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Feeding and grazing in Lake George, Uganda

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The fauna of Lake George is dominated by herbivores, in particular the fish *Tilapia nilotica* and *Haplochromis nigripinnis*, and the cyclopoid copepod *Thermocyclops hyalinus*. Digestion, and the assimilation of carbon from algae, by these herbivores were studied in detail. It was found that, contrary to previous observations reported in the literature, both fish and zooplankton were able to digest and assimilate blue-green algae. The diurnal feeding patterns of the herbivores were examined, and methods devised for assessing, in terms of carbon, the daily ingestion of algae. Hence, using biomass data, the total amount grazed by the herbivores was calculated. Estimates of carbon requirements at other trophic levels were made, as was an assessment of the required level of net production by the algae for comparison with figures for standing crop and net algal production measured by other means.

Food selection by secondary and tertiary producers is discussed, and in several species age correlated changes in selectivity were examined. Both the major herbivorous species of fish adopt phytoplankton feeding after a period of carnivorous or omnivorous feeding as fry. *Thermocyclops hyalinus* is herbivorous all its life, but the size of particle taken changes with age. There are more species of carnivorous than herbivorous fish and these exploit a wider variety of food sources; the few species studied also show changes in food preference with age.

INTRODUCTION

The Royal Society–I.B.P. team was established to investigate productivity at all trophic levels in Lake George. Previous workers (Fish 1952, 1955) have concluded that blue-green algae, the dominant elements of the phytoplankton, are not digested by herbivores and therefore do not enter into the food chains. Blue-green algae are known to be ingested by the dominant herbivores in this lake, and thus the question of whether or not these species can digest and assimilate blue-green algae is critical to any interpretation of the relationship between primary and secondary production in the lake.

Digestion and assimilation of algae

The digestion of algae by the herbivorous fish in Lake George was studied by D. J. W. Moriarty (1973). From this investigation it appeared that enzymic digestion occurred in the intestine, but only after acid lysis of the algal cells had already taken place. The lowest pH value recorded in the stomach of *Tilapia nilotica* was 1.4. Experiments *in vitro* indicated, by the degree of subsequent digestion by intestinal enzymes, that lysis was more effective at this pH than at any higher value (figure 1). Very little digestion occurred after algae had been subjected to acid concentrations at or above pH 2.0. Experiments in which ¹⁴C labelled monospecific cultures of algae were fed to fish in the laboratory showed

that *T. nilotica* could assimilate a maximum of 70 to 80% of ingested carbon from the blue-green algae *Microcystis* sp. and *Anabaena* sp., and the diatom *Nitzschia* sp. *Haplochromis nigripinnis* assimilated a similar proportion of carbon from *Microcystis*. *Tilapia nilotica* assimilated a maximum of about 50% of ingested carbon from the green alga *Chlorella* sp. (table 1), (Moriarty, D. J. W. & Moriarty, C. M. 1973). The proportion of carbon assimilated was, however, not always maximal.

In the stomach of *Tilapia nilotica* and of *Haplochromis nigripinnis* in the lake, acid secretion follows a diurnal cycle associated with feeding (figure 2). Secretion starts when feeding begins, at or before dawn, and in *T. nilotica* low pH values are

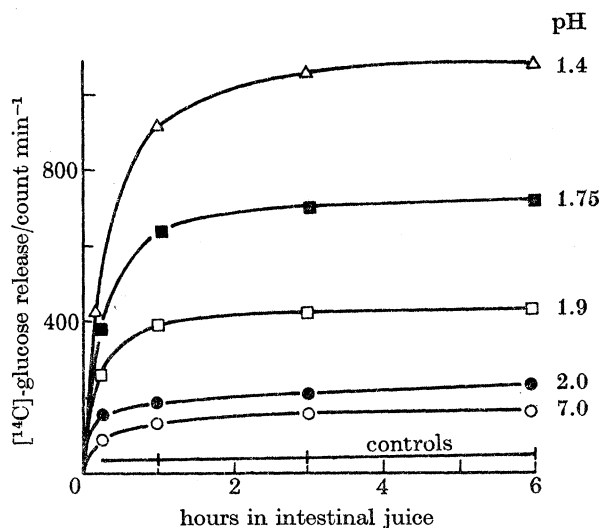


FIGURE 1. Digestion of blue-green algae after treatment with acid at various pH values. This is measured by the release of glucose from storage polysaccharides in lake algae (mainly *Microcystis* spp.), labelled with ^{14}C (Moriarty, D. J. W. 1973).

TABLE 1. PERCENTAGE ASSIMILATION OF CARBON FROM DIFFERENT SPECIES OF ALGAE BY *TILAPIA NILOTICA* AND *HAPLOCHROMIS NIGRIPINNIS* (MORIARTY, D. J. W. & MORIARTY, C. M. 1973)

	assimilation as percentage of carbon ingested		
	average	range	no. of experiments
by <i>Tilapia nilotica</i> ,			
from <i>Microcystis</i> spp.	70	67-73	6
<i>Anabaena</i> sp.	75	68-82	4
<i>Nitzschia</i> sp.	79	78-81	2
<i>Chlorella</i> sp.	49	45-52	3
by <i>Haplochromis nigripinnis</i> ,			
from <i>Microcystis</i> spp.	71	56-80	7

not obtained throughout the stomach until feeding ceases at sunset. When feeding begins the stomach is contracted and most of the algae pass straight through the stomach into the intestine. These algae will remain undigested. As feeding continues the stomach expands, but nevertheless a large proportion of the ingested algae passes through the anterior end of the stomach only. Consequently, this material is not subjected to pH values of less than about 2.0, and its subsequent digestion and assimilation will, therefore, be low. A smaller proportion of

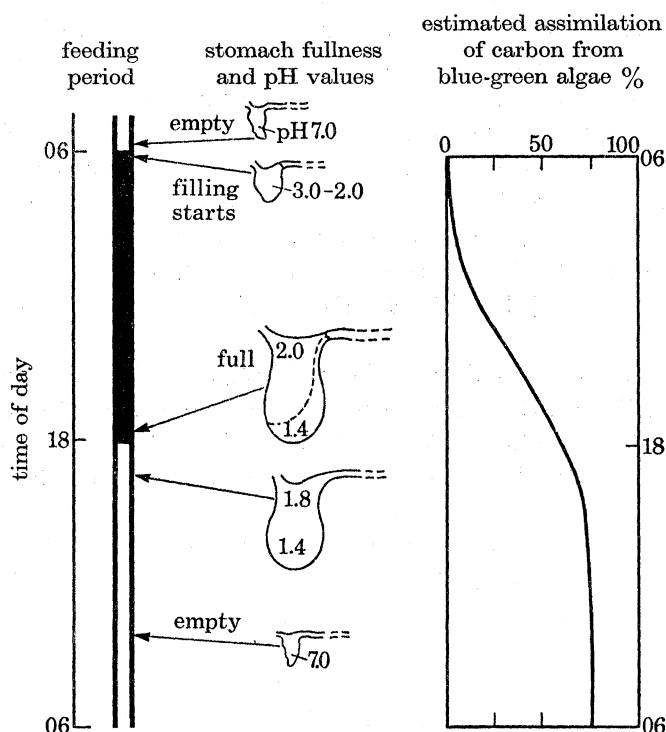


FIGURE 2. Diurnal cycle of feeding in *Tilapia nilotica*, stomach acidity, and digestion of algae in the intestine. The graph of carbon assimilation from blue-green algae which have been eaten during the feeding period shown, and which are present in the intestine, is a tentative estimate based upon data from Moriarty, D. J. W. (1973), and Moriarty, C. M. & Moriarty, D. J. W. (1973).

the ingested algae passes into the fundus of the stomach, where it accumulates as feeding proceeds, and is subjected to pH values of less than 2.0. There is a certain amount of mixing of the algae from the fundus with algae from the anterior part of the stomach, that is, with algae which would not otherwise be subjected to pH values of less than 2.0. As a result of this mixing, a certain proportion of algae that do not pass through the main body of the stomach before entering the intestine nevertheless will be digested and ultimately assimilated. Acid secretion continues for some time after feeding has ceased and algae accumulated in the stomach, except for a small proportion near the pylorus, are subjected to pH values of less

than 2.0. These algae are completely lysed and their subsequent digestion and assimilation is almost complete. The effect of this varying degree of exposure to acid is to cause a gradation through the day from zero to maximum in the proportion of ingested blue-green algal cells lysed, and therefore digested and assimilated.

