TROPHIC INTERRELATIONSHIPS AMONGST CICHLID FISHES IN A TROPICAL AFRICAN RESERVOIR (LAKE CHIVERO, ZIMBABWE)

By

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Abstract

The diet of seven cichlid fish species of Lake Chivero was investigated from October 2004 to April 2005. *Oreochromis niloticus* and *O. macrochir* were microphages feeding on a wide range of algae of which *Microcystis* sp., made up >50% of their diet, while the rest of the food items were chlorophytes, diatoms, zooplankton, insects and detritus. *Tilapia sparrmanii* and *T. rendalli* were primarily macrophages consuming plant material and filamentous algae, but also fed on diatoms and zooplankton. The small species *P. acuticeps* and *P. philander* had a catholic diet comprising of algae, zooplankton, plant material, fish and detritus. *Serranochromis robustus* was a carnivore and fed mainly on fish. They were no ontogenetic diet shift for all species except for S. *robustus* and *P. acuticeps.* Diet shift occurred at 50mm SL*,* were the major food item in the diet of small < 50mm size classes was zooplankton whereas the larger fish included a wider range of food items in their diet. Dietary overlap was low and insignificant in most species, except for *O. macrochir*/*P. philander* and *T. sparrmanii*/*P. philander* in the 51-100mm size-class and *O. niloticus* and *O. macrochir* among the larger fish species (>100 mm). Competition among the small species and the juveniles of the large species may be reduced by abundant food resources, habitat preferences, ontogenetic diet and habitat shifts. Direct competition between *O. niloticus and O. macrochir* may result in the exclusion of the latter .The cichlid species in the lake were grouped into three major feeding group microphages, macrophages and carnivores and omnivores. These feeding guilds utilise most of the available food niches in the lake, except for zoo benthos and gastropods.

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INTRODUCTION

The Cichlidae is one of the largest and most distributed freshwater fish families and over 70% of known cichlids are found in Africa (Ribbink, 1991; Fryer and Iles, 1972). They are one of the six main families (Cichlidae, Embiotocidae, Pomacentridae, Odacidae, Scaridae and Labridae) in the suborder Labroidei of the order Perciformes (Stiassny, 1991). Members of this family have a general perciform body plan but a combination of distinctive features sets them apart from the other labroid families. In cichlids the lateral line is interrupted and they have one nostril opening on each side of the snout (Barlow, 2000). The dorsal and anal fins are composed of spinous and soft-rayed sections and the pelvic fins are located in the thoracic position. The arrangement of their digestive tract is unique, with the stomach consisting of an extendable blind pouch, the left-hand exit to the intestine and the first intestinal loop on the left hand side (Zihler, 1982). The head is incompletely covered with scales and the mouth is protractile and the jaws are lined with teeth which vary in structure and number according to the diet (Fryer & Iles, 1972). The plasticity of feeding behaviour in cichlids has been attributed to the structure and function of the outer jaws which complex making them amongst the most adaptively prehensile of any family of fishes (Liem, 1991; Barlow, 2000).

The cichlids possess pharyngeal jaws, located just anterior to the oesophagus, which are fused to the dorsal and ventral elements of the gill arches to produce the basipharyngeal joint, a feature unique to the family (Helfman *et al.*, 1997). The pharyngeal teeth are armed with a variety of teeth, the nature of which depends on the type of food eaten by a species. The reorganization of the musculature and the jaw articulation of the lower and upper plates has led to a series of complex and powerful movements in the mastication of prey (Nshombo, 1991). The development and diversification of the pharyngeal jaws, together with changes to the outer jaws and dentition is a critical feature which has enabled cichlids to exploit a wide range of food resources and given them the potential to evolve further feeding specializations (Liem, 1991).

The adaptive radiation of the feeding habits of cichlid fishes in the East African lakes is a commonly cited example (Fryer & Iles, 1972; Lowe–McConnell, 1987; Ribbink, 1991). Most cichlids retain sufficient trophic flexibility to adapt to changes in the availability of food and to opportunistically feed on prey types that are not normally utilized (Yamaoka, 1991; Lowe–McConnell, 1987; Liem, 1991). The cichlids display a wide range of morphological and ecological adaptations, enabling them to occupy many different freshwater niches (Lowe-McConnell, 1975; Fryer & Iles, 1972), which Ross (2000) attributes to their robustness, tolerance and flexibility, and overall plasticity. They have a remarkable physiological hardiness, adaptability and general level of tolerance to most potentially limiting environmental variables (Philippart & Ruwet, 1982; Chervinski, 1982).

This study investigated trophic interrelationships amongst the cichlid fishes in Lake Chivero, a eutrophic impoundment on the Manyame River. The lake was built in 1956 to supply water to the city of Harare. Secondary uses include commercial and sport fisheries industry, the supply of water for irrigation, tourism and water sports (Magadza, 2003). It has a capacity of 247 million cubic metres, a mean depth of 9.4m and a surface area of 26.3 km^2 (Burke & Thornton, 1982). Its catchment area is 2136 km^2 (Munzwa, 1982) and inflow is mainly from the Manyame, Mukuvisi and Marimba rivers (Nhapi *et al*, 2002). Sewage and industrial effluent is discharged into these rivers and the lake has been eutrophic since the 1960s (Munro, 1966; Marshall, 1997; Magadza, 2003). The lake has suffered from various water quality problems, the most important of which are severe blooms of blue-green algae and the accelerated growth of macrophytes, notably the water hyacinth *Eichhornia crassipes*. Severe fish kills caused by anoxia and ammonia toxicity at overturn, or poisoning from the ingestion to toxic blue-green algae (Moyo, 1997).

Marshall (1982) listed 26 fish species in Lake Chivero of which 21 were indigenous, the rest having been introduced from various parts of the world. But the number has changed since then because of introductions (*Oreochromis niloticus* and *Serranochromis robustus*) and species which were once numerous have not been recorded recently and may have disappeared from the system e. g., the African mottled eel *Anguilla bengalensis labiata*, and the eastern bottlenose *Mormyrus longirostris* (Gratwicke *et al.*, 2003).

The study investigated patterns in resource use amongst the cichlid species present in the lake. The generalised riverine species, *Pseudocrenilabrus philander* and *Pharyngochromis acuticeps* are small, omnivorous species and are common in shallow, sheltered areas of the Lake Chivero (Marshall & Lockett, 1976, Brendock *et al*, 2003). The predatory cichlid *Serranochromis robustus* was introduced from the Upper Zambezi and became widely distributed throughout Zimbabwe by the 1970s (Toots, 1970; Toots & Bowmaker, 1976) although it was absent from Lake Chivero at this time (Marshall, 1982), only becoming established there rather later in the 1980s or 1990s (the date of their introduction is uncertain).

