

Feeding biology of the hottentot, *Pachymetopon blochii* (Val.), with an estimate of daily ration

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Gut content analysis shows the hottentot to be an omnivore, consuming a wide variety of algae and invertebrate prey. Amphipod crustaceans and rhodophytes are the dominant food items, although hydroids, echinoderms and molluscs are also eaten in smaller quantities. Geographic variation in the diet was negligible, although seasonal trends were marked. A progressive change in diet occurs with fish size, larger individuals consuming progressively more algae. The hottentot diet differs from those of a number of co-occurring sparids in being far more generalized. Hottentot feed throughout the diel cycle, although feeding activity is markedly higher during the rising tide. The feeding cycle is further modified by a tendency to select particular food items at night. Available mathematical feeding rate simulation models for continuously feeding fish were improved to incorporate an asymptotic consumption rate. The resultant model was used to calculate daily consumption rates for hottentot, giving a value of 2.5% body weight per day. This is compared with values calculated using earlier models, and with published feeding rate values for other species.

Ontleding van die buikinhoud dui aan dat die hottentot 'n omnivoor is wat 'n groot verskeidenheid alge en ongewerwelde prooi eet. Amfipode skaaldiere en rodofoete is die oorheersende voedselkomponente, alhoewel hidroïede, ekinoderme en molluske ook in kleiner hoeveelhede geëet word. Geografiese dieetverskeidenheid was gering, alhoewel seisoenings opmerklik was. Daar is 'n toenemende verandering in dieet teenoor visgrootte, met die gevolg dat groter visse al hoe meer alge eet. Die dieet van hottentotte verskil van dié van 'n aantal spariede, wat saam met hottentotte aangetref word, aangesien dit baie meer uitgebrei is. Hottentotte wei die hele dag deur, alhoewel weiding baie meer aktief is tydens die stygende gety. Die weidingsiklus is verder gewysig deur die neiging om snags spesifieke voedselitems uit te soek. Verbeterings is aan beskikbare wiskundige voedingstemosimuleermodelle aangebring ten einde 'n asimptotiese verbruikingskoers in te sluit. Die resulterende model is gebruik om daaglikse verbruikingskoerse vir hottentotte te bereken, met 'n resultaat van 2,5% ligmaansmassa per dag. Hierdie resultaat word vergelyk met waardes wat met vroeëre modelle bereken is, en ook met gepubliseerde voedingskoerswaardes van ander spesies.

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The hottentot fish, *Pachymetopon blochii* (Val.), is a sparid endemic to southern Africa. It occurs commonly in and around kelp beds and on subtidal reefs, from Luderitz to the mouth of the Breede River (van der Elst 1981). It forms a major component of the western Cape commercial handline catch and has been identified as an important carnivore in the kelp bed community (Velimirov, Field, Griffiths & Zoutendyk 1977). Preliminary observations on the diet of this species have been conducted (Stander & Nepgen 1968; Nepgen 1977). These were not, however, quantitative, nor did they consider variation in the diet with area, season or fish size. By contrast this study presents quantitative information on the feeding habits of *P. blochii* and considers change in diet with area, season and fish size. Comparisons are also drawn with sympatric sparids.

No attempts have been made to determine the diel rhythms of feeding and elimination of any of the commercially important South African linefish species, nor to estimate their rate of food consumption. One of the principal reasons for this is the practical difficulty in obtaining adequate samples of fish over a regular time series. The hottentot fish is, however, readily captured by handline at all times of day and is thus an ideal experimental animal for the estimation of diel feeding patterns and daily ration. An attempt was thus made to

utilize hottentot to develop suitable techniques by which these parameters may be estimated in the field.

Methods

Diet

Most of the 737 fish examined were obtained through fish dealers or from commercial hand-line fishermen at the four sampling sites shown in Figure 1 between February 1984 and July 1985. A single large sample of hottentot, covering the full size range, was also collected in the Dyer Island area in March 1984, by fishing with handlines from a Sea Fisheries Research Institute research vessel. Since the majority of these fish were longer than 200 mm total length, smaller individuals were also speared by SCUBA divers at Partridge Point, False Bay.

The total length and fork length of each fish were measured in millimeters, and the mass determined in grams. The stomach and hindgut were then removed and preserved in buffered 10% formalin. After determining the settled volume, stomachs contents were analysed under a stereo dissecting microscope. Gut contents were identified to the lowest possible taxon and assigned a visual percentage volume (Hyslop 1980). Percentage frequency of occurrence (Hynes 1950) was calculated for each food category as well as for major food classes. The

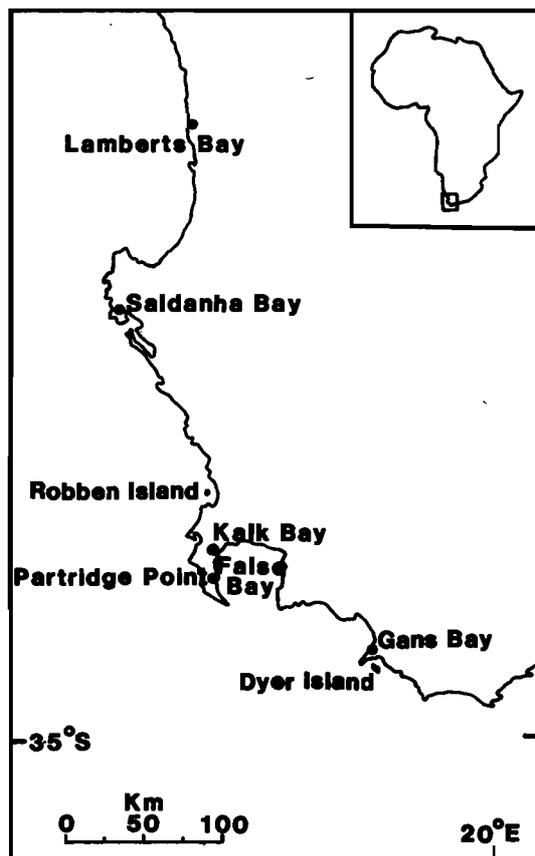


Figure 1 Map of the Cape west and south-west coast showing the four sites at which hottentot samples were collected.

data for each month, from each area, were then grouped according to size class. The 96 samples resulting from this grouping were subsequently summarized to provide a generalized view of the diet of *P. blochii*, and to test for a change in diet with area, size, and season.

As arc-sine is the suggested transformation for percentage data (Zar 1974), this was adopted. Preliminary tests on the raw data, using other transformation choices, also indicated that an arc-sine transformation yielded the most promising results for the classification and ordination analyses.