The first faecal material derived from any feeding period is green, because the first algae to enter the intestine have not been affected by acid. Faeces resulting from the mixture of algae from the anterior and posterior parts of the stomach are voided next, and are green-brown in colour, the brown fraction being due to lysed and digested algae. Any diatoms appearing in these faeces will have been completely digested because pH values of 2.0 are low enough to destroy their cell membranes. This mixture of digested diatoms and undigested blue-green algae could explain why Fish (1952, 1955) thought that the diatoms were utilized as food but the blue-green algae were not. Faeces resulting from the algae accumulated in the stomach at the end of the feeding period are brown, because these algae have been subjected to strong acid. In colour and consistency, this well-digested faecal material resembles the Lake George sediment, which could explain the observations of Fish (1955) that *Tilapia nilotica* in Lake George feeds on the bottom sediment.

Having shown that pure cultures of certain algal species in Lake George are assimilated by *Tilapia nilotica*, experiments were carried out to determine the average degree of assimilation of ingested carbon from the community of phytoplankton occurring naturally in the lake. Because it was impossible to measure this directly, the natural feeding rhythm of the fish was simulated in the laboratory, and the average degree of assimilation over a 24 h period was determined. The results obtained show that *T. nilotica* assimilated an average of about 43 % of ingested carbon, and *Haplochromis nigripinnis* an average of about 66 % (Moriarty, D. J. W. & Moriarty, C. M. 1973).

The same monospecific culture of *Microcystis* used to feed the fish was used also to determine the degree of assimilation of carbon by *Thermocyclops hyalinus*. Copepodids and adults assimilated about 35 % of ingested carbon, and the nauplii about 58 % (M. P. Tevlin unpublished). Although these results were obtained with a laboratory culture of *Microcystis*, they should be similar for *T. hyalinus* in the lake, since it feeds mainly on *Microcystis* throughout its life cycle.

Utilization of primary production

That all three herbivores have a diurnal cycle of ingestion was established by observation throughout 24 h. With this approach it was possible to quantify the total daily ingestion, and by applying this figure to the population biomass, to indicate the total grazing of phytoplankton by herbivores in the lake. Estimates of the amount of algae necessary to sustain organisms at higher trophic levels have been made, and hence a rough assessment of the total daily loss from the phytoplankton community could be made. This estimate can be compared with the net primary production as measured by standard techniques.

Moriarty, C. M. & Moriarty, D. J. W. (1973) showed by measuring dry weight of stomach and intestinal contents every 2 h for 24 h, that *Tilapia nilotica* and *Haplochromis nigripinnis* have a diurnal cycle of feeding.

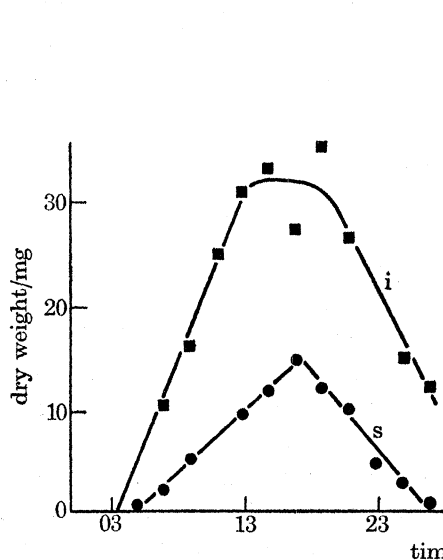


FIGURE 3

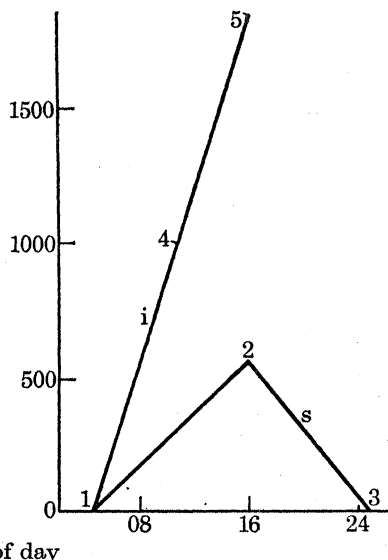


FIGURE 4

FIGURE 3. The diurnal changes in dry weight of stomach (s) and intestine (i) contents of *Haplochromis nigripinnis* (average total length 7.3 cm). Samples of fish were taken from the lake at 2 h intervals, and the gut contents removed and dried to constant weight (Moriarty, C. M. 1973).

FIGURE 4. Weighted regression lines of change in dry weight of stomach (lines 1-2, 2-3), and intestine (line 1-4) contents during the day, of *Tilapia nilotica*, average total length 19.0 cm. Line 4-5 is an extrapolation of line 1-4 (from Moriarty, C. M. & Moriarty, D. J. W. 1973).

In both species feeding begins at or before dawn, and the dry weight of stomach contents increases steadily until feeding stops. This generally occurs just before sunset (about 19.00 h), and is followed by a gradual decrease in the dry weight of stomach contents. Emptying of the stomach into the intestine is generally completed by about 01.00 to 02.00 h, and the intestinal contents decrease as defaecation proceeds. A typical feeding pattern is shown in figure 3.

A method for quantifying daily ingestion by *Tilapia nilotica* and *Haplochromis nigripinnis*, based on this diurnal feeding pattern, is illustrated in figure 4. The weighted regression lines 1 to 2 and 2 to 3 show the increase and decrease respectively in the dry weight of stomach contents with time. As feeding proceeds, in this case from 05.00 to 16.00 h, food passes from the stomach to the intestine. Initially, the passage rate of food from stomach to intestine is given by the slope of the weighted regression line 1-4. Point 4 represents the time at which defaecation of new food begins. Between this time and that at which feeding ceases (2) it was impossible to measure the rate at which stomach contents are emptied into the

304 D. J. W. Moriarty and others (Discussion Meeting)

intestine. It was assumed, therefore, that the rate represented by the slope of 1–4 would be constant throughout feeding, so that this line could be extrapolated to point 5, at which time feeding ceased. Point 5 gives, therefore, an estimate of the total food entering the intestine during feeding. This, together with the amount accumulated in the stomach (point 2), gives an estimate of total ingestion for the day. The quantities ingested are linearly related to the weight of the fish, as given by the following regression equations:

$$\text{for } T. \textit{ nilotica} \quad y = 271 + 13.3x, \quad (1)$$

$$\text{for } H. \textit{ nigripinnis} \quad y = -29.6 + 21.9x, \quad (2)$$

where y is the dry weight of phytoplankton ingested in mg per day and x is the wet weight of fish in grams. The equation for *H. nigripinnis* is only an approximate guide to ingestion by this species because insufficient data were available for one of the parameters on the rate of stomach emptying. These equations were derived from studies with *T. nilotica* in the size range 15 to 23 cm total length and with *H. nigripinnis* from 5 to 8 cm total length. They are not applicable to the juvenile and omnivorous stages of either species, and they may be inaccurate for individuals whose sizes lie outside the range studied. In order to obtain estimates for ingestion by the whole population of these species it was necessary to assume, however, that the equations do apply to all phytophagous members of the population. Since much of the biomass of both species is made up of individuals within the size ranges studied, there are probably no serious errors introduced by this assumption. Thus, for any population of fish equations (1) and (2) become:

$$\text{for } T. \textit{ nilotica} \quad I = n271 + 13.3B, \quad (3)$$

$$\text{for } H. \textit{ nigripinnis} \quad I = -n29.6 + 21.9B, \quad (4)$$

where I is the total ingestion in mg dry weight per day in the area occupied by the fish, n is the number of fish, and B is their biomass in grams fresh weight.

