The effect of temperature on the rate of passage of food in the smallmouth yellowfish, *Barbus aeneus* Burchell (Teleostei, Cyprinidae)

D.H. Eccles

Institute for Fresh Water Studies, Rhodes University, Grahamstown

The effect of temperature on the rate of gut evacuation in *Barbus aeneus* was investigated in two ways. In the first, juvenile fish, kept under conditions of constant temperature, were fed marked food items and the time elapsing until these appeared in the faeces was noted. In the second, fish of a range of sizes were caught in the P.K. le Roux dam and immediately placed in cages in the dam to prevent their access to food. Groups of fish were sacrificed at intervals and the contents of standardized gut sections weighed. The field experiment was carried out in summer and in winter. The laboratory experiment yielded the relationship: $P = 6270 \times T^{-2{,}11}$ where P is the passage time in hours and T is the temperature in °C. This gives passage times of the order of 8 h at 25°C and 39 h at 11,5°C. The field experiment indicated that there was an exponential relationship between degree of fullness and rate of evacuation, and that complete evacuation required about 24 h in summer, but more than 5 days in winter.

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Die invloed van temperatuur op die tempo van dermlediging by *Barbus aeneus* is op twee maniere ondersoek. Eerstens is jong visse wat onder konstante temperature in die laboratorium aangehou is, gemerkte voedselitems gevoer en die tydsverloop totdat dié items in die faeces verskyn, aangeteken. Tweedens is visse van verskillende groottes in die dam gevang en onmiddellik in hokke in die dam geplaas om sodoende hul toegang tot voedsel te verhoed. Groepe visse is met tussenposes verwyder en die inhoud van gestandaardiseerde dermseksies geweeg. Die eksperimente in die hokke is in die somer sowel as in die winter gedoen. Die laboratoriumeksperimente het die volgende verband laat blyk: $P = 6270 \times T^{-2{,}11}$ waar P die tydsverloop in ure van voedsel deur die dermkanaal is en T die temperatuur in °C. Dit gee tye van 8 h by 25°C en 39 h by 11,5°C. Die eksperimente in die hokke het 'n eksponensiële verwantskap tussen dermvolheid en tempo van lediging getoon. Volkome lediging het ongeveer 24 h in die somer geneem, maar meer as 5 dae in die winter.

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D.H. Eccles
Present address: c/o Ministry of Agriculture, Fisheries and Food,
Directorate of Fishery Research, Lowestoft,
NR33 4HT, United Kingdom

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Barbus aeneus Burchell, previously known as *B. holubi* Steindachner (Hocutt & Skelton 1983), is an important constituent of the ichthyofauna of the P.K. le Roux Dam, a large impoundment on the Orange River, South Africa (Allanson & Jackson 1983). Because this species is likely to be an important component of any large-scale fishery in this dam, or in the larger H.F. Verwoerd Dam situated further upstream, a study of its diet was undertaken (Eccles, in press a). Since the rate of evacuation of the stomach is known to vary with temperature (Elliott & Persson 1978) it was necessary to know not only the quantity of the gut contents, but also the rate of passage of these at various temperatures, before daily consumption could be estimated.

Elliott & Persson (1978) reviewed previous approaches which have been made to this question. In a study of the time required for the emptying of the stomach in trout, where the stomach contents can be removed completely without difficulty, they found that an exponential model was the best predictor of emptying rates.

In cyprinids there is no pyloric sphincter, and thus no true stomach, although the anterior part of the intestine is often expanded into a 'pseudogaster' (Harder 1975). It is therefore possible that in cyprinids the use of stomach pumps may withdraw contents not only from the pseudogaster but also from the intestine posterior to this. For this reason stomach pumps were not used in the present study, two other approaches bring used to estimate the effect of temperature on food passage times. The first was the laboratory measurement of the time required for the passage through the whole gut of marked food items. The second was a field study of the rate of decrease of the gut contents of fish enclosed in cages which allowed free circulation of water but which excluded food items. These two methods approximated the extremes of the conditions which can be encountered in the field, namely a super-abundance of food and, on the other hand, starvation.