The red-breasted tilapia, *Tilapia rendalli,* and the banded tilapia, *T. sparrmanii* are both indigenous to the system although *T. rendalli* were stocked in 1956 to improve commercial fishing and reduce weed growth (Lewin, 1957). It was established by 1962, making up 20 % of the landed catch (Marshall, 1982) and its success was attributed to the presence of extensive beds of water lilies (*Nymphaea* sp.) and associated plants (Munro, 1966). It was implicated in the destruction of these macrophyte beds by Junor (1969) but it is more likely that the increasing severity of algal blooms prevented their growth and led to their destruction (BE Marshall, personal communication). *Tilapia sparrmanii was* first recorded in the lake by Munro (1966) but it remained scarce until at least the 1980s (Marshall, 1982). Its numbers have increased sine then and it is now an important member of the lake's fish assemblage.

The green-headed tilapia *Oreochromis macrochir* was also introduced in 1956 (Lewin, 1957) and rapidly become the most important species in the lake displacing the native *O. mossambicus* which had never been numerous (Marshall, 1982). It made up < 10% of the commercial catch in 1963 but this had risen to 60% by 1972 (Marshall, 1982). Its success was attributed to the permanent blooms of blue green algae, a major constituent in the fish's diet. *Oreochromis macrochir* is a microphage, feeding on algae, periphyton and other small organic particles, while juveniles feed on diatoms (Minshull, 1978). The Nile tilapia, *O. niloticus,* was first recorded from the lake in 1992 suggesting that it was stocked into the lake in the middle or late 1980s. Its diet also consists of blue-green algae, diatoms and macrophytes detritus (Trewavas, 1983, Lowe-McConnell, 1991; Njiru *et al.*, 2004) so the two microphages (*O. macrochir* and *O. niloticus*) may be in competition for the same food resources. *Oreochromis niloticus* supplanted *O. macrochir* as most the important commercial species in 1998 and it currently makes up to 50% of the landed catch (Table 1)

A fundamental question about the ecology of cichlids is how sympatric species sharing the same food resources are able to coexist, because ecological differentiation is a necessary condition for coexistence (Hardin, 1960). Resource partitioning has enabled many fish species to coexist in tropical communities through varied array of morphological and ecological adaptations (Lowe-McConnell, 1987). The problem of coexistence cannot be approached only by stomach content analysis. In a recent review of the feeding ecology of cichlids in the great lakes Yamoaka, (1991) indicates that species that have been regarded as sharing the same trophic requirements show slight but distinct interspecfic differences in feeding behaviour, feeding sites and habitat. Differences in resources use do not automatically imply competition is occurring; physiological requirements, phylogenetic constraints and differential susceptibility to predation can also produce species differences in resource use (Helfman *et al.*, 1997).

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Table 1. The mean relative abundance (no. of fish/ setting/net) of fish in Lake Chivero, 1992-2002. The symbol ● = species present but <1% of the total number of fish. Data from Lake Chivero Fisheries Research Centre records.

	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002
Mormyrus longirostris	●								●		
Cyphomyrus discorhynchus	●	●	●	●	●	●		●		●	●
Marcusenius macrolepidotus	2.73	2.03	0.64	0.29	0.29	0.33	0.25	0.21	0.28	0.16	0.24
Labeo cylindricus	0.48	0.21	0.55	0.62	0.13	0.28	0.32	0.22	0.18	0.02	0.06
Labeo altivelis	2.79	1.23	1.56	0.51	0.36	0.24	0.14	0.11	0.11	0.10	0.15
Barbus radiatus	●				●						
Barbus trimaculatus	●	●	●	●				●			
Barbus paludinosus	●	●	●	●	●	●	●	●	●		
Cyprinus carpio							●	●	●	●	0.2
Hydrocynus vittatus	●	●	●	●			●	●	0.46	0.23	0.03
Brycinus imberi	0.69	0.32	●	●	●	●	●	●	●	0.08	●
Clarias gariepinus	1.21	0.90	1.27	1.10	1.56	1.82	1.50	0.74	0.84	1.11	1.28
Micropterus salmoides	●	●	●	●	●	●	●	●	●	●	●
Pseudocrenilabrus philander		●	●	●		●	●				
Pharyngochromis acuticeps	0.40	0.49	1.45	1.31	1.21	2.95	2.43	1.21	0.81	0.01	0.20
Sargochromis codringtonii	●	●	●	●		●	●				
Serranochromis robustus	0.12	0.24	0.58	0.56	0.47	0.54	0.45	0.26	0.09	0.05	
Tilapia rendalli	0.38	0.64	0.40	0.42	0.35	0.34	●	●		●	●
Tilapia sparrmanii	0.63	0.65	1.25	1.46	1.01	0.83	0.69	0.25	0.33	0.16	0.03
Oreochromis mossambicus	●	●	●	●	●	●	●	●	●	●	
Oreochromis niloticus	●	●	●	0.79	0.93	0.94	8.74	4.66	4.48	3.89	2.76
Oreochromis macrochir	10.92	11.32	12.95	20.98	8.39	5.02	2.23	1.39	1.83	1.42	1.03
Total	20.52	18.40	21.10	28.52	15.07	13.90	17.11	9.19	9.56	7.32	6.01

Pianka (1974) argues that equating overlap with competition is misleading as they may often be an inverse relationship between overlap and competition. If resources are not in short supply, two organisms can share them without detriment to one another. Thus, extensive niche overlap may actually be collated with reduced competition. Similarly disjunct niches may often indicate avoidance of competition in situations where it could be potentially severe. Causal factors responsible for difference in resource use are rarely known (Ross, 1986) because of the shortcoming of both experimental and observational studies in demonstrating competition in nature (Schoener, 1974). Through the process of inference descriptive studies can provide strong circumstantial evidence to support or reject the hypothesis of interspecfic competition and the strength of such evidence is dependent on strength of comparison based on interspecfic, or temporal and spatial variation (Winemiller, 1989).

Little research has been conducted on the feeding ecology of fish communities in Lake Chivero. In one of the few comprehensive studies Munro (1967), investigated five species in-depth and made observations on 6 less important species. Caulton (1975) and Minshull (1978) gave information on the food habits of *T. rendalli* and *O. macrochir.* The objective of this study was to investigate the diet and possible resource partitioning in the cichlid fishes of Lake Chivero and to determine the extent of overlap in the diets of the small species and juveniles of the large species. The occurrence of ontogenetic shifts in the diet of these cichlids was investigated across size classes to determine the degree of resource partitioning amongst the adult fish. It was hypothesized that the diets of the small species and the juveniles of large ones overlap and they compete with each other but this overlap would decrease as they get older and more specialised in their diet. The young of teleosts are typically zooplanktivorous and feed by active visual capture of zooplankton (Lazzaro, 1987). This could be a bottleneck in the provision of food to juveniles leading to competition for resources but as they grow and become more specialized their feeding niches are more likely to diverge and competition should decrease.