The biomass of fish is greatest around the shorelines of the lake, and least at its centre (Burgis *et al.*, this volume). This unequal distribution pattern of herbivorous fish must result in more intense grazing on the phytoplankton of inshore regions. To quantify this regional difference, grazing rates were calculated for inshore and midlake areas (table 2), inshore areas being defined as lying within 100 m of any shore, the remaining area being considered mid-lake. For calculation of overall grazing rates, a mean figure for fish biomass over the whole lake was used (J. J. Gwahaba, personal communication) from which a mean daily grazing rate of 34 mg C m⁻² was calculated.

The raptorial stages of *Thermocyclops hyalinus* also showed a diurnal cycle of feeding. Ingestion rates were determined at 3 h intervals for 24 h by feeding freshly collected animals with ¹⁴C labelled lake algae. The uptake of radioactive material was measured after a feeding period short enough to preclude defaecation of ¹⁴C labelled pellets. The radioactivity of the feeding medium (expressed as

counts $\text{min}^{-1} \text{ml}^{-1}$), and its carbon content (as $\mu\text{g C ml}^{-1}$, determined by the method of Ganf & Milburn 1971), were measured. Thus, ingestion was expressed directly in terms of carbon. Corresponding defaecation rates (at intervals over 3 h) were measured, on some occasions, by counting the number of faecal pellets voided by

TABLE 2. CALCULATED TOTAL DAILY INGESTION OF PHYTOPLANKTON BY *TILAPIA NILOTICA* AND *HAPLOCHROMIS NIGRIPINNIS* IN INSHORE AND MIDLAKE REGIONS OF LAKE GEORGE

	mg (dry weight) $\text{m}^{-2} \text{day}^{-1}$		mg C $\text{m}^{-2} \text{day}^{-1}$	
	mid-lake	inshore	mid-lake	inshore
<i>Tilapia nilotica</i>	34	360	11	120
<i>Haplochromis nigripinnis</i>	57	110	19	36
total	91	470	30	156

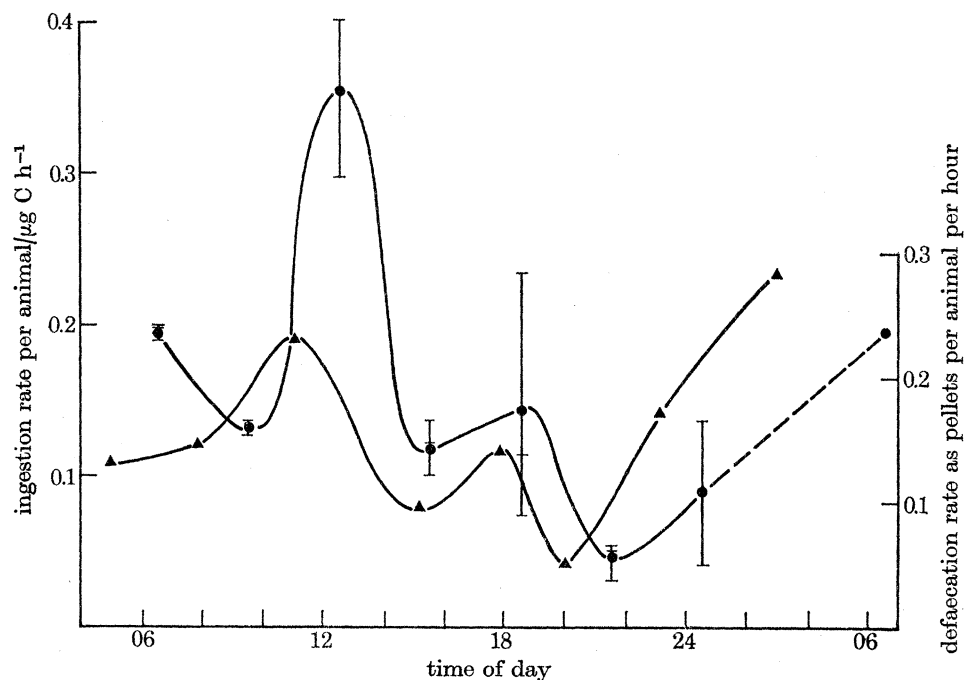


FIGURE 5. Diurnal variation in ingestion (●) and defaecation (▲) rates of *Thermocyclops hyalinus*. The area beneath the ingestion curve gives the total ingestion for that day, in this case $0.34 \mu\text{g C}$ per adult per day. Lines above the points show the range of values obtained. (M. P. Tevlin unpublished.)

freshly collected animals feeding on lake algae. The mean ingestion and defaecation rates per individual generally showed two or three peaks of feeding activity in each 24 h period (figure 5). The only period during which no feeding activity was recorded was between about 12.00 and 18.00 h, corresponding to the period when thermal stratification commonly occurs in the lake.

Feeding by the nauplii of *Thermocyclops hyalinus* was not investigated in detail, but the available data show that feeding activity was greatest at night. Of the other herbivorous zooplankton occurring in the lake, only *Daphnia barbata* was studied. Analysis of gut fullness indicated that the level of feeding activity did not vary appreciably during a 24 h period (A. Duncan, personal communication).

Results of the type illustrated in figure 5 were used to calculate the total daily ingestion of carbon by planimetric integration of the area beneath the ingestion curve. Mean figures obtained by this method are detailed in table 3*a*.

TABLE 3. DAILY INGESTION DATA FOR *THERMOCYCLOPS HYALINUS*

method	developmental stage	$\mu\text{g C}$ ingested per animal per day	\pm s.d.	no. of experiments	corrected to lake concentrations
(a)	adult	0.33	$\pm < 1\%$	2	0.86
	late copep.	0.18	—	1	0.47 †
	nauplius	0.38	—	1	0.38
(b)	adult	0.28–0.43	—	1	0.73–1.12
(c)	adult	0.31	$\pm 52\%$	8	0.81
	late copep.	0.12	$\pm 11\%$	4	0.31

Methods used (see text): (a) Planimetric integration of area beneath curve of diurnal ingestion rate. (b) Quantification of individual peaks of ingestion and their summation. (c) Laboratory method.

† In subsequent calculations, this value of 0.47 $\mu\text{g C}$ ingested by late copepodids was used rather than the mean of 0.47 and 0.31 $\mu\text{g C}$. This is because the ingestion rate for late copepodids obtained by method (a) is considered to be more accurate than that obtained in (c). Greater experimental difficulty was experienced with method (c), particularly in manipulating sufficiently large numbers of copepodids in the time available before the animals began to defaecate the ^{14}C labelled food. As a result consistent results were not always obtained. Adult animals, because of their larger size, could be selected and handled more rapidly. Techniques for handling copepodids were improved before the method of planimetric integration, (a), was carried out.

