THE BIOLOGY OF CLARIAS GARIEPINUS (BURCHELL, 1822) IN LAKE SIBAYA, KWAZULU, WITH EMPHASIS ON ITS ROLE AS A PREDATOR

by

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Length 33½ inches
Greatest breadth 5½
Length longest cirrhus 7

P.D 69
A 53
C 18
P 10
V 6
M.B. 5

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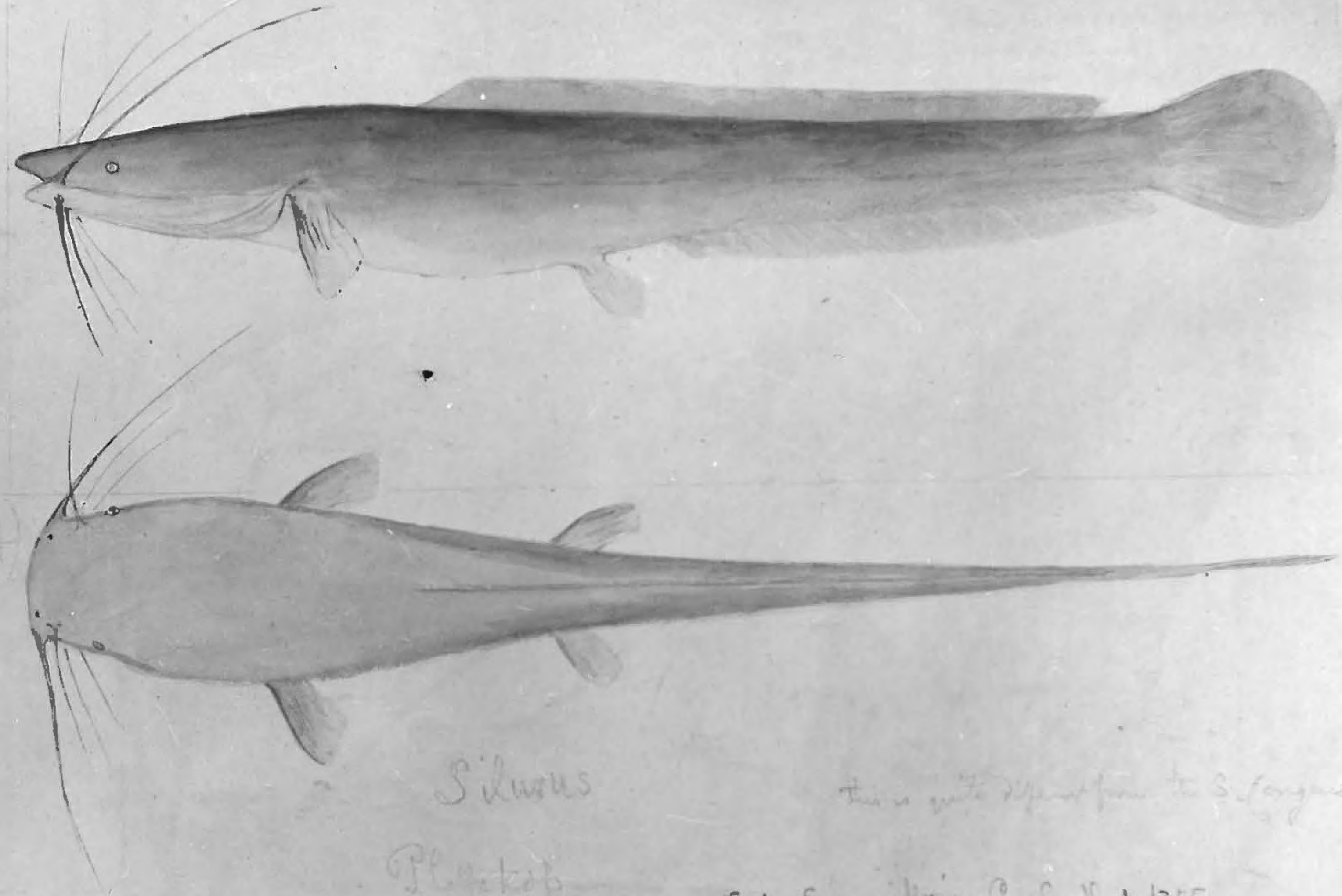

392

Silurus

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Frontispiece: Photograph of William Burchell's original sketch of Clarias gariepinus, dated 3.11.1811. His formal description of the catfish appeared 11 years later (Burchell, 1822). Photo: L. Luckhoff, courtesy Africana Museum, Johannesburg.

RESUME

Aspects of the biology of the sharptooth catfish, Clarias gariepinus (Burchell, 1822) were studied in a clear coastal lake (Lake Sibaya, KwaZulu.).

Catfish reach maturity towards the end of the first year (total length 200-250mm) and breed in summer. Gonadal maturation is cyclical, and most fishes are ripe between September and January each year. Maturation stages and fecundity are described. Twenty-two catfish spawning runs were witnessed. There were no large aggregations of catfish before the Summer rains, as reported in some impoundments and rivers, but catfish accumulated on the shallow terrace immediately before a spawning run. Spawning usually took place in flooded marginal areas after heavy rain on dark calm nights. Peak activity occurred between 20h00 and 02h30. Pre-nuptial aggression, courtship and mating are described and illustrated in detail for the first time from field observations. Gonadal products are released while in amplexus and fertilized externally. The eggs have an adhesive disc for attachment to plants, and develop rapidly. Early development and feeding are described.

The growth rate of catfish was determined using rings on the pectoral spines, and validated using recent techniques. C.gariepinus in Lake Sibaya grow rapidly and remain in good condition to a length of 500mm, but larger catfish have a poor growth rate and condition, and few exceed 650mm. The modal length and weight of the Sibaya population is intermediate between that of other populations but the number and condition of larger catfish in Lake Sibaya is lower. Other studies on C.gariepinus growth are reviewed. Very high and low first year increments obtained previously may be due to methodological errors, but catfish do appear to have variable growth rates. The size reached by C.gariepinus is reviewed.

Catfish are equipped morphologically and behaviourally to feed on a wide variety of prey in different situations, but they usually feed at night on exposed, active benthic organisms. Social hunting facilitates the capture of prey which is too fast or manoevrable for a single predator. Food preferences are scored by three different methods and presented for the total catfish population and for different length groups, seasons, and habitats. Juveniles feed more often and on a greater variety of prey, and their condition is better than that of adults. The proportions of several food items in the diet changed at different lake levels as marginal areas became inundated. In particular, increasing lake levels resulted in a change in relative density of three cichlid prey in the shallow water feeding area of catfish. This situation provided the opportunity to study the effect of changing cichlid density on predation by catfish.

The world literature on factors influencing the predator-prey relationship in fish is reviewed and several key factors are identified. The interaction of fish predators and prey in Africa, and particularly Lake Sibaya, is examined in detail, and prey density, modified by accessibility, is found to be an important factor.

The effect of cichlid prey density on catfish predation was therefore investigated using field collections and experimental observations. Catfish prey on the cichlid species with greatest relative abundance, with some deviations which can be explained in terms of accessibility. The experimental results also describe feeding periodicity, imitative hunting and the effect of water depth, day-night light intensity changes and predator number on predation efficiency on cichlids. Catfish predation is discussed in terms of recent predation theory, and it is concluded that their ability to switch from one prey to another as prey availability (= density + accessibility) changes, is an an important aspect of their success as predators.

