

**The food and feeding behaviour of *Clarias gariepinus* (Pisces : Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids**

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# The food and feeding behaviour of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with emphasis on its role as a predator of cichlids

The morphological and behavioural adaptations for feeding, and the food of *C. gariepinus* in Lake Sibaya are described. *C. gariepinus* is equipped to feed on a wide variety of food items, from minute crustaceans to fish. Predation is more efficient on invertebrate prey. Most feeding takes place at night on active benthic organisms, but they may also feed during the day and at the water surface. Individual bottom foraging is the normal mode of feeding although catfish may also feed in groups at the water surface. The advantages of social hunting are discussed.

Food preferences are scored by three different methods and presented for the total catfish population and for different length groups, seasons, habitats and lake levels. Increasing lake levels during the study period resulted in a change in the relative density of three cichlid prey in the shallow water feeding area of *C. gariepinus*. The effect of changing cichlid densities on catfish predation was studied using field collections and experimental observations. *C. gariepinus* was found to feed on whichever cichlid prey was in greatest abundance, with some deviations which can be explained in terms of prey accessibility and other factors. An important aspect of their success as predators is their ability to switch from one prey to another as prey availability (= density + accessibility) changes.

Predation by *Clarias* species on cichlids in Africa is reviewed, and the movements and interaction of *C. gariepinus* and three cichlid species in Lake Sibaya are described in detail. Catfish predation is discussed in terms of recent predation theory, and their role as predators of cichlids is tentatively postulated as three-fold:

- (a) to enhance species fitness by removing enfeebled individuals, i.e. to act as a "cleaner"
- (b) to restrict the distribution of prey under certain conditions, i.e. to act as a "restrictor"
- (c) to dampen fluctuations in prey abundance, i.e. to act as a "regulator".

The relative importance of these roles is unknown at this stage, and may change at different lake levels and in different ecosystems.

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## INTRODUCTION

The way in which an omnivorous predatory fish, *Clarias gariepinus* (Burchell, 1822) utilizes the food resources of a lake with a fluctuating shore line is examined in this paper. Two feeding strategies are possible: (a) the predator is euryphagic and feeds on a variety of organisms according to their availability; (b) the predator is stenophagic and feeds on a narrow range of organisms which are available at all lake levels.

The catfish *C. gariepinus* is shown here to use the first strategy. Their wide array of anatomical adaptations for feeding (reviewed below) allows *C. gariepinus* to feed on a wide variety of organisms in different situations. This equipment is used to best effect by feeding in different ways according to the accessibility, size and density of the prey. Feeding is performed both individually and in groups. The main body of the paper describes the food preferences of *C. gariepinus* at different lake levels, and the results of an experiment to test the selectivity of the catfish for fish prey at different densities. Finally, the role of *C. gariepinus* as a predator in Lake Sibaya is discussed.

The only previous study of *C. gariepinus* feeding in Lake Sibaya is by Minshull (1969) who examined 53 specimens. Crustacea, mainly the crown crab *Hymenosoma orbiculare* Desmarest, formed 44% of the food, and fish, mainly small cichlids and the goby *Glossogobius giuris* (Hamilton-Buchanan), 32%. Other food items were insects, mainly terrestrial forms (12%), gastropod molluscs (10%) and small quantities of algae and diatoms. Bruton & Boltt (1975) reported on the stomach contents of an additional 164 specimens of *C. gariepinus* and found that 33% contained fish remains, of which 9% were identifiable as cichlids.

## STUDY AREA

Lake Sibaya ( $32^{\circ}40'S$ ,  $27^{\circ}25'E$ ) is a natural freshwater lake situated on the sandy coastal plain of south-east Africa. The lake has an area of  $65 \text{ km}^2$ , a maximum depth of 40 m and a mean depth of 13 m (Hill, 1969). The bathymetry is shown in Fig. 1. Present basin profiles suggest that Lake Sibaya was originally an estuarine basin which became isolated from the sea by longshore dune formation (Hill, 1969, 1975).

Lake Sibaya consists of a large main basin into which open two smaller basins and two long arms. The numerous basins and arms result in a well-developed shore line with a length of 144 km. The northern and south-western shores of the three basins shelf gradually into deeper water. On the western, eastern and south-eastern shores, and along the northern and western arms, deep water occurs close inshore and the shallow littoral terraces end in a steep slope. Diagrammatic profiles of the lake shore are given in Fig. 2. The shores of the lake are sandy with no rock apart from isolated outcrops of ironstone on the north-eastern shores.

The lake level is subject to wide fluctuations dependant on local rainfall, runoff and seepage. Simulated and directly-read month-end lake levels from 1914 to 1974 had a vertical range of 3.5 m (Pitman & Hutchison, 1975). During the study period (1970 to 1976) the lake level fluctuated through 3.06 m. These changes had a marked effect on

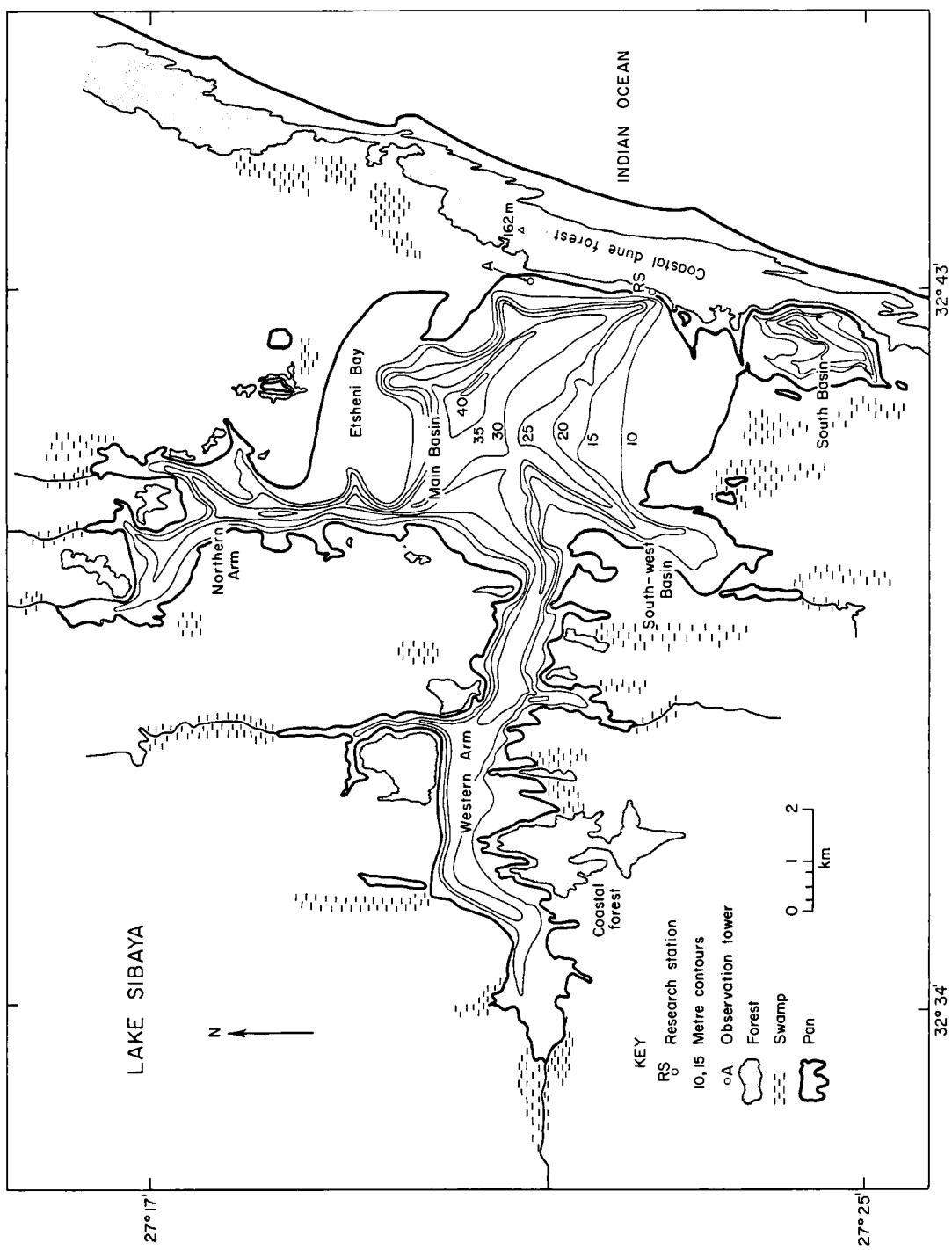


FIG. 1. Map of Lake Sibaya. Bathymetry modified from Hill (1975).

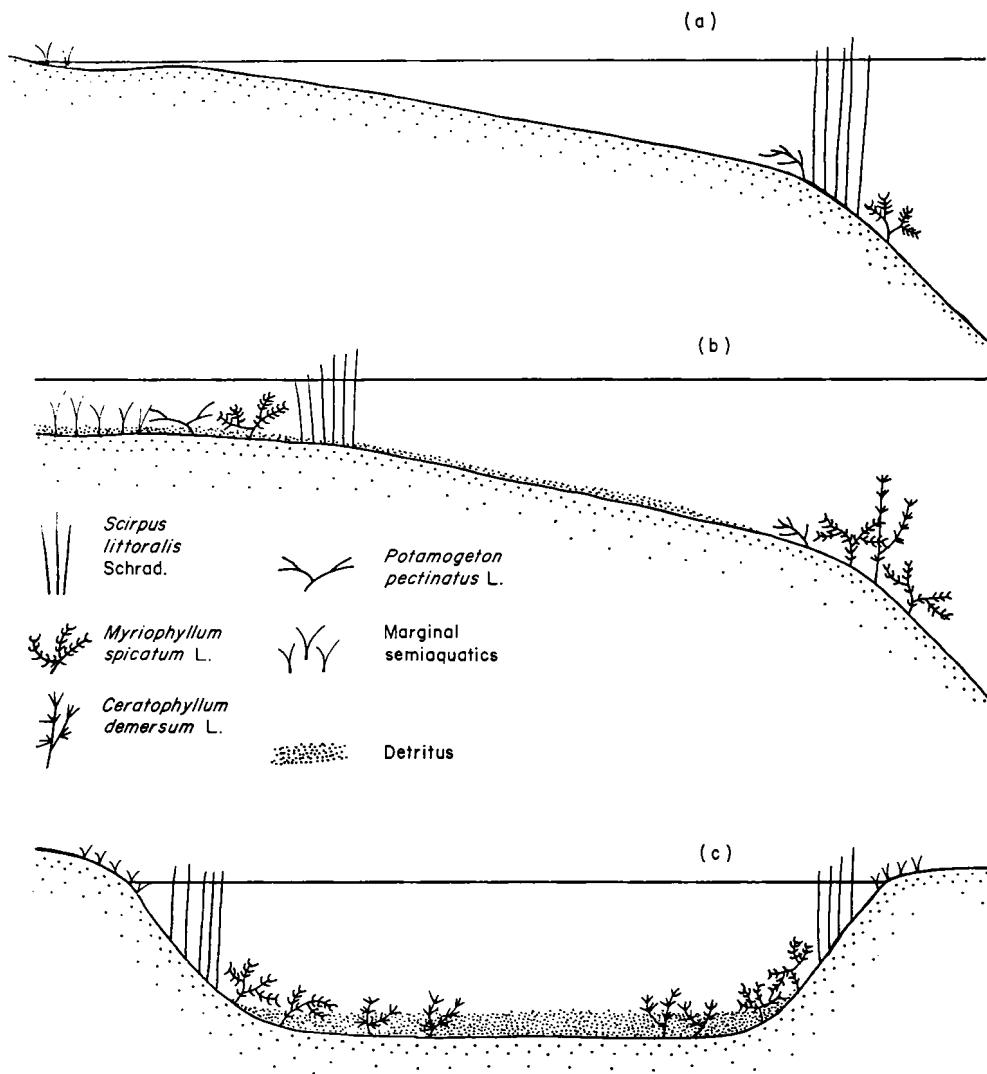


FIG. 2. Diagrammatic profiles of different inshore habitats in Lake Sibaya. (a) Terrace and slope at low lake level. (b) Terrace and slope at high lake level. (c) Sheltered bay.

the nature of sublittoral, littoral and marginal habitats as extensive areas of shore line have a gradual slope and are therefore readily inundated.

Seven main habitats can be distinguished in Lake Sibaya on the basis of flora, fauna, bottom profiles and depth: marginal, littoral terrace, steep slope, gradual slope, bay, profundal and limnetic. These habitats, and the distribution of plants, fish and especially *C. gariepinus* are described by Bruton (1978).

The cichlid fish *Sarotherodon mossambicus* (Peters) which is the most important fish prey of *C. gariepinus* in Lake Sibaya, mainly inhabits slope and inshore habitats at a depth of less than 12 m. *S. mossambicus* juveniles are abundant on the littoral terraces

especially during the day in summer. At low lake levels they represent more than 90% of the fish catch on the terrace, whereas at higher lake levels other cichlids as well as gobiids also occur there (Bruton & Boltt, 1975; Bruton, 1978).

The most common zooplankter is *Pseudodiaptomus hessei* (Mrâzek), which occurs at a low mean density of less than six individuals per litre (Hart & Allanson, 1975). The standing crop of phytoplankton contains less than 5 mg chlorophyll per litre, and has a maximum carbon fixation rate of  $239 \text{ mg m}^{-2} \text{ d}^{-1}$  (Allanson & Hart, 1975). Both values are very low for a warm subtropical lake.

The distribution and abundance of the benthos is described by Boltt (1969), Boltt, Hill & Forbes (1969), Allanson, Bruton & Hart (1974) and Appleton (1977). The crown crab *Hymenosoma orbiculare*, and the molluscs, *Bellamya capillata* (Frauenfeld) and *Melanoides tuberculatus* (Müller) are the commonest large invertebrates of the epifauna. The amphipod *Grandidierella lignorum* Barnard is the dominant infaunal component to a depth of about 20 m, but in deeper water the tanaid *Apseudes digitalis* Brown, is more common. The shrimp *Caridina nilotica* (P. Roux) is abundant in marginal habitats and occurs at varying densities in sheltered plant beds and the profundal zone. Other important benthic Crustacea are the isopods *Cyathura carinata* (Kröyer) and *Pontogeloides latipes* Barnard, the amphipod *Corophium triaenonyx* Stebbing, and the shore crab *Potamon sidneyi* Rathbun. The most conspicuous littoral insects are the burrowing mayfly *Povilla adusta* Navás, and odonatan nymphs. Molluscs (12 species) are abundant in sheltered bay habitats.

Open water temperatures measured at a fixed buoy over 20 m from 1970 to 1976 varied from  $18^\circ$  to  $28^\circ\text{C}$  (Hart & Allanson, 1975, and pers. obs.). Terrace and marginal habitat temperatures ranged between  $16^\circ\text{C}$  (rarely  $13^\circ\text{C}$ ) and  $36^\circ\text{C}$  (rarely  $41^\circ\text{C}$ , pers. obs.). Oxygen levels are usually high at all depths and rarely fall below 60% saturation. Secchi disk readings varied between 2.7 and 3.5 m. The lake water is alkaline, pH 8.3 and has a high chloride ion concentration,  $135 \text{ mg/CL}^{-}/\text{C}$ , but is otherwise fresh (Allanson & van Wyk, 1969).

## METHODS

Field observations on *C. gariepinus* feeding behaviour, which cover a  $3\frac{1}{2}$  year period from 1973 to mid-1976, were made from boats, a 7 m high tower in shallow water, and using SCUBA and free-diving gear. Catfish for food analyses were collected in three stages (Table I). In the first stage they were caught incidentally during another research programme. The second, main stage involved regular monthly collections from January 1974 to December 1975, and the third an intensive two month collection (March, April, 1976) for comparison with the previous two. The collecting methods are described by Bruton (1978).

As the collections were made at low, intermediate and high lake levels, the effect of the changing ecology of marginal areas on the diet of *C. gariepinus* could be determined. This was the main value of the first and third collections. The second collection also served to define the diet of the catfish population as a whole and in different length groups, seasons and habitats.

Many catfish caught during the study were not used for food analysis because their stomach contents, or lack of contents, were influenced by the collecting method. In such cases, the whole catch was used for another purpose or discarded. Catfish caught in gillnets or on longlines which were not serviced within three hours (usually due to deteriorating lake conditions) were ignored. Catfish caught in traps, seine nets, trawl nets or using rotenone were treated with caution as they

readily ingested other fish in the catching apparatus or after poisoning. Newly-ingested fish, as well as longline bait, could easily be distinguished from real prey.

Regularly serviced longlines and gillnets provided the best catfish for food analyses. The most successful method was to use a "factory boat" and dinghy so that the gear could be serviced half-hourly or hourly, and the newly caught fishes processed immediately on the spot.

As a concurrent tagging programme was performed, a modified Seaburg (1957) stomach pump was tried for flushing the stomachs of live fish. Examination of the stomachs of 25 flushed fish indicated that 100% recovery of medium sized prey such as *Hymenosoma orbiculare*, *Melanoides tuberculatus*, *Bellamya capillata* and small fish was obtained, but very small items such as *Grandidierella lignorum* and chironomids, and large items such as *Potamon sidneyi* and *Sarotherodon mossambicus*, were not always removed successfully. This method was therefore not used (a more promising "gastric lavage" method is described by Foster, 1977).

TABLE I

*Details of the study period, lake level range, collection methods and fish caught during the study of the food of C. gariepinus in Lake Sibaya*

Study period	Lake level range (m)	Collection methods	Number of <i>C. gariepinus</i> caught (with stomach contents)	<i>C. gariepinus</i> total length range (mm)
1970-1972	0.92-1.71 (low lake level)	Seine net, rod and line	92	300- 700
January 1974- December 1975	1.83-3.03 (intermediate)	Mainly longlines, gillnets, handnets	469	12-1088
March-April 1976	3.86-3.98 (high)	Mainly longlines, gillnets, handnets	123	246-836

Stomachs were cut open immediately and the contents flushed out and preserved in 10% formalin. Intestinal contents were biased towards items which are digested slowly and contained no food items not found in the stomach; they were therefore ignored. Recently ingested prey organisms in the stomach with a weight of more than one gram were identified as far as possible, counted, dried and weighed to 0.01 g. Partly digested, fragmented and small items were identified, counted and measurements made of a representative body parameter viz. carapace width (crustaceans), standard length (fish) or total length (insects and molluscs). To determine the body weight of these small or partly digested items, representatives of the same species were collected in the lake and decalcified, dried, weighed and measured along the relevant body parameter. Reconstructed weights were then determined from a regression line relating this body parameter to dry weight. The use of reconstructed weights for fragmented or partially digested prey is recommended, as use of dry weights of prey fragments alone may underestimate the contribution of a food item. Reconstructed weights are regularly used by Russian workers (*vide* Popova, 1967), but rarely by others.

An important criticism of the use of stomach contents in food preference studies is that small or soft-bodied prey may be digested before recovery. Small prey were, however, well-represented in the stomach contents of Sibaya catfish (*Grandidierella lignorum*, *Caridina nilotica* and cichlid fry represented 28.3, 11.0 and 7.0% of all prey) indicating that the stomachs were examined before digestion of these items. Instances where only parts of prey are ingested would also bias results—only two such incidents were recorded when one leg each of *Potamon sidneyi* was taken.

Careful consideration was given to the method of expressing food preferences. At least 14 useful methods have been suggested by various authors (Hess & Swartz, 1941; Hynes, 1950; Pillay, 1952; Ivlev, 1961; Karamchandani & Desai, 1961; the workers mentioned by Windell, 1968; Hellawell & Abel, 1970; Hobson, 1974; Yurochko, 1976). In an omnivore like *C. gariepinus*, consideration of the numbers only will not give a good representation of the importance of different foods because of large differences in size. Frequencies are also biased in favour of small items, though less so, whereas weight measurements favour large items, which take longer to digest completely. For a proper assessment of the food of *C. gariepinus*, frequency, numbers and weight of food items have been taken into account and expressed in the following ways:

- (a) Frequency of occurrence: the percentage of stomachs examined (with contents) in which the food item appeared
- (b) numerical method: the number of individuals of each food type in all stomachs expressed as a percentage of the total number
- (c) dry weight method: percentage contribution to total prey dry weight by each food organism (weight determined directly, or indirectly as described above).

The latter two methods were only used for the 17 most common food items as defined by the frequency method. A composite analysis, combining the placings of the other three methods, was also used.

## RESULTS

### *Anatomical adaptations for feeding*

*C. gariepinus* has a remarkable array of anatomical adaptations for feeding which allow it to take prey ranging in size from a minute zooplankter to a fish half its own length. Euryphagy is an important adaptation for a fish which feeds in a variety of habitats and in fluctuating marginal areas of lakes and rivers.

Gosline (1973) considers that the ancestral cypriniform fish from which the modern catfish (Siluriformes) are derived was a compressed, small-mouthed, bottom-feeding form which caught small prey by grasping and sucking. From the structures associated with feeding in this ancestral form evolved the three main lines of feeding specialization of modern cypriniform fishes, i.e. the bite of characins, the suction and bite of catfishes, and the "pipette" suction of cyprinids. The specializations for feeding found in modern catfish have probably been tailored by two major factors: (a) their benthic feeding habit; (b) their predominantly nocturnal activity.

The mouths of benthophage fishes vary widely in form from small to large, protrusile to non-protrusile, and from a large to a small gape, depending on the method of food collection. The wide mouth, vertical gape, long circumoral barbels, and ability to depress the hypobranchial apparatus are anatomical features which facilitate the mode of benthic feeding practised by *C. gariepinus*, i.e. "sink" sucking (described below).

*C. gariepinus* has a wide, rounded caudal fin typical of fishes which ambush their prey, in contrast to fast swimming predators, such as the tigerfish *Hydrocynus vittatus* Castelnau, which have lunate caudal fins and chase the prey. Adaptations which have relevance to both bottom feeding and low visibility (i.e. feeding at night, or in murky or deep water) include the retention of the palatine-maxillary articulation as a hinge for probing movements of the maxillary barbel independent of the mouth (Alexander, 1965), reduction in the importance of the eyes, development of an abundant network of sensory organs on the body, head, lips and barbels (Angelopoulos, 1947) and the further development of the suck and bite method of food intake. The sensory equipment of *C. gariepinus* is

adapted to nocturnal feeding in common with that of many other siluroids (e.g. *Ictalurus lacustris* (Rafinesque), Bailey & Harrison, 1948; Ghanaian catfish, Lowe-McConnell (1975)).

*C. gariepinus* is equipped with four pairs of unbranched barbels of which the maxillary is the longest and most mobile, followed by the outer mandibular, inner mandibular and nasal pairs. The barbels are densely packed with sensory organs, which are particularly prominent in larval catfish. The nature of these sense organs has not been investigated in *C. gariepinus*.

