Food and feeding habits of *Oreochromis mossambicus* (Peters) in hypertrophic Hartbeespoort Dam, South Africa

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The diet of 745 *Oreochromis mossambicus* (Peters) of less than 0,5 up to 2000 g wet mass, in Hartbeespoort Dam, was determined from stomach content analysis. Samples of fish were selected to cover a whole annual cycle. Small fish fed initially on zoobenthos and zooplankton, but fish with a mass of over 4 g fed increasingly on *Microcystis aeruginosa* Kützing and detritus until these food items formed the dominant food source in *O. mossambicus* over 8 g. Some cannibalism was encountered in fish up to 64 g in the summer months. The ratio of intestinal length to total length of fish ranged from 0,58 in the smaller fish to 11,02 in larger fish and this indicated that there was an ontogenetic adaptation from a carnivorous to a phytoplanktivorous/detritivorous diet. Feeding in juvenile fish studied over 24 h was found to be most intense in the early morning and late afternoon but remained high throughout daylight hours decreasing considerably at night. The daily ingestion rate of food in *O. mossambicus* in Hartbeespoort Dam was estimated at 453 mg/g of fish. This comprised 45% *M. aeruginosa* and 55% detritus. It was apparent that of this matter ingested only a small percentage would be assimilated. *Oreochromis mossambicus* shows feeding and breeding preadaptations which enable it to successfully exploit a lacustrine environment. These adaptations enable it to maintain a large population in Hartbeespoort Dam despite frequent winter mortalities caused by water temperatures below their tolerance limits.
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Die dieet van 745 *Oreochromis mossambicus* (Peters) met nat massas van minder as 0,5 g tot 2000 g in die Hartbeespoortdam, is bepaal deur maaginhoudanalise. Vismonsters teenwoordigend van alle stadiums in 'n eenjaarsiklus is geselekteer. Klein vissies het aanvanklik zoobenthos en zooplankton gevreet, maar visse van meer as 4 g het al hoe meer *Microcystis aeruginosa* Kützing en detritus verkies, totdat hierdie items die dominante kossoorte geword het in *O. mossambicus* oor 8 g. In die somermaande het kannibalisme in visse onder 64 g voorgekom. Die verhouding tussen ingewandlengte en totale vislengte het van 0,58 in kleiner vissies tot 11,02 in die groter visse gewissel. Dit het daarop gedui dat daar 'n ontologiese aanpassing van 'n roofagtige dieet tot 'n dieet van phytoplankton/detritus in hierdie visspesies plaasgevind het. In jong visse is die voedingsaktiwiteit, bestudeer oor 24 h, in die vroeë oggend en laat namiddag die bedrywigste. Dit het algemeen hoog gebly gedurende die dag maar gedurende die nag het dit aansienlik verminder. Die daaglikse voedselinname van *O. mossambicus* in die Hartbeespoortdam is bepaal as 453 mg/g vis. Die voedsel het 45% *M. aeruginosa* en 55% detritus bevat. Dit blyk dat net 'n klein persentasie van die voedsel geassimileer is. *Oreochromis mossambicus* is vooraf aangepas vir voeding en aanteel in mere wat dit moontlik maak om 'n groot bevolking in die Hartbeespoortdam te handhaaf ten spyte van herhaalde wintervrektes veroorsaak deur lae watertemperature.
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The hypertrophic Hartbeespoort Dam is rich in phytoplankton growths which are dominated by *Microcystis aeruginosa* Kützing for the major portion of the year (Robarts 1984). The dam supports a fish population comprising *Clarias gariepinus* Burchell, *Cyprinus carpio* Linnaeus and *Oreochromis mossambicus* (Peters) as the three dominant species, with a further nine less abundant species (Cochrane 1984).

This paper concentrates on the food and feeding habits of *O. mossambicus* in Hartbeespoort Dam. The feeding ecology of *O. mossambicus* has been extensively examined in aquaculture projects or in waters where the fish have been introduced (see Trewavas 1983). Throughout its natural distributional area in southern Africa, several studies on the feeding biology of this species have been undertaken [Munro 1967 (Trewavas 1983 notes that the species studied by Munro 1967 was probably the closely related *O. mortimeri* (Trewavas).); Bruton & Boltt 1975; Bowen 1976, 1979; Whitfield & Blaber 1978].

This paper presents the first study to examine in detail the feeding behaviour of this species in a phytoplankton-rich, hypertrophic subtropical lake. An attempt was also made to assess why *O. mossambicus* has maintained high population levels in spite of the frequent recordings of winter mortalities (see Trewavas 1983) and deteriorating water quality (Cochrane 1984).