A second method of quantifying daily ingestion by raptorial stages of *Thermocyclops* depended upon recurrence of the peaks of feeding activity at certain times, which could be anticipated to within about 2 h. Freshly collected adult animals were fed ^{14}C labelled lake algae about 3 h before the expected feeding peak. At 1 h intervals for the next 6 h, a number of individuals was taken from the feeding vessel and the radioactivity per animal measured. This figure was converted to ingested carbon per animal as described above (p. 305). The carbon uptake per animal was plotted against time, and the apex of this curve was taken to be the amount of carbon ingested during that feeding period (M. P. Tevlin personal observations). The apices of the first two expected feeding peaks were well-defined and ingestion values readily obtained. The third, however, was of longer duration, and a distinct apex was not observed since defaecation and ingestion of ^{14}C labelled material was occurring simultaneously. Nevertheless, from the data available, it was possible

to estimate the probable upper and lower limits of ingestion during that period. Calculated values for the three feeding periods are shown below:

- first peak 0.092 $\mu\text{g C}$ per adult *T. hyalinus*,
- second peak 0.14 $\mu\text{g C}$ per adult *T. hyalinus*,
- third peak 0.05 to 0.20 $\mu\text{g C}$ per adult *T. hyalinus*.

The total daily ingestion was taken to be the sum of these amounts (table 3b).

A laboratory method for measuring ingestion involved supplying a known number of animals with lake algae for 24 h, and counting the total number of faecal pellets produced as a result of ingestion during this period. In separate experiments, animals (of the same developmental stage) with full guts were deprived of food and allowed to defaecate completely. Thus, the mean number of faecal pellets produced from a full gut was obtained. By dividing this figure into the daily total, the number of times the gut filled per day was calculated. The mean amount of carbon in one full gut was determined by feeding previously starved animals on ^{14}C labelled algae for 40 min (i.e. long enough to fill the gut, but not to start defaecating) and measuring the uptake of radioactive material; this was converted into $\mu\text{g C}$ as described above. Hence the total carbon uptake per individual per day was calculated as the product of the mean carbon content per full gut, and number of times the gut was filled per day (Tevlin 1973). The results are given in table 3c.

Table 3 shows that the results obtained by these three methods of measuring total ingestion are consistent. However, the figures could not be applied directly to animals in the lake, because the concentrations of zooplankton and phytoplankton used in the experiments were five to ten times higher than in the lake (except for those experiments on nauplii in which lake concentrations were used). Experiments to assess the effect of concentration showed that ingestion rates at lake concentrations were 2.6 times greater than those at the experimental concentrations. Thus, the measured total daily ingestions (except of the nauplii) were multiplied by 2.6 to make them applicable to animals feeding at lake concentrations (table 3). Using biomass data from Burgis (1973) the total ingestion by the whole *Thermocyclops hyalinus* population in the lake was calculated to be 504 $\text{mg C m}^{-2} \text{ day}^{-1}$ (table 4).

Total grazing and other losses from the phytoplankton

The total daily intake of phytoplankton by the herbivores has been estimated at 34 mg C m^{-2} for the fish, and 504 mg C m^{-2} for *T. hyalinus*, over the whole lake (table 4). Zooplankton grazing by species other than *T. hyalinus* was not measured, but was considered unlikely to alter the total grazing figure significantly because of their relatively small biomass (see Burgis, 1974). The total daily loss by grazing from the phytoplankton (538 mg C m^{-2}) is very much less than the mean standing crop of algae in the lake, which is about 30 g C m^{-2} and shows little variation (G. G. Ganf, personal communication).

Grazing by the plankton and fish does not, however, account for all the loss from the phytoplankton population. Export of algae from the lake occurs with outflow via the Kazinga Channel, but no quantitative data are available. It is thought that losses by this means are relatively small since the rate of flow down the Channel is slow. Terminal sedimentation of algae within the lake occurs, but again, no quantitative data are available. In addition to these losses, the benthic animals feed on sedimented algae, both live and moribund, and presumably, on the decomposers associated with them. A tentative quantitative estimate of benthic ingestion was

TABLE 4. TOTAL DAILY INGESTION OF PHYTOPLANKTON
BY THE MAJOR HERBIVORES IN LAKE GEORGE

	mg (dry weight) $\text{m}^{-2} \text{ day}^{-1}$	mg C $\text{m}^{-2} \text{ day}^{-1}$
<i>Tilapia nilotica</i>	53	17.5
<i>Haplochromis nigripinnis</i>	50	16.5
<i>Thermocyclops hyalinus</i>	—	504
total		538

TABLE 5. RATE OF SEDIMENTATION OF PHYTOPLANKTON MATERIAL AS FAECES
OF THE MAJOR HERBIVORES IN LAKE GEORGE

	ingestion mg C $\text{m}^{-2} \text{ day}^{-1}$	assimilation %	faeces mg C $\text{m}^{-2} \text{ day}^{-1}$
<i>Tilapia nilotica</i>	17.5	43	6.5
<i>Haplochromis nigripinnis</i>	16.5	66	6.5
<i>Thermocyclops hyalinus</i> (raptorial stages)	333	35	216
<i>Thermocyclops hyalinus</i> (nauplii)	171	58	72
		total faeces	about 300

made by using calculated population growth and respiration values in terms of carbon (J. P. E. C. Darlington, unpublished). Total daily assimilation of carbon by the benthos was obtained by summing population growth and respiration, assimilation of 15 % being assumed. The total daily ingestion by the benthos was estimated by this means at 1 g C m^{-2} .

Of this $1 \text{ g C m}^{-2} \text{ day}^{-1}$, using assimilation efficiencies of 43 % for *Tilapia nilotica*, 66 % for *Haplochromis nigripinnis*, 58 % for *Thermocyclops* nauplii and 35 % for the raptorial stages of *T. hyalinus* (see p. 302), about $300 \text{ mg C m}^{-2} \text{ day}^{-1}$ could be supplied by the faeces of planktonic herbivores (table 5). The remaining $700 \text{ mg C m}^{-2} \text{ day}^{-1}$ required to maintain the benthic fauna must be derived from the phytoplankton, either directly or through the decomposers. Thus, in addition to a daily planktonic grazing of about 540 mg C m^{-2} the phytoplankton must supply $700 \text{ mg C m}^{-2} \text{ day}^{-1}$ for the benthic grazers. This total of $1240 \text{ mg C m}^{-2} \text{ day}^{-1}$ is a minimum estimate of the net primary production required to maintain both planktonic and benthic organisms at higher trophic levels. Net primary production must exceed this minimum estimate to account for the outflow and sedimentation losses mentioned above.

Net primary production has been estimated by standard limnological techniques, as $600 \pm 800 \text{ mg C m}^{-2} \text{ day}^{-1}$ (Ganf 1972). Although there is considerable variation resulting from such factors as differences in light intensity, the mean rate is somewhat less than the estimated daily average of 1240 mg C m^{-2} taken by the 'grazers'. The discrepancy increases if attempts are made to include outflow and sedimentation losses. With the standard techniques for direct measurement of primary production it is difficult to make allowances for the complex interactions between supply and demand of oxygen and carbon dioxide for photosynthesis, photorespiration and dark respiration (Ganf & Viner, this volume). It is possible that estimates of total grazing could provide a useful independent assessment of minimum net primary production.

Food selection by herbivores

It has been shown above that the important herbivores in Lake George not only ingest, but can readily digest and assimilate blue-green algae, including *Microcystis* spp. Like many other specialized feeders, the young of the two dominant herbivorous fish species develop their characteristic adult feeding habits as they grow. The fry occupy a different niche or trophic level from the adults of their species.