In *C. batrachus* (L.) the barbels are both tactile and gustatory in function (Srivastava & Sinha, 1961; Agrawal & Rajbanshi, 1965; Rajbanshi, 1966; Singh, 1967; Welsch & Storch, 1969). Taste buds and mucous glands are found on the barbels and lips. Each barbel consists of an outer epidermis, a basement membrane and a dermis made up of connective tissue containing blood vessels and bundles of nerve fibres. The central core of the dermis has a cartilaginous axial skeleton (Agrawal & Rajbanshi, 1965; Singh, 1967).

Movable barbels projecting radially from the head enable *C. gariepinus* to scan a much larger volume of water. Upon contacting a food item, the catfish immediately turns towards the prey and lunges from the correct distance away. Accurate seizure of food upon contact requires that precise sensory information of its location reaches the central nervous system. Beidenbach (1971) showed in *Ictalurus punctatus* (Rafinesque) that "glide units" signal the radial distance from the head along a given barbel, and "position units" the displacement of the barbel from a resting position. Input from cutaneous chemoreceptors may distinguish food from inedible items. Barbels act as probes during foraging and when moving between obstructions, and as a forwardly directed "seine" (Gosline, 1973) which may limit the chance of escape by prey.

*C. gariepinus* has small eyes with a lateral and antero-dorsal field of view. Judging from the eye position, direct anterior, posterior and ventral vision is not possible. The eyes have little apparent role in food fixation. Stationary prey is often bypassed by hungry swimming catfish unless the prey makes direct contact with some part of the predator's body. Individual swimming prey is detected up to 100 mm away, in clear and murky water, by direct contact or via eddies detected by the barbels. Turbulence caused by a shoal of prey is detected from a greater distance. A naturally blinded catfish in an enclosure caught food on the substrate with the same apparent efficiency as sighted companions during the day and night. Movements of other catfish, and changes in light intensity, may be sensed visually. The role of olfaction and the lateral line system in prey detection is unknown in *C. gariepinus* but is likely to be important. *Clarias* species have electric receptors although they produce no continuous electric current themselves (Lissman & Machin, 1963).

The posterior half of the body in *C. gariepinus* is compressed and muscular with a wide caudal peduncle and large rounded caudal fin (sometimes truncate) for steady forward movement during foraging. The dorsal and anal fins are long and high to act as turning aids and keels, but can be depressed.

*C. gariepinus* is negatively buoyant and has a bi-lobed swim bladder (as in *C. mossambicus*; Gee, 1970) connected to the oesophagus via a narrow pneumatic duct (Angelopoulos, 1947; Petrick, 1975). According to Alexander (1965), the swim bladder of *Clarias* species is reduced to compensate for the buoyancy given by air carried in the suprabranchial chambers, and apparently has little hydrostatic function (and no gas gland, Petrick,

1975) although it is an important component of the Weberian apparatus. Observations on *C. gariepinus* in Lake Sibaya and in a pond indicate that the suprabranchial chamber is used for buoyancy regulation during feeding. Air is retained in the chamber when a stationary, near-vertical position is required as in surface feeding, but expelled for sudden downward escape movements and for slow bottom foraging. Between feeding bursts, catfish rest with the body at an angle of 20–90° from the substrate when air is in the chamber, or flat on the substrate when most of the air is expelled (similar behaviour is reported in *C. batrachus* by Devaraj, 1972). Fry and fingerlings commonly rest between feeding periods in a vertical position among plant stems, or in a horizontal position under flotsam at the surface, by retaining air in the suprabranchial chamber. In *Clarias magur* (Ham. Buch) air in the suprabranchial chamber minimizes the effort required for movements to the water surface for breathing (Naqvi, 1966).

The mouth of *C. gariepinus* is wide, subterminal, transverse and capable of considerable vertical displacement for engulfing large prey or large volumes of water during filter feeding. When opened, the volume of the buccopharyngeal chamber is increased by lowering the hyoid apparatus, thus creating a strong negative pressure in the vicinity of the food which is carried towards the mouth in the consequent current of water (Gosline, 1973, in catfishes and personal observations). This gross form of suction, a "sink" effect, is in contrast to the more specialized "pipette" suction action in which water flows rapidly down a narrow tube as in cyprinids (Gosline, 1973) and many other fishes (including the "ntaka" of Lake Malawi; Iles, 1960). Alexander (1967) found that most teleosts take food into their mouth by sucking, and later (1970) that the catfish *Ictalurus melas* (Rafinesque), which feeds in a similar way to *C. gariepinus* develops a negative pressure of ~80 cm which may be retained for 60 msec, when feeding. Tanaka (1973) demonstrated in the nurse shark *Ginglymostoma cirratum* (Bonnaterre) that suction feeding is particularly suited to a benthic predator.

Once the food has been sucked into the mouth, the jaws are snapped shut and the prey is prevented from escaping by broad bands of recurved teeth on the premaxillary and dentary bones. The vomerine and upper and lower pharyngeal bands of teeth also perform this function as well as that of incapacitating the prey, which is then swallowed whole. Small prey may be expelled from the mouth then sucked in again several times before ingestion.

The teeth are numerous, small, cardiform and backwardly directed. The premaxillary, mandibular and pharyngeal teeth are conical and sharp, whereas the vomerine band has mainly granular molar-like teeth with variable numbers of conical teeth, usually on the distal margins (Plate I). The teeth of large catfish are noticeably more worn and rounded than in small fishes, especially on the vomerine band. As the vomerine tooth band has no ventral partner, crushing and gripping of the prey takes place against the hyoid apparatus which bulges upwards to form a tongue.

*C. gariepinus* has long gillrakers on the anterior borders of the five branchial arches, and additional gillrakers on the posterior margin of the third and fourth arches, which interdigitate with those from the anterior row of the next arch. The number of gillrakers increases with length, although the scatter is wide (Fig. 3; and Jubb, 1967) as found in *C. mossambicus* (Worthington, 1933), *C. lazera* (Mills, 1956; Jocque, 1977) and *C. senegalensis* C. & V. (Thomas, 1966). Murray (1975) investigated the efficiency of filter-feeding by means of gillrakers in *C. gariepinus* in an attempt to explain why catfish smaller than

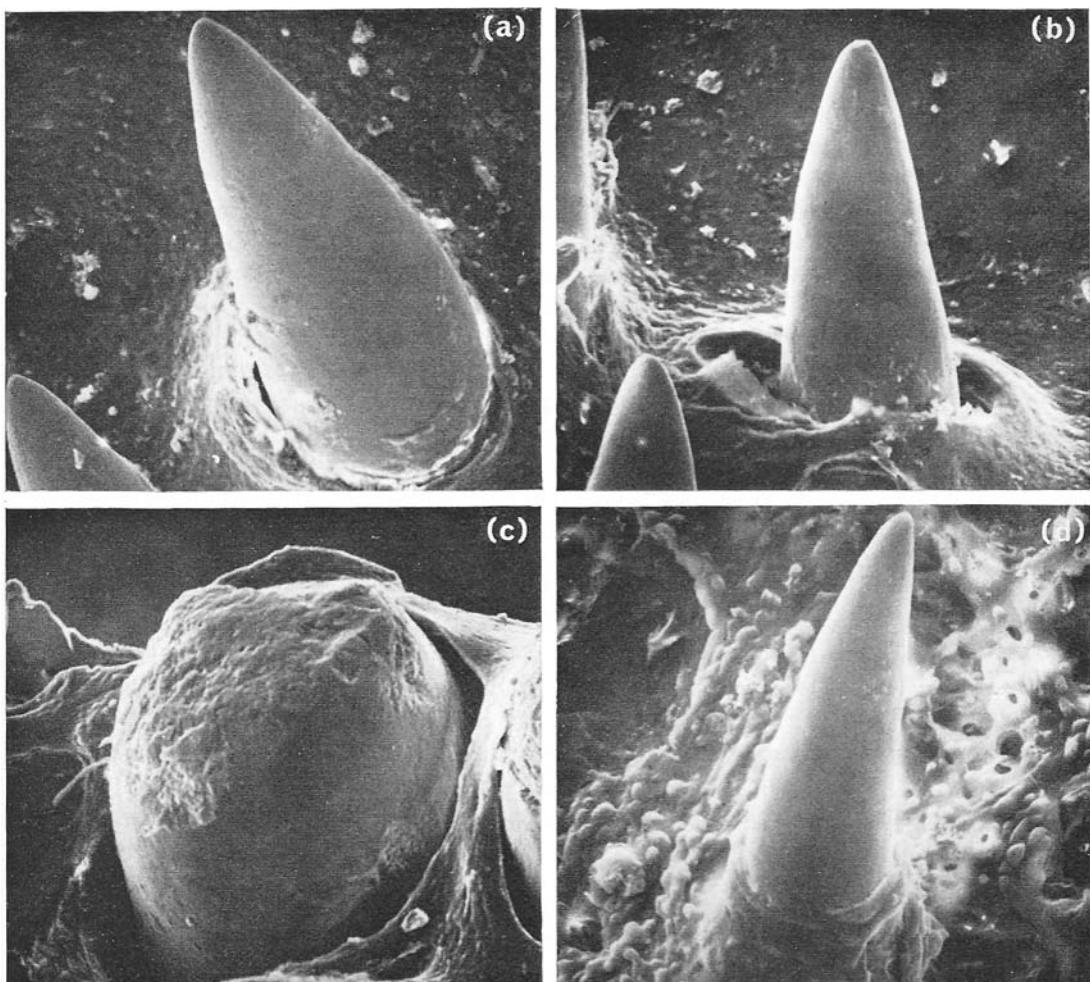


PLATE I. Scanning electron micrographs of the teeth of *C. gariepinus* from Lake Sibaya. (a) Premaxillary. (b) Mandibular. (c) Vomerine. (d) Pharyngeal. ( $\times 150$ ).

400 mm TL do not feed on zooplankton (Munro, 1967; Schoonbee, 1969; Bowmaker, 1973, in *C. gariepinus*; Jackson, 1961a, in *C. mossambicus*) whereas large catfishes do. Murray found that the straining surface area increased isomorphically with fish length, and the space between rakers linearly with fish length. Characteristics of the straining apparatus did not explain the absence of filter feeding in small catfish in natural conditions, but rather indicated that smaller fish should be more able to utilize zooplankton. Small captive catfish readily fed on zooplankton (as reported by Bruton, 1979), and the relative size or absolute volume of the buccal cavity, or the habitat occupied by juveniles, were offered as explanations for the lack of filter-feeding in juveniles.

The mean width between developed gillrakers varied between  $< 0.1$  and  $0.6$  mm (Murray, 1975) thus allowing retention of particles of greater minimum width than the above figures.

The oesophagus is short and dilatable and opens into a distinct distensible muscular stomach. The intestine is simple and thin-walled. Little mastication is performed in the buccopharynx as the prey is crushed in the muscular stomach to facilitate digestion. Mechanical digestion was followed in *C. gariepinus* using the X-ray technique of Molnar *et al.* (1967), with *Sarotherodon mossambicus* as prey. In two experiments (X-ray exposure time 0.5 sec at 65 kV) the prey was tumbled through 180° several times in the first 3 hours. Fish prey is also turned throughout the digestion period in the silurid catfish, *Silurus glanis* L. (Molnar *et al.*, 1967).

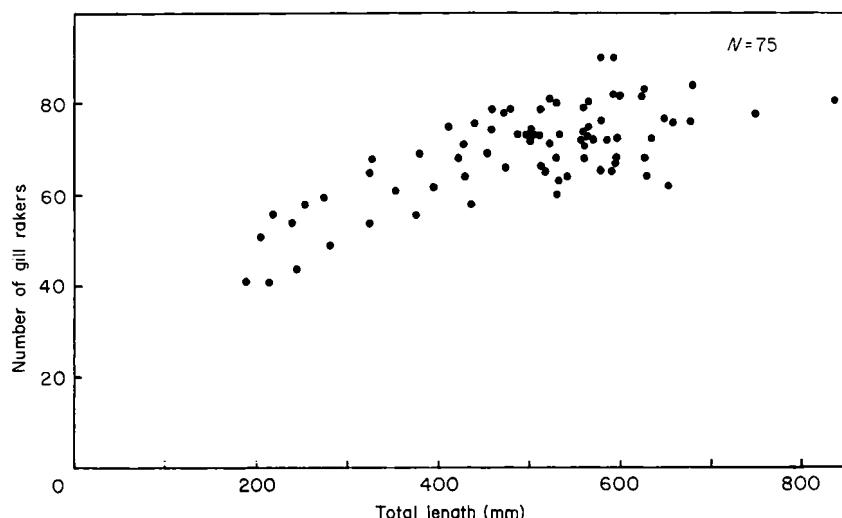


FIG. 3. Scatter diagram of the total number of gillrakers on the first gill arch against the total length of *C. gariepinus* from Lake Sibaya.

The histology and functional morphology of the digestive tract of *Clarias batrachus* an Asian clariid, has been described by Khanna (1966). The buccopharynx and oesophagus secrete large amounts of mucus which lubricates the prey for swallowing. In the stomach the food is crushed by movements of the muscular stomach wall, as in *C. gariepinus*, and digested by means of enzymes secreted from simple digestive glands. The intestinal epithelium is mainly absorptive and the rectum is muscular and mucus-secreting to aid defaecation.

There are no studies of digestion in *C. gariepinus* but some information is available on *C. batrachus* and *C. mossambicus*. In *C. batrachus* the pH in the stomach is 5.9 and protease and amylase are present (Agrawal & Verma, 1966). Protease is present in the stomach and intestine of *C. mossambicus* with maximal activity at pH 4 and pH 6 in the respective tissues (Cockson & Bourne, 1972). Enzyme activity in the stomach is about four times that in the intestine.

#### *The feeding behaviour of C. gariepinus*

Four modes of feeding were observed: two performed by individual catfish (foraging and shovelling), one by individuals or groups (surface feeding) and one by groups alone (formation feeding).

- (a) Individual foraging (Fig. 4(a)) is the normal mode of feeding in terrace and profundal habitats and plant beds. The catfish swims slowly forward, swaying the head slightly from side to side with the barbels extended forwards in a cone. When prey is detected or flushed, the catfish darts rapidly and accurately forward. The predator-prey interaction is not usually prolonged. If a lunge is unsuccessful, the predator continues foraging, though its subsequent route may be altered. Although searching is random in the sense that orientated reactions to food objects can only be made after detection, elements of non-randomness are also found: places not recently traversed are favoured over those just successfully explored, and the locality where prey has just been caught or detected may be searched with special attention. The tendency for catfish to move into shallower water for feeding is also an element of non-randomness, suggesting that they are concentrating their foraging in areas where ample food has previously been found. If new food sources, such as terrestrial insects on the water surface, and rich feeding beds, such as flooded marginal pools, are found the destination of future explorations is altered. Insofar as food preferences depend on chance experiences of individuals, differences in diet will develop among members of the same population feeding in different habitats. The most abundant, mobile organism in any habitat is likely to be detected and ingested most often by catfish.

Organisms caught by *C. gariepinus* during benthic foraging include *Grandidierella lignorum*, *Pontogeloides latipes*, *Cyathura carinata*, Chironomidae, *Bellamya capillata*, *Melanoides tuberculatus*, *Bulinus* spp, *Potamon sidneyi*, *Hymenosoma orbiculare* and gobiid and cichlid fish. The catfish rarely venture further than 1 m from the substrate when foraging so that midwater fish in sheltered areas e.g. *Tilapia sparrmanii* A. Smith, *T. rendalli swierstrae* Gilchrist & Thompson, *Gilchristella aestuarius* (Gilchrist), *Hepsetia breviceps* (Val.) and *Barbus paludinosus* Peters, were rarely taken.

When stationary, *C. gariepinus* erects the barbels in a cone in front of the head; any prey touching the barbels is immediately detected and grasped (this observation has also been reported by Jubb, 1965).

- (b) Individual shovelling: Where deposits of detritus such as decomposing *Scirpus* stems cover the substrate, *C. gariepinus* feeds by shovelling the sloping anterior portion of the head under the detritus, lifting the detritus up and taking any organisms which are exposed. This method is practised in sheltered bays, on the terrace edge and in flooded marginal areas, for capturing odonatan nymphs, *Caridina nilotica*, chironomids and *M. tuberculatus*. Some detritus is also ingested. Thomas (1966) states that *C. senegalensis* "does not normally grub around in sediments in search of food", but this mode of feeding was repeatedly observed in *C. gariepinus*.
- (c) Surface feeding: Small *C. gariepinus* (< 200 mm TL) occasionally feed by positioning the body perpendicularly with the barbels spread across the water surface (Fig. 4(b)). A strong current of water is drawn into the mouth from the water surface, and expelled through the gill openings. Large items, such as terrestrial insects which have fallen onto the water surface, are occasionally taken but this method is particularly efficient for filter feeding on neuston and plankton (aquarium observations). Body position is maintained by gentle undulatory movements of

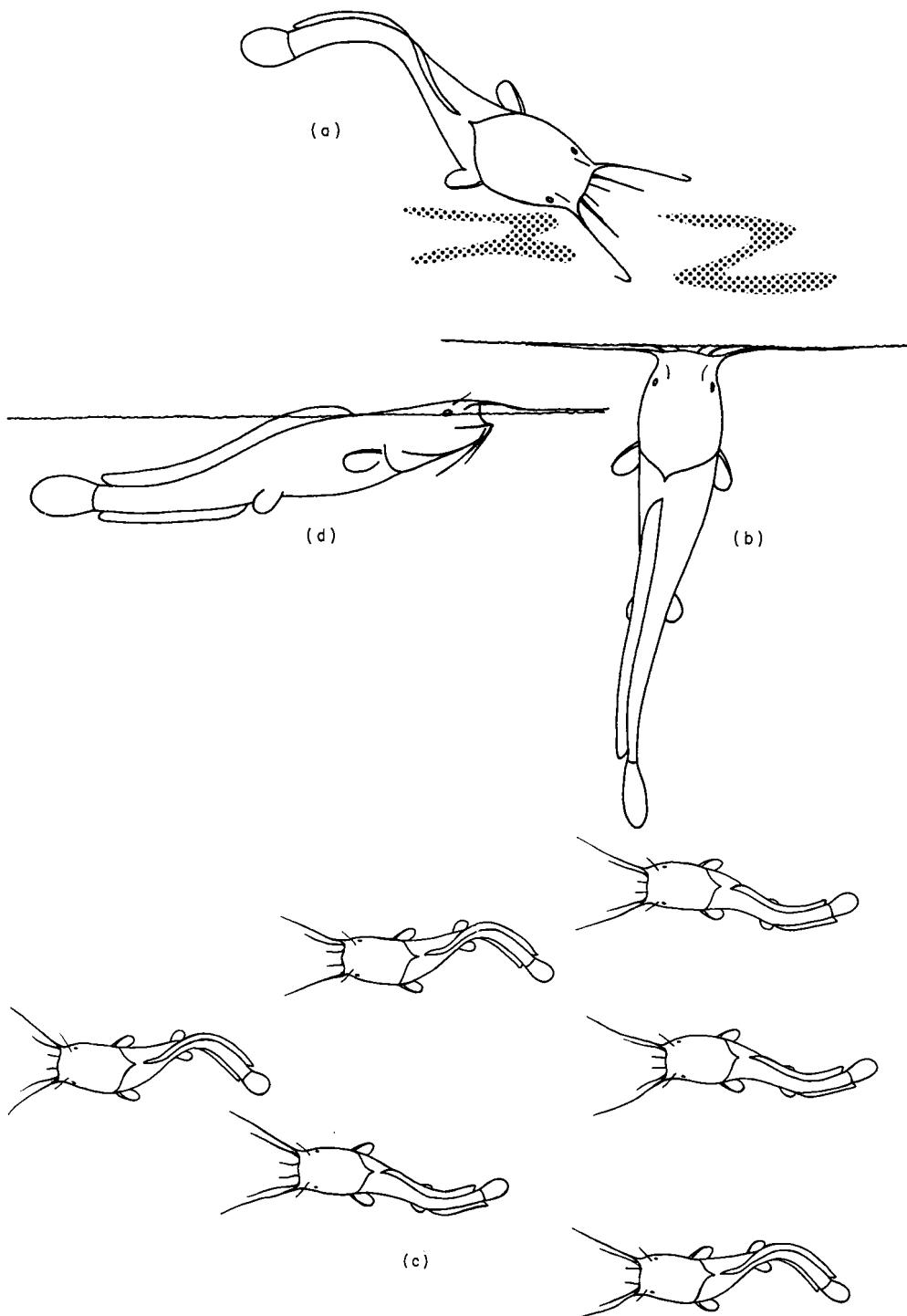


FIG. 4. Different modes of feeding in *C. gariepinus* in Lake Sibaya. (a) Individual foraging. (b) Perpendicular surface feeding. (c) Horizontal surface feeding. (d) Formation feeding at the surface.

the tail, or, in very small catfish, by positive buoyancy and the surface tension of the water on the outspread barbels.

Larger *C. gariepinus* surface feed at an angle of about 60°. Food is sucked into the mouth accompanied by loud smacking noises as the mouth is opened and closed. Surface feeding takes place singly and in groups, and occurred most often after heavy rain caused debris, especially terrestrial insects and plant fragments, to form a scum on the water surface. The catfish, in groups numbering up to 50 or 60 individuals, bobbed up and down so that the mouth was alternately partially exposed and then submerged. On rising, a strong current of water and scum was sucked into the mouth. After three or more minutes at one place the group submerged and swam just beneath the water surface to another site 1–2 m distant, where they resumed their feeding routine. This behaviour continued for up to 40 min and was always accompanied by loud sucking noises and "smacks" caused by the catfish hitting the ventral side of the head against the water surface, as in courtship (Bruton, 1979a). The catfish remained in a tight group throughout the feeding period and appeared to be stimulated into more intensive activity by the close presence and foraging behaviour of other catfish. These surface feeding shoals could be approached to within 3 or 4 m in a small boat. The prey of a sample of 16 catfish caught while surface social hunting in this way consisted of terrestrial Orthoptera, Coleoptera, Hymenoptera, Hemiptera, aquatic Mollusca and plant debris. The value of this form of ritualized feeding behaviour is not clear as social behaviour does not appear to increase predation efficiency, although the combined sensory ability of the group may reduce the risk of predation by aerial predators, e.g. fish eagle *Haliaëtus vocifer* (Daudin).