Materials and Methods

Determination of diet by stomach content analysis

Between December 1980 and March 1984 *O. mossambicus* were collected with seine nets in the littoral regions of Hartbeespoort Dam. Fish up to 10 cm total length (TL) were preserved whole in 4% formaldehyde immediately after capture. Larger fish were killed, measured, weighed and their stomachs were removed and preserved in 4% formaldehyde.

In the laboratory, stomach contents of fish were removed and examined under a dissecting or compound microscope and the contents were divided into 11 food type categories (Table 1). The stomach contents were then further analysed using two separate techniques: (a) Percentage frequency occurrence of food type, where the number of stomachs in which each food type occurred was recorded and expressed as a percentage of the total number of stomachs examined and (b) A visual estimate of the volumetric abundance of each food type was made, and recorded as a percentage of the entire stomach contents. The number of times food types were found in the stomachs of fish at densities equal to or greater than 20% of the total stomach contents were noted. The total number of occurrences of all food types combined, in concentrations equal to or greater than 20% of stomach contents, were then summed and the abundance of each food type was determined as a proportion of the total.

Stomach contents of fish were examined taking cognizance of sizes of fish and season of the year. As the length of a fish increases in a linear fashion, the mass of this fish increases in relation to its volume, which is approximately a cubic increase. For this reason it was decided to base size classes of fish on mass, rather than total length. An equation to convert fish wet mass (g) to total length (cm) was developed and can be used to convert the known mass of a fish to its predicted length.

Total length of fish (cm) = 1,38078 + 0,32607 log e mass (g). (From 707 sets of data $r^2 = 0,9924$.)

Intestinal length of fish in relation to their size

During several collecting trips, 65 *O. mossambicus* of various sizes were killed, their mass and length, measured and their entire gut tract removed. In the laboratory the unstretched gut length, from the end of the stomach to the cloaca, was measured under water. If not measured immediately, material was stored overnight in a cool room.

Feeding periodicity and quantity of material ingested

When juvenile *O. mossambicus*, already feeding on a diet representative of adult fish, were plentiful in the littoral regions of the dam, feeding activity in these fish was examined over 24 h according to some modifications of the methods used by Bowen (1976). Samples of 20 to 40 juvenile fish (6 to 10 cm TL) were collected between 9 and 10 February 1984 at 2-h intervals from the littoral regions of the dam, along the northern shore, with a seine net. Half the fish collected on each occasion were immediately fixed in 4% formaldehyde and the other half were held alive in aquaria filled with lake water filtered through a 287-µm mesh net. These aquaria were left floating in the littoral region of the dam to ensure that water temperatures were kept as near as possible to those of the dam. Since the water was filtered it could be assumed that feeding ceased during this period. Exactly 3 h after capture the fish kept in aquaria were fixed in formaldehyde.

In the laboratory all fish collected as described above were transferred to a 40% iso-propyl alcohol solution and left for 10 days before further processing. After measuring the mass and length of each fish the entire intestinal tract of each was removed. The stomach and intestines were picked clean on the outside and each, together with contents, was then separately placed in a glass vial of known mass. The fish plus liver and remaining mesentery removed from the intestines was placed in a third vial. All vials were now dried to constant mass in an oven at 80°C for 60 h, and the mass measured to 0,0001 g.

In a separate experiment 31 juvenile fish, collected in the same manner as previously described, were taken alive to the laboratory, held in 100-ℓ aquaria and starved for a period of seven days. They were then killed and gut and fish mass were determined as above. Stomach and intestine masses of these fish were assumed to represent their mass when empty. Empty stomach and empty gut masses were regressed against fish masses and the two equations so derived were then used to calculate empty stomach or empty whole gut masses for the size range of fish collected over the 24-h period. These data were used to determine the stomach content masses from fish collected in the diurnal study.

Regression equations of maximum stomach or whole gut contents mass (mg) against fish mass (g) were developed from fish killed immediately after capture which had the greatest quantity by mass of food in their guts. To enable comparison of samples of fish collected over the 24 h period, the median mass of all 397 fish collected was determined and used as a standard mass.

To convert the mass of stomach or whole gut contents of a fish to the equivalent mass of that of a standard fish, the mass of the sample fish was entered into the appropriate regression equation and the corresponding maximum stomach or gut content mass for that size fish was determined. The actual measured stomach or whole gut content mass was then expressed as a proportion of the calculated maximum. This proportion was then multiplied by the calculated maximum gut content mass of a standard fish and this then indicated the stomach or whole gut content mass of each fish expressed as a standard. Standardized mean stomach and mean whole gut content masses were used for further calculations.

