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Food and feeding ecology of *Oreochromis niloticus* (LINNAEUS, 1758) juveniles in Lake Awassa (Ethiopia)

By C. TUDORANCEA, C. H. FERNANDO and J. C. PAGGI

With 10 figures and 4 tables in the text

Abstract

A total of 3087 *Oreochromis niloticus* juveniles in L. Awassa were measured for size frequency distribution, and the diet of 445 specimens of 10 to 50 mm length was analyzed. The breeding of *O. niloticus* in L. Awassa is continuous with a high peak in February–April. As soon as the juveniles are released by females at about 10 mm standard length, they become omnivorous, feeding chiefly on benthic and attached organisms. The blue greens and the benthic diatoms such as *Synedra, Cymbella, Neidium* and *Gomphonema,* represent a significant component of the diet in terms of frequency of occurrence, numerical percentage and relative importance. Animal food, and in particular Chironomidae larvae and some adult insects, represent the bulk of the diet as a percentage of food volume in the juveniles of less than 25–30 mm SL. As the juveniles approach the upper end of this size their feeding becomes predominantly herbivorous and the animal component decreases in importance. The change in diet with increase in fish size may reflect a change in habitat and they may affect the condition factor whose values were significantly higher in the early stages. *O. niloticus* juveniles showed a diurnal feeding pattern.

Introduction

In recent years there has been a rapidly growing interest in tilapias due to the increased importance of these fish as a cheap source of animal protein in tropical countries. Tilapias, a group of species of the family Cichlidae whose taxonomy was revised by TREWAVAS (1983), represent by far the largest component of the commercial inland fish catch in Africa (FRYER & ILES 1972). An important reason for the success of the tilapias is their ability to thrive on a wide variety of readily available foods. Most of the previous studies on feeding behaviour of tilapias have dealt mainly with the diet of adults with little reference to the diet of juveniles (FISH 1955; BOWEN 1978, 1979; COSTA & ABEYSIRI 1978; SPATARU & ZORN 1978; DE SILVA 1985; DE MOOR et al. 1986).

Little information exists on the feeding ecology of *Oreochromis niloticus (= Tilapia nilotica)* which is the most abundant and widely distributed cichlid of commercial value in the eastern African Rift Valley. The physiology of digestion of

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commercially exploited *O. niloticus* in Lake George was well documented by Moriarty (1973), Moriarty & Moriarty (1973a, b) and Moriarty et al. (1973). These studies also include a few references to feeding in juveniles. Pantastico et al. (1982, 1985) investigated the feeding preferences of juvenile tilapias using algae under experimental conditions. There are no studies regarding feeding ecology of *O. niloticus* juveniles under natural conditions. Information on the natural food and feeding habits of tilapia juveniles will clarify some trophic relationships in tropical waters which are still rather obscure in comparison with those in the temperate region. Also the feeding ecology of the young fish determines the rate of recruitment to the fishery and therefore influences the potential yield of the fishery.

In the present paper, we present data on the feeding ecology of newly hatched tilapias until they reach a size of 50 mm standard length. Our data is based on one year study of material collected in Lake Awassa, Ethiopia.

Description of the lake

Lake Awasse (Fig. 1) is located at an altitude of 1680 m in the central part of the Ethiopian Rift Valley (7°33′N, 38°29′E). It has a surface area of 88 Km^2 (Herrmann, pers. comm.), a maximum depth of 22 m, and an average depth of 11 m. Lake Awassa is a discontinuous warm polymictic lake in accordance with the revised classification of lakes by Lewis (1983). Baxter et al. (1965) stated that this lake is probably polymictic. The bottom water temperature at 15 m depth was usually 2° or 3° less than the surface water temperature and no prolonged thermal stratification developed. The water is alkaline, with pH between 8.75 (Aug. 1984) and 9.05 (March 1985). The conductivity (K_{25}) ranged between 827 μScm^{-1} (May 1984) and 922 μScm^{-1} (April 1984) and averaged 854 μScm^{-1} (Kifle 1985). The predominant ions are Na^+, and $HCO_3^- + CO_3^=$. The annual mean concentrations of these were 158.6 $mg.l^{-1}$ and 8.40 $mg.l^{-1}$ respectively. Transparency, as measured by Secchi disk, had values between 65 cm (Jan. 1985) and 95 cm (Dec. 1984).

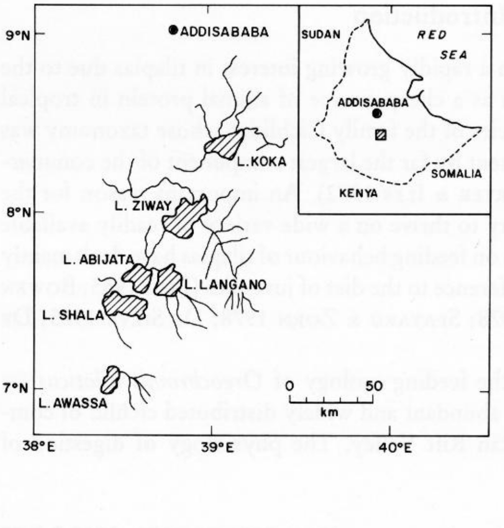

Fig. 1. Some of the Ethiopian Rift Valley Lakes.

The annual water level fluctuates in relation to the seasonal variation in precipitation in its watershed. Longer term fluctuations have also been noted (BAXTER et al. 1965). This area is characterized by an eight month rainy season (March to October) having its peak during July–September, and a four month dry season (November–February) (GAMACHU 1977).

The littoral is covered by an extensive belt of submergent and emergent rooted vegetation which extends about 150 m offshore. The shallow area between 0.5 and 1 m depth is usually covered by *Potamogeton* spp. and the waterlily *Nymphaea coerulea*. Further offshore down to 3–4 m depth is a subzone dominated by the emergent plant *Paspalidium geminatum*.

Lake Awassa supports a commercial fishery. The fish fauna of the lake consists of two species of *Barbus (B. intermedius* and *B. cf. amphigramma)*, the catfish *Clarias lazera* and *Oreochromis niloticus*. Of these, *O. niloticus* accounts for almost the total fish catch, which is sold both locally and in the capital Addis Ababa 250 km away.

Materials and methods

Fish juveniles were collected monthly during April 1984 to March 1985 in shallow water less than 0.5 m depth, using a 0.5 cm mesh seine. The mesh size was small enough to catch even the early stages of juveniles, and fish up to a size of about 50 mm in standard length were caught. The fish were immediately preserved in 10% formaldehyde. To obtain data of diel feeding activity, juveniles were caught every 6 hrs during 24 hrs on three occasions (October 1984, January 1985 and March 1985).

To assess recruitment during the year, a total of 3087 individuals were measured (standard lenght) in the laboratory for monthly size frequency distribution.