As individuals of *Tilapia nilotica* increase in size they show changes in diet which are related to their changes in habitat. The fry inhabit the littoral and swampy regions of the lake, and ingest a wide variety of plant and animal material including aufwuchs, detritus, rotifers, copepods, hydracarinae and various insects. At this stage their feeding behaviour involves active pursuit and 'pecking' at particles in the water. As the juvenile *T. nilotica* grow larger and move further offshore, they ingest an increasing proportion of phytoplankton until, when they are more than 6 cm long, they feed almost entirely on phytoplankton. Aquarium observations show that from this stage onwards the fish feed by a 'gulping' action resembling exaggerated respiratory movements, and that some zooplankters are able to avoid capture by swimming away from the feeding current. When live zooplankton was added to tanks of lake water in which the fish were feeding, there was no increase in the number of zooplankton remains found in the faeces after a fixed feeding period. However, after heat-killed zooplankton was added to the water, a sevenfold increase was observed (Moriarty, C. M. 1973).

The species composition of the phytoplankton ingested by large *T. nilotica* in the lake was examined in detail. Counts of several algal species in the stomachs of fourteen fish were compared with counts from an integrated column water sample collected at the same time and place, and their frequency distributions were found to be different. For each algal species Ivlev's coefficient of electivity was calculated; it is defined (Ivlev 1961) as:

$$\frac{(r-p)}{(r+p)},$$

where r is the percentage abundance of the species in the gut contents, and p is the

percentage abundance of that species in the environment. Results for five algal species (figure 6) show that there was a marked positive selection for the colonial blue-green alga *Microcystis*, the filamentous blue-green alga *Lyngbya*, and the colonial diatom *Melosira*, and negative selection for the small blue-green alga *Anabaenopsis* and the diatom *Synedra*.

This suggests that selection is based upon the size, and perhaps the shape, of the food particles. Collection of particles from the incurrent water involves a mucous-filtration mechanism, the effectiveness of which may well depend upon the particle size (Greenwood 1953).

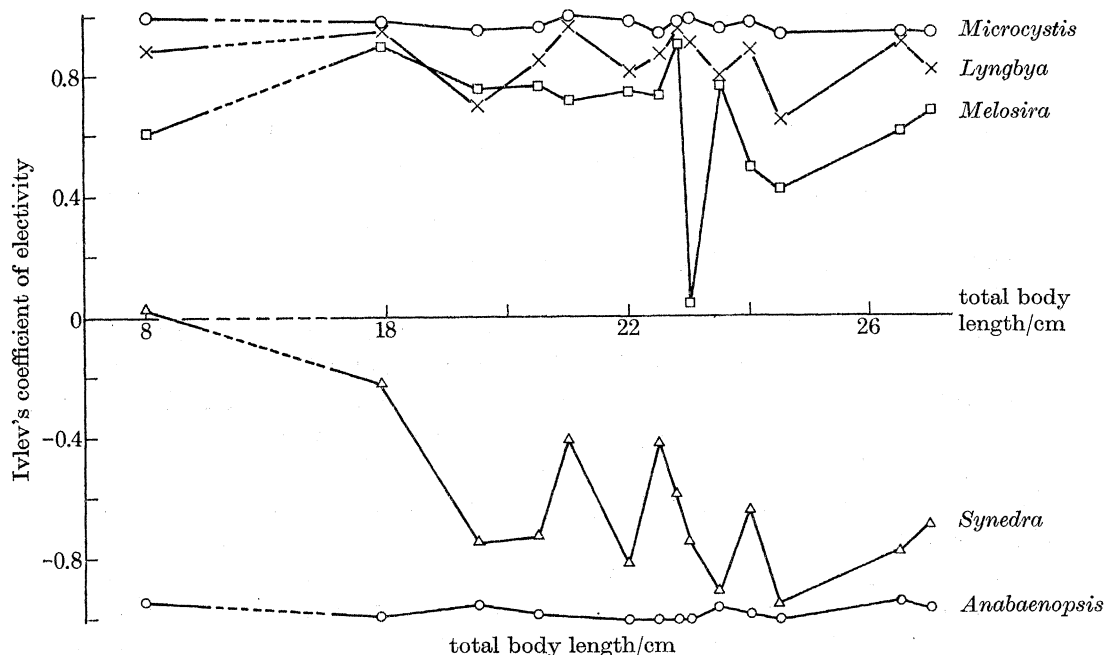


FIGURE 6. Graph of Ivlev's coefficient of electivity for five genera of planktonic algae ingested by *Tilapia nilotica*, against total length of the fish (after Moriarty, C. M. 1973).

All growth stages of *Haplochromis nigripinnis*, including the fry, are distributed throughout the lake. As much as 70% of the food particles taken in by fry are zooplankters, and Ivlev's coefficient suggests that there is some selectivity towards different components of the zooplankton (figure 7). There is positive selection for the larger cladoceran species *Daphnia* and *Moina*, which is greatest in the larger fish. For the smaller crustaceans, *Ceriodaphnia* and the copepods, there appears to be no selection by small fish (less than 5 cm long) and only weak selection, positive and negative respectively (for the *Ceriodaphnia* and copepods), by larger fish. The proportion of zooplankton in the total intake decreases as the fish approach maturity, when 97% of the particles ingested are phytoplankton (figure 8). Only the large colonial species of algae are found in the guts, including *Microcystis* spp.

and *Aphanocapsa*, together with diatoms bound in the mucilaginous sheaths of the colonies (Moriarty, C. M. 1973).

Only one other phytoplankton-eating fish, *Tilapia leucosticta* Trewavas, occurs in Lake George. The gut contents of individuals of this species caught in mid-lake areas show a preponderance of blue-green algae over other possible food items,

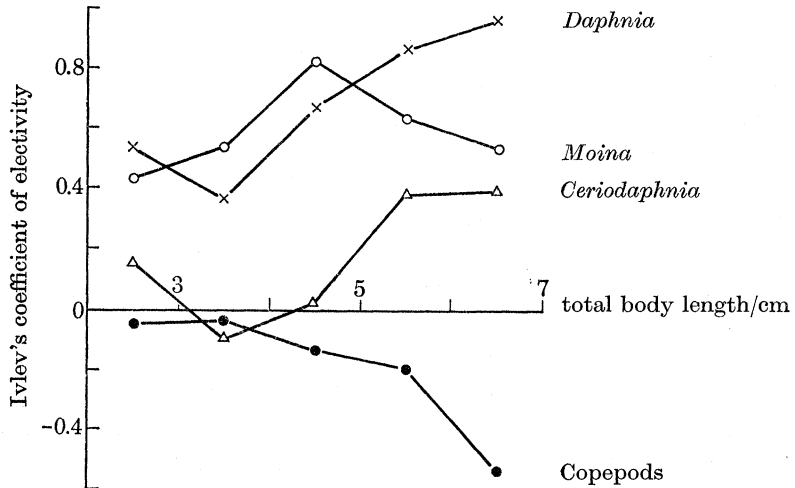


FIGURE 7. Graph of Ivlev's coefficient of electivity for four groups of planktonic crustaceans ingested by *Haplochromis nigripinnis* females and juveniles. Each point represents the gut contents of five individual fish whose total lengths are within the 1 cm size range indicated (Moriarty, C. M. 1973).