The cichlids in Lake Chivero were expected to separate into three groups: (a) microphages (*O. macrochir*, *O. niloticus*) (b) macrophages (*T. rendalli*, *T. sparrmanii*) and (c) carnivores and omnivores (*P. philander*, *P. acuticeps*, *S. robustus*). The following research questions were addressed: (a) is there an overlap in the diets of small species and juveniles of large ones and do they compete with each other? (b) Is there any size related dietary shift in the food habits of these cichlids and does it reduce competition amongst adults?

METHODS

Fish were collected from Lake Chivero with gill nets ranging from 12 mm to 120 mm mesh size, an electro fisher, and a beach seine net. Specimens were sorted according to species, measured to standard length and weighed after which their stomachs were dissected out and preserved in 5% formalin for 24 hrs to allow fixation of tissues and then transferred to 75% alcohol for storage. The contents of each stomach were suspended in 100ml of water per gram of stomach contents and examined under an inverted microscope. Each item in the diet was identified to the lowest possible taxonomic level and counted.

The diet was first determined by the frequency of occurrence method, which records the percentage of stomachs containing a particular food item out of the total stomachs containing food (Hyslop, 1980). The food items were then combined into broader taxonomical or functional categories for quantitative comparisons. These diet categories were chlorophytes, cyanophytes, diatoms, microfauna (zooplankton, insects and protozoa), fish, macrophytes, detritus and unidentified items. The point system was used to estimate the contribution of each food category by evenly spreading all contents from each gut in the counting cell chamber and examining under microscope. The area occupied by each food category in the chamber was later converted to the percentage of each food category. Broader food categories were not used for numerical analyses, because (1) lower taxonomic categories generally represented one or more renewable resources, and (2) lumping resources states often inflates niche overlap values (Winemiller, 1989).

The fish were grouped into 50-mm size classes so that ontogenetic shifts in diet could be determined. Some indices were used to interpret feeding, as follows: (1) the vacuity index (VI) is the number of empty stomachs as a percentage of the total number of stomachs examined; (2) the gut fullness GF) is an average of the relative fullness of all stomachs examined on a scale of 0 (empty) to 4 (fully distended with food). (3) Diet diversity was estimated by Levin's (1968) standardized index of niche breadth. This index is calculated by:

$$B_i = \frac{1}{n-1}\left[\left(\frac{1}{\sum p_{ij}}\right)-1\right]$$

where B_i = Levin's standard index for predator '*i*'; 'P_{ij}'= proportion of diet for predator for predator '*i*' that is made up of prey '*j*'; '*n*'= number of prey categories.

Diet similarities were calculated from Pianka`s (1973) symmetrical measure of niche breadth in which:

$$O_{jk} = O_{kj} = \frac{\sum (P_{ik} P_{ij})}{\sqrt{(\sum P_{ik}{}^2 \sum P_{ij}{}^2)}}$$

where O_{jk} and O_{kj} = symmetric niche overlap coefficient between species *j* and species *k,* and P_{ik} and P_{ij} = the proportions of the *i*th resource used by the *j*th and *k*th species. For each index, values may range from near zero (indicating a specialized diet or almost no overlap) to 1.0 (even use of food resources or indicating a complete overlap).

The classification and definition of the rate of overlap was compared with Langton (1982) low overlap = 0.0-0.29, moderate overlap = 0.30-0.59 and high overlap (biologically significant) = 0.6-1.00.

RESULTS

Seven of the nine cichlid species known to occur in Lake Chivero were collected during this study; the two that were not collected were *Oreochromis mossambicus*, now rare or possibly extinct in the lake, and *Sargochromis codringtonii*, which was introduced in the 1970s but has rarely been caught since. Where available, a subsample of 20 specimens of each size class per species was dissected for stomach content analysis. The largest sample was of *O. niloticus* (N = 171) and also covered the largest size range from 51 mm to greater than 300 mm. *Oreochromis macrochir* was represented by a smaller sample (N = 79) extending over a smaller size range from 51 mm to 250 mm (Table 2). None of the specimens of three small species, *Pharyngochromis acuticeps* (N= 88), *Pseudocrenilabrus philander* (N = 53) and *Tilapia sparrmanii* (N = 33), exceeded 100 mm in length.

The last two species, *T. rendalli* (N =37) and *S. robustus* (N = 89) can grow to a large size but the specimens collected in this study were all small ones, being less than 100 mm and less than 200 mm in length respectively. For all the species, the vacuity index (VI) was low in the small size classes (< 150mm) and generally increased in large size classes. The gut fullness (GF) was relatively high in *O. niloticus, O. macrochir, T. sparrmanii* and *T. rendalli* (3.0 ± 0.9 to 4.0 ± 0.0) and low in the *P. acuticeps, P. philander and S. robustus* (1.5 ± 1.0 to 3.1 ± 1.2).

Table 2. The dietary attributes of the stomachs collected from cichlid fish species in Lake Chivero, November 2004 - March 2005. N = total number of stomachs examined, VI=vacuity index, and GF = mean stomach fullness.

Species	Size class (mm SL)	N	VI (%)	GF
Oreochromis niloticus	51-100	23	13.0	3.8 ± 0.4
	101-150	27	7.4	3.5 ± 0.5
	151-200	29	31.0	3.0 ± 0.9
	201-250	34	41.2	3.7 ± 0.5
	250-300	28	28.6	3.1 ± 1.1
	>300	30	33.3	3.3 ± 0.9
O. macrochir	51-100	22	16.7	3.5 ± 0.6
	101-150	24	21.4	3.6 ± 0.5
	151-200	14	18.2	3.5 ± 0.7
	>200	19	47.4	3.6 ± 0.7
Tilapia sparrmanii	51-100	23	21.5	3.9 ± 0.6
	>100	10	0.0	4.0 ± 0.0
T. rendalli	51-100	27	3.6	3.9 ± 0.6
	>100	10	30.0	4.0 ± 0.0
Pharyngochromis acuticeps	<50	24	28.6	1.5 ± 1.0
	51-100	69	71.0	3.1 ± 0.9
Pseudocrenilabrus philander	<50	24	20.8	1.9 ± 1.4
	51-100	29	20.8	2.6 ± 1.2
Serranochromis robustus	51-100	25	16.0	1.5 ± 1.0
	101-150	29	34.5	3.1 ± 1.2
	>200	35	51.4	2.9 ± 1.1

Oreochromis niloticus was a microphage and its diet consisted almost entirely of algae over all size classes with a wide range of species being eaten (Table 3). Other food items included rotifers, especially in the smallest and largest size classes, zooplankton and some insects and other items. The major difference between the diet of the 50-100 mm size class and the other sizes was the size spectrum of the prey ingested. The 50-100 mm size class consumed small food items consisting mainly of desmids such as *Ankistrodesmus*, *Scenedesmus*, *Trachelomonas*, filamentous algae, diatoms and detritus, while the diet of the other size classes consisted of larger items including zooplankton, colonial algae and coarse plant detritus. This suggests that 100mm SL may be a critical length after which diet include larger food. Because of this, there was no significant dietary overlap between the 51-100 mm size class and any of the other size classes

Table 3. The diet (% occurrence) of *Oreochromis niloticus* in relation to length, Lake Chivero, November 2004-March 2005. N = number of stomachs examined, B = Levin's standardised index of niche breadth.