Table 1. Number of fish investigated in each size class (standard length) during the period April 1984–March 1985.

Size class (SL) mm.	10–15	15.1–20	20.1–25	25.1–30	30.1–35	35.1–50
No. of fish	179	105	93	36	21	11

The guts of 445 randomly selected specimens were examined for food items. The number of specimens dissected for each size group are given in Table 1. For counting of small organisms, such as algae and Protozoa, in the gut contents, an ordinary microscope slide and coverslip method was used (BROWER & ZAR 1977). Larger animal organisms were enumerated in full using a microscope. The identifications were made to the most detailed taxonomic level possible. The gut contents were analyzed using three seperate methods: a) Percent frequency of occurrence, which gives the percentage of guts containing a particular food item out of the total guts containing food. This method gives a general indication of the food spectrum and also illustrates changes in diet with age or increase in size (FAGADE 1971, COSTA & ABEYSIRI 1978, HAMMER 1985); b) Numerical method, which expresses the relative abundance of a particular food category as a percentage of that food item of the total gut contents, and c) A volumetric method which gives the relative importance of a particular food item as a volume percentage of that food item of the total volume of gut contents. This method appears to give a better indication of the contribution of various food items to the diet (Spataru 1976, Spataru & Zorn 1978, Maitipe & De Silva 1985). By sampling the feeding habitat we calculated the volume of the food items at ingestion. The algae were measured in three dimensions under a microscope and various formulae were used to calculate their volume depending on their geometrical shape (Trevisan 1978). The volume of animal food items was calculated by comparing them with geometric solids of similar shape (Hyslop 1980, Bowen 1983).

Since each of the three methods used emphasizes the importance of different foods, the „relative importance index" (RI) (George & Hadley 1979, Hyslop 1980) which combines the values obtained by the three methods was calculated:

$$RI = 100\, AI_a \sum_{a=1}^{n} AI, \text{ where}$$

AI = absolute importance index = % frequency of occurrence + % total numbers + % total volume, for food item, and n = number of different food items.

As a measure of fish condition we used a modified Fulton's condition coefficient (Bagenal 1978) calculated by the following formula:

$$K' = \frac{W}{L^b} \times 100, \text{ where}$$

L is the standard length (SL), W is the weight of fish, and b = 3,26 is the slope of the regression line expressing the weight – length relationship for the juveniles between 10 and 50 mm length. The arcsine transformed data (Zar 1974) were used to calculate the condition factor.

To illustrate the diel changes in feeding behaviour the following index of fullness was calculated:

$$IF = \frac{w}{W} \times 100 \text{ where}$$

w is the weight of gut contents and W is the weight of fish. Gravimetric information was obtained by weighing the entire gut contents after evaporating by standing in air.

Results

1. Size frequency distribution

Oreochromis niloticus is a maternal mouthbrooding species. The eggs are held in the mouth of the female and the young are subsequently released. Detailed information on breeding habits in African cichlids is found elsewhere (Fryer & Iles 1972, Philippart & Ruwet 1982).

The brooding and the release of juveniles usually take place in shallow water. The juveniles released live in natural nurseries along the shore in water less than 50 cm depth. As they grow they move further offshore into the vegetation and then into the pelagial zone (Fig. 2 A).

The size frequency distribution of the *O. niloticus* fry population in Lake Awassa is shown in Fig. 2 A and B. The juvenile population is characterized by the dominance of individuals of 10 to 24 mm length (SL). Very few individuals below 10 mm SL (1%) were captured during the year which suggests that they are not released by the parent before reaching this size. On one sampling occasion a brooding female having about 70 larvae in its mouth was captured. Most of the larvae were 9–10 mm long which also indicates that the release of the young does not take place before the larvae are 10 mm long. Likewise only a small number of individuals longer than 25 mm were captured during the year which suggests that at this size the juveniles start moving further offshore and cannot be easily caught.

Judging from the number of new recruitments to the population (Fig. 2B) one can say that *O. niloticus* in Lake Awassa has a main breeding season during the period February–April with a peak in March which coincides with the beginning of the small rains. A second, less pronounced breeding peak occurred in October–November which coincides with the end of the rainy season. New recruits were also noted in other months of the year (except August and December 1984) but they occurred in low percentages. This suggests that at least part of the population may continue breeding for the rest of the year but at a very low intensity.

2. Composition of the diet

The diet of *O. niloticus* juveniles in L. Awassa displayed a high diversity consisting of 26 species of blue-greens, greens and diatoms and representatives of all major freshwater animal invertebrate taxa except molluscs (Table 2). Detritus also occurred very frequently. Fish scales and some other unidentifiable remnants were sometimes found.

The algae occurred more frequently than the animals. Diatoms have the highest frequencies of occurrence (100%) followed in descending order by green algae (Chlorococcales) and the blue-greens. Among the diatoms the Pennales were found more frequently with *Synedra* spp., *Cymbella* spp., *Neidium* sp. and *Gomphonema* sp., each occurring in more than 60% of the fish investigated. The green algae *Scenedesmus* spp. and *Botryococcus braunii* occurred in frequencies of 40 to 50%, while each of the blue-green algae occurred in less than 40% of the guts analyzed.

Among the animals, rotifers occurred most frequently in the diet (56%), followed in descending order by insects, Cladocera and Copepoda. A total of 16 taxa of rotifers were identified in *O. niloticus* guts, but only the Bdelloidea group and *Lecane bulla* occurred in almost 30% of the fish dissected. Chironomid larvae occurred also in almost 30% of the guts investigated. The littoral cladoceran *Macrothrix laticornis* and cyclopoids had frequencies of occurrence of 20% and 18% respectively. Terrestrial insects which fall into the water are also taken in by fish.

Fig. 3 shows that once the juveniles are released at about 10 mm length they start feeding on both algae and animals. This diet spectrum characterizes all the size groups up to 50 mm length with some changes in the frequency of occurrence of some food items with increase in fish size. The diatoms and rotifers seem to be taken at a constant rate by the juveniles of all sizes. The Chlorophyceae displayed a slight increase and the Cyanophyceae a slight decrease in occurrence with increase in juvenile size. Except for insects and Protozoa, which did not show any particular pattern, the other animal groups decreased in their percentage frequency of occurrence with increase in fish size.

