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The diet of largemouth bass, *Micropterus salmoides*, in Lake Naivasha, Kenya

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Lake Naivasha is a freshwater lake situated in the eastern rift valley of Kenya. Only five species of fish are present, all of which have been introduced. Of these, *Oreochromis leucostictus*, *Tilapia zillii* and *Micropterus salmoides* (largemouth black bass) support an important gillnet fishery with bass also being taken for sport. Until bass reached 260 mm F.L. they depended upon invertebrate food organisms. Thereafter crayfish, fish and frogs became increasingly important the larger the size of the bass. The most important invertebrate prey species was the water boatman, *Micronecta scutellaris*, followed by chironomid and culicid pupae. Zooplankton was consumed but only in large quantity by fish smaller than 80 mm. For bass over 260 mm the crayfish, *Procambarus clarkii*, was the principal food. The largemouth bass in Lake Naivasha are generalized macro-predators, feeding principally on free-living animals of a kind most likely to be found in the littoral zones.

Key words: *Micropterus salmoides*; largemouth bass; diet; feeding; Lake Naivasha.

I. INTRODUCTION

The largemouth bass, *Micropterus salmoides* (Lacépède), is native to North America where it inhabits both rivers and still waters although it is most common in small, shallow lakes or the shallow bays of larger ones (Wheeler, 1978). The species has fine sporting and eating qualities, prompting its introduction to the waters of many temperate and tropical countries, where it has often become established (Maitland & Campbell, 1992), as in Lake Naivasha, Kenya.

Lake Naivasha is a freshwater lake, approximately 150 km^2 in area, situated in the eastern rift valley about 100 km north of Nairobi. It lies in a closed basin at an altitude of 1890 m above sea level and receives 90% of its water from the perennial River Malewa, the remaining input coming from two ephemeral streams, rainfall and ground seepage. The lake is mostly between 4 and 6 m deep, and is subject to considerable fluctuations in water level. Water temperatures are generally in the range 20–25° C. Dominant vegetation types are belts of papyrus (*Cyperus papyrus* L.) around the margins, large stands of submerged macrophytes [principally *Najas pectinata* (Parl.)] and floating mats of *Salivinia molesta* Mitch. and, recently, *Eichhornia crassipes* (Mart.). An overview of the lake and its ecology can be found in Harper *et al.* (1990).

The single native fish species, the endemic *Aplocheilichthys antinorii* (Vinciguerra), was last recorded in 1962 (Elder *et al.*, 1971). Fish introductions began in 1925, with bass released in 1929, during the 1940s and in 1951 (Muchiri

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& Hickley, 1991). Other species present today are *Oreochromis leucostictus* (Trewavas), *Tilapia zillii* (Gervais), *Barbus amphigramma* Boulenger and *Poecilia reticulata* Peters (guppy). The two tilapias and the bass form an important commercial fishery (Muchiri & Hickley, 1991) with all three species being exploited using gillnets and the bass also being taken by rod and line for sport.

Several authors (e.g. Naivasha Fisheries Department, pers. comm.; Siddiqui, 1977; Muchiri & Hickley, 1991; Muchiri *et al.*, 1994) have suggested that more species could be introduced into Lake Naivasha to diversify the fish community and increase commercial catches. Muchiri (1990) has provided data on the feeding habits of the two tilapias and the principal purpose of this paper is to report on the food requirements of the bass. In addition, the study provides an insight into the feeding of this popular fish in a non-native environment.

II. MATERIALS AND METHODS

Most fish were obtained by gillnetting, the nets being set in gangs comprising 30 m lengths of mesh sizes 11, 15, 20, 24 and 35 mm (knot to knot). A few samples were taken by electric fishing and traps were used to catch the smallest specimens. Collections were made annually from 1987–1991 from major habitat types, namely open water, submerged macrophyte beds, rocky shore and the marginal vegetation fringe. Stomachs were removed from representative samples from across the size range, for each habitat type in each sampling year. Gut contents were examined with the aid of a × 20 binocular microscope. Ingested matter was identified to categories ranging from broad taxonomic groups to individual species according to reasonable limits of identification.