Catfish predate more efficiently on invertebrates, but feed largely on fishes after the first year. This preference for fish prey is probably related to food quality, as fishes contributed over 75% of the energy content of all ingested food, as well as abundant protein and the correct amino acid balance.

Finally, I conclude that the role of <u>C.gariepinus</u> as a predator on <u>S.mossambicus</u> is three-fold:

(a) to enhance species' fitness by removing enfeebled individuals i.e. to act as a 'cleanser'

(b) to restrict the distribution of prey under certain conditions i.e. act as a 'restricter'

(c) to dampen fluctuations in cichlid abundance i.e. act as a 'regulator'.

The relative importance of these roles may alter at different lake levels in Lake Sibaya in response to changes in the vulnerability of fish prey.

ACKNOWLEDGEMENTS

This project was supervised during its early stages by the late Dr R.E. Boltt, whose untimely death in April 1975 robbed us of an inspiring colleague. Professor B.R. Allanson, who had always had a lively interest in my research, took over supervision during the final two years. I benefitted greatly from Professor Allanson's clear grasp of the real issues at hand and his appreciation of the difficulties of field work. As director of the Institute for Freshwater Studies, he also provided facilities and funds for research at Lake Sibaya Research Station.

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INTRODUCTION

Taxonomic and zoogeographic studies dominated African ichthyology for many years, and it is only in the last 30 years that biological investigations have come to the fore. Many of the earlier biological studies relied on the analysis of commercial catches, which could only yield information on part of the fish population. A vast amount of data were collected, but an understanding of the populations involved often evaded the investigator. It was an important step, therefore, when *in situ* autecological studies were started, using a variety of collecting gear and other techniques. These studies were particularly successful when they were combined with an integrated research programme on other aspects of the ecology of the water body in question. The need for an integrated approach to freshwater ecology was appreciated by the organising committee of the International Biological Programme in 1962, and the success of one of their African projects (Lake George, Uganda; Greenwood, 1976) is testimony to their foresight.

Another, smaller freshwater ecology project (partly sponsored by the PF section of the South African IBP) was initiated by Professor B.R. Allanson of the Institute for Freshwater Studies at Rhodes University, on Lake Sibaya in KwaZulu. This programme included studies of the origin, physico-chemical limnology, primary production and the distribution, ecology and ecophysiology of the dominant animals of Lake Sibaya.

The fish studies (reviewed where relevant in the text) revealed an interesting fauna dominated by cichlids and gobiids (Appendix 1). The most abundant cichlid, *Sarotherodon mossambicus*, was studied in detail, and found to grow rapidly in the first year, and breed precociously. Their growth rate, as well as their condition, decreased after maturity and individual fishes reached a very small final size compared with other populations of the same species. *S.mossambicus* was also shown to perform diel horizontal movements into warm water during the day and back into deeper water at night.

The observed growth pattern and movements of *S.mossambicus* in Lake Sibaya may be due to abiotic and/or biotic factors. Abiotic factors include wave action, water depth and water temperature, and biotic factors the availability and quality of food, and the effect of predators. Bruton (1973) initiated a study on the effect of the abiotic factors on tilapia movements. This study was continued by Bowen (1976), who also investigated the influence of food availability and food quality. Preliminary analyses of the stomach contents of a prominent predator in the lake, the catfish *Clarias gariepinus*, revealed that considerable numbers of *S.mossambicus* were eaten. Predation by catfish was therefore identified as an additional factor influencing *S.mossambicus* movements.

Meanwhile, studies of the benthic invertebrates, especially the crown crab Hymenosoma orbiculare, and small fish species revealed that C.gariepinus was omnivorous, and impinged on the biology of nearly all organisms in the lake. A detailed study of the catfish in Lake Sibaya became an obvious priority, especially against a background of detailed biological studies of its main prey, S.mossambicus and H.orbiculare. The catfish study had two main aims:

(a) to define the role of C.gariepinus in Lake Sibaya, with special emphasis on its effect on the main fish prey, S.mossambicus. This programme would also provide a preliminary assessment of the impact of catfish on other vertebrate and invertebrate prey, and contribute to our understanding of trophic pathways in Lake Sibaya;

(b) to investigate the predator:prey relationship of Clarias and tilapia, and contribute to our knowledge of the ethology of predation, particularly in an African context. Several researchers have recognised that the major limitation in our understanding of predator-prey relationships in fish is in relation to population dynamics (Popova, 1967; Nikolsky, 1969; Weatherley, 1972). I was fortunate at Lake Sibaya to have the opportunity to study these effects.

Previous studies on African fish predators have been concerned with the quantities of prey consumed, and to a lesser extent, the conditions under which prey are taken. There have been no detailed studies on the ethology of predation. The world literature (reviewed below) contains references to studies on the feeding ecology of sheatfish, sharks and other omnivorous fishes, but these studies have not established the principles of predation by an omnivore, as Holling (1965, 1966) has done for an ambushing insect predator, and Beukema (1968) for a small carnivorous fish. Omnivores are potentially interesting predators, whose main characteristic is that they can switch from one prey to another as prey accessibility changes (although few are as euryphagous as Clarias). Omnivores are more common than stenophages among fishes and it is therefore essential that their feeding ethology is known if we are to understand the predation process fully. The present study can be considered a contribution to the first step along this road.

Before embarking on the main study on feeding and predation, it was necessary to obtain background information on the habitat preferences, distribution, breeding and growth of C.gariepinus in Lake Sibaya. These earlier studies also filled an important gap as previous work on C.gariepinus (reviewed in the relevant chapters) is sparse when one considers that this species is one of the most widespread and prominent fishes in southern Africa.

Some important aspects of the biology of C.gariepinus, such as aerial respiration, mortality and population dynamics, were beyond the scope of this study, either because they were not directly related to the main theme, or because they could not be studied at a field station with the equipment available.

This was primarily a field study, and I tried to take advantage of my situation by living with the fishes as much as possible. Extensive use was made of diving gear for underwater observations, and many valuable hours were also spent observing the fishes from above water platforms and boats. In contrast to many previous 'lucky dip' type studies, in which the researcher necessarily analysed catches taken blindly from the depths with a net, I have endeavoured to sample the fishes meaningfully using a wide variety of gear backed up by diving observations.

Throughout this dissertation I have compared my findings with those of other workers on this and related *Clarias* species. This approach has allowed me to describe their life history characteristics, and evaluate their role as predators, in a wide variety of ecosystems.

A DESCRIPTION OF LAKE SIBAYA

Lake Sibaya ($32^{\circ}40'$E, $27^{\circ}25'$S) is the largest natural freshwater lake in South Africa. The lake is situated on the seaward edge of a broad coastal plain of recently deposited tertiary sands in Tongaland, northern KwaZulu (Fig. 1). A row of high forested coastal sand dunes separate the lake from the sea. The lake surface, with an area of about 65km^2, is approximately 21m above mean sea level.