The rate of change in gut contents mass (ΔG), the faecal production rate (FPR) and the ingestion rate (IR) were calculated as follows:

$$\Delta G_{(t)} = \frac{G_{(t+2)} - G_{(t)}}{2}$$

$$\mathrm{FPR}_{(t)} = \frac{G_{(t)} - GH_{(t)}}{3}$$

$$\mathrm{IR}_{(t)} = \Delta G_{(t)} + \mathrm{FPR}_{(t)},$$

where $G_{(t)}$ and $G_{(t+2)}$ are mean masses of gut (or stomach) contents at selected times t and $(t+2)$ 2 h later. $GH_{(t)}$ is the mean mass of gut contents of fish caught at time (t) but held for 3 h and (t) is all rates expressed per hour or at time (t). Calculated food ingestion and faecal production rates were used to estimate daily food intake and faecal production.

Results and Discussion

Influence of season and size of individuals on the diet of *O. mossambicus*

The most frequently encountered food types in stomachs of *O. mossambicus*, ranging from less than 0,5 g to greater than 800 g wet mass, are summarized in Table 1. Detritus was a major component in all size categories of fish, the lowest percentage occurrence of detritus being found in stomachs of fish with masses of between 1,0 and 4,0 g. Zooplankton were most frequently found in this size category of fish indicating that there was a transition from benthic grubbing to planktonic feeding during this stage of the life cycle. Stomachs of *O. mossambicus* with a mass of over 4 g showed increasing occurrences (Table 1), and contained greater quantities, of *Microcystis* and detritus (Figure 1). Fish below 1 g fed mostly on zoobenthos (Table 1).

Figure 1 shows the percentage abundance of food types, found in concentrations equal to or greater than 20% of gut volume in various size ranges of *O. mossambicus* over the four seasons. Spring refers to data gathered between September and November, summer to data gathered from December to February, autumn to data gathered between March and May, and winter to data collected between June and August.

Because the breeding season of *O. mossambicus* was limited to the warmer months (October to March in Hartbeespoort Dam) small fish were only recorded during spring and summer (Figure 1). Fish up to 4 g fed predominantly on protein rich zoobenthos, consisting almost entirely of chironomid larvae, and zooplankton, comprising mostly Cladocera (*Daphnia* sp.). During the summer period fish from 0,5 to

Table 1 Occurrence of food items in stomachs of *O. mossambicus* as a percentage of fish examined

Food types	Mass of fish (g) 0 – 0,50	0,51 – 1,0	1,01 – 2,00	2,01 – 4,0	4,01 – 8,0	8,01 – 16,0	16,01 – 64	64,01 – 150	150,01 – 800	> 800
Microcystis	11	–	–	4	44	58	41	50	36	66
Diatoms	–	–	–	–	–	1	6	17	32	62
Desmids	–	–	–	–	–	–	1	17	4	26
Filamentous algae	–	–	–	–	1	1	2	17	40	72
Plant matter	9	33	15	4	10	3	1	17	24	49
Detritus	55	73	37	27	65	80	58	83	52	68
Zooplankton	23	20	57	80	20	4	11	–	32	24
Zoobenthos	45	67	31	4	7	6	5	–	16	15
Insects	2	13	6	14	8	3	8	–	–	–
Fish	13	30	39	38	16	10	26	–	–	2
Fish eggs	–	–	–	–	–	1	2	–	–	–
Number of fish	47	30	54	56	105	205	132	6	25	85

