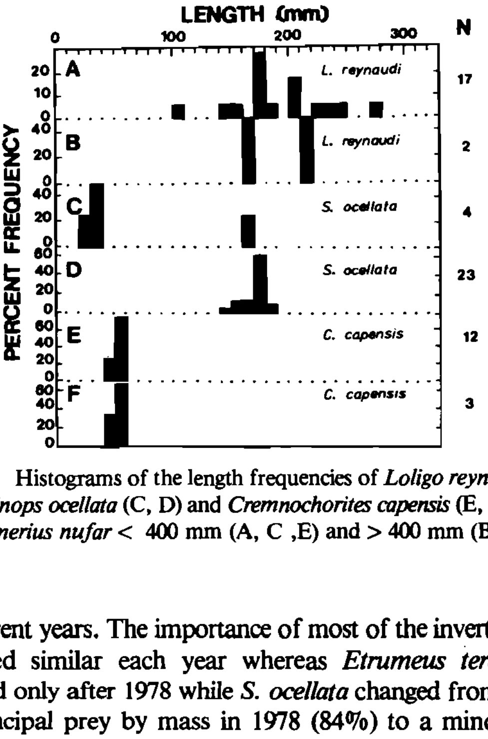

Figure 6 Histograms of the length frequencies of *Loligo reynaudi* (A, B), *Sardinops ocellata* (C, D) and *Cremnochorites capensis* (E, F) taken by *Cheimerius nufar* < 400 mm (A, C ,E) and > 400 mm (B, D, F).

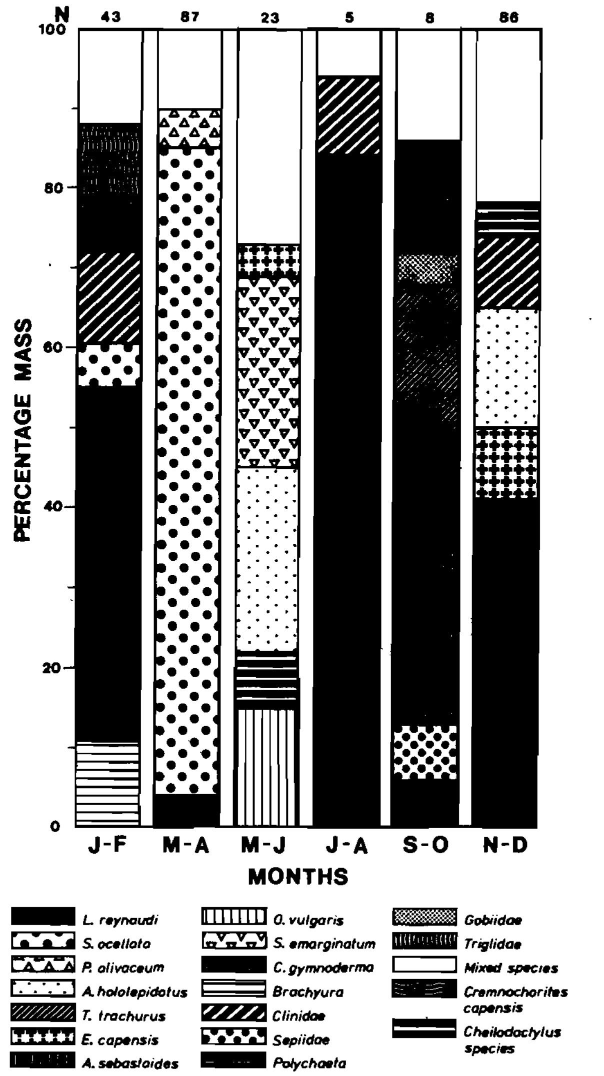

Figure 7 The percentage composition by mass of prey of *Cheimerius nufar* of 201 – 700 mm in bi-monthly periods, all years combined. *N* is the sample size.

in different years. The importance of most of the invertebrates remained similar each year whereas *Etrumeus teres* was collected only after 1978 while *S. ocellata* changed from being the principal prey by mass in 1978 (84%) to a minor prey in subsequent years. *Engraulis capensis* was only recorded after 1979. Minor species fluctuated in abundance in stomach contents, occasionally being absent, but this is almost certainly caused by the small sample available. More important species, such as clinids and gobies, were recorded throughout the study.

In the wild, fish of 150 – 400 mm usually occur in loose aggregations over low to moderate profile reefs (0,2 – 3 m high), or swim along the sandy bottom gullies which transect them. Individuals or several dozen fish may be present and aggregations are generally not organized into tightly packed schools. Most of the individuals swim around apparently uninfluenced by other conspecifics or are widely spaced, but swimming in the same direction, about 0,2 – 1 m above the substrate. Occasionally two or three form a small school or pack, and swim over the reef together. Observations of hunting behaviour were confined to searches and chases, no instances of successful prey capture were observed in the wild. Four behavioural sequences were seen in the aquarium, usually over flat reefs, especially those which are covered with mussels.

(i) 'Quartering' — individuals swim closer to the reef, about 10 – 20 cm over it. The proximity may depend on the type of prey being hunted. Swimming speed more or less doubles from 'cruising speed' and the fish appeared more alert, with eyes directed to the substrate.

(ii) 'Speculative dive' (Figure 8) — the predator swims rapidly at a cave or towards the surface of the reef, as if about to take a prey item, but rapidly decelerates, stopping about 1/3 of a body length away from the reef. It then remains immobile for a few seconds, the eyes fixed ahead on the reef. This was interpreted as a behavioural ruse to alarm cryptic prey into alarm escape, whereupon they may be taken. No successful attacks were witnessed to confirm this interpretation. It is also possible that fish saw a movement on the reef and stopped to investigate it further.

(iii) 'Hover' — the fish searches the reef while hovering over it, remaining immobile from a few seconds to a minute (Figure 8). While hovering the predator was observed examining the substrate, searching for prey. Position was maintained by fanning the pectoral fins, and the caudal fin appeared to undulate along its length. Periodically, a dart was made to the substrate to secure prey items which were probably small invertebrates.

(iv) 'Move off' — after an unsuccessful hunt the fish moved

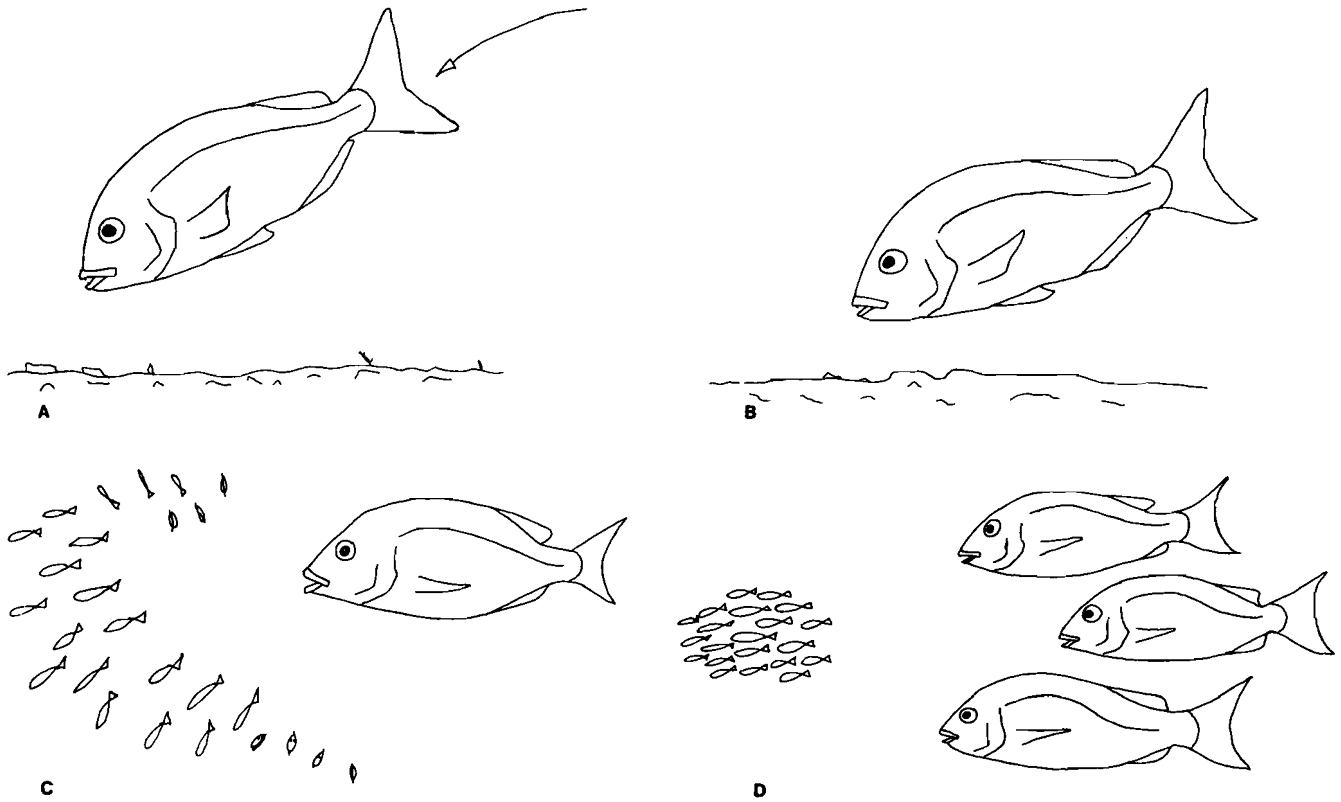

**Figure 8** Hunting behaviour of *Cheimerius nufar*: A: 'speculative dive' B: 'hovering', C: attacking schooled prey, D: 'herding' prey.

off fairly slowly, to accelerate and repeat the behaviour nearby. *C. nufar* were usually coloured plain off-white over sand, but had about five broad red vertical bars across the body near reefs, although this was not a clearcut difference. The bars were seen at different times of the day.

Different behaviour was noted when schooling fish were hunted in the aquarium. Interactions between the predators and a mixed school of juveniles (*Trachurus trachurus, Sarpa salpa* and *Pomadasys olivaceum*) were observed and the following features were noted:

(i) 'Cruising' — fish swam around the tank 0,4 – 1 m above the substrate, at a relatively slow speed, showing no sign of appetitive behaviour.

(ii) 'Approach' — the predators swam towards the school of fish at cruising speed.

(iii) 'Feint' — the predator swam slowly towards the prey which retreated. The 'feint' would consist of a moderate speed charge which would not be carried through. This may have been to test for weak members of the school.

(iv) 'Attack' (Figure 8) — the attack initially took the same form as the 'feint' but was more determined. The predator swam rapidly through the school which opened up to avoid the attack. To counter this, *C. nufar* twisted and turned rapidly, presumably chasing individual prey. The ensuing chaos prevented observation of successful attacks. Vertical chases occurred occasionally when shrimps or prawns were disturbed and flicked away in escape. *C. nufar* responded by chasing, turning and snapping, following the course of the prey, often only catching it at the water surface.

(v) 'Group attack' — this was essentially the same as 'attack' behaviour, but was practised by 2 – 5 predators simultaneously. There was no evidence of organization *per se*, but mutual facilitation seemed evident as the attacks appeared to be more aggressive and determined, and the skirmishes lasted longer. The school of prey was broken up more effectively as prey reacted simultaneously to several predators. This would presumably make it easier for a single susceptible prey to be picked and attacked.

(vi) 'Herding' (Figure 8) — this was seen on only two occasions and may be a rare occurrence. Following an intense skirmish over an artificial reef by four *C. nufar*, the school of prey gravitated towards the point of least attack and started to swim away. The school was very tightly packed (occupying 1/3 – 1/6 of their normal volume), swam fast and was followed by the predators, about 30 cm behind the prey. They swam around the reef, were subjected to one or two further attacks after which the predators left. In the wild the school may have escaped from a high threat area to open water or possibly a cave, whichever would provide a refuge. Whether this was in fact herding or simply the predators following prey is uncertain.

Clearly there are two different behavioural sequences which are used to catch prey: the individual reef-orientated behaviour, and the schooling-prey orientated attack patterns. The two patterns show how the behaviourally different prey groups described above are attacked and overcome. The reactions of prey to different attack strategies will be discussed below.