Lake Sibaya consists of a large main basin into which open two smaller basins in the south and south-west. Two long arms stretch towards the north and west. The bathymetry of Lake Sibaya is illustrated in Fig. 2 (a foldout under the back cover). The maximum depth is 40m and the mean depth 13m (Hill, 1969). 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). The shores of Lake Sibaya are sandy with no rock apart from isolated outcrops of ironstone on the north-eastern shore of the main basin. The numerous arms and bays result in a well-developed shore line with a length of 144km. The northern and south-western shores of the three basins shelve gently into deeper water. On the western, eastern and south-eastern shores, and along the northern and western arms, deep water often occurs close inshore. Shoreward of the slope are open terraces which fluctuate in depth according to lake level. Extensive shallow pools form in the marginal zone at low lake level. Diagrammatic profiles of the lake shore are given in Fig. 3.

The lake level is subject to considerable fluctuations dependent on local rainfall, runoff and seepage. Simulated month-end lake levels for Lake Sibaya from 1914 to 1969 are given by Pitman and Hutchinson (1975). During this 55 year period, lake level rose and fell 3,5m. During the period of my stay at Lake Sibaya lake level fluctuated through 2,7m,(Fig. 4). These changes have a profound effect on the nature of sublittoral, littoral and marginal habitats as extensive areas of shoreline are gently sloping and therefore readily inundated.

Seven main habitats in Lake Sibaya, with notes on the distribution of fish

Seven main habitats can be distinguished in Lake Sibaya on the basis of flora, bottom profiles, substrate type and depth. A full description of these habitats and their fauna and flora is given by Allanson *et al* (1974). A checklist of the fishes of Lake Sibaya is given in Appendix 1.

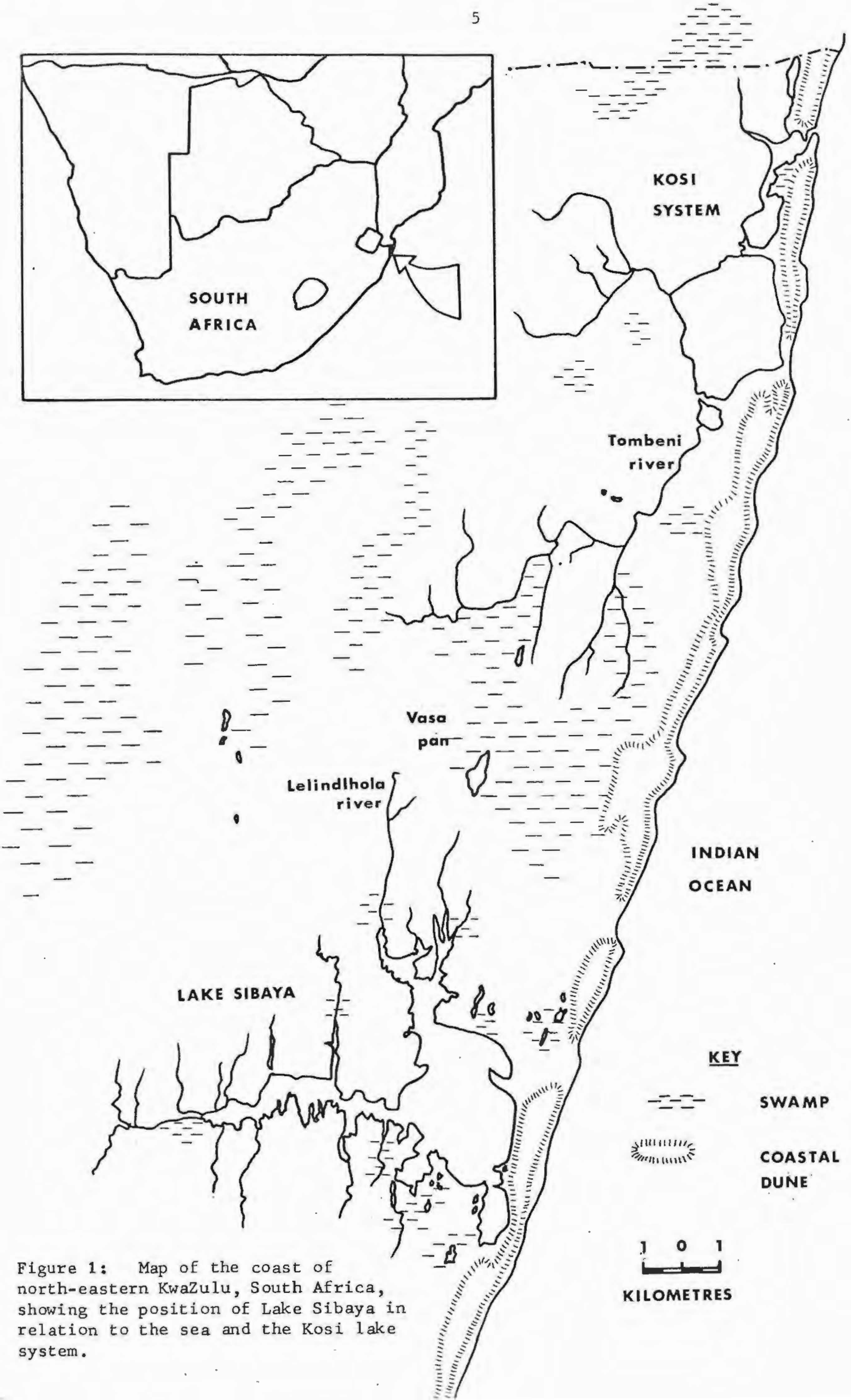


Figure 1: Map of the coast of north-eastern KwaZulu, South Africa, showing the position of Lake Sibaya in relation to the sea and the Kosi lake system.

