FEEDING ECOLOGY OF *OREOCHROMIS ESCULENTUS* (GRAHAM) (PISCES:CICHLIDAE) IN LAKE KANYABOLI, KENYA.

BY

STEPHEN V. OPIYO B.Sc. (Hons) (NAIROBI)

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DECLARATION

This thesis is my original work and has not been presented for a degree in any University.

19/6/92

Stephen V. Opiyo Date

This thesis has been submitted for examination with my approval as University supervisor.

10/7/92

Prof. Stephen Dadzie Date
Department of Zoology
University of Nairobi

DEDICATION

This thesis is dedicated to my parents Mr. Amoth Owira and the late Mrs. Joyce Amoth.

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Abstract

The food and feeding habits of *Oreochromis esculentus* in Lake Kanyaboli were investigated from September 1989 to August 1990 during which a total of 1305 fish stomachs were examined. The diet consisted of a broad spectrum of food types, including phytoplankton, zooplankton and detrital material. The blue-green algae (Cyanophyta) and green algae (Chlorophyta) were the principal food types, constituting about 70% and 24% respectively by numbers, of the foods consumed . Diatoms (Bacillariophyta), euglenoids (Euglenophyta) and zooplankton were also consistently present in the diet of this species. *O. esculentus* of different sizes in Lake Kanyaboli fed on similar food types. The diet composition remained the same throughout the year as did the composition of phytoplankton in the water. Diatom and zooplankton components of the diet were digested while most blue-green and green algae as well as euglenoids passed out through the gut undigested.

O. esculentus tended to select the Bacillariophyta and zooplankton, which are digestible, and, to some extent, the euglenoids. This species, however, rejected blue-green and green algae, which it was not capable of breaking down.

O. esculentus in Lake Kanyaboli fed during the day, and digested and assimilated food at night. It fed actively from 0700h until 1700h, when peak feeding

activity occurred. Thereafter, digestion progressed steadily until 0600h when 90% of the fish had empty stomachs.

The presence of a lower pharyngeal bone armed with slender teeth hooked at the distal end, an upper pharyngeal bone with teeth cusped at the distal end, a poorly developed i.e. less mascularized sac-like stomach and an intestine of considerable length (standard length to intestine length ranged from 1:4 to 1:14), all attest to the phytoplanktivorous diet of *O. esculentus*.

Both male and female *O. esculentus* exhibited isometric growth. The overall length-weight relationship was given by: $\text{Log } W = -4.523 + 3.022 \text{ Log } L$. There was no significant difference in the condition of fish of different sizes or sexes, or at different times.

CHAPTER ONE

INTRODUCTION

The cichlid fish, *Oreochromis esculentus* (Graham) is indigenous to Lakes Victoria, Kyoga, Nabugabo and Kanyaboli (Graham, 1929; Greenwood, 1953; Lowe-McConnell, 1955; Welcomme, 1964; Bailey, 1968). It has, however, been introduced into several reservoirs in East Africa (Bailey, 1968). From the beginning of this century to the 1960s it formed the mainstay of the commercial fishery in Lake Victoria (Graham, 1929; Worthington, 1929; Fryer, 1961; Welcomme, 1964 , 1966). Tilapiine catches per night have now decreased from 50-100 fish per 50 m long gillnet (of 127mm stretched mesh) in 1905 (Worthington and Worthington, 1933) to less than 0.5 fish in 1970 (Ssentongo, 1972). The tilapiine fishery has declined from a mean monthly catch of 6.0 metric tons in 1969 to 0.3 metric tons in 1976 (Benda, 1979). The decline in the catches of *O. esculentus* in Lake Victoria have been attributed to a variety of factors including overfishing (Graham, 1929; Ssentongo, 1972; Kudhongania, 1973; Benda, 1979; Muller and Benda, 1981; Bergstrand and Cordone, 1971; Gulland, 1972; LVFS, 1950-1960; FAO, 1972) and predation by the introduced Nile perch, *Lates* *niloticus* (L.) (Okemwa, 1984; Okemwa *et al.*, 1982; Ogutu-Ohwayo, 1985; Hughes, 1986). The Lake Victoria fishery is now dominated by *L. niloticus*, *Rastrineobola argentea* (Pelligrin) and introduced *O. niloticus* (L.). (Kenya Govt., 1989).

Although *O. esculentus* is presently faced with extinction in the Winam Gulf of Lake Victoria, it is found in large quantities in Lake Kanyaboli situated about 16 km North East of Lake Victoria, contributing about 60% to the total catch (Okemwa, 1981). The continued abundance of *O. esculentus* in Lake Kanyaboli could be due to the absence of the predaceous *L. niloticus* from that lake. Lake Kanyaboli's fisheries and limnology have been little studied. With the exception of preliminary surveys of the fish, coupled with baseline limnological studies (Okemwa, 1981; Mavuti, 1989) no other research has been carried out on the lake. The study of food and feeding habits of fish are of great importance since they have implications for fish growth rates, development, fecundity and condition. Within a species fish show temporal and spatial variability in feeding habits. Failure to take account of this variability has often resulted in conflicting or incomplete observations (De Silva, 1973; Staples, 1975).

Results of studies on food habits of *O. esculentus* in East African lakes have consistently shown that the species is a phytoplanktivore which digests only the diatom component of the phytoplankton while blue-green and green algae pass through the gut undigested (Graham, 1929; Worthington, 1929; Fish, 1951; Welcomme, 1964). Zooplankton have also been reported in the diet although in insignificant amounts (Fish, op. cit.). In the past two decades or so, however, no research work has been carried out on the feeding ecology of the species in East Africa. With dynamic changes in physico-chemical conditions, productivity and ichthyofauna of East African lakes, food habits may well be changing.

In reservoirs where *O. esculentus* has been introduced, the species never grows to a large size. It has been suggested (Welcomme, 1962; Bailey, 1968) that stunted growth in the reservoirs is due to a low density of diatoms in the water column. Contrary to the above observations, Lowe-McConnell (1975) reported that several species of the tilapiines including *O. esculentus* grow large and delay sexual maturity in deep large lakes, whereas in small water bodies, floodplain pools, fish ponds and aquaria, they breed at small sizes and young ages but develop quite quickly to maturity. The author noted that this ability of tilapiines to mature at a small size and early age despite rapid growth rate is an adaptation to ensure rapid population growth of the species in environments where the danger of desiccation is greatest.

Despite the proximity of Lakes Victoria and Kanyaboli, the stocks of *O. esculentus* inhabiting them show great differences in body size. Whereas *O. esculentus* in Lake Victoria grow to a large size (30-40 cm TL), individuals from the Lake Kanyaboli stock are stunted and attain sexual maturity and breed when very small (10 cm TL) (per. obs.). This stunted growth phenomenon is very undesirable to fishermen and fish merchants because such stunted fish have low market value.

From available data (Talling, 1961; Evans, 1960; Nyamu, 1986; Kibaara, 1989) there are three main phytoplankton groups in Lake Victoria, namely Cyanophyta, Chlorophyta and Bacillariophyta. The presence of adequate amounts of digestible algae i.e. diatoms, in the water column could be responsible for the large size of *O. esculentus* in Lake Victoria. In Lake Kanyaboli, however, data on phytoplankton composition and abundance are lacking and no explanation for the reduced size of the species has been advanced. The present investigations were undertaken in an attempt to examine reasons for the small body size of the *O. esculentus* population in Lake Kanyaboli. In this study the food habits and condition of *O. esculentus* in Lake Kanyaboli were examined.

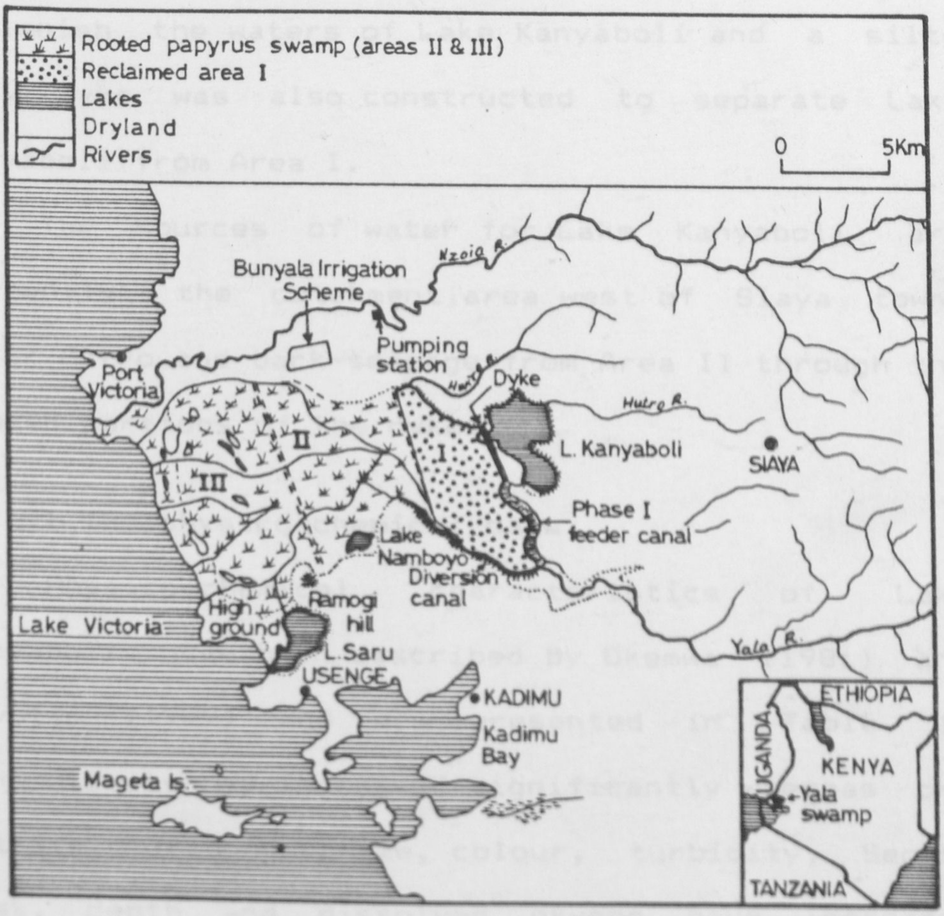
1.1 THE STUDY AREA

Lake Kanyaboli (Fig.1) is located between latitudes 0° 05′N, and 0° 02′N and longitudes 34° 09′E and 34° 11′E, at an altitude of 1156 m above sea level. It has an area of 10.5 km^2 and an average depth of 2.5 m. The lake is located on the eastern edge of the Yala swamp, on the northern shore of Lake Victoria (Mavuti, 1989).

The Yala swamp covers an area of 17,500 ha. and is bounded on the North by the Hwiro and Nzoia Rivers and on the South by the Yala River. Part of the swamp has been reclaimed for agriculture and there is a continuing controversy between conservationists and politicians regarding the reclamation of the remaining portion. Before reclamation of the swamp started in the early 1970s, the Yala River flowed first through the eastern part of the swamp into and through Lake Kanyaboli before discharging into the main swamp (see areas II and III, in Fig. 1).

Fig. 1 Map of Yala Swamp showing its environs.

Source: Mavuti 1989.


Rooted papyrus swamp (areas II & III)
Reclaimed area I
Lakes
Dryland
Rivers
0
5Km
Nzoia R.
Bunyala Irrigation Scheme
Pumping station
Dyke
Hutro R.
Port Victoria
II
III
I
L. Kanyaboli
SIAYA
Phase I feeder canal
Lake Namboyo
Diversion canal
High ground
Ramogi hill
Lake Victoria
L. Saru
USENGE
KADIMU
Kadimu Bay
Yala R.
Mageta Is.
ETHIOPIA
UGANDA
KENYA
Yala swamp
TANZANIA

During the reclamation of Area I in the swamp a diversion canal was constructed which changed the direction of flow of the Yala River. Thus, instead of the river flowing through Area I into Lake Kanyaboli, it now flows through Areas II and III into Lake Victoria. A feeder canal was constructed to replenish the waters of Lake Kanyaboli and a silt-clay dyke was also constructed to separate Lake Kanyaboli from Area I.

The sources of water for Lake Kanyaboli are currently the catchment area west of Siaya town, River Hutro and back-seepage from Area II through the broken portions of the dyke.

1.1.1 The physico-chemical data

Physico-chemical characteristics of Lake Kanyaboli have been described by Okemwa (1981) and Mavuti (1989) and are presented in Table 1. Conductivity has increased significantly whereas pH, nitrate, orthophosphate, colour, turbidity, Secchi disk, depth and dissolved oxygen have increased slightly or remained the same from 1981 to 1989. Small increases in nitrates in the lake are probably the result of increased use of fertilizers in the reclaimed area of Yala Swamp. The northern section of the lake is more turbid than the southern

Table 1. Some morphometric and physico-chemical data of Lake Kanyaboli.

Parameter	Year 1981	1989
Surface area (km^2)	10.5	10.5
Maximum depth (m)	2.5	3.0
Transparency	0.75	1.0
p^H	7.25	9.0
Conductivity (K_{20}Hmho.cm^{-1})	630	950
Nitrate (mg N. l^{-1})	0.4	0.6
Orthophosphate (µg P l^{-1})	0.14	0.2
Iron (µg Fe. l^{-1})	0.03	*
Colour (units)	188	*
Turbidity (FTU)	51	04
Secchi disk (m)	0.75	*
DO (ppm)	5.4	*
Bottom	fine mud	fine mud

Note: The asterisks indicate parameter not determined

DO = Dissolved oxygen

Source: Okemwa (1981) and Mavuti (1989).

especially during the rainy seasons, owing probably to surface run-offs from quarries on the northern lakeshore.

1.1.2 The Biota

Lake Kanyaboli is surrounded by dense growth of aquatic vegetation dominated by *Cyperus papyrus* L. interspersed with other aquatic macrophyte species, including *C. dives* Del., *Hibiscus diversifolius* Jacq., *Leersia hexandra* Sw., *Ludwigia leptocarpa* (Nutt.) Hara., *Commelina africana* L., *Crassocephalum picridifolium* (Dc.). S. Moore., *Fimbristylis subaphylla* Boeck., *Phragmites karka* (Retz.) Steud., and *P. mauritianus* Kunth., *Ipomea rubens* Choisy., *Cyclosorus striatus* (Schumach.) Ching., *Typha domingensis* Pers. and *Pteris* species.

The southern and northern sections of Lake Kanyaboli were once divided by a mass of firmly rooted papyrus (Okemwa, 1981). The papyrus which separated the two sections of the lake have been uprooted and now exist as "papyrus islands", and there is now free movement of water between the two sections of the lake. The macrophytes that surround the lake are of considerable ecological value, because they act as nursery grounds for young fish, and harbour various animal groups including annelids, insects, molluscs, reptiles, birds and mammals.

Discrete clumps of free floating "papyrus islands" with diameter ranging from one to twenty metres are prominent features in the lake. The direction and rate of movement of the "papyrus islands" is determined by the direction and speed of wind. As they move, these islands collect and destroy fishing gears such as gillnets, long lines and even beach seines. Therefore they exert a negative impact on commercial exploitation of the ichthyofauna. When these "islands" die, they sink to the bottom, decompose and form a fine black mud.

The present ichthyofaunal community of Lake Kanyaboli is composed of *O. esculentus* (Graham), *O. variabilis* (Boulenger), *O. niloticus* (L), *Haplochromis* spp., *Clarias mossambicus* (Peters), and *Protopterus aethiopicus* (Heckel). According to local fishermen several other genera, such as *Labeo*, *Barbus*, and *Bagrus*, which used to inhabit the lake have disappeared since the construction of the silt clay dyke and the diversion canal.

CHAPTER 2

LITERATURE REVIEW

The importance of the tilapiines as food fish in Africa has long been recognised. Research on various aspects of the biology of tilapiine species started at the beginning of this century (see review by Thys, 1968) and has continued to the present day.

2.1 Species composition and relative abundance

Okemwa (1981) and Mavuti (1989) reported the presence of nine species of fish in Lake Kanyaboli including *Oreochromis esculentus*, *O. variabilis*, *O. leucostictus*, *Tilapia zillii*, *Clarias mossambicus*, *Protopterus aethiopicus*, *Xenoclarias* and the multispecies haplochromines. Other fish genera including *Barbus*, *Labeo*, *Mormyrus* and *Synodontis*, have disappeared since the construction of the silt-clay dyke. Considerable information exists on the composition and abundance of the Lake Victoria ichthyofauna based on commercial catches (LVFS, 1950-1960) and experimental trawls (Kudhongania, 1973; Benda, 1979, 1981). There have been recent declines in the catch of species endemic to Lake Victoria, namely *O. esculentus*, *O. variabilis*, *Bagrus docmac*, *Barbus altinialis*, *Mormyrus* sp., *Haplochromis* spp., *Marcusenius* sp. and *Labeo victorianus*, but an increase in the catch of introduced species especially the Nile perch, *Lates niloticus* and *O. niloticus* (Bergstrand and Cordone, 1971; Gulland, 1972; Benda, 1979). *O. esculentus* dominated the Lake Victoria fishery up to the 1960s (Gee, 1968). A sharp decline in catches of this species started in the 1970s and has continued until now. Presently, insignificant numbers of this species are caught in the trawls in the Winam Gulf (Okemwa, 1984). Data on the abundance of fish in Lake Kanyaboli are scanty. During a preliminary survey of the fish in Lake Kanyaboli, Okemwa (1981) determined the relative abundance of fish in the fisheries catch and found that *O. esculentus* contributed about 60% of the total fish caught. No data exist on the ichthyomass of the different fish species inhabiting the lake.

2.2 Feeding ecology

The tilapiines are well known for their ability to colonise and effectively exploit unstable shallow water habitats in the tropics and sub-tropics (Lowe-McConnell, 1975). Their success in these habitats has been attributed to their ability to rapidly alter both life history characteristics and feeding habits in response to changes in the environment (Fryer and Iles, 1972; Bowen, 1982).

2.2.1 Food habits

Due to the evolution of structural and physiological specialisations, the cichlid fishes of the Great African Lakes exhibit a great diversity of feeding habits which has enabled them to exploit a large variety of food sources. Among the cichlids, phytoplanktivores, carnivores, detritivores and macrophyte feeders are encountered (Fryer and Iles, 1972).

Reports on the feeding habits of *O. esculentus* show that its diet consists principally of phytoplankton. Only the diatoms are digested whereas the blue-green and green algae pass undigested through the gut (Graham, 1929; Worthington, 1929; Fish, 1951; Greenwood, 1953; Lowe-McConnell, 1956; Welcomme, 1966). Limitations on the digestive capabilities of *O. esculentus* affect its growth in reservoirs where they are often in poor condition and remain under-sized owing perhaps, to a lack of diatoms in the water (Fish, 1951; Payne, 1971). In certain instances the water may be green with phytoplankton and *O. esculentus* may feed heavily on algae but, due to small numbers of digestible diatoms, the fish starve. Other food types, namely insect larvae and planktonic crustaceans occur less frequently in, but may contribute significantly to the diet of *O. esculentus* (Fish, 1955). Gut contents of *T. esculenta*

(= *O. esculentus*) caught in the vicinity of Nyumba ya Mungu Dam in Tanzania were found to be made up almost entirely of algae dominated by the genera *Cyclotella, Melosira, Nitzschia* (diatoms) and *Microcystis* (blue-green alga). The absence of macrophyte, detrital, animal, and inorganic materials was an indication that the fish fed on plankton (Bailey and Denny, 1978).

Other tilapiines have also been reported to feed on phytoplankton. *O. nigra*, like *O. esculentus*, feeds mainly on phytoplankton and/ or epiphytic algae, digesting the diatom fraction but passing blue-green and green algae undigested (Whitehead, 1958). Phytoplankton is the main component of the diet of *Sarotherodon galilaeus* and *T. mariae*; however traces of higher plant tissue, a few rotifers and copepods have been found in insignificant proportions in their stomachs (Corbet *et al.*, 1973). During a study of *T. galilaea* (=*S. galilaeus*) in Lake Kinneret in Israel, Spataru (1976) found that Chlorophyta, Cyanophyta and Chrysophyta were the main components of the diet. Occasionally, Cladocera, Rotatoria, remnants of cephalic capsules of Chironomida, chaeta of Oligochaeta, statoblasts of Bryozoa and spicules of Spongilla were also found in *S. galilaeus* guts.

2.2.2 Prey digestibility

Although blue-green and green algae are often not digested by tilapiines, there appear to be exceptions. D.J.W. Moriarty and C.M. Moriarty (1973) reported that *T. nilotica* (=*O. niloticus*) can assimilate a maximum of 70-80% of the carbon in the blue-green algae *Microcystis* and *Anabaena*, whereas 50% of the carbon was assimilated from green alga, *Chlorella* sp. Because the fish assimilated more carbon from blue-green algae than from green algae under similar conditions, the authors contended that the cellulose cell wall of green algae was more resistant to lysis.

According to Moriarty (1973) and Payne (1978) the tilapiine species that digest blue-green and green algae have stomach pH of 2.0 or less, and acidic conditions in the stomach contribute to the lysis of algal cell walls. *O. niloticus*, whose stomach pH does not fall below 2.5, keeps the food in the stomach for a long period of time to facilitate the lysis of blue-green and green algal cells (Harbott, 1975).

In Lake Kinneret, Spataru (1976) examined ingested food items in different parts of the gut of *T. galilaea* (=*S. galilaeus*) in order to estimate the digestibility of various food types and found clear differences in the degree of disintegration of different algal species along the intestinal tract. The majority of the Chlorophyta and all Cyanophyta and Euglenophyta species passed through the gut whole with internal pigments intact, and only *Cosmarium laeve* and *Coelastrum microporium* were digested in Autumn and Winter respectively. Because Chrysophytes were often in a disintegrated condition in the oesophagus and stomach, it was assumed that they were dead when ingested.

2.2.3 Seasonal changes in diet composition

Seasonal changes in food availability may be caused by changes in the habitats available for foraging, changes due to life history patterns of food organisms, and changes in the feeding behaviour of the fish themselves (Wootton, 1990). Fish species with catholic diets often show changes in the taxonomic composition of diets whereas species that have a more specialised diet show changes in the proportion rather than the composition of ingested food types (Wootton, op. cit.). No elaborate seasonal changes in the diet of tilapiines has been reported.

2.2.4 Variation in diet in different localities

Some fish species show differences in diet in different locations. Bailey (1975) (cited by Trewavas, 1983) found the diet of *O. pangani* to consist of diatoms, filamentous algae and fragments of macrophyte tissue. It was however reported by Bailey and Denny (1978) in Nyumba ya Mungu Reservoir that the same species feeds predominantly on periphyton. Similarly, *O. niloticus* in Lake Awasa fed mainly on *Botryococcus braunii* (colonial chlorophyte) while the same species in Lake Zwai fed on *Microcystis* species (cyanophyte) (Getachew, 1986).

2.2.5 Food in relation to size of fish

The diet of some fishes changes as they grow because of morphological changes that accompany their growth. The question of whether the diet of a particular fish species remains stable throughout its life or changes with increasing size is of considerable biological interest since it determines whether there is competition between juveniles and adults for food in situations where there is food scarcity.

Welcomme (1966) reported that the adults of *O. esculentus* (>7.0 cm SL) in Lake Victoria fed on phytoplankton, mainly *Melosira* and occasionally *Nitzschia*, *Stephanodiscus* and *Surriella*, whereas the juvenile's (<7.0 cm SL) diet consisted predominantly of bottom material. Larger individuals of *O. guineensis* (>6.0 cm TL) browse on the decaying leaves of macrophytes while juveniles feed principally on algae, particularly filamentous blue-green algae (Payne, 1978).