### *Petrus rupestris* (Valenciennes 1830) — red steenbras

A total of 751 *P. rupestris* measuring 55 – 1310 mm FL were collected from anglers and by spearfishing and rotenone sampling (Figure 9). Of these, 113 specimens contained stomach contents (15,1%) and the balance had empty stomachs or had regurgitated during capture. Those with stomach contents measured from 55 – 1186 mm FL. Seventy-eight of the fish with stomach contents were collected by line fishing, 33 by spearfishing and two from rotenone stations. Freshly ingested prey were discounted from the latter. The prey were similar by each collection method considering size and locality and

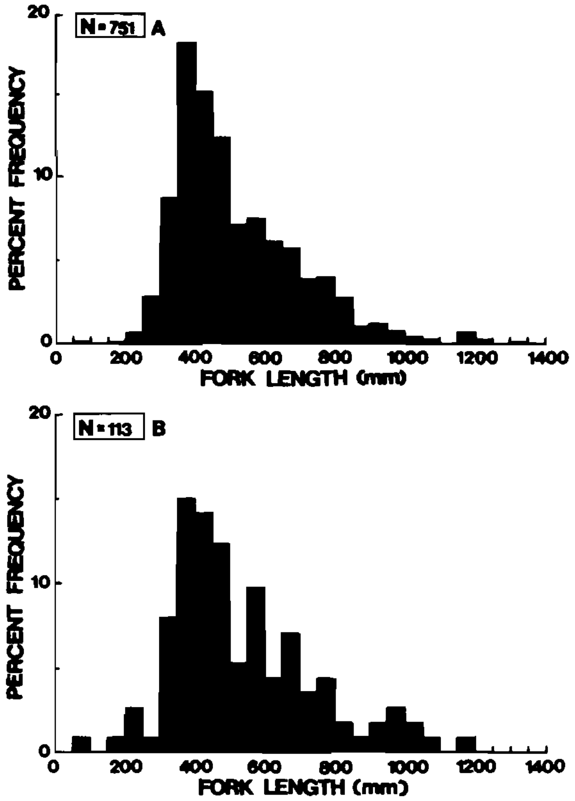

**Figure 9** Histograms of the length frequencies of the entire sample of *Petrus rupestris* (A) and those with stomach contents (B).

were therefore lumped for analysis. The fullest stomach recorded was 5,5% of total mass.

The prey of *P. rupestris* is presented in Table 2, grouped according to predator size and the principal prey species are shown in Figure 10. One juvenile of 55 mm, collected from Tsitsikamma Coastal National Park in a rotenone station, contained seven mysids, *Mysidopsis similis* (Wooldridge pers. comm.), and one small, well-digested carid shrimp. *M. similis* is typical of reefs and sheltered caves, suggesting that predation occurs around the reef. The first record of fish in the diet is from a specimen of 190 mm which had taken three gobies.

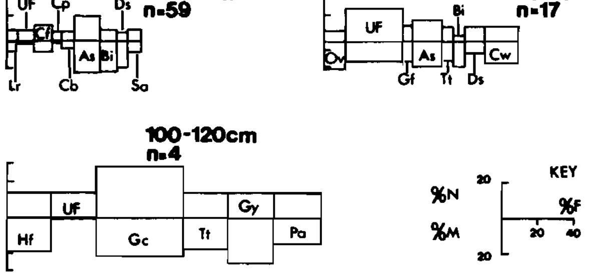

**Figure 10** The principal prey of *Petrus rupestris*. The size range of each group and the number of stomachs is shown. As: *Acanthistius sebastoides*, Bi: *Boopsoidea inornata*, CA: Caridea, Cb: *Chirodactylus brachydactylus*, Cf: *Cheilodactylus fasciatus*, CL: Clinidae, Cm: *Chatrabus melanurus*, Cp: *Cheilodactylus pixi*, Cw: *Conger wilsoni*, Ds: *Diplodus sargus*, Gc: *Genypterus capensis*, Gs: *Galeichthys* sp., GO; Gobiidae, Gy: *Gymnocrotaphus curvidens*, Hf: *Haploblepharus fuscus*, Lr: *Loligo reynaudi*, MYS: Mysidacea, Ov: *Octopus vulgaris*, Pa: *Pachymetopon aeneum*, Sa: *Sarpa salpa*, Tt: *Trachurus trachurus* UF: Unidentified fish.

The only invertebrate taken by *P. rupestris* between 201 and 400 mm was *Loligo reynaudi*, it made up 3% of the number and 0,2% of the mass of prey. Fish made up the majority of the diet (98%N, 99,8%M), 80% by number and 89% by mass being reef-associated species. The principal prey species were the fingerfins, *Cheilodactylus pixi* and *C. fasciatus*.

The 401 – 700 mm group took four invertebrate groups: sepiids, *Loligo reynaudi*, unidentified benthic ocotopods and *Octopus vulgaris*, which represented 13% of the number and 15% of the mass of prey taken. The rockcod, *A. sebastoides*, was the principal prey species, while the fingerfin *C. fasciatus* ranked second. Reef-associated fish comprised 70% by number and 74% by mass of prey. Species which are associated with sand areas but also occur on reefs, such as *Pomadasys olivaceum* and *Galeichthys* species made up 9% by number and 7% by mass of the prey. The pelagic *Trachurus trachurus* was a minor item, 1% by number and 4% by mass.

The 701 – 1000 mm size group took five invertebrate prey types: prawns, *Scyllarides elisabethae*, sepiids, *Loligo reynaudi* and *Octopus vulgaris*. Crustaceans were minor prey (6%N, 1%M) whereas the cephalopods were more dominant (13%N, 16%M). Reef fish accounted for 28% by number and 34% by mass of prey, demersal soft bottom or ubiquitous species made up 22% of the number and 27% of the mass taken. Pelagic prey constituted 13% by number and 12% of the mass ingested.

Four fish between 1001 and 1200 mm were collected. Forty-three per cent of prey by number were reef fish, 29% were associated with soft substrata and 14% were pelagic. These groups represented 59%, 22% and 19% of the prey mass, respectively.

The percentage similarity by mass of prey taken by the various predator size groups is shown in Figure 11. The 701 – 1000 mm and 401 – 700 mm are clearly most similar (54%), while the 50 – 200 mm group has no prey in common with larger conspecifics, although the sample size is very small.

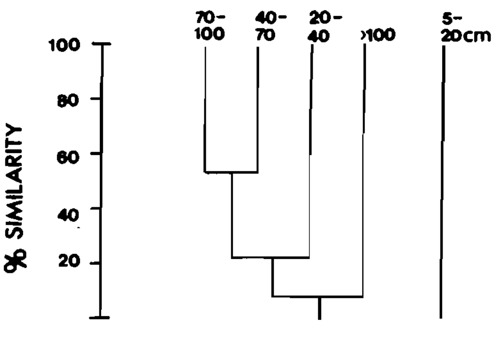

**Figure 11** Similarity dendrogram of diets of *Petrus rupestris* size groups, according to prey mass.

The prey of *P. rupestris* is presented on a regional basis in Table 3. Broader size class groupings are used because there were insufficient data to use smaller size groups in this analysis. Those collected at East London show the greatest

**Table 2** The prey of *Petrus rupestris*, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g. The habitat of fish prey is indicated by the letters: (P) pelagic, (S) soft substrata, (R) reef and (U) ubiquitous

| | 50 – 200 mm | | | 201 – 400 mm | | | 401 – 700 mm | | | 701 – 1000 mm | | | 1001 – 1200 mm | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Crustacea | | | | | | | | | | | | | | | |
| Mysidacea | 50,0 | 63,6 | 5,6 | | | | | | | | | | | | |
| Caridea | 50,0 | 9,1 | 1,9 | | | | | | | | | | | | |
| Penaeidea | | | | | | | | | | 5,9 | 3,1 | 0,1 | | | |
| *Scyllarides elisabethae* | | | | | | | | | | 5,9 | 3,1 | 0,8 | | | |
| Mollusca | | | | | | | | | | | | | | | |
| Sepiidae | | | | | | | 1,7 | 1,4 | 0,2 | 5,9 | 3,1 | 0,1 | | | |
| *Loligo reynaudi* | | | | 3,2 | 2,5 | 0,2 | 6,8 | 5,7 | 0,4 | 5,9 | 3,1 | < 0,1 | | | |
| Octopoda (Benthic) | | | | | | | 3,4 | 2,9 | 0,9 | | | | | | |
| *Octopus vulgaris* | | | | | | | 3,4 | 2,9 | 13,4 | 11,8 | 6,3 | 15,7 | | | |
| Chondrichthyes | | | | | | | | | | | | | | | |
| *Haploblepharus fuscus* (R) | | | | | | | | | | | | | 25,0 | 14,3 | 19,0 |
| Osteichthyes | | | | | | | | | | | | | | | |
| Unidentified fish | | | | 12,9 | 10,0 | 5,0 | 8,5 | 7,1 | 0,6 | 35,3 | 18,8 | 11,1 | 25,0 | 14,3 | 0,3 |
| *Gonorynchus gonorynchus* (S) | | | | | | | 1,7 | 1,4 | 0,7 | | | | | | |
| *Etrumeus teres* (P) | | | | | | | | | | 5,9 | 3,1 | 1,9 | | | |
| *Galeichthys* sp. (S) | | | | | | | 1,7 | 1,4 | 1,8 | 5,9 | 9,4 | 11,2 | | | |
| *Genypterus capensis* (S) | | | | | | | | | | | | | 50,0 | 28,6 | 22,3 |
| Cheilodactylidae (R) | | | | | | | 1,7 | 1,4 | 0,2 | | | | | | |
| *Cheilodactylus fasciatus* (R) | | | | 19,4 | 15,0 | 36,1 | 10,2 | 8,5 | 5,9 | | | | | | |
| *Cheilodactylus pixi* (R) | | | | 25,8 | 22,5 | 20,6 | 5,1 | 5,7 | 1,2 | | | | | | |
| *Chirodactylus brachydactylus* (R) | | | | 6,5 | 5,0 | 8,8 | 6,8 | 5,7 | 4,4 | | | | | | |
| *Acanthistius sebastoides* (R) | | | | 3,2 | 2,5 | 0,7 | 15,3 | 14,3 | 19,0 | 17,7 | 12,5 | 13,9 | | | |
| *Trachurus trachurus* (P) | | | | 3,2 | 2,5 | 4,5 | 1,7 | 1,4 | 4,2 | 5,9 | 9,4 | 10,0 | 25,0 | 14,3 | 18,6 |
| *Argyrosomus hololepidotus* (S) | | | | | | | | | | 5,9 | 3,1 | 3,4 | | | |
| *Pomadasys olivaceum* (S) | | | | | | | 3,4 | 2,9 | 2,2 | | | | | | |
| *Boopsoidea inornata* (R) | | | | 3,2 | 2,5 | 6,2 | 8,5 | 7,1 | 16,7 | 5,9 | 3,1 | 13,7 | | | |
| *Diplodus sargus* (R) | | | | | | | 6,8 | 5,7 | 14,3 | 11,8 | 9,4 | 5,9 | | | |
| *Gymnocrotaphus curvidens* (R) | | | | | | | | | | | | | 25,0 | 14,3 | 25,6 |
| *Pachymetopon aeneum* (R) | | | | 3,2 | 2,5 | 2,5 | 1,7 | 1,4 | 0,4 | | | | 25,0 | 14,3 | 14,2 |
| *Polysteganus undulosus* (R) | | | | | | | 1,7 | 1,4 | 0,3 | | | | | | |
| *Pterogymnus laniarius* (S) | | | | | | | 3,4 | 2,9 | 1,8 | | | | | | |
| *Sarpa salpa* (R) | | | | 3,2 | 2,5 | 2,0 | 8,5 | 7,1 | 5,3 | | | | | | |
| *Spondyliosoma emarginatum* (R) | | | | | | | 3,4 | 2,9 | 0,9 | | | | | | |
| Gobiidae (R) | 50 | 27,3 | 92,5 | | | | | | | | | | | | |
| Clinidae (R) | | | | 19,4 | 15,0 | 7,2 | 3,4 | 2,9 | 0,6 | | | | | | |
| *Clinus* spp. (R) | | | | 3,2 | 2,5 | 0,7 | | | | | | | | | |
| *Clinus superciliosus* (R) | | | | | | | 1,7 | 1,4 | 2,2 | | | | | | |
| *Clinus venustris* (R) | | | | 3,2 | 2,5 | 1,8 | | | | | | | | | |
| Tripterygidae (U) | | | | 3,2 | 2,5 | 0,5 | | | | | | | | | |
| *Cremochorites capensis* (U) | | | | 3,2 | 2,5 | 0,4 | | | | | | | | | |
| *Scorpaena scrofa* (R) | | | | | | | 1,7 | 1,4 | 0,8 | | | | | | |
| *Conger wilsoni* (U) | | | | | | | | | | 17,7 | 9,4 | 12,1 | | | |
| *Chatrabus melanurus* (R) | | | | 9,7 | 7,5 | 2,8 | 3,4 | 2,9 | 1,7 | 5,9 | 3,1 | < 0,1 | | | |
| Totals | 2 | 11 | 1,1 | 31 | 40 | 442,4 | 59 | 70 | 2649,2 | 17 | 32 | 1681,7 | 4 | 7 | 1828 |

difference in prey compared to similar-sized fish elsewhere, although there is overlap with prey such as *Cheilodactylus pixi*, benthic octopods, *Conger wilsoni* and *Tharbacus melanurus*. Thus, although they are taking similar types of prey, *Scorpaena scrofa, Pterogymnus laniarius, Polysteganus undulosus* and *Etrumeus teres* are not recorded from *P. rupestris* further south. This difference probably results from the warmer and deeper water (60 – 100 m) that characterizes the fishing areas for *P. rupestris* off East London.