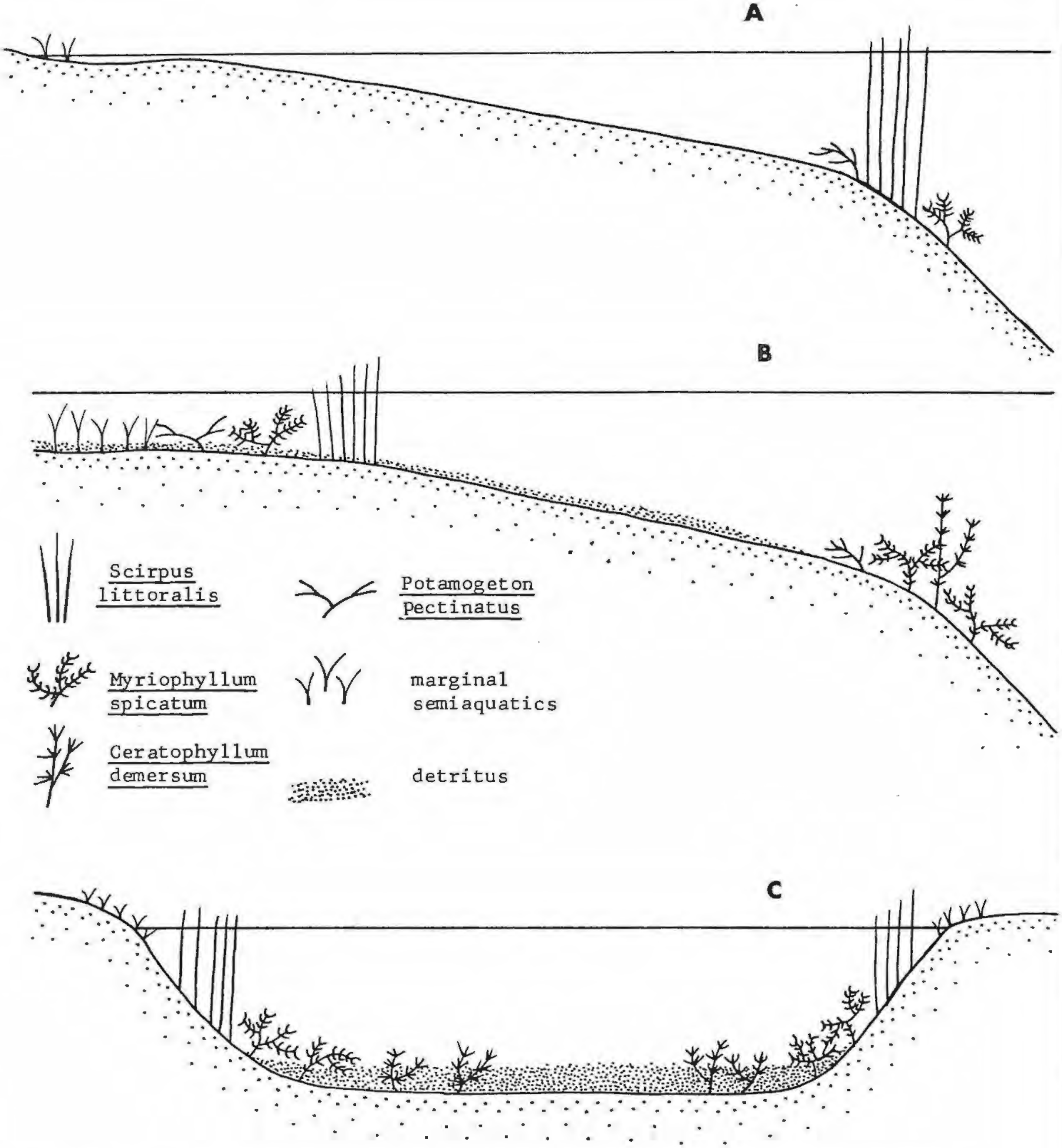


Figure 3: Diagrammatic profiles of different inshore habitats in Lake Sibaya.

A. Terrace and slope at low lake level

B. Terrace and slope at high lake level

C. Sheltered bay

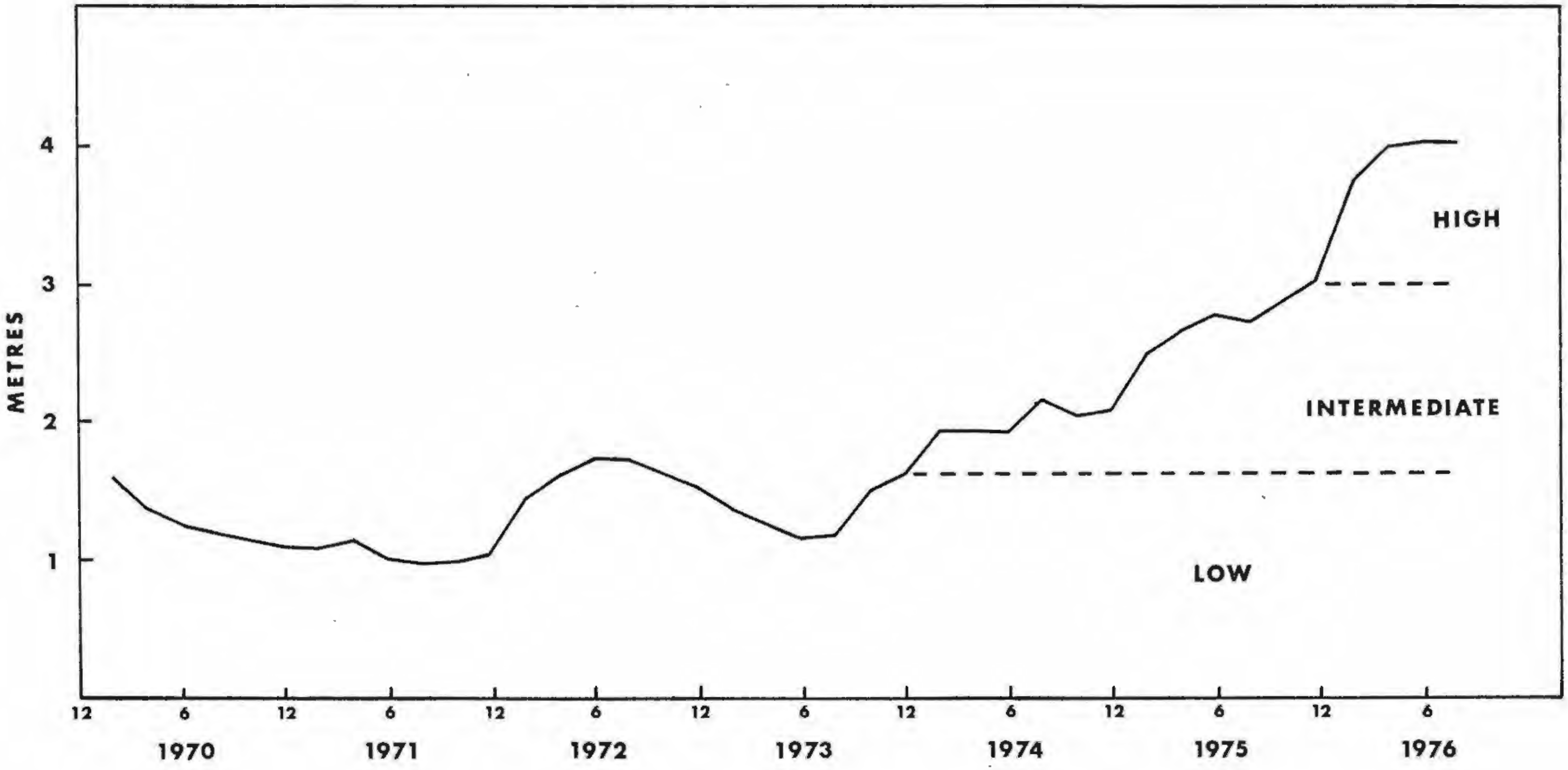


Figure 4: Month end lake levels at Lake Sibaya as measured on a Department of Water Affairs 'OH' level recorder at Lake Sibaya Research Station. The arbitrary lake level categories used in this study are also shown.

The nature of *marginal habitats* changes most markedly at different lake levels. On a receding or low lake level, extensive barren, sandy beaches with wide shallow pools are characteristic of gently sloping shores (Fig. 5). On steeply sloping and sheltered shores emergent macrophytes *Phragmites mauritianus* and *Scirpus littoralis* fringe the shore. At increasing and high lake levels, marginal beaches, pools, adjacent grassland and forest fringes are inundated, and extensive well-vegetated marginal pools are created (Figs 6 and 7). The extent of this inundation is shown on Fig. 7. Often, adjacent swamps and lakelets are joined to the main lake. A diversity of semi-aquatic plants become established along the shore including *Andropogon amplectens*, *Imperata cylindrica*, *Cladium mariscus*, *Haemarthria altissima*, *Juncus kraussii*, *Panicum meyerianum*, *Erogrostis gangetica* and *Harpochloa falx*. The sheltered shallow pools provide cover for many fish and invertebrate species which inhabit offshore macrophyte beds at low lake levels. On the eastern shore of the main basin the lake abuts directly on climax coastal dune forest. Here, a band of *Acacia karroo* on the lake edge is drowned at high lake levels and provides a tangled inshore habitat. Marginal habitats are inhabited by all the fish species known from Lake Sibaya (see Appendix 1) except *Labeo molybdinus* and *Marcusenius macrolepidotus*.