In Lake George, *O. niloticus* (>6.0 cm TL) ingests mainly phytoplankton whereas *H. nigripinnis* (>5.0 cm TL) feeds mainly on the blue-green alga *Microcystis*. Smaller fish of both species are omnivorous (Moriarty, 1973). In *T. shirana chilwae* considerable changes in the diet occur as the fish grow (Green, 1972). Small individuals (<10 cm TL) feed on zooplankton but the diets of bigger fish show increased proportions of higher plant materials and diatoms. Similarly, the juveniles (8-18 cm TL) of *O. mossambicus* feed on zooplankton while the adults feed mainly on phytoplankton (Green op. cit.). Whyte (1975) found that the juveniles of *S. galilaeus* primarily feed on insects at the water surface (chaoborids and chironomids), whereas the adults are exclusively phytoplanktivorous feeding mainly on blue-green algae and desmids. Young *H. nigripinnis* are opportunistic feeders and take benthic, mid-water and emergent invertebrates as well as aufwuchs and plant fragments, but switch to fish prey, i.e. *Oreochromis* spp. and *Haplochromis* juveniles, as they grow. Individuals of the benthic predator *H. angustifrons* feed on benthic invertebrates throughout their life but show a change in diet with growth (Moriarty, 1973). The small fish feed on ostracods and copepods while the larger individuals feed on dipteran larvae. Bowen (1979) found that both juveniles and adults of *O. mossambicus* are benthic detrital feeders but occupy different feeding zones. The juveniles feed in shallow inshore areas whereas the adults feed in deeper waters.

Similar changes in the diet have been reported in other teleostean species in African freshwaters. For instance, young of Nile perch prey mostly on invertebrates while the adults are mainly piscivores (Ogari and Dadzie, 1988). In *Bagrus docmac*, the juveniles feed on aquatic insects and crustaceans but become piscivorous at a length of 18 cm (Okach and Dadzie, 1987).

2.2.6 Diel feeding periodicity

The diel feeding periodicity of fish may vary with species, habitat, season and the distribution, abundance, and behaviour of prey. According to Nikolsky (1963) the intensity of feeding depends on the condition of the fish with fat fish consuming less food than lean ones. At present there are no data available on the diel feeding periodicity of *O. esculentus*. A few investigations have been conducted on diel feeding patterns in other cichlids. Moriarty (1973) found that *O. niloticus* and *H. nigripinnis* in Lake George are diurnal feeders and begin feeding at or near dawn. According to Man and Hodgkiss (1977), *S. (=O.)*

mossambicus in Plover Cove Reservoir feeds during the day with the feeding intensity being maximal between 1200 and 1500 hours, then slows progressively so that stomachs are completely empty by 0000 to 0300 hours. Diurnal feeding behaviour has also been reported in *S. shiranus chilwae* (Bourn, 1974), *S. alcalicus grahami* (Coe, 1966, 1967) , *T. busumana* in Lake Busumtwi (Whyte, 1979) and in the tilapiines in Lake Kamburu (Dadzie *et al.* 1979). Contrary to the diurnal feeding behaviour of the above cichlids, *S. (O.) galilaeus* and *T. discolor* feed at night between 1800 and 0500 hours (Whyte, 1975).

The piscivore *B. docmac* in Lake Victoria feeds principally at dusk and dawn (Okach and Dadzie, 1987). Aloo (1988) investigated the diel feeding patterns of blackbass, *Micropterus salmoides* in Lake Naivasha and found that this species is a diurnal feeder with feeding peaks at dawn, around noon and towards dusk.

2.3 Food selection

Several authors have investigated the ability of fishes to actively select certain prey items among a range of available types. In herbivorous *O. niloticus* in Lake George, there is a marked positive selection for the blue-green alga *Lyngbya* and a colonial diatom

Melosira but a negative selection for the blue-green alga *Anabaenopsis* and diatom *Synedra* (Moriarty, 1973). The selection appeared to be based on size and the shape of the food particles. In *H. nigripinnis*, the fry are zooplanktivores and exhibit selection for different sizes of zooplankton. Smaller fish (< 5.0 cm TL) showed positive selection for the smaller crustacean *Ceriodaphnia* whereas larger fish showed positive selection for the larger Cladoceran species such as *Daphnia* and *Moina* and the smaller crustacean *Ceriodaphnia* (Moriarty op. cit.).

Spataru (1976) reported that *T. galilaea* show preference for *Peridinium* (a pyrrophyte) but show negative selection for other groups of algae namely: Chlorophyta and Cyanophyta, with selectivity values between 0 and 1, but they occur incidentally in the gut when they are mechanically swallowed together with *Peridinium*.

Spataru and Gophen (1987) investigated food selection by the cichlid fish, *Tristramella sacra* in Lake Kinneret and found low indices of electivity for both phytoplankton and zooplankton during most parts of the year. From December to August there was positive selection for phytoplankton but a negative selection for zooplankton in April. However, during September – November the selection was inverted, positive for zooplankton and negative for phytoplankton.

2.4 Feeding structures

The feeding apparatus and digestive tract limit the range of potential food items that can be consumed and digested efficiently (Lagler, *et al.*, 1963; Bowen, 1982).

2.4.1 Jaw

The oral teeth of tilapiines are located on the jaws. Dentition is often intimately related to the nature of the food and to the method employed for its collection. Generally, the jaw teeth of cichlid fishes occur in one to five rows (Bowen, 1982). Cichlid teeth are basically of three types: unicuspid, bicuspid and tricuspid (Fryer and Iles, 1972).

In some cases, cichlid tooth structure not only varies from species to species but also through an individual's lifetime as consequence, dentition of adults can be strikingly different from that of juveniles. Such variations have been observed in *Chilotilapia rhoadesii* where changes occurred both in dentition and in the shape of the jaw as the fish develop (Trewavas, 1935, cited by Fryer and Iles, 1972).

it has been reported (Lanzing and Higginbotham, 1976) that *T. mossambica* (*O. mossambicus*) develops villiform, bicuspid and tricuspid teeth on the upper and lower jaws but with the bicuspids being concentrated along the outer edge of the jaw.

2.4.2 Pharyngeal bones

In cichlids the grinding processing of foods, equivalent to mastication in other fishes, usually takes place in the throat or pharynx with the assistance of flattened pharyngeal bones (Fryer and Iles, 1972). The upper pharyngeal bone is located at the roof of the pharynx and is a complex of three bones which lie close together and function as a single unit. The lower pharyngeal bone, on the other hand, is made up of two bones firmly united into a single bone usually more or less triangular in shape (Fryer and Iles op cit.).

Foods that are ingested must pass between the upper and lower pharyngeal bones. Both pharyngeal bones are endowed with teeth whose number, size and morphology differ from species to species depending on their food habits. Forward and backward sliding of the upper bones in combination with upward and downward movement of the lower bone facilitate the crushing and tearing of food, and food passage into the oesophagus. The form and armature of the pharyngeal bones vary in different species depending on the nature of foods it deals with. Phytoplankton feeders have numerous rows of teeth that curve backwards and some strong teeth at the posterior end of the lower bone. In contrast, piscivorous species are armed with fewer, stouter teeth which are sharp and point backwards, suitable for gripping and forcing solid foods into the oesophagus (Fryer and Iles, op cit.).

Greenwood (1953) reported that the hooked crown of the upper pharyngeal teeth of *T. esculenta* (*O. esculentus*) are used for raking a mixture of mucus and phytoplankton towards the oesophagus. The lower pharyngeal teeth, on the other hand, are pointed and lack distinct cusps. In *O. mossambicus*, the dorsal pharyngeal teeth have a peculiar hook-like extension at the tip, whereas the ventral pharyngeal teeth tend to curve posteriorly (Lanzing and Higginbotham, 1976).

The pharyngeal mill reduces the size of food particles by breaking or cutting the food into smaller units thereby facilitating peristaltic mixing and increasing surface area for exposure to digestive enzymes in the gut (Bowen, 1982). In *T. esculenta* (*O. esculentus*), algal filaments and large colonies are broken into smaller fragments (Greenwood, 1953). In *S. mossambica* (*O. mossambicus*) and *S. melanotheron* detrital aggregates are broken into fine fragments (Bowen, 1976; Pauly, 1976). The mechanical disruption of macrophyte cell walls by pharyngeal apparatus in *T. rendalli* increase the efficiency with which food is digested (Caulton, 1976).

2.4.3 Stomach

The degree of development of the stomach varies according to the diet of fish. In some herbivores there is virtually no stomach whereas some piscivores have large pouch-like stomachs (Wootton, 1990). It has been reported that the stomach of tilapiines is separated from the intestine by a sphincter and the fluid the stomach contains has a low pH (Moriarty, 1973; Bowen, 1976; Caulton, 1976).

2.4.4 Intestine

Great differences occur in the intestine lengths of herbivorous and carnivorous fishes. In herbivorous fishes the intestine is several times the length of the body whereas in carnivorous, and particularly piscivorous fish the intestine is usually very short. It has been reported (Kapoor *et al*., 1975) that there is a correlation between diet and the gut length to body length ratio.

The relationship between gut length and the body length of *T. esculenta* (=*O. esculentus*) has been found to vary with the sexual state of the fish (Welcomme, 1966). The gut, excluding the stomach, is 8.1 ± 1.4 times the standard length (Welcomme, op. cit.). Variations in the gut/body length ratio between fish of various sexual states indicate that the gut tends to be shorter in breeding fish and spent females which are mouth-brooding and do not feed. Data for *T. rendalli*, *S. melanotheron* and *S.* (= *Oreochromis.*) *mossambicus* show that the ratio of the intestine length to fish standard length is between 7:1 and 10:1 (Caulton, 1976; Pauly, 1976). The Indian cyprinid, *Labeo horie* feeds on detritus and has a gut length that is 21 times its body length (Bond, 1979). In *Cichlasoma urophthalmus*, a carnivorous cichlid the intestine length is 2.2 times the fish standard length (Martinez-Palacios and Ross, 1988).

Sometimes changes occur in the diet and form of the alimentary canal as fish grow. In *M. cephalus* the ratio of the gut length to body length increases with age (Blaber, 1976). The ratio of the total gut length to fish standard length ranged from 2:10 for fish of 120mm to 6.5:1.0 for fish of 500mm (Blaber op. cit.).

2.5 Length-weight relationship

Establishment of length-weight relationships has two functions. First, lengths, which are easier to measure, can be readily converted to weights using appropriate length-weight regressions. Secondly, it is possible to determine the condition of fish using length-weight relationships (Le Cren, 1951).

The length-weight relationship is often expressed by the general mathematical formula (Le Cren, 1951):

$W = aL^b$ where,

W = weight (g)

L = standard length (cm)

a = constant

b = exponent

In most cases the value of b falls between 2.0 and 4.0, with a mean near 3.0. When the value of b is close to 3.0 the fish is said to exhibit isometric growth, whereas allometric growth occur when the value of b varies greatly from 3.0 (Bagenal and Tesch, 1978). A logarithmic transformation of this equation gives a linear relationship:

$$\text{Log } W = \text{Log } a + b \text{ Log } L$$

In this transformed equation b becomes the slope of the equation and log a is the intercept of the line on the y-axis.

Reports on length-weight relationships of various fish species inhabiting African water bodies are still scanty. Investigations of length-weight relationship of fish have, from time to time, been carried out in reservoirs and ponds. In a study of fish in man-made Lake Kamburu, Dadzie *et al.* (1979) computed the values of "b" for four teleostean fish species and found them to vary with species. The values were 3.0, 3.1, 2.6 and 2.0 for *Tilapia*, *Barbus*, *Labeo* and *Mormyrus*, respectively. The authors concluded that *Tilapia* and *Barbus* exhibit isometric growth. In the same lake, Dadzie (1985) observed no differences in length-weight relationships between sexes, even within the same month of the year, in the African carp, *Labeo victorianus*. The respective values for "a" and "b" were -1.6 and 2.9 for males, -1.6 and 2.9 for females.

In a study of pond raised *T. zillii*, Dadzie and Wangila (1980) computed length-weight relationships for males and females and found the values of "a" and "b" for males to be -1.7 and 3.4 respectively, while the corresponding values for the females were -1.7 and 3.4. The authors concluded that growth in this stunted *T. zillii* population was not isometric. In Nyumba ya Mungu Reservoir, however, all four tilapiines studied exhibited isometric growth (Bailey and Denny, 1978). The values of "a" and "b" respectively were -1.8 and 3.0 for *Sarotherodon (Oreochromis) jipe*, -1.8 and 3.0 for *S. (O.) pangani*, -1.7 and 3.0 for *S. (O.) esculentus*, and -1.9 and 3.1 for *T. rendalli*. There were no significant differences in the slopes for different species. In Jatiluhur reservoir in Indonesia, Hardjamulia *et al.* (1987) found *O. niloticus* to exhibit isometric growth.

In Lake Victoria, Okach (1981) found that growth patterns were similar for male and female *B. docmac* up to a length of 35 cm, beyond which females became heavier than males for a given length, probably owing to the development of egg-ladden ovaries in gravid females. "b" in the length-weight regression was found to be 3.1 and the author concluded that the species exhibits isometric growth. Also in Lake Victoria, Mwalo (1981) computed length-weight regressions for two species of *Synodontis* and found the values of "a" and "b" to be -2.3 and 3.5 for male and -2.3 and 3.6 for female *S. afrofischeri*, and 2.2 and 3.3 for male and -2.0 and 3.1 for female *S. victoriae*.

From the study of length-weight relationships in fish populations from temperate region, Callander (1969) found that there was a tendency for the value of "b" to be about 3.0. Bailey (1972) found the values of "b" in *Nothobranchius guentheri* to be 3.8 in females and 3.3 in males. Bannister (1975) computed length-weight relationships for male and female *Coryphaena hippurus* and found that "b" and "a" values for females were 2.9 and -4.7 and for the males were 3.0 and -4.8. The author concluded that the weight of this species is proportional to the third power of the fork length (FL).

2.6 Condition

Condition factor is often used as a measure of the plumpness, fatness or "well being" of a fish, and varies with age-group, sex, season, habitat, and reproductive state (Tesch, 1971; Bagenal and Tesch, 1978)

Payne (1975) determined the relative condition factor for immature and mature *B.liberiensis*, using somatic weights in order to elucidate the effect of gonadal development on the condition but reported lack of significant changes in the somatic conditions after spawning. Welcomme (1966) calculated coefficient of condition of the introduced tilapiines from standard lengths and found them to be high, an indication that the stocks are healthy. The condition factors of tilapias in Lake Victoria were: 4.1, 4.3 and 4.1 for *T. nilotica*, (*O. niloticus*), *T.leucosticta* (*O. leucostictus*) and *T. zillii* respectively (Welcomme, op cit.). The corresponding values for the same fishes from Lake Albert where all the three species are endemic were 4.1, 3.9 and 4.2. (Welcomme, op. cit.).

Dadzie *et al.* (1979) followed monthly changes in the condition of four lacustrine fish species i.e. *Tilapia*, *Barbus*, *Labeo* and *Momyrus* in Lake Kamburu and found their condition factors to be 3.0, 3.1, 2.6 and 2.0 respectively. In the same lake, Dadzie (1985) noted monthly fluctuations in the relative condition of *Labeo cylindricus*, but with no marked differences between the sexes. Both sexes reached maximum condition at the beginning of the spawning period in October. Females showed minimum condition factors after spawning in April.

Dadzie and Wangila (1980) found the mean K_n value for pond raised *T. zillii* to be 1.01 with no significant differences among size-classes. Even though the fish were runted their relative condition approached unity, an indication of good condition. Although fish became progressively smaller through successive generations due to runting their condition still remained good.

2.7 OBJECTIVES

The specific objectives of the research were:

1.1 To determine the relative abundance of *O. esculentus* in Lake Kanyaboli.

1.2 To study the food and feeding habits.

1.3 To examine and describe the anatomy of the feeding structures in *O. esculentus*.

1.4 To determine the length-weight relationships and condition of *O. esculentus* in Lake Kanyaboli.

CHAPTER 3

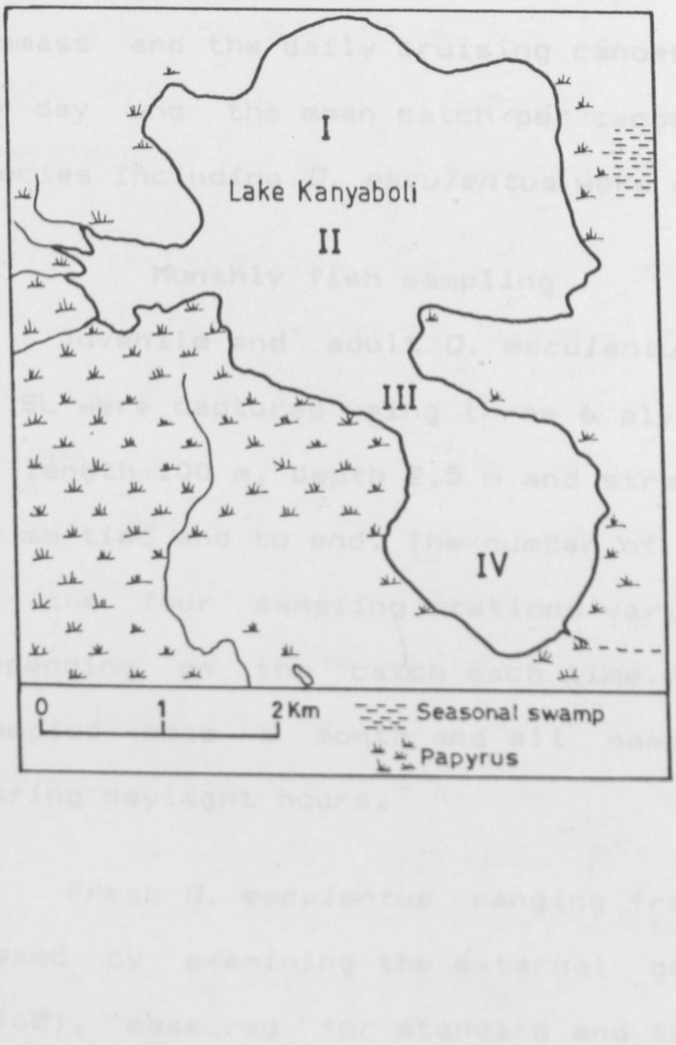
MATERIALS AND METHODS

3.1 Trial sampling

At the initial stage of this project four sampling stations in Lake Kanyaboli were randomly chosen to establish the general distribution of *O. esculentus*. The fish were caught using four fleets with seven gillnets in each fleet. The gillnets in each fleet were each 100 m long; had stretched mesh sizes of 28 mm, 38 mm, 47 mm, 63 mm, 76 mm, 101 mm and 114 mm; and were tied end to end to give a sum total length of 700m. At each station a fleet of gillnets was set parallel to the shore at 7.00 p.m., left overnight and examined between 6.00 a.m. and 7.00 a.m. the following day. During the first week of this survey, the gillnets were manipulated by fishermen and destroyed by the free floating "papyrus islands". For this reason, the use of gillnets was discontinued and replaced with beach seines. The results of the one-week gillnet survey showed that *O. esculentus* was ubiquitous, being present at all sampling stations.

The same four sampling stations used in preliminary surveys were used for the monthly beach seine sampling. These stations were of varied depths as follows: Station I (1.5 m); Station II (3.7 m); Station III (1.8 m); Station IV (2.6 m), and covered the northern and southern sections of the lake.

Fig. 2 Map of Lake Kanyaboli showing the sampling stations.


I
Lake Kanyaboli
II
III
IV
0
1
2 Km
Seasonal swamp
Papyrus

3.2 Relative Abundance

Fish from the commercial catches at the main landing beach - Gang Nyalaji, were separated into different species i.e. *O. esculentus, C. mossambicus, P. aethiopicus, Haplochromis* spp. and other tilapiines (*O. niloticus, O. variabilis* and *O. leucostictus*) and their biomass measured in kg daily. The number of canoes that went fishing each day was recorded. From the daily biomass and the daily cruising canoes, catch per canoe per day and the mean catch per canoe per month of each species including *O. esculentus* were determined.

3.3 Monthly fish sampling

Juvenile and adult *O. esculentus* measuring 26-200 mm SL were captured using three 6 ply beach seines, each of length 100 m, depth 2.5 m and stretched mesh size of 25 mm tied end to end. The number of hauls made at each of the four sampling stations varied from 2 to 10 depending on the catch each time. Each station was sampled once a month and all samples were obtained during daylight hours.

Fresh *O. esculentus* ranging from 26-200 mm SL were sexed by examining the external genitalia (Bailey, 1968), measured for standard and total lengths to the nearest mm, weighed to the nearest g using a pan balance, then dissected. The stomach of each fish was excised and its contents weighed in g, and then preserved in 4% formalin. The rectums of the corresponding fishes were also excised and their contents preserved in 4% formalin. In the laboratory, stomach and rectum contents were stirred in order to separate the organisms, then were examined under a binocular microscope at a magnification of x 100. Food items were identified to the generic level using identification keys in Edmondson (1959), Prescott (1969), Pennak (1978), and Needham and Needham (1975).

To estimate the number of food items in the plankton, four replicate samples of water were collected every month from each of the four sampling stations using an "integrated water sampler", i.e. a flexible tube with a bore of 32 mm and length of 3.0 m. The sampler was lowered through the water column, closed at the top and hauled to the surface using a rope tied to the lower end. Water samples were placed in 500 ml plastic bottles and immediately fixed and preserved in Lugol's solution (Vollenweider, 1974). Another set of water samples from the same stations and at the same times as the phytoplankton samples, were preserved in 4% formalin for zooplankton counting. In the laboratory, 100 ml of the preserved sample were placed in a narrow 100 ml glass cylinder and left to stand for 12 hours, allowing plankton to settle to the bottom. Half of this volume was removed by sucking out the upper 50ml with a pipette. The remaining 50 ml was thoroughly shaken to ensure the random distribution of plankton before pipetting a 1 ml sub-samples into a Sedgewick-Rafter cell, and the plankton were identified to the generic level and counted under a microscope at x 100. 25 fields in each of four Sedgwick-Rafter sub-samples were counted and the average count for each genus was noted. The percentage contribution of each genus in the water was computed.

The macrobenthos was sampled quantitatively with a 12 cm by 12 cm Ekman grab. Ten grabs were taken from each station on each sampling date and sieved through sieves of mesh size 2 mm, 1 mm and 0.5 mm. The benthic fauna retained on the sieves were removed and preserved in 4% formalin, examined under a dissecting microscope at x 24, identified to the lowest possible taxon using the keys of Pennak (1978), then counted. Macrobenthos sampling was carried out monthly for 12 months. It was however observed that *O. esculentus* in Lake Kanyaboli did not feed on macrobenthos.

Feeding habits were determined using the following methods:

The fullness index which gives the relative contribution of food weight to the total weight of the fish was determined according to Ogari and Dadzie's (1988) modification of Blegvads's (1917) index of fullness:

$$\text{Fullness index} = \frac{\text{Fresh weight of the stomach contents (g)}}{\text{Total fresh weight of fish (g)}} \times 100$$

The frequency of occurrence of each food item was determined according to Hynes (1950) as the number of stomachs in which a prey item occurred expressed as a percentage of the total number of stomachs examined. In the numerical analysis, (Hyslop, 1980) estimates of the number of phytoplankton cells and zooplankton in stomach contents were made by suspending preserved gut contents from individual fish in known volumes of water, then sub-sampling using a pipette. Sub-samples were placed in a Sedgewick-Rafter cell and counts made of the various food items, as for the plankton samples. Diatoms, green algae, euglenoids, rotifers and copepods were counted as individuals, whereas blue-green algae were counted as coenobial or colonial units. Prey digestibility was determined by comparing the composition and relative proportions of undigested food types in the stomach and in the rectum.