For each sample the number of guts in which each food item occurred was recorded and expressed as a percentage of the number of guts containing food (% occurrence). The % abundance of different foods in individual guts was calculated as the count of a food item expressed as a percentage of the total count for all food items. To assess the relative importance of each dietary taxon consumed, a prominence value (*PV*) was calculated from the product of its % abundance and the square root of its % occurrence. This was based on the scheme of Wilhm (1967), as adopted by Hickley & Bailey (1987). Finally, to compare overlap with other species, prominence values were used to calculate a similarity coefficient as described by Wilhm (1967). A similarity of 0·6 was adopted as the point at which competition for food could be suspected (after Wallace, 1981).

Diel changes in stomach fullness were examined by lifting gillnets at different times of the day. Nets set at 18.00 hours were not lifted until 06.00 hours but otherwise nets were set to fish for 2–3 h only, a new gang being deployed to replace each one that was lifted. (The large number of resident *Hippopotamus amphibius* L. prevented setting and lifting of nets during the hours of darkness on the grounds of safety.) Entire bass stomachs were removed and weighed, emptied, re-weighed and the weight of the contents obtained by subtraction.

III. RESULTS

GUT CONTENTS

The contents of 1261 bass stomachs were examined in total. There was no evidence of capture techniques having induced regurgitation of food. Thirty-seven taxonomic categories were established for the ingested material of which 16 represented single species, with the rest equating to several species within a class, order or family (Table I). Excluded from Table I, with means for both abundance and occurrence less than 1%, are Oligochaeta, Hirudinea,

TABLE I. The mean percentage abundance (Ab) and occurrence (Occ) of different food materials in the stomachs of largemouth bass of different size groups where either mean exceeded 1%

	Length range (mm):					
	20–60		60–260 Sample size		260–500	
	42		1086		133	
	Ab	Occ	Ab	Occ	Ab	Occ
Food item:						
Naias pectinata leaf	—	—	P	3	—	—
Salvinia molesta root	—	—	P	1	—	—
Conchostraca	—	—	1	8	—	—
Cladocera	33	57	6	9	—	—
Ostracoda	—	—	P	5	—	—
Copepoda	44	56	P	2	—	—
Procambarus clarkii	P	3	4	19	52	63
Zygoptera nymph	—	—	P	5	—	—
Anisoptera nymph	—	—	P	1	—	—
Trichoptera larva	—	—	P	4	—	—
Chaoborus pupa	—	—	1	5	—	—
Culicid pupa	—	—	3	9	—	—
Chironomid larva	—	—	4	42	P	2
Chironomid pupa	—	—	14	60	1	2
Other Diptera larva	—	—	P	1	—	—
Diptera adult	—	—	P	1	—	—
Micronecta scutellaris	20	55	63	90	17	14
Anisops	—	—	1	5	P	1
Laccocoris	—	—	—	—	1	1
Arachnida	—	—	P	1	—	—
Gastropoda	—	—	P	1	P	1
Xenopus tadpole	—	—	P	2	—	—
Xenopus adult	—	—	—	—	10	13
Anura adult	—	—	—	—	4	6
Barbus amphigramma	—	—	—	—	P	1
Micropterus salmoides	—	—	P	1	9	9
Tilapia zillii	—	—	P	1	2	2
Poecilia reticulata	3	17	P	1	—	—
Fish indet.	—	—	1	1	4	6

Data are combined for all habitats (submerged macrophyte, rocky shore, open water and marginal vegetation) for the years 1987–1991 inclusive. *P*=present at <1%.

Ephemeroptera nymph, Lepidoptera larva, Corixida, Coleoptera adult, terrestrial insect and *Oreochromis leucostictus*.

The most common invertebrate taken by the bass was the water boatman *Micronecta scutellaris* (Stal.), followed by chironomid and culicid pupae. Zooplankton was consumed but only in significant quantities by fish under 80 mm long. Of the larger prey types, the crayfish, *Procambarus clarkii* (Girard), was an important food. Where bass were piscivorous they took all four other species plus their own kind, with *T. zillii* and bass the most frequently consumed.