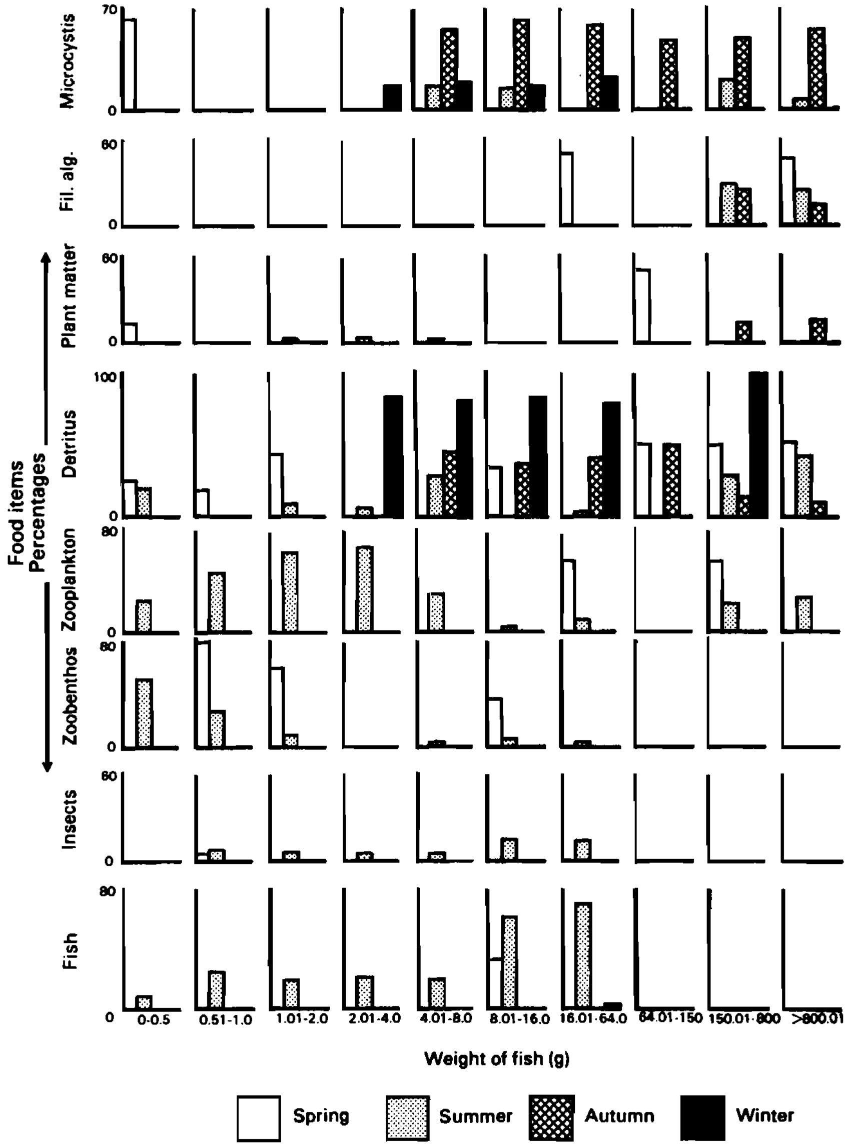

Figure 1 The percentage abundance of food items in concentrations greater than 20% of total stomach contents in various size groups of *O. mossambicus* during the four annual seasons. The number of individuals in each size class is as in Table 1.

64 g frequently fed on fish and terrestrial insects as well as aquatic Hemiptera (Naucoridae, Notonectidae). Filamentous algae (*Cladophora* sp.) and vascular plant remains were occasionally found in stomachs of subadult and adult *O. mossambicus*, and in some stomachs *Cladophora* sp. made up 100% of the diet. *Microcystis aeruginosa* formed a large component of the diet in fish with a mass of over 4 g during autumn and detritus was the most abundant food item found in larger fish during winter and spring (Figure 1).

On a seasonal basis it thus appeared that *O. mossambicus* (mostly smaller fish) showed a preference for zoobenthos in spring. In summer smaller fish showed a preference for zooplankton, insects and fish, while larger fish relied on detritus, filamentous algae and *Microcystis*. This dependance on detritus and *Microcystis* became more pronounced in autumn and winter when these two food types formed the majority of stomach contents of all fish of over 4 g (Figure 1).

Intestinal length of fish in relation to their size

Kruger & Mulder (1973) noted, for a number of South African fish species, that the gut length of fish relative to their body length, gave a good indication of their main dietary requirements. Carnivores had a ratio of gut length to total or fork length of 0,96 – 1,18. With omnivores this increased to 1,70 – 2,30 and with herbivores (they included *O. mossambicus* in this category) it ranged from 7,2 – 7,9. The final category, detritus feeders, ranged from 10,0 – 17,3. Bowen (1976) found the gut length to body length ratio of 121 formalin-preserved *O. mossambicus* to give a mean value of 3,93. Unfortunately he did not include the size range of fish used in his study.

Figure 2 summarizes the findings of this study and shows that the gut length to body length ratio increased with an increase in body length. It ranged from a minimum of 0,58 for fish under 2 cm long, to 11,02 for fish over 35 cm long. The most marked change occurred in fish before they were 5 cm in length which corresponded to a mass below 2,02 g.