In order to establish whether *O. esculentus* selects certain food types, comparisons were made between the quantity of various food types in the stomach and in the environment. This was accomplished by determining the numbers of various food types in fish stomachs, in the water column, and on the bottom of the lake.

Food selection was determined using Chesson's (1983) prey preference index using the formula which assumes no food depletion, and a constant number of food types.

$$\alpha_i = r_i/n_i \;/\; \sum r_j/n_j \qquad i = 1,\ldots,m$$

where

αi = preference for prey type i

n_i = number of items of type i present in the environment

r_i = number of items of type i in the consumer diet.

m = number of types in the environment.

Chesson's prey preference index ranges from 0 to 1, where the values close to 0 indicate lack of selection whereas values close to 1 indicate strong selection. Since five food types were examined for preference, in the case of no preference for any particular food type, the α value for each food type would be 0.20. For this study therefore, food was selected when the α value was > 0.20.

For the diel feeding periodicity study, *O. esculentus* were captured in the open water of the lake by seining for 20-30 minutes at hourly intervals. Captured fish were weighed to the nearest 1 g, dissected, the stomach excised and its contents weighed to the nearest 0.1 g. Variations in the weight of the stomach contents relative to fish weight were used in determining diel rhythms in feeding behaviour. This exercise was conducted once in April 1990. Brooding females were not used in this study because they had empty stomachs at all time.

3.4 FEEDING STRUCTURES

The jaws, lower and upper pharyngeal bones, stomach and the intestine of *O. esculentus* ranging from 30-200 mm SL were dissected. The upper and lower jaws were examined under a dissecting microscope at magnification x 24 in order to determine the number of rows of teeth, and teeth morphology. The upper and lower pharyngeal bones were also examined under a dissecting microscope and their structures noted. Teeth on both the upper and lower pharyngeal bones were scraped and examined under a binocular microscope in order to determine their morphology. Measurements were made of the lengths and widths of surfaces occupied by teeth and the entire lower pharyngeal bones. From these measurements, the surface area of toothed surfaces were computed and correlated with fish standard length.

For scanning electron microscopy of oral and pharyngeal teeth of *O. esculentus*, the upper and lower jaws, and upper and lower pharyngeal bones were carefully dissected and the attached flesh removed. Jaws and pharyngeal bones were kept in a dry plastic container and allowed to dry. They were cleaned in 90% alcohol, coated with gold in a sputter chamber, and then examined at different magnifications under a scanning electron microscope, JEOL Model JSM - T100, and photographed.

The structure of the stomach was noted. Finally, the intestines of fish were uncoiled and their lengths measured in mm. and the ratio of the intestine to fish standard lengths were computed. The relationship between intestine length (IL) and Standard length (SL) of fish was described by the allometric equation:

$$IL = aSL^b$$

where,

IL = gut length (mm)

SL = standard length (mm)

a = constant

b = exponent

3.5 LENGTH-WEIGHT RELATIONSHIP

The length-weight relationships were determined using least squares regression analyses using the equation (Le Cren, 1951).

$w = aL^b$

where,

w = weight of fish (g)

L = standard length (mm)

b = exponent

a = constant

The least squares regression coefficients were calculated from the logarithmically transformed data i.e. $\log w = \log a + b \log l$.

Calculations of length-weight relationship were made separately for male and female *O. esculentus* for the whole study period and the resulting slopes slopes , were tested for any significance differences using t statistic. The result of the test showed that there was no significant difference between the slopes, $t = 0.48$; d.f. 1301; $p > 0.05$. The outcome of the test justified pooling of length-weight relationship data for the two sexes.

For detailed analyses, monthly log transformation of length-weight data for each sex was regressed and analysis of covariance test was carried out to determine whether there were significant differences in the monthly slopes of either sex. Similarly, regressions were calculated according to size-classes and their slopes tested using covariance test.

To determine the type of growth pattern exhibited by the species, isometry test was performed by calculating $\hat{t}$ statistic (Pauly, 1984).

$$\hat{t} = (s.dx/s.dy)\ (|b-3|)/\sqrt{(1-r^2)}/\sqrt{(n-2)}$$

Where;

s.dx = standard deviation of $\log_{10}$ value of length.
s.dy = standard deviation of $\log_{10}$ value of weight.
n = number of fish used in analysis
r^2 = coefficient of determination

3.6 CONDITION

The relative condition (K_n) of individual *O. esculentus* was calculated by the method described by Tesch (1971).

$$K_n = \hat{w} / w$$

where,
$\hat{w}$ = observed weight
w = expected weight

Each K_n value represents the deviation of a particular fish from the mean weight- for- length of all fish. The relative condition was calculated monthly for males and females and according to size-classes. Analysis of variance was carried out to determine whether there was significant variation in k_n across months and size-classes.

CHAPTER 4

RESULTS

4.1 FISH SPECIES COMPOSITION AND RELATIVE ABUNDANCE IN LAKE KANYABOLI

4.1.1 Species composition

The present resident fish community of Lake Kanyaboli consists of the following species: *O. esculentus*, *O. niloticus*, *O. variabilis*, *O. leucostictus*, *Tilapia zillii*, *Clarias mossambicus*, *Xenoclarias*, sp. *Protopterus aethiopicus* and *Haplochromis* species.

4.1.2 Relative abundance

Table 2 shows mean monthly catch rates of different ichthyofauna in Lake Kanyaboli. The mean catch per canoe per month of *O. esculentus* varied from 18 kg in January to 36 kg in June. The mean catch per canoe per year of this species was the highest, being 26.4 kg as compared to the mean catches of the other fish. The mean annual catch rates for the other species were as follows: *P. aethiopicus* 3.0 kg, *C. mossambicus* 1.0 kg, *Haplochromis* spp. 1 kg and other tilapiines 1 kg. The mean overall catch per canoe per year was 34 kg.

Table 2. Mean monthly catch rates (kg/canoe) of the ichthyofauna in Lake Kanyaboli.

	Month												
	S	O	N	D	J	F	M	A	M	J	J	A	$\bar{x}$
O. esculentus	20	20	27	30	18	27	31	24	28	36	29	27	26.4
P. aethiopicus	3	2	3	2	2	2	4	2	2	5	3	3	2.6
C. mossambicus	1	1	1	1	1	2	3	1	1	1	1	1	1.3
Haplochromis spp.	1	1	1	1	1	1	1	1	1	1	1	1	1.0
Other tilapiines	1	1	1	1	1	1	1	1	1	1	1	1	1.0

Note: $\bar{x}$ = Mean

4.2 Feeding Ecology

4.2.1 Food habits

The monthly dietary composition of *O. esculentus* from September 1989 to August 1990 based on 1045 specimens from all stations combined is summarised in Table 3. A total of 12 genera of blue-green algae (Cyanophyta), 15 genera of green algae (Chlorophyta), 4 genera of diatoms (Bacillariophyta), 3 genera of euglenoids (Euglenophyta), 4 genera of rotifers, and detritus were observed in the diets of *O. esculentus* in Lake Kanyaboli. Generally the dietary composition of *O. esculentus* in the lake remained the same throughout the year with the possible exception of a few very rare food items such as *Cosmarium*, *Filinia*, and *Keratella*.

Table 4 and Fig. 3 depict the mean frequency of occurrence of different food items in the stomachs of *O. esculentus*. The blue-green algae *Microcystis*, *Merismopedia*, *Lyngbya*, *Spirulina*, *Coelosphaerium* and *Chroococcus* occurred more frequently in the diet (86.9%, 80.3%, 88.6%, 86.1%, 62.1% and 66.4% respectively) than other blue-green algae.

Amongst the planktonic chlorophytes, *Scenedesmus* and *Ankistrodesmus* occurred most frequently in the diet, at frequencies of 87.6%, and 67.9%. Four planktonic diatom species namely, *Fragilaria*, *Navicula*,

Table 3. Monthly dietary composition of *O. esculentus* in Lake Kanyaboli.

Food item	S	O	N	D	J	F	M	A	M	J	J	A
CYANOPHYTA												
Merismopedia	+	+	+	+	+	+	+	+	+	+	+	+
Spirulina	+	+	+	+	+	+	+	+	+	+	+	+
Chrococcus	+	+	+	+	+	+	+	+	+	+	+	+
Coelosphaerium	+	+	+	+	+	+	+	+	+	+	+	+
Microcystis	+	+	+	+	+	+	+	+	+	+	+	+
Oscillatoria	+	+	+	+	+	+	+	+	+	+	+	+
Lyngbya	+	+	+	+	+	+	+	+	+	+	+	+
Nostoc	+	+	+	+	+	+	+	+	+	+	+	+
Aphanocapsa	+	+	+	+	+	+	+	+	+	+	+	+
Synechocystis	+	+	+	+	+	+	+	+	+	+	+	+
Nodularia	+	+	+	+	+	+	+	+	+	+	+	+
Gomphosphaeria	+	+	+	+	+	+	+	+	+	+	+	+
CHLOROPHYTA												
Scenedesmus	+	+	+	+	+	+	+	+	+	+	+	+
Pediastrum	+	+	+	+	+	+	+	+	+	+	+	+
Coelastrum	+	+	+	+	+	+	+	+	+	+	+	+
Crucigenia	+	+	+	+	+	+	+	+	+	+	+	+
Ankistrodesmus	+	+	+	+	+	+	+	+	+	+	+	+
Staurastrum	+	+	+	+	+	+	+	+	+	+	+	+
Closterium	+	+	+	+	+	+	+	+	+	+	+	+
Tetraedron	+	+	+	+	+	+	+	+	+	+	+	+
Kirchneriella	+	+	+	+	+	+	+	+	+	+	+	+
Selenestrum	+	+	+	+	+	+	+	+	+	+	+	+
Elakotothrix	+	+	+	+	+	+	+	+	+	+	+	+
Chlorella	+	+	+	+	+	+	+	+	+	+	+	+
Botryococcus	+	+	+	+	+	+	+	+	+	+	+	+
Korshikoviella	+	+	+	+	+	+	+	+	+	+	+	+
Cosmarium	−	+	−	−	+	+	+	−	−	+	−	+
BACILLARIOPHYTA												
Navicula	+	+	+	+	+	+	+	+	+	+	+	+
Stephanodiscus	+	+	+	+	+	+	+	+	+	+	+	+
Nitzschia	+	+	+	+	+	+	+	+	+	+	+	+
Fragilaria	+	+	+	+	+	+	+	+	+	+	+	+
EUGLENOPHYTA												
Phacus	+	+	+	+	+	+	+	+	+	+	+	+
Trachelomonas	+	+	+	+	+	+	+	+	+	+	+	+
Euglena	+	+	+	+	+	+	+	+	+	+	+	+
ZOOPLANKTON												
Brachionus	+	+	+	+	+	+	+	+	+	+	+	+
Filinia	+	+	+	+	+	+	+	+	+	+	+	+
Keratella	−	−	−	+	−	+	−	−	−	−	+	+
Polyarthra	−	−	+	−	+	+	+	−	−	−	+	+
Detritus	+	+	+	+	+	+	+	+	+	+	+	+
Sample size	80	88	80	151	167	110	83	82	73	145	124	122

Note: + indicate presence of food item
- indicate absence of food item

Table 4. Mean percentage frequency of occurrence of food items in diets of *O. esculentus* from September 1989 to August 1990.

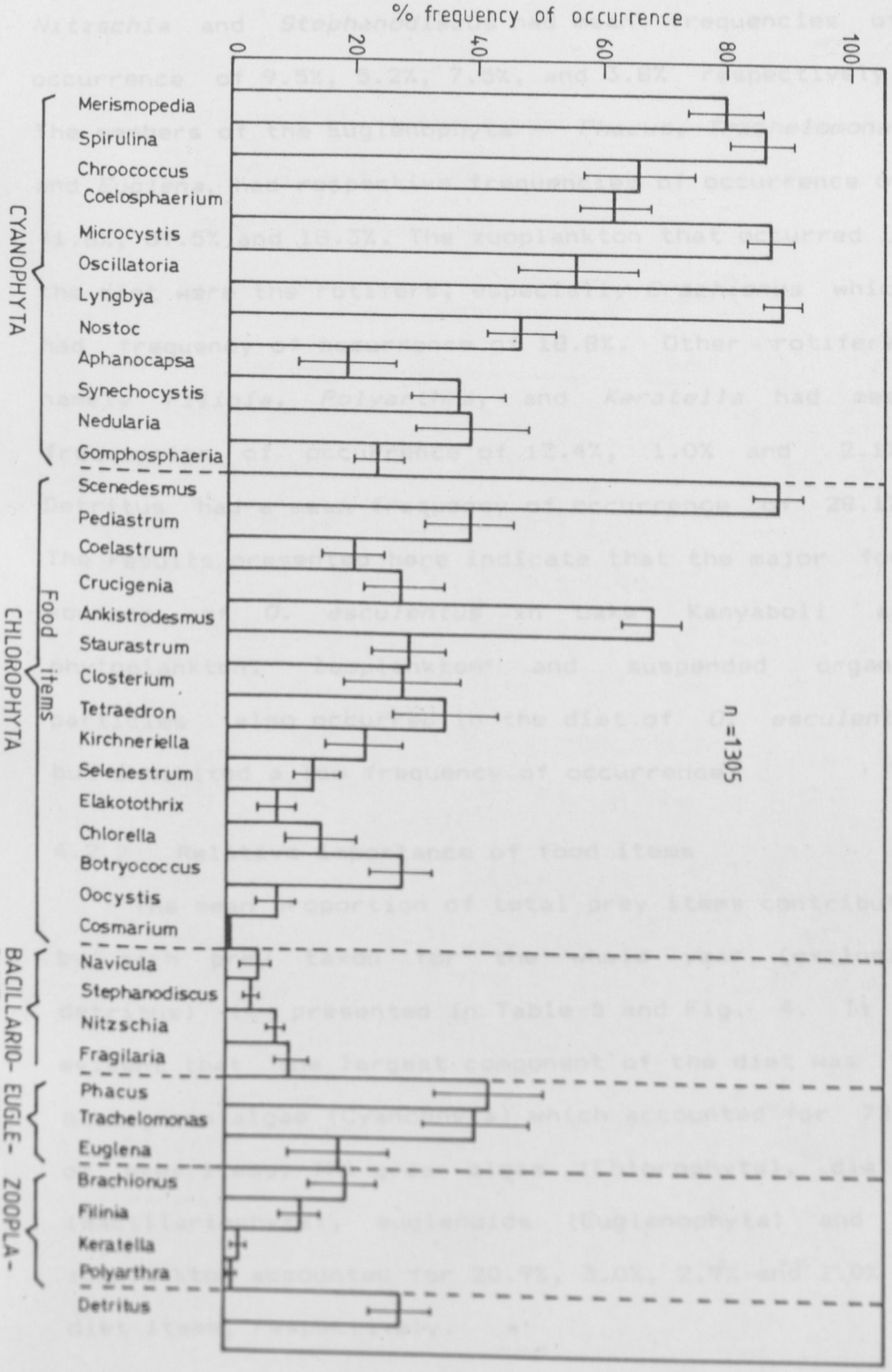
Food item	Mean frequency of occurrence (%)
CYANOPHYTA	
Merismopedia	80.33 ± 11.73
Spirulina	86.08 ± 8.60
Chroococcus	66.42 ± 18.53
Coelosphaerium	62.08 ± 10.97
Microcystis	86.92 ± 6.52
Oscillatoria	55.67 ± 18.73
Lyngbya	88.58 ± 6.24
Nostoc	46.67 ± 11.30
Aphanocapsa	19.42 ± 17.92
Synechocystis	36.75 ± 15.40
Nodularia	38.58 ± 17.95
Gomphosphaeria	23.56 ± 7.95
CHLOROPHYTA	
Scenedesmus	87.58 ± 6.49
Pediastrum	38.58 ± 13.89
Coelastrum	19.92 ± 9.76
Crucigenia	28.25 ± 14.19
Ankistrodesmus	67.92 ± 8.99
Staurastrum	28.50 ± 11.77
Closterium	27.75 ± 19.39
Tetraedron	35.42 ± 16.82
Kirchneriella	21.50 ± 11.67
Selenestrum	14.08 ± 7.24
Elakotothrix	8.00 ± 6.15
Chlorella	14.83 ± 10.89
Botryoccoccus	27.50 ± 9.59
Oocystis	8.33 ± 6.12
Cosmarium	0.42 ± 0.90
BACILLARIOPHYTA	
Navicula	5.17 ± 4.35
Stephanodiscus	3.75 ± 1.66
Nitzschia	7.50 ± 7.10
Fragilaria	9.50 ± 4.60
EUGLENOPHYTA	
Phacus	41.58 ± 17.13
Trachelomonas	39.50 ± 17.10
Euglena	18.33 ± 15.52
ZOOPLANKTON	
Brachionus	18.75 ± 13.02
Filinia	12.37 ± 5.83
Keratella	2.14 ± 2.48
Polyarthra	1.03 ± 1.56
Detritus	28.08 ± 10.08

Note: The number of fish studied = 1305

± indicate standard deviations

Fig. 3 Mean percentage frequency of occurrence of different food items from September 1989 to August 1990.

Vertical bars indicate standard deviations.


% frequency of occurrence
0
20
40
60
80
100
CYANOPHYTA
Merismopedia
Spirulina
Chroococcus
Coelosphaerium
Microcystis
Oscillatoria
Lyngbya
Nostoc
Aphanocapsa
Synechocystis
Nedularia
Gomphosphaeria
CHLOROPHYTA
Scenedesmus
Pediastrum
Coelastrum
Crucigenia
Ankistrodesmus
Staurastrum
Closterium
Tetraedron
Kirchneriella
Selenestrum
Elakotothrix
Chlorella
Botryococcus
Oocystis
Cosmarium
BACILLARIO-PHYTA
Navicula
Stephanodiscus
Nitzschia
Fragilaria
EUGLE-NOPHYTA
Phacus
Trachelomonas
Euglena
ZOOPLA-NKTON
Brachionus
Filinia
Keratella
Polyarthra
Detritus
Food items
n =1305

Nitzschia and *Stephanodiscus* had mean frequencies of occurrence of 9.5%, 5.2%, 7.5%, and 3.8% respectively. The members of the Euglenophyta - *Phacus*, *Trachelomonas* and *Euglena*, had respective frequencies of occurrence of 41.6%, 39.5% and 18.3%. The zooplankton that occurred in the diet were the rotifers, especially *Brachionus* which had frequency of occurrence of 18.8%. Other rotifers, namely *Filinia*, *Polyarthra*, and *Keratella* had mean frequencies of occurrence of 12.4%, 1.0% and 2.1%. Detritus had a mean frequency of occurrence of 28.1%. The results presented here indicate that the major food sources of *O. esculentus* in Lake Kanyaboli are phytoplankton. Zooplankton and suspended organic particles also occurred in the diet of *O. esculentus* but exhibited a low frequency of occurrence.

4.2.2 Relative importance of food items

The mean proportion of total prey items contributed by each prey taxon for the whole year (excluding detritus) is presented in Table 5 and Fig. 4. It is evident that the largest component of the diet was the blue-green algae (Cyanophyta) which accounted for 72.3% of prey items. The green algae (Chlorophyta), diatoms (Bacillariophyta), euglenoids (Euglenophyta) and the zooplankton accounted for 20.9%, 3.0%, 2.9% and 1.0% of diet items, respectively.

Table 5. Mean relative abundance (%) of the major food groups in the gut of *O. esculentus* over the study period.

Food type	Abundance (%)
Cyanophyta	72.29 ± 3.34
Chlorophyta	20.86 ± 2.29
Bacillariophyta	3.04 ± 1.25
Euglenophyta	2.93 ± 0.95
Zooplankton	1.04 ± 0.41

Note: The number of fish examined = 1305

± indicate standard deviations

Fig. 4 Mean relative abundance of major food types in the stomach of *O. esculentus* from September 1989 to August 1990.

Vertical bars indicate standard deviations.

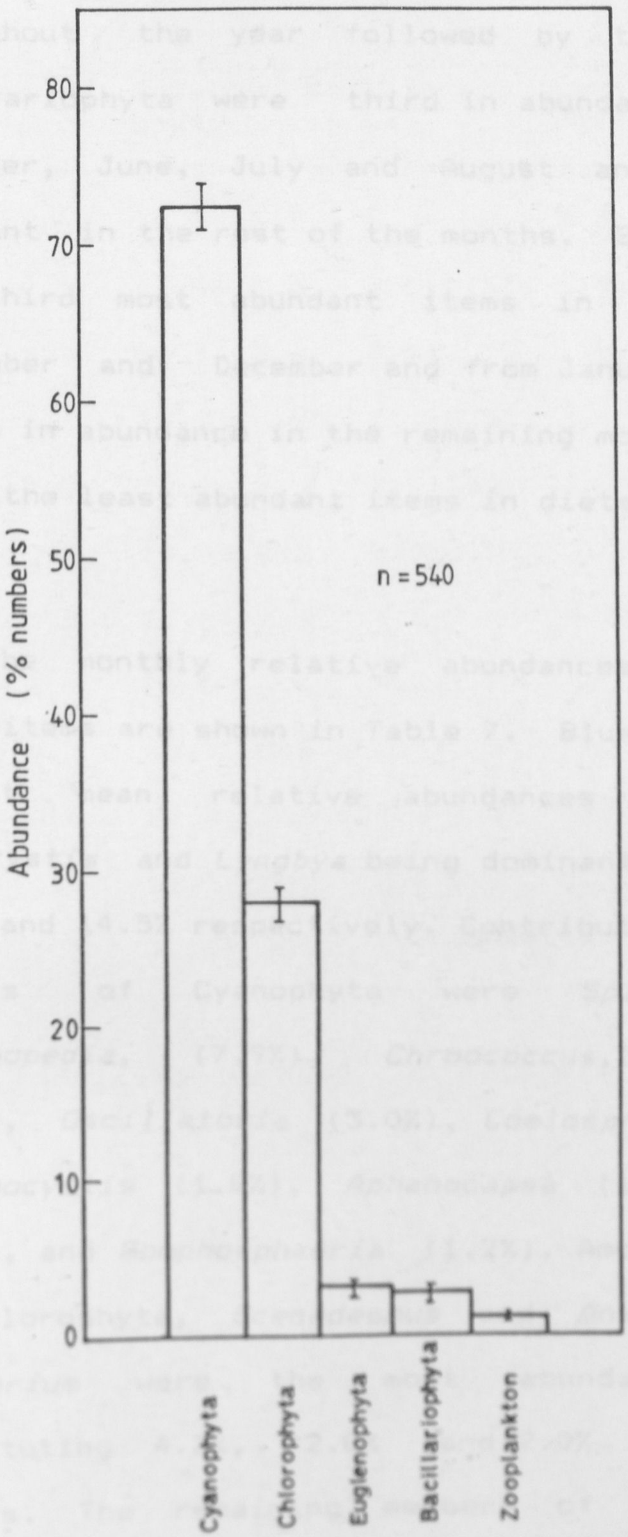

Abundance (% numbers)
80
70
60
50
40
30
20
10
0
n = 540
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
Food type

Table 6 and Fig. 5 depict monthly variations in the relative abundance of major components of the diet. It is clear that the Cyanophyta dominated the diet throughout the year followed by the Chlorophyta. Bacillariophyta were third in abundance in October, November, June, July and August and fourth most abundant in the rest of the months. Euglenophyta were the third most abundant items in the diet during September and December and from January to May but fourth in abundance in the remaining months. Zooplankton were the least abundant items in diets throughout the year.