The prey is more similar between Algoa Bay and the south

**Table 3a** The prey of *Petrus rupestris* taken off East London, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g

| | 50 – 400 mm | | | 401 – 700 mm | | | 701 – 1200 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Crustacea | | | | | | | | | |
| Penaeidea | | | | | | | 20 | 11,1 | 0,9 |
| *Syllarides elisabethae* | | | | | | | 20 | 11,1 | 6,5 |
| Mollusca | | | | | | | | | |
| Sepiidae | | | | 14,3 | 12,5 | 4,3 | | | |
| Octopoda (Benthic) | | | | 14,3 | 12,5 | 3,8 | | | |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | 100,0 | 50,0 | 37,5 | 14,3 | 12,5 | 2,9 | 60,0 | 33,3 | 50,6 |
| *Gonorynchus gonorynchus* | | | | 14,3 | 12,5 | 16,7 | | | |
| *Etrumeus teres* | | | | | | | 20,0 | 11,1 | 16,2 |
| *Cheilodactylus pixi* | 100,0 | 50,0 | 62,5 | | | | | | |
| *Polysteganus undulosus* | | | | 14,3 | 12,5 | 6,7 | | | |
| *Pterogymnus laniarius* | | | | 28,6 | 25,0 | 44,8 | | | |
| *Scorpaena scrofa* | | | | 14,3 | 12,5 | 21,0 | | | |
| *Conger wilsoni* | | | | | | | 40,0 | 22,2 | 25,7 |
| *Chatrabus melanurus* | | | | | | | 20,0 | 11,1 | 0,1 |
| Totals | 1 | 2 | 0,8 | 7 | 8 | 105 | 5 | 9 | 200,2 |

**Table 3b** The prey of *Petrus rupestris* taken from Algoa Bay and environs, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g

| | 50 – 400 mm | | | 401 – 700 mm | | | 701 – 1300 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Mollusca | | | | | | | | | |
| *Loligo reynaudi* | 7,7 | 6,3 | 0,9 | 4,5 | 3,8 | < 0,1 | 7,7 | 4,8 | < 0,1 |
| *Octopus vulgaris* | | | | | | | 7,7 | 4,8 | 7,5 |
| Chondrichthyes | | | | | | | | | |
| *Haploblepharus fuscus* | | | | | | | 7,7 | 4,8 | 11,6 |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | | | | 9,1 | 7,7 | 0,2 | 30,8 | 19,0 | 3,0 |
| *Galeichthys* sp. | | | | | | | 7,7 | 14,2 | 6,3 |
| *Genypterus capensis* | | | | | | | 15,4 | 9,5 | 13,6 |
| Cheilodactylidae | | | | 4,5 | 3,8 | 0,9 | | | |
| *Cheilodactylus fasciatus* | 7,7 | 6,3 | 1,3 | 9,1 | 7,7 | 11,5 | | | |
| *Cheilodactylus pixi* | 30,8 | 25,0 | 71,7 | 9,1 | 11,5 | 1,9 | | | |
| *Chirodactylus brachydactylus* | | | | 9,1 | 7,7 | 2,4 | | | |
| *Acanthistius sebastoides* | | | | 13,6 | 15,4 | 38,6 | 7,7 | 4,8 | 4,7 |
| *Trachurus trachurus* | | | | | | | 7,7 | 4,8 | 11,3 |
| *Argyrosomus hololepidotus* | | | | | | | 7,7 | 4,8 | 1,9 |
| *Pomadasys olivaceum* | | | | 4,5 | 3,8 | 0,9 | | | |
| *Boopsoidea inornata* | | | | 4,5 | 3,8 | 12,4 | 7,7 | 4,8 | 7,7 |
| *Diplodus sargus* | | | | | | | 7,7 | 9,5 | 3,1 |
| *Gymnocrotaphus curvidens* | | | | | | | 7,7 | 4,8 | 15,6 |
| *Pachymetopon aeneum* | 7,7 | 6,3 | 9,8 | 4,5 | 3,8 | 1,6 | 7,7 | 4,8 | 8,7 |
| *Sarpa salpa* | | | | 13,6 | 11,5 | 16,9 | | | |
| *Spondyliosoma emarginatum* | | | | 9,1 | 7,7 | 3,8 | | | |
| Gobiidae | 7,7 | 18,8 | 0,9 | | | | | | |
| Clinidae | 23,1 | 18,8 | 4,4 | 4,5 | 3,8 | 1,8 | | | |
| *Conger wilsoni* | | | | | | | 7,7 | 4,8 | 5,0 |
| *Chatrabus melanurus* | 23,1 | 18,8 | 10,9 | 9,1 | 7,7 | 7,1 | | | |
| Totals | 13 | 16 | 112,4 | 22 | 26 | 645,1 | 13 | 21 | 3001,7 |

coast areas, although there are some differences. One interesting feature of the small-group fish is that the dominance of *C. pixi* and *C. fasciatus* in the diet changes between these areas. This may be attributable to distributional preferences, *C. pixi* being found in warmer waters (Smith 1980).

A scatter diagram of the length of *P. rupestris* and its prey is shown in Figure 12. There is a concomitant increase in size of prey with growth although the prey vary between 7 and 69% of predator length. Octopod mantle lengths are 7 – 13% of predator length.

**Table 3c** The prey of *Petrus rupestris* taken from Tsitsikamma Coastal National Park and Mossel Bay, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g

| | 50 – 400 mm | | | 401 – 700 mm | | | 701 – 1300 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Crustacea | | | | | | | | | |
| Mysidacea | 5,3 | 21,2 | < 0,1 | | | | | | |
| Caridea | 5,3 | 3,0 | < 0,1 | | | | | | |
| Mollusca | | | | | | | | | |
| Sepiidae | | | | | | | 33,3 | 11,1 | 0,3 |
| *Loligo reynaudi* | | | | 10,0 | 8,3 | 0,6 | | | |
| Octopoda (Benthic) | | | | 3,3 | 2,8 | 1,1 | | | |
| *Octopus vulgaris* | | | | 6,7 | 5,6 | 18,7 | 33,3 | 11,1 | 13,0 |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | 15,8 | 9,1 | 6,6 | 6,7 | 5,6 | 0,7 | | | |
| *Galeichthys* sp. | | | | 3,3 | 2,8 | 2,5 | | | |
| *Cheilodactylus fasciatus* | 26,3 | 15,2 | 47,8 | 13,3 | 11,1 | 4,3 | | | |
| *Cheilodactylus pixi* | 15,8 | 12,1 | 3,0 | 3,3 | 2,8 | 1,1 | | | |
| *Chirodactylus brachydactylus* | 10,5 | 6,1 | 11,7 | 6,7 | 5,6 | 5,4 | | | |
| *Acanthistius sebastoides* | 5,3 | 3,0 | 1,0 | 20,0 | 16,7 | 13,4 | 66,7 | 33,3 | 30,2 |
| *Trachurus trachurus* | 5,3 | 3,0 | 6,1 | 3,3 | 2,8 | 5,8 | 33,3 | 33,3 | 54,9 |
| *Pomadasys olivaceum* | | | | 3,3 | 2,8 | 2,7 | | | |
| *Boopsoidea inornata* | 5,3 | 3,0 | 8,3 | 13,3 | 11,1 | 19,0 | | | |
| *Diplodus sargus* | | | | 13,3 | 11,1 | 19,9 | 33,3 | 11,1 | 1,6 |
| *Sarpa salpa* | 5,3 | 3,0 | 2,7 | 6,7 | 5,6 | 1,6 | | | |
| Clinidae | 15,8 | 9,1 | 8,1 | 3,3 | 2,8 | 0,2 | | | |
| *Clinus* spp. | 5,3 | 3,0 | 1,0 | | | | | | |
| *Clinus superciliosus* | | | | 3,3 | 2,8 | 3,1 | | | |
| *Clinus venustris* | 5,3 | 3,0 | 2,4 | | | | | | |
| Tripterygiidae | 5,3 | 3,0 | 0,7 | | | | | | |
| *Cremnochorites capensis* | 5,3 | 3,0 | 0,5 | | | | | | |
| Totals | 19 | 33 | 330,3 | 30 | 36 | 1899,1 | 3 | 9 | 308 |

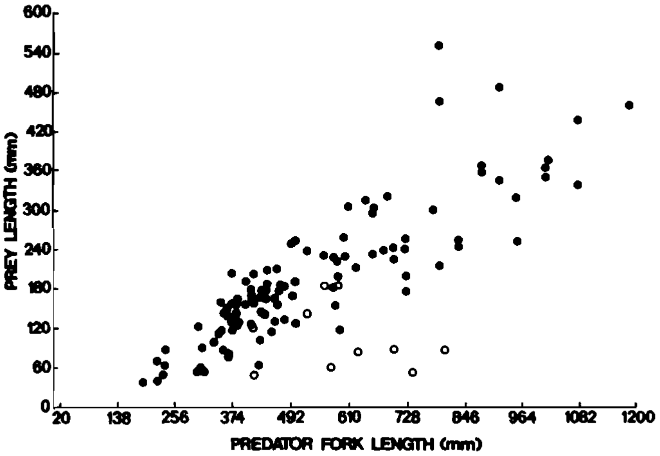

**Figure 12** Scatter diagram of prey length against length of *Petrus rupestris*. Cephalopods are shown by open circles and fishes by closed circles.

The lengths of more common prey are shown in Figure 13 for the different size groups of *P. rupestris*. Although there is overlap, there is a trend for larger predators to take larger prey.

*P. rupestris* is either solitary or occurs in loosely grouped packs of two to ten fish when 200 – 1000 mm in length. Below this size they are rarely seen. A single fish of 55 mm was collected at a rotenone station, suggesting that they are solitary at this size. On reefs where several individuals occur over a wide size range, they appear to act independently, swimming in different directions over the reef. Occasionally two or three of approximately the same size swim in the same direction, giving the impression of an opportunistic 'pack' formation. The 'pack' may remain loosely associated for several minutes (often disappearing out of sight after this) or break up, the members diverging and taking different routes over the reef. They 'cruise' over the reef, close to gullies, drop-offs and caves, 50 cm to 1 m above the reef. Periodically they will swim up sheer reef faces of 8 to 10 m. On high relief reefs large fish (> 500 mm) are often more common in deeper (20 – 25 m) waters.

The author has never observed successful pack hunting but the phenomenon is suggested by catches of 5 – 10 *P. rupestris* of the same size at one reef with the same prey in their stomachs (*Genypterus capensis* and small catsharks), suggesting that they will attack abundant schooling prey.

Individual hunting was observed on several occasions. *P. rupestris* exhibits two modes of attack, depending on the prey.