		Length class (mm)					
		51-100	101-150	151-200	201-250	251-300	>300
N		23	27	29	34	28	30
B		0.7	0.6	0.6	0.6	0.7	0.7
Cyanophyceae	*Merismopedia*	12.5	20.0	53.9	5.0	40.0	13.7
	Microcystis	93.7	10.0	92.3	100.0	100.0	91.7
	Oscillatoria	87.5	50.0	53.9	33.3	40.0	75.0
	Spirulina		20.0	15.8	16.7	30.0	25.0
	Anabaena	68.8					66.7
Euglenophyceae	*Trachelomonas*	81.3	100.0	76.9	91.7	60.0	91.7
	Phacus	31.3	20.0	7.7	16.7	20.0	41.7
	Euglena	31.3	10.0	15.8	8.3	50.0	25.0
Chlorophyceae	*Ankistrodesmus*	87.5	10.0	7.7	25.0		58.3
	Asterococcus	25.0	90.0	100.0	75.0	100.0	58.3
	Closterium	37.5	30.0	7.7		10.0	
	Chlamydomonas		10.0			10.0	
	Coelastrum		20.0	7.7	16.7	50.0	
	Cosmarium	50.0	50.0	30.8	52.0	30.0	8.3
	Eudorina			7.7		20.0	
	Filamentous algae	68.8	70.0	20.0	33.3	50.0	13.7
	Pediastrum	81.3	90.0	92.3	100.0	100.0	100.0
	Scenedesmus	100.0	80.0	92.3	75.0	100.0	83.3
	Staurastrum	68.8	30.0	61.5	50.0	60.0	50.0
	Gonium	75.0	70.0	76.9	75.0	90.0	100.0
	Tetrastrum	18.8		23.1	33.3	20.0	58.3
Diatomophyceae	*Cycotella*	93.8	90.0	69.2	75.0	80.0	91.7
	Cymbella	43.8	40.0	7.7			16.7
	Gomophonema	12.5	40.0	15.8		30.0	8.3
	Melosira	68.8	90.0	100.0	100.0	100.0	75.0
	Navicula	62.5	80.0	84.6	75.0	100.0	41.7
	Pinnularia	12.5	50.0	23.1	25.0	60.0	41.7
	Synedra	37.5	30.0	69.2	58.3	40.0	58.3
Dinophyceae	*Ceratium*	6.3			8.3		
Rotifers	*Brachionus*	68.8	20.0	15.8	8.3		75.0
	Keratella	18.8	20.0			20.0	33.3
	Platyias						41.0
Cladocera	*Daphnia*				8.3		
	Bosmina	18.8	30.0	84.6	91.7	100.0	50.0
	Cladocera remains	31.3	10.0	7.7			16.7
Copepods	Calanoida				8.3	10.0	8.3
	Cyclopoid	6.3	10.0	15.8	16.7	20.0	13.7
	Nauplius larvae	6.3		76.9	66.7	80.0	25.0
Rhizopoda	*Centropyxis*	37.5	40.0	53.9	58.3	70.0	58.3
Insects			10.0		16.7		
Plant detritus		81.3	100.0	92.3	100.0	100.0	66.7
Detritus		31.3	30.0				

although the diet of all the other size classes overlapped extensively (Table 4). Apart from the differences in the 51-100 mm size class there was no other evidence of an ontogenetic shift in the diet in *O. niloticus*.

Table 4. Dietary overlap among different size classes of *Oreochromis niloticus* from Lake Chivero, November 2004-March 2005. The values are Pianka`s (1973) symmetrical measure of niche breadth coefficients: significant values (>0.60), indicated in bold font, imply an extensive overlap in the diet with no biologically significant differences in the diet of different size classes.

SL (mm)	>300	251-300	201-250	151-200	101-150
50-100	0.402	0.451	0.400	0.415	0.428
101-150	**0.797**	**0.827**	**0.831**	**0.834**	
151-200	**0.877**	**0.934**	**0.977**		
201-250	**0.891**	**0.931**			
251-300	**0.826**				

The other microphagous cichlid in the lake was *O. macrochir*, which like *O. niloticus* also fed primarily on algae (Table 5). *Microcystis* made up 50% of its diet, while the rest of the food items were chlorophytes, diatoms, zooplankton, insects and detritus. The 50- 150mm size-classes consumed mainly diatoms and algae, while the diet of the 151-200 size-class consisted mostly of zooplankton and algae dominated by *Microcystis*, *Gonium* and *Phacus*. Fish > 200mm SL mainly fed on the cyanobacterium *Microcystis*. There were some significantly low dietary overlaps between size classes but these were not consistent and it is not clear if there was any ontogenetic change in diet (Table 6).

Table 5. The diet (% occurrence) of *Oreochromis macrochir* in relation to length, Lake Chivero, November 2004-March 2005. N = number of stomachs examined, B = Levin's standardised index of niche breadth.

		Length class (mm)			
		51-100	101-150	151-200	>200
N		22	24	14	19
B		0.8	0.8	0.8	0.7
Cyanophyceae	*Merismopedia*	25.00	63.6	66.7	
	Microcystis	100.0	100.0	100.0	100.0
	Oscillatoria	75.0	81.8		75.0
	Spirulina				12.5
Euglenophyceae	*Trachelomonas*	75.0	100.0		87.5
	Phacus	25.0		66.7	25.0
	Euglena	25.0			50.0
Chlorophyceae	*Ankistrodesmus*	25.0			75.0
	Asterococcus	75.0	100.0	66.7	37.5
	Closterium	50.0	18.2		
	Cosmarium	75.0	90.9		12.5
	Filamentous algae	75.0	90.9	33.3	37.5
	Pediastrum	25.0	72.7		100.0
	Scenedesmus	100.0	100.0	33.3	100.0
	Staurastrum	25.0	9.09		37.5
	Gonium	75.0	27.3	33.3	87.5
	Tetrastrum			66.7	50.0
Diatomophyceae	*Cycotella*	75.0	90.9		12.5
	Cymbella		81.8	66.7	25.0
	Gomophonema	75.0	81.8		25.00
	Melosira	75.0	72.73		100.0
	Navicula	100.0	90.9		87.5
	Pinnularia	75.0	81.8	33.3	12.5
	Synedra	25.0			50.0
Rotifers	*Brachionus*		72.73	100.0	37.5
	Keratella				37.5
Copepods	Nauplius larvae			100.0	25.0
Cladocera	*Bosmina*	75.0	81.82	33.33	50.
	Cladocera remains	25.0	63.6		25.0
Rhizopoda	*Centropyxis*			33.3	
Insects				100.0	
Plant detritus		100.0	9.1	33.3	100.0
Unidentified material		75.0	90.9		33.3

Table 6. Dietary overlap among different size classes of *Oreochromis macrochir* from Lake Chivero, November 2004-March 2005. The values are Pianka`s (1973) symmetrical measure of niche breadth coefficients: significant values (>0.60), indicated in bold font, imply an extensive overlap in the diet with no biologically significant differences in the diet of different size classes.