Social hunting by catfish swimming nearly parallel to the water surface was observed on five occasions in Lake Sibaya, all between 2000 and 0100 hrs on dark nights over deep water (20–35 m). Small groups of adult catfish (estimated total length 400–600 mm) swam slowly in the same direction in a regular formation (Fig. 4(c)). Individual catfish were 200–1500 mm apart, and arranged diagonally. The catfish swam with their mouths wide open and the upper jaw protruding slightly above the water surface (Fig. 4(d)). The maxillary barbels, which reach a length of 160 mm in an 800 mm TL *C. gariepinus*, were spread out over the water surface at an angle of about 45° in front of the mouth, and probably functioned as a unidimensional funnel to direct food items on the water surface into the mouth. The catfish were orientated at an angle of 20 to 40° from the water surface (Fig. 4(d)), and kept the mouth open for up to 30 sec before suddenly snapping it closed, submerging briefly as a group, and then resuming the formation again, usually swimming in a slightly different direction. Group size ranged from 3 to 13 (average 7). No surface feeding catfish were caught. Several sources of food were available to these fishes:

- (a) flotsam, mainly terrestrial insects caught in the surface film
- (b) neuston, especially the alga *Botryococcus braunii* Kütz. which occasionally accumulates in large numbers, and Cladocera, such as *Moina* spp. which are trapped in the surface film
- (c) plankton, especially *Pseudodiaptomus hessei*, zoeae of *Hymenosoma orbiculare* and larvae of the planktophagous fish *Gilchristella aestuarius*, all of

which are large enough to be trapped by gillrakers with a gap of 0·6 mm (as found in *C. gariepinus*; Murray, 1975).

Zooplankters are generally sparse in Lake Sibaya and, although they undergo a vertical migration, they do not accumulate in large numbers at the immediate water surface (Hart, 1973). A more likely source of food is flotsam, especially if the catfish can locate the convergence zones of Langmuir spirals after a heavy wind, a feeding tactic adopted by the percichthyid *Morone chrysops* (Rafinesque) in Lake Mendota (McNaught & Hasler, 1961).

Worthington (1932) made similar observations on "*C. lazera*" in East African lakes where they were often "seen swimming slowly along the water surface, with their long barbels projecting into the air, skimming dead insects off the surface. On one occasion large numbers were observed doing this out in the open water after a cloud of lake flies had passed, and when the surface of the lake was littered with the bodies and pupa cases of these flies."

Bowmaker (1973) observed similar behaviour in *C. gariepinus* in Lake Kariba: "*Clarias* were, for most of the year, commonly seen feeding in shoals at the water surface as follows: The body was held at approximately 30° to the water surface with the tip of the upper jaw and nasal barbels protruding from the water. The mandibular and maxillary barbels were usually spread and curved up to the water surface and along it. Up to four or five fish would swim quietly and slowly along in this position within a few metres of each other, gulping in water from the first few millimetres of the water surface, and, apparently filtering the zooplankton from it." *C. gariepinus* caught by Bowmaker in the open lake had fed mainly on plankton, especially *Diaphanosoma* spp. and a diaptomid sp. Jubb (pers. comm., 1976) observed vundu, *Heterobranchus longifilis* C & V (another southern African clariid catfish), surface feeding in a similar way in Lake Kariba. Their stomachs contained large quantities of zooplankton.

During surface feeding both *C. gariepinus* and *H. longifilis* swim with the mouth held open in a fixed position (although Bowmaker mentions "gulping") and water flows through the orobranchial chamber and past the gills. No sucking takes place. Walters (1966) identified the "bow pressure wave" as the main problem to be overcome in feeding by planktivorous fish. He showed in *Euthynnus affinis* (Cantor) that the feeding mechanism is virtually dragfree when the mouth and orobranchial chamber are open and distended, and that the fish feeds by swimming over its food, rather than by sucking it in. Field observations indicate that *C. gariepinus* feeds in the same way when swimming in groups on the water surface.

- (d) Formation feeding: in shallow water is performed by groups of *C. gariepinus* (400–800 mm TL) along shallow gently-sloping sandy beaches and in sparsely-vegetated marginal pools. A tightly-knit group in a rough sickle-shaped formation (Fig. 5) swim slowly inshore near the water surface with their mouths open, herding shoals of small (20–80 mm TL) cichlids (especially *Sarotherodon mossambicus*, *Tilapia sparrmanii* and *Pseudocrenilabrus philander*). When a water depth of 50–100 mm is reached the catfish suddenly close their mouths with a loud noise, open them again and swim forwards with the mouth wide open and partly above the water surface. These loud, sudden actions cause the prey to panic and jump in all directions. The catfish swim steadily inshore, opening and closing their mouths more or less in unison. The prey are eventually encircled and form a dense, panic-stricken

mass and are readily captured by the catfish. When all the prey have dispersed or been eaten, the catfish submerge and swim alongshore before reforming as a pack and swimming inshore as a group again. This cycle may continue every few minutes for over an hour, although it usually terminates after 20–30 min. The groups observed in Lake Sibaya all numbered from 15 to 40 individuals, but larger groups have been observed feeding in this way in the Dobi River, Botswana

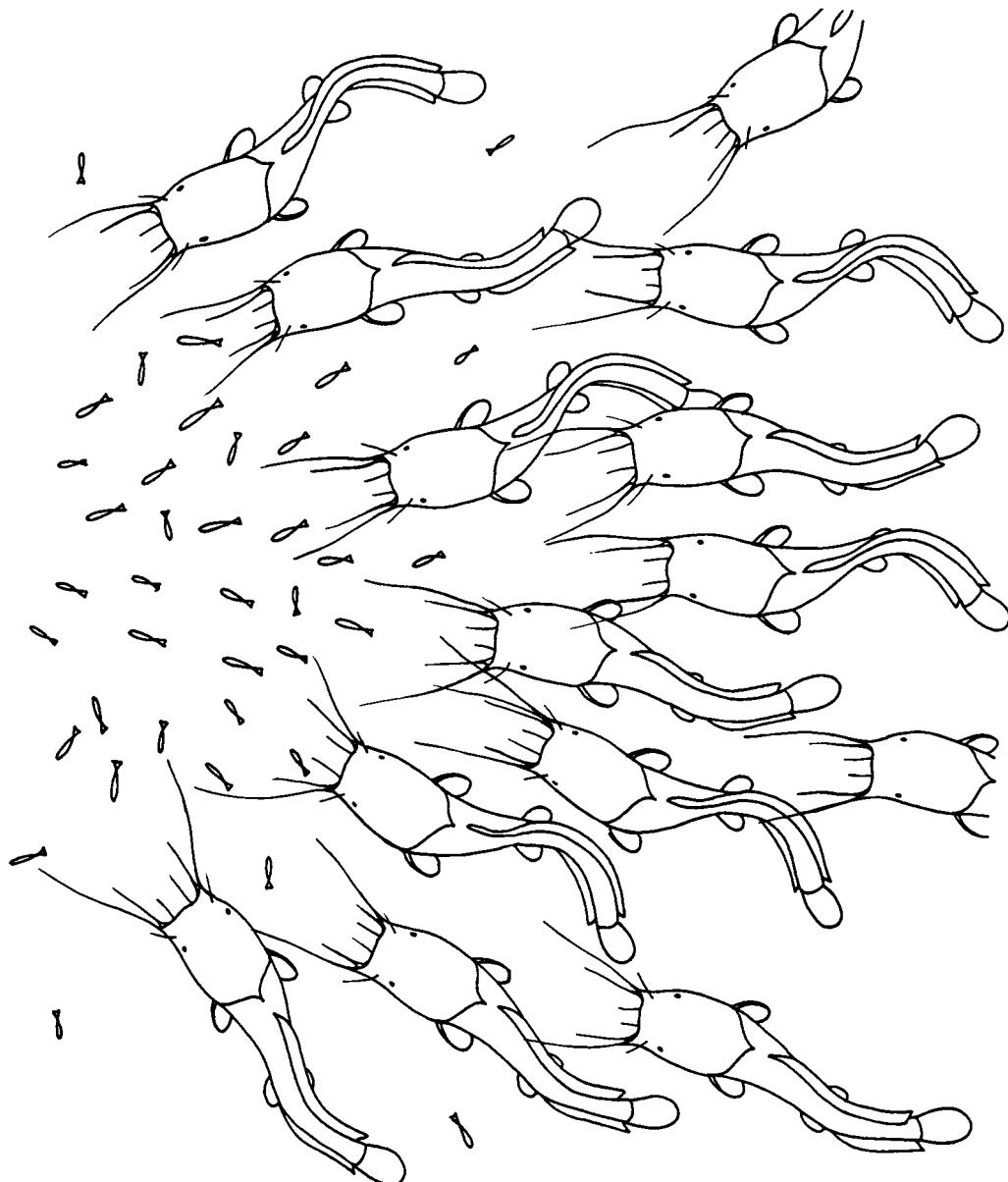


FIG. 5. Pack-hunting by *C. gariepinus* in shallow water. The prey are small cichlids.

(Donnelly, 1966, in *C. ngamensis* Castelnau, about 400 individuals) and in Nyamithi Pan, Ndumu Game Reserve, Zululand (Pooley, 1972, in *C. gariepinus*, 75–100 individuals).

Donnelly (1966) observed *C. ngamensis* (from 0·5 to 1 kg) foraging upstream in column formation at the water surface at a time when the river was subsiding. This behaviour occurred at about 0300 hrs to the accompaniment of loud noises produced every 30 sec by each fish thrusting its head out of the water and snapping it down again with some force. In the bays the catfish "rushed into the shallows like a seine net until many were crawling around on the sand out of the water". Pooley observed a close semi-circular formation of catfish (1·5–2·5 kg) surrounding small fish in very shallow water. Both Donnelly and Pooley noted that the prey were encircled in small inlets.

Similar, though less co-operative, social hunting behaviour was observed by van der Waal (pers. comm., 1976) and Bell-Cross (1974, 1976, pers. comm.) in *C. gariepinus*. van der Waal reports from Lake Liambezi in the Caprivi strip, South West Africa, that young prey fish move from the floodplain back into *Vossia* beds adjacent to the main river channel when the floods of the Zambezi river recede. Here "thousands" of *C. gariepinus* hunt in packs which chase prey fish to the water surface. The panicking prey are caught amid loud clapping noises made by the catfish. The main prey are *Barbus paludinosus* Peters, *B. haasianus* David, *Nannocharax* spp. and small cichlids. *C. ngamensis* were seen hunting in shoals for *Alestes lateralis* Boulenger.

Bell-Cross (1974, 1976) reports similar behaviour in *C. gariepinus* and *C. ngamensis* on floodplains in the Upper Zambezi river. As the flood water recedes, small prey species, and juveniles of large species, move into the main river. Packs of catfish patrolled the edge of the floodplain and attacked the prey as it attempted to enter deeper water. The water at the point of capture was about 3 m deep. The shoals of *Clarias* (with *C. gariepinus* far more numerous than *C. ngamensis*) numbered several hundred fishes in the range one to 10 kg (average about 4 kg). The prey numbered thousands and included mainly *Alestes lateralis*, *Micralestes acutidens* (Peters), *Nannocharax multifasciatus* (Boulenger), *Barbus fasciolatus* Günther, *B. haasianus*, juvenile *Tilapia* and *Sarotherodon* spp., *Pseudocrenilabrus philander* and *Ctenopoma multispinis* Peters. Tait (1965) and Williams (1971) had previously noted heavy predation by *C. gariepinus* on small fishes, particularly *P. philander*, under similar conditions in the Kafue river catchment in Zambia.

Social hunting has not, to my knowledge, been reported in other large African siluroid catfishes, e.g. *Dinopterus*, *Chrysichthys*, or *Bagrus* of the Great Lakes, nor for Siluriformes elsewhere, but there seems every likelihood that such behaviour occurs in at least some of these groups, e.g. in *Dinopterus loweae* (Jackson), which feeds in open water habitats in Lake Malawi, often at the water surface (Jackson, 1959).

Orlova & Popova (1975) report that predatory fishes in the Volga river, especially *Silurus glanis*, are found in their densest concentrations during the downstream migrations of young semi-diadromous fishes. The predators lurk in channels near the shore. They did not specify, however, whether the predators actually hunted in groups.

### *Discussion on social hunting*

Social hunting, i.e. organized hunting by a group of animals which potentially benefits all the individuals in the group, is practised by many animals including communal spiders, army ants, squid, fish, reptiles, birds and mammals (Wilson, 1972; Redakov, 1973; Curio, 1976). A wide variety of fishes, both freshwater and marine, use social hunting techniques to capture large, scattered or elusive prey (Bruton, in prep.) but few have reached the level of organization described above in *Clarias* species.

In *C. gariepinus* social hunting grades from mere scrambling, when individuals dart to the surface for flotsam or feed on carcasses, to highly co-operative and synchronized behaviour, as in surface and shallow water formation feeding. The behaviour reported by van der Waal and Bell-Cross, in which packs of *C. gariepinus* and *C. ngamensis* attacked dense shoals of prey fish forced to move in one direction at the water surface, is an intermediate stage.

Organized social hunting in *C. gariepinus* has several possible functions:

- (a) to locate dispersed prey, particularly when feeding on neuston at the water surface
- (b) disorientate elusive prey e.g. *Sarotherodon mossambicus*, and cause them to lose their normal defensive shoaling synchronization and become more vulnerable
- (c) restrict the prey spatially by herding it to the water surface or into shallow water inlets
- (d) herd prey away from shelter.

The combined effect is for social hunting to increase the predation efficiency of the individual predator, and allow it to capture prey which is normally too elusive or dispersed. Other possible advantages of social hunting in fishes are discussed by Bruton (in prep.).

### *Food preferences of C. gariepinus in Lake Sibaya*

The diet of *C. gariepinus* caught at intermediate lake level is examined in detail first, and then compared with the findings at low and high lake levels.

The food preferences of all catfish examined at intermediate lake level are given by frequency of occurrence in Table II for all food items, and by number and dry weight for the 17 most important prey in Table III. In Fig. 6 these results are plotted for the four major prey classes.

The food class appearing in most stomachs was Crustacea (Table II, 77%), followed by fish, insects and molluscs, and the most important prey species or groups were *H. orbiculare*, *G. lignorum*, *C. nilotica*, *S. mossambicus*, odonatan nymphs, chironomid larvae, *P. adusta* and *G. giurus*.

The class contributing the highest number of prey organisms was Crustacea (Table III, 65.1%) followed by fish (mainly fry), insects and molluscs. The most numerous prey species were *G. lignorum*, *H. orbiculare*, *C. nilotica*, *P. adusta*, cichlid fry, chironomid larvae and odonatan nymphs.

As a class, fishes contributed the greatest proportion of total prey dry weight (Table III, 75%) followed by crustaceans, insects and molluscs. The most important food species in

TABLE II  
*The food of C. gariepinus at intermediate lake levels (1974-75) in Lake Sibaya*  
—frequency analysis

Food species or group	Frequency of occurrence in stomachs examined	% of total no. of stomachs examined
Fish: Total	239	50·9
<i>Sarotherodon mossambicus</i>	91	19·4
<i>Pseudocrenilabrus philander</i>	41	8·7
<i>Cichlid fry</i>	28	6·0
<i>C. gariepinus</i> eggs	5	1·1
<i>Glossogobius giurus</i>	39	8·3
<i>Croilia mossambica</i>	8	1·7
<i>Aplocheilichthys</i> spp.	41	8·7
<i>Barbus</i> spp.	10	2·1
<i>Gilchristella aestuarius</i>	6	1·3
Unidentified fish	59	12·6
Crustacea: Total	361	77·0
<i>Hymenosoma orbiculare</i>	231	49·3
<i>Potamona sidneyi</i>	30	6·4
<i>Caridina nilotica</i>	116	24·7
<i>Grandidierella lignorum</i>	122	26·0
<i>Corophium triaenonyx</i>	10	2·1
<i>Afrochiltonia capensis</i>	9	1·9
<i>Apseudes digitalis</i>	9	1·9
<i>Cyathura carinata</i>	44	9·4
<i>Pontogeloides latipes</i>	31	6·6
Unidentified Crustacea	35	7·5
Insecta: Total	177	37·7
<i>Povilla adusta</i>	67	14·3
Odonatan nymphs	68	14·5
Hemiptera	15	3·2
Trichoptera	6	1·3
Chironomid larvae	73	15·6
Terrestrial Coleoptera	42	9·0
Terrestrial Hymenoptera	8	1·7
Terrestrial Orthoptera	11	2·3
Other terrestrial insects	9	1·9
Unidentified Insecta	1	0·2
Mollusca: Total	103	22·0
<i>Melanoides tuberculatus</i>	54	11·5
<i>Bellamya capillata</i>	28	6·0
<i>Bulinus</i> spp.	35	7·5
<i>Corbicula africana</i>	7	1·5
Arachnida	10	2·1
Plant debris	42	9·0
Diatoms	12	2·6
Sand	46	9·8

Number of catfish examined with stomach contents = 469.

Total number of catfish examined = 683.

TABLE III  
*The food of C. gariepinus at intermediate lake levels (1974–75) in Lake Sibaya—  
numerical and dry weight analyses of most important food items*

Food species or group	Dry weight analysis		
	Numerical analysis		Percentage of total prey dry weight
	No. individual prey	Percentage of total	
Fish: Total	695	12·5	75·0
<i>S. mossambicus</i>	126	2·3	60·6
<i>P. philander</i>	44	0·8	5·3
Cichlid fry	383	6·9	2·6
<i>G. giurus</i>	38	0·7	4·9
<i>Aplocheilichthys</i> spp.	104	1·9	1·6
Crustacea: Total	3615	65·1	18·6
<i>H. orbiculare</i>	1302	23·5	7·1
<i>C. nilotica</i>	606	10·9	0·6
<i>P. sidneyi</i>	27	0·5	10·7
<i>G. lignorum</i>	1548	27·9	0·1
<i>P. latipes</i>	44	0·8	0·04
<i>C. carinata</i>	88	1·6	0·07
Insecta: Total	1014	18·3	4·5
Odonata nymphs	197	3·6	2·0
Chironomid larvae	350	6·3	0·1
<i>P. adusta</i>	388	7·0	0·7
Terrestrial insects	79	1·4	1·7
Mollusca: Total	225	4·1	1·9
<i>M. tuberculatus</i>	44	0·8	0·7
<i>B. capillata</i>	77	1·4	1·1
<i>Bulinus</i> spp.	104	1·9	0·1

Number of catfish examined with stomach contents = 469.

Total number of catfish examined = 683.

Total number of prey found in 469 stomachs = 5549.

the dry weight analysis were *Sarotherodon mossambicus*, *Potammon sidneyi*, *Hymenosoma orbiculare*, *G. giurus* and *P. philander*.

Animals of marine or estuarine origin were well-represented in the catfish diet, occurring in 87% of all stomachs examined (with contents). They were, in order of frequency of occurrence, *H. orbiculare*, *G. lignorum*, *G. giurus*, *Hepsetia breviceps*, *Gilchristella aestuarii*, *Croilia mossambica* Smith, *Corophium triaenonyx*, *Apseudes digitalis*, *Cyathura carinata* and *Pontogeloides latipes*.

One incidence of cannibalism (ignored in previous analyses) was recorded—a male *C. gariepinus* measuring 1088 mm TL (weight 8790 g) contained a *C. gariepinus* measuring 280 mm TL, weight 217 g. In Barberspan, four large *C. gariepinus* (TL 1245 mm, 1156 mm, 1028 mm, 610 mm) had ingested four remarkably large *C. gariepinus* prey (TL 610 mm, 381 mm, 254 mm, 356 mm; Groenewald, 1964). *Clarias mossambicus* in a stream in Lake Victoria ingested small *C. mossambicus* and *C. carsoni* (TL 20 mm and 60 mm respectively),

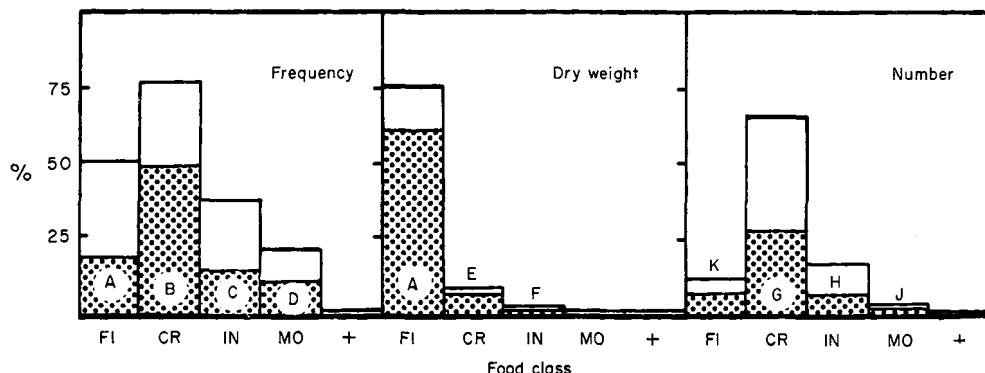


FIG. 6. The percentage contribution of different prey classes to the diet of 469 *C. gariepinus* caught at intermediate lake level in Lake Sibaya, analysed by frequency, dry weight and number, with the dominant prey species or group shaded. Food classes: FI, Fish; CR, Crustacea; IN, Insecta; MO, Mollusca; +, Other. Dominant prey: A, *S. mossambicus*; B, *H. orbiculare*; C, Chironomid larvae; D, *M. tuberculatus*; E, *P. sidneyi*; F, Odonatan nymphs; G, *G. lignorum*; H, *P. adusta*; J, *Bulinus* spp.; K, Cichlid fry.

but in both cases the predators were also small (TL 77 mm and 150 mm respectively, Corbet, 1961). Small *C. gariepinus* killed by rotenone are readily consumed by larger catfish in Lake Sibaya.

*C. gariepinus* ingested 1.75 times more *B. capillata* than *M. tuberculatus* (Table III), although the latter species was 17 times more common in belt transects measured by SCUBA divers in Lake Sibaya (Boltt, 1969). This marked selection of the thin-walled globose snail rather than the heavy-walled spiralled one may be related to the relative ease with which *B. capillata* can be crushed. Similar selection for thin-shelled snails was found by Stein *et al.* (1975) in carp *Cyprinus carpio* L.

The almost total lack of planktonic food in the diet of Sibaya catfish is in contrast to findings elsewhere (Groenewald, 1964; Munro, 1967; Schoonbee, 1969; Bowmaker, 1973; Murray, 1975). The only planktonic organisms recorded were *Pseudodiaptomus hessei* (four stomachs) and *Spirogyra* spp. (one stomach). The low standing crop of zooplankton in Lake Sibaya (Hart & Allanson, 1975) probably accounts for the dependence of *C. gariepinus* on benthic food items. As mentioned above, *C. gariepinus* have been seen feeding on the water surface at night, as they do in Lake Kariba for plankton, but none of these surface feeders has been caught.

#### Food preferences by predator length

The food preferences of catfish in different total length groups is presented in Table IV for prey species and groups, and in Fig. 7 for the major prey classes. A composite analysis, using the placings of the most important food items as determined by dry weight, frequency and number, is also presented in Table IV. In this analysis the highest rated food species or group scores one point, the second highest two points, etc. The most important food items would therefore have the lowest score when the placings are summed.