The monthly relative abundances of individual diet items are shown in Table 7. Blue-green algae had highest mean relative abundances in diets, with *Microcystis* and *Lyngbya* being dominant, accounting for 19.7% and 14.5% respectively. Contributions by the other members of Cyanophyta were *Spirulina* (8.6%), *Merismopedia*, (7.9%), *Chroococcus*,(6.2%), *Nostoc*, (3.8%), *Oscillatoria* (3.0%), *Coelosphaerium* (2.8%), *Synechocystis* (1.8%), *Aphanocapsa* (1.3%), *Nodularia* (1.3%), and *Gomphosphaeria* (1.2%). Amongst the members of Chlorophyta, *Scenedesmus* and *Ankistrodesmus* and *Closterium* were the most abundant diet items constituting 4.3%, 2.8% and 2.0% of the diet by numbers. The remaining members of the Chlorophyta

Table 6. Monthly relative abundance (%) of the major food groups in the diet of *O. esculentus*.

Month	Cyanophyta	Chlorophyta	Bacillariophyta	Euglenophyta	Zooplankton
S	73.9±11.6	20.8± 4.5	1.8±1.1	2.3±1.2	1.2±0.3
O	75.1± 9.3	18.9± 3.3	3.3±1.3	1.9±0.7	0.8±0.5
N	73.4±15.9	20.1± 3.6	3.9±0.7	1.8±1.0	0.8±0.3
D	69.2± 3.6	24.9±10.7	2.4±0.3	2.7±0.6	0.8±0.2
J	70.2± 7.8	21.4± 8.6	3.2±1.2	3.8±0.7	1.4±0.4
F	76.0±10.2	19.4± 8.2	0.5±0.2	3.3±1.1	0.8±0.2
M	68.9±11.9	21.6± 7.3	3.8±0.9	4.8±1.5	0.9±0.6
A	66.9± 6.9	24.8± 4.1	3.2±1.0	4.3±1.9	0.8±0.3
M	76.0± 9.3	18.7± 3.6	2.3±0.5	2.4±0.5	0.6±0.1
J	76.1± 6.8	17.2± 7.0	3.5±1.5	2.3±0.7	0.9±0.2
J	67.9±13.1	21.5± 5.5	5.6±2.3	3.0±0.2	2.0±0.4
A	72.0±15.5	21.0± 6.3	3.0±1.1	2.5±0.8	1.5±0.3

Note: ± indicate standard deviations.

Fig. 5 Monthly variation in the relative abundance of the major food types in the diet of *O. esculentus*

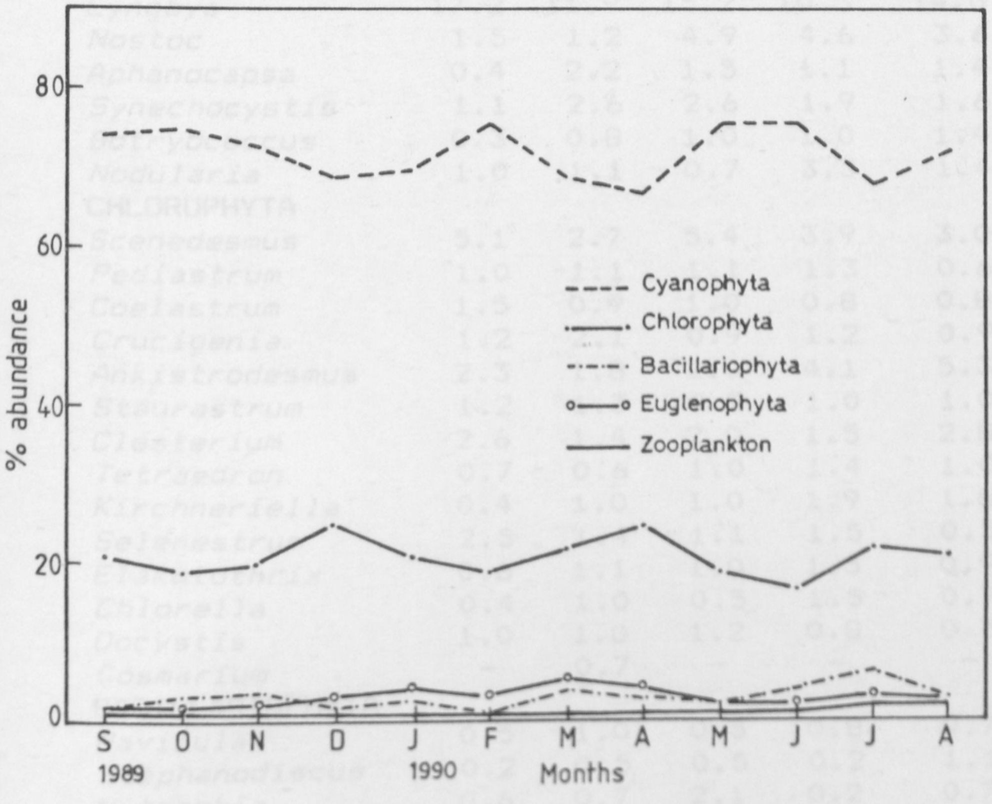

% abundance
80
60
40
20
0
Cyanophyta
Chlorophyta
Bacillariophyta
Euglenophyta
Zooplankton
S
O
N
D
J
F
M
A
M
J
J
A
1989
1990
Months

Table 7. Monthly relative abundance (numbers) of individual food items in the gut of *O. esculentus*

FOOD TYPE	Sept	Oct	Nov	Dec	Jan	Feb
CYANOPHYTA						
Merismopedia	11.7	7.7	2.8	7.7	11.1	11.0
Spirulina	12.2	4.8	8.7	7.7	8.4	12.3
Chroococcus	6.0	10.0	7.8	7.4	3.9	4.4
Coelosphaerium	2.9	2.9	2.6	2.7	3.7	1.4
Microcystis	16.1	26.5	23.4	19.2	13.4	9.8
Oscillatoria	2.4	1.3	0.6	1.6	2.1	0.3
Lyngbya	17.2	11.9	15.2	10.3	14.0	23.5
Nostoc	1.5	1.2	4.9	4.6	3.6	3.5
Aphanocapsa	0.4	2.2	1.5	1.1	1.4	1.6
Synechocystis	1.1	2.6	2.6	1.9	1.6	2.7
Botryococcus	0.3	0.8	1.0	1.0	1.4	0.8
Nodularia	1.0	1.1	0.7	3.3	1.4	0.8
CHLOROPHYTA						
Scenedesmus	5.1	2.7	5.4	3.9	3.0	4.7
Pediastrum	1.0	1.1	1.1	1.3	0.6	0.8
Coelastrum	1.5	0.9	1.0	0.8	0.8	1.6
Crucigenia	1.2	2.1	0.9	1.2	0.9	1.3
Ankistrodesmus	2.3	1.8	2.0	4.1	5.3	2.0
Staurastrum	1.2	1.3	0.9	1.0	1.0	1.3
Closterium	2.6	1.4	2.0	1.5	2.8	0.8
Tetraedron	0.7	0.6	1.0	1.4	1.0	0.8
Kirchneriella	0.4	1.0	1.0	1.9	1.8	1.7
Selenestrum	2.5	1.4	1.1	1.5	0.5	2.5
Elakotothrix	0.6	1.1	1.0	1.5	0.9	1.1
Chlorella	0.4	1.0	0.5	1.5	0.7	0.8
Oocystis	1.0	1.0	1.2	0.8	0.7	-
Cosmarium	-	0.7	-	-	-	-
BACILLARIOPHYTA						
Navicula	0.5	1.0	0.5	0.8	0.7	-
Stephanodiscus	0.2	0.5	0.5	0.2	1.1	0.2
Nitzschia	0.6	0.7	2.1	0.2	0.7	0.3
Fragilaria	0.5	1.1	0.8	1.2	0.7	-
EUGLENOPHYTA						
Phacus	1.0	1.2	0.7	1.0	1.1	1.0
Trachelomonas	0.6	0.6	0.7	1.9	1.3	1.5
Euglena	0.7	0.1	0.4	0.8	1.4	0.8
ZOOPLANKTON						
Brachionus	0.4	0.8	0.6	0.8	0.7	0.8
Filinia	0.8	-	0.2	-	0.7	-

Table 7 (cont.)

FOOD TYPE	Mar	Apr	May	Jun	Jul	Aug	Mean
CYANOPHYTA							
Merismopedia	11.1	6.7	3.7	7.4	10.2	3.5	7.9
Spirulina	7.2	8.9	9.0	5.1	9.8	9.4	8.6
Chroococcus	4.3	3.6	5.8	6.6	6.1	9.0	6.2
Coelosphaerium	1.8	1.6	2.6	5.4	2.7	3.0	2.8
Microcystis	16.2	15.2	25.9	30.9	18.6	22.3	19.8
Oscillatoria	3.4	3.0	2.2	2.5	2.9	1.4	2.0
Lyngbya	14.6	16.2	14.8	11.6	11.5	13.1	14.5
Nostoc	5.4	6.6	5.7	1.7	2.0	4.8	3.8
Aphanocapsa	1.2	1.3	2.1	0.9	0.8	1.4	1.3
Synechocystis	1.7	1.1	1.3	2.7	1.2	1.2	1.8
Botryococcus	0.8	0.8	1.0	0.8	1.2	1.1	0.9
Nodularia	1.1	1.1	1.8	0.9	0.8	1.8	1.3
CHLOROPHYTA							
Scenedesmus	3.9	4.8	4.5	3.4	5.2	4.7	4.3
Pediastrum	1.1	1.3	1.2	0.9	1.0	1.1	1.0
Coelastrum	0.8	1.2	1.1	0.8	0.9	1.0	1.0
Crucigenia	1.2	1.6	1.0	1.4	1.1	1.2	1.3
Ankistrodesmus	2.5	4.3	2.2	1.8	2.7	2.2	2.8
Staurastrum	1.0	1.1	1.0	0.9	1.2	1.7	1.1
Closterium	1.9	2.6	1.8	1.4	2.3	2.4	2.0
Tetraedron	1.2	1.2	1.2	0.6	1.1	0.7	1.0
Kirchneriella	1.6	0.8	1.6	0.9	1.0	1.1	1.2
Selenestrum	1.1	1.6	1.2	0.8	0.8	1.1	1.3
Elakotothrix	1.2	1.9	0.8	0.8	1.0	1.4	1.1
Chlorella	0.8	0.8	0.3	1.2	1.2	0.9	1.0
Oocystis	1.0	0.8	-	0.8	0.8	1.4	0.8
Cosmarium	1.1	-	-	0.7	-	-	0.2
BACILLARIOPHYTA							
Navicula	1.0	1.0	-	0.9	1.1	0.7	0.7
Stephanodiscus	1.2	0.3	1.0	0.8	1.2	0.9	0.7
Nitzschia	0.8	1.1	1.3	0.7	1.7	0.7	0.9
Fragilaria	0.8	0.8	-	1.1	1.6	0.7	0.8
EUGLENOPHYTA							
Phacus	1.1	1.4	1.2	1.1	1.1	0.8	1.1
Trachelomonas	2.1	2.1	1.2	1.2	1.1	0.9	1.3
Euglena	1.1	0.8	-	-	0.8	0.8	0.6
ZOOPLANKTON							
Brachionus	0.9	0.8	0.6	0.9	1.1	0.7	0.8
Filinia	-	-	-	-	0.9	0.8	0.3

numerically constituted less than 2.0% of the diet. The members of the zooplankton and Bacillariophyta accounted for less than 1% of the diet. The mean relative abundances of members of Euglenophyta i.e. *Phacus*, *Trachelomonas* and *Euglena* were 1.1%, 1.3% and 0.6% respectively. There were monthly variations in the proportion of each food item in the diet. *Polyarthra* and *Keratella* occurred in insignificant quantities.

4.2.3 Seasonal changes in the diet composition

There was some monthly variation in the proportions of *O. esculentus* that fed on various food items, but diet composition was remarkably stable (Table 8).

4.2.4 Diet in relation to size of *O. esculentus*

O. esculentus in Lake Kanyaboli fed principally on phytoplankton and also on zooplankton and detritus regardless of size differences. The percentage frequency of occurrence of different food items in 691 juveniles and 354 adults is illustrated in Table 9 and Fig. 6. From these results it is apparent that the food items that frequently occur in the stomachs of the adults such as *Microcystis*, *Merismopedia*, *Lyngbya*, *Spirulina*, *Coelosphaerium*, *Chroococcus*, *Oscillatoria*, *Scenedesmus* and *Ankistrodesmus* are the same ones that frequently occur in the stomachs of the juveniles. Some food items occurred in greater proportion in the juveniles than in

Table 8. Monthly percentage frequency of occurrence of different food items in the stomach of *O. esculentus*.

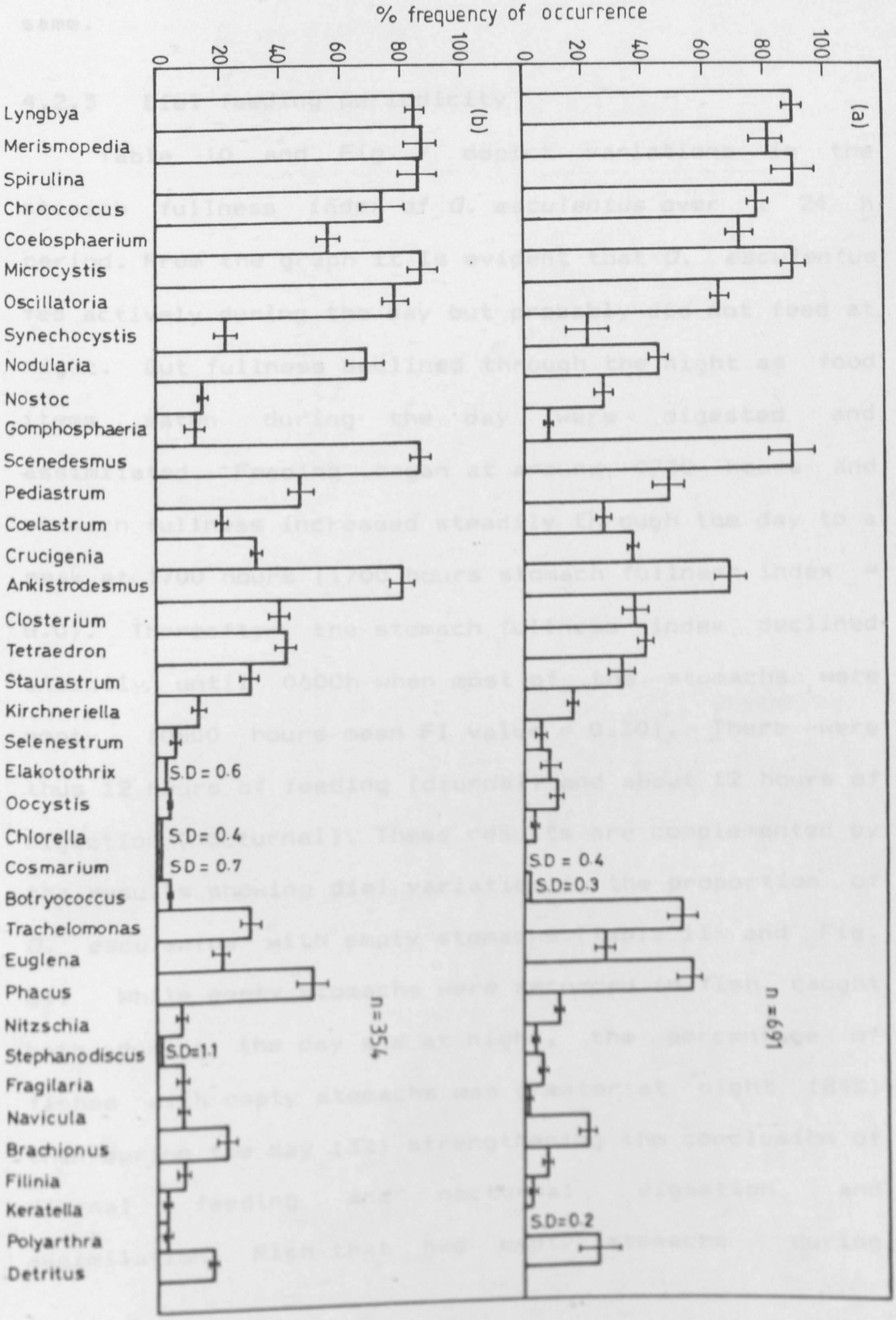
Food item	Monthly percentage frequency of occurrence											
	S	O	N	D	J	F	M	A	M	J	J	A
CYANOPHYTA												
Merismopedia	86	73	90	82	90	81	72	68	53	89	88	92
Spirulina	79	70	88	89	94	86	96	86	71	89	90	95
Chroococcus	46	27	67	57	65	66	78	54	74	88	85	90
Coelosphaerium	54	46	63	61	57	47	66	62	71	87	67	64
Microcystis	89	73	85	88	90	90	96	85	77	94	86	90
Oscillatoria	41	33	44	42	59	60	62	31	54	68	85	89
Lyngbya	86	79	85	85	95	93	96	82	95	97	83	87
Nostoc	65	67	58	73	72	49	56	32	39	25	22	12
Aphanocapsa	2	14	23	8	39	44	8	61	14	9	4	7
Synechocystis	27	48	57	32	66	43	19	13	32	35	43	26
Nodularia	29	42	31	42	36	20	15	30	58	31	47	82
Gomphosphaeria	11	7	17	3	6	23	5	14	1	5	19	26
CHLOROPHYTA												
Scenedesmus	87	76	88	75	94	89	84	90	91	94	88	95
Pediastrum	44	30	42	22	17	34	46	48	21	43	55	61
Coelastrum	7	12	23	19	23	23	28	38	16	14	31	5
Crucigenia	15	6	28	19	13	19	36	39	29	36	50	49
Ankisrodesmus	69	55	60	68	74	58	64	63	66	75	76	87
Staurastrum	26	18	35	15	25	22	40	33	17	18	40	53
Closterium	15	6	15	7	26	22	14	37	24	44	66	57
Tetraedron	31	21	42	18	14	25	44	53	35	22	50	70
Kirchneriella	36	12	34	31	34	10	34	8	12	25	10	12
Selenestrum	11	16	4	21	7	19	6	16	22	27	12	8
Elakotothrix	12	16	9	1	15	2	7	5	3	5	19	2
Chlorella	14	17	21	5	15	13	24	43	8	6	5	7
Botryococcus	3	5	12	19	29	43	29	64	37	16	16	57
Oocystis	2	5	4	3	2	7	11	20	19	8	12	7
Cosmarium	0	1	0	0	0	0	0	0	0	3	0	12
BACILLARIOPHYTA												
Navicula	4	3	7	7	1	6	3	2	1	4	17	7
Stephanodiscus	4	6	2	6	4	5	2	3	6	2	3	2
Nitzschia	11	3	5	1	1	3	10	1	2	14	19	20
Fragilaria	2	5	12	7	15	16	8	4	11	15	7	2
EUGLENOPHYTA												
Phacus	29	18	46	26	41	67	56	62	14	37	52	51
Trachelomonas	43	18	22	24	45	62	64	61	24	29	52	30
Euglena	15	6	15	13	16	49	36	9	1	9	43	8
ZOOPLANKTON												
Brachionus	24	18	22	10	3	23	8	8	11	18	52	28
Filinia	4	1	8	3	1	4	0	0	0	5	50	13
Keratella	0	0	0	2	0	1	0	2	0	0	0	2
Polyarthra	0	0	1	0	3	2	0	0	0	0	4	1
Detritus	33	36	27	25	21	29	54	35	29	21	21	16
Sample size	80	88	80	151	167	110	83	82	73	145	124	83

Table 9. The percentage frequency of occurrence of individual food items in juvenile (<70 mm SL) and adult (>70 mm SL) *O. esculentus*.

	% Frequency of occurrence	
Food item	Juveniles	adults
Detritus	25.2 ± 7.3	17.9 ± 2.7
CYANOPHYTA		
Lyngbya	91.2 ± 11.2	84.6 ± 6.3
Merismopedia	82.9 ± 15.0	87.2 ± 9.8
Spirulina	89.7 ± 6.3	85.9 ± 11.7
Chroococcus	76.8 ± 12.2	74.4 ± 13.8
Coelosphaerium	66.3 ± 8.2	56.4 ± 7.7
Microcystis	89.2 ± 4.7	87.2 ± 10.3
Oscillatoria	65.0 ± 13.1	78.2 ± 6.7
Synechocystis	22.7 ± 4.1	23.1 ± 5.9
Nodularia	44.6 ± 6.9	69.2 ± 12.3
Nostoc	27.0 ± 6.6	15.2 ± 4.7
Gomphosphaeria	8.6 ± 2.1	12.8 ± 6.1
CHLOROPHYTA		
Scenedesmus	89.4 ± 13.4	85.9 ± 6.9
Pediastrum	47.6 ± 10.5	47.4 ± 7.5
Coelastrum	27.2 ± 5.3	20.5 ± 4.3
Crucigenia	36.3 ± 4.9	33.3 ± 3.0
Ankistrodesmus	67.8 ± 13.3	79.5 ± 7.9
Closterium	37.3 ± 8.0	39.7 ± 5.4
Tetraedron	39.8 ± 3.7	42.3 ± 7.1
Staurastrum	31.5 ± 7.7	30.8 ± 5.6
Kirchneriella	16.4 ± 5.3	12.8 ± 4.1
Selenestrum	6.1 ± 1.7	6.4 ± 2.3
Elakotothrix	8.8 ± 2.6	2.6 ± 0.6
Oocystis	10.8 ± 4.1	3.8 ± 1.0
Chlorella	4.3 ± 2.0	1.3 ± 0.4
Cosmarium	1.3 ± 0.4	1.1 ± 0.7
Botryococcus	2.0 ± 0.3	3.9 ± 0.9
EUGLENOPHYTA		
Trachelomonas	51.9 ± 10.2	30.8 ± 4.7
Euglena	27.2 ± 5.5	20.5 ± 5.8
Phacus	54.7 ± 9.4	51.3 ± 10.3
BACILLARIOPHYTA		
Nitzschia	11.8 ± 2.3	7.7 ± 2.3
Stephanodiscus	3.8 ± 0.4	1.3 ± 1.1
Fragilaria	6.1 ± 2.1	7.7 ± 4.2
Navicula	4.0 ± 1.4	7.7 ± 1.9
ZOOPLANKTON		
Brachionus	20.7 ± 5.3	23.1 ± 6.6
Filinia	8.1 ± 3.1	9.0 ± 3.2
Keratella	3.2 ± 0.6	2.6 ± 1.4
Polyarthra	1.1 ± 0.2	3.1 ± 1.0
Total number of stomachs examined	897	455

Note: ± indicate standard deviations

Fig. 6 Mean percentage frequency of occurrence of different food items in the juveniles (a) and adults (b) of *O. esculentus*. Vertical bars indicate standard deviations.