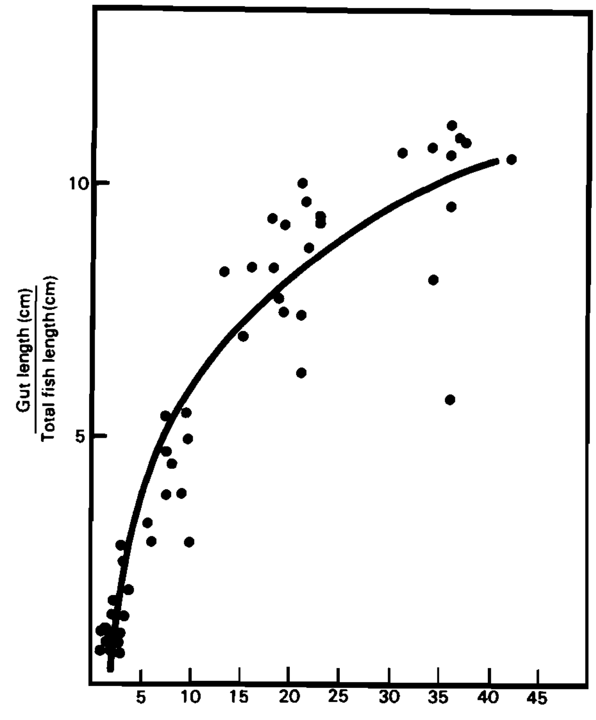

Figure 2 Regression curve of total length (TL) against the ratio of gut length to total length of fish. $y = -2{,}03 + 3{,}37 \log \mathrm{TL}$; $r^2 = 0{,}91$ ($n = 65$).

These results suggest that during its ontogeny there are anatomical and physiological developments, which enable *O. mossambicus* to change from a diet initially relying almost entirely on protein rich animal matter to one with increasing quantities of plant matter, algae and detritus.

Feeding periodicity and quantity of material ingested

The mass of mean stomach or whole gut contents, and the 95% confidence intervals, for each group of fish collected and killed immediately at 2-h intervals over 24 h, are presented in Figure 3a and b. The rate of change in gut contents (ΔG), faecal production rate (FPR) and rate of food ingestion (IR) are presented in Figure 3c – e.

The greatest feeding activity during a 24-h period, based on both stomach fullness and ingestion rates (Figure 3a & e), was between 06h30 and 08h30 in the morning and between 17h30 and 19h30 in the evening. Feeding activity remained high throughout daylight hours, and the faecal production rate was also higher during the daylight hours than at night. The highest rate occurred between 17h30 and 19h30 (Figure 3d). There was a notable decrease in feeding activity, evidenced by the degree of stomach and whole gut fullness, during darkness (Figure 3a and b).

Ingestion rates (IR) are the sum of two calculated variables ΔG and FPR which were determined from data with widely ranging variation (Figure 3b). This would mean that there would frequently be no statistical differences between many of the estimated ingestion rates. However, general trends in feeding rates indicated that fish do feed at varying rates over a 24-h period. Higher feeding activity occurred during daylight and might also be expected when calm windless conditions prevailed as was found by Bowen (1976).

The daily ingestion and faecal production rates of *O. mossambicus* juveniles were estimated as the mean hourly ingestion and faecal production rates multiplied by 24 (Table 2). This gave an estimate of 453 mg food ingested and 314 mg of matter defaecated per gram of fish per day (both fish food and faecal matter expressed as dry mass). The daily ingestion estimate is higher than values calculated from data produced by other workers (Moriarty & Moriarty 1973; Bowen 1976; Caulton 1982) which ranged from 65 – 272 mg food per gram of fish. A high temperature may influence feeding activity and Caulton (1978) found that an increase in water temperature from 18 to 30°C led to a more than three-fold increase in the ingestion of plant matter in *Tilapia rendalli* (Boulenger).

Table 2 The amount of food matter ingested (mg) per gram of fish and an estimate of the amount assimilated using figures obtained from de Moor & Scott (1985)

	Food ingested (mg)	Food assimilitated (mg)	Matter defaecated (mg)
Total	453	139	314
Microcystis	204	103	101
Detritus	249	36	213
Energy (J)[a]	1 575	795	–

[a] The energy content of the food was determined from *Microcystis* only.

Food low in nutritional value is ingested at a slower rate than food of an intermediate nutritional value (Taghon & Jumars 1984). However, the ingestion rate was found to decrease once the nutritional value of the food became very high (Jobling 1981). An abundance of high nutritional food led to an increased ingestion rate but a decrease in the assimilation efficiency of food (Pandian & Raghuraman 1972). It appears, therefore, that food matter ingested by *O. mossambicus* in Hartbeespoort Dam was of intermediate nutritional value or else present in abundance. Either of these factors could have led to a high rate of ingestion.

Gut contents of fish collected over the 24 h consisted predominantly of *Microcystis* and detritus which was charac-