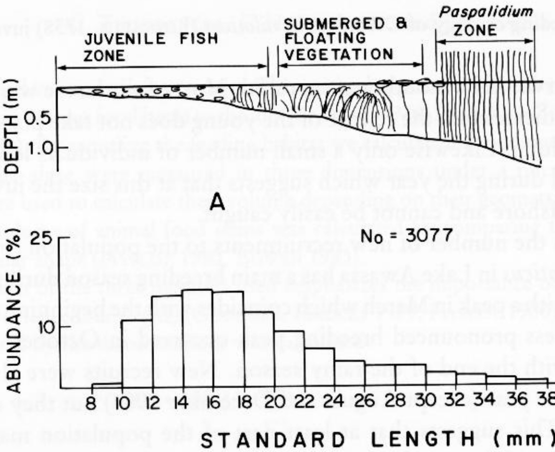

Fig. 2. Annual (A) and monthly (B) size frequency distributions of *Oreochromis niloticus* juveniles in shallow depths (less than 50 cm) of Lake Awassa. N = no. of individuals.

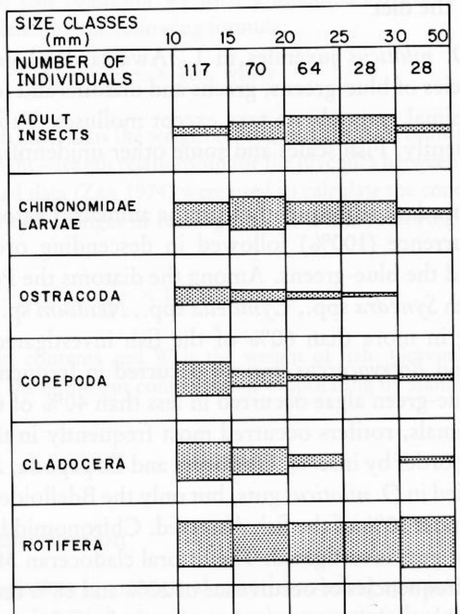

Fig. 3. Percentage frequency of occurrence of various food items in the guts of *O. niloticus* juveniles in L. Awassa.

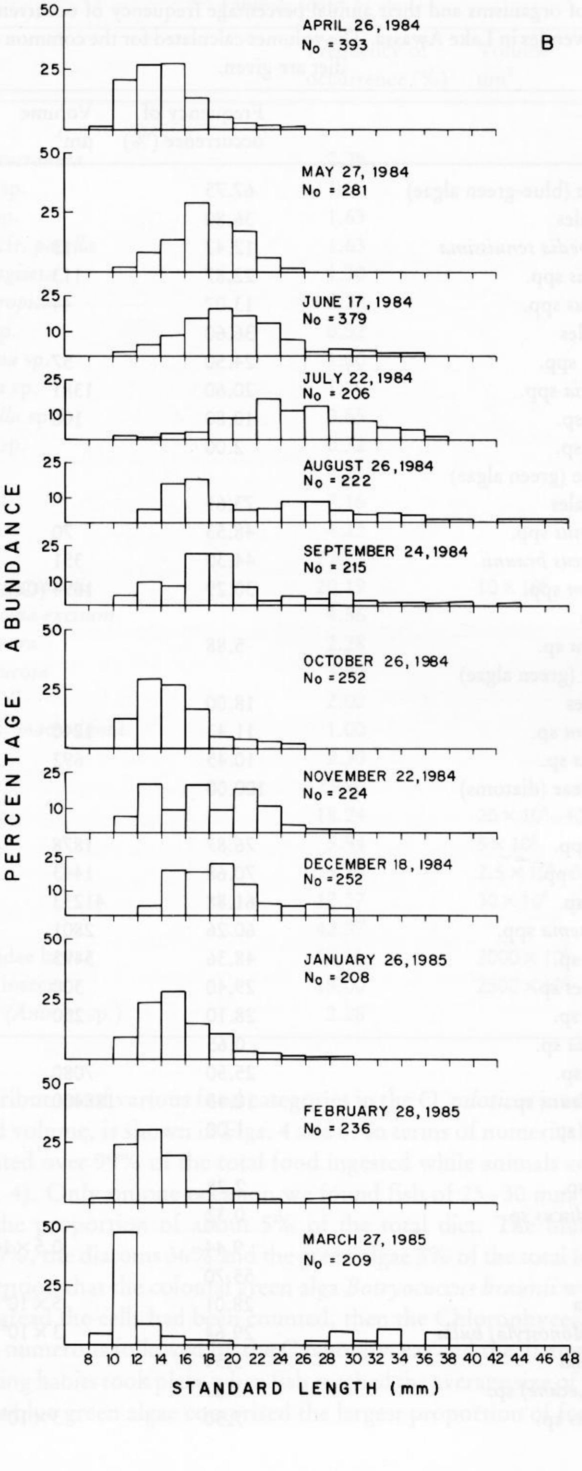
APRIL 26, 1984
No = 393
B
MAY 27, 1984
No = 281
JUNE 17, 1984
No = 379
JULY 22, 1984
No = 206
AUGUST 26, 1984
No = 222
SEPTEMBER 24, 1984
No = 215
OCTOBER 26, 1984
No = 252
NOVEMBER 22, 1984
No = 224
DECEMBER 18, 1984
No = 252
JANUARY 26, 1985
No = 208
FEBRUARY 28, 1985
No = 236
MARCH 27, 1985
No = 209
PERCENTAGE ABUNDANCE
STANDARD LENGTH (mm)
8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46 48

Fig. 2B.

Table 2. List of organisms and their annual percentage frequency of occurrence in the diet of *O. niloticus* juveniles in Lake Awassa. The volumes calculated for the common organisms in the diet are given.

Organisms	Frequency of occurrence (%)	Volume μm^3
Cyanophyceae (blue-green algae)	67.75	
Chroococcales	36.80	
Merismopedia tenuissima	12.42	13
Microcystis spp.	22,87	113
Chrococcus spp.	13.07	44
Oscillatoriales	36.60	
Rivularia spp.	24.50	57
Oscillatoria spp.	20.60	1381
Lyngbya sp.	10.80	106
Spirulina sp.	2.00	
Chlorophyceae (green algae)		
Chlorococcales	73.61	
Scenedesmus spp.	48.53	70
Botryococcus braunii	44.30	351
Pediastrum spp.	30.29	1694 (Cenobium)
Ulotrichales		
Microspora sp.	5.88	
Charophyceae (green algae)		
Zygnematales	18.00	
Cosmarium sp.	11.43	1240
Mougeotia sp.	10.45	692
Bacillariophyceae (diatoms)	100.00	
Pennales		
Synedra spp.	76.87	1878
Cymbella spp.	70.68	1443
Neidium sp.	61.88	41233
Gomphonema spp.	60.26	2801
Amphora sp.	48.36	5493
Achnanthes sp.	29.40	300
Nitzschia sp.	28.10	250
Hantzschia sp.	0.65	
Navicula sp.	25.50	7080
Cymatopleura sp.	10.45	188400
Cocconeis sp.	1.00	
Centrales		
Melosira sp.	2.28	
Stephanodiscus sp.	0.32	
Protozoa	9.44	0.5×10^6
Rotifera	55.70	
Bdelloidea	28.01	5×10^6
Lecane (Monostyla) bulla	29.64	3×10^6
Lecane luna	5.54	
Lecane (Lecane) sp.	1.63	
Brachionus sp.	7.50	$3 \times 10^6 – 5 \times 10^6$

Table 2. (cont.)