Interpretation of the data was facilitated by two methods of cluster analysis proposed by Field, Clark & Warwick (1982). The first of these utilized the group average sorting method and Bray-Curtis measure of similarity, to derive a dendrogram showing percentage similarity between different groups of fish. This was complemented by non-parametric multi-dimensional scaling, which uses the same similarity matrix to produce an ordination diagram depicted in a two-dimensional form.

Early runs of the entire data set identified samples in which the stomachs of all fish were packed with an individual, usually planktonic taxon. These outliers were excluded from subsequent runs in order to facilitate interpretation of more general size related, geographical, or seasonal trends.

Diurnal feeding cycle and estimation of daily ration

Any estimate of feeding periodicity or daily ration,

based on an analysis of stomach contents, requires a knowledge of the rate of simultaneous gastric evacuation. This was determined by capturing a sample of 140 fish over a 45-min period of intensive handline fishing, in < 10 m of water, at a site off Robben Island. Stomach eversion in fish did not occur. The specimens were transferred to food-free holding tanks on the research vessel, where they were continuously supplied with fresh sea water pumped from the study site. Eleven of the fish were sacrificed immediately upon capture, their fork lengths recorded and the stomach and hindgut of each removed and frozen separately. The remainder of the catch, confined to the tanks, were sampled in the same way at 3-h intervals over a 36-h period.

Although Thorpe (1977) found that serial sampling of fish, denied access to food, underestimates the digestion rate, a modification of his method was adopted in this study, as it was felt this would give a more accurate result. The sampling technique used differed from that of Thorpe (1977) in that only one catch, rather than successive catches made at 3-h intervals, was serially sampled.

Owing to the difficulties of weighing fish on board ship, fork length measurements were converted to mass equivalents using the regression equations given by Nepgen (1977).

After removing excess surface moisture by blotting, stomach contents were weighed to the nearest milligram and sorted under a stereo-dissecting microscope. In order to standardize the effect of variation in fish size, the data were converted to express the stomach contents mass as a percentage of wet fish body mass.

As enzymatic reactions follow an exponential relationship (Fabian *et al.* 1963, in Elliott & Persson 1978), it is assumed that gastric evacuation also proceeds exponentially (Elliott 1972; Doble & Eggers 1978; Elliott & Persson 1978; Lane, Kingsley & Thornton 1979). The gastric evacuation rate constant (R) was thus determined using the equation

$$St = So e^{-Rt}$$

where So is the quantity of food in the stomach at the start of the experiment (t_0), and St is the stomach content mass at each successive sampling period (t).

Diel feeding activity and ration were assessed by collecting a further sample of 15 fish at 3-h intervals over 24 h. All material was obtained by handlining off dinghies at Robben Island, as the presence of dense kelp beds in the natural habitat of the hottentot made gill-netting prohibitive. The fish were processed as described above although the stomach contents were sorted into major taxa and each prey group was assigned a visual percentage by volume.

In order to model the feeding and elimination cycles, it was assumed that the pattern of feeding and elimination follows a 24-h cycle. The amount of food consumed by a fish can be expected to increase to an asymptote as the fish becomes satiated (Elliott & Persson 1978), thereby following a Von Bertalanffy-type

relationship. The equation

$$St = S_{\infty} (1 - e^{-k(t-t_0)})$$

was thus applied to the feeding portions of the cycle, where S_{∞} is the stomach content mass at infinity and k is a constant. As suggested by Hughes (1986), the full data set, and not just a single mean stomach mass per time interval, was utilized in estimating the parameters of the equation.

Using ETAL1, a programme developed by Gaschutz, Pauly & David (1980) for iteratively fitting von Bertalanffy-type curves to irregularly spaced data, curves were fitted to the individual data for the feeding phases. The resultant constants S_{∞} , k and t_0 were then used to predict the start (St_0) and end percentage stomach mass (St) values of each feeding phase. These were subsequently used to determine the constant b , in the exponential equation

$$St = S' e^{-bt}$$

describing the elimination phases, where S' is the stomach content mass at the start of the elimination phase. As compensation must be made for simultaneous ingestion during the elimination phase, the rate b , determined from this will differ from the elimination rate (R), calculated earlier.

In order to estimate the gross daily consumption (C_g), it is necessary to correct for elimination that may occur during periods of nett increase in stomach content mass (feeding phases), and equally, any feeding that may take place during periods of nett elimination. The consumption for each feeding or elimination phase will therefore be the sum of the instantaneous elimination rate and the nett increase in stomach contents mass for that period, and is described by the general equation

$$C = [St' - St] + \int_t^{t'} RS dt$$

where t and t' are the time at the start and end of each period, respectively.

As the Von Bertalanffy-type relationship predominates during periods of nett increase in stomach content mass, the Von Bertalanffy parameters must be incorporated into the integration when determining the consumption for the feeding phase (C_f). The general equation can thus be re-written as:

$$C_f = St' - St + RS_{\infty} \left[t + \left(\frac{e^{-k(t-t_0)}}{k} \right) \right] \Bigg|_t^{t'}$$

Similarly, the exponential relationship will predominate during periods of nett elimination and these parameters must be incorporated accordingly when estimating consumption during the elimination portion (C_e) of the cycle, giving:

$$C_e = St' - St + RSt \left(\frac{e^{-bt'}}{-b} \Bigg|_t^{t'} \right)$$

The daily ration (C_g), is then calculated by obtaining the sum of the consumption rates determined for the two feeding and the two elimination phases.

$$C_g = C_{f1} + C_{e1} + C_{f2} + C_{e2}$$

Finally, in order to test the applicability of this model, our data were fitted to the original Bajkov method (in Elliott & Persson 1978), the corrected Bajkov method (Eggers 1979) and the model proposed by Elliott & Persson (1978).

Results

Diet

Of the 737 *P. blochii* stomachs sampled, 86% contained food, the remaining stomachs being empty. The mean percentage volume and percentage occurrence, of the major prey classes recorded in these pooled data are presented in Table 1, together with comparable percentage occurrence data from Nepgen (1977). Bait organisms (pilchard, squid, redbait, rocklobster and white mussel), were found in 33,5% of the stomachs, but were not considered in the analysis. Pilchard was found to be the most common bait used.

Of the major prey categories, the most important were amphipods, represented in 64% of the stomachs examined and contributing 30% by volume to the diet. Of this volume one third comprised caprellids, of which *Caprella cicur* and *C. aequilibrata* were the most common. The remainder was dominated by *Paramoera capensis* and *Jassa falcata*, the former species contributing approximately half of the total volume of amphipods recorded. The amphipod species represented, and the proportion of the dominant species in the diet, remained relatively constant throughout the sampling area. Nepgen (1977), found *Caprella* species only in stomachs also containing algae, but this association was not apparent in the present study. This suggests that hottentot selectively prey on amphipods whilst feeding amongst understorey algae, rather than accidentally ingesting them whilst grazing, as proposed by Nepgen (1977).