% frequency of occurrence
0
20
40
60
80
100
(a)
(b)
Lyngbya
Merismopedia
Spirulina
Chroococcus
Coelosphaerium
Microcystis
Oscillatoria
Synechocystis
Nodularia
Nostoc
Gomphosphaeria
Scenedesmus
Pediastrum
Coelastrum
Crucigenia
Ankistrodesmus
Closterium
Tetraedron
Staurastrum
Kirchneriella
Selenestrum
Elakotothrix
Oocystis
Chlorella
Cosmarium
Botryococcus
Trachelomonas
Euglena
Phacus
Nitzschia
Stephanodiscus
Fragilaria
Navicula
Brachionus
Filinia
Keratella
Polyarthra
Detritus
S.D = 0.6
S.D = 0.4
S.D = 0.7
S.D=1.1
n=354
S.D = 0.4
S.D=0.3
S.D=0.2
n=691

the adults and vice versa. On the whole, however, the dietary composition of juveniles and adults was the same.

4.2.5 Diel feeding periodicity

Table 10 and Fig. 7 depict variations in the stomach fullness index of *O. esculentus* over a 24 h period. From the graph it is evident that *O. esculentus* fed actively during the day but probably did not feed at night. Gut fullness declined through the night as food items eaten during the day were digested and assimilated. Feeding began at around 0700 hours and stomach fullness increased steadily through the day to a peak at 1700 hours (1700 hours stomach fullness index = 8.0). Thereafter the stomach fullness index declined steadily until 0600h when most of the stomachs were empty, (0600 hours mean FI value = 0.30). There were thus 12 hours of feeding (diurnal) and about 12 hours of digestion (nocturnal). These results are complemented by the results showing diel variation in the proportion of *O. esculentus* with empty stomachs (Table 11 and Fig. 8). While empty stomachs were recorded in fish caught both during the day and at night, the percentage of fishes with empty stomachs was greater at night (84%) than during the day (3%) strengthening the conclusion of diurnal feeding and nocturnal digestion and assimilation. Fish that had empty stomachs during

Table 10. Diel variation in fullness index of *O. esculentus*.

Time	No. of fish examined	Mean fullness index
1900	12	6.67 ± 2.56
2000	26	4.82 ± 2.13
2100	14	5.68 ± 1.58
2200	23	5.66 ± 2.20
2300	14	4.91 ± 2.72
2400	18	3.40 ± 2.59
0100	12	3.59 ± 2.40
0200	19	2.43 ± 3.08
0300	13	3.28 ± 2.04
0400	16	1.76 ± 1.93
0500	15	0.97 ± 1.42
0600	19	0.30 ± 0.64
0700	17	0.68 ± 0.67
0800	15	2.59 ± 1.66
0900	19	3.51 ± 2.00
1000	17	3.07 ± 1.21
1100	37	4.46 ± 1.59
1200	18	4.34 ± 2.00
1300	11	4.60 ± 1.91
1400	21	5.87 ± 1.04
1500	14	7.06 ± 1.50
1600	14	6.95 ± 1.54
1700	13	8.02 ± 2.11
1800	22	7.61 ± 1.66

Note: ± indicate standard deviation

Fig. 7 Diel feeding periodicity of *O. esculentus*. Vertical bars indicate standard deviations.

Figures in parentheses indicate sample size.

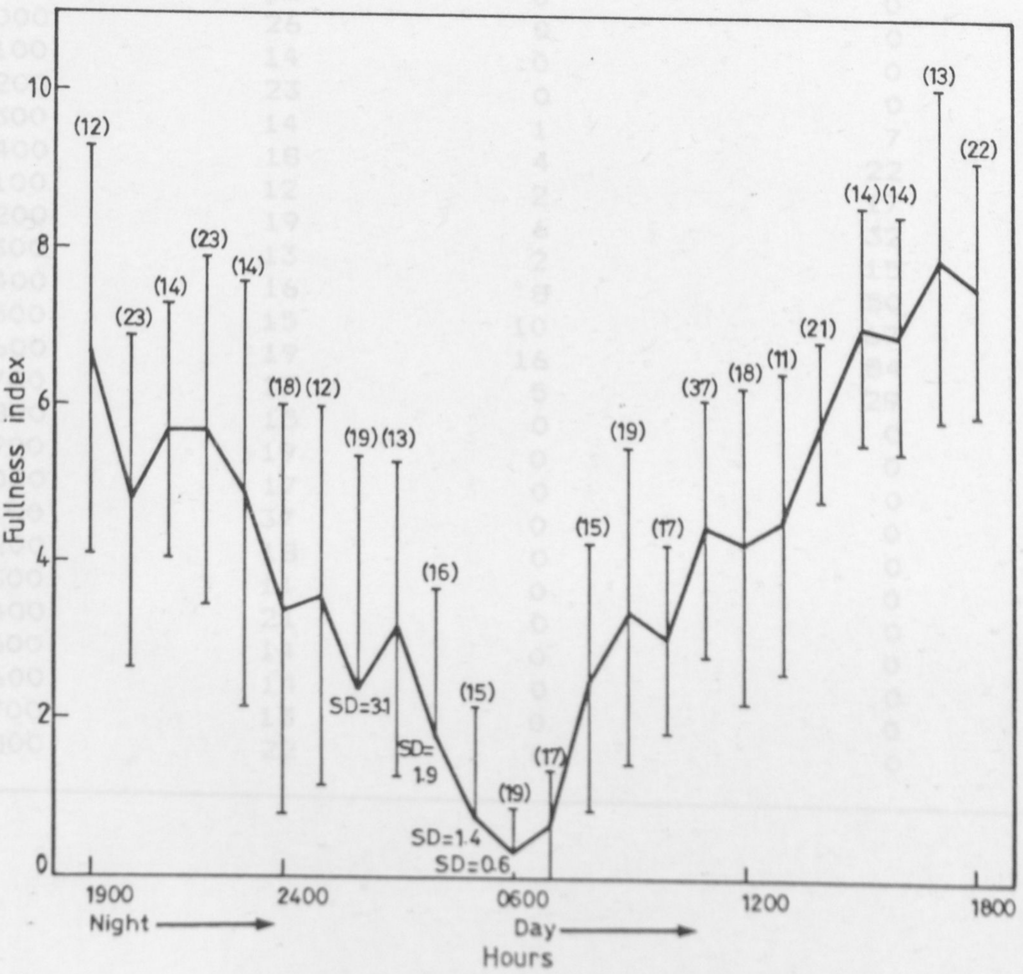
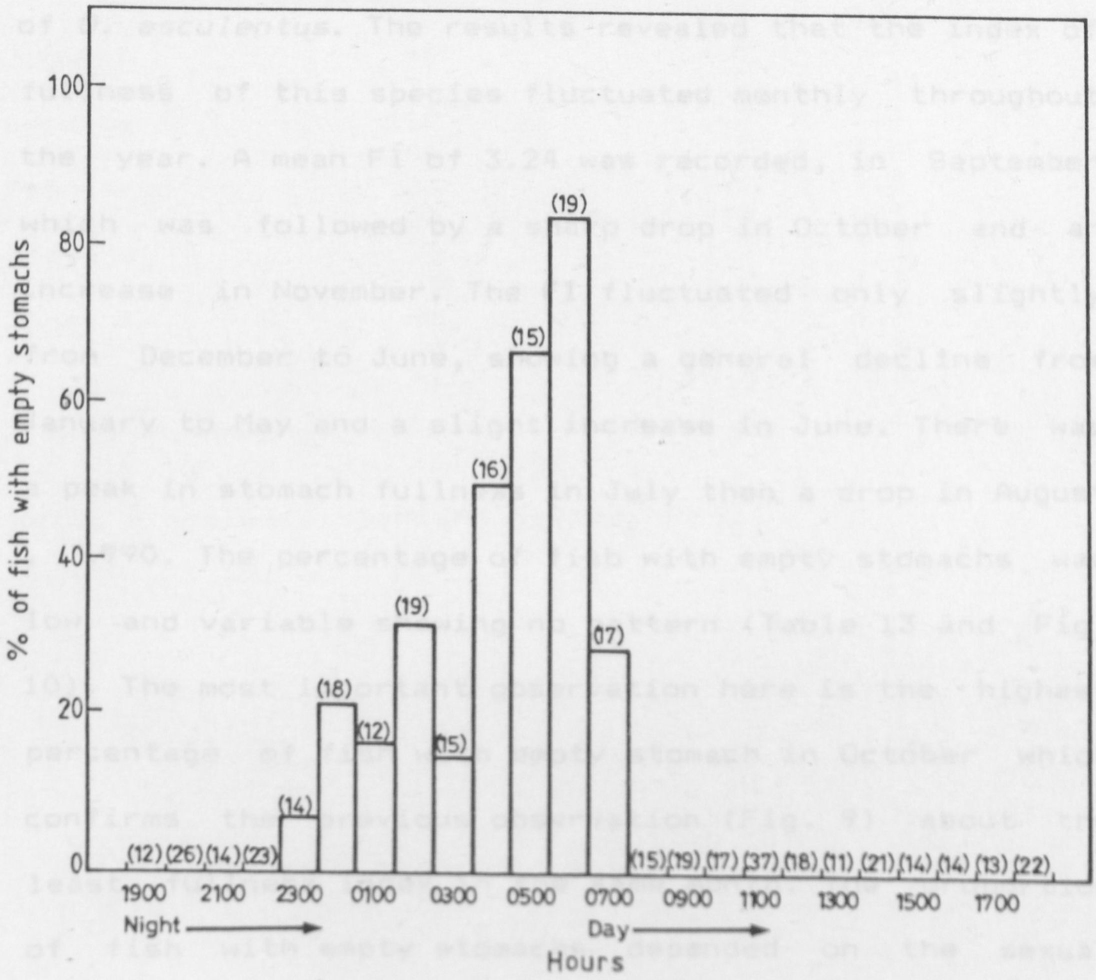

Fullness index
10
8
6
4
2
0
(12)
(23)
(14)
(23)
(14)
(18)
(12)
(19)
(13)
SD=3.1
(16)
SD=1.9
(15)
SD=1.4
(19)
SD=0.6
(17)
(15)
(19)
(17)
(37)
(18)
(11)
(21)
(14)
(14)
(13)
(22)
1900
2400
0600
1200
1800
Night
Day
Hours

Table 11. Diel changes in the number and percentage of *O. esculentus* with empty stomachs.

Time	No fish examined	No fish with empty stomachs	% number of fish with empty stomachs
1900	12	0	0
2000	26	0	0
2100	14	0	0
2200	23	0	0
2300	14	1	7
2400	18	4	22
0100	12	2	17
0200	19	6	32
0300	13	2	15
0400	16	8	50
0500	15	10	67
0600	19	16	84
0700	17	5	29
0800	15	0	0
0900	19	0	0
1000	17	0	0
1100	37	0	0
1200	18	0	0
1300	11	0	0
1400	21	0	0
1500	14	0	0
1600	14	0	0
1700	13	0	0
1800	22	0	0

Fig. 8 Diel variation in the percentage of *O. esculentus* with empty stomachs. Figures in parentheses indicate sample of fish examined.


% of fish with empty stomachs
0
20
40
60
80
100
(12)
(26)
(14)
(23)
(14)
(18)
(12)
(19)
(15)
(16)
(15)
(19)
(17)
(15)
(19)
(17)
(37)
(18)
(11)
(21)
(14)
(14)
(13)
(22)
1900
2100
2300
0100
0300
0500
0700
0900
1100
1300
1500
1700
Night
Day
Hours

the day were mainly the mouth-brooding females.

4.2.6 Monthly variation in feeding activity

The index of stomach fullness and the percentage of fishes with empty stomachs were evaluated monthly. Table 12 and Fig. 9 depict monthly indices of fullness of *O. esculentus*. The results revealed that the index of fullness of this species fluctuated monthly throughout the year. A mean FI of 3.24 was recorded, in September which was followed by a sharp drop in October and an increase in November. The FI fluctuated only slightly from December to June, showing a general decline from January to May and a slight increase in June. There was a peak in stomach fullness in July then a drop in August , 1990. The percentage of fish with empty stomachs was low and variable showing no pattern (Table 13 and Fig. 10). The most important observation here is the highest percentage of fish with empty stomach in October which confirms the previous observation (Fig. 9) about the least fullness index in the same month. The proportion of fish with empty stomachs depended on the sexual state of female fishes, because mouth-brooding females had empty stomachs. This investigation provides further evidence that female *O. esculentus* brood the eggs and fry, and do not feed during the brooding period. Males and non-brooding females fed throughout the year.

Table 12. Mean monthly fullness index of *O. esculentus*

Month	No of stomachs examined	Fullness index
September	73	3.2 ± 0.4
October	46	2.0 ± 1.3
November	131	3.4 ± 0.5
December	119	3.3 ± 0.3
January	144	4.2 ± 2.5
February	84	3.9 ± 1.8
March	24	3.3 ± 0.7
April	76	3.1 ± 1.7
May	55	2.9 ± 1.2
June	86	3.6 ± 1.4
July	90	6.0 ± 2.6
August	56	4.2 ± 2.3

Note: ± indicate standard deviations

Fig. 9 Monthly variation in the fullness index of *O. esculentus*. Vertical bars indicate standard deviations. Figures in parentheses indicate number of fish examined.

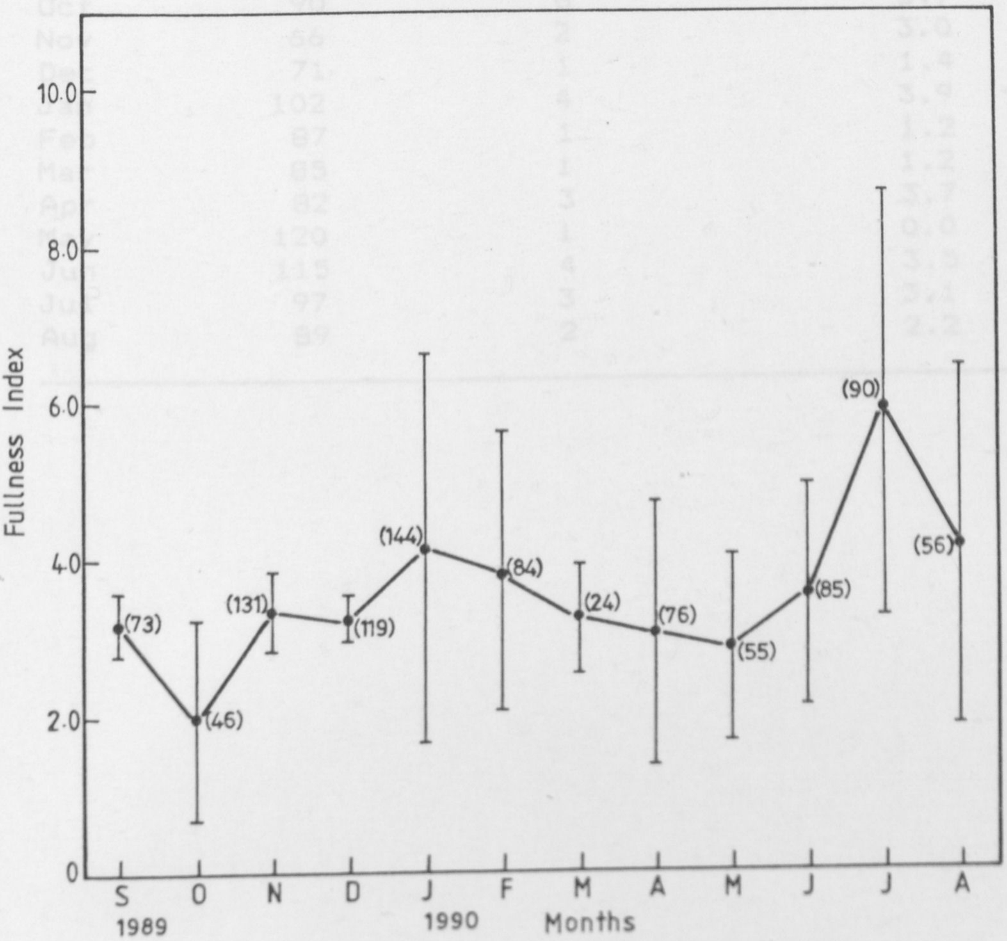
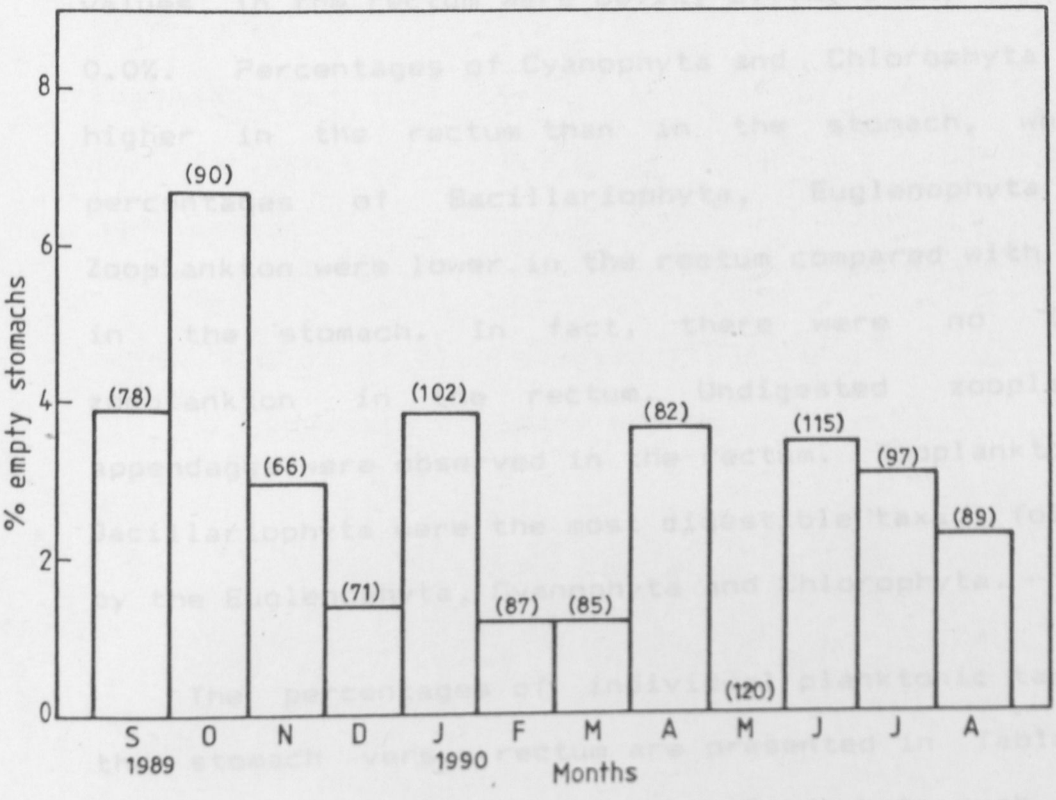

Fullness Index
10.0
8.0
6.0
4.0
2.0
0
(73)
(46)
(131)
(119)
(144)
(84)
(24)
(76)
(55)
(85)
(90)
(56)
S
O
N
D
J
F
M
A
M
J
J
A
1989
1990
Months

Table 13. Monthly variation in the percentage number *O. esculentus* with empty stomachs.

Month	No of fish examined	No of empty stomachs	% number of fish with empty stomachs
Sep	78	3	3.8
Oct	90	6	6.7
Nov	66	2	3.0
Dec	71	1	1.4
Jan	102	4	3.9
Feb	87	1	1.2
Mar	85	1	1.2
Apr	82	3	3.7
May	120	1	0.0
Jun	115	4	3.5
Jul	97	3	3.1
Aug	89	2	2.2

Fig. 10 Monthly variation in the proportion of *O. esculentus* with empty stomachs. Figures in parentheses indicate number of fish examined.


% empty stomachs
0
2
4
6
8
(78)
(90)
(66)
(71)
(102)
(87)
(85)
(82)
(120)
(115)
(97)
(89)
S
O
N
D
J
F
M
A
M
J
J
A
1989
1990
Months

4.2.7 Food digestibility

Table 14 and Fig. 11 illustrate the percentages of different food types in two regions of the gut, viz in the stomach and in the rectum. The percentages of the Cyanophyta, Chlorophyta, Bacillariophyta, Euglenophyta, and Zooplankton in the stomach were 63.2%, 26.5%, 4.4%, 4.0% and 1.9%, respectively, whereas corresponding values in the rectum were 65.2%, 29.9%, 1.6%, 3.3% and 0.0%. Percentages of Cyanophyta and Chlorophyta were higher in the rectum than in the stomach, whereas percentages of Bacillariophyta, Euglenophyta and Zooplankton were lower in the rectum compared with those in the stomach. In fact, there were no intact zooplankton in the rectum. Undigested zooplankton appendages were observed in the rectum. Zooplankton and Bacillariophyta were the most digestible taxa, followed by the Euglenophyta, Cyanophyta and Chlorophyta.

The percentages of individual planktonic taxa in the stomach versus rectum are presented in Table 15. The proportion of members of the Cyanophyta such as - *Spirulina*, *Chroococcus*, *Coelosphaerium*, *Lyngbya*, *Nostoc*, and *Nodularia* and *Gomphosphaeria* were lower in the stomach than in the rectum. *Microcystis* and *Synechocystis* occurred in the same proportion in both regions of the gut. The proportions of *Merismopedia*,

Table 14. Mean percentage number of the major food groups in the stomach and in the rectum of *O. esculentus.*

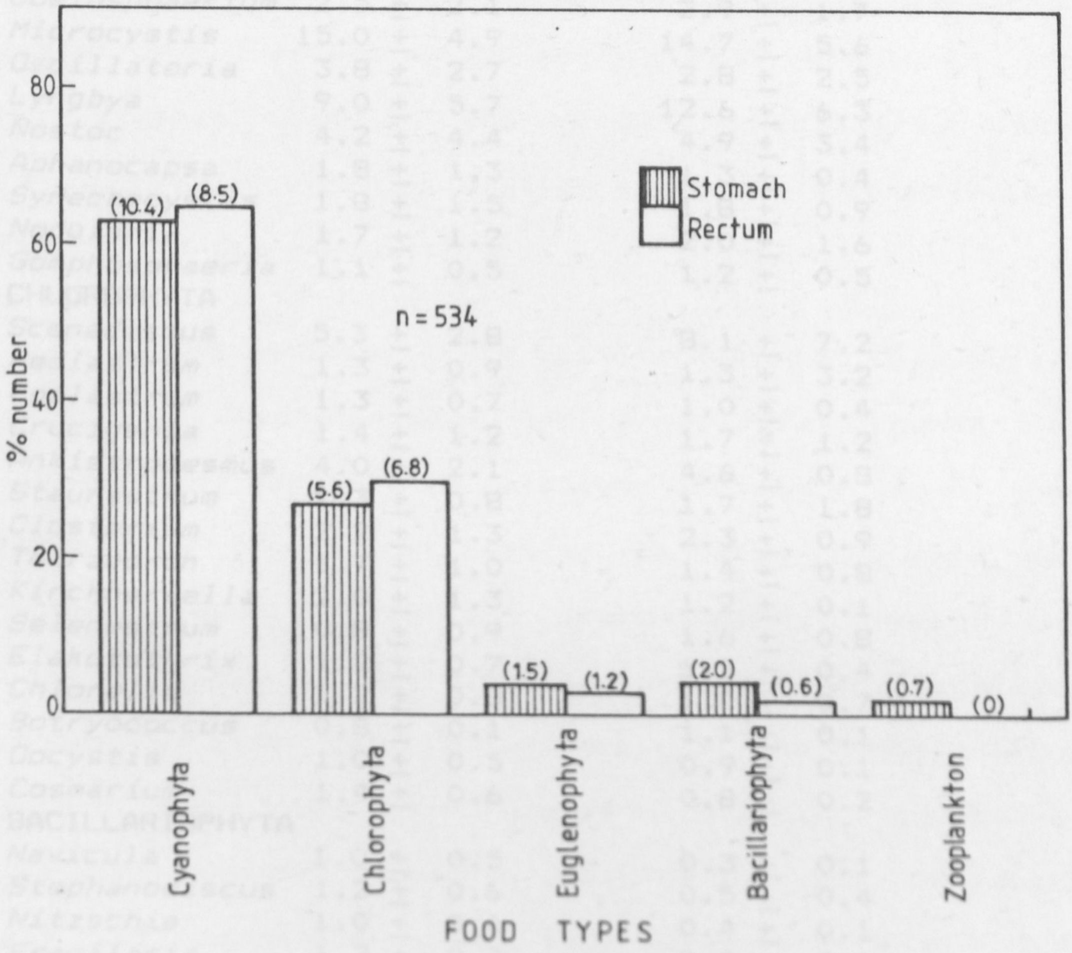
Food Type	% in stomach	% in rectum
Cyanophyta	63.2 ± 10.4	65.2 ± 8.5
Chlorophyta	26.5 ± 5.6	29.9 ± 6.8
Euglenophyta	4.0 ± 1.5	3.3 ± 1.2
Bacillariophyta	4.4 ± 2.0	1.6 ± 0.5
Zooplankton	1.9 ± 0.7	0.0 ± 0.0

Note: Number of fish studied = 534

± indicate standard deviations

Fig. 11 Mean percentage of various food items in the stomach (a) and rectum (b) of *O. esculentus*.