- 20–50 mm TL: The most important prey class by all methods was Crustacea, followed by insects and molluscs. No fish were taken.
- 50–100 mm TL: the predominant food class by frequency and number was Crustacea, followed by insects, fish and molluscs, whereas the dry weight analysis

rated insects above fish, crustaceans and molluscs. The insect component consisted largely of odonatan nymphs and *P. adusta*, and the fishes mainly of cichlid fry. *C. nilotica*, *G. lignorum* and *H. orbiculare* were the important Crustacea. *Clarias theodorae* Weber inhabits streams and, at high lake levels, flooded marginal areas in Lake Sibaya. Eighteen stomachs contained odonatan nymphs (78% of stomachs), *P. adusta* (50%), *Caridina nilotica* (39%), chironomid larvae (17%) and *M. tuberculatus* (11%). They may therefore compete with small *C. gariepinus* for food.

- (c) 100–300 mm TL: Fish were the most important food item by weight followed by Crustacea, but insects form an important component which is in contrast to the diet of larger catfish. In the length range 100–200 mm TL, cichlid fry form the

TABLE IV  
Summary of the food preferences of different length groups of *C. gariepinus* in Lake Sibaya

<i>C. gariepinus</i> total length group (mm)	Method of stomach analysis	Dominant food	Subdominant food (in order of preference)
20–50 (N = 19)	Frequency	<i>G. lignorum</i>	Chironomid larvae, <i>C. nilotica</i> , <i>C. carinata</i>
	Numerical	<i>G. lignorum</i>	Chironomid larvae, <i>C. nilotica</i> , <i>C. carinata</i>
	Dry weight	Odonatan nymphs	<i>C. nilotica</i> , chironomid larvae, <i>C. carinata</i>
60–100 (N = 37)	Frequency	<i>P. adusta</i>	Chironomid larvae, <i>C. nilotica</i> , <i>C. carinata</i>
	Numerical	<i>G. lignorum</i>	<i>C. nilotica</i> , chironomid larvae, <i>G. lignorum</i>
	Dry weight	Odonatan nymphs	<i>P. adusta</i> , <i>C. nilotica</i> , chironomid larvae
100–300 (N = 93)	Composite	<i>P. adusta</i>	Cichlid fry, <i>P. adusta</i> , <i>H. orbiculare</i>
	Frequency	<i>C. nilotica</i>	<i>C. nilotica</i> , <i>G. lignorum</i> , cichlid fry
	Numerical	<i>G. lignorum</i>	Odonatan nymphs, <i>P. adusta</i> , <i>H. orbiculare</i>
300–700 (N = 291)	Dry weight	Cichlid fry	<i>C. nilotica</i> , cichlid fry, <i>H. orbiculare</i>
	Frequency	<i>H. orbiculare</i>	<i>P. philander</i> , <i>P. sidneyi</i> , <i>S. mossambicus</i>
	Numerical	<i>H. orbiculare</i>	<i>G. lignorum</i> , <i>C. nilotica</i> , <i>Bulinus</i> spp.
700+ (N = 29)	Dry weight	<i>S. mossambicus</i>	<i>P. sidneyi</i> , <i>H. orbiculare</i> , <i>P. philander</i>
	Composite	<i>H. orbiculare</i>	<i>S. mossambicus</i> , <i>G. lignorum</i> , <i>P. sidneyi</i>
	Frequency	<i>S. mossambicus</i>	<i>B. capillata</i> , <i>P. sidneyi</i> , chironomid larvae
	Numerical	<i>S. mossambicus</i>	<i>H. orbiculare</i> , chironomid larvae, <i>B. capillata</i>
	Dry weight	<i>S. mossambicus</i>	<i>P. sidneyi</i> , <i>G. giurus</i> , <i>H. orbiculare</i>
	Composite	<i>S. mossambicus</i>	<i>P. sidneyi</i> , <i>B. capillata</i> , <i>H. orbiculare</i>

N = number of stomachs examined with contents.

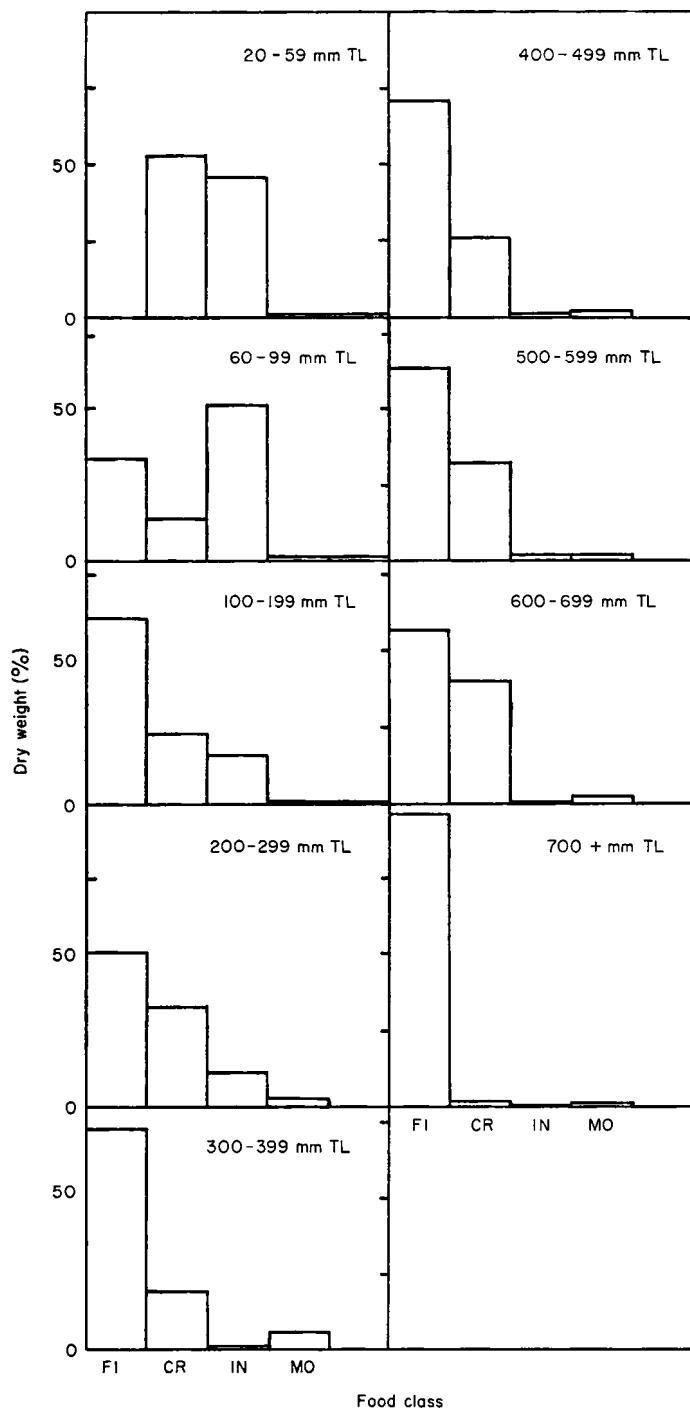


FIG. 7. The percentage contribution to total prey dry weight of major prey classes for different length groups of *C. gariepinus*. Abbreviations as in Fig. 6.

bulk of the fish component, whereas in larger catfish, juvenile *S. mossambicus* and *P. philander* are more important.

- (d) 300–700 mm TL (large juvenile and adult fishes) feed predominantly on fish, especially *S. mossambicus*, and Crustacea, mainly *H. orbiculare*. Insects are unimportant in the diet as these fishes feed mainly in exposed or deep sandy areas where insects are uncommon.

This size group of *C. gariepinus* has also been observed to feed in Lake Sibaya on frogs (*Rana* spp., *Hyperolius* spp.), the fruit of fig trees *Ficus* spp., fish regurgitated by the cormorant *Phalacrocorax carbo* (L.), *Sarotherodon mossambicus* fry (released by mouth-brooding females caught in a seine net), fledgling weavers *Ploceus* spp. and cormorants *Phalacrocorax carbo*, rotting flesh on cow and crocodile carcasses, and *Hippopotamus amphibius* L. dung. A large group was seen feeding with crocodiles on a hippopotamus carcass in Ndumu Game Reserve, Zululand, in 1970. Other diverse items which have appeared in *C. gariepinus* stomachs include young water fowl, berries, grass seeds, a small crocodile (Bell-Cross, 1974), swallows and cormorant eggs (Groenewald, 1961), ducklings (Groenewald, 1964), a small mammal and remains of a snake (van der Waal, 1972). *C. mossambicus* have also been seen feeding on a crocodile carcass (Jackson *et al.*, 1963) young *Phalacrocorax* sp. (Corbet, 1959) and fish embryos (Greenwood, 1965).

- (e) 700 mm TL +: Large adults which rarely enter shallow water, and feed predominantly on *S. mossambicus*.

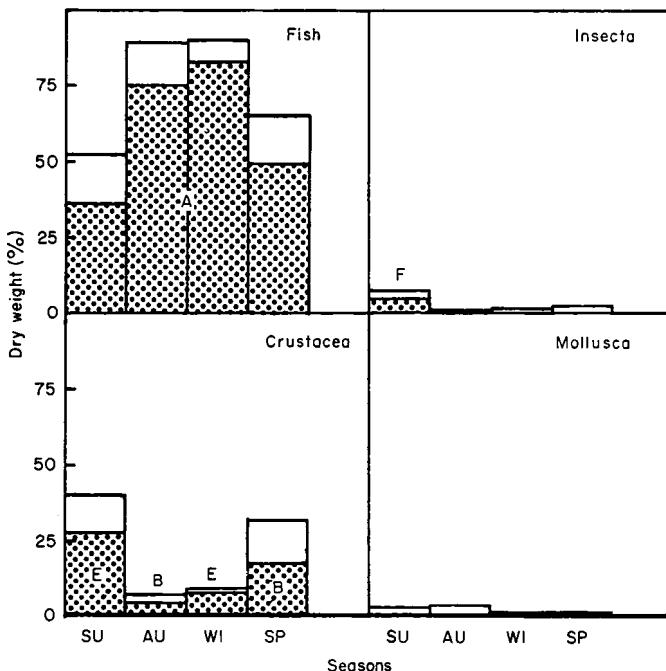


FIG. 8. The percentage contribution to total prey dry weight of major prey classes for *C. gariepinus* caught in different seasons. The dominant prey species or group is shaded. Seasons: SU, summer; AU, autumn; WI, winter; SP, spring. Other abbreviations as in Fig. 6.

### Food preferences by season

The relative contribution to total prey dry weight of the four major prey classes in different seasons is plotted in Fig. 8. Insects and molluscs were taken in low proportions throughout the year, with the highest insect catch in summer. Fish, mainly *Sarotherodon mossambicus* contributed a greater proportion of prey weight in autumn and winter than in spring and summer. The mean weight of *S. mossambicus* prey was higher in autumn and winter (15.8 and 23.0 g) than in spring and summer (2.7 and 3.2 g) in catfish in the length range 300–600 mm TL. Crustacea contributed more to prey weight in spring and summer than in autumn and winter, although Boltt (1969) found that *Hymenosoma orbiculare*, the main crustacean prey, is more abundant in Lake Sibaya in the cooler months. Their absence from the terrace during this period (Boltt, 1969) may account for their smaller contribution to the catfish diet in winter. *Caridina nilotica* and *Grandidierella lignorum* were taken mainly in spring and summer.

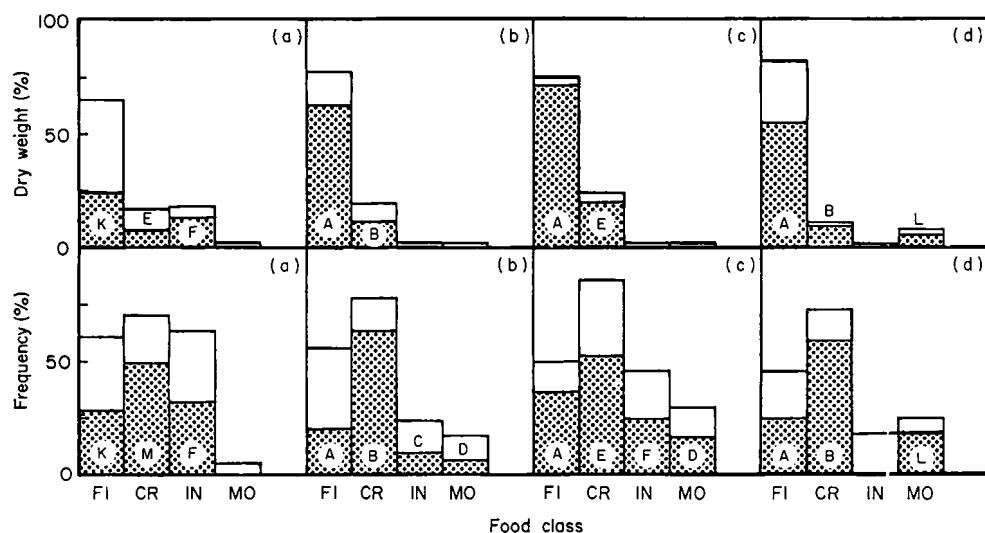


FIG. 9. The percentage contribution to total prey dry weight (upper histograms) and frequency of occurrence (lower histograms) of major prey classes of *C. gariepinus* in different habitats. The dominant prey species or group is shaded. Habitats: (a) marginal; (b) terrace; (c) sheltered bay and slopes; (d) profundal. Dominant prey (in addition to those in Fig. 6): L, *B. capillata*; M, *C. nilotica*; N, *P. philander*.

### Food preferences by habitat

The relative contribution to total prey dry weight and frequency of the four main prey classes in different habitats is plotted in Fig. 9. Fish contributed the greatest proportion of prey dry weight in all habitats, whereas Crustacea occurred in most stomachs in all habitats. Insects were taken most often in marginal and bay habitats, and molluscs in bay and profundal habitats.

### Food preferences by prey microhabitat

Too little is known of the density of the diverse prey of *C. gariepinus* in Lake Sibaya to calculate forage ratios (*vide* Thomas, 1966) but data on prey microhabitat preferences

and accessibility are presented in Table V. Prey organisms common in the different microhabitats but rarely taken by catfish are also listed. The larvae of *Povilla adusta* are normally tubicolous but swim about actively in the dark (Hartland-Rowe, 1958; Petr, 1970; my own observations). Thomas (1966) noted that the absence of silken cases of *P. adusta* in *Clarias senegalensis* stomachs containing the larvae indicated that they were taken while out of their burrows at night, a result confirmed for *C. gariepinus* at Lake Sibaya. *P. adusta* is therefore included in category F. Although they build burrows in the sand, *Grandidierella lignorum* was included in category G as the majority of those eaten by *C. gariepinus* (over 80%) were appetitive males which had probably left their burrows at night (Boltt, pers. comm., 1973).

TABLE V  
Microhabitat and accessibility of prey available to, and taken by *C. gariepinus* in Lake Sibaya

Prey microhabitat	Accessi- bility	Common* prey not or rarely taken by catfish	Prey frequently taken by catfish	% of total prey dry weight	% of total prey number
(a) Permanently sheltered in sand	Low	Tubificid and naidid oligochaetes	Chironomid larvae	0·1	6·4
(b) Swimming in midwater or near water surface	Moderate	<i>T. sparrmani</i> <i>T. rendalli</i> <i>Barbus viviparus</i> M. Weber	<i>Aplocheilichthys</i> spp.	1·6	1·9
(c) Exposed on plants or plant debris	High	Trichopteran nymphs	Odonatan nymphs Some <i>Bulinus</i> spp.	2·2	4·6
(d) Sheltering under or in association with plant debris	Moderate		Some <i>P. sidneyi</i> Some <i>C. nilotica</i>	5·7	5·7
(e) Associated with water surface	High	Adult aquatic insects	Terrestrial insects	0·6	1·7
(f) Swimming close to substrate (within about 1 m)	High		<i>S. mossambicus</i> , <i>P. philander</i> cichlid fry, <i>P. adusta</i> , <i>G. giurus</i>	75·3	17·9
(g) Temporarily sheltered in substrate or living on substrate- water interface	High	<i>Ceratonereis</i> <i>keiskama</i> Day (Polychaeta), tadpoles.	<i>H. orbiculare</i> , <i>G. lignorum</i> , some <i>C. nilotica</i> , some <i>P. sidneyi</i> , <i>P. latipes</i> , <i>C. carinata</i> , <i>B. capillata</i> , <i>M. tuberculatus</i> , some <i>Bulinus</i> spp.	14·5	61·8

\*According to Boltt (1969) and Allanson *et al.* (1974).

The majority of prey taken (89·8% by weight, 79·7% by number) lived in close proximity to the substrate: water interface (sections F and G, Table V). Highly accessible prey was taken in preference to prey with moderate or low accessibility. Tadpoles are common in sheltered shallow water, yet they were not recorded in the diet of *C. gariepinus* in Lake Sibaya. *C. mossambicus* and *C. senegalensis* are known to eat tadpoles (Corbet, 1961; Thomas, 1966).

The composition of the diet of catfish in Lake Sibaya does not correspond with the relative proportions of common benthic organisms reported by Boltt (1969). *Hymenosoma orbiculare*, *Caridina nilotica* and *G. lignorum* were well-represented in the diet, but *Bellamya capillata*, *Melanoides tuberculatus*, *Corophium triaenonyx* and *Apseudes digitalis* which are common in the benthos, were less prominent than shallow water insects such as odonatan and *P. adusta* nymphs. Selection is thought to be a function of two closely-related factors—prey activity and prey exposure. *H. orbiculare* swim off the substrate when disturbed and are readily detected (but not necessarily caught) by catfish, as are odonatan nymphs and *C. nilotica*. Both *G. lignorum* males and *P. adusta* nymphs are active above the substrate at night. In contrast, the molluscs, as well as *C. triaenonyx* and *A. digitalis* are less active, remain on the substrate and would probably be less detectable by a predator relying largely on mechanoreception. This possibility is investigated further below.

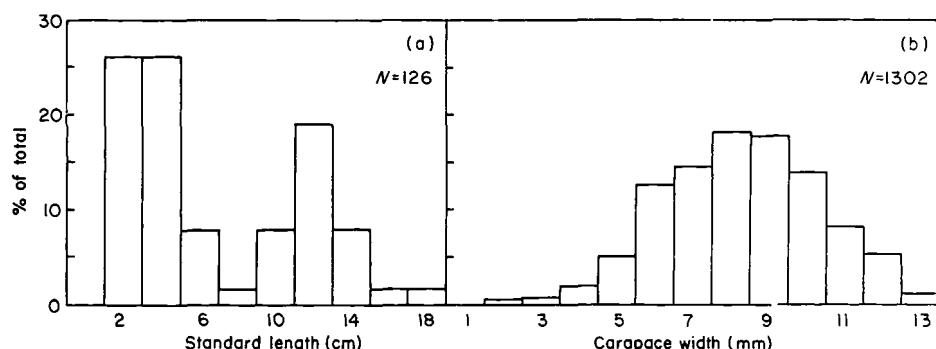


FIG. 10. The size structure of *S. mossambicus* (a) and *H. orbiculare* (b) prey of *C. gariepinus* in Lake Sibaya.

#### Size structure of the main prey

The size structure of *H. orbiculare* and *S. mossambicus* prey is given in Fig. 10. Catfish preyed on large benthic *H. orbiculare* and not their planktonic zoeae. The mean size taken (8.3 mm) is about the mean size of *H. orbiculare* in the benthos of Lake Sibaya (9 mm, Forbes & Hill, 1969). *S. mossambicus* prey consisted mainly of fry, small juveniles and intermediate size adults. Few *S. mossambicus* in the standard length range 80–120 mm, or larger adults over 150 mm SL, were taken. The absence of the latter can be accounted for by their relative paucity in the *S. mossambicus* population and by their large size, but the absence of the intermediate size cichlids requires another explanation. Bruton & Boltt (1975) found that most young adult male *S. mossambicus* spend their first year in offshore waters, so that the population structure of *S. mossambicus* on the terrace is bimodal and resembles that given in Fig. 10 for catfish prey. These findings suggest that *C. gariepinus* may feed mainly on the size classes of *S. mossambicus* which frequent terrace waters.

The standard length of 71 *S. mossambicus* prey which could be measured accurately is plotted against catfish total length in Fig. 11. The prey are grouped in three size classes—fry (10–20 mm SL); juveniles (20–80 mm) and small adults (120–150 mm). In general, prey size increased linearly with predator length ( $R = 0.86$ ) although large catfish were

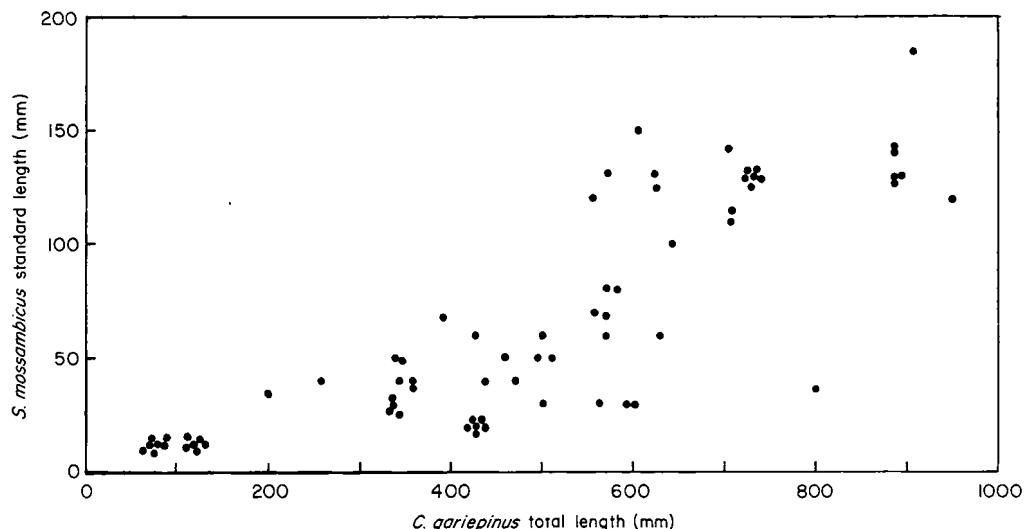


FIG. 11. The relationship between total length of predator (*C. gariepinus*) and standard length of prey (*S. mossambicus*) for a sample of 71 *S. mossambicus* from Lake Sibaya.

observed to eat some cichlid fry and small juveniles. The largest *S. mossambicus* found in a catfish stomach measured 185 mm SL.

#### *Prey diversity and number*

The sample of catfish used in this study consumed over 55 different food species or groups, and further collecting would doubtless reveal additional items. Individual catfish stomachs contained up to 10, rarely 13, different food species (average 3.1, Table VI). Catfish in the total length range 60–400 mm contained the greatest variety of food species and the highest number of individual food items, but dispersion around the mean was high. Corbet (1961) found as many as six different prey species in a single *Clarias mossambicus* stomach.