In the category 'Other crustaceans', isopods had the highest frequency of occurrence. Nepgen (1977), in contrast, reported only a few unidentified isopod remains. Although they contributed only 1,3% to total volume, a high diversity of isopods was encountered. Of the 37 species recognized, *Exosphaeroma truncatitelson*, *Exosphaeroma laeviusculum* and *Cymodocella sublevis* occurred most frequently from Lamberts Bay to False Bay, whereas *Dynamenella huttoni* and *Dynamenella doixus* were more common from False Bay eastwards. Isopods were usually found in stomachs also containing algae but this association was not exclusive, suggesting that these crustaceans are selectively ingested.

Other crustaceans contributing significantly to the percentage volume were mysids, stomatopods and adult as well as larval crabs. With the exception of mysids, which occur in resident swarms in kelp beds and around sublittoral reefs, the percentage occurrence of these crustaceans in the diet was low. Decapods, primarily crabs, *Plagusia chabrus*, were less common than reported by Nepgen (1977). Together with rocklobster, *Jasus lalandii*, which occurred in less than 1% of fish, these prey were unimportant in the diet of *P. blochii*.

Table 1 Percentage volume and percentage occurrence of the individual food items recorded in the stomachs of hottentot during this study and the study by Nepgen (1977)

Prey item	This study		% Occ. Major group	Nepgen (1977) % Occ.
	% Vol.	% Occ.		
Amphipods			64,3	
Caprellids	9,27	41,11		
Gammarids	20,47	60,24		
Other crustaceans			38,6	29,1
Cirripeds	0,61	2,58		
Decapods	2,61	4,48		
Isopods	1,33	14,79		
Megalopa	1,75	2,85		
Mysids	3,51	9,63		
Ostracods	0,28	9,63		
Stomatopods	2,03	2,58		
Tanaids	<0,01	0,41		
Algae	18,73		34,19	58,9
Hydroids	11,37		29,58	5,4
Echinoderms			3,0	36,3
Crinoids	2,80	2,31		
Echinoids	0,02	0,54		
Holothurians	<0,01	0,14		
Ophiuroids	0,99	2,17		
Molluscs			30,0	11,8
Small molluscs	1,36	29,71		
<i>Haliotis</i>	0,05	0,13		
<i>Loligo</i>	0,40	0,54		
Others				
Anemones	0,37	0,54		<1,0
Echiuroids	<0,01	0,27		
Eggs	<0,01	2,40		
Nematodes	0,03	2,85		
Polychaetes	3,82	13,98		7,5
Pycnogonids	0,19	2,17		<1,0
Sand grains	<0,01	7,90		
Sipunculids	0,04	1,90		<1,0
Teleost rems.	0,12	0,13		3,8
Tunicates	0,69	1,78		1,5
Unidentified	16,96	45,18		

Algae were the second most important identifiable component of the diet, occurring in 34% of fish and contributing 19% by volume. The most important group of algae eaten were rhodophytes (84% occurrence). This is not unexpected for a species grazing in the understory of kelp beds where, owing to the shading effect of *Laminaria* and/or *Ecklonia*, this algal group is prolific (Branch & Branch 1981). The species most commonly recorded correspond with those mentioned by Simons (1976), Field, Griffiths, Griffiths, Jarman, Zoutendyk, Velimirov & Bowes (1980) and Branch & Branch (1981) as being the dominant forms in the sublittoral zone, many being epiphytic or parasitic on the kelp plants

themselves. An interesting observation is the abundance of *Porphyra capensis* in the fish sampled. The presence of this species (dominant in the littoral zone), showed that the fish fed in the intertidal at high tide.

There appeared to be a close correlation between algae and hydroids in the stomachs, the latter making up 11% of the diet by volume. As the two groups occur together, hydroids often growing epiphytically on the algae, it would be expected that, whilst grazing unselectively on the reef the hottentot will simultaneously ingest both taxa. *Obelia geniculata* occurred most frequently in samples from Lamberts Bay, whereas *Plumularia setacea* and *Aglaophenia pluma* were common from the Saldanha Bay and False Bay areas. *Eudendrium* was the only genus recorded in fish from the Dyer Island area, hydroids contributing a negligible proportion of the diet of fish in this area.

Echinoderms were uncommon in the diet, although Nepgen (1977) found them to be the second most important prey item in his study. Crinoids and brittle stars were the most frequently encountered, with echinoid spines and individual holothurians in a few samples only. When present, crinoids usually contributed significantly to individual stomach contents. It was noticed that these crinoids all had well-developed gonads, the high calorific value of gonad material (Field *et al.* 1980), probably influencing their selection. Most of the molluscs ingested were small species, juveniles or larval forms. With the exception of a few samples containing juvenile squid (*Loligo reynaudii*), or small abalone (*Haliotis parva*) these small bivalves and gastropods contribute minimally to the percentage volume of food eaten, this largely being a function of their low relative densities.

The majority (76,7% vol.; 76,3% occ.) of the category 'Others' consisted of polychaete worms of which *Gunnarea* spp., *Nereis* spp. and *Syllis* spp. were the most common. Soft-bodied animals, such as worms, tunicates, anemones and fish may, however, be the major contributors to the large unidentifiable fraction of the stomach contents and hence be under-represented in the results. As bait was found in 33% of the stomachs analysed, well digested and hence unrecognizable bait organisms may also contribute significantly to the unidentifiable remains. The time elapsed between catching and preserving the sample also plays a role in the proportion of unidentifiable material in the gut, since in some cases the samples obtained when the day had been hot, or when the fishermen returned later than usual, were in an advanced state of digestion, making positive identification of prey items difficult.

Having analysed the pooled data there was reason to suspect that the diet of hottentot may be influenced by fish size, geographical location and season. The data were thus segregated in order to test for consumption patterns associated with these variables.

