Diet of the cyprinid fish *Barbus aeneus* (Burchell) in the P.K. le Roux Dam, South Africa, with special reference to the effect of turbidity on zooplanktivory

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Barbus aeneus is one of the most important fishes in the P.K. le Roux Dam, being found over the whole surface and on the bottom down to the thermocline or to 30 m. It is omnivorous, but its diet varies with size. Below a length of 100 mm it feeds mainly on zoobenthos, from 101 – 300 mm zooplankton is the principal food but in larger fish vegetable food becomes increasingly important. *B. aeneus* is the principal vertebrate consumer of zooplankton in the dam, but takes only the larger species which are located visually. The quantity of zooplankton in the diet was related, not to its density, but to light and transparency which were the most important non-seasonal influences on the diet. Seasonal effects were marked, zooplankton being most important during summer and autumn while empty stomachs were most frequent in winter and spring. In rivers, larger *B. aeneus* feed on bigger invertebrates and on vegetable material. These are limited in the P.K. le Roux Dam and sub-adults experience high mortality once they can no longer feed efficiently on zooplankton. The size at which this occurs is determined largely by turbidity, and this should be taken into consideration in formulating management policies.
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Barbus aeneus is een van die belangrikste vissoorte in die P.K. le Roux-dam. Dié vis kom oor die hele oppervlak en die bodem tot by die termoklien of tot op 'n diepte van 30 m voor. Hulle is omnivore, maar die dieet varieer met grootte. Visse kleiner as 100 mm voed hoofsaaklik op soöbentos, visse tussen 101 – 300 mm op soöplankton, maar by groter visse is plantaardige voedsel meer belangrik. *B. aeneus* is die vertebraat wat die meeste soöplankton in die dam verbruik, maar vreet slegs die groter spesies wat visueel opgespoor kan word. Die hoeveelheid soöplankton in die dieet hou nie verband met die digtheid van die soöplankton nie, maar wel met lig en deursigtigheid wat die belangrikste nie-seisoenale invloede op die dieet is. Seisoenale invloede is duidelik. Soöplankton is gedurende die somer en herfs baie belangrik terwyl leë mae hoofsaaklik in die winter en lente voorkom. In riviere voed groter *B. aeneus* op invertebrate en op plantmateriaal. Hierdie voedselbronne is beperk in die P.K. le Roux-dam en die mortaliteit onder onvolwasse visse is hoog wanneer hulle nie meer op soöplankton kan voed nie. Die grootte waarby dit gebeur word grootliks bepaal deur turbiditeit, en dié feit behoort in aanmerking geneem te word wanneer bestuursbeleide geformuleer word.
S.-Afr. Tydskr. Dierk. 1986, 21: 257 – 263

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Received 28 March 1984; accepted 26 November 1985

Before informed decisions can be made about the development of a new fishery the potential annual yield must be estimated. In existing fisheries this is done by observing the effect of exploitation on the recruitment, growth rate and structure of the exploited populations. Such techniques are of limited value in newly established impoundments where the stocks are often dominated by single year classes of those species which benefited immediately from the new conditions. It may take several years for the fish populations to approach an equilibrium and, even then, information on the effects of exploitation is unlikely to be available. In such cases the morphoedaphic index and similar parameters (Oglesby 1977) are often used to indicate potential yields. These are usually based on physical and chemical measurements, without reference to the structure of the ecosystem, and fail to take into account differences between water bodies in the efficiency of energy transfer between trophic levels.