Methods

Laboratory

In the laboratory study it was not possible to keep larger fish under the constant temperature conditions of the experiment and only juvenile fish, ranging in mass from 3 to 40 g, were used. These were kept in a constant environment room and were acclimatized at the experimental temperature for a period of at least four days prior to the experiment.

Between experiments the fish were kept communally in metal-framed glass aquaria measuring 60 × 30 cm, with a water depth of approximately 20 cm. These were supplied with a continuous flow of conditioned and aerated water from the Municipal supply, the outflow being through a syphon opening at the bottom of the tank so that faeces and detritus were removed with the outflow. The water level was maintained by leading the syphon to a cup with an overflow set at the desired height. During the holding period the fish were fed on a commercially available aquarium food which was supplemented with live *Daphnia* when these were available. The light regime was controlled by automatic switches set to give equal 12-h periods of light and dark and was maintained at the same period during the experiments.

During the experiment the fish were segregated in individual aquaria. For the smaller fish, up to 10 cm long, these were constructed from 5-ℓ wine bottles (Figure 1). The bottoms of these were removed and, in each, a small hole was drilled in the side to serve as an outlet and a glass funnel with a stem diameter of 1 cm was cemented to the neck with silicone rubber. A tube of soft plastic was attached to the stem of the funnel. A vial was inserted into the free end of the tube to collect any faecal pellets produced. Vials could be changed rapidly simply by pinching the tube and replacing the old vial with an empty one. A false floor, consisting of a plastic grid with a mesh sufficiently large to allow faecal pellets to fall through, but too small to permit the fish to become jammed, was cemented in the 'shoulder' region of each flask to prevent the fish from becoming jammed in the neck of the bottle. A syphon, inserted through the outlet hole, led from below the grid to an external cup which could be raised or lowered to control the water level. Waste products and any foul water resulting from putrefaction in the funnel were removed through this system, but the inlet of the syphon was fitted with a screen of fine mesh nylon which prevented the loss of faecal pellets or food organisms.