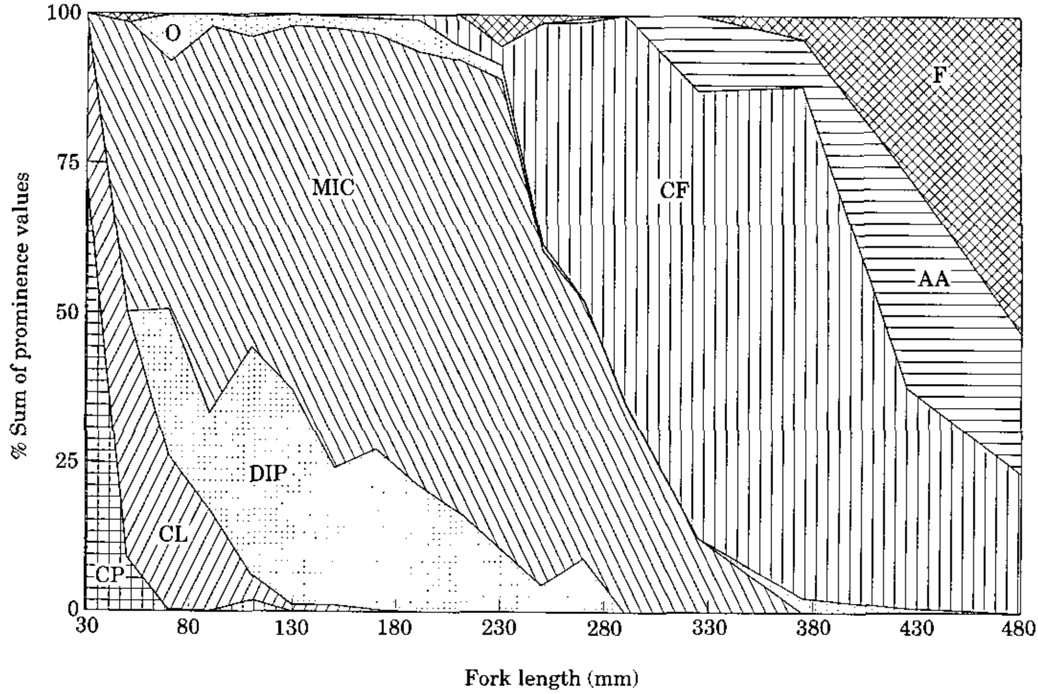

FIG. 1. The percentage of the sum of all prominence values represented by the different food materials in the stomachs of largemouth bass plotted against fish length. Data are combined for all habitats (submerged macrophyte, rocky shore, open water and marginal vegetation) for the years 1987–1991 inclusive. Key: CP, Copepoda; CL, Cladocera; DIP, Dipteran pupa; MIC, *Micronecta*; O, other items; CF, crayfish; AA, anura adult; F, fish.

DIET IN RELATION TO FISH SIZE

There were major changes in bass diet as the fish increased in size (Table I; Fig. 1). For the smallest fish (20–40 mm) the principal prey were copepod crustaceans. Thereafter copepods were replaced by cladocerans, dipteran pupae and *Micronecta*, the latter reaching 65% abundance and 90% occurrence in 80–260 mm fishes. For larger bass, crayfish became the single most important prey, with frogs and fish featuring predominantly only in the diets of very large specimens.

DIET IN DIFFERENT HABITATS

Micronecta and chironomid pupae were the most important foods in all four habitats (Table II). In particular, trichopteran larvae were found only in the rocky shore samples, *Anisops* was absent from bass from open water and was associated with submerged or marginal vegetation and *Chaoborus* pupae were taken by fish caught away from the shoreline in the submerged macrophytes and open water. Among larger bass, crayfish prominence was high in samples from the rocky shore, open water and marginal vegetation, but low near submerged macrophytes. *Micronecta* ranked first in guts from both the off-shore and shoreline vegetated sites. Gastropods were eaten among submerged macrophytes but not by the smaller fish. Fish and frogs were most important in

TABLE II. The ranked importance of food items found in stomachs of largemouth black bass based on prominence value (*PV*) for different habitats for the years 1987–1991 combined where *PV*>1

(a) Bass 60–260 mm F.L.

Taxonomic group	Submerged macrophyte		Rocky shore		Open water		Marginal vegetation	
	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*
Micronecta scutellaris	1	660·9	1	695·0	1	589·9	1	531·5
Chironomid pupa	2	141·1	2	84·4	2	151·8	2	153·4
Procambarus clarkii	3	33·2	4	35·7	7	21·0	3	79·0
Cladocera	5	22·5	5	25·7	3	36·1	4	64·5
Chironomid larva	4	30·1	6	19·8	5	33·8	5	28·6
Culicid pupa	11	1·6	3	44·8	4	35·0	6	26·3
Chaoborus pupa	7	14·0			6	27·3		
Conchostraca	10	5·4	8	6·5	9	12·8	8	10·1
Anisops	6	15·9	9	1·1			7	15·8
Fish	9	5·7			8	16·7	11	2·8
Trichoptera larva			7	14·4				
Anura tadpole	8	6·5			10	4·6		
Copepoda							9	9·3
Zygoptera nymph							10	7·1

(b) Bass 260–500 mm F.L.