Impoundments are colonized by species already present in the river system concerned and the transfer efficiency between trophic levels will depend on how successfully these adapt to lacustrine conditions. This is especially important where the reservoir is so large or so deep that the bulk of the primary and secondary production is planktonic rather than benthic. The P.K. le Roux Dam, on the Orange River in South Africa, is such a lake. It was formed by the closure of the dam wall at Vanderkloof in the northern Cape Province. Its physical, chemical and biological characteristics were described by Allanson & Jackson (1983). A number of factors limit the productivity of the dam (Allanson, Beuthin, Jansen & Selkirk 1983). It lies in a semi-arid area and receives most of its inflow from the H.F. Verwoerd Dam but, since this is mostly drawn from below the thermocline, it is relatively cool. This is reinforced by the prevailing aridity and windiness which lead to high rates of evaporative cooling so that, despite long hours of sunshine and high air temperatures, the surface temperature rarely reaches 25°C and the bulk of the epilimnion seldom exceeds 22°C in summer. The dam is highly turbid owing to the presence of colloidal clay particles, and transparency, as measured by Secchi disc, rarely exceeded 30 cm during the period of the study. This not only limited primary production by restricting photosynthesis but also, by restricting solar heating to the superficial waters, increased heat losses by radiation and evaporation, and contributed to the generally cool regime of the lake.

The dam contains only ten species of fish (Allanson & Jackson 1983). The most abundant of these are *Labeo capensis* (Smith), a benthic detritivore, and *Barbus aeneus* (Burchell), formerly known as *B. holubi* Steindachner (Hocutt

& Skelton 1983), which is found regularly over the whole of the water body and which is omnivorous, taking a wide variety of food including zooplankton (Schoonbee 1969; Mulder 1973; Gaigher & Fourie 1984). These two species form the bulk of the stocks which would be available for commercial exploitation and were the main species of fish examined during an investigation into the fisheries production potential of the dam (Allanson & Jackson 1983). The present study, which formed a part of this investigation, was designed to ascertain the degree to which *B. aeneus* utilized the available resources.

Material and Methods

A total of 681 fish, from 10–547 mm in fork length, were examined. Most were caught in gill nets but drift nets, seine nets, a purse seine and a surface trawl were also used. The length and mass of the fish were measured to the nearest 1 mm and 0,1 g respectively. The gut was severed where it entered and left the body cavity and the alimentary viscera were preserved in 10% formalin.

To minimize the effects of digestion and of passage of food through the gut, quantitative studies were limited to fish which had been caught in nets set for no longer than 2 h. These included few specimens of 50–150 mm or longer than 300 mm. To increase cover in these size ranges additional fish were obtained from gill nets set overnight, but these were used only in the qualitative evaluation of food preferences. Information was also obtained from nets set in deep water down to 48 m and *B. aeneus* was found down to the thermocline to a limit of 30 m but because these nets were set for over 2 h, the deep-water fish were considered only in the qualitative studies.

In cyprinid fish there is no true stomach, but the anterior part of the intestine is often expanded to form a 'pseudogaster' (Harder 1975). The gut was divided into a number of sections delimited by regularly occurring points of inflection (Eccles 1986b), the first being the pseudogaster, and the contents of each were removed. Bias in estimation of the diet, owing to the fact that most individuals were caught in daylight, was minimized by recording the contents of each section separately.

Food items were classified into the following broad categories: zoobenthos, zooplankton, adult insects with aquatic larvae, terrestrial arthropods, fish, phytoplankton, phytobenthos, angiosperms, angiosperm detritus, miscellaneous, empty. For each section the contents were examined and the three most abundant categories were ranked. Categories estimated to form less than 5% of the total were disregarded. If fewer than three categories were present the lower ranks were represented as 'negligible'.

After gross estimation of the diet the samples were weighed. In samples of less than about 250 mg the individual items were enumerated and measured but larger samples were thoroughly mixed before subsampling for detailed examination. The samples were then oven-dried at 65°C for 48 h to obtain a standard dry mass and were finally ashed at 515°C for 6 h to obtain the mass of the ash residue. Where subsamples had been taken the dry and ash masses of the original sample were estimated. The ash-free dry mass was recorded as a percentage of the live mass of the fish.

Two measures of diet were used, firstly a qualitative assessment of the frequency of an item as the principal component in any section of the gut and secondly, a quantitative dietary index, $I_{d,x}$, which was computed for each item using the equation: $I_{d,x} = 10MP/F$ where:

M = ash-free dry mass of the original contents,

P = estimated percentage of the total contents attributable to item '*x*' where second- and third-ranked items were assumed to form 30% and 20% respectively, appropriately weighted if one or both of these ranks was 'negligible',

F = live mass of the fish,

10 = a raising factor for convenience.