Figures in parentheses indicate standard deviations.



% number
0
20
40
60
80
(10.4)
(8.5)
(5.6)
(6.8)
(1.5)
(1.2)
(2.0)
(0.6)
(0.7)
(0)
Stomach
Rectum
n = 534
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
FOOD TYPES

Table 15. Percentage number of different food items in the stomach and in the rectum of *O. esculentus*.

Food item	Percentage number in stomach	Percentage number in rectum
CYANOPHYTA		
Merismopedia	10.3 ± 5.7	5.2 ± 2.2
Spirulina	8.2 ± 4.2	9.4 ± 4.3
Chroococcus	3.8 ± 2.5	6.4 ± 3.5
Coelosphaerium	2.5 ± 2.1	2.9 ± 1.7
Microcystis	15.0 ± 4.9	14.7 ± 5.6
Oscillatoria	3.8 ± 2.7	2.8 ± 2.5
Lyngbya	9.0 ± 5.7	12.6 ± 6.3
Nostoc	4.2 ± 4.4	4.9 ± 3.4
Aphanocapsa	1.8 ± 1.3	1.3 ± 0.4
Synechocystis	1.8 ± 1.5	1.8 ± 0.9
Nodularia	1.7 ± 1.2	2.0 ± 1.6
Gomphosphaeria	1.1 ± 0.5	1.2 ± 0.5
CHLOROPHYTA		
Scenedesmus	5.3 ± 2.8	8.1 ± 7.2
Pediastrum	1.3 ± 0.9	1.3 ± 3.2
Coelastrum	1.3 ± 0.7	1.0 ± 0.4
Crucigenia	1.4 ± 1.2	1.7 ± 1.2
Ankistrodesmus	4.0 ± 2.1	4.6 ± 0.8
Staurastrum	1.3 ± 0.8	1.7 ± 1.8
Closterium	2.2 ± 1.3	2.3 ± 0.9
Tetraedron	1.7 ± 1.0	1.4 ± 0.8
Kirchneriella	2.0 ± 1.3	1.2 ± 0.1
Selenestrum	0.8 ± 0.9	1.6 ± 0.8
Elakotothrix	1.2 ± 0.7	1.2 ± 0.4
Chlorella	1.2 ± 0.8	1.0 ± 0.7
Botryococcus	0.8 ± 0.1	1.1 ± 0.1
Oocystis	1.0 ± 0.5	0.9 ± 0.1
Cosmarium	1.4 ± 0.6	0.8 ± 0.2
BACILLARIOPHYTA		
Navicula	1.0 ± 0.5	0.3 ± 0.1
Stephanodiscus	1.2 ± 0.6	0.5 ± 0.4
Nitzschia	1.0 ± 0.4	0.4 ± 0.1
Fragilaria	1.2 ± 0.7	0.4 ± 0.1
EUGLENOPHYTA		
Phacus	1.6 ± 1.0	1.0 ± 0.8
Trachelomonas	1.3 ± 0.7	1.3 ± 0.7
Euglena	1.1 ± 0.6	1.0 ± 0.5
ZOOPLANKTON		
Brachionus	1.0 ± 0.5	0.0 ± 0.0
Filinia	0.9 ± 0.6	0.0 ± 0.0

Note: Number of fish used for this analysis = 534

± indicate standard deviations

Oscillatoria and *Aphanocapsa* were higher in the stomach than in the rectum.

Among the members of the Chlorophyceae, *Coelastrum, Tetraedron, Kirchneriella, Chlorella, Oocystis* and *Cosmarium* were higher in the stomach than in the rectum while *Scenedesmus, Crucigenia, Ankistrodesmus, Closterium, Selenestrum* and *Botryococcus* were lower in the stomach than in the rectum. *Pediastrum* and *Elakotothrix* occurred in similar proportions in both the stomach and the rectum.

All the members of the Bacillariophyta (*Navicula, Nitzschia, Stephanodiscus* and *Fragilaria*) showed a tendency to decline in relative abundance from the stomach to the rectum. Similar patterns occurred in Euglenophyceae (*Phacus* and *Trachelomonas*) except in *Euglena* which occurred in similar proportions in the two regions of the gut. The members of the zooplankton reached the rectum disintegrated with only appendages remaining and could therefore not be counted. Although the Bacillariophyta and the zooplankton are found only in small quantities in the diet, they may be more useful to *O. esculentus* nutritionally.

4.2.8 Food selection

For the study of food selection, a comparison was made between food items in the gut and algae and zooplankton in the plankton of the lake. From Table 16 and Fig. 12 it is evident that the relative abundances of food items in the water and those in the gut of the fish were different, indicating that the fish is capable of selecting its food. The proportions of different food types in the diet and in the water fluctuated monthly as follows: The proportion of the Cyanophyta was higher in the diet than in the environment during January, February and June but were lower than those in the environment during the remaining months. The monthly difference between the proportion in the diet and in the environment was however small except in June when it was pronounced.

The proportion of Chlorophyta in the stomach was higher in the diet than in the environment during the months of September, November, December, March, April, July and August but was lower during the remaining months. However the differences were slight.

Proportions of the Euglenophyta were higher in the diet than in the environment throughout the year. The same pattern is reflected in the Bacillariophyta except in October when its proportion in the water was higher

Table 16. Monthly variation in the proportions of the major food types in the stomach and in the environment, and an index of food preference.

a) Cyanophyta

Month	% in diet	% in water	α
Sep	73.9	87.2	0.032
Oct	75.1	71.1	0.139
Nov	73.4	79.2	0.026
Dec	69.2	79.8	0.048
Jan	70.2	68.7	0.037
Feb	76.0	71.5	0.048
Mar	68.9	80.6	0.031
Apr	66.9	75.4	0.108
May	76.0	79.3	0.029
Jun	77.1	17.7	0.030
Jul	67.9	83.1	0.023
Aug	72.0	80.3	0.074

b) Chlorophyta

Month	% in diet	% in water	α
Sep	20.8	12.0	0.065
Oct	18.9	21.4	0.112
Nov	20.1	18.8	0.029
Dec	23.4	19.0	0.068
Jan	21.4	31.3	0.025
Feb	19.4	27.9	0.032
Mar	21.2	16.5	0.047
Apr	24.8	20.2	0.149
May	18.7	19.7	0.029
Jun	17.2	82.1	0.001
Jul	21.5	15.5	0.039
Aug	21.0	17.5	0.099

c) Euglenophyta

Month	% in diet	% in water	α
Sep	2.3	0.8	0.109
Oct	1.9	1.4	0.172
Nov	1.8	1.4	0.036
Dec	2.7	0.7	0.215
Jan	3.8	1.3	0.107
Feb	3.3	0.3	0.500
Mar	4.3	2.5	0.063
Apr	4.3	2.9	0.179
May	2.4	1.1	0.066
Jun	2.3	0.2	0.105
Jul	3.0	0.8	0.102
Aug	2.5	1.6	0.128

Table 16 (cont.)

d) Bacillariophyta

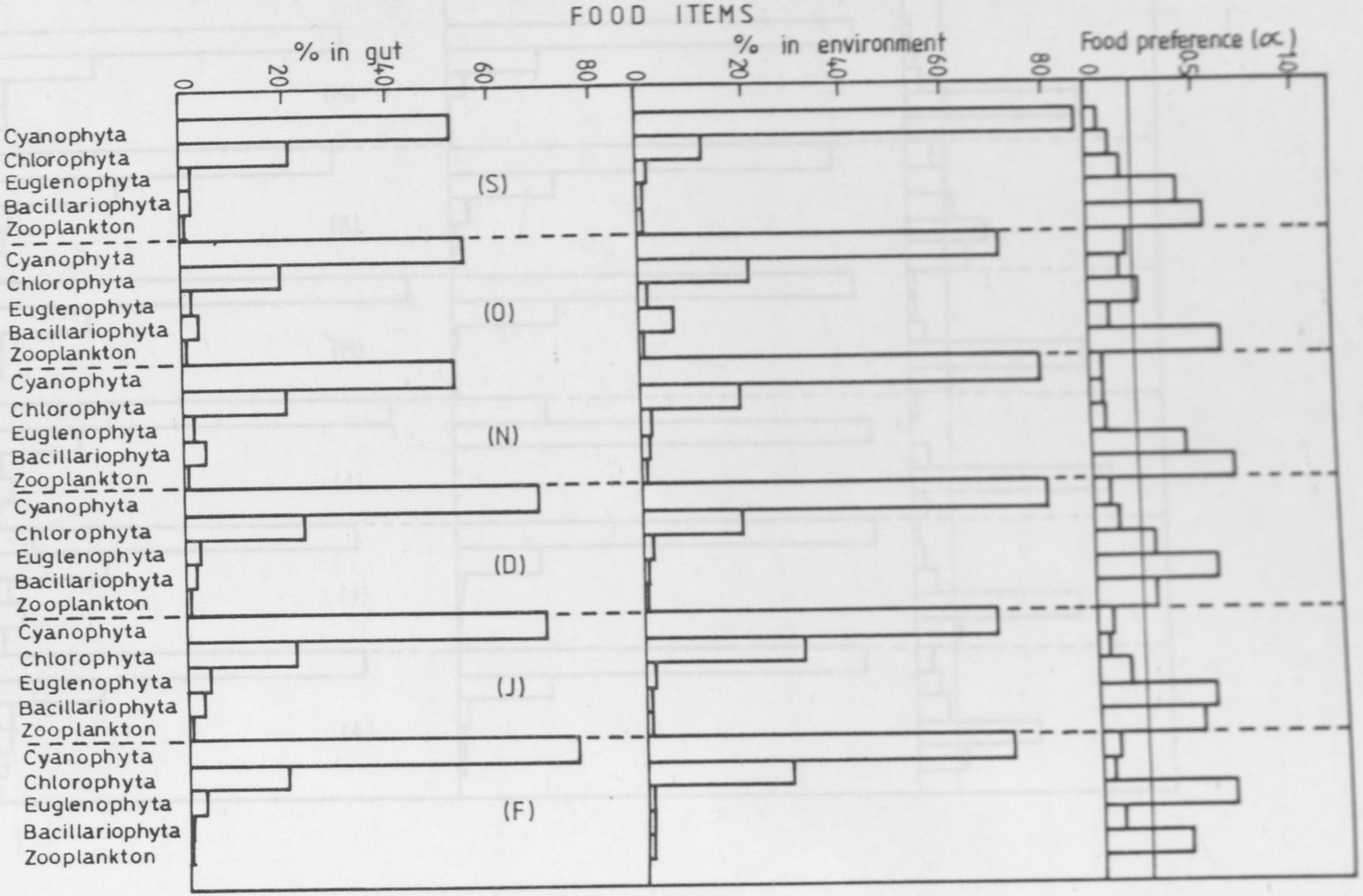
Month	% in diet	% in water	α
Sep	1.8	+	0.340
Oct	3.3	5.9	0.070
Nov	3.9	0.3	0.358
Dec	2.4	0.3	0.445
Jan	3.2	0.3	0.444
Feb	0.5	0.4	0.057
Mar	3.8	0.0	0.694
Apr	3.2	1.2	0.323
May	2.3	0.1	0.695
Jun	3.5	0.03	0.802
Jul	5.6	0.8	0.659
Aug	3.0	0.5	0.493

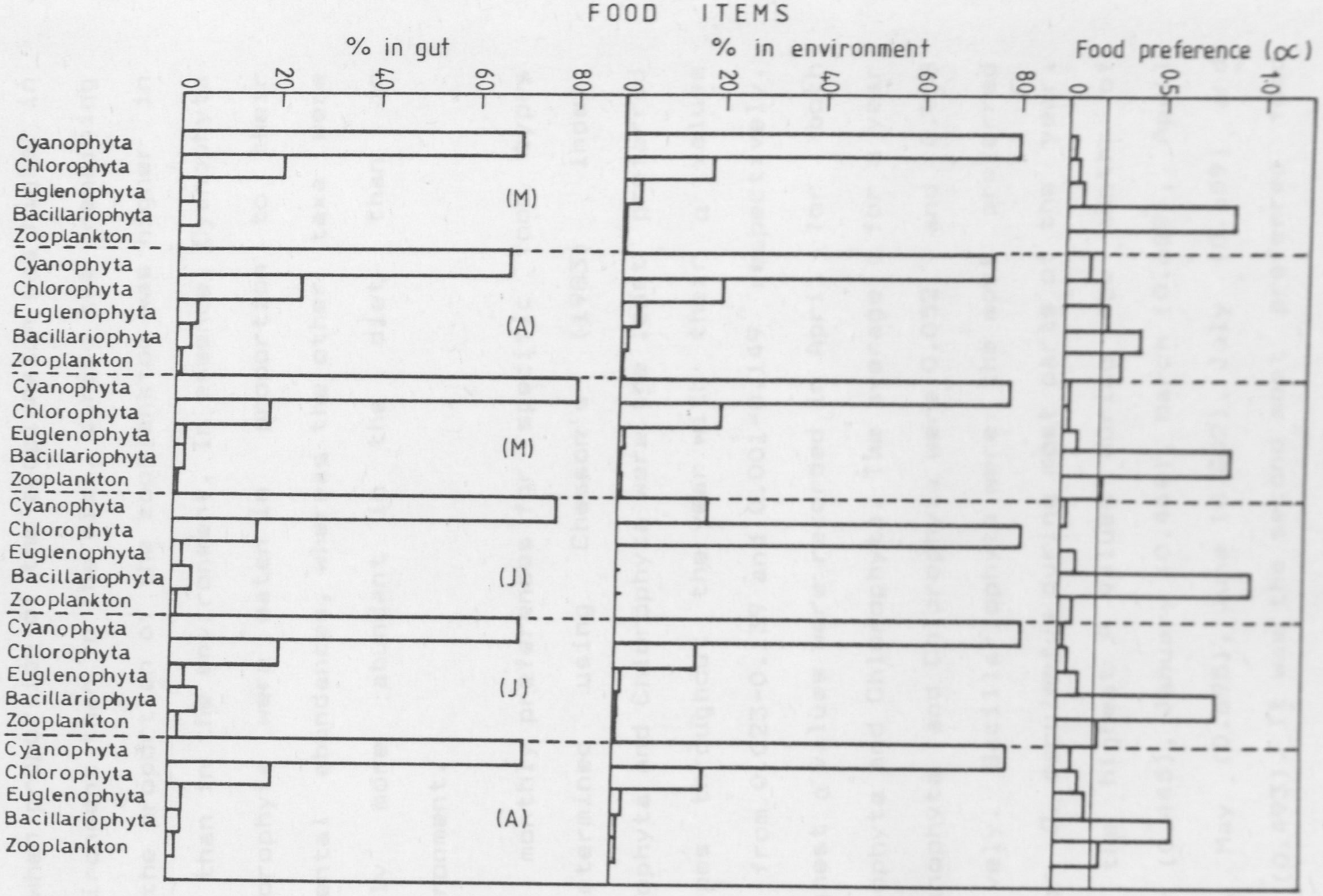
e) Zooplankton

Month	% in diet	% in water	α
Sep	1.2	+	0.454
Oct	0.8	0.2	0.507
Nov	0.8	0.04	0.551
Dec	0.8	0.2	0.223
Jan	1.4	0.13	0.388
Feb	0.8	0.1	0.364
Mar	0.9	0.2	0.164
Apr	0.8	0.4	0.242
May	0.6	0.1	0.181
Jun	0.9	0.1	0.062
Jul	2.0	0.3	0.177
Aug	1.5	0.6	0.206

Note: + indicates food type was present but in very small quantities.

Fig. 12 Monthly variation in the proportions of the major food types in the stomach and in the environment, and an index of food preference.


FOOD ITEMS
% in gut
0
20
40
60
80
% in environment
0
20
40
60
80
Food preference (α)
0
0.5
1.0
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(S)
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(O)
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(N)
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(D)
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(J)
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(F)


FOOD ITEMS
% in gut
% in environment
Food preference (α)
0
20
40
60
80
0
20
40
60
80
0
0.5
1.0
Cyanophyta
Chlorophyta
Euglenophyta
Bacillariophyta
Zooplankton
(M)
(A)
(M)
(J)
(J)
(A)

than in the environment. Similarly, with the exception of June when proportion of the zooplankton was higher in the environment than in the diet, during the remaining months the proportion of the zooplankton was higher in the diet than in the environment. In essence, Cyanophyta and Chlorophyta were eaten in proportion to their environmental abundances, whereas the other taxa were relatively more abundant in the diet than in the environment.

The monthly preferences for specific food types were determined using Chesson's (1983) index. The Cyanophyta and Chlorophyta were the least preferred food types throughout the year with their α values ranging from 0.023-0.139 and 0.001-0.149 respectively. The highest α values were recorded in April for both the Cyanophyta and Chlorophyta. The average α for a year for Cyanophyta and Chlorophyta were 0.052 and 0.058 respectively. Bacillariophyta were the most preferred food for *O. esculentus* during most parts of the year. It had the highest α values during the months of December (0.445), January (0.444), March (0.659), April (0.323), May (0.695), June (0.802), July (0.659) and August (0.493). It was the second most preferred food during September and November with respective α values of 0.340 and 0.358. The Bacillariophyta was however least preferred in October (α = 0.07). The average α for the year was the highest being 0.448.

Euglenophyta were most preferred prey type in February ($\alpha = 0.500$), second most preferred in October ($\alpha=0.172$) and June ($\alpha=0.05$) but third most preferred item during the remaining months and had mean α value of 0.149.

Finally, zooplankton were most preferred in September, October and November with the α values of 0.454, 0.507 and 0.551 respectively. It was the second most preferred food type in December (0.223), January (0.388), February (0.364), March (0.164), April (0.242), May (0.181), July (0.177) and August (0.206). The average α for zooplankton for the whole year was 0.293.

From the results, it is evident that the order of *O. esculentus* selectivity for food items was Bacillariophyta, Zooplankton, Euglenophyta, Cyanophyta and Chlorophyta. It is apparent that the food types that showed highest digestibility, i.e. zooplankton and diatoms (Bacillariophyta), were selected for. Thus *O. esculentus* selected the most profitable prey (in terms of digestibility) it encountered. Since the rate of encounter with the most profitable preys - Zooplankton and Bacillariophyta was low due to to their low numbers, the next profitable prey - Euglenophyta was included in the diet. Due to the fact that even the Euglenophyta were few and the chances of their being encountered was also low, the variety of items ingested was expanded to include the less profitable Cyanophyta and Chlorophyta to increase the profitability of getting a reasonable quantity of the preferred food items.

4.3 Feeding structures

4.3.1 Dentition

The oral teeth located on the upper and lower jaws of *O. esculentus* are not of a uniform type (Plates 1 A & B). From the plate it is evident that each jaw carries three rows of teeth. The longest teeth are found on the outermost areas of the jaw, the middle row of teeth are of intermediate size, and the innermost row of teeth are the shortest.

The oral teeth of the outer row are bicuspid with one of the cusps always much longer than the other (Plates 1 E & F). The teeth are flattened distally to form blades, and the distal ends are stained brown. Closer examination of the teeth reveal that some portions of the cusps are worn so that the teeth appear tricuspid (Plate 1 E). The distal regions of inner and middle rows of oral teeth, on the other hand, are tricuspid (Plates 1 C & D). This species does not show morphological changes in dentition with size.

Plate 1 Scanning electron micrographs of lower jaw teeth of *O. esculentus* showing:

A - Rows of jaw teeth (inside view) x75.

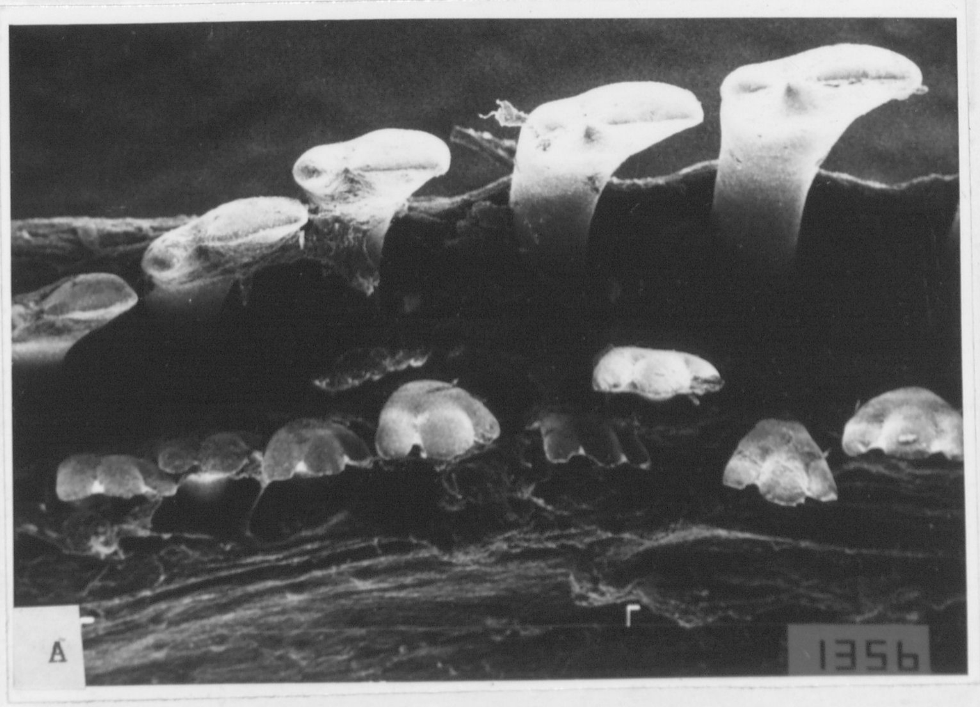
B - Rows of jaw teeth (outside view) x75.