Taxonomic group	Submerged macrophyte		Rocky shore		Open water		Marginal vegetation	
	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*
P. clarkii	5	48·8	1	603·6	1	502·1	2	445·2
M. scutellaris	1	204·4	3	102·2	3	90·0	1	504·2
Chironomid pupa	4	110·7			2	226·3	3	5·2
Anura adult	2	196·2	2	125·5				
Fish	3	151·3	4	30·6			4	4·8
Chironomid larva	6	21·2			4	61·5		
Gastropoda	7	8·5						
Laccocoris			5	5·2				

The taxonomic groups are listed in overall rank order.

the submerged macrophyte and rocky shore samples and were absent in those from open water.

CHANGE IN DIET WITH TIME

Separating data for the five sampling years showed large differences in the consumption of certain food items. *Micronecta* was the most important organism in guts of 60–260 mm bass throughout the sampling period (Table III). Chironomid pupae were second most predominant overall but ranked second only in 1989 and 1990. In 1987 *Chaoborus* pupae were second, although this was the only year in which they were taken. Similarly, culicid pupae (1991), *Anisops*

TABLE III. The ranked importance of food items found in stomachs of largemouth black bass based on prominence value (*PV*) for the years 1987 to 1991 inclusive for all habitats combined where *PV*>

(a) Bass 60–260 mm F.L.

Taxonomic group	1987		1988		1989		1990		1991	
	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*
Micronecta scutellaris	1	583·8	1	825·4	1	483·6	1	622·0	1	592·
Chironomid pupa	7	6·0	3	37·5	2	264·0	2	199·5	3	52·
Cladocera	4	61·5	7	1·1	3	89·9	4	17·6	5	35·
Procambarus clarkii	3	80·1			5	28·8	3	68·1	7	8·
Culicid pupa									2	155·
Chironomid larva	8	5·7	4	37·0	4	79·4	5	14·7	6	11·
Chaoborus pupa	2	82·7								
Conchostraca									4	49·
Anisops			2	44·8						
Fish	5	42·3					8	2·6		
Anura tadpole	6	22·1								
Trichoptera larva			5	9·8			6	6·0		
Zygoptera nymph			6	3·3	6	6·7				
Copepoda							7	5·8		

(b) Bass 260–500 mm F.L.

Taxonomic group	1987		1988		1989		1990		1991	
	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*	Rank	*PV*
P. clarkii	2	257·0	2	130·1	2	183·4	1	612·6	1	1000
M. scutellaris			1	595·5	1	334·9	2	363·3		
Anura adult	1	462·8	4	28·1	5	6·5	3	12·6		
Chironomid pupa					3	168·9				
Fish	3	151·3	3	69·0			4	12·6		
Chironomid larva					4	41·4				
Laccocoris			5	13·1						
Gastropoda					6	4·2				

The taxonomic groups are listed in overall rank order.

(1988) and Conchostraca (1991) achieved relatively high prominence in 1 yr only.

Large bass took large prey items (Fig. 1), namely crayfish, fish and frogs in 1987 and crayfish alone in 1991. However, in 1988–1990 *Micronecta* maintained high status, ranking first or second, and in 1989 chironomid pupae were important.

PREY SIZE

The relationship between bass size and their prey size was investigated in cases where prey fish (Fig. 2) and crayfish (Fig. 3) were not too digested to be measured. In general, both fish and crayfish increased in length relative to increase in length of bass. The smallest fish consumed were a juvenile bass at 15 mm, a guppy at 18 mm and a *Tilapia* fry at 20 mm. The smallest crayfish