Geographic variation

An initial similarity analysis of the edited data failed to group samples in any clear pattern based on collection

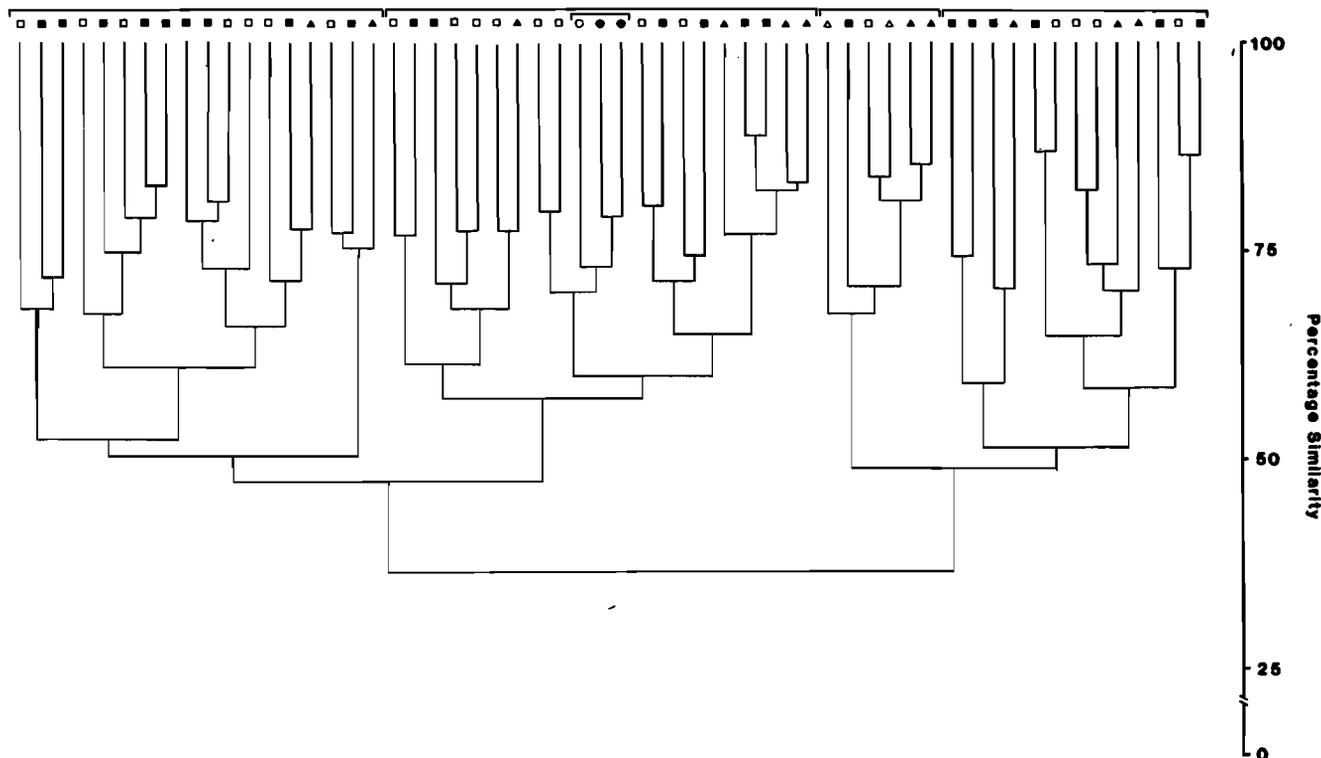


Figure 2 Cluster analysis classification of the dietary data of *P. blochii* showing indistinct clustering by locality. (○ = Gans Bay, ● = Kalk Bay, ▽ = Saldanha Bay and ▼ = Lamberts Bay).

site (Figure 2). This may in part be attributable to variations in the size frequency distributions of fish collected from the four localities.

A further test was thus conducted maintaining the size variable constant by examining only the size class 250–300 mm, which was well represented in all study sites. These data did separate out into four groups at the 50% similarity level, although only the Lamberts Bay and Saldanha Bay data formed coherent clusters. A pictorial representation of the diets of these four groups of fish is shown in Figure 3. This analysis suggests that fish sampled at Dyer Island consumed proportionally more algae by volume than in other areas. This corresponds with the results of Nepgen (1977), who reported a decline in the proportion of crustaceans in the diet from west to east. Of further interest is that hydroids, well represented in samples from other localities, were not recorded in fish from this area. A possible explanation for this could be that, in the event of a high availability of algae, the fish may exhibit selective preference for algae rather than hydroids.

Seasonal trends

Subsequent data selection, keeping both the locality and size variables constant (size class: 250–300 mm, locality: Lamberts Bay), indicated that seasonal changes in diet can also be distinguished, in both the classification and multidimensional scaling methods (Figure 4).

When presented graphically (Figure 5), the reasons for these seasonal trends become more noticeable. The data suggest that during the warmer months the

hottentot consumes proportionally more algae than amphipods. During autumn and winter, however, the volume of algae eaten decreases. These trends were not, however, as strongly evident in data from other sites.

Many of the algae occurring in kelp beds are less abundant during winter. *Hymenema*, for example, is washed up in large quantities during May and June. This may be due to increased wave action, or, as in the case of the epiphytic and parasitic species (e.g. *Carpoblepharis* spp.), a decrease in the availability of host plants, for *Ecklonia* and *Laminaria* exhibit a decline in biomass during the winter months (N. Jarman, Sea Fisheries Research Institute, Cape Town, pers. comm.). As these genera are those most commonly recorded in the diet of *P. blochii*, the seasonal variation in both percentage occurrence and percentage volume of algae is not unexpected. The seasonal change in the diet, identified by the cluster analysis, is thus most likely attributable to the fluctuation in availability of this food source in the environment.

Variations in diet with fish size

Although initial cluster analysis failed to segregate pooled samples of different sized fish into clear size-related groups, this was attributed to interference from other variables, such as season. By selecting a month in which a full size range of fish was collected at each sampling station, and re-running the program, a change in diet with size could be identified.

The most noticeable trend in the changing proportions of the various food categories in fish of increasing size, is