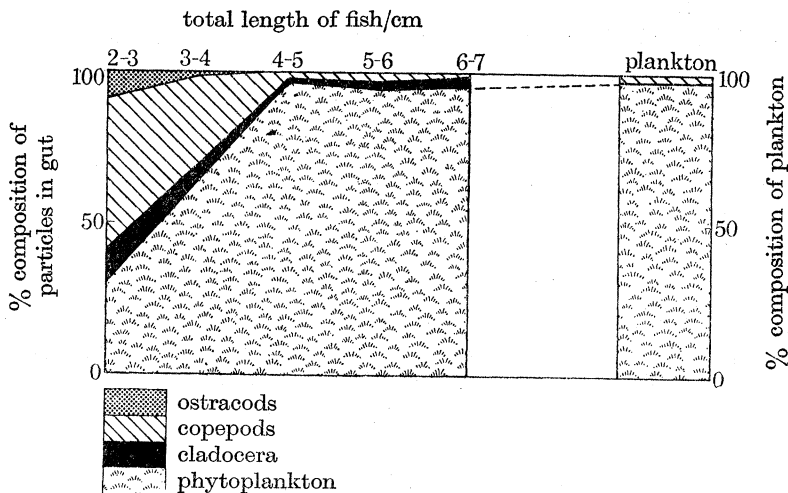


FIGURE 8. Numerical percentage composition of the total particles present in the guts of *Haplochromis nigripinnis* females and juveniles. The total gut contents of five individual fish were counted for each 1 cm size range of fish (after Moriarty, C. M. 1973). For comparison, the numerical percentage composition of the plankton is shown, as counted in vertical haul residues sieved through a plankton net with 4 meshes/mm (100 meshes/in).

whereas fish caught in inshore regions had ingested detrital material (Dunn 1971). Since this species is more abundant inshore than offshore (Burgis *et al.*, this volume), it is essentially a detritivore.

Thermocyclops hyalinus is a phytoplankton feeder throughout its development, but the mechanism of feeding and the size of particles taken differ in the different developmental stages. Adults and copepodids are raptorial feeders upon the large colonies of *Microcystis* spp., which consist of numerous cells bound together with mucilage. The animals can be seen to grasp a colony with their many-pointed maxillae and maxillipeds, while the sharp mandibles break off smaller pieces for ingestion. Microscopic examination of the gut contents revealed *Microcystis* cells which had been ingested without apparent rupture, suggesting that the function of the mandibles is simply to break off pieces of a suitable size for ingestion, and not to masticate the algae. Such mouthparts are typical of carnivorous species of cyclopoid (Fryer 1957) to which *T. hyalinus* is very closely related. Raptorial *T. hyalinus* individuals were observed to attack, and apparently feed from, moribund Cladocera, but this was not common. Laboratory cultures of raptorial stages were maintained on *Microcystis* taken from the lake. Subsequent feeding, assimilation and growth measurements showed that their daily carbon requirements could be adequately supplied from this source alone (M. P. Tevlin, personal observation).

Naupliar stages of *Thermocyclops* are not raptorial, and are unlikely to be capable of ingesting algal particles greater than *ca.* 10 μm diameter. Examination of their gut contents usually showed the presence of single *Microcystis* cells (*ca.* 8 μm diameter). Laboratory observations on the nauplii suggest that the animals simply ingest suitably sized particles that they encounter in their movements through the water.

The role of bacteria in naupliar nutrition has not been determined. Growth studies on *in vitro* cultures of nauplii show normal growth when the nauplii are kept in that fraction of lake water that has passed through a 400-mesh net (i.e. with a pore size of 40 μm).

The remaining herbivorous zooplankton species are small filter feeders that are unable to ingest the large algal colonies. The scarcity of algal particles of a suitable size may partially explain why Cladocera are not more abundant in Lake George (Burgis *et al.*, this volume). Adult *Daphnia barbata* can ingest particles about 60 μm in diameter, and their gut contents include green algal cells and brown material (A. Duncan, personal communication). Laboratory observations of behaviour, and the fact that *Daphnia* tends to be most abundant at the bottom of the water column, suggests that most feeding activity occurs close to the mud surface.

Food selection by carnivores

By comparison with the secondary producers, the tertiary producers show a greater species diversity, especially in inshore regions. They are exploiting a wider variety of food sources than the herbivores, and though some species are very selective in their choice of food, others, especially some of the fish, are opportunists.

Predation on fish

Predation on the fish population has not been quantified, nor are its effects clear, but some qualitative observations can be made.

Of the piscivorous species of fish in Lake George, the most abundant is *Haplochromis squamipinnis* Regan. It shows a change in food selection with age, the young fish being opportunistic feeders taking benthic, midwater and emergent

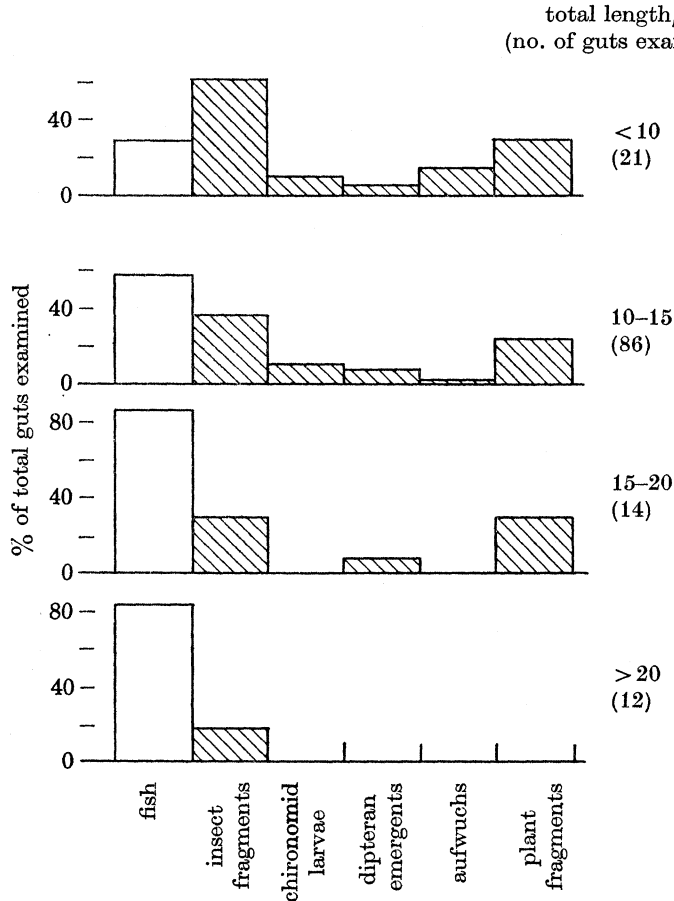


FIGURE 9. Histograms of the percentage of the total guts examined (excluding empty guts) in which six categories of food item occurred, in four 5 cm size ranges of *Haplochromis squamipinnis* (after Dunn 1972).

insects, as well as aufwuchs and plant fragments. As it grows, the young *H. squamipinnis* specializes increasingly on fish as a source of food (figure 9). Although it is the largest species of *Haplochromis* found in the lake, it is of moderate size, mature females being 15 to 25 cm long and the males rather less. Thus predation by this species will fall most heavily on the young stages of *Tilapia* spp. and on the *Haplochromis* spp. Young *H. squamipinnis* are most abundant close to shore where

they feed on fish fry. Only limited shelter is available for the prey in this region, which may contribute to the success of this predator. (Dunn 1972, and personal observations).

The other important piscivorous fish, *Bagrus docmac* (Forsk.), *Clarias lazera* Val., and *Protopterus aethiopicus* Heckel, are much larger fish than *Haplochromis squamipinnis* and are therefore able to take larger prey. *Protopterus* also eats molluscs in some areas. Other fish species also take fish fry, although their principal food source is different; for instance *H. angustifrons* Boulenger which feeds largely on benthic invertebrates will occasionally take small fish.

Haplochromis taurinus Trewavas is a localized inshore species which feeds on the embryos and larvae of cichlid fishes. By analogy with related species from Lake Victoria it seems probable that *H. taurinus* feeds by sucking the young out of the mouths of brooding females (Greenwood 1973).

Predation by piscivorous birds may be high, especially in the shallow water close to shore. Herons, ibises and storks feed along the shore line, and fish eagles and several species of kingfisher hunt in inshore regions. Cormorants and darters feed inshore and over the sandy shoals, while pelicans and terns feed over the entire area of the lake.