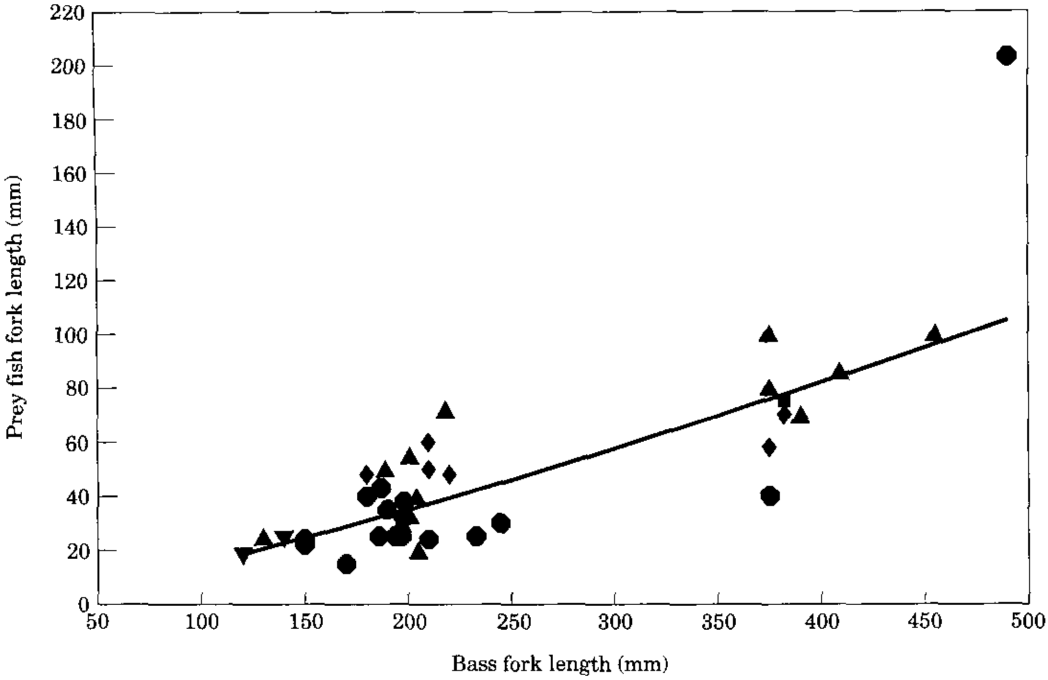

FIG. 2. Size of prey fish found in stomachs of bass of different sizes for the period 1987–1991. The equation of the solid line is $\log_{10} PF = 1{\cdot}226 \log_{10} l - 1{\cdot}278$ ($r=0{\cdot}802$) where PF=prey fish F.L. (mm) and l=bass F.L. (mm). Sample size, 39. Key: ●, bass; ■, *Oreochromis*; ▲, *Tilapia*; ◆, *Barbus*; ▼, guppy.

specimens taken had carapace lengths of 4 mm. The biggest prey were a 100 mm *T. zillii* and a 203 mm bass. The carapace of the largest recorded crayfish measured 50 mm (98 mm T.L.).

DIEL FEEDING PATTERN

Largemouth bass generally fed during the daytime (Fig. 4) with low levels of stomach fullness at 06.00 hours increasing to a maximum at about 16.00 hours. It is probable that most food was consumed at a steady rate from dawn until late afternoon.

COMPARISON WITH OTHER SPECIES

Muchiri (1990) recorded detritus as the principal component of the tilapia diet. Detritus is the most abundant food material available to fish in Lake Naivasha and its importance has been noted previously by Malvestuto (pers. comm.) and Siddiqui (1977). Of the other foods eaten by *O. leucostictus*, various algae, especially planktonic forms, were predominant and free-living insects such as *Micronecta* featured infrequently. In contrast, *T. zillii* consumed significant amounts of macrophyte and relatively large quantities of insect material, notably *Micronecta*.

Whilst there was apparent competition between the tilapias until detritus was discounted (Muchiri, 1990), serious overlap in feeding did not occur (Table IV). The two size groups of bass were reasonably close to each other at a similarity of