SL (mm)	201-250	151-200	101-150
50-100	**0.801**	0.285	**0.865**
101-150	**0.713**	0.342	
151-200	0.361		

Tilapia sparrmanii is a small species and none of the fish collected exceeded 150 mm in length. Although it fed on algae, it also took larger particles with plant detritus being an important food item with a frequency of occurrence of 78% and 50% in the 50-100mm and >100mm size classes, respectively (Table 7). The main constituents of the diet were diatoms and chlorophytes, especially filamentous algae, which were a conspicuous component of their diet. The dietary overlap between the two size classes was high (0.920) and highly significant (>0.60) and there was no evidence of an ontogenetic change.

Although *T. rendalli* is larger than *T. sparrmanii* only small specimens were caught in this study with only 10 specimens greater than 100mm being collected. It was primarily a macrophage and ingested mainly plant material, but also fed on diatoms, zooplankton and filamentous algae (Table 7). The dietary overlap between the 51-100mm SL and >100mm SL size classes was high and significant (0.864) with no evidence of ontogenetic change.

Table 7. The diet (% occurrence) of *Tilapia sparrmanii and T. rendalli* in relation to length, Lake Chivero, November 2004-March 2005. N = number of stomachs examined, B = Levin's standardised index of niche breadth.

		T. sparrmanii		*T. rendalli*	
		51-100 mm	>100 mm	51-100 mm	>100 mm
N		23	10	27	10
B		0.7	0.7	0.8	0.5
Cyanophyceae	*Chroococcus*				14.6
	Merismopedia	27.8		5.9	14.6
	Microcystis	66.7	90.0	17.7	28.6
	Oscillatoria	50.0	40.0	76.5	42.9
	Spirulina	50.0			14.6
Euglenophyceae	*Anabaena*				28.6
	Trachelomonas	72.2	40.0	29.4	42.9
	Phacus	33.3	20.0		
	Euglena	16.7			
Chlorophyceae	*Ankistrodesmus*		20.0	17.7	14.3
	Asterococcus	44.4	60.0		
	Closterium	11.1		5.9	
	Cosmarium	50.0	20.0	41.2	28.6
	Filamentous algae	72.0	60.0	100.0	71.4
	Pediastrum	83.3	80.0	17.7	42.9
	Scenedesmus	72.2	80.0	70.6	71.4
	Staurastrum	66.7	60.0	5.9	14.6
	Gonium	83.3	70.0	11.8	28.6
	Tetrastrum		20.0		
Diatomophyceae	*Amphora*				14.3
	Cycotella	100.0	80.0	47.6	71.4
	Cymbella	38.9	20.0		
	Gomophonema	72.0	40.0		
	Gyrosigma	5.6			14.3
	Melosira	88.9	70.0	29.4	57.1
	Navicula	94.4	90.0	5.9	71.4
	Pinnularia	77.8	50.0	5.9	28.6
	Synedra	55.6	20.0		
Rotifers	*Brachionus*	38.9	20.0	35.3	14.6
	Keratella		20.0		
Cladocera	*Bosmina*	5.6	30.0	5.9	14.6
	Cladocera remains	61.1	30.0	5.9	
Copepods	*Calanoida*		20.0	35.3	14.6
	Nauplius larvae	11.1	20.0		
Rhizopoda	*Centropyxis*	27.8	20.0	35.3	28.6
Plant detritus		77.8	50.0	100.0	100.0

Pharyngochromis acuticeps and Pseudocrenilabrus philander are small species and none of the fish collected exceeded 150 mm in length. *Pharyngochromis acuticeps* was an omnivore that utilised a wide spectrum of food resources including algae, diatoms, detritus and zooplankton (Table 8). The dietary overlap between <50mm and 51-100mm size-classes was low (0.083) with the smaller fish feeding mostly on zooplankton while the larger ones were generalists, utilizing diatoms, detritus and fish. This indicated an ontogenetic diet shift in this species (Figure 1).

Table 8. The diet (% occurrence) of *Pharyngochromis acuticeps and Pseudocrenilabrus philander* in relation to length, Lake Chivero, November 2004-March 2005. N = number of stomachs examined, B = Levin's standardised index of niche breadth.

		P. acuticeps		*P. philander*	
		<50	51-100	<50	51-100
N		24	64	24	29
B		0.6	0.7	0.5	0.7
Cyanophyceae	*Microcystis*		8.7	35.7	33.3
	Oscillatoria		4.4		33.3
Euglenophyceae	*Trachelomonas*			21.4	66.7
	Phacus		43.5		
	Euglena		39.1		
Chlorophyceae	*Ankistrodesmus*		4.4		
	Asterococcus			7.1	11.1
	Closterium			7.1	33.3
	Cosmarium		4.4	14.3	
	Filamentous algae		43.5	42.9	33.3
	Pediastrum		43.5		44.4
	Scenedesmus		4.4	35.7	66.7
	Gonium		39.1		
Diatomophyceae	*Cycotella*		13.0	42.9	77.8
	Cymbella		52.2	7.1	
	Gomophonema		4.4	14.3	
	Melosira		4.4	35.7	66.7
	Navicula	50.0	13.0	21.4	44.4
	Pinnularia		4.4	14.3	22.2
	Synedra			14.3	33.3
Rotifers	*Brachionus*		37.8		
	Keratella	25.0	4.4	7.1	11.1
Cladocera	*Daphnia spp*	25.0			
	Bosmina		4.4		33.3
Copepods	*Cyclopoid*	25.0	4.4	21.4	33.3
	Calanoida	75.0	4.4	35.7	55.6
Rhizopoda	*Centropyxis*		17.4	50.0	33.3
Plant material			13.0	78.6	88.9
Fish			56.5	28.6	22.2
Unidentified material			56.5	92.9	88.9