Up to 5000 tonnes of fish are removed from the lake each year by the commercial fishery. About 80 % of this consists of *Tilapia nilotica*, and the catching methods are selective as to size. The effects of this fishery are discussed in some detail in Burgis *et al.* (this volume).

Predation on zooplankton

In terms of biomass the dominant predators on zooplankton are the larval stages of *Chaoborus* spp. (Diptera, Nematocera). The food preference of the larvae varies in different instars (table 6; L. M. McGowan, unpublished data), and the instars are unevenly distributed, young larvae being concentrated inshore and older larvae extending into the mid-lake area. As a result of this distribution, the predation pressure exerted by the populations of larval *Chaoborus* on other components of the zooplankton is not uniform. Small zooplankters, such as rotifers and copepod nauplii, will be under heavier predation pressure close to shore than in the midlake region, since these animals form the major food source for the young *Chaoborus* larvae. In addition to this overall pattern, the *Chaoborus* larvae often occur in dense swarms in the plankton, so that the intensity of predation by the larval population varies very markedly. Most fourth and late third-instar *Chaoborus* larvae show a diurnal cycle of activity, burying themselves in the bottom sediments during the day and emerging into the water column at night to feed. It is possible that this cycle is linked with the diurnal cycle of feeding activity of *Thermocyclops* (M. P. Tevlin, personal observation). The copepod *Mesocyclops leuckarti* Kurz is also a planktonic predator taking cyclopoids as well as cladocerans.

By comparison with the *Chaoborus* species, predation by fish in the midlake area is relatively slight. *Haplochromis pappenheimi* (Boulenger) is the only fish

species in the lake which selectively feeds on zooplankton throughout its life, though the mechanism by which it selects animals from the total plankton is not known. Predation by *H. nigripinnis* fry on the zooplankton has already been discussed (p. 310). The surface-feeding, generalized carnivores *Aplocheilichthys eduardianus* David & Poll, and *A. pumilus* Boulenger take a proportion of zooplankton in their diet. Experiments in which a mixture of equal numbers

TABLE 6. DISTRIBUTION OF, AND FOOD SELECTION BY, DIFFERENT INSTARS OF *CHAOBORUS* SPP. LARVAE (L. M. MCGOWAN, UNPUBLISHED)

instar	distribution	prey organisms observed in the pharynx
1	predominantly inshore	ROTIFERS
2	predominantly inshore	ROTIFERS, nauplii, copepods
3	ubiquitous	rotifers, nauplii, COPEPODS, COPEPODIDS
4	ubiquitous	rotifers, <i>Daphnia</i> , ostracods, COPEPODS

Capitals, main components; lower case, other components.

Thermocyclops, *Daphnia* and *Ceriodaphnia* were offered to *A. eduardianus* in the laboratory, showed that the fish selected the Cladocera (M. P. Tevlin, unpublished observations).

Inshore, predation on the zooplankton by fish fry may be important. The paucity of large cladocerans in the inshore areas could well be correlated with this predation pressure (Burgis *et al.*, this volume).

Where dense swarms of *Chaoborus* larvae occur they are eaten by a great variety of fish. For instance, adult *Haplochromis nigripinnis* are sometimes found with their stomachs full of *Chaoborus* larvae instead of the usual phytoplankton. Similarly, *Chaoborus* and chironomid pupae ascending through the water column to emerge, or in the process of emerging, are frequently ingested by fish which are not otherwise carnivorous.

Predation on the benthos

Haplochromis angustifrons is the most important benthic predator throughout most of the lake; over mid-lake mud areas it is the only benthic predator except for the occasional young *H. squamipinnis*. At one mid-lake site, where the standing crop of benthos was $0.77 \text{ g (d.w.) m}^{-2}$, a minimum estimate for the daily take-off by the *H. angustifrons* population was $0.03 \text{ g (d.w.) m}^{-2}$, or 4% of the total standing crop.

Individuals of *H. angustifrons* feed on benthic invertebrates throughout life, but show a change in feeding selectivity with growth (figures 10, 11). Gut content analyses show small fish select ostracods and copepods, while larger individuals select dipteran larvae. This may indicate size discrimination, since the crustaceans are about 1 mm in linear dimensions while the size range of dipteran larvae is from 1 to 18 mm in length. The distribution of the different instars of chironomid larvae in the gut contents (figure 12) shows that young instars are taken mainly by small fish and older instars by larger fish. This suggests that the upper limit to the size

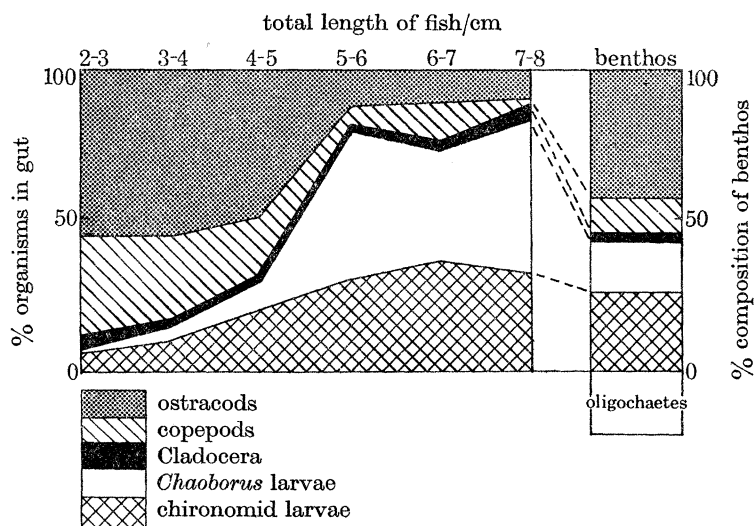


FIGURE 10. Numerical percentage composition of the total organisms present in the guts of *Haplochromis angustifrons* females and juveniles. The total gut contents of five individual fish were counted for each 1 cm size range of fish. For comparison, the numerical percentage composition of the benthos is shown, as counted in the residues of six Jenkins cores (enclosing the population occurring from 10 cm above the mud surface to 40 cm below it), retained in a wire sieve with 1.6 meshes/mm (40 meshes/in) (J. P. E. C. Darlington, unpublished). *N.B.* Oligochaetes are graphed as being in excess of 100 % of the benthos. This is because oligochaetes were not found in the guts of *H. angustifrons*, but if they were ingested it is probable that their remains would not have been recognized. They are, therefore, to be excluded from the comparison.

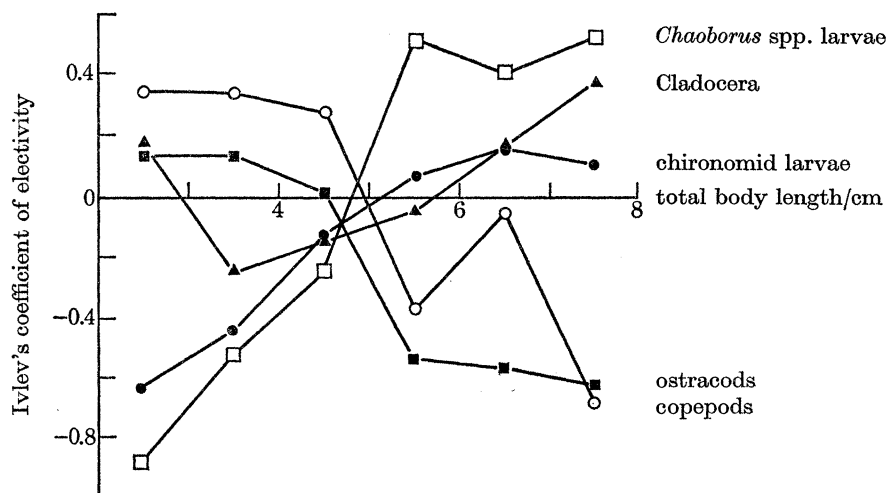


FIGURE 11. Graph of Ivlev's coefficient of electivity for five groups of prey organisms ingested by *Haplochromis angustifrons* females and juveniles. Each point represents the gut contents of five individuals whose total lengths are within the 1 cm size range indicated (J. P. E. C. Darlington, unpublished).

of prey selected is set by what can be swallowed, and the lower limit depends on a sieving mechanism whose 'mesh' coarsens as the fish grows. Laboratory observations indicate that the fish feed by sucking mud into the mouth, passing it through the buccal chamber, and expelling waste material through the opercular opening. The gill arch morphology shows peculiarities which may represent an adaptation to this mode of feeding (P. H. Greenwood, personal communication).