Terrace habitats are gently sloping littoral shelves between the shore and the slope (Fig. 8). The substrate is sandy with variable amounts of detritus. At low lake level, *Scirpus littoralis* often forms a fringe near the deep edge of the terrace, (Fig. 9) but at high lake level this fringe is found inshore and submerged macrophytes (*Potamogeton pectinatus*, *P.schweinfurthii*, *Myriophyllum spicatum*) become established on the deep edge. Terrace habitats varied in depth from 1m to 3,7m on the lakeward edge at different lake levels, and temperature and light regimes, and the effect of wave action, were modified accordingly. At low lake levels, *S.mossambicus* is the only fish which inhabits the terrace in large numbers, but at high lake levels two other cichlids, *Tilapia sparrmanii* and *Pseudocrenilabris philander*, the gobies *Glossogobius giurus* and *Croilia mossambica*, and a clupeid *Gilchristella aestuarius*, are also common. Catfish generally feed on the terrace after dark.

Gradual sloping habitats replace terraces on windward shores. They have an inshore curtain of *S.littoralis*, *P.mauritianus* and *Typha latifolia*, and beds of *M.spicatum*, *P.pectinatus* and *Ceratophyllum demersum* in deeper water beyond the influence of wave action. This habitat grades into the profundal at about 15m although macrophytes rarely extend deeper than 9m. Substrates consist of stabilised sand with a thin layer of flocculent material (Fig. 10) and variable amounts of macrophyte debris. The fish fauna is the same as that of the terrace, with the addition of the mormyrid, *Marcusenius macrolepidotus*.

Steep slopes are found on the deep edge of the terrace, and represent a contracted transition zone from terrace to profundal habitats. These slopes,

Figure 5: Large marginal pools and shallow terraces at low lake level in Lake Sibaya. A view along the eastern shore of the south basin in November 1971. Lake level 0,94m.

Figure 6: Flooded grassland at increasing lake level on the east shore of the south basin. November 1972. Lake level 1,51m.

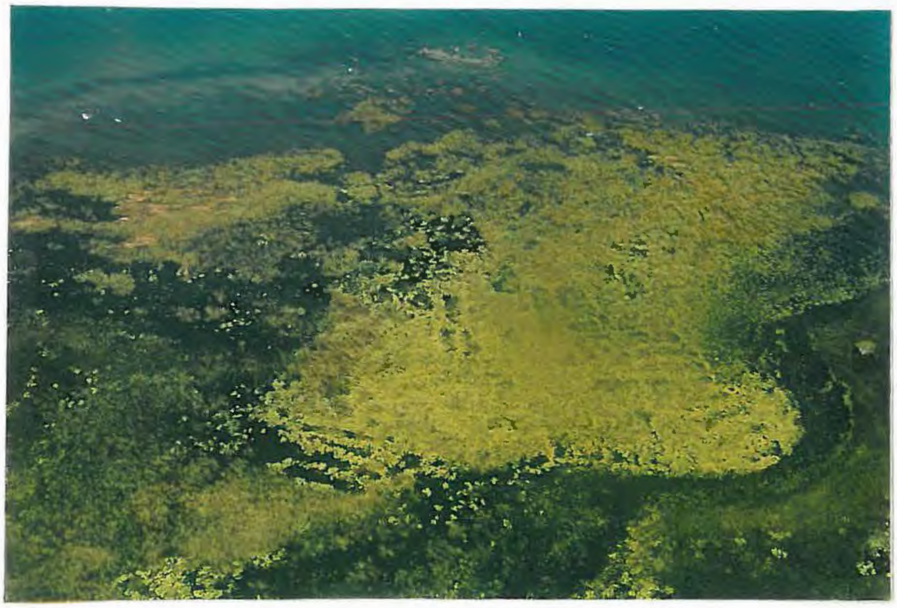


Figure 7: Flooded marginal grassland and swamp at increasing lake level on the north-western shore of the main basin. (July, 1976; lake level 4,03).

Figure 8: The wide terrace and flooded Acacia fringe on the eastern shore of the main basin at Lake Sibaya Research Station. (July, 1976, lake level 4,03m).

Figure 9: Shallow terrace on the western shore of the main basin at low lake level (July 1972).

Figure 10: Underwater photograph of detritus layer, snail Bellamya capillatus and a submerged macrophyte, Potamogeton pectinatus, at 7m depth in a gradual slope habitat.

at an angle of 20° - 30° from horizontal, usually extend to about 15m, but at the deep point (Fig. 2) they reach as far as 40m. The sandy substrate is generally unstable but dense beds of *P.schweinfurthii*, *P.pectinatus*, *M.spicatum* and *C.demersum* are found to a depth of 7m. Cyprinid, cyprinodont, cichlid and gobiid fishes are common. *C.gariepinus* are often encountered in slope habitats.

Sheltered bays are characterised by steep slopes close to shore and flat bottoms covered with a layer of organic ooze. Aquatic macrophytes are common (Figs 11 and 12), and include abundant water lilies, *Nymphaea capensis*. This habitat harbours a diverse assemblage of invertebrates and all 18 species of fish known from Lake Sibaya have been collected there.

The profundal zone begins at about 15m. There are no macrophytes and substrates consist of stabilised sand with a layer of detritus which in some places e.g. centre of the south basin, exceeds 1m in depth. Gobiids, *C.gariepinus* and *P.philander* commonly inhabit this zone.

The limnetic zone is sparsely populated with fish and the only permanent pelagics are the planktivores, *Gilchristella aestuarius* and *Atherina breviceps*. The standing crop of phytoplankton contains less than 5 mg chlorophyll per litre, and has a maximum carbon fixation rate of 239mg m^{-2}d^{-1} (Allanson & Hart, 1975). Both values are very low for a warm subtropical lake.

Physical and chemical characteristics

The open waters of the lake are basically homothermal and no persistant thermal stratification has been observed, probably as a result of frequent high velocity winds which blow from the north and south (Allanson & van Wyk, 1969). Open water temperatures measured at a fixed buoy over 20m from 1970 to 1976 varied from 18° to 28°C (Hart & Allanson, 1975, and personal observations). Terrace and marginal habitat temperatures ranged between 36°C (rarely 41°C) and 16°C (rarely 13°C, personal observations). Oxygen levels are high at all depths and rarely fell below 60% saturation. Secchi disc values vary between 3,0 and 3,5m, and 1% of midday incident light energy is recorded seasonally between 14 and 17m. The waters are alkaline, pH 8,6, and have a high chloride ion concentration, 135 mg/CL^{-}/C, but are otherwise fresh (Allanson & van Wyk, 1969).