(i) Solitary prey. The behaviour was similar to that of *C. nufar*. The quartering and speculative dive sequence was as follows: swimming speed increases and the predator swoops down to the reef, often darting into a cave or rushing around an obscuring rock. The aim of these manoeuvres appears to be to take a suitable prey by surprise and to initiate an attack before the prey is aware of the proximity of the predator. When in the open prey seem to freeze or move away when *P. rupestris* is about five body lengths away.

(ii) Schooling prey. This behaviour is similar to that of *C. nufar* when attacking schooling fishes. In *P. rupestris* it

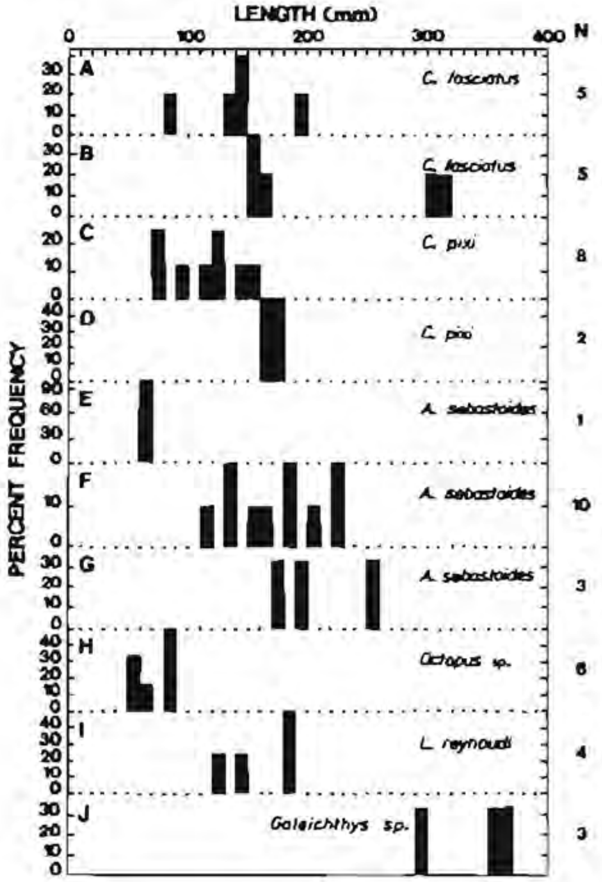

**Figure 13** Histograms of the length frequencies of *Chellodactylus fasciatus* (A, B), *Cheilodactylus pixi* (C, D), *Acanthistius sebastoides* (E, F, G), *Octopus* sp. (H), *Loligo reynaudi* (I) and *Galeichthys* sp. (J), taken by *Petrus rupestris* of 200 – 400 mm (A, C, E), 401 – 700 mm (B, D, F), 701 – 1000 mm (G) and all sizes (H, I, J).

**Figure 14** *Petrus rupestris* of about 500 mm attacking a school of *Sarpa salpa*.

**Figure 15** A specimen of *Acanthistius sebastoides* of 184 mm recovered from the stomach of a *Petrus rupestris* of 480 mm. The tooth puncture marks, which are indicated with arrow heads, show that it had been attacked from behind across the ventral surface.

has been seen most frequently in attacks on *Sarpa salpa*, a herbivore which crops algae throughout the day in schools of 20 to several hundred (pers. obs.). The members of the school feed simultaneously with their heads down and the bodies between 10° and 90° to the surface of the reef. Cropping is an active process. One or two individuals change from the feeding position, bring their heads into a horizontal position over the rock, then turn and swim off to another patch. The other members join them and vigorous feeding resumes. This active grazing causes the fish to shimmer and reflect light on the shallow reefs. They may attract passing *P. rupestris*, which often come in low on the reef, making a rush at the school (Figure 14). The school either opens up (if large) or darts away to another patch to resume grazing when the threat has passed. The attack pattern may be repeated several times by *P. rupestris*. As was found with *C. nufar*, some of the approaches, which appear to be undermotivated, may serve to scare off the school to reveal any weak or slow individuals.

Examination of prey in stomach contents revealed that fish were invariably in the head-first position, although tooth marks on prey (Figure 15) reveal they are attacked from behind. This suggests that they are rotated to the head-first position before being swallowed. This was observed in the wild using the following procedure: a *Pachymetapon aeneum* of about 110 mm was shot with a Hawaiian sling and a multiprong spear. It was removed and a single hook passed through the body beneath the dorsal fin so that it swam in a normal position. It was still alive and swimming although bleeding slightly. It was lowered 10 – 15 m below a SCUBA diver, using a monofilament line. A *P. rupestris* of 558 mm FL observed it, swam up to it from behind and bit it. The prey was chewed several times (presumably to kill it) with the powerful canines, then rotated in the mouth. At one stage it had the fish pinned against a reef while rotating it. The hand-line was kept slack throughout and did not appear to affect any of the behavioural sequence. The fish was swallowed head first and the predator was hooked. The prey was regurgitated while the fish was being subdued. Line fishermen have frequently reported that whole fish bait is chewed by *P. rupestris*.

### *Polysteganus praeorbitalis* (Günther 1859) — Scotsman

A total of 74 *P. praeorbitalis* between 202 and 668 mm FL were examined between February 1978 and December 1981 (Figure 16). Thirty-five of 202 – 632 mm FL had prey remains in their stomachs (47,3%). Of these, 31 were caught by line and four were shot. The fullest stomach recorded was 3,1% of total mass.

The prey of *P. praeorbitalis* is listed in Table 4 and presented in Figure 17 for three size groups. The 200 – 300 mm group took some copepods and penaeids (17%N, 3%M). Fish were the dominant prey (79%N, 86%M) and all of these were reef-associated or ubiquitous. Clinids and *Cremnochorites capensis* were the principal components (41%N, 52%M). In the 301 – 400 mm group, crabs (6%N, 4%M), and demersal cephalopods (6%N, 20%M) were minor prey while fish again dominated the diet (85%N, 75%M). Clinids and *Cremnochorites capensis* were the dominant prey (23%N, 28%M). The 401 – 700 mm group took fewer crustaceans (5%N, 1%M)

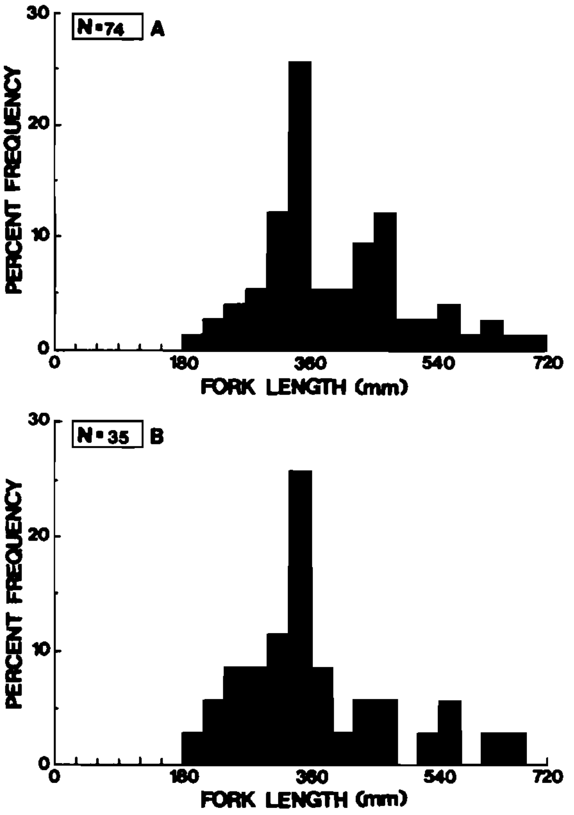

**Figure 16** Histograms of the length frequencies of the entire sample of *Polysteganus praeorbitalis* (A) and those with stomach contents (B).

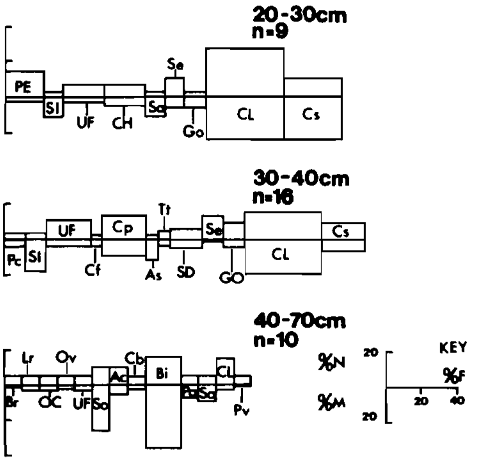

**Figure 17** The principal prey of *Polysteganus praeorbitalis*. The size range of each group and the number of stomachs is shown. Ac: *Ammodytes capensis*, As: *Acanthistius sebastoides*, Bi: *Boopsoidea inornata*, BR: Brachyura, Cb: *Chirodactylus brachydactylus*, Cf: *Cheilodactylus fasciatus*, CH: *Cheilodactylidae*, CL: Clinidae, Cp: *Cheilodactylus pixi*, Cs: *Cremnochorites capensis*, GO: Gobiidae, Lr: *Loligo reynaudi*, OC: Octopoda (benthic) Ov: *Octopus vulgaris*, Pa: *Pachymetopon aeneum*, Pc: *Plagusia chabrus*, Pv: *Pavoclinus* spp. Sa: *Sarpa salpa*, SD: Sparidae, Se: *Spondyliosoma emarginatum*, SI: Sepiidae, So: *Sardinops ocellata* Tt: *Trachurus trachurus* UF: Unidentified fish.

and cephalopods (16%N, 7%M). Bony fishes were the principal prey (79%N, 92%M). A pelagic species, *Sardinops ocellata* (11%N, 26%M), and a fish normally associated with sandy substrata, *Ammodytes capensis* (11%N, 6%M), were taken while reef-associated fish such as *Boopsoidea inornata* and clinids made up 53% of the number and 58% of the prey mass taken.

The percentage similarity by mass of prey taken by these predator size groupings are shown in Figure 18. The two groups of small fish are clearly most similar, while the large fish are only 12% similar to these two.

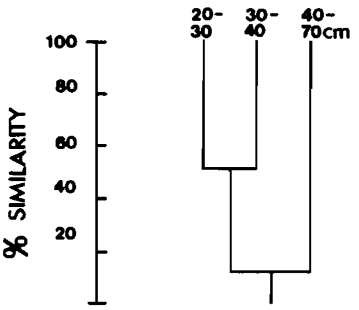

**Figure 18** Similarity dendrogram of diets of *Polysteganus praeorbitalis* size groups, according to prey mass.

The relationship between *P. praeorbitalis* length and the size of prey taken is presented in Figure 19. There is a concomitant increase in size of prey taken with growth and an apparent avoidance of small prey by larger predators. The smallest ratio of prey to predator length is 8% and largest is 49%. Clinids varied between 11% and 38% of predator length: *Cremnochorites capensis* varied between 14 and 21%; *Cheilodactylus pixi* between 14 and 28%; *Spondyliosoma emarginatum* between 8 to 15%; and *Sarpa salpa* was 31% of predator length. The mantle lengths of octopods were between 8 and 10%, and *L. reynaudi* was 49%, of the predator fork length.

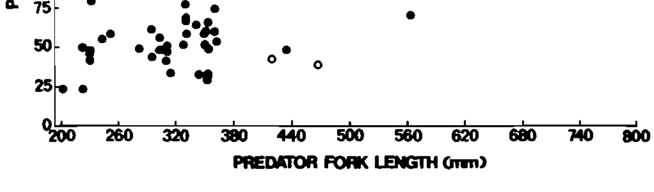

**Figure 19** Scatter diagram of prey length against fork length of *Polysteganus praeorbitalis*. Cephalopods are shown by open circles and fishes by closed circles.