Organisms	Frequency of occurrence (%)	Volume µm³
Rotifera		
Mytilina mucronata	2.28	
Epiphanes sp.	1.63	
Colurella sp.	1.63	
Lepadella cfr. *patella*	1.63	
Filiania longiseta	1.30	
Keratella tropica	2.28	
Keratella sp.	0.32	
Sinantherina sp.	1.00	
Trichocerca sp.	1.00	
Cephalodella sp.	0.65	
Notomata sp.	0.32	
Nematoda	4.23	
Oligochaeta	7.16	
Acarina	4.23	
Cladocera	29.31	
Macrothrix laticornis	20.19	10×10^6
Diaphanosoma excisum	4.56	
Moina micrura	2.28	
Alona verrucosa	3.90	
Alona davidi	2.00	
Leydigia cf. *macrodonta*	1.00	
Ephippia	2.30	
Copepoda	23.80	
Cyclopoida	18.24	$20 \times 10^6 - 40 \times 10^6$
Harpacticoida	5.54	5×10^6
Nauplii	5.86	$2.5 \times 10^6 - 3.5 \times 10^6$
Ostracoda	12.37	30×10^6
Insecta	42.37	
Chironomidae larvae	28.66	$2000 \times 10^6 - 7850 \times 10^6$
Terrestrial insects	19.00	$2500 \times 10^6 - 17675 \times 10^6$
Hemiptera (*Anisops* sp.)	2.28	

The contribution of various food categories in the *O. niloticus* juvenile diet both as number and volume, is shown in Figs. 4 and 5. In terms of numerical percentages, algae represented over 99% of the total food ingested while animals comprised less than 1% (Fig. 4). Only on one occasion we found fish of 25–30 mm length taking Protozoa in the proportion of about 5% of the total diet. The blue green algae represented 60%, the diatoms 36% and the green algae 3% of the total food ingested. We should mention that the colonial green alga *Botryococcus braunii* was counted as colonies. If instead the cells had been counted, then the Chlorophyceae would have been the most numerous followed by the Cyanophyceae and the diatoms. A marked change in feeding habits took place when fish reached the average size of 27.5 mm. Up to this size the blue green algae comprised the largest proportion of food (69%). At this stage the diatoms increase in their numerical importance representing over 81% of the total food taken in by the junveniles larger than 30 mm length. The diatoms *Synedra, Neidium* and *Cymbella* alone comprised about 59% of the total diet of the fry longer than 30 mm. There seems to be a slight tendency for an increase in the number of green algae and a decrease in the number of diatoms in the guts with increasing fish size but confirmation of this tendency requires more information on feeding habits of the juveniles over 50 mm length.

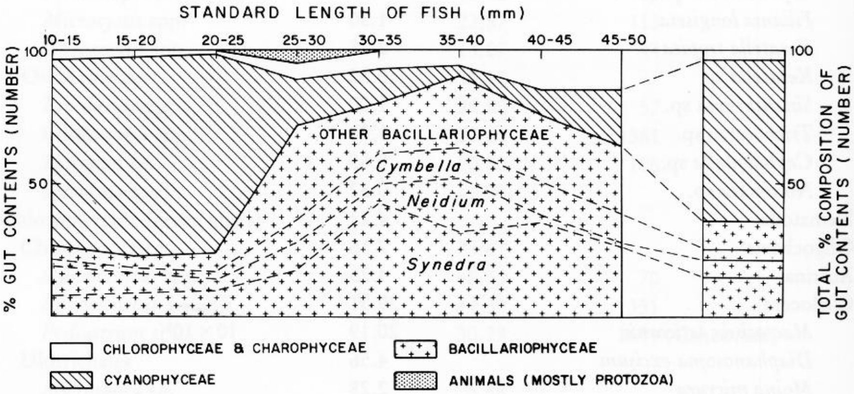

Fig. 4. Numerical percentage composition of food components in the *O. niloticus* juvenile guts with increase in fish size. The total percentage of the gut contents for all specimens investigated is shown.

A different picture is obtained when the importance of various food items are shown as percentage volume. Fig. 5 indicates that animals comprise the major part of the fish diet (77%) while the algae are in second place making up 23% of the total volume. The main bulk of food is made up by Chironomidae larvae (45%) and adult insects (25%). Other groups of benthic organisms such as Ostracoda, Nematoda, Hydracarina and Oligochaeta, although taken in, amount to less than 2% of the total volume. The sessile Protozoa and the zooplankton (rotifers, cladocerans and copepods) also contributed very little to the diet of *O. niloticus* juveniles (4% and 2% respectively).

A marked change in feeding preference occurred again when the fish reached an average size of 27.5 mm (size class 25.1–30 mm) length. It appears that the fish below this size rely to a great extent on animal protein provided in particular by chironomid larvae (48%) and other insects (27%). The algae made up only 17% of the total gut content volume of the early stages of juveniles. The individuals over 30 mm shifted to a diet consisting mostly of algae (70.50%). The largest proportion of algae was made up by the green alga *Botryococcus braunii.*

On a seasonal basis it appears that the major part of the diet of *O. niloticus* juveniles during the dry season (November–February) is made up of chironomid larvae. They represent an important food item for the fry in the rainy season as well, particularly for the earlier stages (10–15 mm SL) (Fig. 6). During the rainy season

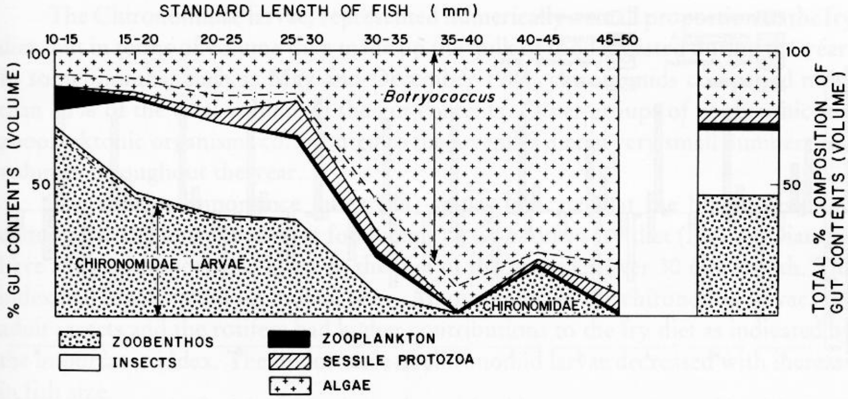

Fig. 5. Volumetric percentage composition of the food items in the *O. niloticus* juvenile guts with increase in fish size. The total percentage composition of the gut content for all specimens analysed is shown.