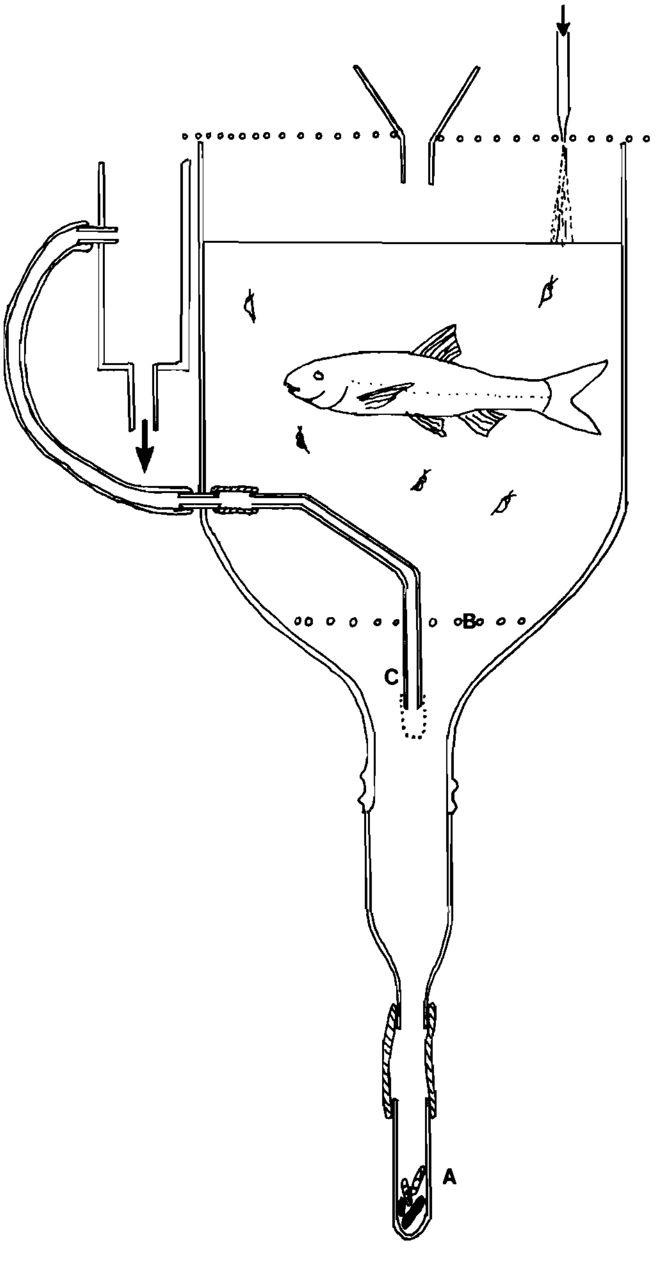

Figure 1 Design of aquaria used for measurement of food passage rates in isolated juvenile *B. aeneus*. A. Collecting vial for faecal pellets; B. False floor; C. Outlet syphon.

Larger fish, which could not fit comfortably in the small aquaria, were individually isolated in the holding tanks from which all faeces and detritus were removed at the beginning of the experiment. To prevent the loss of faecal pellets or food organisms through the syphon, this was covered with a cage which did not interfere with the water flow.

In all cases wastes were removed by a continuous flow of water directed into the tank through a narrow jet which entrained air bubbles to ensure aeration. The tops of the aquaria were covered by grids of expanded metal to prevent the fish from jumping out. Short, wide glass funnels were inserted through these grids to allow the introduction of food.

For at least a day prior to an experiment, and for its duration, the fish were fed on *Daphnia* which were cultured in bulk in outdoor tanks. Other animals which occurred in these tanks, such as notonectids and the larvae and pupae of Chironomidae and Culicidae, were separated from the *Daphnia* for use as marker items, but the main marker item was *Daphnia* which had been placed in a suspension of carbon black until their guts were filled with this material, after which they were rinsed in clean water. Faecal pellets containing these marked *Daphnia* were of an intense black colour, in contrast to the normal brown of those derived from unmarked *Daphnia*. Pellets containing the remains of insect markers could easily be identified by their structure and by the presence of head capsules.

During the experiments the standard food was unmarked *Daphnia*, which were added to the aquaria as they became depleted so that food was available to the fish at all times. From time to time marker items were introduced instead of unmarked *Daphnia*. The markers were followed, after they had been eaten, by further unmarked food so that marked faecal pellets were separated by unmarked ones. The collection vials were examined at intervals and any containing faecal pellets were removed, the time being noted. In the larger tanks faecal pellets were removed manually by pipette so that it was not possible, in these cases, to ensure that no re-ingestion took place. When examinations were made during the dark periods a red light was used to minimize disturbance to the fish.

After a series of markers, with intervening unmarked food, had been offered to the fish and recovered in the faeces the experiment was terminated and the fish returned to the holding aquaria for acclimation to the next experimental temperature.

Six series of experiments, lasting between two days at 25°C and four days at 11,5°C, each involving between 14 and 20 individual fish, were run in the laboratory. In each day the faeces were examined at intervals of no more than 2 h over a 16-h period and occasionally during the remaining 8 h.

Field

Fish were captured in shore seine-nets or in purse seines used at the surface offshore, and were immediately enclosed in cages and returned to the dam or sacrificed to serve as controls. Two experiments were undertaken; in March, 1980, when the water temperature was about 22°C, and in August 1980 when it was about 12°C. In March a total of 74 fish, ranging in mass from 27 to 312 g (fork length 11,3–25,3 cm) were used, but nine were excluded from consideration for reasons given later. Fewer fish were available in August and a total of 34, ranging in mass from 83 to 314 g (fork length 13,3–25,7 cm) were studied.