The effects of a number of environmental factors on diet were analysed.

Solar time: Time (h) since local sunrise.

Solar period: To eliminate seasonal differences in day length, records were related to sunrise, noon, sunset and midnight. Day and night were each divided into six equal sections and ten periods defined: dawn, early morning, late morning, early afternoon, mid-afternoon, late afternoon, evening, early night, midnight (2 sections), pre-dawn (2 sections).

Light index: $(I_l) = T - T^2/D$ where T is solar time and D is length of daylight.

In addition to these the daily wind run, change in water level over the previous 7 and 14 days, distance from the dam wall, distance offshore and depth of capture were recorded.

Other environmental factors routinely monitored at standard stations by the Institute of Freshwater Studies of Rhodes University (Allanson *et al.* 1983; Hart, Allanson & Selkirk 1983) included temperature (°C) at 1 m depth, Secchi-disc visibility (m), chlorophyll *a* concentration (μg ℓ^{-1}) and the biomasses (mg m^{-2}) of the crustacean zooplankton species. Where the dates of recordings did not coincide with fishing dates values were interpolated.

Seasons were defined in relation to the thermal regime of the dam:

Spring (September–November) — positive heat balance, thermal stratification not well established.

Summer (December–February) — thermal stratification well established.

Autumn (March–May) — negative heat balance, stratification decaying.

Winter (June–August) — dam almost homothermal.

Relationships were investigated using statistical procedures available in the 'Statistical Package for the Social Sciences' (SPSS) (Nie, Hull, Jenkins, Steinbrenner & Bent 1975) at the computer centre, Rhodes University.

Results

Figure 1 shows, for each length group, the seasonal percentage frequency of principal dietary items. Animal food predominated in the smaller fish but became progressively less important until, at a length of about 400 mm, vegetable material was the major item. Zooplankton was eaten by all size classes but zoobenthos predominated in the smallest fish. In fish of 101–300 mm zooplankton was the principal component in over 50% of all gut sections including those which were empty.

The abundance of zooplankton in the dam fluctuated considerably over short periods, particularly in summer, and also showed great seasonal variation (Hart, Allanson & Selkirk 1983). This is reflected in the increasing importance of zooplankton in the diet from spring to summer and its decline in autumn and winter. The seasonal patterns for zoobenthos and for empty sections were complementary to that for zooplankton and, in fish below 350 mm length, phytobenthos and angiosperm material were more important in winter. No clear seasonal trends were apparent for terrestrial arthropods,