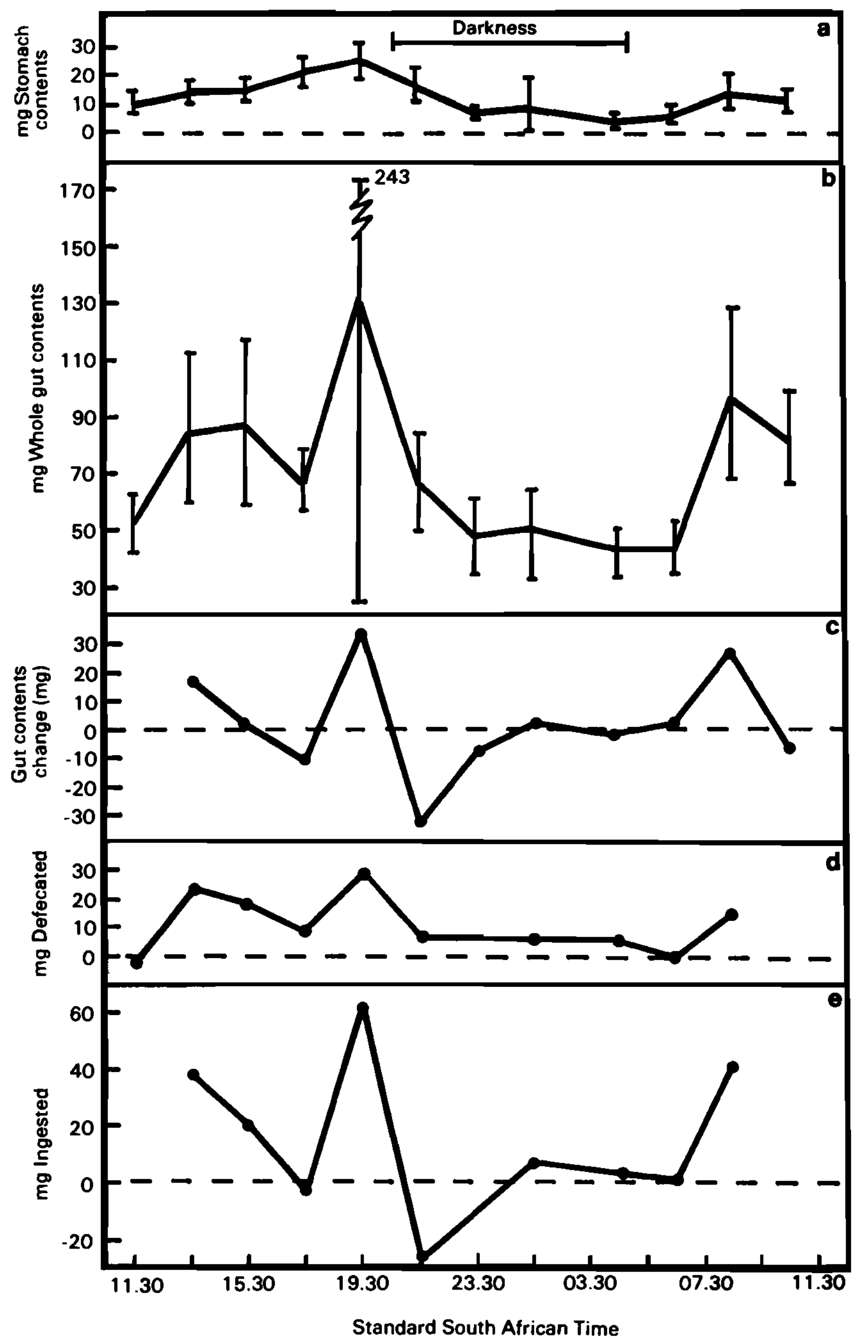

Figure 3 The diel feeding activity of *O. mossambicus* on 9 and 10 February 1984. (a) Mean and 95% confidence intervals for standardized fish stomach contents. (b) The same for total gut contents. (c) Mean masses of faeces deposited. (d) Calculated faecal production. (e) Calculated masses of food ingested. The 95% confidence intervals are expressed as ± t (0,05; $N-1$) times the standard error and c, d, e expressed in mg/h.

teristic for this size of fish in autumn (Figure 1). If, according to de Moor & Scott (1985), 50,8% of *Microcystis* ingested was assimilated and assuming that 45% of the diet was *Microcystis* (Figure 1) then 103 mg *Microcystis*, 0,65 mg phosphorus, or 795 J of energy would be assimilated per gram of fish per day (Table 2). Caulton (1982) showed that aquarium-held fish consumed less than half the quantity of food consumed by fish in their natural environs. With a larger quantity of food being ingested there would thus be a considerable reduction in the quantity of food being assimilated. It follows that there would be a much lower assimilation efficiency for *Microcystis* ingested by *O. mossambicus* in its natural environs (where the algae occur in a mixed diet), than when compared with aquarium-held fish whose only food source was *Microcystis* (de Moor & Scott 1985). The mixed diet of fish in natural habitats leads to a differential assimilation efficiency of the varius food items, from which individual assimilation efficiencies would be very difficult to determine.