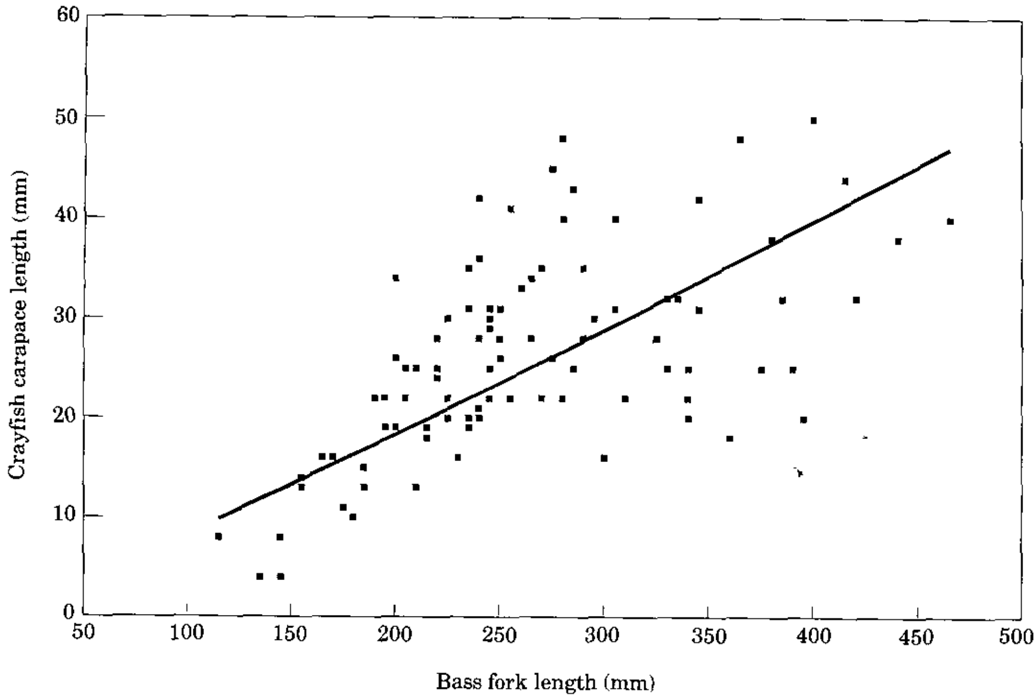

FIG. 3. Size of crayfish found in stomachs of bass of different sizes for the period 1987–1991. The equation of the solid line is $\log_{10} CF = 1{\cdot}118 \log_{10} l - 1{\cdot}311$ ($r = 0{\cdot}682$) where CF=crayfish carapace length (mm) and l=bass F.L. (mm). Sample size, 94.

TABLE IV. Similarity coefficients (after Wilhm, 1967) for the diets of bass and two species of tilapia based on the prominence value of food items taken

	Micropterus salmoides (60–260 mm)	*Micropterus salmoides* (260–500 mm)	*Oreochromis leucostictus*
M. salmoides (260–500 mm)	0·42	—	—
O. leucostictus	0·07	0·05	—
Tilapia zillii	0·29	0·30	0·64 (0·24)

The value in parentheses excludes detritus from the comparison.

0·42 and to *T. zillii* at 0·29 and 0·30. The very different diets of bass and *O. leucostictus* produced similarity coefficients of only 0·07 and 0·05.

IV. DISCUSSION

Generally, juvenile largemouth bass commence feeding on zooplankton and macro-invertebrates and then, as they grow, progress to larger prey items such as crayfish, fish and frogs (Maitland & Campbell, 1992). However, in Lake Naivasha, insect prey were the principal source of food until bass reached 260 mm F.L. (Fig. 1). Keast & Eadie (1985) showed year 1 bass of only