(February–October), the green algae particularly *Botryococcus braunii* comprise a large proportion of the juvenile diet mainly for individuals over 30 mm length.

A month by month contribution of various food items by number and volume to the diet of *O. niloticus* is shown in Fig. 7. The numerically dominant algae in the fish diet troughout the year are the diatoms which were exceeded by the blue-green algae only in March and April. The green algae which contributed little numerically to the fish diet, represent by volume a major food particularly during the heavy rain season (July–October). Unfortunately there is no information on the seasonal changes in density of various algae in the lake, so the algal diet of *O. niloticus* juveniles could not be related to such changes during the year.

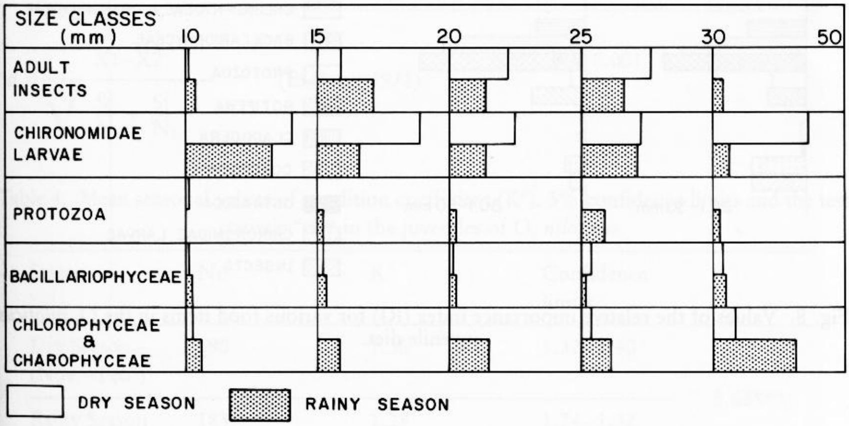

Fig. 6. Volumetric percentages of food components with increase in fish size during the dry (Nov.–Feb.) and rainy (Mar.–Oct.) seasons. Only foods which represented more than 5% of the gut contents are shown.

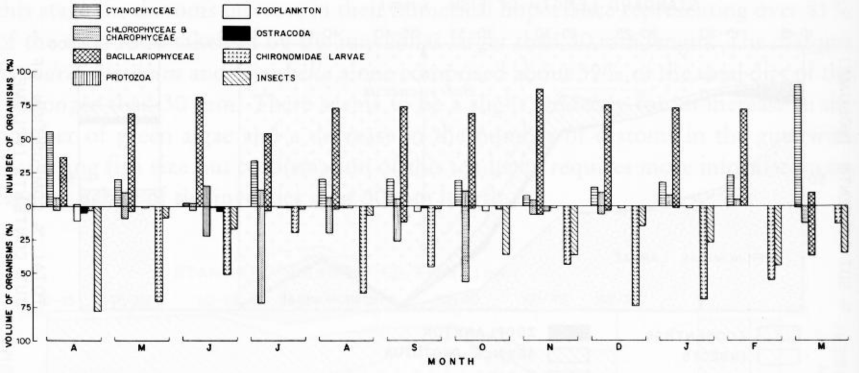

Fig. 7. Monthly percentage composition by number and volume of the food components in the *O. niloticus* juvenile guts during the April 1984 – March 1985 interval.

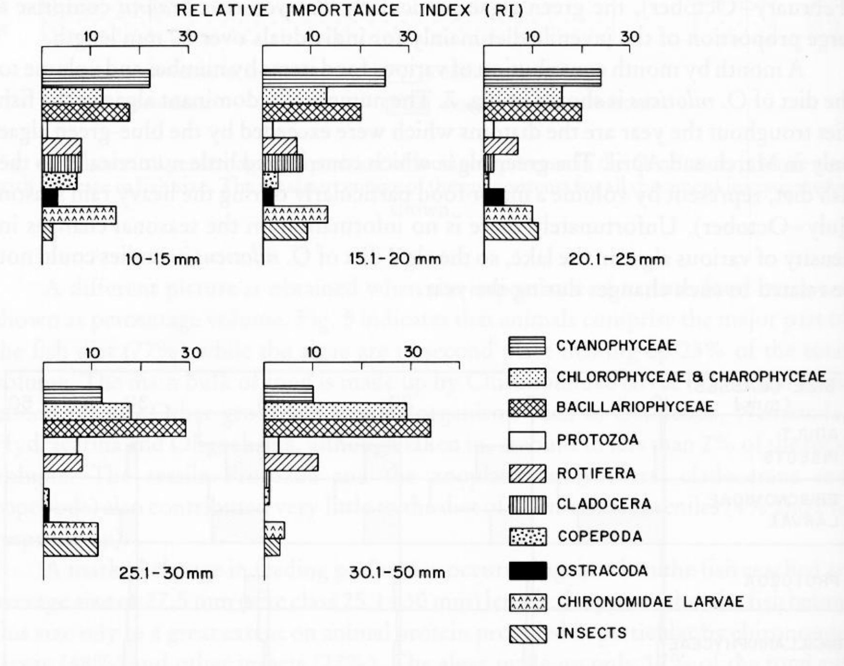

Fig. 8. Values of the relative importance index (RI) for various food items in the *O. niloticus* juvenile diet.

The Chironomidae larvae, represented numerically a small proportion to the fry diet, but in terms of volume they made up the bulk of food ingested during the year. In some months, such as May and December 1984, chironomids comprised more than 70% of the total volume of the gut contents. Other groups of zoobenthic and zooplanktonic organisms contributed to the juveniles diet in very small numbers and volumes throughout the year.

The relative importance index (RI) values indicate that the blue-greens and diatoms are the most important food items of *O. niloticus* fry diet (Fig. 8). Diatoms have a higher importance index in the diet of the juveniles over 30 mm length. The index had lower values for animal prey. Among animals, the chironomid larvae, the adult insects and the rotifers had higher contributions to the fry diet as indicated by the importance index. The importance of chironomid larvae decreased with increase in fish size.

The condition coefficient (K′) value for juveniles below 30 mm SL is significantly higher than that for juveniles between 30 and 50 mm SL (Table 3). This suggests better nutrition for the early fry stages which have an important animal component in their diet. Also the condition coefficient value is significantly higher for juveniles collected during the dry season than during the rainy reason (Table 4). Nutrition and the fish growth thus appear to be better in the dry season (November–February).

Table 3. Mean condition coefficient (K′), 5% confidence limits, and the test statistic "d"* in the juveniles of *O. niloticus* of different sizes.