Groups or 'packs' of *P. praeorbitalis* were observed on three occasions during this study in the shallows at Cape Recife in depths of 4 – 9 m. About five fish measuring about 300 mm FL were swimming more-or-less abreast. Although in loose formation, about 300 to 500 mm apart, they appeared to be aware of each others' movements as they maintained this formation for most of the observation period. The swimming formation of the pack is probably effective for searching a wide area. Occasionally individuals separated, examining objects among the scattered reefs. On one occasion

**Table 4** The prey of *Polysteganus praeorbitalis*, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g. The habitat of fish prey is indicated by the letters: (P) pelagic, (S) soft substrata, (R) reef and (U) ubiquitous

| | 200 – 300 mm | | | 301 – 400 mm | | | 401 – 700 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Polychaeta | | | | 6,3 | 2,1 | 0,4 | | | |
| Crustacea | | | | | | | | | |
| Copepoda | 11,1 | 3,4 | 0,3 | | | | | | |
| Penaeidea | 22,2 | 13,8 | 2,3 | | | | | | |
| Brachyura | | | | 6,3 | 2,1 | 0,7 | 10,0 | 5,3 | 0,5 |
| *Plagusia chabrus* | | | | 12,5 | 4,3 | 3,7 | | | |
| Mollusca | | | | | | | | | |
| Sepiidae | 11,1 | 3,4 | 11,1 | 12,5 | 4,3 | 18,1 | | | |
| *Loligo reynaudi* | | | | | | | 10,0 | 5,3 | 2,6 |
| Octopoda (Benthic) | | | | 6,3 | 2,1 | 1,7 | 10,0 | 5,3 | 3,0 |
| *Octopus vulgaris* | | | | | | | 10,0 | 5,3 | 1,7 |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | 22,2 | 6,9 | 3,1 | 25,0 | 10,6 | 4,2 | 10,0 | 5,3 | 2,6 |
| *Sardinops ocellata* (P) | | | | | | | 10,0 | 10,5 | 25,7 |
| *Ammodytes capensis* (S) | | | | | | | 10,0 | 10,5 | 5,7 |
| Cheilodactylidae (R) | 22,2 | 6,9 | 4,9 | | | | | | |
| *Cheilodactylus fasciatus* (R) | | | | 6,3 | 2,1 | 4,1 | | | |
| *Cheilodactylus pixi* (R) | | | | 25,0 | 12,8 | 9,0 | | | |
| *Chirodactylus brachydactylus* (R) | | | | 6,3 | 2,1 | 2,1 | 10,0 | 5,3 | 1,5 |
| *Acanthistius sebastoides* (R) | | | | 6,3 | 2,1 | 12,0 | | | |
| *Trachurus trachurus* (P) | | | | 6,3 | 4,2 | 4,1 | | | |
| Sparidae (U) | 11,1 | 3,4 | 1,2 | 18,8 | 6,4 | 4,6 | | | |
| *Boopsoidea inornata* (R) | | | | | | | 20,0 | 15,8 | 35,5 |
| *Pachymetopon aeneum* (R) | | | | | | | 10,0 | 5,3 | 7,5 |
| *Sarpa salpa* (R) | 11,1 | 3,4 | 12,3 | | | | 10,0 | 5,3 | 10,0 |
| *Spondyliosoma emarginatum* (R) | 11,1 | 10,3 | 6,1 | 12,5 | 12,8 | 2,1 | | | |
| Gobiidae (U) | 11,1 | 3,4 | 6,1 | 12,5 | 8,5 | 5,5 | | | |
| Clinidae (R) | 44,4 | 27,6 | 24,0 | 43,8 | 14,9 | 20,1 | 10,0 | 15,8 | 2,8 |
| *Clinus berrisfordi* (R) | 11,1 | 3,4 | 3,1 | | | | | | |
| *Pavoclinus* spp. (R) | | | | | | | 10,0 | 5,3 | 0,9 |
| *Cremnochorites capensis* (U) | 33,3 | 10,3 | 24,5 | 25,0 | 8,5 | 7,6 | | | |
| *Chorisochismus dentex* (R) | 11,1 | 3,4 | 1,0 | | | | | | |
| Totals | 9 | 29 | 16,3 | 16 | 47 | 72,4 | 10 | 19 | 388,8 |

three of the five were observed with alternating pale and dark horizontal bands along the body, but the cause of this colour pattern change is unclear, nor was it obvious why the other individuals had the more uniform colouration. As they were sexually immature, it is unlikely to have been sex-related.

### *Epinephalus guaza* (Linnaeus 1758) — yellowbelly rockcod

During this study 319 fish between 250 and 875 mm were collected from anglers and spearfishermen (Figure 20). Of these, 90 (301 to 700 mm TL) had prey remains in their stomachs. Fifty-seven of these were collected by line and 33 by speargun. As the prey were similar irrespective of collection method the data were combined. The highest stomach content mass was 10,3% of body mass.

The prey of *E. guaza* is listed in Table 5 and the principal species are shown in Figure 21. The 300 – 400 mm group took penaeids and several crabs including *Plagusia chabrus*. The crustaceans made up 70% by number and 58% by mass. *Octopus vulgaris* made up 9% of the number and 24% of the mass of prey. The fish component was made up of reef species exclusively. Prey of the 401 – 500 mm group included penaeids and brachyurans (50%N, 36%M) and octopods (15%N, 34%M). A wider spectrum of fish (9 taxa) was found in this group and all were reef-associated or ubiquitous species, representing 35% of the number and 31% of the mass of prey. Crustaceans were major prey of the 501 – 700 mm group (61%N, 20%M). Carids were represented by a large number (31) of *Plesionika* sp. from the stomach of a fish from East London. *Plagusia chabrus* was important by frequency (24%), number (11%) and mass (12%). *Octopus vulgaris* was the most dominant cephalopod prey taken (21%F, 11%N and 50%M). Thirteen fish taxa were identified. The wide range of species taken in low numbers caused them to become insignificant individually, consequently none except *C. wilsoni* are shown in Figure 21. Reef fish comprised 8% by number and 4% by mass of the diet while conger eels made up 4% of the number and 8% of prey mass.

The percentage similarity by mass of prey taken by these predator size groupings is shown in Figure 22. This shows the two smaller size classes to be most similar.

A scatter diagram of prey length against total length of *E. guaza* is presented in Figure 23. The ratio between prey and predator length varied between 4 and 108%. The smallest prey

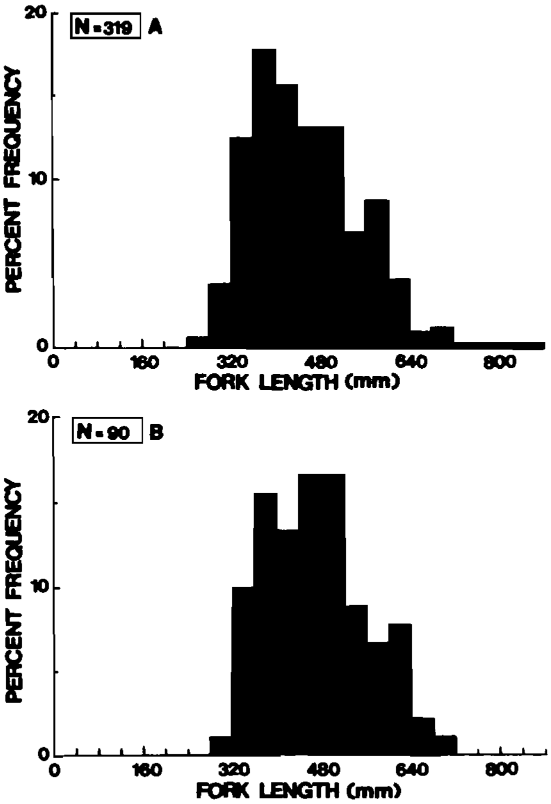

**Figure 20** Histograms of the length frequencies of the entire sample of *Epinephelus guaza* (A) and those with stomach contents (B).

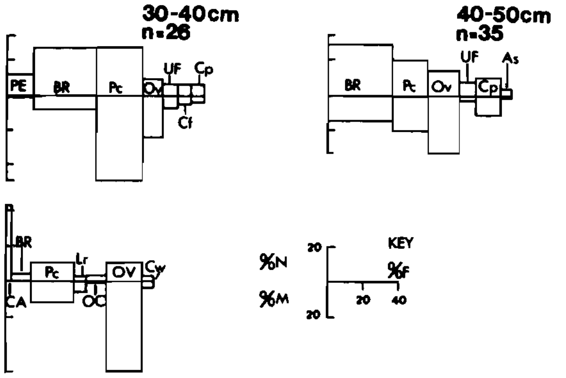

**Figure 21** The principal prey of *Epinephelus guaza*. The size range of each group and the number of stomachs is shown. As: *Acanthistius sebastoides*, BR: Brachyura, Cf: *Cheilodactylus fasciatus*, Cp: *Cheilodactylus pixi*, Cw: *Conger wilsoni*, Lr: *Loligo reynaudi*, OC: Octopoda (benthic) Ov: *Octopus vulgaris*, Pc: *Plagusia chabrus*, UF: Unidentified fish.

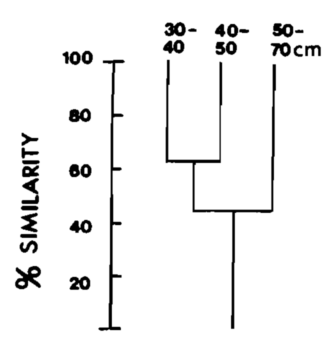

**Figure 22** Similarity dendrogram of diets of *Epinephelus guaza* size groups, according to prey mass.

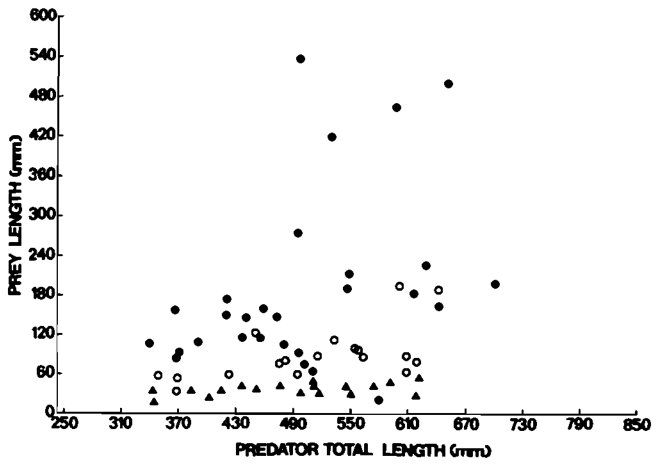

**Figure 23** Scatter diagram of prey length against length of *Epinephelus guaza*. Cephalopods are shown by open circles, fishes by closed circles and crabs by triangles.

taken were crustaceans, such as *Plagusia chabrus* (5 – 10% of predator length) and carideans, while the largest were conger eels, which have very elongate bodies. Apart from the conger eels, most fish taken were between 15 and 56% of the predator length. Mantle lengths of octopods taken varied between 9 and 32% of the predator total length. The conger eels varied between 77 and 108% of the total length and were folded in the stomach. Apart from the eels, the prey size taken over the range shows considerable overlap.

## Discussion

### *Cheimerius nufar*

The forked tail, narrow caudal peduncle and the 4 – 6 strong canine teeth in each jaw show that *C. nufar* is an active carnivorous fish. The deep body and well-developed dorsal fin suggest that the species can manoeuvre rapidly. Such attributes are important to a predator which feeds over reefs on active prey. The strong canines and large gape (10% FL) are important for grasping and subduing prey. The disruptive colour pattern of dark bars on a pale background camouflages it over reefs and sand (Cott 1957; Norman & Greenwood 1963; Edmunds 1974).

*C. nufar* exhibits clear changes in predation with growth. Initially small crustaceans, especially mysids, form the bulk of the diet and feeding appears to be concentrated over reefs (Buxton, Smale, Wallace & Cockcroft 1984), and the 15 elongate gillrakers are important for trapping small prey. The 100 – 200 mm size group in this study had taken fewer mysids but a larger proportion of benthic invertebrates and reef fish. These being larger specimens than recorded in the previous study, they appear to represent a later stage in predatory behaviour.