The cages were cylinders of nylon curtaining with a mesh small enough to exclude *Metadiaptomus* and the larger zooplankton organisms which are the main food of *B. aeneus* in the P.K. le Roux Dam, where the experiments were carried out (Eccles, in press a). They were 1 m in diameter and 1 m high and were supported on the outside by 1-m diameter hoops of 15-mm diameter high-density polyethylene water pipe. The upper hoop was filled with air and the lower with water and additional floats and weights were attached to stretch the cages, which were moored in the water just below the surface. Some of the fish in one cage in the March experiment were found to have ingested faecal material and so were excluded from the experiment. For the August experiment the cages were modified by the inclusion of a floor of 10 mm stretched mesh knotless fishing net which allowed the faeces to fall through to the bottom of the cage where they were out of reach of the fish.

All the fish in one cage were caught at the same time and were sacrificed at the same time after a pre-determined interval. Fish caught at the same time were sacrificed immediately as controls. After death the fish were weighed and measured and the guts removed and preserved in 10% formalin. They were subsequently dissected, divided into five sections on the basis of a consistent pattern of coiling (Figure 2) (Eccles, in press b). The contents of each section were removed, dried, weighed, ashed and re-weighed. The ash-free dry mass of the contents was expressed as a fullness ratio, the percentage it formed of the live mass of the fish.

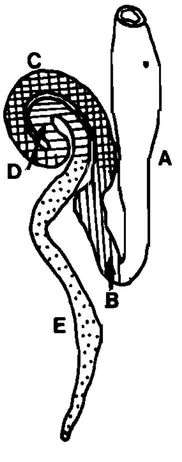

Figure 2 Gut of 63-mm *B. aeneus* showing sections considered in the food exclusion experiment. Sections B–D increase in length at a greater rate than sections A and E during growth.

The percentage of the total fish mass represented by the ash-free dry mass for particular food items was calculated to derive a dietary index for that item for each gut section and for the entire gut (Eccles, in press a).

Results

Laboratory experiments

There was wide variation between individuals in food passage rates, especially at lower temperatures when some individuals appeared not to feed at all, or certainly passed no faeces containing food given in the period of the experiment. In such circumstances the use of a mean value for the passage time is not possible. Instead the time between feeding a marker and its appearance in the faeces was taken for the median fish in the series. This provided standardized estimates of passage time which agreed quite closely with the mean passage times at temperatures at which all the test fish passed marked items. When fitted against temperature (Figure 3) these followed a power curve which can be expressed as:

$$P = 6270 \times T^{-2,11}$$

where P is passage time in hours, T is temperature (°C).

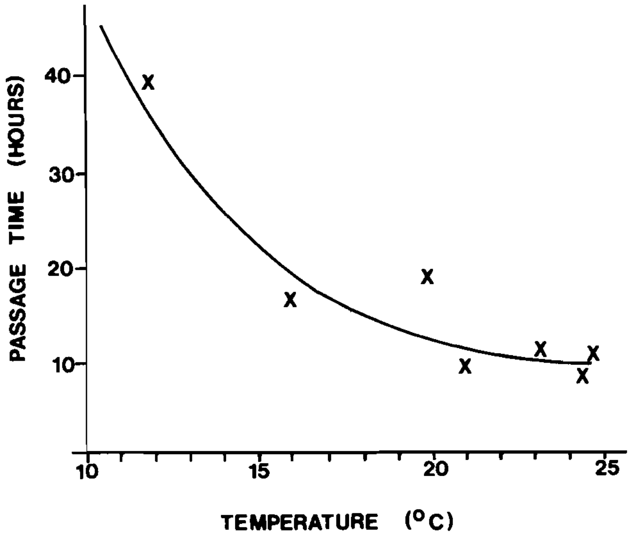

Figure 3 Relationship between time for food to pass through the gut (P) and temperature (T°C) in juvenile *B. aeneus*.