The major faunal components other than fish

The diversity of fauna is greatest in sheltered marginal vegetation (83 taxa), and permanently submerged plant beds (55 taxa) and least on the terrace (29 taxa), and in the profundal and pelagic zones (24 and 16 taxa respectively; Allanson *et al*, 1974).

The most common zooplankter is *Pseudodiaptomus hessei* which occurs at a low mean density of less than six individuals per litre (Hart & Allanson, 1975).

Figure 11: The western arm of Lake Sibaya showing sheltered bays and inlets (July, 1976; lake level 4,03m).

Figure 12: Sheltered bay habitat in the western arm (June, 1976). Photo: A. Bruton.

The distribution and abundance of the benthos is described by Boltt (1969), Boltt *et al* (1969), Allanson *et al* (1974) and Appleton (1976). The crown crab, *Hymenosoma orbiculare* and the molluscs, *Bellamya capillata* and *Melanoides tuberculata* are the commonest large invertebrates of the epifauna. The amphipod *Grandidierella lignorum* is the dominant infaunal component to a depth of 20m, but in deeper water the tanaid *Apseudes digitalis* is more abundant. The shrimp *Caridina nilotica*, 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* and *Pontogeloides latipes*, the amphipod *Corophium triaenonyx* and the shore crab *Potamon sidneyi*. The most striking littoral insects are the burrowing mayfly *Povilla adusta* and odonatid nymphs. Molluscs are abundant in sheltered bay habitats and marginal pools.

Collecting, measuring, tagging and observation methods

Collecting methods

Most catfish were caught in the main basin of Lake Sibaya, but representative samples were also taken from the smaller basins, and the northern and western arms. A variety of methods were used to catch catfish in all depths and habitats. Each method secured catfish in particular size classes and condition, and the catches were therefore used for different purposes (Table 1).

TABLE 1

The methods used to catch C.gariepinus in Lake Sibaya. The habitats sampled, and the number and use of catfish caught using each method are also given.

Collecting method	Number caught	Habitat sampled	Catch used for the study of
Gillnets	928	Terrace, slope, profundal, bay	Growth, distribution and diet
Fixed lines and longlines	714	Terrace, slope, profundal, bay	Growth, distribution and diet
Fishtraps	385	Marginal, bay, stream	Juvenile ecology
Fonya thrust baskets and handnets	228	Marginal	Spawning runs
Rod and line	75	Terrace, slope, profundal, bay	Diet
Seine and trawl nets	58	Terrace, slope	Distribution
Total	2388		

The length frequency of the catch using different gear is given in Fig. 13. This figure is discussed in the chapter on 'Growth'.

Gillnets: A fleet of 60, 80, 120 and 160mm stretch mesh multi-filament nylon gillnets were used. The nets were bottom set in shallow and deep water, and lifted every three to six hours.

Fixed lines: Catfish drown within a few hours if they are held beneath the water surface, as in gillnets, and a method was therefore devised which yielded live, undamaged fish. Fixed lines consisted of a pole to which was attached a spring and a length of dacron line, a running sinker, swivel, steel trace and a single hook baited with fresh tilapia fillets. The pole was driven into sand at the lake edge and the baited line thrown into deeper water. This

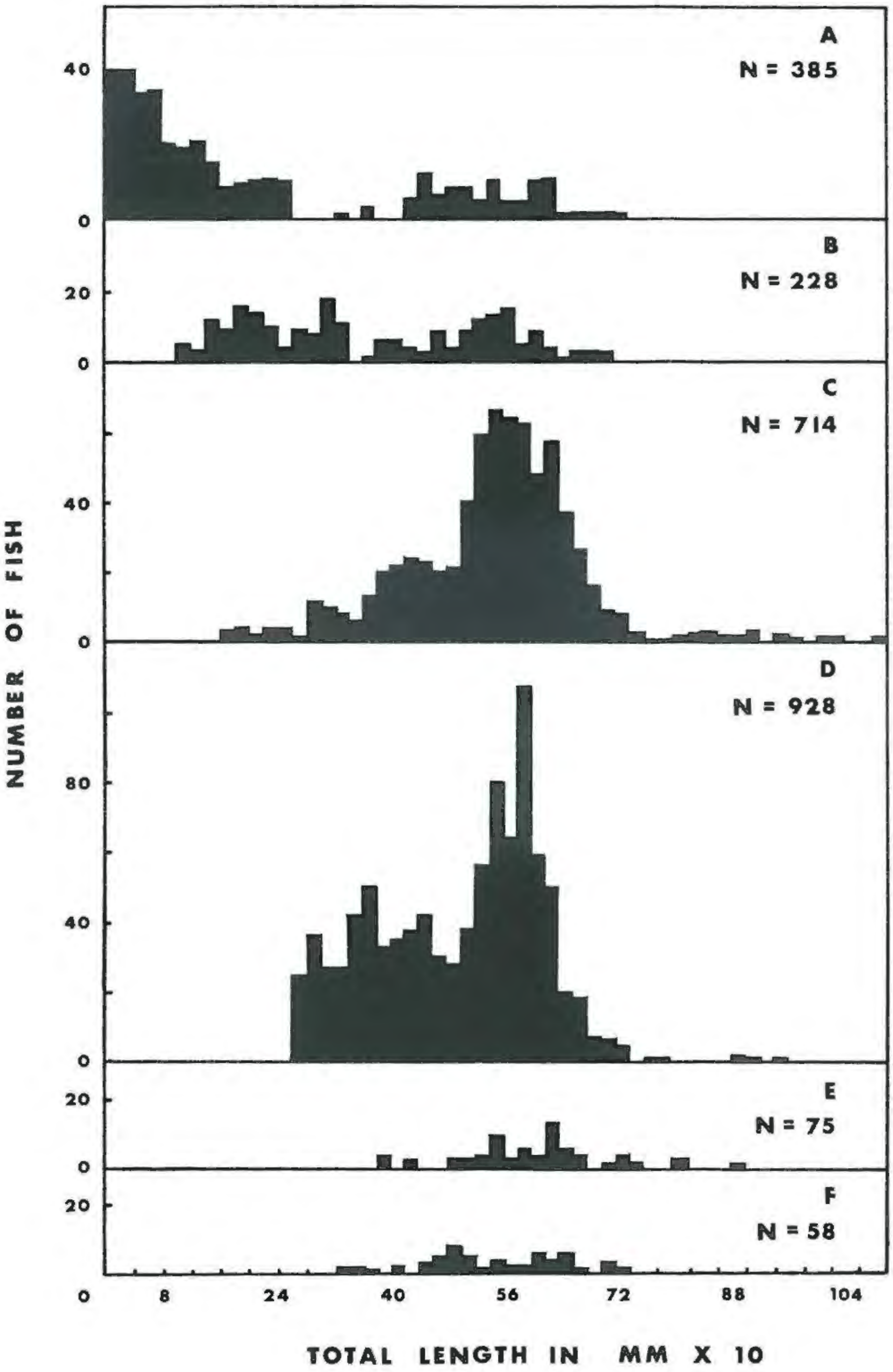


Figure 13: The length frequency of C.gariepinus caught in Lake Sibaya using different gear. A: Handnets and fonya baskets. B: Fishtraps. C: Fixed lines and longlines. D: Gillnets. E: Rod and line. F: Seine and trawl nets.

apparatus allowed tethered catfish to rise to the surface for aerial breathing. The spring was added in an attempt to reduce damage to the catfish's mouth, but this damage was still considerable. Furthermore, fixed lines could only be operated from the lake edge. A longlining method was therefore used which allowed tethered fish to play the line against a floating buoy, and which could be used in all parts of the lake.