According to Coetzee & Baird (1981a), the age of the 100 – 200 mm group is about 0 to 1 year. The 201 – 400 mm size group is between 1 and 7 years and the largest group is about 7 to 16 years. The 201 – 400 mm size group was the most numerous collected ($n = 179$) and consequently a large number of prey categories were recorded from them ($n = 45$). The prey included all those taken by the small group, except *Mysidopsis* spp. and *Macropatasma africanum*, although these prey may have been represented in the family groupings of the 201 – 400 mm size group. Similarly the largest group (> 401 mm) only had one species unrepresented in the middle size group, *Sarpa salpa*. Despite this overlap there was a clear

**Table 5** The prey of *Epinephelus guaza*, according to size of predator. The totals are number of stomachs (F), number of items (N) and prey wet mass, g. The habitat of fish prey is indicated by the letters: (P) pelagic, (S) soft substrata, (R) reef and (U) ubiquitous

| | 300 – 400 mm | | | 401 – 500 mm | | | 501 – 700 mm | | |
|---|---|---|---|---|---|---|---|---|---|
| Prey | %F | %N | %M | %F | %N | %M | %F | %N | %M |
| Crustacea | | | | | | | | | |
| Caridea | | | | | | | 3,4 | 43,1 | 2,1 |
| Penaeidea | 15,4 | 12,1 | 1,4 | 2,9 | 2,2 | 0,2 | | | |
| Brachyura | 34,6 | 27,3 | 7,9 | 37,1 | 28,3 | 14,1 | 10,3 | 4,2 | 0,5 |
| Megalopae larvae | 3,8 | 3,0 | 0,1 | | | | | | |
| *Plagusia chabrus* | 26,9 | 27,3 | 49,0 | 20,0 | 19,6 | 21,3 | 24,1 | 11,1 | 11,9 |
| *Pseudodromia* sp. | | | | | | | 3,4 | 1,4 | 0,7 |
| Macrura | | | | | | | 3,4 | 1,4 | 5,1 |
| Mollusca | | | | | | | | | |
| Sepiidae | | | | | | | 3,4 | 1,4 | 0,2 |
| *Loligo reynaudi* | | | | | | | 6,9 | 2,8 | 6,1 |
| Octopoda (Benthic) | | | | 2,9 | 2,2 | 0,1 | 10,3 | 4,2 | 0,5 |
| *Octopus vulgaris* | 11,5 | 9,1 | 24,1 | 17,1 | 13,0 | 33,8 | 20,7 | 11,1 | 50,3 |
| Chondrichthyes (U) | | | | | | | 3,4 | 1,4 | 0,2 |
| Osteichthyes | | | | | | | | | |
| Unidentified fish | 7,7 | 6,1 | 7,6 | 8,6 | 6,5 | 3,3 | 3,4 | 1,4 | 1,7 |
| Bothidea (S) | | | | | | | 3,4 | 1,4 | 7,1 |
| *Cynoglossus capensis* (S) | | | | | | | 3,4 | 1,4 | 1,9 |
| Cheilodactylidae (R) | | | | 2,9 | 2,2 | 0,1 | | | |
| *Cheilodactylus fasciatus* (R) | 7,7 | 6,1 | 5,3 | 2,9 | 2,2 | 2,2 | | | |
| *Cheilodactylus pixi* (R) | 7,7 | 6,1 | 3,9 | 14,3 | 10,9 | 11,1 | 3,4 | 1,4 | 0,3 |
| *Chirodactylus brachydactylus* (R) | | | | 2,9 | 2,2 | 2,8 | 3,4 | 1,4 | 0,6 |
| *Acanthistius sebastoides* (R) | | | | 5,7 | 4,3 | 2,1 | | | |
| *Boopsoidea inornata* (R) | | | | | | | 3,4 | 1,4 | 2,6 |
| *Diplodus cervinus* (R) | | | | 2,9 | 2,2 | 1,8 | | | |
| *Lithognathus mormyrus* (S) | | | | | | | 3,4 | 1,4 | < 0,1 |
| *Pachymetopon aeneum* (R) | | | | | | | 3,4 | 1,4 | 0,2 |
| *Spondyliosoma emarginatum* (R) | | | | | | | 3,4 | 1,4 | 0,2 |
| Clinidae (R) | 3,8 | 3,0 | 0,7 | 2,9 | 2,2 | 4,7 | 3,4 | 1,4 | 0,1 |
| Congridae (U) | | | | | | | 3,4 | 1,4 | 3,3 |
| *Conger wilsoni* (U) | | | | 2,9 | 2,2 | 2,4 | 6,9 | 2,8 | 4,4 |
| Totals | 26 | 33 | 216,3 | 35 | 46 | 674 | 29 | 72 | 1644,0 |

trend of fish becoming more dominant and crustaceans less important, especially by mass. The largest group took crustaceans occasionally which were insignificant by mass (1,2%). Octopods are apparently less important prey of the larger fish. *C. nufar* attains 800 mm and 7 kg, which is considerably smaller than *P. rupestris*, but more similar to *P. praeorbitalis* (van der Elst 1981).

Coetzee & Baird's (1981a) study of 64 *C. nufar* stomachs collected from Algoa Bay shows a similar pattern. These authors recorded only four positively identified fish prey species while a large proportion of the fish (23,5%) was unidentified. Although both *Loligo* spp. and *Octopus* spp. were recorded, they were at lower percentages and these variations are probably attributable to differences in methodology and the use of otoliths and beaks in this study to ensure accurate prey identification. Coetzee & Baird (1981a) also studied hindgut contents. While this may hold as an additional aid, it is clear from their results that retention of organisms with hard exoskeletons and the lack of reliably identified fish reduces the benefit of this analysis. Furthermore, it is possible that the higher incidence of crustaceans in the hindgut results from the gut contents of the prey remaining in the predators' gut. Hindguts were not used in this study as small otoliths are usually totally eroded in the stomach before passing through to the hindgut, and the amorphous material which usually remains is biased towards prey which resist digestion. Hindgut analyses, therefore, rarely throw additional light on the prey of top predatory teleosts which could not be obtained from stomach content analyses.

Druzhinin's (1975) work on feeding of *C. nufar* in the Gulf of Aden region revealed that no less than 10 species of fish were taken and that the diet also included crustaceans and octopods. The fish he recorded are representatives of both pelagic and demersal groups indicating that although the species taken were different to the present study, the feeding behaviour is essentially the same.

The scatter diagram of prey size to predator size clearly showed a wide prey size range available to *C. nufar*, although the spread of the data suggests that it preys opportunistically on suitable abundant prey. Prey of 30 to 350 mm is taken by this species although predators smaller than 200 mm have a considerably smaller maximum prey size (about 35 mm). Predators larger than about 400 mm avoid prey smaller than about 100 mm, although this may be related to the availability of prey. Even this size group occasionally takes small crustaceans such as crabs. That prey of up to 84% of predator length is taken is surprising, considering that *C. nufar* does not have dentition suitable for cutting through prey. Furthermore, the large prey under consideration are *Loligo reynaudi* and *Argyrosomus hololepidotus*. While it is possible that squid could be torn apart during a feeding frenzy, this would be more difficult with large teleosts. It is possible that these large specimens were taken either as sections partially ingested by other predators such as seals or sharks or that they were taken as rejected heads of cleaned fish from anglers. The latter explanation is unlikey as kob are popular eating fish which are usually gutted but not headed at sea. However the lengths of these large fish were calculated from otolith measurements and the entire fish was not recovered from stomachs. Therefore partial ingestion is the most likely explanation for this apparent anomaly. Small fish of less than 190 mm (54%) of the predator length are more dominant and are probably close to the largest prey size normally ingested whole by *C. nufar*. Starck (1970) has recorded that *Lutjanus griseus* take prey up to 135% of its own length. He found that the large items that cannot be swallowed whole are shaken apart, although the majority of items are swallowed whole. Considering the similar dentition of *C. nufar*, this behaviour may also have occurred here. Another example of partial ingestion of prey has been recorded by Macpherson (1983) working on predation of *Genypterus capensis*, and in this instance it was hypothesized that the behaviour is a feeding optimization strategy.

The variable sample size evident in the bi-monthly analysis of stomach contents resulted from fluctuations in catches. Both Coetzee & Baird (1981b) and Smale & Buxton (1985) showed variations in the catch per unit effort of this species in Algoa Bay. Although caught throughout the year, *C. nufar* appears to be most common in catches between October and April (Smale & Buxton 1985). Diving has confirmed that *C. nufar* occurs inshore throughout the year (unpublished data). The causes of fluctuations in catches are not clear but may well represent larger predators responding to patchy distribution of prey. The importance of schooling fishes such as *Sardinops ocellata* to larger individuals, particularly in March – April 1978, suggests that this predator responds very strongly to highly abundant prey. This probably accounts for the dominance of clupeids and engraulids from November to April, when they appear to move into shallow coastal waters. *L. reynaudi* appears sporadically in the diet, perhaps coincidental with spawning activity of the squid (Smale 1983). Demersal fish make up the bulk of the prey through the rest of the year.

The peak of *S. ocellata* in the diet of *C. nufar* in 1978 and the subsequent appearance of *E. capensis* conforms well with data collected for other predators, such as *Argyrosomus hololepidotus* (Smale & Bruton 1985).

### *Petrus rupestris*

*Petrus rupestris* is a large demersal carnivore associated with reefs. It has a robust body and relatively thick caudal peduncle and a broad, forked tail. The powerful jaws bear 4 – 6 strong canine teeth which are used to attack and masticate prey, including the heavily spined *Galeichthys* species. It is likely that the catfish is killed and the spines either forced down or broken prior to ingestion. This dentition probably also explains the fairly close correlation of prey size to predator size. Evidently *P. rupestris* normally hunts relatively large prey. The selection of large prey by big specimens may be related to the gill raker structure, which changes ontogenetically from elongate rakers to shorter, broad structures (personal observation), while the gape is about 10% of fork length.

The prey of *P. rupestris* are mostly reef-associated species and the rest are either found over sandy areas or are pelagic, but may have been close to reefs when taken. Most of the dominant prey are either solitary or found in small groups. Unlike *C. nufar*, crustaceans were not recorded from fish larger than 200 mm and it appears that *P. rupestris* is less of a generalist predator than *C. nufar*. A progression of prey was recorded from mysids to cryptic small reef fish to suprabenthic species such as sparids (*Diplodus sargus, Gymnocrotaphus curvidens*). Large specimens (> 900 mm) are uncommon in inshore waters (< 30 m) and tend to move offshore onto deep reefs (40 – 100 m), where specimens up to 50 kg are caught.

No other detailed studies of feeding have been made although Nepgen (1982) recorded four fish with stomach contents from False Bay. These contained no pelagic fish but *Spondyliosoma emarginatum* and *Clinus* sp. were found. Other prey he records are mantis shrimp, amphipods and *Turbo sarmaticus* and the remains of a brittlestar in one stomach. Regrettably no details of predator size were given. The invertebrates recorded do not accord with observations made in this study. Anecdotal information by Stander & Nepgen (1968) showed that *P. rupestris* occurs over rocky banks and that *Octupus*, clinids, small roman (*Chrysoblephus laticeps*) and other reef fish are taken. Again no size is documented but these records agree with this study although *C. laticeps* was not recorded here.

### *Polysteganus praeorbitalis*

*P. praeorbitalis* has a deep. laterally compressed body and a forked tail. The gape is 10% FL and the first gill arch has 20 – 25 elongate gill rakers (van der Elst 1981) which probably serve to retain small prey when feeding. The jaws bear 4 – 6 canine teeth and it is clearly an active piscivore which hunts over reefs. Although crustaceans are commonly taken by fish smaller than 400 mm, fish are the dominant prey of all size groups. The dominance of small fishes such as the clinids and tripterygiids is reduced and larger fish, such as sparids, are taken to a greater extent. The cheilodactylids are most important as prey of *P. praeorbitalis* between 301 and 400 mm. A minor proportion of the teleosts taken were pelagic but may have been taken as they swam close to reefs.

*P. praeorbitalis* is uncommon in the south-eastern Cape where it is usually encountered in shallow water (< 20 m). No other study on the feeding of *P. praeorbitalis* has been published although van der Elst (1981) notes that it takes large crabs, crayfish, a variety of reef fish and squid. These observations made from Natal appear to agree with the results of this study although crayfish, which are rare in the shallows of the eastern Cape, were not found during this investigation.