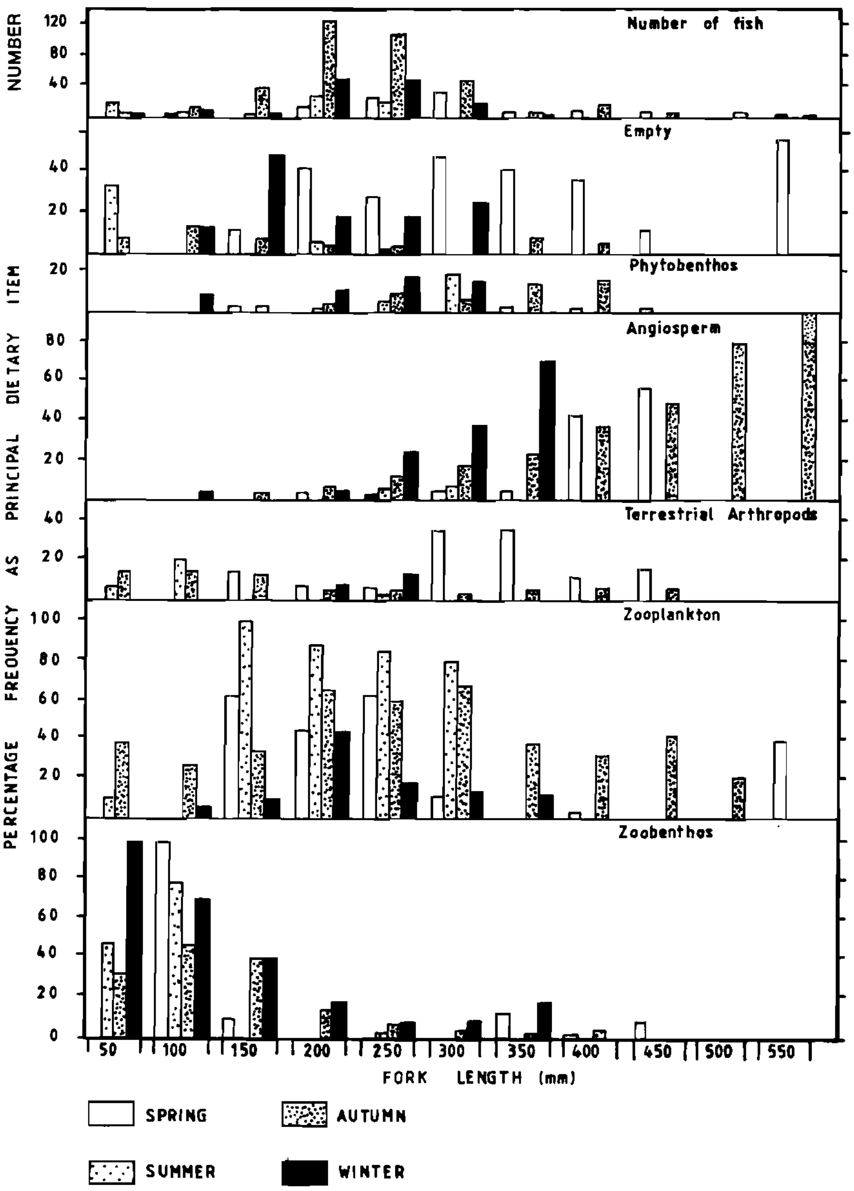

Figure 1 Seasonal variation in the relation between the principal dietary component and the fork length of *B. aeneus*. The effects of diurnal changes in diet were minimized by recording the contents of each section of the gut separately.

although these were the principal component in 8% of all cases.

Because the frequency of dietary zooplankton increased with fish length below 150 mm and decreased above 300 mm, only fish in the size range 151 – 300 mm were considered in analysis of the infuence of factors other than fish length on the diet.

Figure 2 shows the relative frequency of principal dietary items at different solar periods. Zooplankton was taken almost exclusively during daylight, while zoobenthos and angiosperm material were relatively more important at night, although this probably reflected reduced feeding on zooplankton rather than increased use of other resources in the dark, since Figure 3 indicates that there was no diurnal pattern in the quantity of zoobenthos taken.

The effects of environmental factors on the preference and the dietary index for zooplankton were investigated by multiple regression analysis (Tables 1 & 2). Because gut evacuation is dependant on temperature and slows rapidly at lower temperatures (Eccles 1986a) analysis of the effect of light and of time of day was restricted to fish caught at temperatures above 18°C. Figure 4.1 shows that $I_{d,z}$ for the pseudogaster increased from dawn until mid-afternoon and then declined progressively. Figure 4.2 shows that this can be attributed largely to a highly significant correlation with the light index. Figure 4.3 shows the contribution of Secchi-disc visibility to the $I_{d,z}$ of the pseudogaster in fish caught in the daytime for all fish and for fish caught in the winter when zooplankton is less abundant.

Although zooplankton was the major component of the diet of 151 – 300 mm fish, no significant correlations were found between its abundance and $I_{d,z}$. This was probably the result of the great short-term and regional variations in zooplankton abundance (Hart *et al.* 1983). Only the larger species, *Lovenula excellens, Daphnia barbata, D. gibba* and *D. longispina*, were important in the diet. About 70% of the total zooplankton biomass consisted of the copepod *Metadiaptomus meridianus* (Hart *et al.* 1983) but this, together with the small cladoceran *Moina dubia* and cyclopoid copepods, was taken by only a few individuals, mostly at the lower end of the size range.