TABLE VI  
Number of individual prey and prey diversity in *C. gariepinus* stomachs from Lake Sibaya

Catfish TL group (mm)	No. catfish stomachs examined (with contents)	Total no. individual prey	Mean no. prey per stomach	S.E.	Mean no. prey species per stomach	S.E.
0–50	19	186	9.8		2.3	0.88
50–100	37	952	25.7	5.2	3.5	0.64
100–200	42	1088	25.9	6.81	3.8	0.79
200–300	51	889	17.4	8.56	5.0	0.66
300–400	82	744	9.1	5.29	3.3	0.34
400–500	68	407	6.0	1.62	2.3	0.20
500–600	95	754	7.9	1.68	2.7	0.22
600–700	46	334	7.3	2.56	3.1	0.53
700+	29	116	4.0	2.82	1.9	0.18
	469	5470	11.7		3.1	

As shown in Table VII, which gives six examples of diverse stomach contents of *C. gariepinus* in Lake Sibaya, the catfish occasionally consumed large numbers of one prey species. Other examples are: *C. gariepinus* ova (highest number in one stomach: 370), cichlid fry (94), *P. adusta* (59), odonatan nymphs (36), *Bulinus* spp. (Mollusca, 23) and *C. nilotica* (20). All these examples indicate concentrated feeding by the predator on a particular prey. *H. orbiculare* were present in most stomachs, occasionally in large numbers (e.g. 26, 47, 69).

The greatest diversity of animals in Lake Sibaya is found in sheltered vegetation or in permanently submerged beds (Allanson, Bruton *et al.*, 1974). These areas are inhabited mainly by juvenile catfish (< 400 mm TL) whereas areas supporting a less diverse fauna (exposed terraces and deep lake sediments) are inhabited by larger catfish (Bruton, 1978).

TABLE VII

*Six examples of the diversity of prey found in the stomachs of individual *C. gariepinus* caught in Lake Sibaya*

<i>C. gariepinus</i> total length	Stomach contents
269 mm	1 <i>P. philander</i> , 1 <i>P. sidneyi</i> , 32 <i>G. lignorum</i> , 3 <i>C. carinata</i> , 5 Coleopteran larvae, 2 <i>H. orbiculare</i> , 11 chironomid larvae, 6 adult Diptera, 4 <i>C. nilotica</i> , 11 odonatan nymphs, 1 curculionid beetle, 5 <i>G. lignorum</i> .
280 mm	1 <i>A. katangae</i> , 1 odonatan nymph, 6 <i>C. nilotica</i> , 1 <i>C. mossambica</i> , 14 <i>P. adusta</i> , 1 formicid.
386 mm	54 <i>G. lignorum</i> (all males), 1 <i>P. sidneyi</i> , 2 <i>P. adusta</i> , 1 chironomid larva, 2 <i>C. carinata</i> , 2 <i>M. tuberculatus</i>
545 mm	2 <i>P. philadneri</i> , 3 <i>G. giurus</i> , 1 <i>A. katangae</i> , 1 <i>P. latipes</i> , 4 <i>C. carinata</i> , 1 <i>H. orbiculare</i> , 1 <i>Bulinus</i> spp., 1 <i>M. tuberculatus</i>
565 mm	27 <i>H. orbiculare</i> , 3 <i>P. latipes</i> , 1 <i>M. tuberculatus</i> , 15 <i>G. lignorum</i> , 1 Hymenoptera, 1 coccinellid beetle, 1 odonatan nymph, 1 chironomid larva, 1 chrysopid adult, 1 <i>Bulinus</i> ( <i>Physopsis</i> ) sp., 1 <i>C. triaenonyx</i> , fish vertebrae, insect egg.
585 mm	1 <i>P. sidneyi</i> , 6 chironomid larvae, 7 <i>C. nilotica</i> , 2 Coleoptera adults, 1 <i>Segmentorbis</i> spp., 1 <i>P. latipes</i> , fish scales, plant fragments, sand.

#### *Stomach fullness*

An arbitrary estimation of stomach fullness was made and points allocated as follows:

Visual estimation	
of fullness	Points
Distended	10
Full	8
3/4 full	6
1/2 full	4
1/4 full	2
Trace	1
Empty	0

The mean number of points per stomach (fullness index) was determined for each month's sample (Fig. 12(a)). Although this method provides a measure of relative volume of food irrespective of predator size, equal numbers of catfish from each size class were used in the sample as the fullness index varied in different size classes (see below).

Feeding intensity in adult *C. gariepinus* was not high, and, with the exception of fish taken in November, stomachs were on average less than half full (Fig. 12(a)). Small catfish (< 200 mm), which feed largely on small items had higher mean fullness indices (4.9) than medium (200–600 mm TL, 3.8) or large catfish (> 600 mm TL, index 2.6). Similar results are reported by Corbet (1961) in *C. mossambicus*, Groenewald (1964) and Munro (1967) in *C. gariepinus*, and Thomas (1966) in *C. senegalensis*. Regurgitation and digestion by *C. gariepinus* caught in passive gear (gillnets, traps, longlines) in Lake Sibaya may account in part for the low fullness indices obtained.

#### Condition factor

Condition factors also give an indication of feeding intensity if changes in the length-weight relationship due to gonadal maturation are taken into account. The method used for the calculation of condition factor is given in Appendix I. Monthly mean

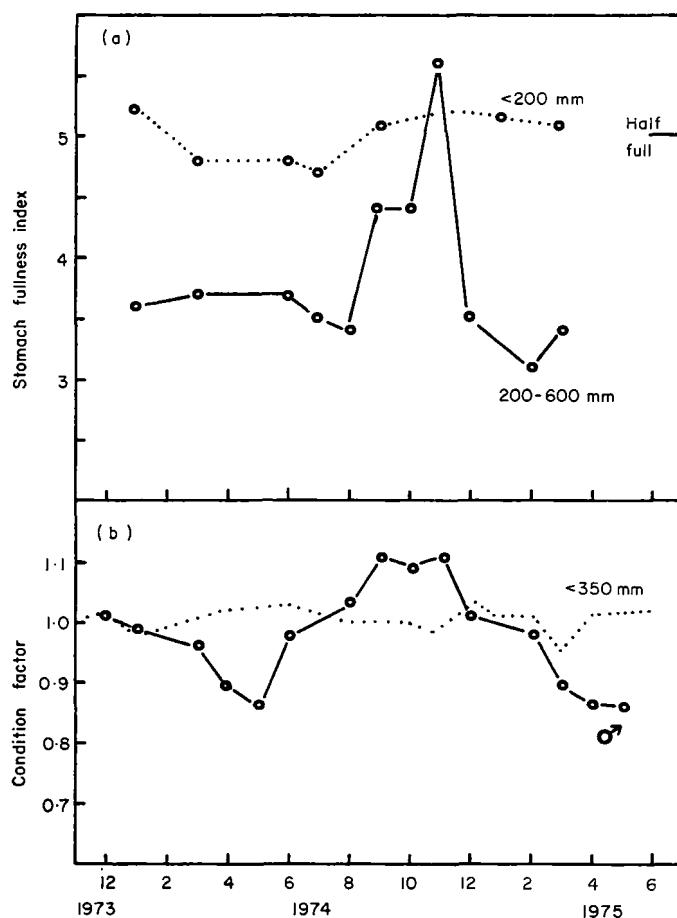


FIG. 12. (a) Monthly stomach fullness indices of small juvenile (< 200 mm TL, dotted line) and large *C. gariepinus* (200–600 mm TL solid line), from Lake Sibaya. (b) monthly condition factors of juvenile (< 350 mm TL, dotted line) and adult male (*C. gariepinus* from Lake Sibaya.

condition factors for adult males and juveniles are given in Fig. 12(b) for the period November 1973 to May 1975. Adult males were used as the mature testis weight is small and has little effect on the length-weight relationship, whereas mature ovaries may constitute up to 12% of total body weight (Bruton, 1979). The condition factor fluctuated more widely in adult males than in subadult catfish. In adult males condition factors were lowest in March, April and May and reached a peak in September, October and November. High condition factors may be due to a high proportion of fat fish and a high proportion of fish with full or near full stomachs.

Loss of condition by adults in midyear coincided with several events—decreasing lake temperatures, less shallow water feeding activity by catfish and an increase in the mean size of prey fish. A possible explanation for the fall-off in condition is that feeding periodicity was reduced in catfish feeding on large items in deeper water. In the warmer months, when *C. gariepinus* regularly entered shallow water, the index of stomach fullness is high, feeding intensity is higher, and the diet consists of larger numbers of small items. *C. senegalensis* also reached peak condition in October after a period of feeding (Thomas, 1966).

TABLE VIII  
*Incidence of parasites in C. gariepinus from Lake Sibaya*

Parasite	No. catfish examined	No. catfish infested	% infested	Mean no** parasites	Range
<b>External</b>					
<i>Dolops ranarum</i> Stuhlmann (Crustacea: Branchiura)	249	84	33.7	5.8	1-15
<i>Limnatis fenestrata</i> Moore (Annelida: Hirudidae)	249	5	2.0	3.6	1-12
<b>Internal</b> (stomach only examined)					
Nematoda	249	27	10.8	9.2	1-12

\*\* per infested catfish

Juvenile catfish which feed throughout the year in shallow water remained in good condition during the whole study period (Fig. 12(b)).

Unlike the population of *C. gariepinus* in the Pongola river, which were heavily infested with internal parasites (Kok, pers. comm., 1976), only 10.8% of a sample of 823 *C. gariepinus* from Lake Sibaya had nematodes in their stomachs (Table VIII). The incidence of an external parasite, *Dolops ranarum* (Stuhlmann) was higher (33.7%), but these crustaceans cause little apparent harm to *C. gariepinus*.

#### *The diet of C. gariepinus at different lake levels in Lake Sibaya*

The diet of *C. gariepinus* at different lake levels is compared in Table IX by frequency of occurrence of different items. Three main trends are apparent:

- (a) The average number of food items per stomach was lower (1.8) at low lake level than at intermediate (4.8) or high lake level (6.9). The catfish diet was therefore

more diverse when marginal areas had been flooded and extensive sheltered water habitats were found around the lake. These habitats support a richer biota than wave-washed terraces and sandy marginal pools which are typical of low lake level.

- (b) The diet at all lake levels was dominated in terms of frequency by *H. orbiculare*, followed by a cichlid fish or *G. lignorum*.
- (c) Prey items varied markedly in importance at different lake levels. The only variation (besides that of the cichlids) which can readily be explained is that of *P. adusta*. As nymphs, these ephemeropterans burrow into submerged dead sedges and trees, and their abundance can be related directly to the availability of suitable substrates. Their abundance at high lake level in Lake Sibaya and in the catfish diet is almost certainly a consequence of the large number of sedges and *Acacia* trees which were drowned on the lake edge. Population explosions of *P. adusta* have also followed the initial flooding of several man-made lakes in Africa (e.g. Volta lake, Petr, 1970).

Some food items which are only common in summer (October–February), such as certain insects with aquatic larval stages, may be underestimated in the diet of high lake level catfish as these collections were only made in March and April.

TABLE IX  
*Frequency of occurrence of major food items of C. gariepinus (TL 300–700 mm)  
at three different lake levels in Lake Sibaya (lake levels defined in Table I)*

	Low N = 92	Lake level Intermediate N = 469	High N = 123
Fish total	31.5	52.9	55.3
<i>S. mossambicus</i>	25.0	20.3	1.6
<i>P. philander</i>	4.3	6.5	36.6
<i>T. sparrmannii</i>	3.3	0.3	12.2
<i>G. giurus</i>	15.2	11.7	10.6
Crustacea total	64.2	85.2	80.5
<i>H. orbiculare</i>	47.8	62.9	75.6
<i>G. lignorum</i>	6.5	21.3	26.8
<i>P. sidneyi</i>	4.3	7.9	0
<i>C. nilotica</i>	10.9	17.5	8.9
Insecta total	15.4	25.4	14.6
Odonatan nymphs	8.7	5.5	0
Chironomid larvae	4.3	6.9	3.3
<i>P. adusta</i> nymphs	2.2	5.2	12.2
Mollusca total	8.7	22.0	23.3
<i>B. capillata</i>	6.5	5.8	8.9
<i>M. tuberculatus</i>	4.3	12.4	8.1
<i>C. africana</i>	0	2.4	11.4
<i>Bulinus</i> spp.	0	5.8	4.9
Mean no. food items per stomach	1.8	4.8	6.9

N = number of stomachs examined with contents.

TABLE X  
Review of the main foods of some large African *Clarias* species

<i>Clarias</i> species	Water system	Method of stomach analysis	Predator length range (mm)	Main prey	Other important food	Number stomachs examined (with contents)	Reference
<i>C. gariepinus</i>	Jukse river Barberspan Vaal river (all Transvaal)	Frequency Frequency Frequency	124-228	Entomostracans & Chironomids <i>Clarias gariepinus</i> Terrestrial invertebrates	Other fish, plankton Fish	Total 104	Groenewald (1964)
Lake McIlwaine (Rhodesia)	Reconstructed volume		200-400	Chironomid pupae	Tanypodinae larvae, Gastropoda, terrestrial insects	102	Munro (1967)
			400-600	Chironomid pupae	Cladocera & Copopeda, Gastropoda	358	Munro (1967)
			600+	Cladocera & Copepoda	Chironomid pupae	105	Munro (1967)
Lake Sibaya (Zululand) Barberspan (Transvaal)	Numerical Volumetric	approx 300-700 0-200 200-400	<i>H. orbicularis</i> Fish (unspecified) Fish	Small cichlids, <i>G. giuris</i> Ephemeroptera Cladocera		53 37 4	Minshull (1969) Schoonbee (1969) Schoonbee (1969)
Shallow pools (Rhodesia)	Frequency	not given	400+ Coleoptera (aquatic adults)	Fish Grape seeds Fish Fish	Filamentous algae Fish <i>Nymphaea</i> seeds Chironomidae	68 not given	Weir (1972)
Olfants river, Transvaal Farm dam, Marble Hall Farm dam, Groblersdal Lolamentes dam, Marble Hall	Volumetric Volumetric Volumetric Volumetric	over 180 over 180 over 180 over 180	Fish Fish Fish Fish	Terrestrial insects Chironomidae Terrestrial insects, detritus	15 16 16 299	van der Waal (1972) van der Waal (1972) van der Waal (1972) van der Waal (1972)	
Leeupan, W. Transvaal Kareepan, Wolmaranstad Elandsriver, nr Marble Hall Lepalona dam, Olfants River Crocodile Hill Dam,	Volumetric Volumetric Frequency	over 180 over 180 over 180 70-180	Chaoboridae, Chironomidae	Cladocera	15	van der Waal (1972)	
Olfants river Lake Kariba Pongola pans (Zululand)	Frequency Frequency	70-180 216-865 100-900	Terrestrial insects Cladocera Fish	Odontan and Ephemeropteran nymphs Copepoda Aquatic insects, Gastropoda	11 34 266	van der Waal (1972) Bownaker (1973) Kok, pers. comm.,	

	Lake St Lucia (Zululand)	Frequency	353–462	<i>Assiminea bifasciata</i> (Gastropoda)	<i>Glossogobius giuris</i>	12	Whitfield, pers. comm.
Hardap dam (South West Africa)	Frequency	242–1482	Fish	Zooplankton		69	Gaigher (1977)
Lake Sibaya	Frequency	21–1088	<i>H. orbicularis</i> Plant detritus	<i>S. mossambicus</i> , <i>G. ligornum</i>	469	This study	
Lower Shire river, Malawi	Frequency	not given	Cichlid fish, humus, filamentous algae	<i>Cycloasteria</i>	491	Willoughby & Tweedie (1976)	
Lake Kariba (margins amongst <i>Salvinia molesta</i> Mitchell).	Frequency	49–542	<i>P. adusta</i>	chironomid larvae (Conchostraca),	37	Mitchell (1976)	
<i>C. mossambicus</i>	Lake Victoria	Frequency	not given	Fish	Insect larvae, molluscs, oligochaetes, prawns and zooplankton	55	Graham (1929)
Lake Malawi (open waters)	Frequency	not given	<i>Haplochromis</i> spp.	<i>Tilapia</i> spp., small <i>Clarias</i>	not given	Lowe (1952)	
Lake Malawi (sheltered creek)	Frequency	330–570	Terrestrial insects	Seeds, fish	8	Fryer (1959)	
Stream, Lake Victoria	Frequency	7–870	Chironomid larvae	Ostracoda, Anisopteran larvae	93	Corbet (1961)	
Lake Victoria (main lake)	Frequency	240–900	<i>Haplochromis</i> spp.	Plants, Gastropoda, C. <i>nilotica</i> , Anisopteran larvae	216	Corbet (1961)	
Victoria Nile	Frequency	100–240	Lithophilic insects	Ostracoda, chironomid larvae			
Victoria Nile	Frequency	770–900	<i>Potamona</i> spp.	<i>P. adusta</i> , <i>Barbus altianalis</i> Bigr.	5	Corbet (1961)	
Uganda	Frequency	not given	<i>Haplochromis</i> spp.	Insect larvae, molluscs, plants	2	Corbet (1961)	
Lake Chilwa	Frequency	not given	<i>Barbus pallidus</i>	Aquatic insects, plant detritus	not given	Greenwood (1966)	
Lochinvar lagoon, Kafue river	Frequency	not given	Fish		2	Kirk (1967)	
<i>C. lazera</i>	Lake George, Uganda	Frequency	not given	<i>Haplochromis</i> spp.	not given	Greenwood (1976)	
<i>C. ngamensis</i>	Lake Piti, Mozambique	Frequency	300–650	Chironomid larvae	10	Personal observations	
<i>C. senegalensis</i>	Nungua Lake, Ghana	Frequency	150+	Chironomid pupae			
	Numerical	150+	<i>Chaochorus</i>	<i>Stenocorixa</i> , tilapia	178	Thomas (1966)	
	Points	150+	Tilapia	Chironomid pupae, <i>Micronecta</i> (Hemiptera) <i>Stenocorixa</i> (Hemiptera), <i>Hemilepidotus</i> (Trichoptera)			

*Review of feeding by **C. gariepinus**, **C. mossambicus** and some other species of **Clarias***

The results of some studies on the food of *C. gariepinus*, *C. mossambicus*, and other species in the subgenus *Clarias* (*Clarias*), are summarized in Table X. In most populations for which there is an adequate sample, adult catfish (> 35 cm TL, but variable, Bruton, 1979a) fed mainly on fish (in a weight analysis) or Crustacea (in a frequency or numerical analysis). Terrestrial and aquatic insects were important in the diet of juvenile and adult catfish which inhabit shallow ponds and littoral areas. Both species fed on a wide variety of prey of different sizes.

Groenewald (1964) described *C. gariepinus* as a clumsy piscivore which also exploits aquatic and terrestrial invertebrates when they are abundant. Munro (1967) found a marked seasonal change in the diet of *C. gariepinus* in Lake McIlwaine, Rhodesia, with greater emphasis on chironomids from September to February (warm months) and on zooplankton in the cool months. In Lakes McIlwaine (Munro, 1967), Barberspan (Schoonbee, 1969) and Kariba (Bowmaker, 1973) zooplankton were more important in the diet of large (> 400 mm TL) than small *C. gariepinus*. Large *C. gariepinus* from the open waters of Lake Kariba contained mainly Cladocera and Copepoda with a body length > 1 mm (Bowmaker, 1973). When freshwater invades estuarine Lake St Lucia in Zululand, *C. gariepinus* is common and feeds mainly on gastropods, gobiid fishes and crabs (A. K. Whitfield, pers. comm., 1976).

*C. senegalensis* Cuv. & Val. in a small man-made lake in Ghana subsisted mainly on organisms swimming in midwater (including tilapia, zooplankton and insects), those swimming close to the sediment or those living on the sediment. Animals under stones, in the sediment or in shallow water or vegetation close to shore were taken less often. Vegetation and detritus were unimportant in their diet.

A small sample of 19 *C. ngamensis* from Lake Piti in southern Mozambique had eaten only chironomid larvae and *Aplocheilichthys* sp. (pers. obs., 1970). This species feeds mainly on molluscs and chironomids in the Pongola floodplain pans in northern Zululand, South Africa (Kok, pers. comm., 1976). Bell-Cross (1976) describes their diet as similar to *C. gariepinus* with a larger component of insects and molluscs.

In summary, *C. gariepinus* and *C. mossambicus* share an euryphagous diet, dominated in adults by fish or Crustacea. The known diet of *C. senegalensis* and *C. ngamensis* more closely resembles that of their smaller anguilliform, shallow-water relatives which are more stenophagous and feed mainly on arthropods (Jackson, 1961a; Jackson *et al.*, 1963; Jubb, 1967; Bell-Cross, 1976; pers. obs. in *C. theodorae*; Jackson *et al.*, 1963; Worthington, 1933; Corbet, 1961 in *C. carsoni*; Jackson, 1961a; Jubb, 1967 in *C. submarginatus* Peters).

*Review of predation by **C. gariepinus** and **C. mossambicus** on cichlids*

This review includes comments on predators other than catfish where the comparison is helpful in a description of the different kinds of predation. The possible influence of predation on speciation is not discussed (for main papers see Worthington, 1937, 1954; Jackson, 1961b; Fryer, 1960, 1965; Fryer & Iles, 1972; Greenwood, 1974).

Cichlids have been reported from the food of many, but not all, *C. gariepinus* and *C. mossambicus* populations. They occur in the diet of *C. gariepinus* in Lake Barberspan (Groenewald, 1964, but not specified by Schoonbee, 1969), in Lake Sibaya (Minshull,

1969; Bruton & Boltt, 1975; this study), in the Elandsriver (van der Waal, 1972), lower Shire river (Willoughby & Tweddle, 1976), Lake Liambezi, Caprivi strip (van der Waal, pers. comm., 1976) and Kafue River (Bell-Cross, 1976). Cichlids probably also formed a part of the "fish" diet reported by various authors in Table X. Cichlids did not occur, or were rare, in *C. gariepinus* diet in sections of the Vaal and Jukskei rivers sampled by Groenewald (1964), in Lake McIlwaine (Munro, 1967; Murray, 1975), in small ponds in Rhodesia (Weir, 1972), in some small dams in the Transvaal (van der Waal, 1972); in the Sinamwenda River, Lake Kariba (Bowmaker, 1973), margins of Sanyati Basin, Lake Kariba (Mitchell, 1976) and in Lake St Lucia (Whitfield, pers. comm., 1976).

Cichlids formed an important part of the diet of *C. mossambicus* in marginal areas of Lake Malawi (Lowe, 1952), in Lake Victoria (Graham, 1929; Corbet, 1961), in Uganda (Greenwood, 1966) and were rare in their diet in streams flowing into Lake Victoria (Corbet, 1961) and in Lake Chilwa (Kirk, 1967). *C. lazera* in Lake George, Uganda, fed predominantly on *Haplochromis* spp. (Greenwood, 1976).