Field observations

In the March experiments the subjects were taken at different times of day, some being taken within 2 h of sunrise and the others about noon. Since there are diurnal effects on feeding (Eccles, in press a), the degree of fullness of the gut differed between the two sets of controls. The results were therefore weighted by adjusting the values for the contents of the first two sections of the gut of those individuals caught in the early morning, thus allowing them to be compared directly with those individuals caught about noon.

In the August experiment both the mass of the original gut contents and the temperatures were lower. All the fish were captured around noon so that there was no necessity to apply any weighting.

Linear, semi-logarithmic and logarithmic curves were fitted to the data. In the winter series correlations were poor and only the first two of the five gut sections showed reductions in fullness index which were significant at the 1% level. In both summer and winter the best fits were with a semi-logarithmic model (Figure 4).

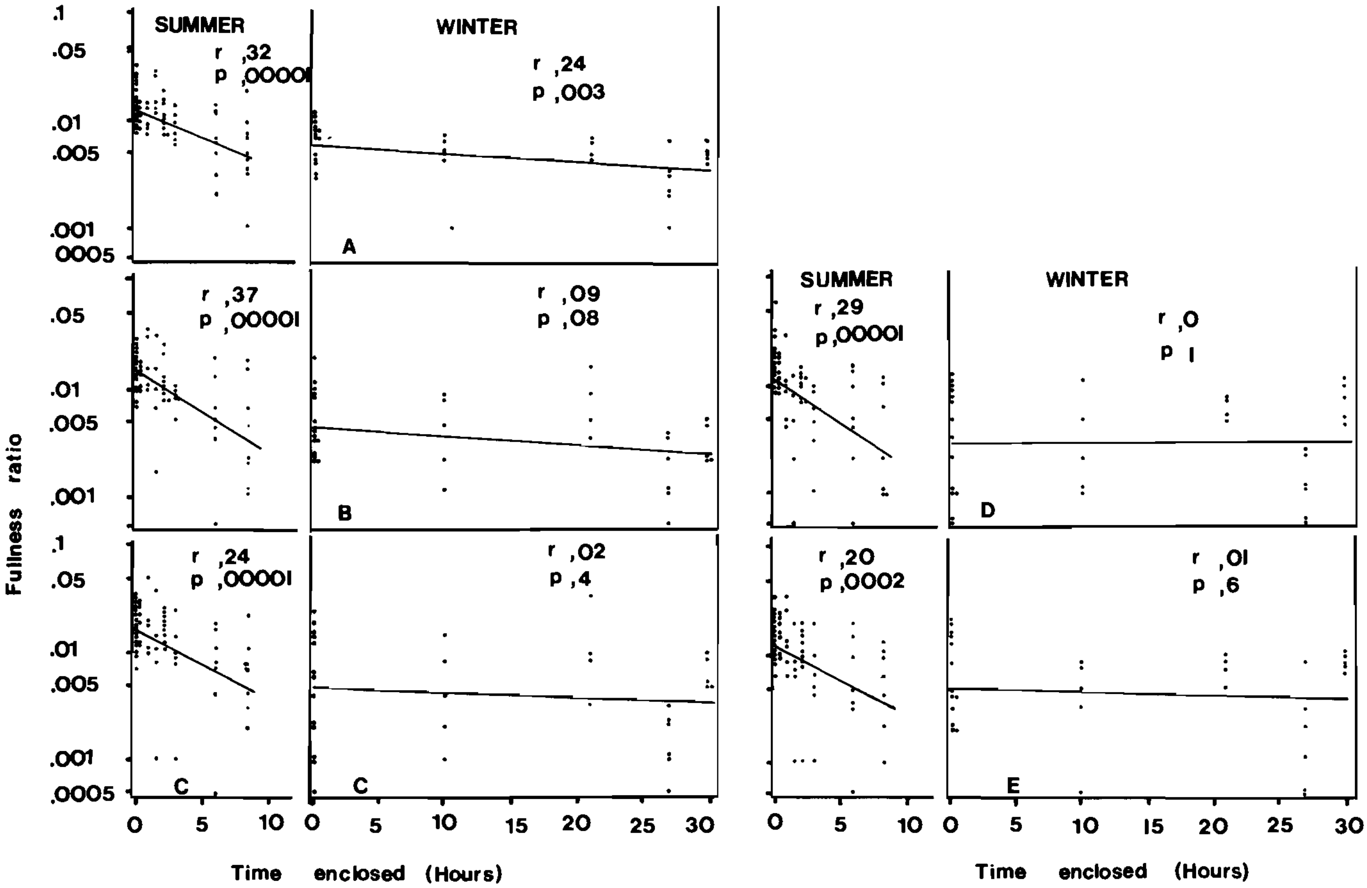

Figure 4 Decrease in contents of sections A–E of gut of *B. aeneus* with time under conditions of food exclusion during winter and summer.

Discussion

The field and laboratory results are not directly comparable since in the former the exclusion of food from the experimental cages will, under an exponential model, result in a reduction of the rate of passage of food. In the laboratory experiment, on the other hand, the constantly available food probably represents a situation rarely found in nature and may have led to an underestimate of passage times in nature. The two sets of results thus encompass the range of conditions which are met in nature, from starvation to a super-abundance of food.

Elliott & Persson (1978) found that an exponential model was the most appropriate for stomach evacuation in fish. The present study confirms this finding in the case of the pseudogaster and the following two sections of the intestine in a stomachless cyprinid, although a linear model accounted for a similar degree of variance in the two final sections.

Extrapolation of the regressions derived from the summer exclusion experiment indicates that, under conditions of starvation, complete emptying of the gut would have occurred after a period of 20–30 h. In winter, emptying is much slower, and a minimum emptying time of about 5 days is indicated for the first two sections of the gut alone, so that complete emptying would be expected to take a minimum of two weeks.