Other factors had little influence on the diet of the fish. Even in fish caught close inshore, or at depths below 10 m, where zoobenthos would be expected to be relatively more

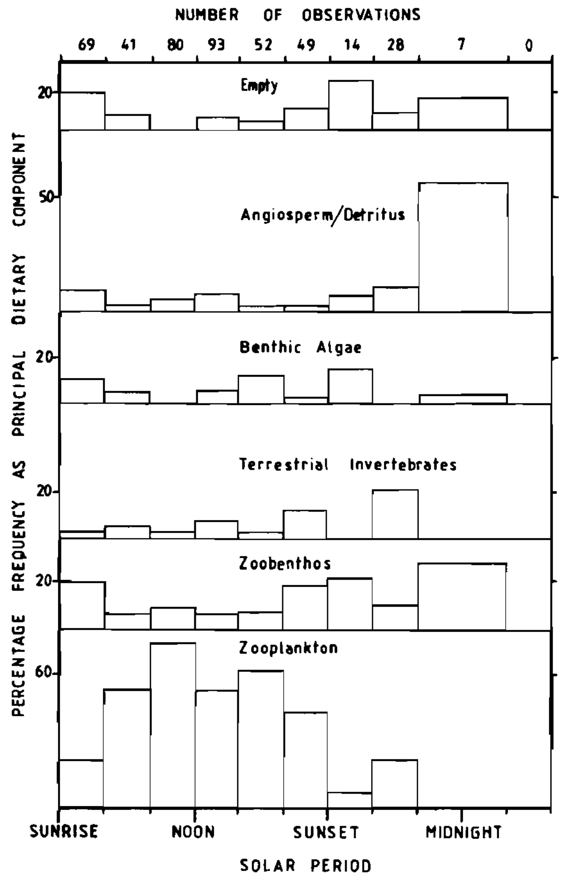

Figure 2 The relation between 'solar period' (see text) and the principal dietary item in the pseudogaster of *B. aeneus* of 150 – 300 mm in fork length. No fish were caught in the pre-dawn period.

available, zooplankton was the predominant, and in some cases the only, dietary item of fish of 151 – 300 mm. However the nets set in deep water were selective for this size range and no smaller fish, which might have exploited zoobenthos, were caught.

Discussion

The normal habitat of *B. aeneus* is in rivers with a regime

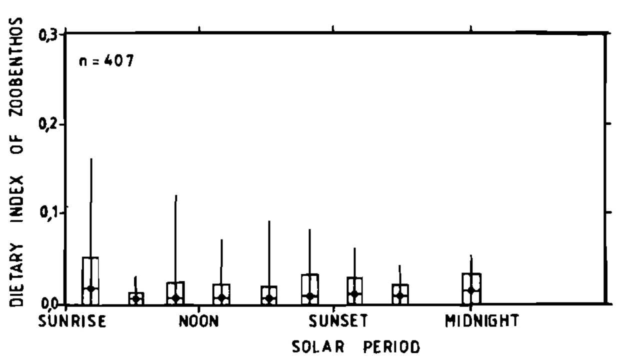

Figure 3 Variation of dietary index of zoobenthos in pseudogaster of *B. aeneus* with solar period for fish caught at temperatures above 18°C.

of summer floods and winter droughts which does not favour the development of potamoplankton. *B. aeneus* is a generalized feeder with a comparatively small mouth. In rivers its diet includes the lamellibranch mollusc *Corbicula*, but larger individuals feed increasingly on the vegetable material which is readily available in the shallow water forming a large part of the riverine environment. In the Orange River downstream from the P.K. le Roux Dam *C. africana*, with shell lengths of up to 17 mm, were an important component of the diet of *B. aeneus* (Skelton & Cambray 1981) but they were never found in the present study of the gut contents of fish from the dam. Although it lacks specific adaptations to planktivory, such as a large gape and fine, closely spaced, gill rakers, *B. aeneus*, because of its generalized behaviour, is able to exploit zooplankton in the lake. Despite its inefficiency as a zooplanktivore, taking only the largest species, this food is the main energy source for *B. aeneus* over much of its life history in the P.K. le Roux Dam.