### *Epinephelus guaza*

*E. guaza* is a benthic reef-associated species usually found near caves. With its cryptic colouration this fish is easily overlooked as it rests on the bottom, stabilizing itself with its paddle-like pectoral fins. Like their congeners, they are ambush predators (Randall 1967; Hobson 1968; Collette & Talbot 1972; Harmelin-Vivien & Bouchon 1976). They lie in wait for a prey to approach closely, then charge and engulf the victim with the large mouth (the gape is 16% TL) and by expanding the operculae. These features are evident from the large head which is 30% of total length. The water engulfed is passed out between 20 – 25 strong and sharply spined gill rakers. The rows of small teeth are ideal for grasping octopods.

Over the size range examined, crabs and octopods were the principal species taken with *Plagusia chabrus* and *Octopus vulgaris* dominating the diet. Reef fish made up the majority of the teleost prey. The large array of prey other than the two species mentioned above suggests opportunism. The importance of the two invertebrates may suggest that they are abundant in the area, but it could also imply that the rockcod is in fact a specialist, which will take other prey when the preferred prey are absent. Although this species can attain 1500 mm (van der Elst 1981) this is considerably larger than the size recorded in this study.

No direct observations on crepuscular or nocturnal behaviour were collected in this study, although both crabs and octopods are more active at night, hunting for food (Altman 1967; Kayes 1974; Nigmatullin & Ostapenko 1976; personal observation). Octopods, however, also forage short distances from their lairs during the day (Smale & Buchan 1981 and this study). When away from their lairs, they are particularly vulnerable to predation. it is not known whether rockcods can successfully attack octopods in their lairs. As freshly ingested specimens of both groups were found during the day, when *E. guaza* is seen to be active on reefs, it is likely that this rockcod is diurnal. Collette & Talbot (1972) record that *E. guttatus, E. adscensionis, E. striatus, E. cruentatus, E. fulvus, Mycteroperca venenosa* and *M. tigris* are common diurnal and crepuscular predators in the Virgin Islands. Starck & Davis (1966) found that rockcods fed by day and night, with a peak at sunset in the Florida Keys. Hobson (1968) found that *Epinephelus labrifrons* feeds throughout the day and night, but perhaps more productively at night. On the other hand, he found that *Mycteroperca roseacea* is principally crepuscular and feeds on schooling flatiron herring, *Harengula thrissina*, when the predator is larger than 300 mm. Harmelin-Vivien & Bouchon (1976) found the serranids from Tulear, Madagascar, feed throughout the day but more actively at night. From these accounts, it appears that feeding times vary between species and that crepuscular or nocturnal feeding by *E. guaza* is also possible.

Although the majority of the fish taken are reef-associated, indicating that most of the feeding is done over reefs, a few, such as bothids and cynoglossids are associated with sandy substrates. These are probably taken by individuals inhabiting the edges of reefs. *Lithognathus lithognathus* is also usually found over sand flats during the day but at dusk it approaches reefs where it would be vulnerable to predation by *E. guaza* (personal observation).

The prey of *E. guaza* changed with increasing predator size. Crustaceans became less important with growth, while octopods and fish became more dominant. Furthermore, the larger specimens took more varied prey than small fish and the maximum size of prey chosen increased with growth. Similar findings were reported for *Epinephelus striatus* in the West Indies (Randall 1967). Harmelin-Vivien & Bouchon (1976) similarly found that prey of small *Epinephelus merra* took brachyurans predominantly while larger fish took few brachyurans but a large quantity of fish and cephalopods.

## Predator – prey interactions

A distinguishing feature of reef fish predator – prey interactions and those of pelagic and open sand environments is that a heterogeneous reef surface, which is covered by encrusting organisms, provides cover for predators and prey. The relief is determined largely by the geological structure. Depth and physical factors such as wave action influence the biotic components and spatial complexity of reefs (Buxton & Smale 1984). Diving observations have revealed that the number and size of fishes and the number of species is generally greater where there is high relief, which is consistent with other studies (Starck & Davis 1966). Over the flat reefs, particularly if there is sand scour, the diversity of invertebrates and fishes is lower (personal observations).

The advantage of cover to prey in avoiding predation is well known and has been described for fish in various habitats including fresh water (Jackson 1961; Greenwood 1965; Keast 1978) and estuaries (Whitfield & Blaber 1978; Blaber 1982). Several studies of marine fishes have highlighted the benefit of structurally complex habitats like reefs as refuges against predation. These include studies by Hiatt & Strasburg (1960) on the coral reefs of the Marshall Islands and by Hobson (1968) in the Gulf of California. Starck & Davis (1966) describe the habits of fishes and the use of shelters by several species. They also describe the use of shelter by individual grunts (Pomadasyidae) once they are detached from schools when pursued by carangids. Similarly, Hartline, Hartline, Szmant & Flechsig (1972) describe how a school of plankton-feeding *Chromis cyaneus* flees to the shelter of a coral head when approached by predators such as carangids, lutjanids and sphyraenids. This escape response ensured that the *Chromis* were safely in the coral head before the predators were close enough to attack. Potts (1980, 1981) has described the reactions of prey to attacks by carangids and shows how schools of lutjanids, mullids and *Gerres* sp. use the advantages of schooling with the spatial complexity of reefs to escape. His descriptions agree well with behaviour seen during this study in reactions between *Sarpa salpa* and other young sparids when subjected to predation by *Cheimerius nufar* and *P. rupestris*. Similarly, other prey such as *Monodactylus falciformis, Gymnocrotaphus curvidens* and *Diplodus sargus* appear to use reef structures in their escape behaviour. Field studies appear to have produced general agreement on the strategic benefit of reefs and other protective structures to prey.

These observations have been confirmed in laboratory studies and in modelling. Ware (1972) examined the feeding behaviour of rainbow trout (*Salmo gairdneri*) presented with different prey sizes and density on substrates of varying complexity. He found that the intensity of predation and total food consumption was inversely related to the complexity of the substrate because a number of prey were able to escape detection by finding cover. Similarly Stein (1977) showed that crayfish suffer less predation with increased substrate particle size, as they have effective refuges. Glass (1971) found that increased structural diversity of aquaria resulted in reduced capture rate of prey (guppies, *Lebistes reticularis*) and fewer attempts at predation by largemouth bass (*Micropterus salmoides*). However at low complexity the prey could be decimated.

Many small reef fishes are seen individually and are characterized by cryptic colouration. They are often immobile for long periods (Hobson 1968, 1974; Feder, Turner & Limbaugh 1974; Helfman 1978). In this study clinids, gobies, cheilodactylids, batrachoidids and the serranid *Acanthistius sebastoides* are examples of this group. They are often associated with small patches of algae or are found in depressions in the reef, where they are easily overlooked. They obviously benefit from crypsis and immobility not only in reducing predation on them but also (presumably) in intercepting their own prey. Observations on 'speculative dives' at the reefs and into caves by predatory sparids were described above and this behaviour is hypothysized to frighten prey into flight and thus make them more vulnerable to attack. This behaviour appears to be specifically aimed at cryptic individual prey. Another attack pattern described was the use of reefs and boulders to conceal the approach of predators. Similar behaviour has been reviewed by Curio (1976) for both terrestrial and aquatic animals. *Epinephelus guaza*, on the other hand, is an ambush predator which lies immobile until prey are close enough to be attacked.

Different hunting tactics were described earlier and these observations show that a change of behaviour is necessary to take different prey types. Individual reef hunting, individual attacks on grouped prey and 'pack' hunting were described. It was observed that the latter two strategies are very similar to attacks by several other predatory species on grouped prey (Hobson 1968, 1978, 1979; Major 1978) and that the prey reacted in a similar manner. Pack hunting was observed in *C. nufar* and *P. praeorbitalis* but not in *P. rupestris*, although circumstantial evidence of it was described. No other observations of hunting behaviour have been made on these species although Penrith (1972) mentions that *P. rupestris* dart into crevices for food, which was called the 'speculative dive' here. Top reef predators examined in this study were apparently diurnal although peaks of activity were not detected, largely because of inadequate diving time, and samples were collected by day from fishermen.

Several common features were found in predation by reef carnivores. Firstly, there is an ontogenetic change of diet, crustaceans becoming less important with an increase in size. Ontogenetic dietary changes with large carnivorous fishes have been shown by numerous authors including Hobson (1968) Harmelin-Vivien & Bouchon (1976), Smale (1984) and Smale & Bruton (1985). Secondly, each of the reef predator's diets comprised reef-dwelling animals although soft bottom demersal species are also taken, probably when close to reefs and vulnerable to these predators. Large (> 400 mm) *Cheimerius nufar* were somewhat of an exception as they largely took pelagic fish, although much of this sample was collected when pilchards, *S. ocellata*, were abundant in Algoa Bay. Nevertheless, pelagic species are more dominant prey of *C. nufar* than other reef fishes. Cephalopods are important prey of all the reef predators discussed here and particularly for *E. guaza*.

These prey species are themselves predators on invertebrate components of the reef fauna, such as crustaceans. This holds for octopods (Smale & Buchan 1981), *Cheilodactylus fasciatus* and *Chirodactylus brachydactylus* (Butler 1975) and some Gobiidae (Butler 1980). Christensen (1978) reported that *Diplodus sargus*, *D. cervinus* and *Sarpa salpa* juveniles feed largely on small crustaceans although *S. salpa* becomes herbivorous when adult (Joubert & Hanekom 1980). Stobbs (1980) recorded that the gobiesocid *Chorisochismus dentex* feeds on small crustaceans, sea urchins and limpets. Similarly, clinids inhabiting rock pools feed largely on small invertebrates (Bennett, Griffiths & Penrith 1983) while *Acanthistius sebastoides* feeds largely on small crabs and fishes (unpublished data). Thus the reef predators examined during this study feed largely on first to third level consumers and the food web is largely reef-based.

There is considerable overlap in prey species and size taken by the four predators considered here. This overlap need not necessarily imply competition if demand for a resource does not exceed supply (Larkin 1956; Birch 1957; Sale 1979). Reduction in potential competition between these species may be related in part to habitat selection, as has been suggested in previous studies (Keast, Harker & Turnbull 1978; Helfman 1978; Sale 1979). None of the predators considered here are very numerous in exploited areas, although *C. nufar* is the most common. This is suggested by the total number of predators examined in this study (3235 *C. nufar*, 751 *P. rupestris*, 74 *P. praeorbitalis* and 319 *E. guaza*), although the figures only provide a rough estimate of relative abundance. At present it appears that these four predators successfully coexist. Fishing pressure is high on carnivorous fishes, which are therefore the first to be removed from exploited reefs (Randall 1982). Competition for food or space is therefore unlikely because of the relatively low density of predators, whereas their prey are generally unexploited.

## Acknowledgements

The co-operation of scores of ski-boat fishermen and spearfishermen is gratefully acknowledged. My colleagues at the Port Elizabeth Museum provided diving back-up and C.D. Buxton was my diving buddy and helped with material collection. I thank the National Parks Board of Trustees for permission to work in the TCNP and J.C. Allen, P.A. Joubert and D.F. Bower for their assistance. Dr H.M. Kok wrote most of the computer programs used in this study and Dr J.H. Wallace and Prof. M.N. Bruton criticized a draft of this paper. W. Mahola and R. Barnard assisted in field collections and Miss M. du Plessis assisted with data checking and final drawings. The Blenkinsop Trust provided funding from 1978 – 1982 and the paper was prepared for publication while I was funded by the South African National Council for Oceanographic Research.

## References

ALTMAN, J.S. 1967. The behaviour of *Octopus vulgaris* Lam. in its natural habitat: a pilot study. *Underwater Ass. Rep.*: 77 – 83.

BENNET, B., GRIFFITHS, C.L. & PENRITH, M-L. 1983. The diets of littoral fish from the Cape Peninsula. *S. Afr. J. Zool.* 18: 343 – 352.

BIRCH, L.C. 1957. The meaning of competition. *Am. Nat.* 91: 5 – 18.

BLABER, S.J.M. 1982. The ecology of *Sphyraena barracuda* (Osteichthyes:Perciformes) in the Kosi system with notes on the Sphyraenidae of other Natal estuaries. *S. Afr. J. Zool.* 17: 171 – 176.

BUTLER, G.S. 1975. An investigation into the biology of two inter- and infra-tidal species of Cheilodactylidae (Pisces:Teleostei). B.Sc. Honours project, Rhodes University.