Although the field results applied to fish denied access to food, they are in broad agreement with the laboratory results obtained under conditions of *ad libitum* feeding, even though the latter was concerned with gut passage time, rather than the time for complete evacuation. Passage time varied from about 7 h at 25°C to 39 h at 11,5°C for the median fish in the series. However at all temperatures there was great individual variation and at the lowest temperature some of the fish had passed no marked food over the period of the experiment.

In the roach, *Rutilus rutilus* L., gut passage rates were found to be considerably faster for fish fed *ad libitum* than values given in the literature for fish fed single meals or minimal meals (Hofer, Forstner & Rettenwander, 1982). Although in the present laboratory study the fish were fed *ad libitum*, the passage times were considerably longer than those found by Hofer *et al.* (1982) which varied from 3–5 h at 24°C to 10–15 h at 10°C. This may be related to the more complex gut morphology of *B. aeneus* (Eccles, in press b) where a complex pattern of coiling of the elongated gut is found. It may also reflect the different climatic conditions under which the species have evolved, since the greatest discrepancy is at lower temperatures. Thus roach would be able to continue feeding at temperatures experienced by *B. aeneus* only for short periods during the winter.

It is impossible to isolate completely the effect of temperature on gut passage time, since passage time under an exponential model is also related to the amount of food in the gut and this itself falls with temperature. However the fact that, in the field experiment, the magnitude of change in evacuation rate for the pseudogaster was found to be similar to that for passage rate in the laboratory, indicates that temperature was the major influence.

Since, in *B. aeneus*, food processing rates fall rapidly at temperatures below 15°C, measures of gut fullness tend to over-estimate food consumption during winter. This leads to an over-emphasis of the importance in the annual energy budget of dietary items taken at this time. For example, although the larvae of *Chaoborus* are an important component of the zooplankton eaten by *B. aeneus* in winter (Eccles, in press a), their total contribution to the annual energy budget is very small.

Daily ration can be estimated from the fresh weight of the gut contents and the passage time as determined in the laboratory. However, where there are substantial diurnal changes in feeding rate, allowances must be made for the exponential decrease in passage rate accompanying decreases in feeding rate. In the absence of fresh-weight estimates, dietary indices for the whole gut can be used to estimate the relative consumption at a range of temperatures.