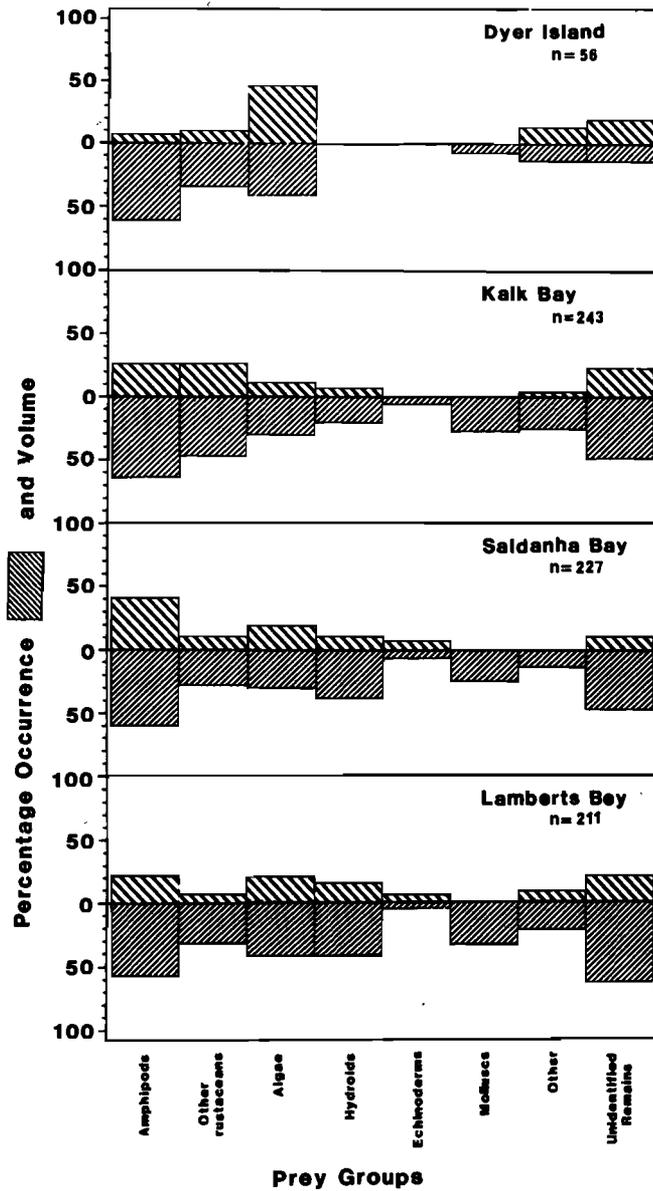


Figure 3 Geographical variation in the mean percentage volume and percentage occurrence of the major prey classes in the diet of *P. blochii* (250–300 mm fork length), recorded at four sites in the south-western Cape (*n* is the sample size).

the progressive decline in the proportion of amphipods eaten and the corresponding increased reliance on algal browsing. Having identified these variables similar changes can be detected in the pooled sample of all fish, and these are shown in Figure 6.

Changing feeding patterns with size were also evident from direct underwater observations of fish in the field. Juveniles were seen occurring singly, or in small groups, leaving the shelter of caves, crevices and overhangs to feed for short periods only. As they attain a size of 150–200 mm, the feeding excursions are prolonged and the fish may join the foraging shoal for extended periods before retreating to cover.

Diel feeding cycle and estimate of daily ration

The course of gut elimination in starved *P. blochii* is

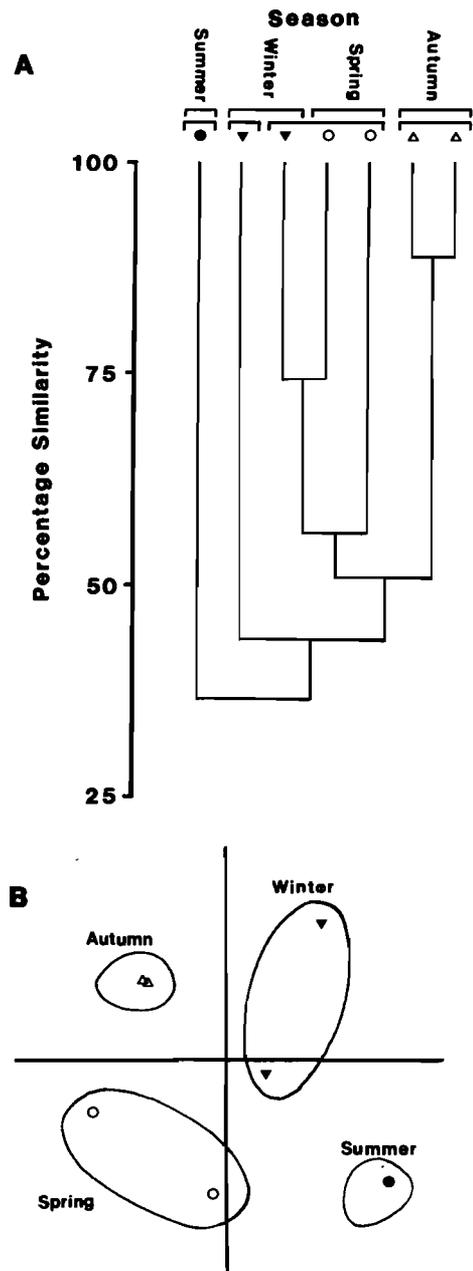


Figure 4 (A) Cluster analysis classification and (B) ordination plot illustrating seasonal trends in the diet of 250–300 mm fork length *P. blochii*, from Lamberts Bay only.

illustrated in Figure 7 and is represented by the equation:

$$St = 1,2675 \times e^{-0,3742t}$$

This indicated that the gut will be 99% evacuated over a period of 12 h 22 min.

Although the fish did not take the bait as readily during certain of the sampling periods, 3-h catches were maintained over the 24-h period, suggesting that at least some of the fish are feeding at all times of day.

Analysis of diel fluctuations in stomach content mass (Figure 8), illustrates that the hottentot exhibits two feeding and elimination cycles daily. These appear to be closely correlated to the tidal cycle, feeding activity

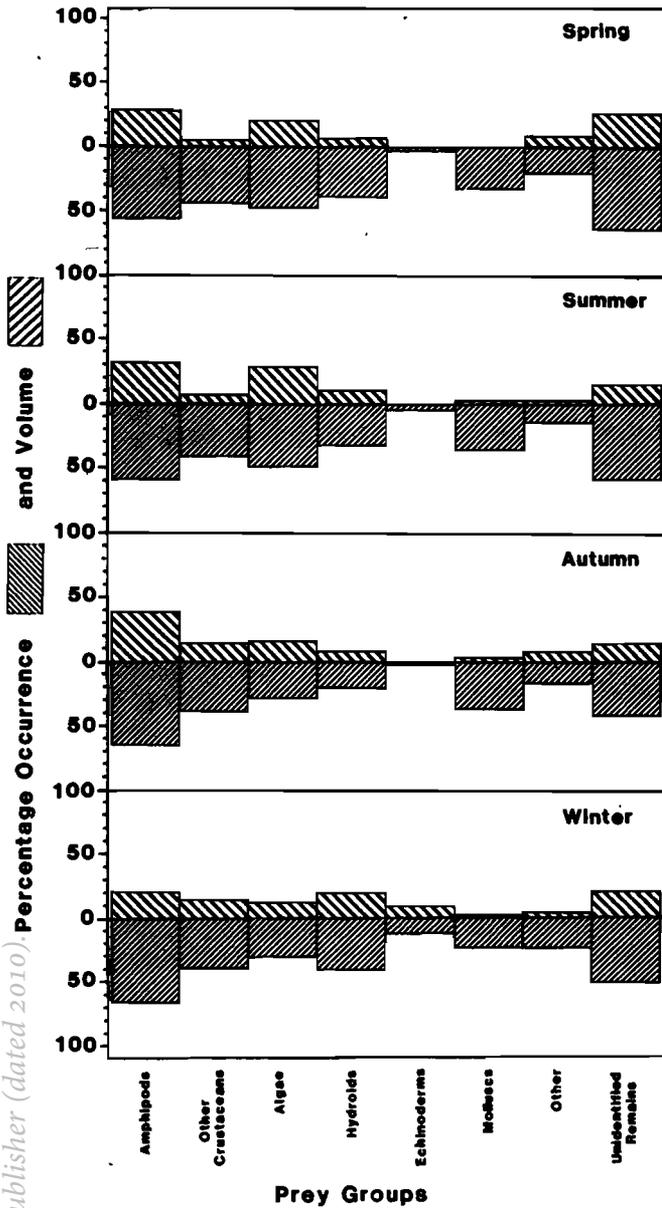


Figure 5 Mean percentage volume and percentage occurrence of the major food items recorded in the diet of *P. blochii*, throughout the year.