*C. gariepinus*, *C. mossambicus* and *C. lazera* may thus prey heavily on cichlids; Fryer & Iles (1972) calculated that *C. mossambicus* consumed more than  $153 \times 10^6$  *Haplochromis* spp. in the Tanzanian waters of Lake Victoria in 1958. These authors also show that smaller cichlids, especially *Haplochromis* spp., are more important prey of *C. mossambicus* than tilapia and other larger cichlids.

Opinions vary as to the "ferocity" of catfish predation. Lowe (1959) and many other authors describe *C. gariepinus* as a "lurker" or "sluggish predator" whereas Bell-Cross (1974, 1976) and the present author agree that catfish can be powerful and fast swimmers and occasionally active chasing predators. Slow, methodical searching is the normal predatory tactic in catfish, especially at night and in still water when feeding on benthic invertebrates and individual fish. More vigorous attacks are sometimes performed in rapids (Bell-Cross, 1976) or during the day when feeding on fishes or groups of fishes.

Ivlev (1961) used the ratio  $\frac{\text{modal size of prey}}{\text{size of predator}}$  (rapacity index) to compare the ferocity of fish predators. Active predators (e.g. *Esox lucius* L.) had indices above 0·2 and "peaceful" or slow predators (*Cyprinus carpio* L., *Abramis brama* L.) indices below 0·2. Ivlev's index is more conveniently multiplied by 100 to give the percentage of prey length in predator length, a ratio used by Jackson (1961b), Gaigher (1970) and Kenmuir (1973) to describe tigerfish, *Hydrocynus vittatus*, predation. The values obtained may vary according to prey availability and predator size. For instance, Popova (1967) has noted that the relative size of fish prey usually decreases with an increase in predator size; in young predators the prey reaches 40–50% predator length, but this value decreases to 20–25% in adults, and to about 10% in large adults.

Small tigerfish eat relatively longer prey than large tigerfish, but the usual ratio is about 25% (range 10–66%; Kenmuir, 1973). The ratio for *C. gariepinus* from Lake Sibaya is 14% (range 5–21%), although cannibalistic *C. gariepinus* in the Vaal River and Hardap dam consumed prey 25–58% of their length (Groenwald, 1964; Gaigher, 1977). In general, tigerfish and catfish can be classified as active and slow predators respectively. Comparable figures for other large freshwater fish predators are 22·8% for pike, *Esox lucius* (> 380 mm; Allen, 1939), 6–37% for *Lates niloticus* (L.) (Hopson, 1972), about 20% for *Hydrocynus forskahlii* Cuv. and 10% for *H. brevis* Günther (Lewis, 1974), and 13–40% for *Bagrus docmac* (Forsk.) (200–600 mm TL, Chilvers & Gee, 1974). The *H.*

*brevis* value is based only on whole ingested fish, but this species is known to commonly bite pieces from larger prey.

When assessing the impact of predation in terms of biomass of prey fish removed from the population, the ferocity or otherwise of the predator is immaterial, for as Fryer (1965) points out, "... the method employed for the capture of the food is no reflection of the amount consumed . . .", although it may influence the choice of prey and prey behaviour (Jackson, 1965; Fryer, 1965). The annual consumption of *Haplochromis* spp. by *Bagrus docmac*, a siluroid predator similar to *C. gariepinus*, was about 75% of the standing stock in Lake Victoria according to Chilvers & Gee (1974). A similar value was obtained for *H. vittatus* which consumed about 80% of the mean standing stock of *Alestes lateralis* in Lake Kariba (Balon, 1972; Chilvers & Gee, 1974), although this prey represented only about 5% of their diet (Matthes, 1968). The huge numbers of cichlids consumed in Lake Victoria by *C. mossambicus* have already been mentioned. Thus, both siluroids and characins may be major piscivores in terms of numbers of prey taken.

#### *The diel horizontal movements of cichlids and C. gariepinus in Lake Sibaya*

During a previous study (1970–73, on *S. mossambicus*, Bruton, 1973) water levels in Lake Sibaya were relatively low (Table I), and the terraces were shallow, wave-washed and sparsely vegetated. A marked diel migration of cichlids onto the terrace in the morning and back onto the slope at night occurred. Small juvenile cichlids fed in shallow, hot inshore areas whereas large juveniles and adults shoaled and fed in mid or deep terrace during the day (Minshull, 1968; Bruton, 1973; Bruton & Boltt, 1975). At night, the cichlids were dispersed on the slope or in mid-water over the slope. The large majority of the terrace and barren slope cichlid population consisted of *S. mossambicus* (88·3%) with lesser numbers of *T. sparrmanii* (3·9%) and *P. philander* (7·5%). Catfish remained in slope and other offshore habitats during the day, and usually entered the terrace at night at low lake levels. During winter (May–July), the number of all fish species entering shallow water decreased.

At intermediate lake level (1974–75, "high lake level" of Bowen, 1976), terrace areas were deeper and less exposed to wave action at substrate level. Higher numbers of *T. sparrmanii* and *P. philander* inhabited the terrace during the day, especially in areas where macrophytes such as *Potamogeton pectinatus* L. had become established. *S. mossambicus* were uncommon on the terrace during the day, occurring mainly in inshore or deep terrace areas but not in the open mid-terrace where they had been so numerous at low lake levels. An invasion of *S. mossambicus* onto the terrace took place between about 2000 and 0100 hrs, but thereafter they were uncommon again (pers. obs. and Bowen, 1976). The proportions of the three cichlids, based on day and night catches, changed slightly with *S. mossambicus* retaining dominance (59·1% of the cichlid population) over *P. philander* (27·7%) and lower numbers of *T. sparrmanii* (13·2%). *C. gariepinus* visited the terrace during the night, and in addition were found in considerable numbers in mid and deep terrace during the day.

At high lake levels, the deepened terrace allowed access of catfish during the day and night. The cichlid populations altered their behaviour, as well as their relative proportions. *P. philander* was dominant (62·2%) followed by *T. sparrmanii* (23%) with *S. mossambicus* sparse (14·8%). *T. sparrmanii* and *S. mossambicus* occupied branch tangles

and flooded vegetation along the inshore margin, whereas *P. philander* was abundant in these areas as well as in mid and deep terrace. *P. philander* and *T. sparrmanii* remained on the terrace during the day and night, whereas *S. mossambicus* mainly occupied the terrace during the night.

At all lake levels the number of cichlids on the terrace decreased during heavy winds (Bruton, 1973; Bruton & Boltt, 1975; Bowen, 1976), particularly at low lake level when wave action reached substrate level.

A pattern therefore emerges in which *S. mossambicus* occupied the terrace (for part of the 24 hour cycle) almost to the exclusion of other cichlids when the water was very shallow and environmental conditions, especially temperature, had wide diel fluctuations. As the lake level increased, terrace water temperatures were moderated, and deeper, more sheltered habitats became available. These changes resulted in increasing occupation of the terrace by cichlids which usually inhabit deeper water or sheltered inshore areas. The extent to which this pattern is dictated by predation and other environmental factors must now be considered. The effect of water temperature will be examined first.

Diel horizontal movements of young cichlids into shallow water along a temperature gradient have been reported by Welcomme (1964) for *Sarotherodon variabilis* (Boulenger), *S. esculenta* (Graham) and *S. zillii* (Gerv.) in Lake Victoria; Coe (1967) for *S. grahami* (Boulenger) in Lake Magadi, Kenya; Donnelly (1969a) for *S. mortimeri* (Trewavas) in Lake Kariba and Caulton (1975) for *T. rendalli* (Boulenger) in Lake McIlwaine. Welcomme (1964) found in Lake Victoria that shallow-sloping or temperature gradient beaches were the usual habitat of young tilapiines, while haplochromines preferred steep-sloping or non-gradient shorelines. At night when temperature gradients were reversed, tilapiines departed to deeper water while haplochromines inhabited the cooler shallows.

Some of the movements of cichlids in Lake Sibaya can be explained in terms of temperature preferenda. *S. mossambicus* is thermophilic, with temperature preferenda between 20° and 35°C depending on size and previous thermal history (Badenhuizen, 1967; Donnelly, 1969b; Josman, 1971). The upper lethal temperature is 38.2°C for small adults (80–120 mm TL, Allanson & Noble, 1964) and 41.7°C for juveniles (25–35 mm TL, Kemp, 1966). *S. mossambicus* also have a rapid rate of temperature acclimation (1°C per 150 min for fishes 80–120 mm TL, Allanson & Noble, 1964). At temperatures below 20°C the metabolic rate declines and *S. mossambicus* becomes lethargic (Josman, 1971) and below 14°C degenerative changes in kidney and blood physiology take place (Allanson & Cross, 1970; Allanson, Bok & Van Wyk, 1971). These wide temperature tolerances explain why *S. mossambicus* can inhabit terraces during the day at all lake levels when water temperatures fluctuate between about 20°C and 40°C, but are absent from terraces at night (or in mid winter) when water temperatures may fall below 16°C.

*T. sparrmanii* fry acclimated at 24.5°C (about the modal water temperature in Lake Sibaya) had upper temperature preferences of 32.2°C whereas adults only selected temperatures up to 30.6°C, in an artificial temperature gradient (Donnelly, 1969b). *P. philander* fry acclimated at 24.5°C had an upper preference limit of 27.2°C whereas adults only selected temperatures up to 25.5°C. At a higher acclimation temperature (29.5°C) both adults and fry adopted a final temperature preferendum of 26.1°C (Donnelly, 1969b). Both these species would thus be excluded from daytime occupation of shallow terrace waters in Lake Sibaya in summer (when temperatures regularly exceed 32°C) as a result of these relatively low temperature preferenda.

Their preference for well-vegetated tangled habitats would be an incentive for *T. sparrmanii* and *P. philander* to inhabit inshore areas at high lake level. On the other hand, *S. mossambicus*, which feeds largely on diatoms which are most abundant in Lake Sibaya in mid and shallow terrace (Bowen, 1976), is more suited to open gradient shores. *S. mossambicus* inhabits deeper open habitats at high lake levels in preference to the terrace. Water temperature, food availability and habitat preferenda can thus explain the broad observed pattern of distribution of these three cichlids in shallow water in Lake Sibaya.

Certain observed movements are, however, unexplained. These include the emigration of *S. mossambicus* from terrace waters at dawn and dusk and the near absence of *S. mossambicus* from the terrace during the day at intermediate and high lake levels. All the abandoned habitats had water temperatures within the normal range of *S. mossambicus*.

Many factors may be responsible for this behaviour, one of which is the threat of predators. Piscivorous birds are present but not abundant at Lake Sibaya and their effect is unknown. *C. gariepinus* is the main fish predator of *S. mossambicus* and other cichlids in Lake Sibaya and their effect was therefore investigated.

*C. gariepinus*, like *S. mossambicus*, perform diel horizontal movements, which may in part be regulated by temperature. Unfortunately, little is known of their temperature preferenda. In Lake Sibaya, they feed in shallow water from 18 to 35°C. In captivity they forage at temperatures above 18°C and become lethargic below about 17°C. Pardue (1970) found experimentally that lower lethal temperatures for *Clarias batrachus* varied from 9.4°C to 12.8°C depending on previous thermal history. The catfish died when subjected to constant temperatures below 18.3°C for periods longer than one month; these deaths were however attributed to increased susceptibility to bacteria and fungi as a result of non-lethal but harmful water temperatures. The little information on catfish temperature preferences therefore indicates that they will not normally forage in terrace waters above 35°C, whereas temperatures below 18°C may only be tolerated for brief periods.

#### *Field and experimental investigations on the effect of different factors on predation by C. gariepinus*

##### *Effect of prey density on predation on cichlids*

*Introduction.* Several important factors which influence the predator-prey relationship between *C. gariepinus* and cichlids in Lake Sibaya can now be identified. These are water depth, day-night light intensity changes, predator density, prey density and water temperature. The effect of the first three factors is described elsewhere in this volume (Bruton, 1979b). Catfish were shown to be more efficient predators on cichlids in shallow waters, at night and in groups. The effect of water temperature on predation was not determined, but the role of prey density is examined here.

An hypothesis, that *C. gariepinus* feeds on cichlid prey in proportion to their relative abundance, was tested to assess the effect of prey density on selectivity. In the next section the relative proportions of cichlid prey on the terrace is compared with their proportions in the diet of *C. gariepinus*. This field test was then re-enacted by exposing *C. gariepinus* to different densities of cichlid prey in an experimental situation and noting their selection of different prey.

*Results of field collections to determine the proportion of cichlids in the diet of C. gariepinus at different lake levels.* In a previous section the distribution of the three cichlids, *S. mossambicus*, *T. sparrmanii* and *P. philander*, on the terrace at three lake levels was described. *S. mossambicus* was numerically dominant at low and intermediate lake levels, but sparse compared with *P. philander* at high lake level, while *T. sparrmanii* constituted a relatively constant proportion of the catch at all lake levels.

These changing proportions of prey fish in the main catfish feeding area provided an opportunity to study the effect of relative prey density on catfish selectivity. Collections of *C. gariepinus* were made on the terrace at the different lake levels, and the proportion of the three cichlids in the catfish diet determined (the collection of cichlids and catfish at low lake level was made during an earlier study; Bruton, 1973). If the proportions of each prey species in the diet and field at each lake level are about the same, the catfish would have taken prey in proportion to its abundance, i.e. relative abundance would have had an important influence on prey selectivity.

The relative abundance of cichlid prey on the terrace and in the catfish diet at different lake levels is compared in Table XI. A *G*-test was used to test for significant differences. In all cases the null hypothesis was that the proportions available (expected to be eaten) were not significantly different from the proportions eaten ( $H_0$ : expected = observed). The expected number was calculated as that proportion of the observed total eaten which the particular prey constituted in the field population, e.g. if a prey formed 88·3% of the field population then the expected number is 88·3% of the total number eaten ( $88\cdot3\% \times 36 = 31\cdot8$  in the first example in Table XI).

Ivlev's electivity index ( $E$ , of Ivlev, 1961) was used to give a clear visual idea of selectivity:

$$E = \frac{P_d - P_f}{P_d + P_f}$$

where  $P_d$  = proportion of each prey in diet  
and  $P_f$  = proportion of each prey in the field.

Using this index, positive selection is expressed by values from +1 to 0, absence of selection by 0, and negative selection by values from 0 to -1.



Ivlev calculated his ratio from the percentage of each prey item in the field and diet, but I have used the observed and expected numbers.

Thus

$$E_i = \frac{P_{ob} - P_{ex}}{P_{ob} + P_{ex}}$$

where  $P_{ob}$  = proportion observed in diet  
 $P_{ex}$  = proportion expected in diet

TABLE XI

*Proportions of S. mossambicus, T. sparrmanii and P. philander on the terrace of Lake Sibaya and in the diet of C. gariepinus on the terrace at different lake levels from 1970-76*

	Cichlid population sampled on the terrace using standardized seine net pulls		Cichlids in diet (number)		Modified electivity index
	number	% of total	Observed	Expected	
<b>Low lake level (1970-72)</b>					
<i>S. mossambicus</i>	4570	88.3	27	31.8	-0.08
<i>T. sparrmanii</i>	204	3.9	3	9	+0.36
<i>P. philander</i>	388	7.5	6	9	+0.36
	5162		36		
			<i>G</i> = 4.880		
			<i>P</i> < 0.05		
			Significant		
<b>Intermediate lake level (1974-75)</b>					
<i>S. mossambicus</i>	2009	59.1	126	101.1	+0.11
<i>T. sparrmanii</i>	449	13.2	2	22.6	-0.84
<i>P. philander</i>	942	27.7	44	47.4	-0.04
	3400		171		
			<i>G</i> = 39.23		
			<i>P</i> < 0.001		
			Significant		
<b>High lake level (1976)</b>					
<i>S. mossambicus</i>	273	14.8	2	9.2	-0.64
<i>T. sparrmanii</i>	424	23.0	15	14.3	+0.02
<i>P. philander</i>	1146	62.2	45	38.6	+0.08
	1843		62		
			<i>G</i> = 9.13		
			<i>P</i> < 0.01		
			Significant		

The null hypothesis, that there was no significant difference between the number of cichlid prey eaten and the number expected to be eaten calculated from the proportions of prey in the terrace population, was tested using the *G*-test of Sokal & Rohlf (1973) which compares observed and expected values. The *G*-statistic given in each case is for two degrees of freedom. The modified electivity index was calculated from observed and expected values as explained in the text.

Ivlev's index (and its modification,  $E_i$ ) has an advantage over other selectivity ratios in that positive and negative ratios can be compared directly and have the same range (in other ratios positive selection usually ranges to infinity).

At all three lake levels the *G*-test indicated that the observed and expected values were just significantly different (Table XI). Nevertheless, as shown by the electivity indices there was a trend towards predation on at least one or two species in proportion to their abundance.

At low lake levels the expected numbers of *T. sparrmanii* and *P. philander* were too low for an accurate assessment of their selection, but *S. mossambicus* was taken approximately in proportion to its abundance. At intermediate lake level, *T. sparrmanii* was taken less often than expected, whereas *S. mossambicus* and *P. philander* were selected according to their relative abundance. At high lake level, *S. mossambicus* was taken less often than expected, whereas the other species were selected according to their relative abundance.

The correlation obtained between observed and expected values is close considering that the collections were made over long periods of time, during which terrace habitats changed markedly. As availability of prey = relative abundance + accessibility, part of the deviation between observed and expected values may be due to different accessibility of the cichlid prey under changing terrace conditions. *T. sparrmanii*, which was negatively selected at intermediate lake level, inhabits vegetated areas and usually feeds, swims and rests above substrate level. They would therefore escape detection by catfish more often than *P. philander* and *S. mossambicus*, which feed and swim on the sand, although they occasionally rest perched on plants. Negative selection of *S. mossambicus* at high lake level may be due to migration into safer offshore areas at dawn and dusk, which was practised during the later stages of intermediate lake level as well (Bowen, 1976).

#### *Experimental observations on selection by C. gariepinus of cichlid prey at different densities*

*Methods.* Field collections indicated that *C. gariepinus* took some cichlid prey approximately in the proportions in which they occurred in the lake. This finding was tested by observing predation by catfish on cichlid prey provided at different densities in a specially-constructed observation pool. The pool, and the means by which the predatory behaviour of *C. gariepinus* was recorded, are described in detail elsewhere (Bruton, 1979b). The amount of feeding activity was measured both by the number of food items eaten and by the number of appetitive actions performed by *C. gariepinus*.

The three cichlid species, *S. mossambicus*, *T. sparrmanii* and *P. philander*, were presented in different proportions out of a total of about 100 prey. Three sets of two experiments were conducted (Table XII). In the first set, the prey species were equally abundant, i.e. each formed 1/3 of the total. This set acted as a control to test selection for different prey at equal densities. In the second set *S. mossambicus* constituted 60% of the prey, *T. sparrmanii* 20% and *P. philander* 10%, and in the third set these proportions were reversed with *P. philander* most and *S. mossambicus* least abundant. The second set therefore reflected approximate cichlid proportions on the terrace at low lake levels, and the third set the proportions at high lake levels. Prey were caught for the experiments using fishtraps off Lake Sibaya Research Station, and introduced into the observation pool 1 hour before each experiment in the absence of predators. The predators were kept in a small enclosure adjoining the pool during the hour preceding experimentation but swam freely in the observation pool during and between experiments. Each experiment lasted 72 hours starting at 0900 hrs. By the end of the experiment about 1/3 of all prey had been eaten. The experiments were carried out under optimal conditions for high predation in the observation pool, i.e. at a water depth of 200 mm, with four catfish in each test (Bruton, 1979b).

An important criticism of experiments of this kind is that prey density and proportions are altered as soon as some prey are eaten. Replacement of destroyed prey is therefore suggested (e.g. Holling, 1966; Beukema, 1968; Colgan, 1973). Replacement was tried through pipes leading from the hide into the observation pool. The catfish soon learnt to associate the pipe with prey

TABLE XII

*Selection of S. mossambicus, T. sparrmanii and P. philander by C. gariepinus in an observation pool (Bruton, 1979b) when the prey are offered in different proportions*

	Prey introduced			Prey eaten (number)		Modified Electivity Index
	Each replicate	Total	% of total	Observed	Expected	
<b>Set 1</b>						
<i>S. mossambicus</i>	34	68	33.3	19	18.3	+0.02
<i>T. sparrmanii</i>	34	68	33.3	15	18.3	-0.10
<i>P. philander</i>	34	68	33.3	21	18.3	+0.07
	102	204		55		
				$G = 1.240$		
				$P > 0.5$		
				Not significant		
<b>Set 2</b>						
<i>S. mossambicus</i>	60	120	66.7	46	40	+0.07
<i>T. sparrmanii</i>	20	40	22.2	9	13.3	-0.19
<i>P. philander</i>	10	20	11.1	5	6.6	-0.14
	90	180		60		
				$G = 3.05$		
				$P > 0.20$		
				Not significant		
<b>Set 3</b>						
<i>S. mossambicus</i>	10	20	11.1	6	6.4	-0.04
<i>T. sparrmanii</i>	20	40	22.2	6	12.8	-0.37
<i>P. philander</i>	60	120	66.7	46	38.6	+0.09
	90	180		58		
				$G = 6.27$		
				$P < 0.05$		
				Significant		

Three sets of experiments were conducted, each replicated twice. Each experiment was conducted in 200 mm deep water using 90 or 102 prey and four catfish, and lasted 72 hours. Water temperatures ranged between 20.3° and 24.3°C. The *G*-statistic given in each case is for two degrees of freedom.

delivery, which interfered with normal searching, and prey usually behaved in an abnormal conspicuous way after delivery, which increased their vulnerability. Other attempts at random replacement of prey without attracting the predator also produced anticipatory behaviour. The high number of prey introduced (90–102), the fact that about 2/3 of this prey remained uneaten after each experiment, and the neutral electivity displayed by the predators meant that there was not a major change in the relative proportions of prey during the experiment, although prey density decreased. The replacement method was therefore not used.

A basic premise of these experiments was that all prey lost had been captured by the catfish. Loss of prey by other sources had to be discounted. Two control experiments lasting two days each were conducted in which a known number of prey were introduced into the pool in the absence of predators. Possible external predators included kingfishers and other piscivorous

birds. No predation took place, nor was any noted throughout the experimental period. Furthermore, no prey deaths were recorded during the main experiments.

The amount of food given to catfish between and during experiments should approximate that eaten in the wild. The normal ration (or average stomach contents) of 350 *C. gariepinus* (300 to 600 mm TL) caught throughout the year in Lake Sibaya using longlines and gillnets was 1·8% body weight (range 0·1 to 10·1%). Baur (1970) obtained a similar value of 1·78% of body weight for *Ictalurus melas* (Rafinesque). The contents of full *C. gariepinus* stomachs weighed, on average, 5% of total body weight ( $N = 62$ ), and up to 6% when distended with arthropods and 8–10% when distended with fish. As catfish feed at least twice in 24 hours, the normal daily ration based on these results would range between 3·6 and 10% body weight. Experimental fishes were fed a diet of 5% body weight, consisting of recently killed cichlids between experiments and live cichlids during experiments.