BUTLER, G.S. 1980. Aspects of the biology of *Caffrogobius caffer* (Günther) (Pisces:Teleostei:Gobiidae) in the Eastern Cape. M.Sc. thesis, Rhodes University.

BUXTON, C.D. 1984. Feeding biology of the Roman *Chrysoblephus laticeps* (Pisces:Sparidae). *S. Afr. J. Mar. Sci.* 2: 33 – 42.

BUXTON, C.D. & SMALE, M.J. 1984. A preliminary investigation of the marine ichthyofauna in the Tsitsikamma Coastal National Park. *Koedoe* 27: 13 – 24.

BUXTON, C.D., SMALE, M.J., WALLACE, J.H. & COCKCROFT, V.G. 1984. Inshore small mesh trawling survey on the Cape south coast. Part 4. Contributions to the biology of some teleostei and chondrichthyes. *S. Afr. J. Zool.* 19: 180 – 188.

CHRISTENSEN, M.S. 1978. Trophic relationships in juveniles of three species of sparid fishes in the South African marine littoral. *Fish. Bull. U.S.* 76: 377 – 388.

CLARKE, M.R. 1962. The identification of cephalopod 'beaks' and the relationship between beak size and total body weight. *Bull. Br. Mus. nat. Hist.* 8: 421 – 480.

COETZEE, P.S. & BAIRD, D. 1981a. Age, growth and food of *Cheimerius nufar* (Ehrenberg, 1820) (Sparidae), collected off St Croix Island, Algoa Bay. *S. Afr. J. Zool.* 16: 137 – 143.

COETZEE, P.S. & BAIRD, D. 1981b. Catch, composition and catch per unit effort of anglers catches off St Croix Island, Algoa Bay. *S. Afr. J. Wildl. Res.* 11: 14 – 20.

COLLETTE, B.B. & TALBOT, F.H. 1972. Activity patterns of coral reef fishes with emphasis on nocturnal – diurnal changeover. In: Results of the Tektite Program: Ecology of Coral Reef Fishes. (Eds) Collette, B.B. & Earle, S.A. *Bull. Los. Ang. Cty Mus. nat. Hist. (Sci.)* 14: 98 – 124.

COTT, H.B. 1957. Adaptive coloration in animals. Methuen & Co., London.

CURIO, E. 1976. The ethology of predation. Springer-Verlag, Berlin.

DRUZHININ, A.D. 1975. Some data on Sparid fishes (Fam. Sparidae) of the Gulf of Aden region. *J. Ichthyol.* 15: 531 – 541.

EDMUNDS, M. 1974. Defense in animals: a survey of antipredator defences. Longmans, New York.

FEDER, H.M., TURNER, C.H. & LIMBAUGH, C. 1974. Observations on fishes associated with kelp beds in southern California. *Fish. Bull. Calif. Fish. Game.* 160: 1 – 139.

FIELD, J.G., CLARKE, K.R. & WARWICK, R.M. 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8: 37 – 52.

GLASS, N.R. 1971. Computer analysis of predation energetics in the largemouth bass. In: Systems analysis and simulation in ecology Vol. 1: 325 – 363. (Ed.) Patten, B.S. Academic Press, New York.

GREENWOOD, P.H. 1965. Predation and its effects on the migration and speciation in African fishes: further comments. *Proc. zool. Soc. Lond.* 144: 310 – 313.

HARMELIN-VIVIEN, M.L. 1981. Trophic relationships of reef fish in Tulear (Madagascar). *Oceanol. Acta.* 4: 365 – 374.

HARMELIN-VIVIEN, M.L. & BOUCHON, C. 1976. Feeding behaviour of some carnivorous fishes (Serranidae and Scorpaenidae) from Tulear (Madagascar). *Mar. Biol.* 37: 329 – 340.

HARTLINE, A.C., HARTLINE, P.H., SZMANT, A.M. & FLECHSIG, A.O. 1972. Escape responses in a pomacentrid reef fish *Chromis cyaneus*. In: Results of the Tektite Program: Ecology of coral reef fishes. (Eds) Collette, B.B. & Earle, S.A. *Bull. Los Ang. Mus. nat. Hist (Sci.)* 14: 93 – 97.

HELFMAN, G.S. 1978. Patterns of community structure in fishes: summary and overview. *Env. Biol. Fish.* 3: 129 – 148.

HIATT, R.W. & STRASBURG, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Mongr.* 30: 65 – 127.

HOBSON, E.S. 1968. Predatory behaviour of some shore fishes in the Gulf of California. *U.S. Fish. Wildl. Serv. Res. Rep.* (73): 1 – 92.

HOBSON, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fish. Bull. U.S.* 72: 915 – 1031.

HOBSON, E.S. 1978. Aggregating as a defence against predators in aquatic and terrestrial environments. In: Contrasts in behaviour. (Eds) Reese, E.S. & Lighter, F.J. Wiley, New York.

HOBSON, E.S. 1979. Interactions between piscivorous fishes and their prey. In: Predator – prey systems in fisheries management. pp. 231 – 242. (Ed.) Clepper, H. Sport Fishing Institute, Washington D.C.

HYNES, H.B.N. 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 19: 36 – 58.

HYSLOP, E.J. 1980. Stomach content analysis — a review of methods and their application. *J. Fish Biol.* 17: 411 – 429.

JACKSON, P.B.N. 1961. The impact of predation, especially by the tigerfish (*Hydrocyon vittatus* Cast.) on African freshwater fishes. *Proc. zool. Soc. Lond.* 132: 603 – 622.

JOUBERT, C.S.W. & HANEKOM, P.B. 1980. A study of feeding in some inshore reef fish of the Natal coast, South Africa. *S. Afr. J. Zool.* 15: 262 – 274.

KAYES, R.J. 1974. The daily activity pattern of *Octopus vulgaris* in a natural habitat. *Mar. Behav. Physiol.* 2: 337 – 343.

KEAST, A. 1978. Trophic and spatial interrelationships in the fish species of an Ontario temperate Lake. *Env. Biol. Fish.* 3: 7 – 31.

KEAST, A., HARKER, J. & TURNBULL, D. 1978. Nearshore fish habitat utilization and species associations in Lake Opinicon (Ontario, Canada). *Env. Biol. Fish.* 3: 173 – 184.

LARKIN, P.A. 1956. Interspecific competition and population control in freshwater fish. *J. Fish. Res. Bd. Can.* 13: 327 – 342.

MACPHERSON, E. 1983. Feeding pattern of the kingklip (*Genypterus capensis*) and its effect on the hake (*Merluccius capensis*) resource off the coast of Namibia. *Mar. Biol.* 78: 105 – 112.

MAJOR, P.F. 1978. Predator – prey interactions in two schooling fishes, *Caranx ignobilis* and *Stoplephorous purpureus*. *Anim. Behav.* 26: 760 – 777.

NEPGEN, C.S. DE V. 1977. The biology of the hottentot *Pachymetopon blochii* (Val.) and the silver fish *Argyrozona argyrozona* (Val.) along the Cape south-west coast. *Investl Rep. Div. Sea Fish. S. Afr.* 105: 1 – 35.

NEPGEN, C.S. DE V. 1982. Diet of predatory and reef fish in False Bay and possible effects of pelagic purse-seining on their food supply. *Fish. Bull. S. Afr.* 16: 75 – 93.

NIGMATULLIN, Ch.M. & OSTAPENKO, A.A. 1976. Feeding of *Octopus vulgaris* Lam. from the north-west African coast. 1 – 3. Shellfish and Benthos Committee I.C.E.S. Charlotenlund, Denmark.

NORMAN, J.R. & GREENWOOD, P.H. 1963. A history of fishes. Ernest Benn, London.

PENRITH, M.J. 1972. The behaviour of reef-dwelling sparid fishes. *Zool. afr.* 7: 43 – 49.

PINKAS, L., OLIPHANT, M.S. & IVERSON, L.K. 1971. Food habits of albacore, bluefin tuna and bonito in California waters. *Calif. Fish. Game Fish. Bull.* 152: 1 – 105.

POTTS, G.W. 1980. The predatory behaviour of *Caranx melampygus* (Pisces) in the channel environment of Aldabra Atoll (Indian Ocean). *J. Zool., Lond.* 192: 323 – 350.

POTTS, G.W. 1981. Behavioural interactions between the Carangidae (Pisces) and their prey on the fore-reef slope of Aldabra, with notes on other predators. *J. Zool., Lond.* 195: 385 – 404.

RANDALL, J.E. 1967. Food habits of reef fishes of the West Indies. *Stud. Trop. Oceanogr.* 5: 665 – 847.

RANDALL, J.E. 1982. Tropical marine sanctuaries and their significance in reef fisheries research. In: N.O.A.A. Technical Memorandum NMFS-SEFC-80. The biological bases for Reef Fishery Management. Proceedings of a workshop held October 7 – 10, 1980 at St Thomas, Virgin Islands of the United States. (Eds) Huntsman, G.R., Nicholson, W.R. & Fox, W.W. Jr. pp. 167 – 178.

SALE, P.F. 1979. Habitat partitioning and competition in fish communities. In: Predator – prey systems in fisheries management. pp. 323 – 332. (Ed.) Clepper, H. Sport Fishing Institute, Washington, D.C.

SMALE, M.J. 1983. Resource partitioning by top predatory teleosts in eastern Cape coastal waters (South Africa). Ph.D. thesis, Rhodes University.

SMALE, M.J. 1984. Inshore small-mesh trawling survey of the Cape south coast. Part 3. The occurrence and feeding of *Arygrosomus hololepidotus, Pomatomus saltatrix* and *Merluccius capensis*. *S. Afr. J. Zool.* 19: 170 – 179.

SMALE, M.J. & BRUTON, M.N. 1985. Predation and prey selectivity by *Argyrosomus hololepidotus* (Osteichthyes: Sciaenidae) in south-eastern Cape waters of South Africa. *S. Afr. J. Zool.* 20: 97 – 108.

SMALE, M.J. & BUCHAN, P.R. 1981. Biology of *Octopus vulgaris* off the east coast of South Africa. *Mar. Biol.* 65: 1 – 12.

SMALE, M.J. & BUXTON, C.D. 1985. Aspects of the recreational ski-boat fishery off the eastern Cape, South Africa. *S. Afr. J. Mar. Sci.* 3: 131 – 144.

SMITH, J.L.B. 1938. The South African fishes of the families Sparidae and Denticidae. *Trans. R. Soc. S. Afr.* 26: 225 – 305.

SMITH, M.M. 1980. A review of the South African cheilodactylid fishes (Pisces: Perciformes) with descriptions of two new species. *Ichthyol. Bull. Rhodes Univ.* 42: 1 – 14.

STANDER, G.H. & NEPGEN, C.S. 1968. Some facts about linefish — with special reference to False Bay. *S. Afr. Shipp. News Fish. Ind. Rev.* 33: 108 – 111.

STARCK, W.A. II. 1970. Investigations of the gray-snapper *Lutjanus griseus*. *Stud. trop. Oceanogr.* 10: 1 – 224.

STARCK, W.A. II & DAVIS, W.P. 1966. Night habits of fishes of alligator reef, Florida. *Ichthyologica Aquar. J.* 38: 313 – 356.

STEIN, R.A. 1977. Selective predation, optimal foraging and the predator – prey interaction between fish and crayfish. *Ecology* 58: 1237 – 1253.

STOBBS, R.E. 1980. Feeding habits of the giant clingfish *Chorisochismus dentex* (Pisces: Gobiesocidae). *S. Afr. J. Zool.* 15: 146 – 149.

VAN DER ELST, R.P. 1981. A guide to the common sea fishes of southern Africa. Struik, Cape Town.

WARE, D.M. 1972. Predation by rainbow trout (*Salmo gairdneri*): The influence of hunger, prey density and prey size. *J. Fish. Res. Bd Can.* 29: 1193 – 1201.

WHITFIELD, A.K. & BLABER, S.J.M. 1978. Food and feeding ecology of piscivorous fishes at Lake St Lucia, Zululand. *J. Fish Biol.* 13: 675 – 691.

WINDELL, J.T. 1968. Food analysis and rate of digestion. In: Methods for the assessment of fish production in fresh waters. I.B.P. Handbook No. 3. (Ed.) Ricker, W.E. Blackwell, Oxford.