Food selection by different sized individuals of *H. angustifrons* may, however, be influenced by the accessibility of the prey. The *Chaoborus* and chironomid larvae burrow into the substrate where they may be beyond the reach of small fish. Furthermore, early instars of chironomids live closer to the mud surface than do later instars, and so might be more readily accessible to small fish. Ostracods and *Daphnia* occur on or near the mud surface, and the copepods in the water column, with the result that these species would be available to fish at all sizes (J. P. E. C. Darlington, personal observation).

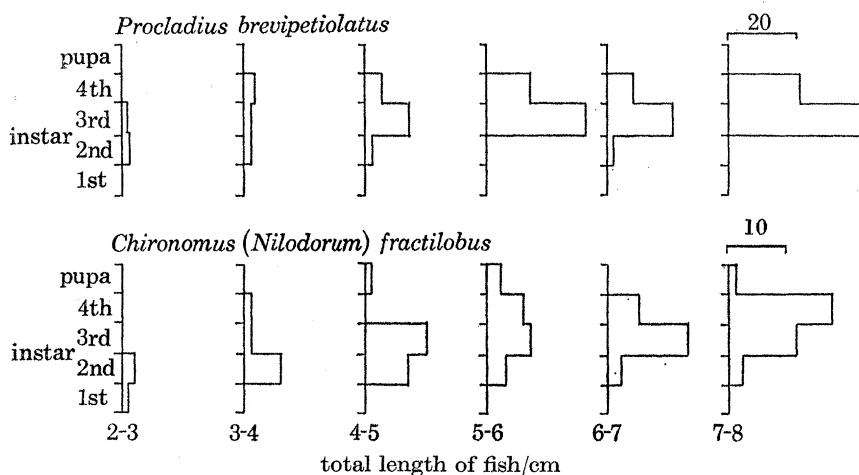


FIGURE 12. Histograms of the total numbers of each instar of two species of chironomid occurring in the guts of *Haplochromis angustifrons* females and juveniles. The total gut contents of five individual fish were counted for each 1 cm size range of fish (J. P. E. C. Darlington, unpublished).

Inshore and over sandy shoals many other species of benthic predators occur. *Haplochromis elegans* Trewavas and *Barbus neglectus* Boulenger are the most abundant, but a number of other species are also present (table 7). All feed mainly on chironomid larvae which are more abundant here than in the mid-lake mud. *Haplochromis mylodon* Greenwood has an enlarged pharyngeal mill which enables it to crush the shells of molluscs, especially *Melanoides tuberculata*, a benthic gastropod which occurs close to shore. Other inshore species of fish, whose overall food intake is more generalized, also include a proportion of benthic invertebrates in their diet; for instance, *H. aeneocolor* Greenwood takes food both from the water column and the substrate, thereby including plant fragments, dipteran larvae and adult aquatic insects in its diet.

Detritus and other feeders

The main detritus feeders are the benthic invertebrates, but very little is known about their feeding habits. The role of *Tilapia leucosticta* as a detritus feeder has been mentioned already (p. 311). Several inshore species of fish ingest detritus, including plant fragments which may be derived from hippopotamus dung. *Haplochromis limax* Trewavas has a dentition adapted for scraping detritus and aufwuchs off solid surfaces (Greenwood 1973).

TABLE 7. SPECIES LIST OF THE FISH IN LAKE GEORGE, WITH NOTES ON THEIR MAIN FOOD (DUNN, UNPUBLISHED OBSERVATIONS)

<i>species</i>	<i>main food</i>
<i>Aplocheilichthys eduardianus</i> David and Poll }	dipteran larvae and emergents
<i>A. pumilus</i> (Boulenger)	
<i>Astatoreochromis alluaudi</i> Pellegrin	molluscs
<i>Bagrus docmac</i> (Förskal)	fish
<i>Barbus altianalis</i> Boulenger }	chironomid larvae (benthos)
<i>B. kerstenii</i> Peters	
<i>B. neglectus</i> Boulenger	
<i>B. perince</i> Rüppell	
<i>Clarias lazera</i> Valenciennes	fish
<i>Ctenopoma muriei</i> (Boulenger)	insect larvae
<i>Haplochromis aeneocolor</i> Greenwood	opportunist omnivore
<i>H. angustifrons</i> Boulenger	benthic invertebrates
<i>H. eduardianus</i> (Boulenger)	phytoplankton and plant material
<i>H. elegans</i> Trewavas	chironomid larvae (benthos)
<i>H. limax</i> Trewavas	aufwuchs
<i>H. macropsoides</i> Greenwood	?
<i>H. mylodon</i> Greenwood	molluscs
<i>H. nigripinnis</i> Regan	phytoplankton
<i>H. pappenheimi</i> (Boulenger)	zooplankton
<i>H. petronius</i> Greenwood	dipteran larvae
<i>H. schubotzi</i> Boulenger }	plant material and insect larvae
<i>H. schubotziellus</i> Greenwood }	
<i>H. squamipinnis</i> Regan	fish (insect larvae when young)
<i>H. taurinus</i> Trewavas	embryos and fry of cichlid fish
<i>Marcusenius nigricans</i> Boulenger	dipteran larvae
<i>Mormyrus kannume</i> Förskal	insect larvae
<i>Protopterus aethiopicus</i> Heckel	fish (and molluscs)
<i>Tilapia leucosticta</i> Trewavas	detritus and phytoplankton
<i>T. nilotica</i> (L.)	phytoplankton

Comments on food selection

The dominant fish species in Lake George are herbivores, but their fry are omnivorous or zooplankton eaters. In turn these species are preyed upon by a variety of fish and other predators, especially when young. Individuals of both *Tilapia* species above a certain size are selectively preyed upon by man.

The zooplankton as a whole shows a paucity of the large forms, such as Cladocera, a characteristic of a 'predated' population (Burgis *et al.*, this volume) and

presumably the result of predation by fish. Smaller zooplankton, especially the dominant *Thermocyclops hyalinus*, are preyed on chiefly by *Chaoborus* larvae. These in turn, especially when they congregate in swarms, are subject to predation by fish in the plankton.

The benthos is preyed upon by one fish species in the midlake, but by many fish species inshore where its biomass is greater (Burgis *et al.*, this volume). Some of these species are fairly specialized in their choice of food, but many are opportunists and take a wide variety of material, including aufwuchs, detritus and natatorial insects.

The calculated grazing rates of the major planktonic herbivores show that only a small proportion of the phytoplankton standing crop is eaten daily (p. 307). The net primary production seems adequate to maintain this cropping rate, and to stand grazing and losses from other sources as well. It is suggested, therefore, that food is not a limiting factor for at least the adult stages of the various vertebrate and invertebrate herbivores of Lake George (see also Viner & Smith, this volume).

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