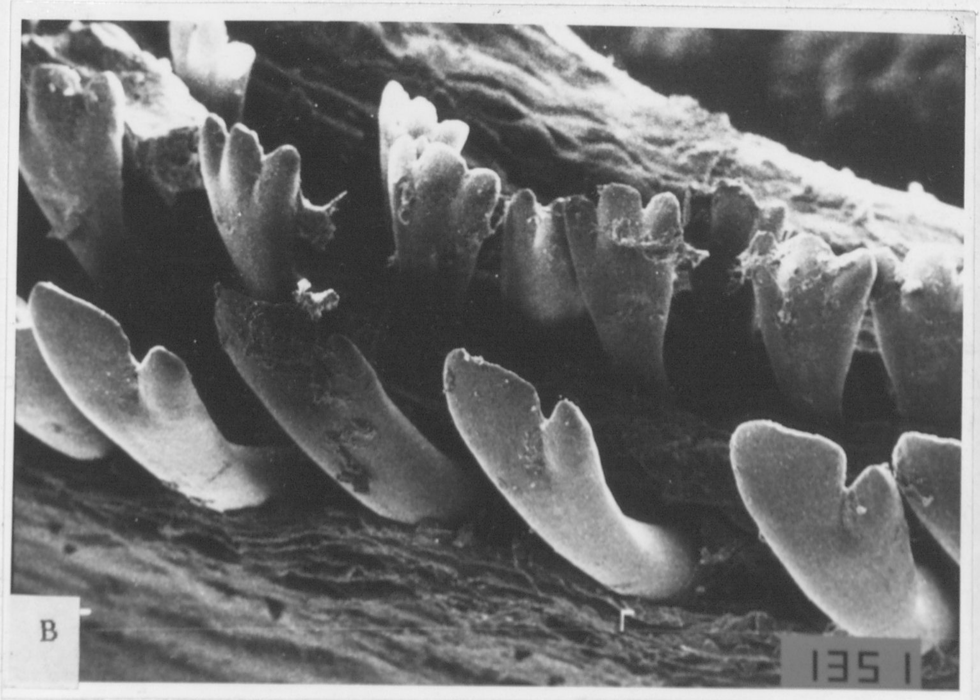
C - Tricuspid jaw teeth x75.

D - Tricuspid jaw teeth x200.

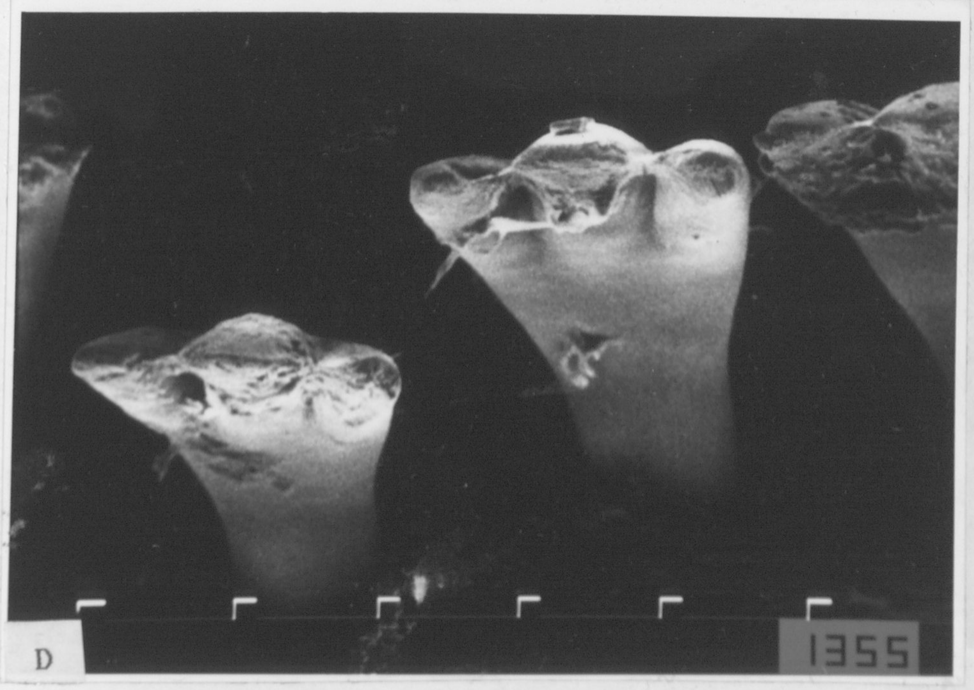
E - Bicuspid jaw teeth (with worn out parts) x150.

F - Bicuspid oral teeth x75.

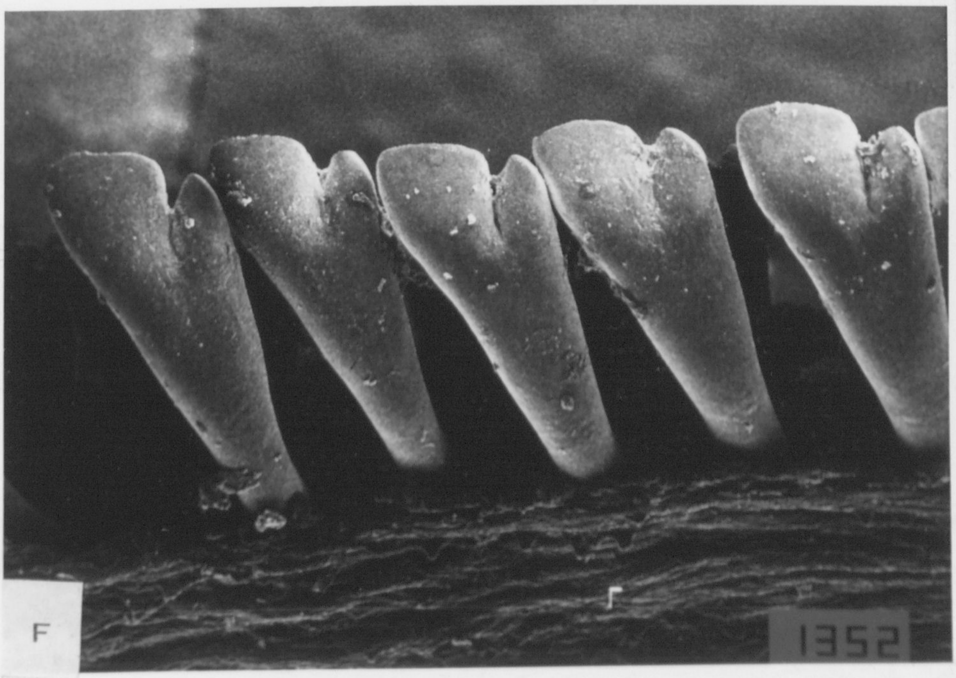

A
1356


B
135 1


C
1354


D
1355


E
1353


F
1352

4.3.2 Pharyngeal bones

The ventral pharyngeal bone is made up of two fused bones and is triangular in outline. It has a central pad with a dense concentration of teeth whose fine distal ends show backward curvature (Plate 2 A). There is greater teeth density in the caudal region (Plate 2 B) of the ventral pharyngeal bone than in the rostral region (Plate 2 A). Similarly, the teeth at the caudal region are of greater length than those at the rostral region. Each tooth looks more like match head at lower magnification (Plate 2 B). Close observation of these teeth at higher magnification reveals that the distal region of each tooth is slender and is hooked posteriorly (Plate 2 C). There is a significant positive correlation between fish standard length and the area of the toothed surface of the lower pharyngeal bone (r - 0.65, $p < 0.05$).

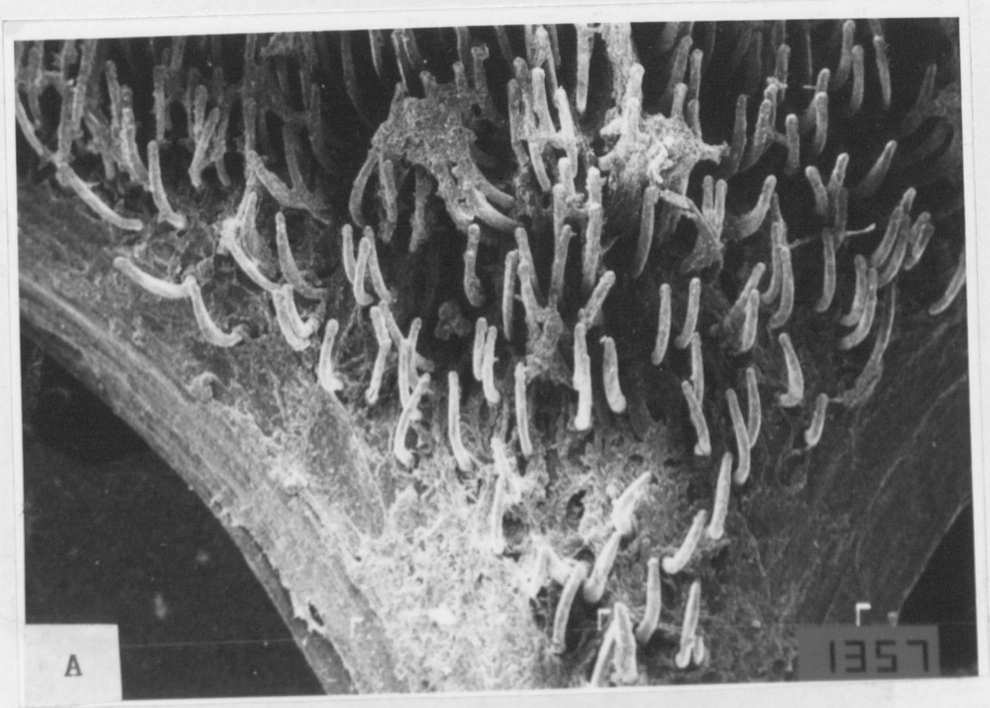
The dorsal pharyngeal bone is made up of three bones which are not fused. The bone is covered by a large number of teeth projecting distally into the pharyngeal cavity. The distal region of each tooth is cusped (Plates 3 A, B & C).

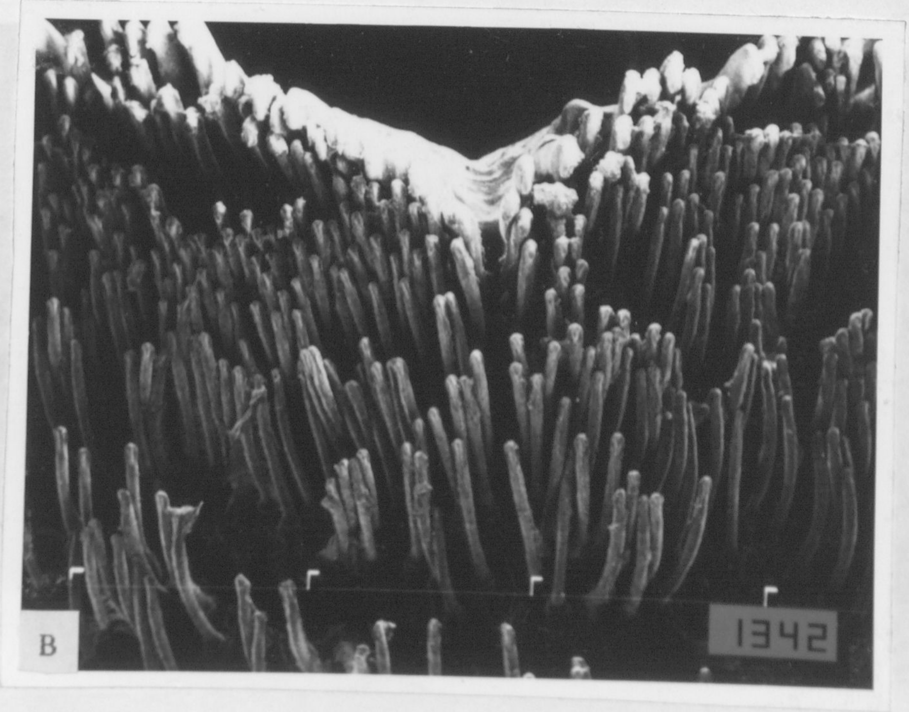
Plate 2 Scanning electron photographs of lower pharyngeal teeth of *O. esculentus* showing:

A - Toothed surface of the rostral region of the lower pharyngeal bone x35.

B - Toothed surface towards the caudal region of the lower pharyngeal bone x35.

C - Lower pharyngeal teeth facing backwards x75.


A
1357


B
1342

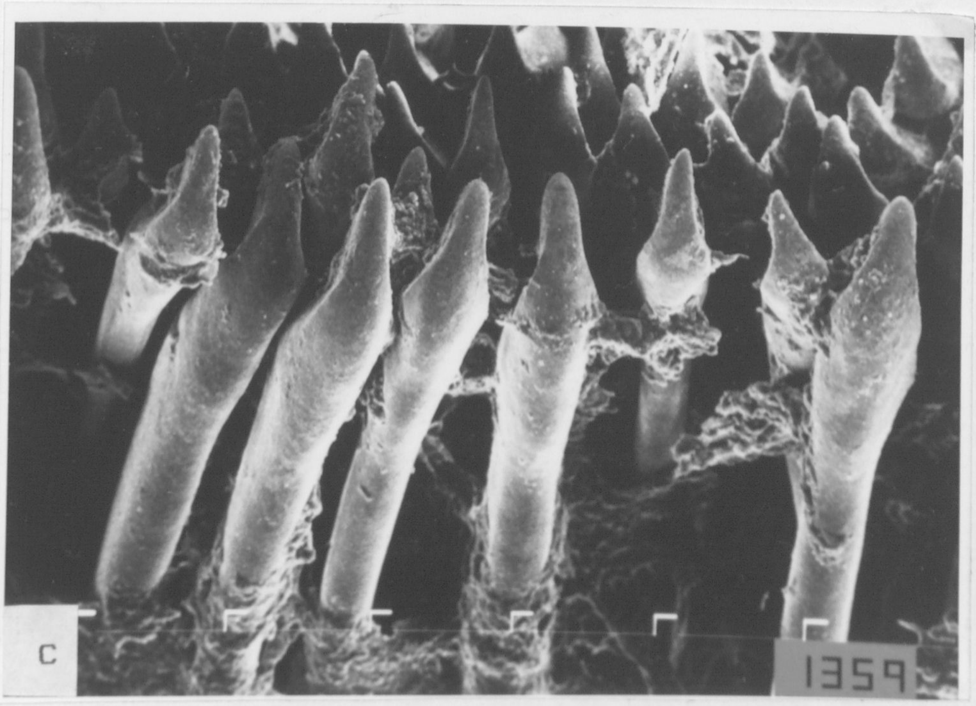
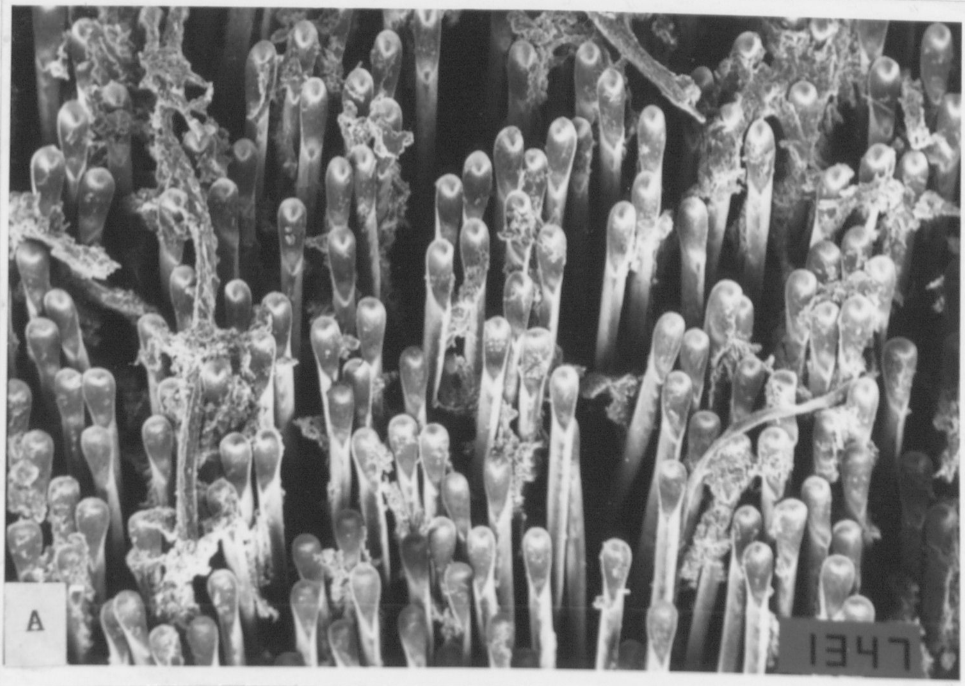

C
1359

Plate 3 Scanning electron photographs of upper pharyngeal teeth of *O. esculentus* showing:

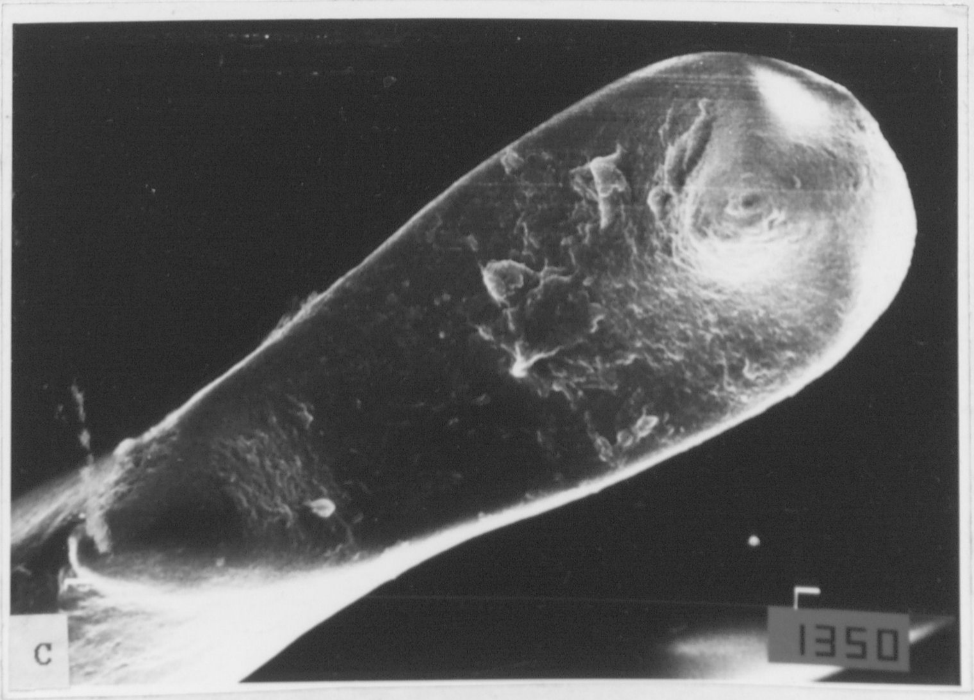
A - Upper pharyneal teeth x75.

B - Upper pharyngeal teeth x200.

C - Tip of Upper pharyngeal teeth x1000.


A
1347


B
1348


C
1350

4.3.3 Stomach

The stomach of *O. esculentus* is a simple distensible sac. It is separated from the duodenum by a pyloric sphincter. Most of the stomach contents were found intact regardless of the time of capture, an indication that it serves primarily as a reservoir where food is stored before it is discharged into the intestine. There was, however, some macerated zooplankton in the stomach. Maceration is most likely carried out using the pharyngeal teeth.

4.3.4 Intestine

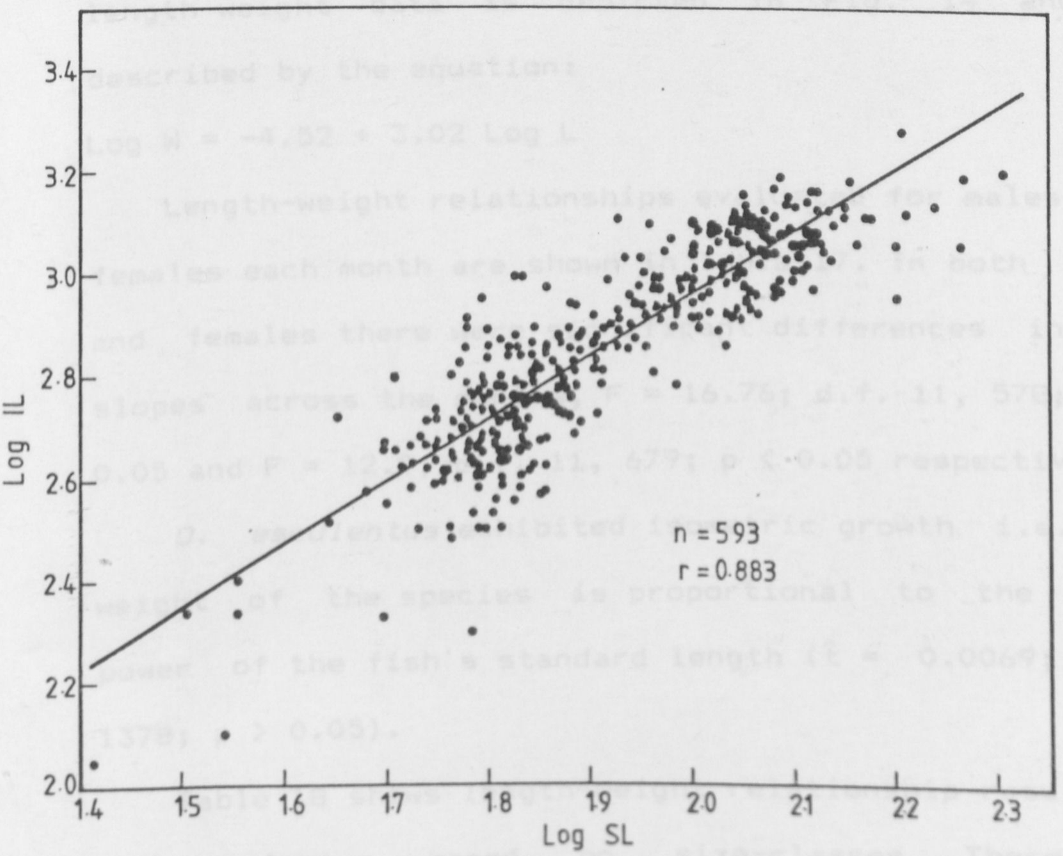
The intestine of *O. esculentus* is delicate and of considerable length. The first portion is thin-walled and transparent, and parasitic nematodes were observed in this region. The ratio of fish standard length to intestine length ranged from 1:4 to 1:14. There is a highly, significant positive correlation ($r = 0.999$, $p < 0.001$) between fish standard length and intestine length (Fig. 13). The relationship between fish standard length (SL) and intestine length (IL) is described by the equation:

$$\text{Log IL} = 0.50 + 1.23\ \text{SL}$$

$$(n = 593,\ r = 0.88).$$

Fishes that were mouth-brooding had shorter intestine compared to others of the same length that were not brooding.

Fig. 13 The logarithmic relationship between fish standard length and the length of the intestine length of *O. esculentus*.


3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
Log IL
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
Log SL
n = 593
r = 0.883

4.4 Length-weight relationship

There was no significant difference between male and female slopes, $t = 0.48$; d.f. 1301; $p > 0.05$. Logarithmic relationship of the pooled male and female length-weight data is depicted in Fig. 14 and is described by the equation:

$$\text{Log } W = -4.52 + 3.02 \text{ Log } L$$

Length-weight relationships evaluated for males and females each month are shown in Table 17. In both males and females there were significant differences in the slopes across the months, $F = 16.76$; d.f. 11, 578; $p < 0.05$ and $F = 12.0$; d.f. 11, 679; $p < 0.05$ respectively.

O. esculentus exhibited isometric growth i.e. the weight of the species is proportional to the third power of the fish's standard length ($\hat{t} = 0.0069$; d.f. 1378; $p > 0.05$).

Table 18 shows length-weight relationship results of *O. esculentus* based on size-classes. There was significant difference in the slopes across the size-classes, $F = 62.78$; d.f. 3, 1364; $p < 0.05$. All the size-classes exhibited isometric growth.