Longlines: consisted of a spherical polystyrene float and wire handle supporting an oil-impregnated hardboard reel (Fig. 14). The reel held a length of dacron line, a running sinker, swivel, steel trace and a single hook. 240 longlines were made in 8 different length categories; thirty lines held 5, 10, 15, 20, 25, 30, 35, 40m dacron line each for use in a water depth corresponding approximately to the line length. This arrangement reduced the incidence of unnecessary line tangles. The longlines were attached via the handle and a snap-swivel to loops spaced at 10m intervals along a surface line (Fig. 14). Each surface line was 300m long and held the entire set of longlines for one depth category. Longlines sets were either laid singly, in which case a buoy, anchor line and anchor were placed at each end, or in a continuous line of varying length, with the anchoring arrangement at each end.

Longlines were set from large or small boats by lowering the upwind anchor and then adding the reel units to each loop on the surface line as the boat drifted downwind. At the end of the surface line another anchor was dropped. The lines were baited with fresh tilapia fillets and allowed to drop onto the lake bottom; slack line was then taken in. Longline sets were serviced from a small dinghy (Fig. 15) by running downwind along the surface line and retrieving each longline at its reel. Tethered catfish were played by hand and landed using a hand net. The bait was changed at every inspection.

Longlines were operated most efficiently by using a 'factory ship' and the service dinghy, so that catfish could be measured, weighed and tagged or gutted within minutes of capture. The longlines could also be serviced continually using this arrangement.

Longlines were successful for catching catfish in good condition at all depths and in a variety of habitats. Landing success ranged from 0 to 30% (average 6,7%) for each 30 unit set. They therefore provided a means of determining catfish density and population structure in different water depths and habitats.

Hooked lines attached to a bottom rope, and multi-hooked longlines suspended from the surface were also tried, but they usually became tangled and yielded catfish in poor condition.

Fishtraps: were designed along the lines of African 'umono' baskets. A rectangular frame with an invaginated funnel at one end was covered with mesh,

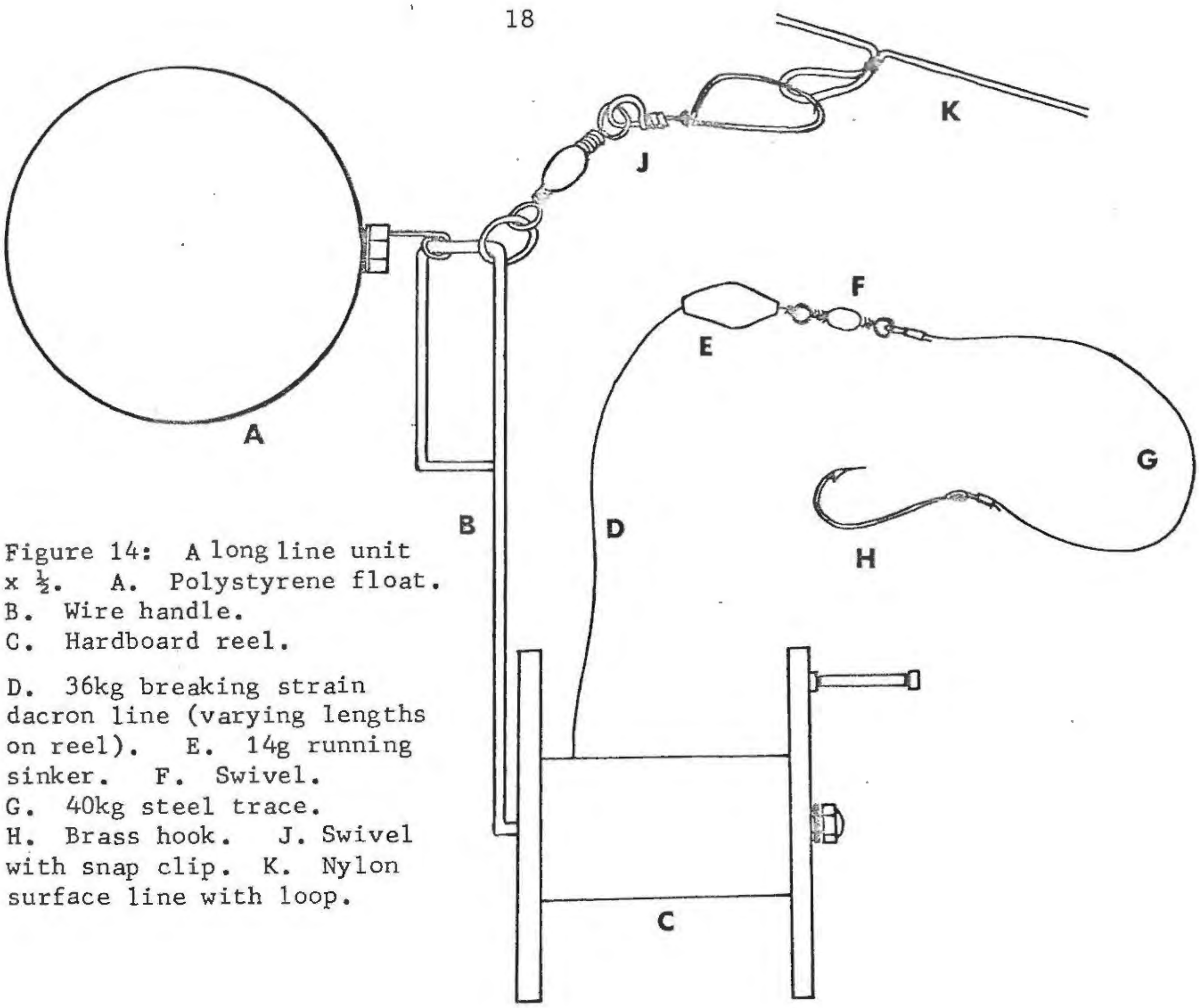


Figure 14: A long line unit x ½. A. Polystyrene float. B. Wire handle. C. Hardboard reel.

D. 36kg breaking strain dacron line (varying lengths on reel). E. 14g running sinker. F. Swivel. G. 40kg steel trace. H. Brass hook. J. Swivel with snap clip. K. Nylon surface line with loop.

Figure 15: The dinghy used for servicing sets of long lines. Two rows of long line floats are visible in the background.

either 1mm nylon gauze or 13mm bar mesh nylon netting. An opening at the opposite end to the funnel was used to remove the catch. The traps were baited with tilapia fillets placed in a gauze bag inside the trap. The volume of the traps varied from 0,2 to 0,5m^3. Fishtraps were laid in shallow water in association with barricades and netting wings. In addition, a standard fyke net with an anterior diameter of 1m was used to catch catfish in streams and channels.

Fonya thrust baskets are open-ended cones made of closely woven sticks (Fig. 16). The basket is thrust over fish in shallow water among dense plants and the catch is removed through a hole in the top. These baskets were the only effective way of catching individual spawning catfish in shallow water.