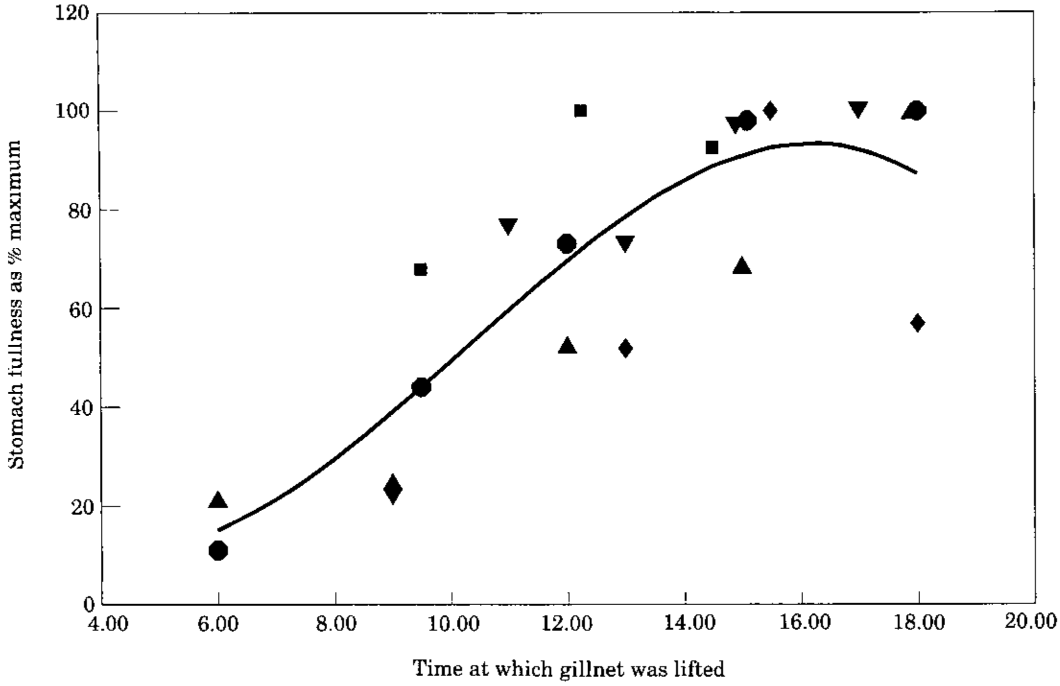

FIG. 4. Bass stomach fullness (*SF*), measured at different times (*t*) of the day, for the years 1988–1992. Stomach fullness is the weight of the stomach contents at the time at which the gillnet was lifted expressed as a % of the maximum content weight recorded for the sampling year. Fish size was in the range 80–260 mm F.L. The equation of the solid line is $SF=48{\cdot}354-19{\cdot}795\,t+2{\cdot}951\,t^2-0{\cdot}096\,t^3$ (proportion of variance explained by regression=72%). Key: ▲, 1988 (n=125); ●, 1989 (n=72); ■, 1990 (n=110); ▼, 1991 (n=220); ◆, 1992 (n=64) where n=number of fish examined.

80–142 mm T.L. in Lake Opinicon, Ontario, to feed almost exclusively on fish and small decapods. Similarly, Carline (1987) states that, sometime in mid-summer of the first year, gizzard shad [*Dorosoma cepedianum* (Lesueur)] began to make up a large portion of the diet of largemouth bass in three lakes in Ohio. In Crab Orchard Lake, Illinois (Lewis *et al.*, 1974) bass over 175 mm S.L. no longer consumed small invertebrates. Mullan & Applegate (1970) reported fish to be the primary food of bass >100 mm T.L. in Beaver reservoir, Arkansas (Applegate *et al.*, 1967), as did Storck (1986) at Lake Shelbyville, Illinois. Here, the largest ate gizzard shad, intermediates ate sunfish, miscellaneous fish and invertebrates and the smallest ate invertebrates; but for the 0 group overall, invertebrates made up only 4–20% of stomach content volume.

Previous reports from Lake Naivasha (Malvestuto, pers. comm.; Siddiqui, 1977) indicate a similar late change in feeding habits with bass up to 200 mm long feeding predominantly on insect prey, especially chironomid pupae and odonate nymphs. Fish in the range 200–300 mm were macro-predators with a food intake of 78% crayfish, the remainder comprising mostly frogs and bass fry. In Peter Lake, Michigan, where bass took invertebrate prey at age II+ (93–188 mm T.L.), Hodgson *et al.* (1989) stated the fish to be foraging atypically, declaring that largemouth bass tend to be more piscivorous and are not normally generalists.

The invertebrates consumed by bass in Lake Naivasha were similar to those eaten by juvenile bass in the U.S.A. and Canada. Hodgson *et al.* (1989) found that, out of 14 different food item categories, large zooplankton, *Chaoborus*, chironomid pupae and odonate nymphs provided the majority of the food intake. Chironomid pupae were especially common during periods of surface emergence. Year 0 bass in Lake Opinicon, Ontario, consumed primarily zooplankton, amphipods, chironomid larvae and ephemeropteran nymphs (Keast & Eadie, 1985). The most common invertebrate prey types listed by Matthews *et al.* (1992) for Lake Texona, Texas, were corixids, ephemeropteran nymphs, the grass shrimp *Palaemonetes*, amphipods and chironomid larvae. Bass smaller than 50 mm T.L. in an Arkansas reservoir, ate mostly copepods and cladocerans (Applegate *et al.*, 1967), as in Lake Naivasha (Fig. 1). Parmley *et al.* (1986) found that bass fry 7·5–10·5 mm T.L. in hatchery ponds in Texas selected copepods. For fish 10·9–22·8 mm T.L. cladocerans made up 65–90% of the number of prey in gut samples and at 22·8 mm T.L. the juvenile bass switched to immature insects (73% abundance).