The above calculations represent the estimated potential energy value of *Microcystis*. Detritus formed the major gut component of *O. mossambicus* (Table 2), and from an additional 249 mg of detritus ingested per gram of fish per day there would be an additional source of energy available. The calculated figures in Table 2, which are derived from estimated food ingested and faecal matter produced as well as determined assimilation efficiencies of *O. mossambicus* fed on a diet of *Microcystis* only (de Moor & Scott 1985), show that only 17% of detritus ingested was assimilated. From the potential energy value of *Microcystis* it was apparent that only a very small percentage of the daily intake of food by fish in the dam was assimilated.

Conclusions

Le Roux (1956) found that juvenile *O. mossambicus*, under 5 cm TL, showed a marked preference for zooplankton. As the fish grew, phytoplankton became the favoured food and when this became scarce they readily fed on plant material. Chironomid larvae were fed on by all sizes of fish. Munro (1967) recorded filamentous algae, diatoms and higher plants as the main diet in 170 *O. mossambicus* he had collected from Lake McIlwaine. [Trewavas (1983) believes that in both above cases this was actually the closely related *O. mortimeri* (Trewavas).] Bowen (1976, 1979) found the diet of all sizes of *O. mossambicus* in Lake Sibaya to consist of periphyton and detrital aggregate. The benthic naviculoid diatom, *Mastogloia elliptica* (Agardh) Cleve, was the dominant food of juvenile fish, whereas adults fed mostly on *Melosira granulata* (Ehrenberg) Ralphs and other sedimented planktonic algae. In Lake Valencia, Venezuela, Bowen (1980, 1981) found *O. mossambicus* feeding on a diet of periphyton and detrital aggregate derived from vascular aquatic plants. Because of the low stomach pH attained (< 2,0) *O. mossambicus* was able to utilize this detritus and even non-protein amino acids were assimilated. Whitfield & Blaber (1978) recorded *O. mossambicus* feeding on benthic diatoms in the brackish waters of Lake St Lucia, where they co-existed with 11 species of mullet. Trewavas (1983) reviews the literature on feeding in *O. mossambicus* and noted that it is a highly opportunistic species which occasionally can turn cannibalistic, but concluded that juveniles were omnivorous whilst adults fed mostly on detritus.

Figure 4 summarizes the abundance of food types found in stomachs of *O. mossambicus*, during its development from small fry through to adults, in Hartbeespoort Dam. Small fish showed a preference for animal protein but there was a major change in the diet of fish of over 4 g in wet mass when *Microcystis* and other plant matter became increasingly important and detritus became the most abundant food type. The anatomical increase in gut length during this developmental stage of the fish (Figure 2) also indicates that a major switch in food preference occurs. Lowe-McConnell (1975) and Bowen (1979) suggest that detritivory is a dietary specialization and that detritus represents a uniform rather than a varied type of diet. McKaye & Marsh (1983) noted that specialized adaptations are used for feeding on a specific food type during times of food shortage. During times of abundance, specialist feeders were observed to revert to a generalist feeding behaviour. It was, however, notable that the Hartbeespoort Dam *O. mossambicus*, although feeding mostly on detritus and *Microcystis*, had a mixture of food types in their gut (Table 1). Mathavan, Vivekanandan & Pandian (1976) found that the mass of 'fingerlings' of *O. mossambicus*, fed on a pure diet of *Spirogyra maxima* (Hass.) Wittrock, actually decreased whereas if this diet was supplemented with goat liver their mass not only increased but they also consumed more *Spirogyra* and showed an increased absorption efficiency. Their study illustrates the importance of a mixed diet and the influence of supplementary animal protein, to ensure optimal growth, in the diet of a herbivorous or detritovorous fish.

Fernando & Holcik (1982) hypothesized that the discrepancy between high primary production and poor fish yields in tropical reservoirs, was due to an under-utilization of the various trophic levels by the fish species present. They suggested that this was due to the general riverine origin of fish species found in lakes. Riverine fish species are adapted to inhabiting mostly the shallow shoreline regions of lakes and their breeding activity is confined to periods when extensive inundation of lake shoreline regions occur, and even then the fish moved upstream into rivers flowing into the lake to breed. Generally lakes show a number of attributes making them significantly different from rivers; a build-up and large standing population of plankton, areas where detritus settles out of the water column forming dense deposits, regions within the same water body with vastly different temperatures, and oxygen saturation ranging from zero to supersaturated. In the family Cichlidae a number of species show preadaptations suited to successfully exploit lacustrine habitats. Because of its nesting and mouth-breeding behaviour the flooding of marginal vegetation is not a pre-requisite for initiating breeding activity in *O. mossambicus* and the ability to utilize planktonic