Spring = October, November

Summer = December, January, February

Autumn = March, April, May

Winter = June, July, August, September.

increasing during the incoming tide, whilst being greatly reduced during the ebb tide, resulting in a nett decline of stomach contents mass. The solutions to the equations fitted to the feeding and elimination phases are presented in Table 2. Gross consumption rates for each of the four phases are also given. The two feeding phases, both corresponding to the flood tides, together accounted for 80 % of total consumption. The remaining 20 % is taken during the periods of nett elimination, over the ebb tides.

As regards the diel rhythm, there was little difference between the consumption patterns by day and by night. As some 41,5 % of the gross daily ration is consumed

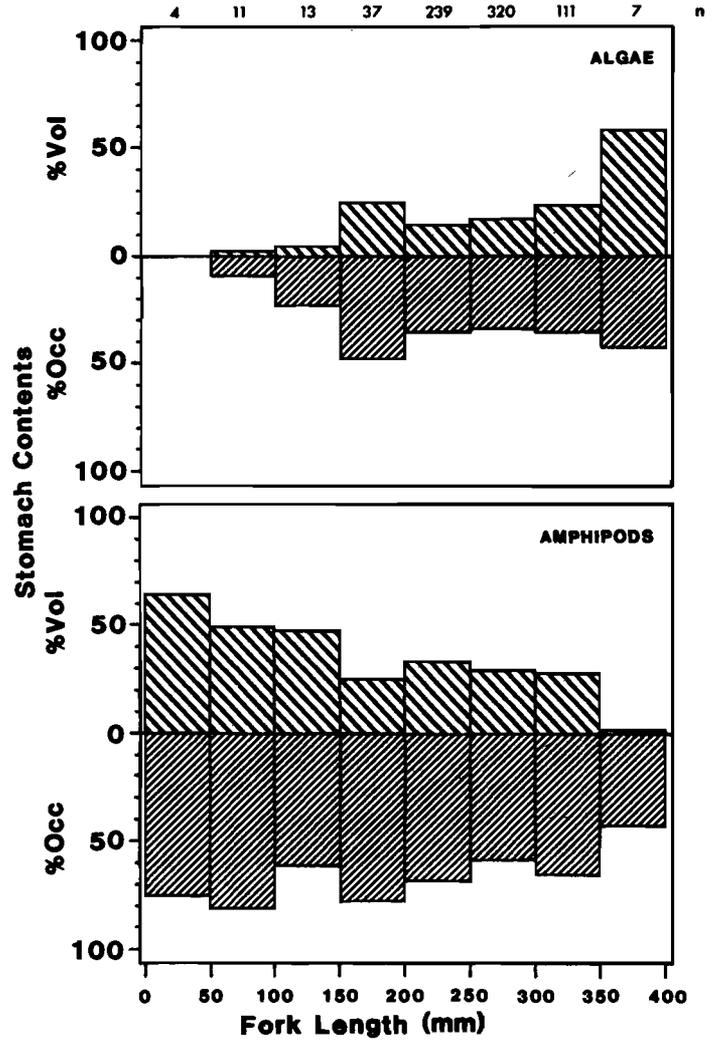


Figure 6 Percentage volume and percentage occurrence of algae and amphipods recorded in the diet of *P. blochii* from all sampling areas (*n* is the sample size) as a function of fish size.

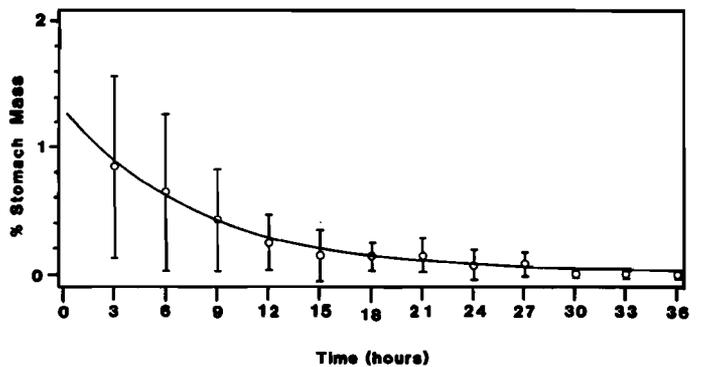


Figure 7 The mean percentage stomach content mass (as a % of body mass) of starved *P. blochii*, showing the exponential gut elimination curve. Vertical bars represent one standard deviation.

during the night, this indicates that feeding is not greatly reduced at this time. A plot of the proportions of each of the major prey groups present in the stomachs, over the 24 h sampling period (Figure 9), however, indicates that

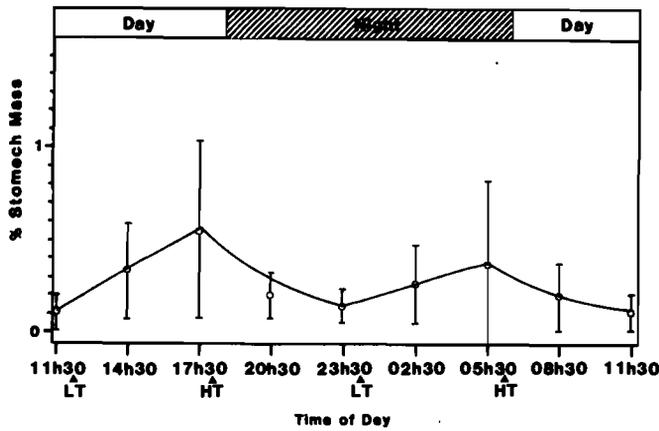


Figure 8 The mean stomach contents mass (as a % body mass) of *P. blochii* over a 24-h period, showing the diurnal feeding cycle. Vertical bars represent one standard deviation.