In many lakes within their home range, largemouth bass diet composition is influenced significantly by the density and sizes of juvenile gizzard shad present (Adams *et al.*, 1982). For example, of bass (175–483 mm T.L.) examined by Lewis *et al.* (1974) in Crab Orchard Lake, Illinois, 71% contained gizzard shad and Storck (1986) reported that gizzard shad was the most important prey species for age II+ largemouth bass. In Lake Naivasha, fish were not as important a component of the diet. The most abundant potential prey species were *O. leucostictus* and *T. zillii*, but Muchiri (1990) noted that these tilapias moved towards macrophyte-covered littoral zones by day. Hence they would be protected from predation by the bass. That lack of availability might influence the low incidence of fish in Lake Naivasha bass diet is supported by results of experimental angling carried out during 1992 (North, unpubl.). Spinning lures representing fish of 45 mm F.L., used in open water and near to marginal vegetation, produced hourly catches of up to 20 bass between 121 and 204 mm F.L. That such small bass took these fish imitations could indicate that prey fish of similar size would be eaten if they were readily available.

When crayfish became abundant in Lake Naivasha in the early 1970s, bass predation on the tilapias was slight (Litterick, pers. comm.). Although low availability could account for low predation on fish, positive selection of crayfish by bass has been noted elsewhere. Predation by largemouth bass was the major factor in reducing a papershell crayfish (*Orconectes immunis*) population by 98% in Northfield Impoundment, Wisconsin (Rach & Bills, 1989) and Taub (1972) commented that bass so reduced populations of *Cambarus diogenes* in an Ohio pond that he was unable to make population estimates. Bryant & Moen (1980) found that stomach samples from bass in Degray reservoir, Arkansas, contained 38% crayfish by weight and Lewis & Helms (1964) reported that largemouth bass preferred crayfish and black bullheads (*Ictaluras melas* Rafinesque) out of six forage items offered them.

Largemouth bass in Peter Lake, Michigan, are opportunistic, feeding on a broad range of prey items in a relatively resource depressed environment (Hodgson & Kitchell, 1987; Hodgson *et al.*, 1989). The relatively low diversity of macro-invertebrates (Clark *et al.*, 1989), and the changes in the food types between habitats and years suggest a similar opportunism by Lake Naivasha bass.

The main recent change in bass diet (Malvestuto, pers. comm.; Siddiqui, 1977) is the importance of *Micronecta*. Clark (1992) found that *Micronecta* was by far the most abundant organism in all habitats and Harper *et al.* (1990) emphasized the rapidly changing nature of Lake Naivasha's ecology. Accordingly, any fish species in the lake that can adapt quickly to new sources of food increases its chance of maintaining its status. Such adaptability could have been the key to the successful establishment of bass as a resident species.

While prey size increased with predator size, the considerable scatter of data points (Figs 2 and 3) probably reflects the fact that maximum size of prey is limited by the mouth gape of the predator whereas minimum size is not. Similar size relationships were recorded at Crab Orchard Lake, Illinois, where 175–200 mm S.L. bass took gizzard shad of 51–100 mm, and for bass of 426–483 S.L. shad measured 138–190 mm (Lewis *et al.*, 1974). Similarly, Snow (1971) noted that larger bass ate larger crayfish. Shelton *et al.* (1979) recorded the maximum size of prey that a largemouth bass could feed on was a third to a half of its body length and Popova (1966) commented that the relative size of prey to predator changes from 40–50% for young predators to only 10% for very large predators.

The daytime feeding habit of bass observed elsewhere (e.g. Hodgson & Kitchell, 1987) was confirmed for Lake Naivasha. Similar findings for *O. leucostictus* and *T. zillii* (Muchiri, 1990) mean that none of the commercially exploited species feeds at night.

In conclusion, *M. salmoides* in Lake Naivasha was a macro-predator, at first taking zooplankton, followed by insect prey, before turning to crayfish, fish and frogs as size increased. Feeding took place in the daytime and individuals tended to feed opportunistically. Principal differences between the bass of Lake Naivasha and those of their native range are the late stage at which they begin to eat large prey items and the low incidence of piscivory.

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