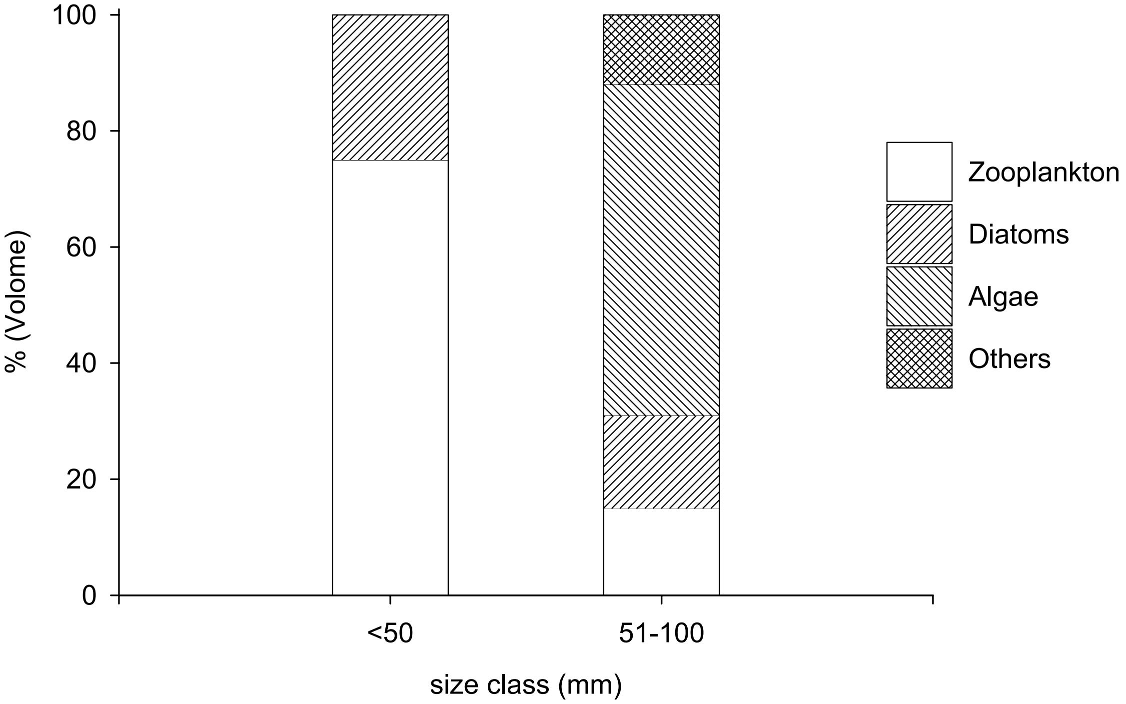

Figure 1: The diet (% volume) of *Pharyngochromis acuticeps* in relation to length, Lake Chivero, November 2004-March 2005, showing the shift that occurred between fish smaller and larger than 50 mm in length

The other omnivorous cichlid in the lake was *P. philander*, which like *P. acuticeps* was generalist feeder (Table 8). There was no ontogenetic diet shift in its feeding habits as both size classes (<50 mm and 51-100mm SL) had similar diets, consisting of algae, diatoms, zooplankton, fish and plant material.

Few large specimens of the predator *S. robustus* were caught and only three size classes could be distinguished. There was a low dietary overlap between the >50mm size-class and any of the other two size-classes. The diet of the <50 mm size-class consisted of zooplankton and insects while >50mm the diet shifted with fish becoming the most important food (Table 9). This was a marked ontogenetic shift with 50 mm apparently being the critical length at which this species became predominantly piscivorous (Figure 2).

Table 9. The diet (% occurrence) of *Serranochromis robustus* in relation to length, Lake Chivero, November 2004-March 2005. N = number of stomachs examined, B = Levin's standardised index of niche breadth.

		Length class (mm)		
		<50	51-100	>200
	N	25	29	35
	B	0.6	0.4	0.0
Cyanophyceae	*Microcystis*		5.3	
Euglenophyceae	*Euglena*	18.2	10.5	
Chlorophyceae	*Cosmarium*		5.3	
	Filamentous algae		5.3	
	Scenedesmus		5.3	
Diatomophyceae	*Cycotella*		5.3	
	Cymbella		5.3	
	Melosira	9.09	5.3	
	Navicula		5.3	
	Pinnularia		5.3	
Cladocera	*Bosmina*	27.3	5.3	
Copepods	*Calanoida*	63.6	21.1	
	Cyclopoid	27.3	15.8	
Rhizopoda	*Centropyxis*	18.2	10.5	
Insects		27.3	5.3	
Plant material		9.1	10.5	
Fish		9.1	84.2	
Unidentified material		63.6	26.3	100.0

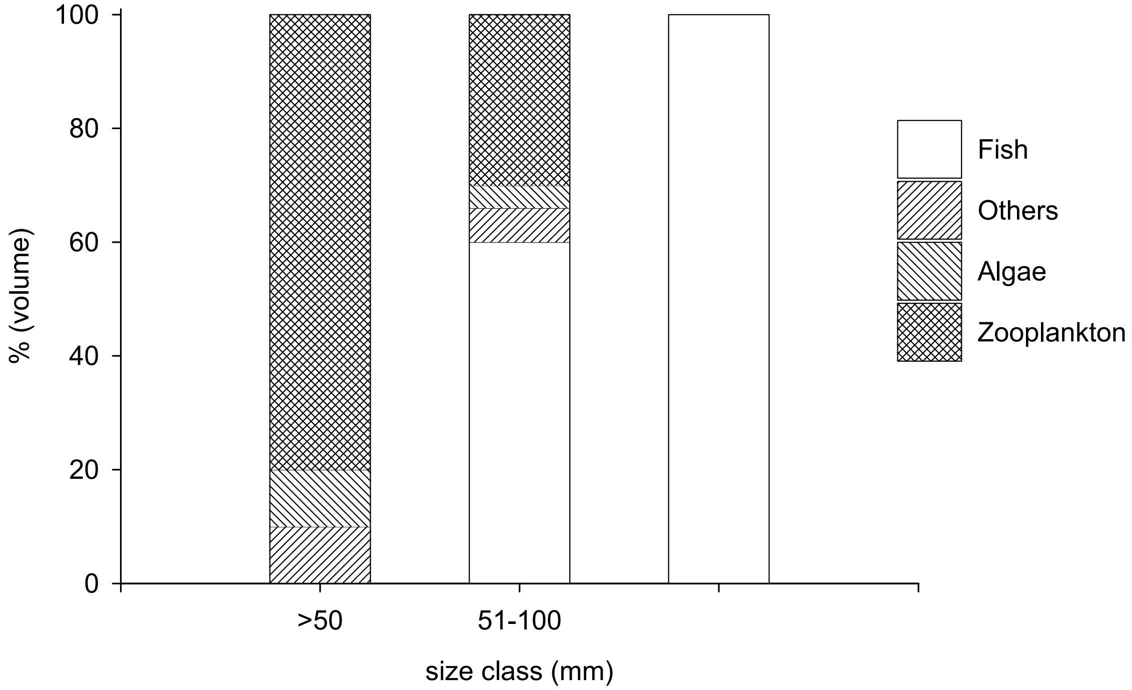

Figure 2: The diet (% volume) of *Serranochromis robustus* in relations to length in Lake Chivero, November 2004-March 2005. Note the diet shift that occurred 50 mm SL.