Table 2(a) S_{∞} , k and t_0 values for the feeding phases of the 24 h feeding cycle of *P. blochii*, and the subsequently calculated St_0 and St_n values and consumption rates (% body mass per day)

Parameter	First feeding phase	Second feeding phase
S_{∞}	15,415	26,839
k	0,005	0,002
t_0	-1,46	-3,672
St_0	0,113	0,146
St_n	0,564	0,383
C_f	1,210	0,827

Table 2(b) S' and b values for the two elimination phases in the 24 h feeding cycle, and the consumption rates (% body mass per day)

Parameter	First elimination phase	Second elimination phase
S'	0,564	0,383
b	0,226	0,203
C_e	0,273	0,225

For the purpose of calculating the equations, curves were assumed to start at $t = 0$.

there are temporal trends in the type of food taken and that these follow a diel rather than a tidal rhythm. By day hottentot appear to graze preferentially on benthic algae, crinoids and hydroids, but in the latter part of the night crustaceans become the most important food item, making up over 60 % of stomach contents.

Discussion

Analysis of the diet of *P. blochii* showed that the species is largely an omnivorous benthic feeder, exhibiting a

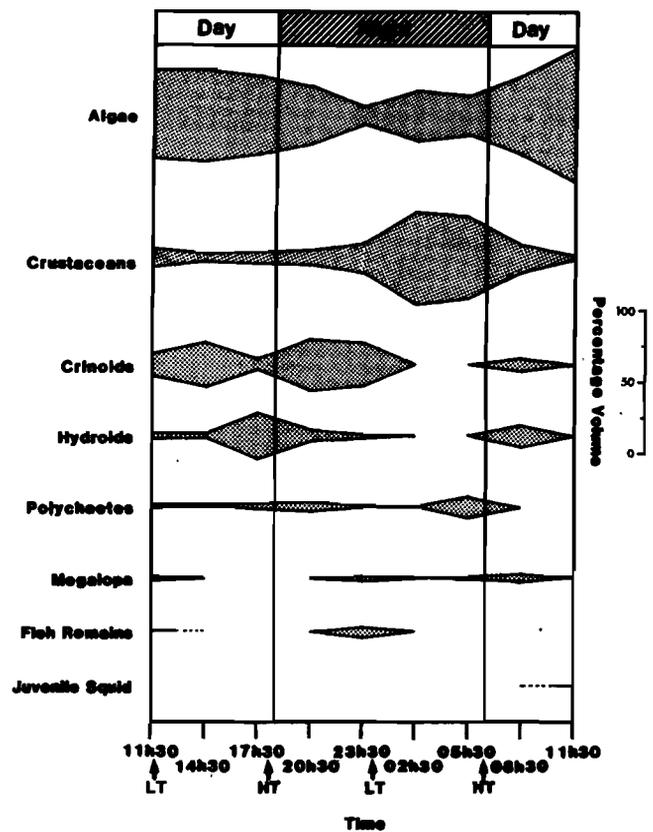


Figure 9 Mean weight of the main food categories in the diet of *P. blochii*, sampled over a 24-h period, expressed as a % of the total weight of all prey items in all fish sampled.

varied preference for a high diversity of organisms occurring in the understory of kelp beds, and on subtidal reefs. Being opportunistic feeders however, they will deviate from their normal grazing behaviour to prey readily on mysids, stomatopods and megalopa, when these are swarming in midwater. The most important components of the diet, in terms of volume, were amphipods, algae and hydroids, together accounting for 60% of the total stomach contents, and 72% of identifiable material.

Although the species found in the stomachs of hottentot are similar to those found by Stander & Neppen (1968) and Neppen (1977), the proportions of the major food items differ. This is most notable in the relatively high proportions of crustaceans, hydroids and small molluscs, and the paucity of echinoderms recorded during the present study.

As Neppen (1977) did not distinguish between size classes in his investigation, this discrepancy in results could be size related. In a species with such opportunistic feeding habits, differences are, however, expected. Differences in depth and geographic location of sampling sites may also influence results. The fact that Neppen (1977) used only the percentage occurrence method in his dietary analysis also means that it is impossible to estimate the relative amounts of each food item present in the stomach.

Considering the highly generalized and opportunistic feeding habits of this species, it is perhaps not surprising

that our similarity analyses were not always able to reveal major systematic variations in diet with locality, season or fish size. What did, however, become evident was the marked increase in the proportions of algae in the diet with increasing fish size and the adoption of the shoaling habit. A similar trend of an early dependence on small Crustacea, followed by a change to an omnivorous or largely vegetarian diet, has been reported for the sea bream (*Archosargus rhomboidalis*) (Vaughan 1978), blacktail (*Diplodus sargus*) and strepie (*Sarpa salpa*) (Christensen 1978).

Comparing the diet of *P. blochii* with those of other South African omnivorous sparids (Table 3), indicates that the hottentot exhibits a preference for algae, second only to *Diplodus sargus* (Joubert & Hanekom 1980, Coetzee 1986). Although the results of Coetzee (1986) indicate a larger preference for amphipods, it must be kept in mind that the figure of 38% occurrence also includes isopods and tanaids. Algae were recorded in the diets of most of the species. It appears, however, that they select the green and brown algae rather than the rhodophytes.

Although Blaber (1974) reported omnivorous habits for juvenile *Rhabdosargus holubi* occurring in estuaries, studies on the feeding biology of other southern African sparids (*Cheimerius nufar*: Coetzee & Baird 1981; Garratt 1986; Smale 1986, *Chrysoblephus puniceus*: Garratt 1986, *Petrus rupestris* and *Polysteganus praeorbitalis*: Smale 1986) have found them to be predators.

As demonstrated by Christensen (1978), Buxton (1984), Garratt (1986) and Smale (1986), the diet of small and large fish may differ considerably. It was therefore not unexpected to find a separation into small, medium and large fish, in the cluster analysis. The poor separation of the clusters, however, indicates that considerable dietary overlap occurs between the size classes and the differences are therefore not distinct.

In view of the reported absence of cellulase in teleosts (Lagler, Bardach & Miller 1962, in Blaber 1974), and the large amounts of apparently undigested plant material present in the hindgut of hottentot, it would be of considerable interest to determine the amount of nutrition that hottentot are able to obtain from algae. The algae may serve merely as a substrate for epiphytic diatoms which are subsequently digested, as found by Blaber (1974) for *R. holubi* and Joubert & Hanekom (1980) for *D. sargus*. Alternatively the seaweeds may be digested to some extent by cellulase-producing gut microflora (Stickney & Shumway 1974), or as suggested by Montgomery & Gerking (1980), nourishment may be extracted from the algae by enzymatic penetration of the cell walls or digestion of cell contents after they are leached from the cells.

Hottentot also appear to exhibit a preference for amphipods, the crustacean fraction of the reported diets of other non-estuarine sparids being dominated by other sub-classes.

Hydroids are poorly represented in the diets of other sparids, with the exception of *P. aeneum*, where they make up 27% of the diet (Buxton & Clarke 1986).