Size (mm)	No.	K′	Confidence limits	d
10–30	252	1.32	1.30–1.40	15.76***
30.1–50	24	1.13	1.10–1.20	

$$*d = \frac{\overline{X}1-\overline{X}2}{\sqrt{\frac{S_1^2}{N_1}+\frac{S_1^2}{N_2}}}$$

(ELLIOTT 1971)

*** P < 0.001

Table 4. Mean seasonal values of condition coefficient (K′), 5% confidence limits and the test statistic "d"* in the juveniles of *O. niloticus*.

Season	No	K′	Confidence limits	d
Dry Season (Nov.–Feb.)	90	1.36	1.32–1.40	5.63***
Rainy Season (Mar.–Oct.)	183	1.28	1.24–1.32	

*d – see Table 3 ***P < 0.001

3. Digestion of food

With regard to the digestibility of foods it would be unrealistic to consider that all food items occurring in the *O. niloticus* juveniles guts are of equal nutritional value. A separate analysis of the gut contents of the intestine and the rectum clearly indicates that in the intestine most of the diatoms were digested while many other algae

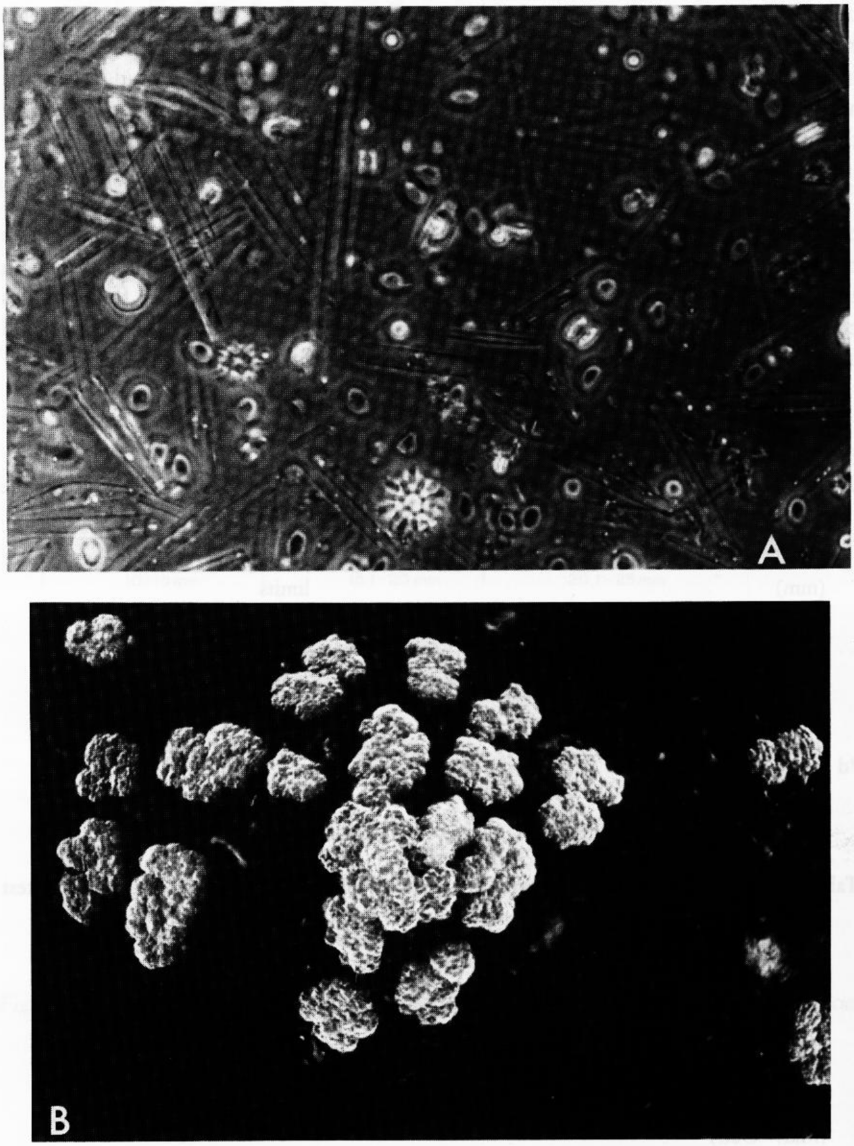

Fig. 9. Digested diatoms mixed with undigested green algae *Scenedesmus* and *Pediastrum* (A) and undigested *Botryococcus braunii* (B) in the posterior intestine of *O. niloticus* juveniles.

remained partly or completely undigested. A similar picture was characteristic for the rectal contents which consisted of empty valves of diatoms while many blue green algae and most if not all of the colonial *Botryococcus braunii* remained undigested. *Botryococcus braunii,* which was ingested in a higher proportion as the juveniles increased in size, could be seen completely undigested along the entire digestive tract (Fig. 9). Other green algae such as *Pediastrum* and *Scenedesmus* also appeared undigested in the rectum. The chitinous parts of arthropods resist digestion while the soft bodied animals like rotifers and oligochaetes are not represented by such indentifiable remains.

4. Diel feeding activity

The index of fullness and the percentage of empty stomachs were computed for the juveniles captured every 6 hours during a 24 hours period on three occasions (Fig. 10). The index of fullness increased from dawn (6.00 h) to midday and decreased from dusk (18.00 h) to midnight. The low values of the index coincides with the highest percentages of empty stomachs. This feeding pattern clearly indicates that *O. niloticus* juveniles feed during the day.

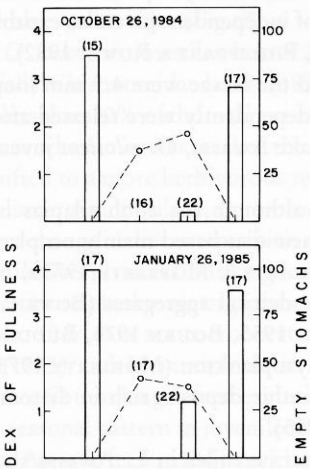

Fig. 10. Diurnal changes in feeding pattern of the *O. niloticus* juveniles at three different dates of the year, based on the index of fullness (o--o--o--o) and the percentage of empty stomachs (vertical columns). The figures in brackets represent no. of fish investigated at each time.

Disussion

Very little information has been reported on the biology and feeding habits of tilapia juveniles in general. Information on feeding in *O. niloticus* juveniles in natural conditions is virtually non-existent.