Based on the gut content analysis of the major cichlids species in the lake some indication of trophic relationship can be seen (Figure 3).Three trophic feeding groups were distinguished: (a) microphytes (*O. niloticus*; *O. macrochir*) (b) macrophytes (*T. sparrmanii, T. rendalli*) (c) carnivores and omnivores (S. *robustus, P. acuticeps, P. philander*). The major food constituent of the microphages is the cyanobacterium *Microcystis* which contributes ≥ 50% by volume of the fish's diet. The other major food items are the chlorophytes and diatoms. *T. sparrmanii* and *T. rendalli* constitute the other feeding guild which consumed mainly macrophytes and filamentous algae. Macrophytes made up about 46 % and 75% in the diet of *T. sparrmanii* and *T. rendalli* respectively.

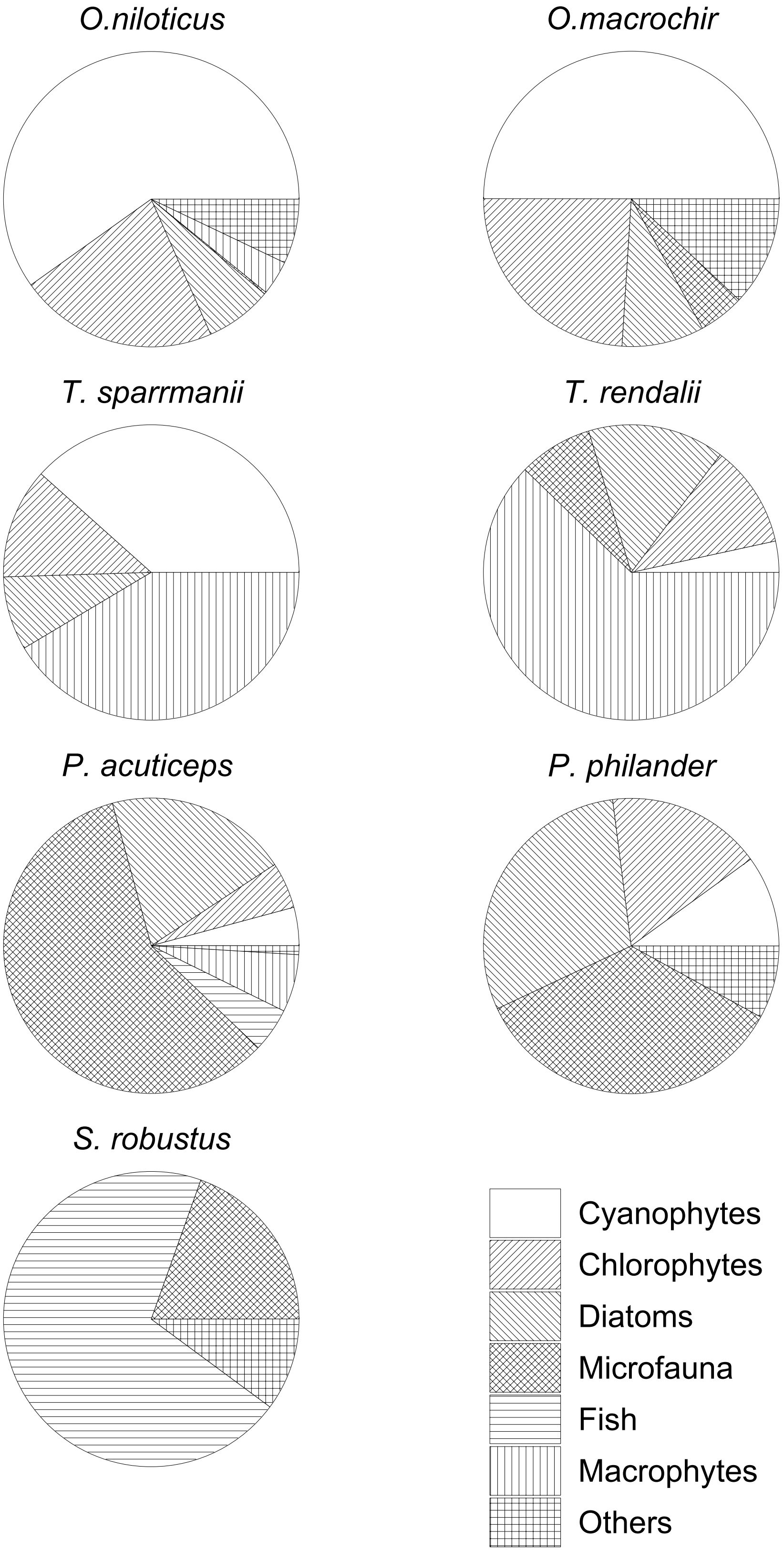

Figure 3. A comparison of the diet (% volume) of cichlid fish species in Lake Chivero. November 2004-March 2005. Microfauna = zooplankton, insects and protozoa

The carnivores and omnivores utilised a varied range of food habits. The small species *P. acuticeps* and *P. philander* had a catholic diet comprising of algae, zooplankton, plant material, fish and detritus. The main constituent of the diet of the two species was zooplankton. *Serranochromis robustus* was carnivorous and its diet consisted of zooplankton and fish. These feeding guilds appear

Table 10. The dietary overlap among very small (<50 mm: upper left panels) and small (51-100 mm: lower right panels) size-classes of cichlid fishes in Lake Chivero, November 2004-March 2005. The values are Pianka`s (1973) symmetrical measure of niche breadth coefficients with significant values (< 0.60) in bold font, na = data not available.

	S. robustus	*P. philander*	*P. acuticeps*	*T. rendalli*	*T. sparrmanii*	*O. macrochir*	*O. niloticus*
O. niloticus	na	na	na	na	na	na	
O. macrochir	na	na	na	na	na		0.382
T. sparrmanii	0.067	0.354	0.164	0.322		**0.842**	0.408
T. rendalli	0.068	0.261	0.185		0.363	0.211	0.465
P. acuticeps	0.515	0.413		0.490	0.440	0.402	0.247
P. philander	0.387		0.395	0.314	**0.682**	**0.779**	0.469
S. robustus		0.160	0.210	0.041	0.054	0.113	0.117

In the very small (<50mm) size class, there was some dietary overlap among the omnivores /predators *S. robustus*, *P. acuticeps* and *P. philander* (values ranging from 0.387 to 0.515) and among the herbivores *T. sparrmanii, T. rendalli* and *P. philander* (0.261-0.354) but it was low and there were no significant overlaps (Table 10). There was a low dietary overlap in most species in the 51-100mm size-class, except for *O. macrochir*/*P. philander* and *T. sparrmanii*/*P. philander*.

There was low overlap in larger fish species (>100 mm), except for *O. niloticus* and *O. macrochir* (Table 11).

Table 11. The dietary overlap among large size classes (> 100 mm) of cichlid fish species in Lake Chivero, November 2004-March 2005. The values are Pianka`s (1973) symmetrical measure of niche breadth coefficients with significant values > 0.60 in bold font, na = data not available.