*Results.* The number of each prey species offered and eaten in the three sets of experiments is given in Table XII.

In the first set, in which prey were equally common, the observed and expected frequencies were not significantly different ( $P > 0\cdot5$ ) and the electivity index was low for all species. The prey were therefore eaten in the proportions in which they were offered under the given conditions.

In the second set, in which *S. mossambicus* was abundant, the observed and expected frequency were also not significantly different ( $P > 0\cdot2$ ). Selectivity was therefore approximately neutral even when the proportions of different prey species differed by a factor of 3.

In the third set, in which *P. philander* was most abundant, the observed and expected frequencies were just significantly different ( $P < 0\cdot05$ ), but the electivity index showed approximately neutral selection for *S. mossambicus* and *P. philander*, and strong negative selection for *T. sparrmanii*. When the data for *S. mossambicus* and *P. philander* only were tested, the observed and expected frequencies were not significantly different ( $P > 0\cdot2$ ). The latter two species were therefore eaten in proportion to their relative density, whereas *T. sparrmanii* was negatively selected.

The general results confirmed the trend found in the field collections that *C. gariepinus* takes the three cichlid species more or less in proportion to their relative density.

There were, however, several cases in which neutral selection did not occur. *T. sparrmanii* were negatively selected in all three sets of experiments reported in Table XII. This finding can be explained by the more secretive, less active behaviour of *T. sparrmanii* compared with the other cichlids. *T. sparrmanii* remained longer in one place, and were less easily flushed by catfish in the observation pool, and as a result the number of "encounters" leading to "discoveries" and the number of "discoveries" leading to "grasps" was lower than for the other species (for definitions of these terms see Bruton, 1979b). *T. sparrmanii* was also negatively selected at intermediate lake level (Table XI) possibly as a result of their habit of living above the substrate.

#### *Observations on predation by C. gariepinus on some invertebrates*

The main experiments were conducted on the cichlid prey of *C. gariepinus* because of their important contribution to prey weight. Invertebrate prey is, however, numerically important in the diet of *C. gariepinus*, and some experiments were therefore also performed to determine their vulnerability to predation by catfish.

In these experiments prey risk was measured by determining the percentage of one appetitive action which led to the next, thus:

$P_{enc}$ : the proportion of "searches" leading to an "encounter"

$P_{disc}$ : the proportion of "encounters" leading to a "discovery"

$P_{gra}$ : the proportion of "discoveries" leading to a "grasp"

$P_{eat}$ : the proportion of "grasps" leading to an "eat".

These appetitive actions are defined by Bruton (1979b), with certain modifications which are given below. This approach to behavioural studies is based on the premise that the predation sequence of *C. gariepinus* is composed of separate elements, as follows:

Search → encounter → discover → grasp → eat.

The effect of different factors on prey risk can be determined by observing to what extent this predation sequence is completed.

*Predation on Hymenosoma orbiculare.* These observations were made in a large glass aquarium, 1500 × 780 × 810 mm deep, enclosed in a black plastic hide with an observation slit.

Experiments using *H. orbiculare* as prey yielded little information as the predators ate over 94% of all crabs offered. The crabs were eaten within 5 min of introduction into the large aquarium without a sandy layer, and up to 30 crabs (the maximum which were provided at one time) were eaten within 15 min by one predator with sand present. Day-night changes in light intensity appeared to have no effect on predation efficiency. All 30 crabs were eaten within 15 min on dark nights (< 50 lx, with a single red light) and during the day (9000–10,000 lx, 2 replicates each) by a single 264 mm TL catfish. Efficient predation during the day and night may be due to the catfish's use of mechano-reception for detecting crown crabs.

Prey risk was expected to be higher in shallow water, as with fish prey (Bruton, 1979b), but different water depths in the aquarium had no effect on predation efficiency; all 30 crabs introduced were eaten within 15 min at depths of 100, 200, 300 and 400 mm (two replicates at each depth) by the single predator. During early encounters 53–81% of the flushed crabs escaped predation by swimming over the cone of barbels, but they were all eventually caught in the small enclosure. *H. orbiculare* has repeatedly been seen evading capture by catfish in Lake Sibaya by swimming over the cone of barbels.

*Predation on small crustaceans.* These observations were made in a small glass aquarium 250 × 250 × 250 mm enclosed in a black plastic hide with an observation slit. Sand from the lake was provided as a substrate.

In an earlier section *C. gariepinus* was shown to feed on infaunal benthos with preference for those forms which are at least partially active above the substrate. Exposure of infaunal benthos for part of the time may thus be an important factor affecting their vulnerability to catfish. This possibility was tested by close observation of predation by two small catfish (85 and 88 mm TL) on small crustaceans. (Experiments with larger catfish and small prey were not possible with the equipment available as prey capture could not be observed in sufficient detail).

Three prominent infaunal species, caught in the lake using a van Veen grab, were used: *Grandidierella lignorum* (Amphipoda: 6–7 mm TL), *Cyathura carinata* (Isopoda: 10–11 mm) and *Apseudes digitalis* (Tanaidacea, 3–4 mm). The prey were delivered individually in a random order from a pipette through a glass tube fixed in position over the

aquarium, with one end under water. Observer movements could not be seen by the catfish. The prey drifted or swam down, landing in different places on the sand according to the direction and intensity of swimming during descent. Prey detected by the predator before reaching the sand were ignored in subsequent analyses, except that they were included in the total ration allowed per experiment. Newly-introduced prey were active on the sand for at least a minute, usually longer, before burrowing. The predator searched constantly during the experiments and readily discovered prey on the sand surface.

A "search" was scored every time the predator crossed from one half of the aquarium to the other and an "encounter" every time an introduced prey reached the substrate before being eaten. A particular encounter ceased one minute after the introduction of each individual prey. Each experiment continued until 30 prey had been eaten (about half an hour) so that satiation of the predator would not affect the results (the catfish used had a capacity for over 60 small crustaceans). Six experiments were conducted with the predators alternated. During the interval between experiments the predator was starved in a separate aquarium and buried prey were removed from the experimental aquarium. If an experiment was not conducted after about 6 hours the catfish were fed 15 small crustaceans each. All experiments were conducted in a dark room. The results are given in Fig. 13.

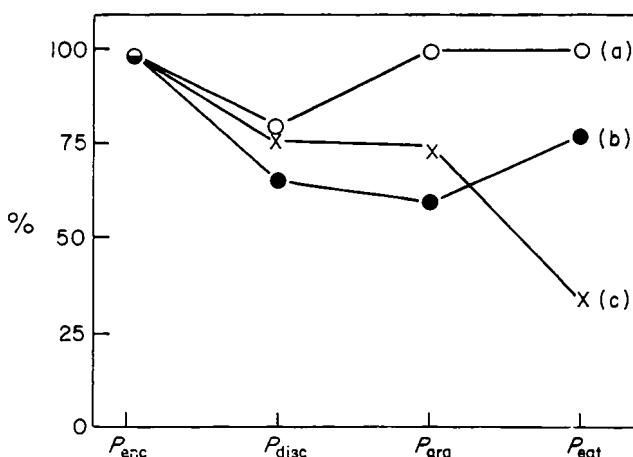


FIG. 13. The proportion of different appetitive actions performed by one *C. gariepinus* in response to small invertebrate prey in a small aquarium. The appetitive actions and abbreviations are defined in the text. Invertebrate prey: (a) *G. lignorum*; (b) *C. carinata*; (c) *A. digitalis*.

$P_{disc}$  was high for all prey, indicating high vulnerability of infaunal benthos on the sand surface. After discovery, all *G. lignorum* were grasped and eaten, whereas only 60–70% of discovered *A. digitalis* and *C. carinata* were grasped. Most grasped *C. carinata* were eaten, whereas most grasped *A. digitalis* were rejected. *G. lignorum* was both the easiest to catch and the most palatable prey, and *C. carinata* were more palatable than *A. digitalis*. This result is confirmed by the observed diet of *C. gariepinus* in the field—*G. lignorum* constituted 27·9% of the diet (numerical analysis), and *C. carinata* and *A. digitalis* only 1·6% and 0·1%.

On three separate occasions 6 hour-starved catfish were allowed to forage for buried prey. When flushed, the three prey species behaved differently. *G. lignorum* swam strongly upwards to about 30 mm above the sand, maintained position briefly, then descended. This is a poor avoidance tactic against catfish as the zone of movement is within the area covered by the circumoral barbels; they were thus frequently detected and, being palatable, eaten. Both *C. carinata* and *A. digitalis* remained buried or moved slowly along the sand surface, and usually escaped detection. *C. carinata* were found more often, probably because of their larger size.

In conclusion, infaunal benthos which is mobile and active above the substrate is more vulnerable to predation by catfish than buried or slow-moving prey; taste may affect  $P_{eat}$ . Other factors, such as prey size, may also be important. Ware (1973) found that prey activity, exposure, density and size were the four major determinants of prey risk to visual fish predators on epibenthos.

Some epifaunal benthos was also introduced into the small aquarium. Twenty specimens each of *Pontogeloides latipes*, small *Caridina nilotica* (< 7 mm TL), small *Hymenosoma orbiculare* (carapace width < 4 mm) and *Povilla adusta* were always grasped when discovered, and eaten when grasped. *C. nilotica* and *H. orbiculare* readily evaded the small catfish by quick movements, and by hiding in *Myriophyllum spicatum* fronds or by burrowing respectively. Molluscs, including small *Bellamya capillata*, *Melanoides tuberculatus*, *Corbicula africana* and *Bulinus* spp. were always neglected on discovery in the small aquarium (20 introductions each).

*Predation on epifaunal benthos.* Observations were also made on predation by 24-hour-starved adult catfish (484 mm to 690 mm TL) on *Bellamya capillata* (20–25 mm TL), *Melanoides tuberculatus* (TL 25–31 mm) and *Potamon sidneyi* (carapace width 30–40 mm) collected in the lake using SCUBA. Thirty each of the molluscs and 10 crabs were introduced into the large observation pool in separate experiments, and subjected to predation by four catfish during the day. Eleven 1-hour experiments were conducted, five on *B. capillata*, three on *M. tuberculatus* and three on *P. sidneyi*. The results, plotted as the proportion of one appetitive action leading to the next, are given in Fig. 14.

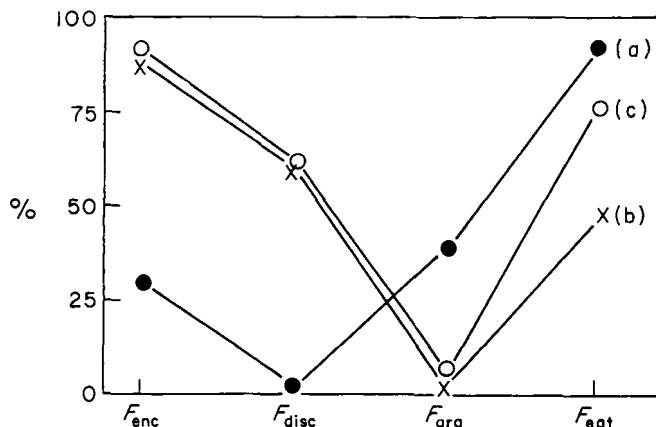


FIG. 14. The proportion of different appetitive actions performed by four *C. gariepinus* in response to large invertebrate prey in an observation pool. The appetitive actions and abbreviations are defined in the text. Invertebrate prey: (a) *P. sidneyi*; (b) *M. tuberculatus*; (c) *B. capillata*.

The encountering efficiency on both snail prey was high as the prey were spread evenly throughout the observation pool and did not clump or evade the predator. About 60% of the encountered molluscs were discovered, but the large majority (over 90%) were neglected on discovery. The snails were only grasped and eaten if a frenzy of social "breathing" occurred (described below) or on an occasion in which the pre-experiment deprivation period was 56 hours instead of 24 hours. The snails were not a preferred prey of *C. gariepinus* under the experimental conditions.

Shore crabs *P. sidneyi* readily evaded "encounter" or "discovery" by catfish, but 40% of those discovered were grasped, and 91% of those grasped were eaten. *C. gariepinus* readily fed on recently killed shore crabs, but rejected rotting crabs.

Diving observations in the lake confirmed that *P. sidneyi* was an elusive but preferred prey, whereas the snails were infrequently taken in relation to their abundance and accessibility.

TABLE XIII  
*Imitative aerial "breathing" in four*  
*C. gariepinus in an observation pool in the*  
*presence and absence of S. mossambicus*  
*prey (50–70 mm TL)*

	Number of rises	
	Abundant food	No food
Initial rise	36	8
2nd rise	13	5
3rd rise	6	3
4th rise	3	1
5th rise	0	0
Total	58	17

An imitative rise was counted every time an initial rise was followed by another rise within 30 sec.

#### *Further observations on predation by C. gariepinus*

##### *Feeding intensity and social "breathing"*

Imitative hunting, in which one catfish is attracted to another by the latter's directed attentions to a prey, is mentioned elsewhere (Bruton, 1979b) as a factor which increases searching intensity. Similar behaviour was observed in Lake Sibaya when large masses of terrestrial insects accumulated on the water surface in shallow water after heavy rain. The loud gulping action of feeding catfish soon attracted others to the site and, if the food resource was small, a "feeding frenzy" soon developed, as commonly observed in sharks (Budker, 1971). This behaviour could be induced by throwing food into shallow water, especially at night.

During a feeding frenzy the catfish become moderately aggressive towards one another, and may tail-slap and perform mouth displays (cf. prenuptial aggression, Bruton, 1979a). Catfish markedly smaller than the group modal size were usually chased away. If the food

resource was large and could not be eaten by the catfish present within about 5 min, aggression gradually became less intense and co-ordinated feeding behaviour ensued, sometimes leading to "social hunting" as described earlier.

Besides the directed response of a catfish to prey, another activity served as a cue for renewed or increased searching behaviour—aerial "breathing". A single catfish (570 mm TL) in the observation pool rose for air about 1–6 times an hour (14 hours observation at different times of the day). When the catfish were in groups the incidence of aerial "breathing" rose to over 10 rises per catfish per hour in the absence of food, and to over 40 with abundant food present. Although *C. gariepinus* is an obligate air-breather under normal circumstances, these rises appear to be far in excess of the respiratory requirements of searching catfish and must have some other function.

A group of rises usually followed close upon one another, suggesting that a rise by one induced a rise by other catfish. The number of rises following an initial rise within 30 sec was therefore counted. As shown in Table XIII, which is based on 16 hours observations, the total number of rises and imitative rises per hour was higher in the presence of food.

Imitative aerial "breathing" often caused previously stationary catfish to start searching, and frequent imitative rises resulted in increased searching intensity. A solitary catfish searched at a speed of 0·3 body lengths/min, whereas a group of four in the absence of food and with moderate social "breathing" (17 rises an hour) searched at 1·1 body lengths/min. In the presence of abundant food, and with intensive social "breathing", searching speed sometimes exceeded 19 body lengths/min in the observation pool. Aerial "breathing" beyond normal requirements may serve as a social signal notifying other catfish of intensive activity, and the presence of food, in a particular area. Loud ritualized aerial "breathing", as well as head and tail slapping on the water surface, also function as social signals during spawning migrations (Bruton, 1979a). Social aerial respiration has also been reported in younggars (*Lepisosteus* spp., Hill, 1972).

#### *Area concentrated searching* (cf. Smith & Dawkins, 1971).

"Area concentrated searching" by *C. gariepinus* was repeatedly observed from the 7 m tower in shallow water. In all cases the rate of turning to one side increased on encountering a concentration of prey, resulting in intensive searching in the immediate vicinity. The catfish also swam more slowly after encountering the prey, although head movements from side to side were more rapid than in search swimming. Observations in the pool and in aquaria showed that, on discovering prey, the barbels were spread to form a wider circumoral cone and thus sample a larger volume of water.

#### *Predation strategy*

Observations on *C. gariepinus* in Lake Sibaya and in the experimental enclosures showed that they habituated to the presence of temporarily uncatchable prey after a few unsuccessful encounters, and thereafter rarely attempted to capture that prey species until conditions changed to their advantage. In particular, repeated attacks made on *S. mossambicus* in the early morning, all of which were fruitless, led the catfish virtually to ignore these cichlids throughout the day. Foraging success also affected the amount of subsequent searching in Rainbow trout *Salmo gairdneri* Richardson. Ware (1972) found that substrate-orientated searching began to wane in trout which did not exceed an average of 0·058 captures sec<sup>-1</sup>.

Seven hours of underwater observations using SCUBA at dusk and by torchlight at night revealed that catfish attacked cichlids after dark when shoaling fish had dispersed and were resting on or near the substrate (Bruton & Boltt, 1975). Individual predators foraged slowly along the sand and touched a stationary cichlid with the maxillary barbel. A quick, accurate suck-snap action followed which was occasionally successful on stationary prey. An individual predator was never seen catching a swimming prey. Thus, when feeding on fish, catfish are more likely to take less mobile individuals, which is in contrast to their strategy with invertebrates.

Catfish change their dorsal and lateral body colour from black to mottled black and green, olive-green, green-brown to light brown, according to ambient light conditions, substrate colour and the presence of vegetation. These colour changes are probably for concealment from visually-orienting predators and prey, as catfish usually match the background colour; they are dark or mottled over mud and in dense macrophyte beds, dark at night, and light during the day on shallow sandy terraces. Their ventral colour is white (rarely variegated with grey) which effects camouflage through counter-shading when lighted from above. Catfish are not always well camouflaged—some individuals which swim from deeper waters onto the terrace retain their dark colouration and would appear to be conspicuous to bird predators.

#### *Predator avoidance tactics by prey*

At low lake level, when the terrace is barren and shallow, cichlids form dense defensive shoals on the terrace during the day (Bruton & Boltt, 1975). Shoaling is less common at high lake level when the cichlids are sparse in mid-terrace but abundant among submerged macrophytes on the slope and in inshore areas among drowned vegetation. The three cichlids had different avoidance tactics: *T. sparrmanii* remained close to dense plant stands and hid individually among foliage; *P. philander* swam rapidly through plants into deeper water and occasionally formed small groups, and *S. mossambicus* usually swam onto the open terrace and formed shoals.

Predator avoidance by fish prey at night was achieved by perching above the substrate in fronds of submerged plants, especially *Potamogeton pectinatus* and *P. schweinfurthii* A. Benn, and by resting in midwater. Both perching and remaining motionless are effective avoidance tactics against catfish. Perching was commonly observed in *G. giurus*, *T. sparrmanii* and *P. philander*, and less commonly in *S. mossambicus*. Resting in midwater occurred mainly in *S. mossambicus*.

*C. gariepinus* flush out crown crabs *Hymenosoma orbiculare* by trailing the mandibular barbels along the sand, in a manner similar to that of marine goatfish *Pseudopeneus* spp. (Mullidae; pers. obs.). When flushed, the crown crabs swim forwards and upwards, then turn rapidly and dive backwards using the paper-thin body as a hydroplane. Those which pass over or to one side of the barbels escape and immediately bury themselves by burrowing backwards into the sand. Others which enter the area enclosed by the circumoral cone of barbels are usually detected and caught.

#### *Diet switching by catfish*

When conditions are unsuitable for capturing fish prey, catfish switch their feeding to crustaceans and insects. If a concentration of vulnerable fish is found, the predator readily switches back, and then resumes invertebrate feeding again as soon as necessary.

When they feed on invertebrates, the catfish may switch from a prey-specific method of feeding, e.g. foraging for crown crabs or surface feeding for flotsam, to a situation-specific method, e.g. grubbing under detritus for whichever food becomes available. There is some evidence that the catfish can also optimize predation by temporal synchrony with a temporarily vulnerable prey, such as appetitive male *G. lignorum* which venture out of their burrows at night. In a broader sense, the recruitment of young catfish in summer when larval insects are most abundant can be regarded as an example of temporal synchrony.

An important reason for the numerical abundance of invertebrates in catfish diet (besides their abundance in the lake) may be their vulnerability to predation by catfish. In the experiments outlined above the predation failure rate, i.e. the percentage of "discovers" which did not lead to "grasps", was 79.3% for catfish preying on fish. The equivalent figure for all crustacean prey tested was 15.3%, and if we exclude *Apseudes digitalis*, which is not a preferred prey, the value is even lower (12.3%). However, these results are biased as the area searched in relation to catfish size in the invertebrate prey experiments was less than in the fish prey experiments, and successful encounters may have led to more intensive searching behaviour. The failure rate obtained for invertebrate prey (12.3%) in *C. gariepinus* was close to values obtained for *Micropterus salmoides* (Lacepede) (10%; Nybergh, 1971). Underwater observations confirmed that *C. gariepinus* was far more efficient at detecting and capturing invertebrate than fish prey.

#### *Discussion on predation by C. gariepinus*

These preliminary studies on catfish predation support Holling's (1961) hypothesis that predator and prey density are the basic components of predation. Relative prey density had a profound effect on selection of three cichlid prey in the lake and in an experimental area. Furthermore, collections of stomach contents showed that invertebrates, which are far more abundant than fishes in the lake, were numerically more important in their diet.

This study has shown, however, that prey density is sensibly combined with prey accessibility when assessing its effect on fish predation. Many prey organisms are abundant but inaccessible to catfish despite the catfish's impressive array of feeding equipment and methods. Most selection by catfish can be explained by taking into account prey availability, if this property includes both prey density and accessibility. Other workers have also found that fish prey selection by African fish predators is determined more by differences in availability (= density + accessibility) than by active preference for one or other prey species, e.g. Gee (1969) for *Lates niloticus* (L.) in three lakes in East Africa; Jackson *et al.*, (1963) for *Bagrus meridionalis* Günther in Lake Malawi, and Chilvers & Gee (1974) for *B. docmac* in Lake Victoria. Their studies applied mainly to predation on haplochromines and not on tilapiines, but this again is a reflection of the availability of the different cichlid groups.

An important aspect of predation by *C. gariepinus* is their ability to switch feeding from one prey to another. Switching relies on the existence of at least two alternate abundant prey. Presumably the extent of switching behaviour will depend on prey diversity. Catfish presented with abundant, diverse food would be expected to switch to different food items more often. On the other hand, those which come in contact with only a few abundant items would rely almost entirely on these items. These trends were followed

by *C. gariepinus* at different lake levels. At low lake levels the shallow water macrofauna of the terraces consisted almost entirely of *S. mossambicus* and *H. orbiculare*, and these items formed the bulk of the catfish diet. At intermediate and high lake level, cichlids were abundant in the shallows and once again formed an important part of the diet. A greater variety of invertebrates was also available, and they formed a major component of the diet. The important point is that catfish did not rely only on offshore fishes and benthic invertebrates at high lake level—they readily switched their feeding to littoral fishes and invertebrates when these became abundant.