Reproduction and the number of spawnings a year for African chichlids is associated with water temperature, light intensity, photoperiod, rains, water level and possibly other factors (Bardach et al. 1972, Balarin & Hatton 1979, Philippart & Ruwet 1982). Based on the size-frequency distribution through the year, *O. niloticus* in L. Awassa has a peak breeding season during February to April. However, there is a low level of breeding more or less continuously for the rest of the year with a less pronounced peak during October to November. This breeding pattern offered us the opprotunity of doing monthly investigations of the diet and feeding preference of *O. niloticus* juveniles. *Oreochromis niloticus* in Lake Ziway, a shallow Rift Valley lake situated North of L. Awassa, displayed a slightly different breeding pattern which was characterized by a marked peak in February and a smaller one in May (Getaneh & Getaneh 1979). Welcome (1967) found that breeding occurs throughout the year. He also mentions the findings of other workers which indicates a seasonal breeding pattern associated with rains.

It was demonstrated in laboratory experiments that the time intervals from egg to hatching and to release of independent juveniles capable of external feeding varies with species (Hanon 1975, Philippart & Ruwet 1982). In *O. niloticus* the hatching took place in 4–5 days and the larvae were 4.5 mm long (Hanon 1975). The first juveniles ready to swim independently were released after 11 days when they were about 8.0 mm length. In Lake Awassa, *O. niloticus* juveniles are released when they reach 10 mm length.

It was reported that although the adult tilapias have a diversified diet, the majority of species have their diet based mainly on plant materials such as phytoplankton (Fish 1955, Moriarty & Moriarty 1973a, b, Spataru 1976, Costa & Abeysiri 1978), periphytic detrital aggregates (Bowen 1981) or macrophytes and associated periphyton (Fish 1955, Bourn 1974, Buddington 1979). *Oreochromis niloticus* adults feed on phytoplankton (Moriarty 1973, Moriarty & Moriarty 1973) as well as on soft benthic deposits rich in diatoms and bacteria and also on epiphytic diatoms (Fish 1955).

The diet of *O. niloticus* juveniles in L. Awassa shows that there is a distinct plasticity in feeding regime. As shown in Table 2, a total of 26 species of algae and 32 animal taxa were found in their diet. Some of these dietary components might have been taken intentionally while others may have entered the gut accidentally. Bowen (1982) emphasized the fact that in order to characterize the diet of a tilapia species it is important to know the food components that consistently occur in the diet over long periods of time.

Although the percentage frequency of occurrence (Table 2 and Fig. 3) does not show the real importance of various prey items in the diet, it gives an indication of an omnivorous feeding pattern based mainly on littoral benthic or periphytic organisms. Except for the pelagic green algae, *Pediastrum*, *Scenedesmus* and *Botryococcus* and the blue-green Chroococcales which together occurred in frequencies ranging from 30%

to 48% of the fish investigated, the rest of the algae occurring in higher frequencies were the diatoms (Pennales) such as *Synedra, Neidium, Cymbella, Gomphonema* and *Amphora* which are benthic organisms (Sze 1986). The diatoms as a group occurred in all the guts analysed (100%). The filamentous blue-green algae (Oscillatoriales) which are littoral organisms occurred as a group in 37% of the guts investigated. The animals which were found in the juvenile diet in relatively high frequencies are also benthic organisms, such as Chironomidae larvae, or littoral species usually inhabiting vegetated areas, such as bdelloid rotifers, the common rotifer *Lecane bulla,* and the cladoceran *Macrothrix laticornis.* Pelagic rotifers and cladocerans were also found in the guts, but they occurred in low frequencies.

In terms of numerical importance, the blue-greens and the diatoms made up over 90% of the total gut contents with a distinct change in their proportions with increase in juvenile size (Fig. 4). The blue-green algae numerically dominated the diet of early fry stages while diatoms became numerically the main food item for the juveniles above 27 mm mean length (25–30 mm). This change in feeding may be related to a change in diatom abundance in the habitats further offshore, inhabited by larger juveniles, rather than to selective feeding. There are indications that diatoms occur in lower densities in shallows of less than 1 m than at deeper parts due to higher light intensity and burial by wave action (Bowen 1978, Sze 1986). Diatoms dominated the *O. niloticus* juvenile diet for a major portion of the year. Only in March and April were they exceeded by the blue-green algae (Fig. 7).

In terms of volume, *O. niloticus* juveniles below 27 mm mean SL consumed mostly animal food, especially Chironomidae larvae (48%) and adult insects (27%), while the algae constituted less than 20% of the total gut contents (Fig. 5). A change in feeding regime also took place when juveniles reached the size class 25–30 mm length. Juveniles above this size shifted to a more herbivorous regime in which algae constituted 70.5% of the total volume. Among algae, *Botryococcus braunii* represented the bulk of the diet. This distinct change in diet composition may again reflect a change in habitat of the growing *O. niloticus* juveniles. Moving further offshore as they grow, the juveniles may encounter more planktonic organisms, in particular pelagic algae, rather than benthic animals. Our data are corroborated by some observations of Moriarty & Moriarty (1973) and Moriarty et al. (1973) who reported that *O. niloticus* individuals above 60 mm length feed exclusively on phytoplankton.

There was no evident seasonal pattern in juvenile feeding (Fig. 6). The fact that *O. niloticus* juveniles in L. Awassa feed mainly on chironomid larvae (volumetric percentage) during the dry season, and on both chironomid larvae and the green alga *Botryococcus braunii* in the rainy season, may reflect the availability of foods at particular times of the year. Switches in feeding habits during the year in relation to the availability of food were also reported in *O. mossambicus* (Maitipe & De Silva 1985) and *Tilapia galilaea* adults (Spataru & Zorn 1978).

It is well known that all fishes in both tropical and temperate regions feed on zooplankton in their early stages (Fernando 1983, Hammer 1985, Gerstmeier 1985). There are indications that zooplankton diversity and production in tropical waters are lower than in temperate regions (Burgis & Dunn 1978, Lewis 1979, Fernando 1980a, b) and this situation may limit recruitment in tropical lakes, leading to low fish yields (Fernando 1980b). However, tilapias show high yields in some tropical lakes and reservoirs in comparison with other fish (Fryer & Iles 1972). Based on this evidence, Fernando (1983) hypothesized that tilapias, with their low number of recruits at each spawning and a high survival rate due to the mouthbrooding, have a low demand per capita for zooplankton in their early stages. These adaptations, as well as the high feeding plasticity of tilapia juveniles, could make tilapias more successful than other fish in tropical waters. As these data show, zooplankton represent an insignificant part in the diet of *O. niloticus* juveniles in L. Awassa. However, zooplankton may play a more important role in the diet of juveniles of other tilapia species as reported by Le Roux (1956), Costa & Abeysiri (1978) and De Moor et al. (1986).

The relative importance index values (Fig. 8) clearly illustrate that *O. niloticus* juveniles below 50 mm SL are omnivores; with the diatoms, blue-green and green algae as the most important foods. The blue-green algae appear to be the most important food in the diet of juveniles below 25 mm SL, while the diatoms and the green algae are the most important foods for juveniles above this size. Animal food, which complements the algal diet, decreases in importance when the juveniles reach about 30 mm in length.