	S. robustus	*T. rendalli*	*O. macrochir*
O. niloticus	0.000	0.385	**0.612**
O. macrochir	0.036	0.463	
T. rendalli	0.026		

DISCUSSION

Food resource partitioning was evident among the cichlid fish species of Lake Chivero during the present study. Dietary overlap was generally low and insignificant in the diets of the small species and juveniles of the large species. Various reasons have been used to explain patterns of resource exploitation, and foremost among them is interspecfic competition, although predation and the effect of environmental factors have recently received greater attention (Schoener, 1974; Winemiller, 1989; Werner & Gilliam, 1984). Diet change can be due to variations in the environmental or biotic interactions, such as competition or predation. Such changes are also a response to the `optimum foraging theory` in which the cost/benefit ratio in catching prey is considered (Helfman *et al*., 1997).

However, many species showed little ontogenetic diet shift. Le-Roux (1956) reported that tilapias all preferred zooplankton at total lengths <50mm. The smallest individuals in Lake Chivero samples were 35-50mm SL, except for *O. niloticus* (minimum 52mm) and *O. macrochir* (minimum 57mm). This could account for the lack evidence of diet shifts in the respective species.

Cichlids are opportunistic and generalized consumers during periods when resources are plenty and switch to a more specialized feeding during periods of relative resource scarcity (Winemiller, 1991; Winemiller & Winemiller, 2003; Lowe-McConnell, 1987). Hence it could be inferred that food resources were not liming in the lake and this could account for the low dietary overlap. The lake is characterised by permanent blooms of blue-green algae and this has led to very high levels of primary productivity (Marshall, 2005).

P. acuticeps and T. sparrmanii occur in a wide range of habitats whilst *P. philander* is more often confined to areas with submerged vegetation (Bell-Cross & Minshull, 1998; Hustler & Marshall, 1991) and this leads to differences in resources use and minimise competition. Competition among the large species has an ontogenetic component that is felt strongly by the young fish. As the fish grow older, their vulnerability to predation decreases and they begin to specialise more on different habitats and food resources. This is illustrated by *O. macrochir* which remain in shallow water until they attain a length of >70mm feeding mainly on diatoms and move into deeper waters after reaching 100 mm in length were they are microphages (Marshall & Lockett, 1976).

Among the large species only *T. rendalli* is known to remain in shallow water feeding macrophytes (Marshall, 1982), but its diet is distinct from the other cichlids and it has no major competitor for food resources. *Serranochromis robustus* is the main open water fish predator in lake after the decline of *Hydrocynus vittatus*, which since 1966 has rarely made up 5% of the total (Marshall, 1982). *Micropterus salmoides,* an exotic fish predator is also present in the lake but it constitutes less than 1% of the landed catch. It was introduced into Zimbabwe in 1932 (Toots, 1970) and is now widespread throughout the country (Gratwicke & Marshall, 2001). The potential for competition among the large fish is reduced by the shift in diet and habitat.

The diet of *P. acuticeps* and *T. rendalli* vary from (Munro, 1967), were insects were a major food component of the fishes diet. The limnology of the lake has changed over the years and in the 1960s the lake was characterized by an extensive macrophyte community of *Typha* sp., *Aponogeton* sp., and *Nymphea caerula.* It is likely that the macrophytes supported a large population of macro-invertebrates and the destruction of these macrophytes beds together with the increasing severity of algal blooms are reflected by the shifts in the diets of the cichlids. This is illustrated by changes in the food habits of *T. rendalli* which is a versatile and an opportunistic feeder whose diet can vary in different habitats and environmental conditions (Minshull, 1969; Junor, 1969; Marshall, 1982). Caulton (1975) found that small (<10mm) size classes of *T. rendalli* fed on diatoms while the sub-adult size classes fed on a variety of food items consisting of cichlid fry, colonial blue-green algae and macrophyte detritus. In the present study it was microphagous, feeding primarily on plant material as it is elsewhere (Philippart & Ruwet, 1982; Chifamba 1990; Winemiller & Winemiller, 2003) and no ontogenetic diet shifts were evident. This may be attributed to the abundant food resources currently in the lake in form of filamentous algae and extensive macrophyte community along the shoreline dominated by floating mats of *Eichhornia crassipes* and the emergent macrophyte *polygonum senegalense.* These mats do not however appear to support a higher diversity of aquatic macro invertebrates and their most important function is habitat provision for the small size classes of fish (Brendonck *et al*., 2003).

Among the adults, there was high dietary overlap between the two microphages *O. niloticus* and *O. macrochir*. The two species are able to digest blue-green algae (Moriarty & Moriarty, 1973) and this is probably is one of the main reasons for the species success in the lake. The two microphages may be in competition for the same food resources. *Oreochromis niloticus* has supplanted *O. macrochir* as most the important commercial species and it is now the most abundant and widely distributed cichlid in the lake, while *O. macrochir* is characterized by low catches and a patchy distribution (Table 1).

O. niloticus is an aggressive competitor, the large males often out-compete other species when spawning places are limited (Lowe-McConnell, 2001). *O. niloticus* has a catholic diet and is know to ingest food items such as macrophytes (Khallaf & Alne-na-ei, 1987), zooplankton, insect and benthic organisms (Philippart and Ruwet, 1982; Bwanika, *et al.*, 2004) and this may be one of the reasons behind its success. It is a highly adaptable species able to exploit new opportunities and expand its realized niche to succefully colonize new habitats and this is illustrated in Lake Victoria, were it has widened its niche to utilise food resources previously eaten by various cichlid and non-cichlid species which no longer occur in the lake (Njiru *et al.*, 2004).

It is of interest to compare the food habits of cichlids in Lake Chivero with Lake Kariba, an oligotrophic lake. In Lake Kariba *P. acuticeps* and *P. philander* feed on chironomids, calanoid copepods and diatoms (Mlhanga, 2000), while the diet of *O. niloticus* consist mainly of chlorophytes and diatoms (Chifamba, 1998). The lake has an estimated primary production of 0.42 g C m^{-2} d^{-1} in comparison to Lake Chivero which is has a primary productivity of 1.64 to 6.03 g C m^{-2} d^{-1} (Robarts, 1982) By contrast the cichlids in Lake Chivero have a diverse food resource base, and the feeding guilds appear to cover most of the available food niches in the lake, except for zoo benthos and gastropods. Benthic and other macro fauna food niches such as gastropods could be in use by other fish species adapted to benthic feeding. *Marcusenius macrolepidotus* is the most abundant Mormyridae in the lake and it feeds primarily on benthic insects, while the now rare *Sargochromis codringtonii* is known to feed on gastropods (Moyo & Fernando, 1999). The abundance of *Microcystis aeruginosa* in the diet of the microphages reflects its dominance in the phytoplankton community of the lake (Brendonck *et al.*, 2003).

Although the results indicate resource partitioning among the cichlid species in Lake Chivero a more detailed study on the biology of the fish species is needed to increase our understanding of interactive processes among the fish communities.

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