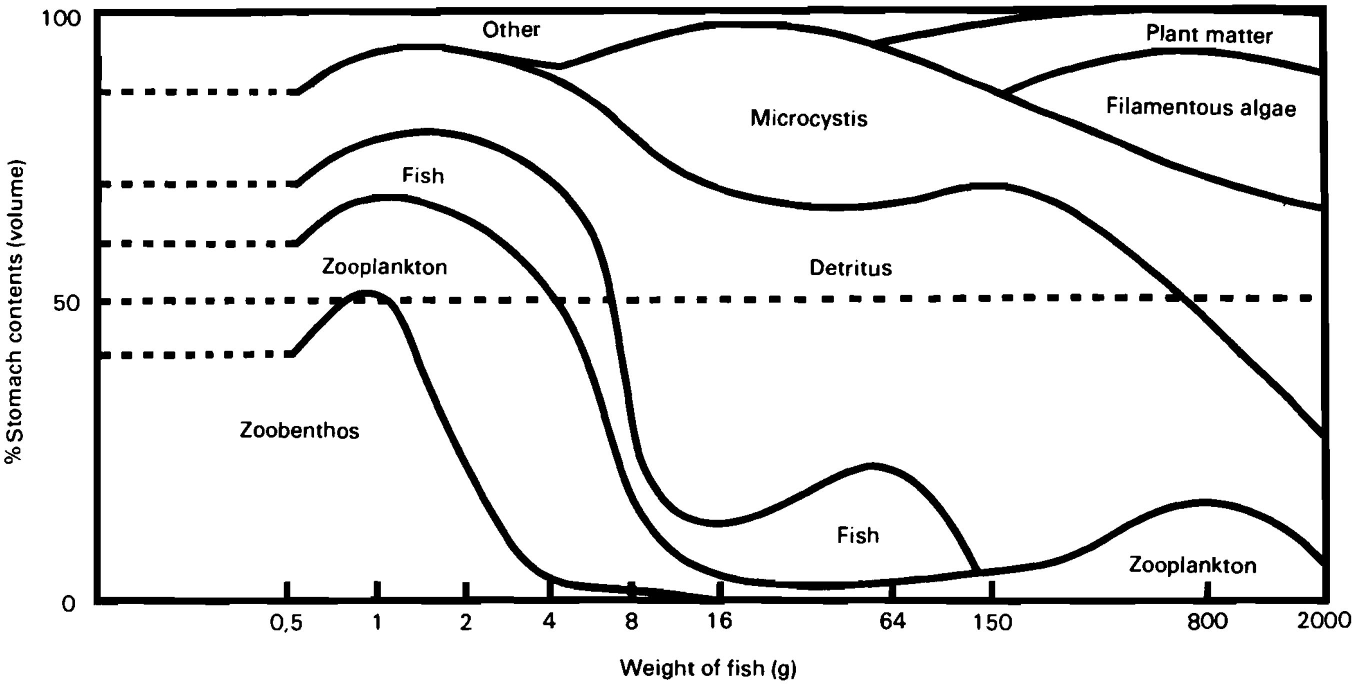

Figure 4 Representation of the major food types expressed as a percentage of stomach content volume with increasing size in *O. mossambicus*.

algae and detritus as a food source further indicate that this species is particularly well adapted for existence in a lacustrine environment. Whitfield & Blaber (1979) noted that *O. mossambicus* could tolerate high salinities and sudden temperature fluctuations but avoided current speeds greater than 10 cm/s. The more than 400-fold increase in fish yields recorded in Lake Parakrama Samudra after the introduction of *O. mossambicus* (Fernando & Holcik 1982), provides further evidence that this species is pre-adapted to the successful exploitation of a shallow lake environment.

Oreochromis mossambicus is at the extreme of its distributional range in Hartbeespoort Dam. In severe winters water temperatures drop to below the minimum tolerated 10°C (du Plessis & Groenewald 1953) and this is often followed by large winter mortalities (Cochrane 1984). In spite of frequent winter mortalities *O. mossambicus* has maintained large population densities. It was evident from field observations that *O. mossambicus* was the only one of the three dominant species to breed in Hartbeespoort Dam in the 1982/83 season and there was a subsequent 81% increase in the total biomass of this species in the 1983/84 season (NIWR 1985). It appears that the prolific breeding of *O. Mossambicus*, up to three broods per year (du Plessis & le Roux 1960), thus allows the build-up of large populations during years when the other dominant species, *C. gariepinus* and *C. carpio*, do not breed. Large blooms of *Microcystis* phytoplankton and an abundance of organic detritus are a consequence of hypertrophy. The ability of *O. mossambicus* to utilize the phytoplankton and detritus as a food source, and its prolific annual breeding cycle with maternal mouth breeding and caring for newly hatched fish, as well as its tolerance to a range of water salinities, thus enable this species to maintain a large proportion of the total fish biomass, even during years when winter mortalities are high.

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