While the relative importance index values are indicative of the dietary spectrum and of changes in importance of various prey items with increase in fish size, they do not indicate the nutritional importance of various foods or their digestibility. As already mentioned, the gut contents in the posterior part of the intestine of *O. niloticus* juveniles in L. Awassa was made up of a mixture of digested diatoms and undigested blue green and green algae, particularly *Botryococcus braunii*. Similar observations were reported for *O. mossambicus* in Sri Lanka by Costa & Abeysiri (1978). These observations draw attention to the selective action of the digestive enzymes and of the nutritional value of different foods. It is well known that the algal wall in general, and in particular the prokaryotic cell wall, cannot be lysed by the digestive enzymes of vertebrates (Bowen 1982). Apparently the diatoms can be easily digested due to the special structure of their valves, which permits a connection between their protoplasm and the surrounding water (Fish 1955). This may explain why diatoms have been reported as an important food for tilapias (Fish 1955, Fryer & Iles 1972, Bowen 1978, 1982, De Moor et al. 1986). Fish (1955) mentioned high yields of *Tilapia* in those areas of Lake Albert where diatoms were dominant and noted signs of malnutrition in tilapias inhabiting areas dominated by the blue-green algae and lacking diatoms. But he also associated high yields of *O. niloticus* in Ferguson Gulf, Lake Turkana, with high abundances of the blue-greens *Spirulina* and *Anabaenopsis*. Hopson & Ferguson (1982) recorded a spectacular yield of fish, mainly *O. niloticus* of 16,000 $Kg.ha^{-1}$ $year^{-1}$ in this gulf, which was still dominated by blue-greens. Moriarty (1973) and Bowen (1976) demonstrated the acid lysis of blue-green algae and bacteria associated with detritus in the stomach of *O. niloticus* and *O. mossambicus* due to the capacity, which is perhaps unique among vertebrates, of producing a gastric milieu below pH 2. The mixture of digested diatoms and undigested blue-green and green algae in the rectum of *O. niloticus* juveniles can be explained at least partly by the gastric digestion mechanisms described by Moriarty (1973) and Moriarty et al. (1973). The undigested algae in the rectum, such as Chroococcales and the greens *Scenedesmus* and *Pediastrum*, are those which passed from the stomach into the intestine without actually being exposed at pH values below 2. The only alga which appears to be completely unaffected by the low pH values in the *O. niloticus* juvenile gut is *Botryococcus braunii*, which otherwise represents the bulk of the diet of juveniles above 30 mm length. This alga is also ingested in large amounts by *O. niloticus* adults in L. Awassa without being digested (TEFERRA, pers. comm.). It is possible that the mucilage which covers the algal colonies, and which is composed of fats (MAXWELL et al. 1968), is resistent even to the low pH in the gastric juice.

Associated with the nutritional value of food is the condition of the fish population reflected in individual growth. BOWEN (1982) underlined the fact that protein is the most important growth limiting factor for herbivorous and detritivorous species such as the tilapias. Different assimilation efficiencies of tilapia feeding on various algae was reported in previous studies (MORIARTY & MORIARTY 1973, DE MOOR & SCOTT 1985, PANTASTICO et al. 1985). It was demonstrated in laboratory experiments that when the diatom *Navicula* and the blue green *Chroococcus* were fed to *O. niloticus* juveniles, the growth and the survival rates of fish as well as the assimilation efficiencies were higher than when juveniles were fed on filamentous blue-green *Oscillatoria*, the green alga *Chlorella* and *Euglena* (PANTASTICO et al. 1985).

To assess the food quality, the digestable protein to digestable food energy ratio has been commonly used (BOYD & GOODYEAR 1971, BOWEN 1979, DE SILVA 1985). A highly significant inverse relationship between the protein to energy ratio and the depth was reported for Lake Sibaya (South Africa) by BOWEN (1979) in *O. mossambicus*. He found that both adults and juveniles of *O. mosambicus* in this lake feed on benthic detrital aggregates made up of diatoms, organic detritus and bacteria. He also reported that the main source of protein in these detrital aggregates is provided by detrital bacteria. In comparing the growth of the adults which feed at depths of 3 to 5 m with that of juveniles which feed at depth less than 30 cm, the author found a better growth in the juveniles than the adults. The difference in growth was associated with the higher protein to energy ratio in the shallows where there is more protein available. If such a relationship between protein content and depth holds also for L. Awassa then it becomes explicable why there is a higher condition coefficient in the juveniles of *O. niloticus* below the length class of 25–30 mm than for the juveniles above this size (Table 3). A very important source of protein available to the early stages of *O. niloticus* is also provided by the animal prey, in particular by chironomid larvae, adult insects and some littoral zooplankton species. The higher condition coefficient for the juveniles during the dry season may also be because during this season chironomid larvae constituted a significant part of the fry gut contents in terms of volume. Zoobenthic and zooplanktonic organisms form important dietary component in *O. mossambicus* in the Hartbeespoort Dam (South Africa) (DE MOOR et al. 1986). There are only a few passing references to the role of animal food in the diet of herbivorous fish to ensure good growth (DE MOOR & SCOTT 1985, MATHAVAN et al. 1976). Information on the significance of animal food in tilapia diet is completely lacking.

The diurnal feeding activities which we observed in *O. niloticus* juveniles of L. Awassa are in accordance with data reported for *O. niloticus* in L. George (MORIARTY et al.) and *O. mossambicus* in South Africa (BOWEN & ALLANSON 1982, DE MOOR et al. 1986). On one occasion (March 1985) we noted that most of juveniles caught around 15 h in the afternoon had the intestines full but their stomachs were either half full or completely empty. This suggests that intensity of feeding may vary at different times of the day. DE MOOR et al. (1986) reported that the highest intensity of feeding activities in *O. mossambicus* in the hypertrophic Hartbeespoort Dam (South Africa) was between 6h30 and 8h30 in the morning and between 17h30 and 19h30 in the evening. The feeding activity intensities of tilapias have been related to water temperature, wave action and changes in water level (BOWEN & ALLANSON 1982, DE MOOR et al. 1986).

The present study of juvenile *O. niloticus* diet and feeding ecology taken together with previous work shows that the breeding of the fish in Lake Awassa, Ethiopia is continuous, with a high and low peak in march and October–November respectively. The juveniles which hatch at 5 mm (SL) are released by the female at about 10 mm SL. They feed on benthic and attached organisms, chiefly diatoms. Although the major component of the diet is algae there is a significant portion of animals included especially in the early stages. As the juveniles reach 30 mm SL they change their diet to pelagic algae mainly and the animal component becomes relatively insignificant. The early stages feed on more nutritious food and the fish show a higher condition coefficient at this time than at a larger size approaching 30 mm.

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