Table 3 Comparison of percentage consumption of various food items by *P. blochii* and other South African omnivorous sparids (not including species occurring in estuaries as juveniles)

Species	Food item				
	Red algae	Green algae	Brown algae	Amphi-pods	Hydroids
<i>Diplodus sargus</i> (Joubert & Hanekom 1980) (Coetzee 1986)	71 %O	63 %O	0	0	0
<i>Rhabdosargus globiceps</i> (Buxton & Kok 1983)	0	3 %V	6 %V	0,6 %V	0
<i>Argyrozona argyrozona</i> (Nepgen 1977)	0	0	<1 %O	5,7 %O	0
<i>Chrysoblephus laticeps</i> (Buxton 1984)	0	0	0	4,6 %V	0
<i>Pachymetopon aeneum</i> (Buxton & Clarke 1986)	0,2 %V	0,3 %V	1,3 %V	0,04 %V	26,6 %V
<i>P. blochii</i> (this study)	16 %V 34 %O	1,8 %V 9,4 %O	1,2 %V 6,3 %O	29,7 %V 64,3 %O	11,4 %V 29,6 %O

Although closely related to *P. blochii*, the blue hottentot consumes less than 2% algae and negligible quantities of amphipods.

In conclusion therefore, *P. blochii* exhibits a strongly omnivorous feeding habit, exhibiting a unique reliance on the combination of algae, amphipods and hydroids as major elements of a highly variable diet. Being an opportunistic feeder, it is capable of exploiting a wide range of food materials available at different depths, areas or seasons. Although dietary overlap exists between *P. blochii* and the sympatric *D. sargus*, the generalist approach to feeding of the hottentot will contribute to co-existence with *D. sargus*.

The pattern of gastric evacuation in hottentot appears to conform closely to the exponential model proposed (Figure 7), complete evacuation taking about 12 h. Hottentot appear to feed continuously over the 24-h period, rather than exhibiting exclusive feeding and elimination phases. Accurate estimates of the evacuation rate could thus not be established *in situ*, as done by Blaber (1974), Staples (1975a), and Doble & Eggers (1978). It was therefore necessary to isolate a sample of fish and subsequently determine the time required for complete gastric evacuation, in a food-free environment.

A number of assumptions are implicit in applying the model to field populations, notably that the pattern of evacuation is independent of the nature and quantity of food being consumed (El-Shamy 1976), and that it is unaffected by capture and transfer of the experimental

individuals. This latter supposition is a serious limitation common to methods proposed for determining gut emptying rate. Although Swenson & Smith (1973) claimed that handling of fish had no effect on the digestion rate, the stress of being hooked, and subsequently transferred to holding tanks, must be considered. This, together with the effect of starvation, noted by Thorpe (1977), suggests that our evaluation of 12 h 22 min for 99% evacuation, may be an underestimate.

The feeding activity exhibited by hottentot appears to be more strongly influenced by the tides than the diel cycle. This has not been recorded in other studies most of which were conducted in fresh water or closed estuarine environments, and which were not subject to tidal influences.

Almost all feeding seems to take place during the rising tide. The reasons for this are obscure, but are presumably related to prey availability. Although some food is taken from the intertidal zone (e.g. *Porphyra capensis*), most is undoubtedly derived from sublittoral resources, and there is no clear reason why this should be more accessible during flood tide. The increase in feeding activity at flood tide does, however, confirm the reports of fishermen, who claim that the fish bite best at this time.

It appears that, although feeding still occurs at night, this is reduced compared with that during daylight. This was further confirmed by night-time diving observations, which showed the fish to be more placid and evenly spaced, usually seeking the cover of caves or crevices in the reef. This contrasts with their daytime behaviour, which involves active grazing in shoals of various sizes. This change in feeding habit is likely to contribute to the observed temporal change in diet. An increase in the relative availability of crustaceans in the plankton is reflected in the higher proportions of this prey in the nocturnal diet. Many benthic crustaceans emerge into the water column at night for feeding, dispersal or reproduction and are thus vulnerable to predation by hottentot at this time.

It can be argued that fishing with hook and line at night will select only those active and hungry fish, thereby strongly biasing the results. Although this may be a limitation, catch rates at night were not significantly different (at the 5% level), from those during daylight hours.

From Figure 8, it becomes evident that, although a von Bertalanffy-type equation was fitted to the feeding portions of the data, the resultant curves are almost linear. As the curves are representative of both consumption and simultaneous elimination, however, the asymptotic nature of the feeding curves would be disguised.

Compared with our model both the original and the corrected Bajkov methods (Elliott & Persson 1978; Eggers 1979) give a lower estimate of daily consumption rate. As the inherent assumption of the Elliott & Persson (1978) model is that feeding rate is constant, its application to the present data will overestimate daily ration, if it is presumed feeding continued during the

elimination phases. If however, it is assumed that feeding ceases during elimination, an underestimate will result. The daily ration, of 2.5% body mass/day, using the present model, differs only slightly from the results obtained using the method of Elliott & Persson (1978), indicating that it offers an acceptable alternative, when dealing with a fish exhibiting continuous feeding.

The estimated ration is close to the 2–4% body mass/day reported for four species of fish by Keast & Welsh (1968), and the 2–6% for yellow perch, as well as the 0.5–4.5% for sockeye salmon reported by Nakashima & Leggett (1978) and Doble & Eggers (1978), respectively.

Thorpe (1977) found a great variation in the daily ration figures in samples from different years, and Nakashima & Leggett (1978) experienced differences of similar magnitude in samples from day to day. Similarly, it has been demonstrated that daily ration and feeding rhythms can vary markedly with season and fish size (Staples 1975b; Nakashima & Leggett 1978), and that water temperature can determine both feeding intensity and digestion rate (Mathur 1973). This indicates that the results of short term, *in situ* experiments provide only a 'snapshot' of the chronological feeding habits and consumption rates of a species. Care must hence be taken in extrapolating these results to apply to all seasons and fish sizes.

An additional complicating factor is the dual influence of the tidal and diurnal cycle on the feeding periodicity. The daily change in the dominant, tidal rhythm will result in a constant variation in the height and position of the feeding peaks. The diurnal influence will subsequently have the further effect of either suppressing or enhancing these peaks, depending on what time of day the high tide occurs.

The consumption rate figure of 2.5% body mass/day calculated for *P. blochii*, must therefore be considered a preliminary one. In attempting to ascertain accurately the feeding chronology and food consumption of a marine teleost, a more extensive sampling programme, involving sampling the complete size range of the population, at short intervals for a period of 48 h or more, regularly throughout the year, must be undertaken. Furthermore, it is suggested that, in a species exhibiting constant feeding, the method of calculating the daily ration proposed here be adopted. Although results obtained with our model may not differ significantly from those obtained using the method of Elliott & Persson (1978), it is considered that this model is more realistic, as it assumes an asymptotic rather than a constant feeding rate.

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