Following this approach it was possible to estimate the effect in the field of temperature on the consumption by *B. aeneus* of zooplankton, which constitutes the principal food of fish from 100–250 mm in length (Eccles, in press a). In summer the dietary index for zooplankton in the gut is about 10 times that found in winter, but the lower temperatures in winter extend the time over which food is retained in the gut three- or four-fold. Using a simple temperature-dependent model the consumption of zooplankton in winter is therefore only about 3% of that in summer (Figure 5). Even this is an over-estimate, since no allowance is made for the exponential effect of smaller quantities of food in the gut in winter, so that the real value for zooplankton consumption in winter is well below 3% of that in summer.

In part, the low winter consumption is a reflection of the low availability of zooplankton at that time (Hart, Allanson & Selkirk 1983). However, in the laboratory experiment a proportion of the fish did not feed, even when offered food *ad libitum*, so that low levels of zooplankton is winter may not, in themselves, impose a severe burden on the fish. A more important factor limiting the growth of *B. aeneus* in the P.K. le Roux Dam may be the extended period of cool conditions, with the whole water body below 12°C for about three months (Allanson, Beuthin, Jansen & Selkirk 1983). Although river temperatures before impoundment reached lower extreme values than those now found in the lake, these would have had little more effect than the present winter temperatures which already inhibit feeding to a large extent. However the period of cold conditions in the river was shorter than that now found in the dam (Pitchford & Visser 1975), while diurnal temperature variations would have allowed some feeding to take place in the day time, even though minimum temperatures would have inhibited feeding for much of the time. Thus in the P.K. le Roux Dam the energetic efficiency of *B. aeneus* is severely limited by the prolongation of cold conditions and, in particular, by the smaller diurnal temperature range and lower maximum temperatures in the dam as compared with the natural conditions in the river.

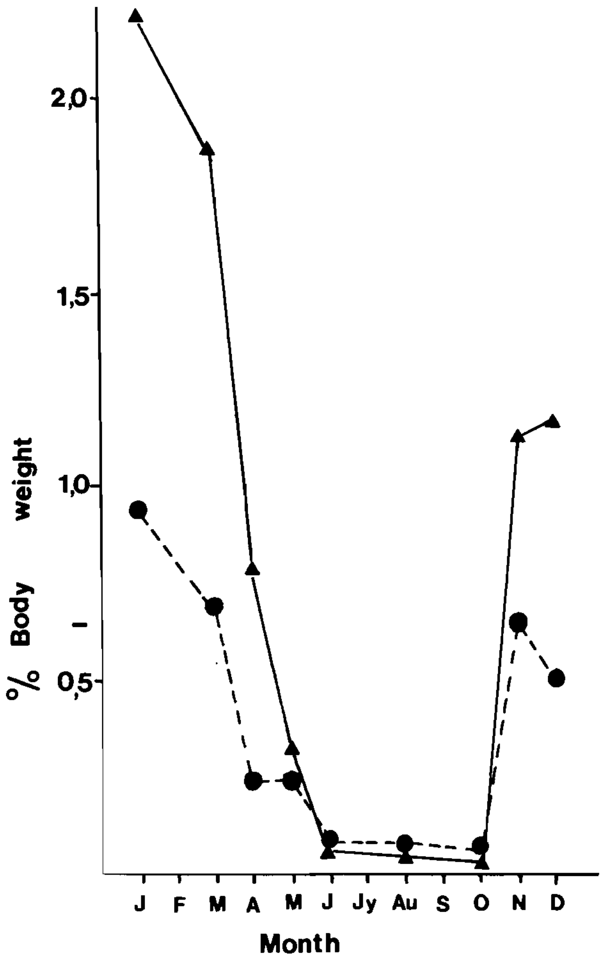

Figure 5 Dietary index for zooplankton ● – – – ●, and estimated equivalent daily consumption ▲———▲, for *B. aeneus* 15–30 cm fork length, caught at different times of year.

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