While frequency of occurrence as the principal dietary item shows that zooplankton is the main food of fish 101 – 300 mm long, it underestimates the true contribution of this item to the energy budget of *B. aeneus*. Zooplankton is taken mainly during the daytime and in the summer, when the total food content is also the highest. The increased frequency of other items at night or in the cooler seasons does not reflect

Table 1 Relative contribution of factors to multiple regression with dietary index of zooplankton in the foregut of smallmouth yellowfish of 15,1 to 30 cm length

	All temperatures		Above 20°C		Below 18°C	
Variables	All fish N = 268	Day time N = 206	All fish N = 97	Day time N = 88	All fish N = 150	Day time N = 97
Light (I_l)	0,14 (0,001)	0,11 (0,001)	0,12 (0,001)	0,05 (0,009)	0,06 (0,033)	0,10 (0,003)
Temperature	neg.	neg.	0,02(–) NS	0,02(–) 0,094	0,05 NS	0,01 NS
Secchi visibility	0,02 (0,005)	0,03 (0,004)	0,06 NS	0,06 NS	0,05 (0,001)	0,07 (0,016)
Lovenula	0,12 NS	0,17 NS	NR	NR	0,01 NS	neg.
Daphnia	0,05 NS	0,04 NS	0,21 NS	0,22 NS	0,03 NS	0,01 NS
Metadiaptomus	0,01 0,05	0,01 NS	0,06(–) NS	0,06(–) NS	0,01 NS	0,04 NS
Moina	neg.	neg.	NR	NR	NR	NR
Distance offshore	0,04 0,07	0,04 (0,038)	neg.	neg.	0,13 (0,001)	0,17 (0,001)
Wind previous day	0,02(–) NS	0,02(–) NS	0,02(–) (0,05)	0,03(–)(0,025)	0,01(–) NS	0,02(–) NS
Distance from dam	neg.	neg.	0,01 (0,001)	neg.	0,01(–)(0,001)	0,01(–)(0,026)
Total r^2	0,41	0,41	0,48	0,45	0,34	0,42

Total r^2 is the proportion of the total variance which can be associated with the combination of the factors listed. The contribution of each factor to total r^2 and its significance level is listed. Negative relationships are indicated by (–). NS indicates that the significance level is less than 95%; neg. signifies that the contribution to r^2 is less than 0,01; NR, no relationship. *Lovenula, Daphnia, Metadiaptomus, Moina* are the abundance of the named genera as mg m^{-2} in upper 10 m. Wind previous day is the total wind run (km) of the previous day.

Table 2 Relative importance of factors in multiple regression with preference index for various food items in the gut of *B. aeneus* (all fish)

	Food items						
	Zooplankton N = 359	Zoobenthos N = 359	Terrestrial arthropods N = 359	Phytobenthos N = 359	Terrestrial angiosperms N = 359	Detritus N = 359	Empty N = 359
Significant factors	Sec 0,30 (0,002)	FL(−) 0,10 (0,000)	Sec(−) 0,01 (0,071)	None	FL 0,15 (0,000)	None	Sec(−) 0,12 (0,080)
	Preyzoo 0,02 (0,003)	Wind(−) 0,03 (0,000)			Wind(−) 0,02 (0,003)		Wind 0,08 (0,000)
	Temp 0,01 (0,003)	Temp(−) 0,02 (0,097)			Lev7(−) 0,01 (0,013)		Temp(−) 0,04 (0,000)
Total r^2	0,39	0,18	0,22	0,05	0,23	0,03	0,26

Total r^2 is the proportion of the total variance which can be associated with a combination of the factors listed. For each factor the contribution to total r^2 and its significance level is listed. Negative relationships are indicated by (−). Contributions less than 0,01 are ignored. N: Number of cases; FL: Fork length; Sec: Secchi disc visibility; Preyzoo: Total of *Lovenula* and *Daphnia*; Temp: Temperature at 1 m; Wind: Wind previous day; Lev7: change in level previous week.

increased consumption of these but is the effect of a reduction of the amount of zooplankton in the diet. Coupled with this is the fact that the rate of digestion and passage of food is much lower in winter, while the lower quantities of food taken then also increase passage times in an exponential manner (Eccles 1986a).