MacArthur (1972) in his “optimal foraging model”, proposed that predator search time is so long in a harsh environment with low prey densities that the predator eats all encountered prey, i.e. it becomes a generalist. Conversely, in a productive environment with a small search time, specialization is favoured. This theory would apply especially to predators which develop a strong “searching image” or “training bias” for a particular prey. Catfish show both generalization and specialization in their diet in productive (or diverse) environments. In ecosystems with abundant, constantly accessible invertebrate populations, such as Lake McIlwaine (Munro, 1967) and the Jukskei River (Groenewald, 1964), *C. gariepinus* is stenophagous, at least as an adult. Conversely, the variety of prey in their diet is greater in Lake Sibaya at high lake level when the population of potential prey is most diverse.

Thomas (1966) discussed the environmental factors which may have led to euryphagy in large African *Clarias* species. According to Thomas, factors which would restrict the food niche of many fishes do not usually affect *Clarias* species strongly. These factors include strong interspecific competition and predation pressure, constant food supply at a low density and harsh physico-chemical conditions. The effect of predation pressure may be reduced by the catfish's large size, well-protected head and pectoral spines. Although catfish are subject to changing physico-chemical conditions as a result of seasonal migrations and changes in water level and oxygen concentrations, their physiological versatility enables them to survive. On the other hand, factors which favour an expansion of the food niche are probably a common feature of their life history. These include strong intraspecific but weak interspecific competition for food, weak predation pressure, a food supply which varies spatially and temporally, high prey species diversity and varying but unrestrictive physico-chemical conditions.

#### GENERAL DISCUSSION ON THE ROLE OF *CLARIAS GARIEPINUS* AS A PREDATOR OF *SAROTHERODON MOSSAMBIKUS* IN LAKE SIBAYA

*S. mossambicus* is well-known throughout the world as a fast-growing, culture fish. Why then does it reach such a small final size in Lake Sibaya? Bruton & Allanson (1974) showed that the growth rate of *S. mossambicus* in the first year is equal to or faster than that of other populations of the same species. However, instead of growing steadily for two or three years and reaching maturity at 250–300 mm TL, *S. mossambicus* in Lake Sibaya reach maturity after one year at 100–120 mm TL. Thereafter growth rates decelerate and individual fishes rarely exceed 200 mm TL. Bowen (1976) investigated the reason for this miniaturization of *S. mossambicus* in Lake Sibaya. He convincingly showed that dietary protein deficiency is the main cause of stunting and poor condition of adult *S. mossambicus*. This malnutrition is brought about by the fact that adults feed on energy rich, but protein-deficient offshore detritus. In contrast, juveniles feed in water shallower

than 1 m which Bowen found had rich concentrations of diatoms, and more important, an abundance of protein-rich detrital bacteria. Clearly, occupation of inshore areas for a part of their diel cycle is an important prerequisite for good growth in Sibaya *S. mossambicus*. Do catfish restrict entry by adult tilapia into these food-rich areas, or are other factors responsible?

Recent work by Caulton (1976, 1977) on a related cichlid, *Tilapia rendalli* suggests that temperature may be the overriding factor dictating the movements and feeding cycles of tilapiines. He showed that ingestion rates and assimilation efficiencies are enhanced by warm temperatures, but the pattern of routine metabolism does not follow the general form expected of poikilotherms. Instead of the characteristic exponential increase in metabolic costs with increasing temperature, there was a plateau over the temperature range characteristic of the daytime inshore habitat of the tilapia species, which resulted in the suppression of the expected high metabolic cost at these warm temperatures. During the day maximal occupation of the preferred temperatures results in optimal energy storage. The maximum retention of this energy gain was facilitated by the fish moving into cool deeper water during the night, when no feeding took place and metabolic energy demands were low.

Since Allanson & Noble (1964) have shown that juvenile *S. mossambicus* have higher preferred temperatures than adults, we can expect that juveniles would feed in shallower water than the adults during the day. This trend was confirmed by Bruton (1973) and Bowen (1976) in Lake Sibaya. Bowen showed that adult *S. mossambicus* feed in deeper water than juveniles although the digestible protein in detritus in these areas is lower. Why have adult *S. mossambicus* not adapted to the prevailing distribution of resources in Lake Sibaya and fed further inshore, despite the increased metabolic energy cost? Apparently adult *S. mossambicus* have an inhibition against entering very shallow water, which is only overridden at certain times during the breeding season (Bruton & Boltt, 1975). This inhibition applies in other lakes as well, but it does not prevent them from attaining a large size and excellent condition there. *S. mossambicus* reaches 432 mm and 1543 g in Inyamithi pan, 60 km north-west of Lake Sibaya (Coke, pers. comm., 1973) and commonly exceeds 350 mm TL in culture ponds (Koura & el Bolock, 1958; Hickling, 1970). All of these systems are shallow. In Lake Sibaya the standing crop of plankton is low due to poor nutrient inflow (Hart & Allanson, 1975; Allanson & Hart, 1975), and the quality of offshore detritus is insufficient to sustain good growth (Bowen, 1976). Because of their inhibition to enter shallow water, adult *S. mossambicus* must feed in these nutrient-poor areas. The obvious conclusion is that the quality of offshore food resources is the main determinant of the growth rate and condition of adult tilapia which do not feed inshore.

Although the diel movements and penetration into shallow water by cichlids have often been interpreted in terms of water temperatures and depth selection, other factors are also involved. Fryer (1961), Jackson (1961b) and Donnelly (1969b) stressed the influence of predators, Caulton (1976) the role of metabolic energy budgets and Bowen (1976) the importance of food quality. Bruton (1973), Caulton (1975) and Bowen (1976) showed that wave action and cloud cover also affect these movements. Clearly, the rhythm and extent of inshore migrations by cichlids are controlled by several factors, and the position of a fish in shallow water is determined by a compromise of several preferences, rather than one preference.

In Lake Sibaya, small *S. mossambicus* grow rapidly and attain a good condition as their higher tolerance of various biotic and abiotic factors allows them to feed on protein-rich detritus in shallow water; adults have a slower growth rate and poor condition as their lower tolerance of shallow water forces them to feed in deeper, less protein-rich areas in Lake Sibaya. The growth pattern, and the inshore movements of *S. mossambicus* into warmer water during the day at low lake level can therefore be explained in terms of various abiotic factors such as water temperature and depth, wave action and cloud cover, and biotic factors such as food quality and distribution. The involvement of a predator need not be inferred as a major controlling influence.

The situation is not as clearcut at intermediate and high lake levels when *S. mossambicus* are largely absent from the terrace during the day, and perform a brief inshore migration into cooler water at night (Bowen, 1976). These movements cannot be explained in terms of known temperature preferenda and metabolic energy budgets, but there is a strong case for the involvement of a predator such as *C. gariepinus*.

Catfish rarely enter terrace waters during the day at low lake level and therefore present little risk to terrace populations of *S. mossambicus*. As the lake level increased, the factors inhibiting catfish occupation of the terrace during the day (possibly risk of predation by fisheagles *Haliaëtus vocifer*, and man) diminished in importance and greater numbers ventured onto the terrace. Meanwhile, as the terraces deepened, water temperatures were moderated and daily maxima did not approach those reached at low lake level. As a result *S. mossambicus* had to venture closer inshore to feed in warm water. In so doing, they exposed themselves to greater predation risk from catfish which, as I have shown, are more efficient at catching *S. mossambicus* in shallow than in deep water. As terrace waters deepened, visibility near the bottom decreased, and the number of catfish on the terrace increased; these factors may also have increased prey risk.

There are other biotic factors which may have led to the exclusion of *S. mossambicus* from the terraces at high lake level. These include competition for food and space with other cichlids, which are present on the terrace in high numbers at high lake levels, and a rearrangement of the food distribution at high lake levels. *P. philander* are the most abundant cichlids in shallow terrace waters, but in contrast to *S. mossambicus*, their diet in Lake Sibaya consists mainly of crustaceans (36% in a frequency analysis) and insects (28%; Minshull, 1969). In contrast, *T. sparrmanii* has a similar diet to *S. mossambicus*, with an additional food source in the form of aquatic macrophytes. However *T. sparrmanii* were not in markedly higher numbers than *S. mossambicus* on the terrace at high lake level (23%; 14.8%) and interspecific competition is unlikely to be a major excluding factor. The influence of lebensraum is unknown. Bowen (1976) found no evidence that there had been a rearrangement of food distribution and quality on the terrace at high lake level after *S. mossambicus* had reversed its migration pattern.

I must conclude that risk of predation by *C. gariepinus* is an important factor excluding *S. mossambicus* from terrace waters at high lake level. Bowen (1976; 108) suggested that "visual recognition of the predator provides sufficient stimulus to override the tendency to seek warmer shallow waters during the day and thus defers movement onto the terrace until dark". While my findings are that individual catfish do not make repeated attacking movements towards uncatchable fish prey, diving observations at high lake level indicated that large numbers of catfish inhabited terrace waters at high lake level, and that prey risk was considerable as a result of social hunting tactics by the catfish. The

counter-adaption of the prey was to feed in terrace waters for as short a time as possible. Their preference for night-time feeding is at this stage unexplained, as Caulton's (1976) results point to advantages of feeding in warmer water, and my observations indicate that catfish predation efficiency is higher at night.

Slobodkin (1968) divided anti-predatory tactics into two categories. The first is the development of escape behaviour and protective mechanisms. Because the evolutionary machinery available to predators is essentially the same as that available to prey this will result in an endless evolutionary race unless some stabilizing influence is found. *S. mossambicus* perform several anti-predation tactics, including perching, shoaling, hanging motionless in midwater, and dispersing, which are successful against a relatively slow-moving, mechanoreceptive bottom-feeding predator. The alternative procedure for the prey is to adjust its fecundity and growth patterns so as to minimize the loss to the population of those animals most subject to predation. Slobodkin (1974) states that a shift of reproductive activity to younger ages is an obvious response to predation in the sense that the greater the fraction of its reproductive contribution an animal has already made, the more expendable it is from the standpoint of the population.

*S. mossambicus* in Lake Sibaya have a maturity length ratio (0.43, Bruton & Allanson, 1974) which is considerably lower than the characteristic value for cichlids (about 0.70, Iles, 1971). According to Iles, low values are typical of dwarfed tilapiine populations and imply that a larger proportion of the population is in an actual or potential reproductive state. Iles (1973) has since emphasized that dwarfing represents an adaptive mechanism involving reproductive and growth characteristics which enable tilapia populations to withstand high mortality rates. Bruton & Allanson (1974) supported this opinion for *S. mossambicus* in Lake Sibaya.

There are several sources of mortality of *S. mossambicus* in Lake Sibaya, but mortality rates are unknown. Fry and fingerlings undoubtedly die in large numbers when marginal pools dry up at low lake levels, and fall prey to invertebrate, fish and bird predators.

The mortality caused by catfish in Lake Sibaya is likely to be on weak, slow, inattentive or cornered fishes, as catfish have been shown to be inefficient at catching free-ranging, healthy *S. mossambicus*, except at night or in groups in shallow water (Bruton, 1979b). Nevertheless the number of prey taken is considerable, and we cannot discount catfish as a source of mortality which may in part have brought about reproductive precocity as an adaptive mechanism in the prey.

How do catfish separate out enfeebled individuals from the prey population? I stated earlier that they became habituated to the uncatchability of tilapia prey during the day, but that they nevertheless occasionally approached prey as if to "test" their vulnerability from time to time. Similarly, catfish "test" prey in the wild—a movement towards a shoal quickly reveals the weaker swimmers (thus making them spatially odd) and leads to increased prey risk to the slowest individuals. From the tower I often observed catfish swimming slowly after a shoal of cichlids, as if to test their cohesiveness. Attacks were sometimes initiated on stray individuals, but incipient attacks were far more common than completed ones. In the experimental areas, tilapia with amputated caudal or pectoral fins quickly fell prey to catfish, whereas healthy fish were rarely caught. Similarly Herting & Witt (1967) found that impairment of the physical condition of *Lepomis gibbosus* (L.) and *Micropterus salmoides* due to injury, parasitism or starvation, resulted in a significant increase in their vulnerability to predation by *Amia calva* L.

A collection of *S. mossambicus* from Lake Sibaya indicated that very few juveniles were unhealthy whereas the proportion of unhealthy adults was high. Only 0·38% of 4670 closely examined juveniles were parasitized and less than 0·1% were injured or malformed. In contrast, over 10% of a sample of 540 adult *S. mossambicus* were parasitized, and the majority had abnormally shaped heads and were in poor condition (Bruton, 1973). Catfish and other predators must have had some role in maintaining the fitness of the juvenile population. The adult population, on the other hand, shows all the indications of low predation pressure (poor condition, slow growth rate, and small size relative to adults in other populations).

There are several reasons why adults would be less subject to predation by catfish in Lake Sibaya. Firstly, *S. mossambicus* larger than 150 mm TL (the approximate length at which adults return to the terrace to breed; Bruton & Boltt, 1975) may be too large for catfish to catch in the clear waters of Lake Sibaya. Catfish prey rarely exceed 20% of the predator's length and a 560 mm predator (the modal length on the terrace, Bruton 1978) would normally take prey less than 110 mm TL. On several occasions while diving I observed catfish longer than 500 mm TL approach adult *S. mossambicus* very closely without attempting to catch them. Similarly, catfish were often seen from the tower swimming among nest-guarding *S. mossambicus* males without causing the cichlids to abandon their nests. No attempt was made to catch the cichlids.

Secondly, the habitat preferences and avoidance strategies of adult *S. mossambicus* reduce their risk of predation by catfish. Adult tilapia rarely enter water shallower than 300 mm and a considerable part of their time is spent in deeper water offshore or in midwater (Bruton & Boltt, 1975). Thus, despite the poor condition of the prey, catfish appear to have little effect on adult populations of *S. mossambicus* in Lake Sibaya.

In conclusion, the role of *C. gariepinus* as a predator on *S. mossambicus* may be summarized as follows:

- (a) to enhance species fitness by removing enfeebled individuals from the juvenile population, i.e. act as a "cleaner";
- (b) to restrict the distribution of prey under certain conditions when prey vulnerability is relatively high, such as at high lake level, i.e. act as a "restrictor";
- (c) to dampen fluctuations in the abundance of cichlid species under certain conditions. The catfish's impact as a "regulator" may be negligible if only enfeebled prey are taken, as these prey would probably die from other causes anyway.

The relative importance of these three roles cannot be defined in detail at this stage, and may be different for different prey or in other systems. For instance, *C. gariepinus* may be more efficient "regulators" in the shallow muddy waters of alluvial pans and swamps, where their efficiency at catching fish prey must be higher. The vulnerability of fish prey under different environmental conditions will most likely determine which role is the most important in a given ecosystem. According to Popova (1967) *Silurus glanis* may also change their role in different systems. In lakes and rivers in Russia where conditions are stable and there is a small supply of food, *S. glanis* acts as a "cleaner". In large lakes with abundant food and a greater diversity and variability of ecological conditions, the predator population is correspondingly larger and they function chiefly as "regulators".

Slobodkin (1961, 1968) introduced the concept of "prudent predation", whereby a predator uses its prey efficiently. A "prudent" predator will consume its prey in such a

way as to maximize its own food supply while at the same time minimizing the possibility that the prey population will be unable to maintain itself and serve as food in the future. From experiments with *Daphnia* sp. as prey, Slobodkin (1961, 1968) concluded that the optimal behaviour of a prudent predator is to take animals which are about to die anyway, i.e. to disrupt the pattern of mortality as little as possible. This behaviour involves taking individuals of low reproductive value. Slobodkin (1961) suggests that the effect of predation on prey populations is either to substitute one cause of mortality for another, or to lower the survival of some particular age group in the population, or both (as shown by Errington, 1946, many years previously). By concluding that "prudent" predators involuntarily are able to take only those prey individuals which are about to die, Slobodkin (1968) implies that predators do not regulate the population numbers of their prey. Maiorana (1976) therefore pointed out that, if this is the case, the predators need not be prudent, as they have no effect on prey survivorship.

Maiorana seems to regard all predators as "regulators", which have a direct effect on population numbers. Some, such as *C. gariepinus*, would appear to be mainly cleansers. Cleansers are also prudent predators, as defined by Slobodkin, and they influence prey survivorship by enhancing species fitness. Under certain conditions, for instance when prey density or vulnerability is high, they may become regulators, and influence survivorship more directly. Furthermore, as Slobodkin (1974) has shown, predation may lead to shifts in fecundity, mortality and growth patterns which lower the reproductive value of preferred prey. Hence, a predator appears to be prudent because the prey individuals it can take have become those with the lowest reproductive value. In fact, this apparent prudence is brought about by adaptations of the prey.

The second major topic which warrants further discussion is the effect of the prey population on the life history characteristics of the predator. In particular, why do catfish switch from an invertebrate diet to a largely fish diet during their ontogeny, when they are apparently more efficient at catching invertebrates? Food quality is the obvious answer. A predator is thought to allocate its resources of time and energy in the most profitable or "optimal" manner, i.e. energy yield from the prey is balanced against the energy cost of catching, ingesting and assimilating that prey (MacArthur, 1972). Bruton (1979b) showed that although fish only contributed 12.5% by number of all prey eaten by *C. gariepinus* in Lake Sibaya, their yield in terms of energy content represented 76.5% of the total.

There is some evidence to suggest that fish food is required by adult *C. gariepinus* if they are to reach a large size (Bruton, 1976). In three well-established impoundments in which *C. gariepinus* would be expected to reach a large size but do not exceed 11 kg (Lakes Kariba, McIlwaine and Barberspan), the adults feed mainly on plankton (Munro, 1967; Bowmaker, 1973; Schoonbee, 1969). Furthermore, Marshall (1977) has shown that the populations of *C. gariepinus* in Lake McIlwaine and other impoundments in Rhodesia, where adults feed mainly on plankton, have declined markedly in recent years. This decline is apparently not due to commercial fishing. In the Vaal River (South Africa), Hardap dam (South West Africa) and Pongola River (Zululand), where adult *C. gariepinus* have an adequate supply of fish food (Groenewald, 1964; Gaigher, 1977; Kok & Gaigher, pers. comm.) the catfish reaches a large size (>17 kg, occasionally >30 kg; Bruton, 1976).

Large adult *C. gariepinus* (>600 mm TL) in Lake Sibaya feed partly on fish, but this

food source is apparently not adequate for the maintenance of good growth and condition, as in juveniles and young adults. As a result, the adults are emaciated and have large heads and thin bodies.

There are several reasons why the quality of food available to large and small catfish in Lake Sibaya is different. Large adults feed mainly in deeper terrace and offshore waters (Bruton, 1978), and their diet consists of a greater proportion of larger *S. mossambicus* (Fig. 11). Bruton (1973) and Bowen (1976) showed that large *S. mossambicus* in Lake Sibaya are in poorer condition than juveniles. The energy yield from adult *S. mossambicus* prey may be less per gram than for juveniles; Caulton (1976) found that *T. rendalli* in poor condition yielded 8·1% less energy per gram than good condition fish. Furthermore adult *S. mossambicus* have several effective avoidance tactics against catfish and, being larger than juveniles, they may be more difficult to catch.

*S. mossambicus* is largely confined to water shallower than 12 m in Lake Sibaya (Bruton & Boltt, 1975) and no other large prey are regularly taken by catfish in deeper water. *Glossogobius giurus*, *Pseudocrenilabrus philander* and *Croilia mossambica* are present in variable numbers in the profundal zone, but they rarely occur in the diet of catfish caught there. Only *Hymenosoma orbiculare* among the profundal benthos contributes significantly to the catfish diet. *Bellamya capillata*, *Melanoides tuberculatus*, *Caridina nilotica* and the various infaunal microcrustacea may be too small, unpalatable and/or sparse to support a large predator. The standing crop of zooplankton is certainly inadequate. Thus poor food quality and low availability of large food items in deep water can be identified as the cause of decreased growth rates and poor condition of large *C. gariepinus* in Lake Sibaya. Their exclusion in a clear lake from shallow littoral areas in which food quality and availability is higher, and their apparent inability to catch midwater fishes in the diverse communities of offshore macrophyte beds, lead to the adult catfish's occupation of the sparse profundal zone. In muddy, shallow lakes and swamps, where large catfish can penetrate into the shallows to feed on littoral fishes without exposing themselves to high predation risks, their growth rate and final size is greater (Bruton, 1976). These areas also provide adequate alternate prey if fishes are not abundant.

There are several parallels between *C. gariepinus* and *S. mossambicus* in Lake Sibaya. In both species the most valuable food resources are found close inshore, and both therefore move into shallow water to feed. These feeding movements are apparently controlled by predation risk and other factors. Both species are food-limited in the larger size groups, and their final size and the condition of adults is lower than in other populations of the same species. Both species are numerically abundant, and their success is largely a result of their ability to utilize a variety of food resources as they become available in the fluctuating littoral zone of Lake Sibaya.

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## APPENDIX I

### *Calculation of condition factor*

The condition factor (*CF*) of fish is usually calculated using either of the following formulae:

where expected weight = geometric mean of the weight distribution for a given length.

$$\text{or } CF = \frac{W}{Tl_b} \dots \dots \dots \quad (2)$$

where  $W$  = actual weight

*b* = exponent from a log:log regression of weight on length for an allometrically-growing species (Tesch, 1968).

Formula (1) has the advantage that a value of one is given for fish in average condition. Values above and below one indicate fish in relatively good or poor condition respectively, in relation to the rest of the sampled population. Calculation of "expected weight" in (1) is, however, a clumsy procedure.

Formula (2) provides an accurate assessment of relative condition as the exponent "b" is taken into account. There is, however, no easy reference to average condition. The advantages of both methods are combined if the following formula is used:

$$CF = \frac{\text{Actual weight}}{\text{Expected weight}} \dots \quad (3)$$

where expected weight: =  $a TL^b$  and  $a$  and  $b$  are the constant and the exponent from a log:log regression of weight on length.

If the length: weight relationship is not linear on a log:log plot for different sexes, or for adults and juveniles, different values must be entered for  $a$  and  $b$  according to the given regression. The length:weight relationship of 862 *C. gariepinus* caught in Lake Sibaya is expressed as follows:

Juveniles 50–350 mm TL,  $W = 0.000006$ ,  $TL^{3.029}$  ( $R^2 = 0.98$ ,  $N = 218$ )

Adult females > 350 mm TL,  $W = 0.00004$ ,  $TL = 2.705$  ( $R^2 = 0.90$ ,  $N = 289$ )

Adult males > 350 mm TL.  $W = 0.00004$ , TL 2.699 ( $R^2 = 0.92$ ,  $N = 355$ )

where  $W$  = weight in grams and,  $TL$  = total length in mm.

of  $a$  and  $b$  were used for the calculation of condition factor using

The relevant values of  $a$  and  $b$  were used for the calculation of condition factor using formula (3).