4.5 Relative condition

The relative condition factor of *O. esculentus* in Lake Kanyaboli was determined on a monthly basis, according to sex (Table 19 and Fig. 15). Generally, the

Fig. 14 Length-weight relationship of *O. esculentus.*

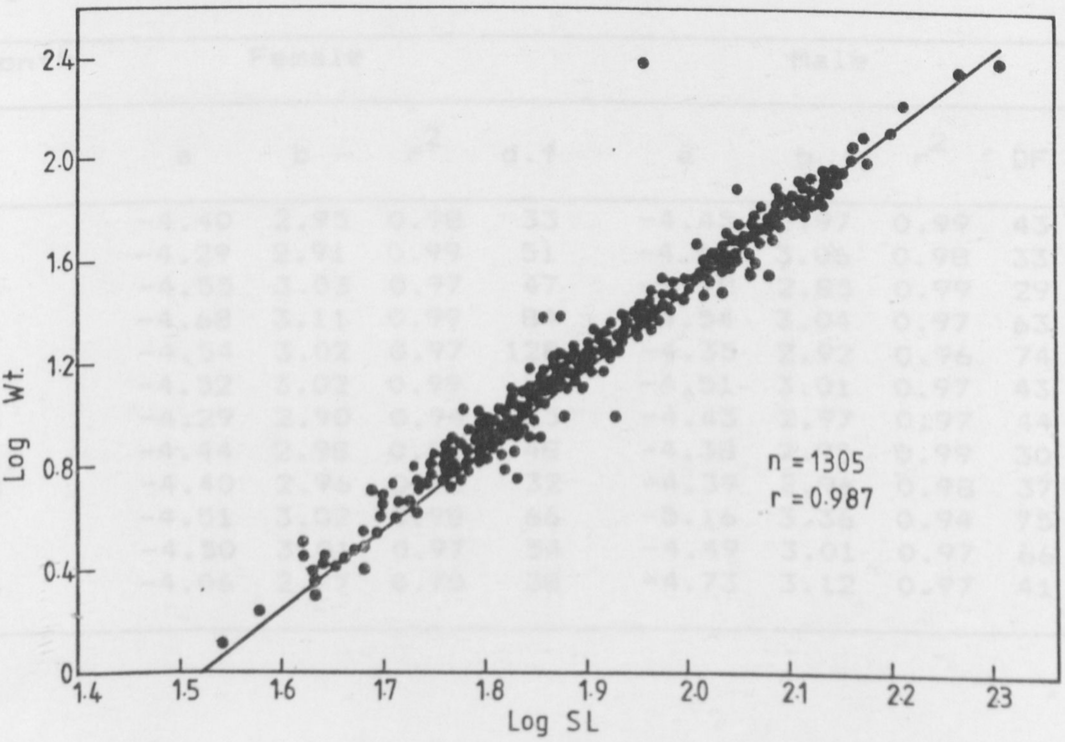

2.4
2.0
1.6
1.2
0.8
0.4
0
Log Wt.
1.4
1.5
1.6
1.7
1.8
1.9
2.0
2.1
2.2
2.3
Log SL
n = 1305
r = 0.987

Table 17. Monthly length-weight relationships for female and male *O. esculentus*.

Month	Female				Male			
	a	b	r^2	d.f	a	b	r^2	DF
S	-4.40	2.95	0.98	33	-4.45	2.97	0.99	43
O	-4.29	2.91	0.99	51	-4.60	3.06	0.98	33
N	-4.55	3.03	0.97	47	-4.18	2.85	0.99	29
D	-4.68	3.11	0.99	84	-4.54	3.04	0.97	63
J	-4.54	3.02	0.97	128	-4.35	2.92	0.96	74
F	-4.52	3.02	0.99	63	-4.51	3.01	0.97	43
M	-4.29	2.90	0.94	35	-4.43	2.97	0.97	44
A	-4.44	2.98	0.96	48	-4.38	2.95	0.99	30
M	-4.40	2.96	0.99	32	-4.39	2.96	0.98	37
J	-4.51	3.02	0.98	66	-5.16	3.36	0.94	75
J	-4.50	3.01	0.97	54	-4.49	3.01	0.97	66
A	-4.06	2.77	0.70	38	-4.73	3.12	0.97	41

Table 18. Length-weight relationships of *O. esculentus* based on size-classes.

Size-class (mm)	a	b	r^2	DF
10 - 49	-5.23	3.49	0.84	38
50 - 99	-4.34	2.92	0.93	1032
100-149	-4.70	3.11	0.89	299
≥ 150	-4.28	2.91	0.89	4
Overall	-4.52	3.02	0.98	1377

relative condition factor of *O. esculentus* in Lake Kanyaboli fluctuated slightly about unity throughout the study period. There were no seasonal variation in k_n , in males (F = 0.13; d.f. 11, 590; p > 0.05) and in females (F = 1.88; d.f 11, 691; p > 0.05). There were also no significant differences in k_n across size-classes, F = 0.389; d.f. 5, 1293; p > 0.05 (Table 20 and Fig. 16).

Table 19. Monthly variation in relative condition factor of female and male *O. esculentus*

Month	Female	Male
Sep	1.01 ± 0.13	1.01 ± 0.12
Oct	1.01 ± 0.10	1.01 ± 0.13
Nov	1.01 ± 0.15	1.01 ± 0.12
Dec	1.00 ± 0.09	1.00 ± 0.10
Jan	1.01 ± 0.12	1.03 ± 0.14
Feb	1.00 ± 0.14	1.01 ± 0.11
Mar	1.01 ± 0.19	1.01 ± 0.12
Apr	1.01 ± 0.14	1.00 ± 0.08
May	1.00 ± 0.06	1.00 ± 0.07
Jun	1.01 ± 0.11	1.01 ± 0.16
Jul	1.01 ± 0.16	1.01 ± 0.11
Aug	1.00 ± 0.14	1.01 ± 0.10

Note: ± indicate Standard deviations

Fig. 15 Seasonal changes in the relative condition factor of female (a) and male (b) *O. esculentus*.

Vertical bars indicate standard deviations.

Figures in parentheses indicate sample size

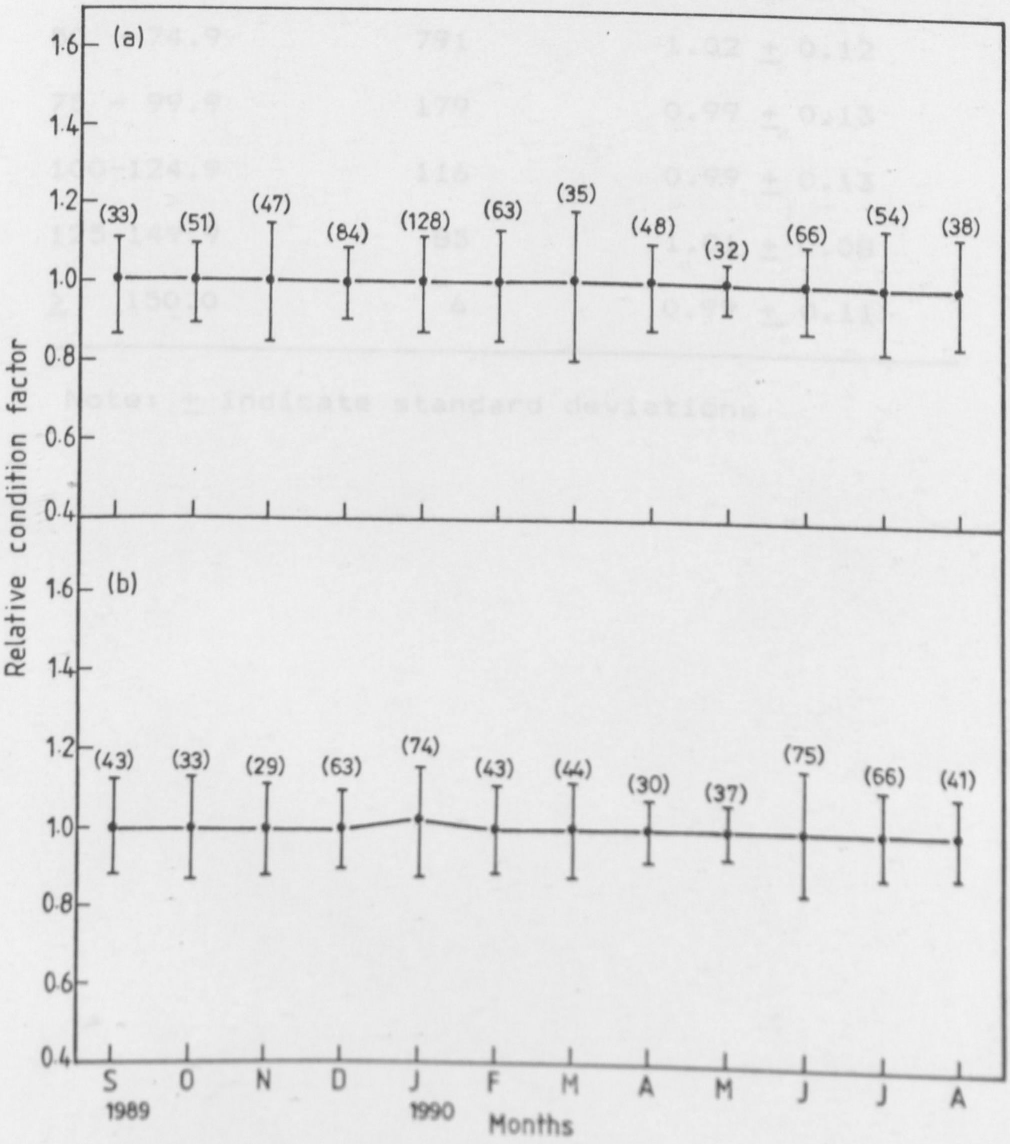

(a)
(b)
Relative condition factor
1.6
1.4
1.2
1.0
0.8
0.6
0.4
(33)
(51)
(47)
(84)
(128)
(63)
(35)
(48)
(32)
(66)
(54)
(38)
(43)
(33)
(29)
(63)
(74)
(43)
(44)
(30)
(37)
(75)
(66)
(41)
S
O
N
D
J
F
M
A
M
J
J
A
1989
1990
Months

Table 20. Relative condition factor of *O. esculentus* based on size-classses.

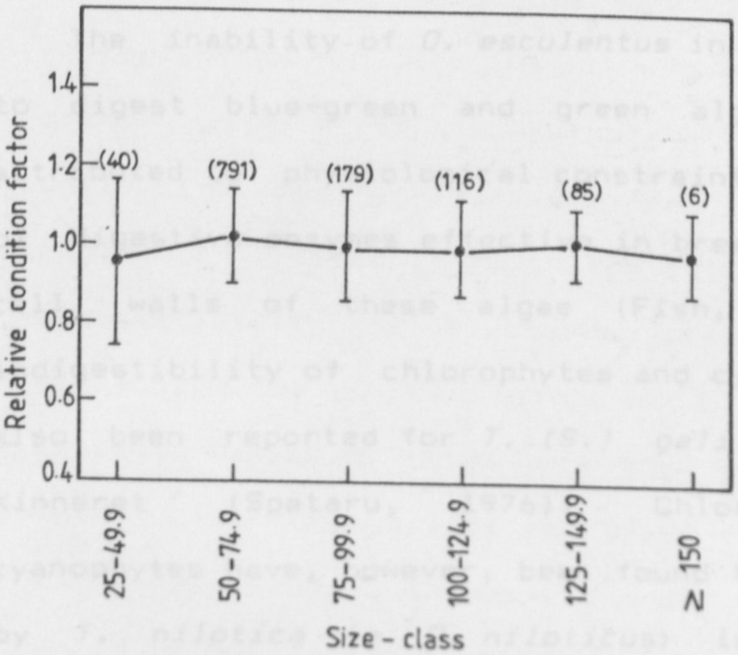
Size-class (mm)	No of fish examined	Relative condition factor
25 - 49.9	40	0.96 ± 0.23
50 - 74.9	791	1.02 ± 0.12
75 - 99.9	179	0.99 ± 0.13
100-124.9	116	0.99 ± 0.13
125-149.9	85	1.01 ± 0.08
≥ 150.0	6	0.99 ± 0.11

Note: ± indicate standard deviations

Fig. 16 Relative condition factor of *O. esculentus* based on size-classes.

Vertical bars indicate standard deviations.

Figures in parentheses indicate sample size.


Relative condition factor
1.4
1.2
1.0
0.8
0.6
0.4
(40)
(791)
(179)
(116)
(85)
(6)
25–49.9
50–74.9
75–99.9
100–124.9
125–149.9
≥ 150
Size - class

CHAPTER 5

DISCUSSION AND CONCLUSIONS

O. esculentus has been reported to feed on all groups of phytoplankton, but to digest only the diatoms while blue-green and green algae pass through the gut undigested (Graham, 1929; Fish, 1951; EAFFRO, 1955/56; Lowe-McConnell, 1956; Welcomme, 1966). Zooplankton and suspended organic matter have also been found in *O. esculentus* stomachs (Fish, 1951).

The inability of *O. esculentus* in Lake Victoria to digest blue-green and green algae has been attributed to physiological constraints, i.e. a lack of digestive enzymes effective in breaking down the cell walls of these algae (Fish, 1951). The indigestibility of chlorophytes and cyanophytes has also been reported for *T. (S.) galilaeus* in Lake Kinneret (Spataru, 1976). Chlorophytes and cyanophytes have, however, been found to be digested by *T. nilotica* (= *O. niloticus*) in Lake Edward (Moriarty, 1973). Digestibility of these algae in this species has been attributed to the production of highly acidic conditions in the stomach, which are believed to aid in the lysis of algal cell walls, thereby exposing their protoplasm to enzymatic activities.

Analysis of *O. esculentus* gut contents in the present study revealed that *O. esculentus* in Lake Kanyaboli feed throughout the year, principally on phytoplankton, and ingest all phytoplankton groups present in the water (Cyanophyta, Chlorophyta, Euglenophyta and Bacillariophyta). Zooplankton and organic matter were also found in stomachs. Members of the Cyanophyta and, to some extent, the Chlorophyta occurred most frequently in the diet. Similarly, these two groups were the most abundant phytoplankton in the water. However, mainly the diatom members of the phytoplankton were digested while the blue-green and green algae, and the euglenoids, passed through the gut undigested. The undigestibility of blue-green and green algae and euglenoids by *O. esculentus* in Lake Kanyaboli is probably because they lack the digestive enzymes which have the ability to digest their algal cell walls. *O. esculentus* has a stomach P^H of 4.0 to 8.0, which is not acidic enough to lyse the cell walls of many algae. Even though the waters of Lake Kanyaboli are green with phytoplankton and *O. esculentus* ingests them, this species has remained stunted, probably because of poor nutrition. Nutrition is poor probably because, highly digestible members of the phytoplankton are rare.

No studies were completed on the algal composition and abundance in Lake Kanyaboli before and after the construction of the dyke that now prevents the River Yala from flowing directly into the lake. It is therefore not known whether there have been changes in phytoplankton composition and abundance over the years. Among physico-chemical parameters which have been measured, Okemwa (1981) and Mavuti (1989) showed that there has been an increase in conductivity. The high conductivity of 950 µmhos/cm was reported by Mavuti (op. cit.). High conductivity could be responsible for the lack of diatoms, such as *Melosira*, which have been reported to survive only in waters with conductivity of less than 600 µmhos/cm. A luxuriant growth of diatoms occurs in the Winam Gulf of Lake Victoria, where conductivity is less than 600µmhos/cm. (Nyamu, 1986; Kibaara, 1989). Changes in land use and water chemistry may contribute to *O. esculentus*' small size in Lake Kanyaboli. Increased input of nutrients and sediment into the lake via agricultural run-off probably results in an increase in water conductivity which, in turn, inhibits the growth of some species of digestible diatoms. The abundance of the blue-green algae, especially *Microcystis* sp., is an indirect indicator of the presence of cultural eutrophication in the lake.

In this study the diet of *O. esculentus* did not vary throughout its life, thus both the juveniles and adults fed principally on phytoplankton and, to a lesser extent, on zooplankton and detritus. This, however, is at variance with Welcomme's (1966) report on the same species in Lake Victoria. The author reported that adult *O. esculentus* were phytoplanktivores while the diets of juveniles (<70mm SL) consisted predominantly of bottom material.

O. esculentus showed a steady increase in stomach content weight from early in the morning to the evening. Stomach content weight declined through the night and the lowest stomach content weights were recorded at dawn. This implies that feeding, digestion, and assimilation take place during the day while only digestion and assimilation occur at night. There are no other results on the diel feeding behaviour of *O. esculentus*; however there are data on the diel feeding periodicity of other Cichlidae. *O. niloticus* and *H. nigripinnis* in Lake George have been reported to begin feeding at or near dawn (C.M. Moriarty and D.J.W. Moriarty, 1973). Dadzie *et al.* (1979) reported that *Tilapia* spp. in Lake Kamburu fed during the day with the highest index of fullness being recorded in the evening. In contrast to the findings of these investigations *Sarotherodon* *galilalaeus* and *T. discolor* feed at night between 1800 and 0500 hours (Whyte, 1975).

Few investigations have been carried out on the food selection of tilapiines in the tropics. Moriarty (1973) reported a marked positive selection for the blue-green alga *Lyngbya* and colonial diatom *Melosira*, but negative selection for the blue-green alga *Anabaenopsis* and diatom *Synedra* in Lake George. The author reported that selection was based on the size and shape of the food particle. *T. (= Sarotherodon galilaeus) galilaea* has been reported (Spataru, 1976) to show a preference for *Peridinium* (a pyrrophyte), but show negative selection for other groups of algae. The above authors used Ivlev's (1961) electivity index as a measure of preference which has, however, been found to suffer from a number of shortfalls (Chesson, 1983).

The results of the present investigation on food selection indicate that *O. esculentus* in Lake Kanyaboli show a preference mainly for the diatoms (Bacillariophyta) and rotifers. Generally, there were low electivity indices for the Chlorophyta and Cyanophyta. It was observed that the foods that were most digestible to *O. esculentus* were the ones selected. Food selection in this species appears to depend on the nutritional value of the food to the fish, i.e. foods that are readily digestible and are therefore profitable are preferred to those that are less digestible.

There are a few reports on the studies of the bucco-pharyngeal anatomy. The limited information indicates that jaw teeth are bicuspid and tricuspid, that the lower pharyngeal teeth are fine and hooked at the distal end and that the upper pharyngeal teeth are cusped at the distal end (Fryer and Iles, 1972; Trewavas, 1983). The results of the present investigations are in general agreement with those of these authors. The anatomical features of *O. esculentus* strongly suggest that this species is a herbivore; an observation supported by the diet analysis. The fine, hooked, lower pharyngeal teeth are adapted for breaking large colonial and filamentous algae. The jaw teeth are in no way related to type of the food it consumes. The presence of a thin-walled sac-like stomach indicates that digestion probably does not occur in the stomach. Stomach contents remained intact over a 24 h period suggesting a lack of gastric digestion. The stomach simply acts as a reservoir for food before it is discharged into the intestine; however, a few macerated zooplankton were found in the stomach. Maceration was probably effected by the pharyngeal teeth. The intestine, which is of considerable length, is typical of herbivores and increases the efficiency of digestion of plant material (Bowen, 1982). The ratio of fish standard length to intestine length observed (1:4 to 1:14) is close to that reported for most tilapiines (1:7 to 1:11) (Bowen, op. cit.). The fact that morphological characteristics of the jaw teeth, pharyngeal teeth, stomach and intestine do not change with size suggest that *O. esculentus* of all size-classes feed on similar food types. Analyses of gut contents confirmed that there were no differences in the diets of *O. esculentus* of different sizes.

In most length-weight relationship studies the regression coefficient b falls between 2.0 and 4.0, with an average value near 3.0. Dadzie *et al.* (1979) have reported isometric growth in *Tilapia* and *Barbus* but allometric growth in *Labeo* and *Mormyrus* in Lake Kamburu. Allometric growth has also been reported in *T. zillii* in fish ponds in Sagana (Dadzie and Wangila, 1980). In Nyumba ya Mungu however, four tilapiines (*Sarotherodon (= Oreochromis) jipe*, *S. (=O.) pangani*, *S. (= O.) esculentus*, *T. rendalli*) exhibited isometric growth. (Bailey and Denny, 1978).

In the present study both male and female *O. esculentus* exhibited isometric growth. This implies that both sexes show similar growth patterns. When length-weight relationships were examined for different size-classes all the size-classes except the smallest exhibited isometric growth. Juveniles below 50mm exhibit allometric growth.

Relative condition factors of fish often fluctuate with respect to age group, sex, season, food availability and reproductive state (Le Cren, 1951; Tesch, 1971; Bagenal and Tesch, 1978). Relative condition departs from unity in only a few species. In most species, condition factors stay relatively constant through time (Weatherly, 1972). Okach (1981) reported that female *B. docmac* had higher condition during the breeding season, and that the juveniles had higher condition factors than adults. The condition factor of pond-raised *T. zillii* showed no significant variation with size (Dadzie and Wangila, 1980). The authors found the runted *T. zillii* to be in surprisingly good condition with an almost uniform relative condition approaching unity. In contrast, a number of fish species including *Esox lucius* (Bregazzi and Kennedy, 1980), *Limanda limanda* (Oretaga - Salas, 1980) and *Cyprinus carpio* (Crivelli, 1981) exhibit fluctuating cycle of condition which reflect their reproductive states. In this investigation there were no cyclical changes in the relative condition of both sexes. The uniform relative condition in *O. esculentus* in Lake Kanyaboli throughout the year is probably due to the fact that this species, like all other tropical tilapiines, does not have a marked breeding season (Dadzie, 1969, 1974; Siddiqui, 1977). Similarly, there were no marked differences in relative condition between sexes similar to the observations of Dadzie and Wangila (1980) on *T. zillii*. Because diets remained the same throughout the year and across size-classes, there was little variation in condition factor.

CONCLUSIONS

1) *Oreochromis esculentus* (Graham) is the most abundant fish species both in numbers and biomass, in Lake Kanyaboli and forms the mainstay of the commercial fishery. The average catch per canoe per day of *O. esculentus* is about 26 kg, while overall catch of all species per canoe per day is about 34 kg.

2) *O. esculentus* in Lake Kanyaboli is principally a phytoplanktivore. In addition to phytoplankton this species also occasionally ingests zooplankton and organic matter including macrophyte fragments.

3) The diet of *O. esculentus* is dominated by blue-green (Cyanophyta) and green algae (Chlorophyta). Diatoms, euglenoids and rotifers constituted a very small proportion of the diet.

4) A large proportion of blue-green and green algae and the euglenoids passed through the gut undisintegrated, whereas a large proportion of the

diatoms and zooplankton were digested.

5) Different sizes of *O. esculentus* fed on similar food types.

6) There were no clear seasonal changes in the diet of *O. esculentus*.

7) *O. esculentus* in Lake Kanyaboli fed during the day. Food in the stomach declined through the night as it was digested and assimilated.

8) The presence of a lower pharyngeal bone armed with slender teeth hooked at the distal end, an upper pharyngeal bone with teeth cusped at the distal end, a poorly developed sac-like stomach and an intestine of considerable length indicate that this species is a phytoplanktivore.

9) Both male and female *O. esculentus* exhibited isometric growth patterns.

10) The relative condition factor of the species was more or less the same throughout the year. Similarly, different sexes did not differ in their condition.

11) The stunted growth of *O. esculentus* in Lake Kanyaboli may be due to inadequate quantities of diatoms in the water.

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