The change from zoobenthos to zooplankton as the main food source for late juveniles is explicable in energetic terms. In the P.K. le Roux Dam there were few submerged macrophytes, such as form shelter for larger invertebrates in rivers, and most of the benthic organisms eaten were small chironomid larvae, many of which were tubicolous. These must be detected by taste rather than vision and so can be located only at short range. The search area for zoobenthos is thus

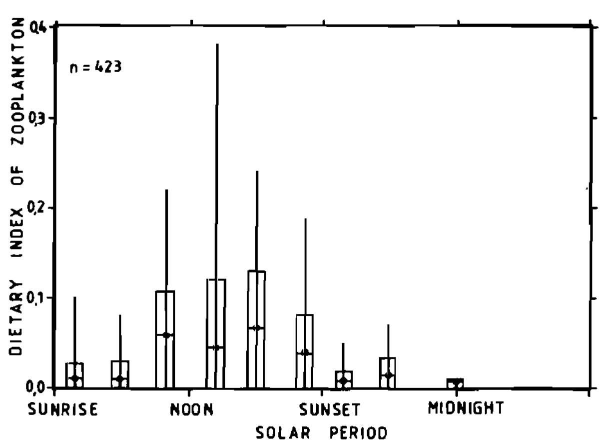

Figure 4.1 Variation of dietary index of zooplankton ($I_{d,z}$) in pseudogaster of *B. aeneus* in relation to solar period for fish caught at temperatures above 18°C and at a light index of 1 or more.

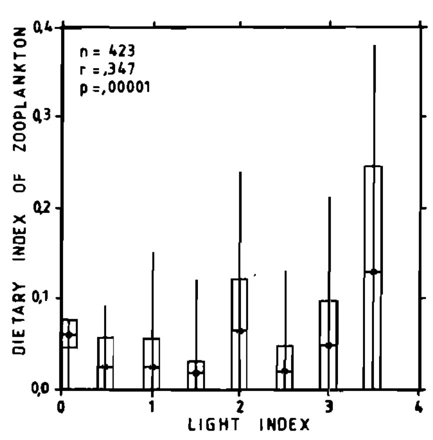

Figure 4.2 Variation of dietary index of zooplankton in pseudogaster of *B. aeneus* with light index (I_l) for fish caught at temperatures above 18°C.

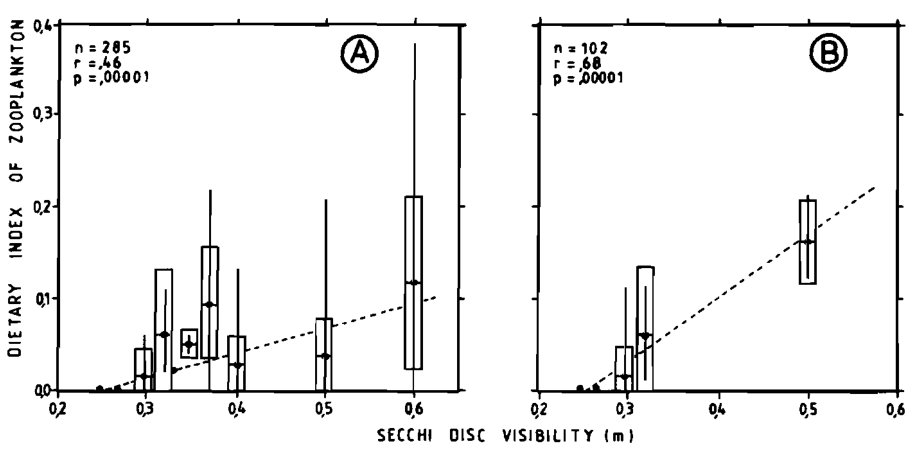

Figure 4.3 Dietary index of zooplankton in the foregut of *B. aeneus* of 151 to 300 mm in length in relation to Secchi disc visibility when light index exceeds 1. A: All fish, B: Fish caught below 17,5°C.

effectively limited to a narrow strip of the bottom, little wider than the span of the barbels. The change to planktivory allows the search area to be extended to a volume determined by the 'reaction distance' which depends not only on characteristics of the prey, such as size and contrast (Confer & Blades 1975), but also on fish size (Breck & Gitter 1983) and on turbidity and illuminance (Vinyard & O'Brien 1976).

The change from zooplankton to plant material is also energetically determined. While swimming speed, and thus the volume searched, is more or less proportional to fish length (Kerr 1971) the maintenance energy requirement increases at a rate between the square and the cube of length (Fry 1957). At the same time the energy required to capture a single prey is proportional to the mass of the predator (Schoener 1969). A stage is therefore reached at which an individual is no longer able to maintain a positive energy balance by feeding on zooplankton and must seek larger, though less energy-rich, foods. If these are not available, as is the case in the P.K. le Roux Dam, starvation will result.

The selection by *B. aeneus* of the larger, but numerically and gravimetrically less abundant, components of the zooplankton and the marked correlation of the dietary index for zooplankton with both light intensity and transparency indicate that these prey are detected visually. This is supported by the observation that, in an aquarium colony fed on zooplankton, the fish held their barbels folded along their lips during daylight but erected them in the dark (Eccles, unpublished). Because of this dependence on vision, zooplankton-feeding *B. aeneus* are adversely affected by turbidity. In the P.K. le Roux Dam the growth of several species, including *B. aeneus*, was positively correlated with transparency (Tomasson & Allanson 1983) and sharp increases in turbidity in 1978 and 1981 were followed by heavy mortality (Jackson, Cambray, Eccles, Hamman, Tomasson & White 1983).

By reducing the volume which can be effectively searched, increased turbidity will lead to a reduction in the length at which the fish can no longer maintain a positive energy balance by zooplanktivory and will be reflected in the distribution of length frequency in the population. At higher levels of turbidity the length at which sub-adult mortality is at a maximum will be reduced and the mean length of the population will be smaller. This possibility was not recognized when the present study began but it could easily be tested in a fish so widespread and important as *B. aeneus* in South Africa.

In the P.K. le Roux Dam benthic primary production is restricted to a narrow strip along the shore and forms less than 1% of total primary production, most of the energy flow being based on phytoplankton and detritus (Hart *et al.* 1983). In such a system the most important fish will be those which can exploit these resources. The main detritivorous species are *L. capensis* and *L. umbratus* (Smith). No species feeds primarily on phytoplankton but both *B. anoplus* Weber and *B. aeneus* feed mainly on zooplankton. The former is abundant only near the shore and *B. aeneus* is more important forming, with *L. capensis*, the bulk of the ichthyomass. Since it is readily caught in surface nets over the whole dam it is one of the two most suitable species for a commercial fishery. Because of the heavy mortality attending the change from zooplankton to inshore resources the size at which this occurs, rather than the size at maturity, should be considered in any management policy (Eccles, Hart, Jackson & Tomasson 1983). Any regulations should be flexible enough to allow rapid changes in permissible mesh size in the event of changes in turbidity, and should allow for the use of different nets for this species in waters of different turbidity values.

Acknowledgements

This work was carried out under the leadership of Prof. B.R. Allanson, as part of a Co-operative Scientific Programme funded by the Council for Scientific and Industrial Research. I am grateful to Professor Allanson, J.A. Cambray, G.L. Christmas, D. Forsyth, Prof. R.C. Hart, P.B.N. Jackson, J. Jansen, W. Selkirk, P. Skelton and T. Tomasson for advice and assistance and to the staff of the Cape Department of Nature and Environmental Conservation for facilities and help in the field. B.P.N. Jackson, S. Jackson, R. Palmer and D. Webster assisted in preparing gut contents.

I am grateful also to the Directorate of Fisheries Research of the United Kingdom Ministry of Agriculture, Fisheries and Food for the provision of office space for the revision of the manuscript.

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