Rod and line was the most effective method for catching catfish in deep profundal zones and well-vegetated bays.

Seine net: The negatively-buoyant, 13mm bar mesh nylon seine net was laid in an arc on the terrace and slope using an outboard-powered launch. The net was allowed to sink before being pulled in and landed on the shore. The seine net had a total width of 5m and a depth of 4m.

A beam trawl net was designed for high speed trawling along the terrace at night. The frame was constructed of galvanised iron piping and measured 3m across and 1,06m high. Two 0,3m stubs of piping projected backwards to support a taut cable which strengthened the trawl frame. The net consisted of an anterior portion 7,3m long made out of 4 x 60mm bar mesh nylon gillnetting panels, and a cod end 1,6m long consisting of a tapering cone of 13mm bar mesh nylon netting. Two ventral hydroplanes were attached to the frame; these depressed the net during forward movement. The trawl net was pulled behind an 8m catamaran powered by 33 and 25hp outboard engines using twin warps of 7mm diameter nylon rope.

The trawl net was only moderately successful as the boats and engines available were not suitable for low speed, high traction work. In addition, the density of catfish on the terrace was usually too low to warrant regular trawling operations. The trawl nevertheless secured moderate catches of terrace catfish at night when seining was impossible due to the distance from shore and risk of crocodile attack.

Measuring techniques

Total lengths were measured to the nearest millimetre from the snout to the end of the tail which was flapped over to one side and spread out. Weight was measured with water drained from the buccal cavity to the nearest gram on an Ohaus triple beam balance (capacity 20kg).

Figure 16: A fonya thrust basket which was used for catching spawning C.gariepinus in shallow water.

Figure 17: The 7m high tower used for observations on C.gariepinus in shallow water. Photo: C. Bruton.

Tagging techniques

723 catfish were tagged using Floy FD-67 spaghetti anchor tags punched into the tough skin separating the opercular and postorbital dermal shields. Tagged fish were released at the site of capture. Tag retention was good on captive fish, but only twenty-three recaptures were made in the lake, of which three had been free for over a year.

Observation techniques

Self-contained underwater breathing apparatus (SCUBA) and free-diving gear were used for observations on catfish behaviour, distribution and density during the day and night, and for surveys of benthic fauna and flora. The efficiency of collecting gear was also established. An interesting observation was that some catfish caught on longlines continued feeding in an apparently normal way, whereas others rested on the bottom for long periods after the initial fight. Underwater observations were made at 15 different sites, and total diving time was in excess of 90 hours.

A 7m high creosote-pole tower (Fig. 17) was erected in mid-terrace (point A, Fig. 2) to provide a platform for observations on catfish movements and searching behaviour. Several reference points were established on the terrace floor so that catfish searching paths could be mapped. Observations were recorded on a tape recorder and in a note book. Day-time observations were made using binoculars, and night-time observations using a spotlight and (for a brief period) infra-red binoculars.

Other methods are mentioned at appropriate places in the text.

A NOTE ON THE TAXONOMIC STATUS OF *C.GARIEPINUS*

The clariids of Africa and south-east Asia form a series which exhibits an overall decrease in size with an increasingly anguilliform body, and a regression of the suprabranchial organisation and roofing of the skull. Within this regressional series, David (1935) sub-divided the genus *Clarias* into three groups which, in descending order, and using the modified terminology of Daget (1962), are termed *C.Clarias*, *C.Clarioides* and *C.Allabenchelys*. The subgenus *C.Clarias* consists of several large catfish whose approximate distributions are as follows:

C.senegalensis,(Cuvier & Valenciennes, 1840)	West Africa (Niger catchment and surroundings)
C.lazera, Valenciennes, 1840	North-east Africa (Syria, lower Nile, Lakes Tana, Albert, Edward, George, Rudolf).
C.mossambicus, Peters 1852	East Africa (Lakes Victoria, Tanganyika Kyoga, Nabugabo, catchment of Lake Malawi).

C.gariepinus (Burchell, 1822)	Southern Africa (Lake Bangweulu, Zambezi to Orange and Umtamnvuna rivers in the south).
C.capensis, Cuvier & Valenciennes, 1840	Natal.

(Distribution data from Worthington, 1933; Crass, 1960; Jackson, 1961; Thomas, 1966; Greenwood, 1966, 1976; Jubb, 1967; Bailey, 1969). These distributions are by no means clearcut, however, as *C.lazera* has been recorded from the Gold Coast (Irvine, 1947) and the Congo system (Bailey, 1969), *C.mossambicus* from Ethiopia (Worthington, 1933) and *C.capensis* from South West Africa (Gilchrist & Thompson, 1913-1917). Various other large *Clarias* have been synonymised with these four species and need not concern us here.

Worthington (1933, 1940) recognised that *C.lazera*, *C.mossambicus* and *C.gariepinus* (and possibly *C.capensis*) form a closely related cline, and may be separated on the width of the vomerine band of teeth as follows:

	Width of vomerine band of teeth in comparison with pre-maxillary band
C.lazera	1½ X
C.mossambicus	1 to 1½ X
C.gariepinus	1 X
C.capensis	vomerine interrupted

According to Crass (1960), *C.capensis* cannot be separated from *C.gariepinus* in Natal using Boulenger's (1908) and Worthington's (1933, 1940) characters, and he therefore synonymised these two species.

Several recent authors have synonymised *C.gariepinus* and *C.mossambicus* (e.g. Jubb, 1967; Bell-Cross, 1976) whereas others have retained the separate species (e.g. Greenwood, 1966; Bailey, 1969). Jubb (1967 and pers.comm., 1977) examined large collections of *Clarias* from the Zambezi River (the Lower Zambezi river is the type locality of *C.mossambicus*), and from the Klasserie-Olifants-Limpopo river system in the Transvaal (31°E, 24,3°S). He found that these populations showed the full range of premaxillary and vomerine tooth band patterns normally attributed to *C.mossambicus* and *C.gariepinus*, and therefore retained the older name *gariepinus*. Similarly, Crass (1960) found that Natal *Clarias* formed a continuous series from an interrupted vomerine band (=*capensis*) through a narrow band (=*gariepinus*) to a wider band (=*mossambicus*).

This trend has now been confirmed for the population of catfish in Lake Sibaya. A collection of 108 *C.gariepinus* from this southern population had the following vomerine and premaxillary tooth band characteristics:

Width of vomerine band of teeth in comparison with premaxillary band	No.	%
$> 1\frac{1}{2}$	2	1,9
$> 1 \quad < 1\frac{1}{2}$	38	35,2
$> \frac{1}{2} \quad < 1$	46	42,6
$< \frac{1}{2}$	1	0,9
gap in vomerine	21	19,4

The failure of this single character to separate C.gariepinus and C.mossambicus cannot justify synonymy at this stage. A thorough revision of the C.lazera - mossambicus - gariepinus group is required which will identify and compare new and more useful characters, both morphological and biological. In the meantime, the three species are referred to separately in this dissertation, although it becomes increasingly obvious that they have very similar life history characteristics.

Throughout this dissertation I have referred to C.gariepinus as 'catfish'. The common name 'tilapia' is used for cichlids belonging to the genera Tilapia and Sarotherodon.

THE HABITAT PREFERENCES AND RELATIVE DENSITY OF C.GARIEPINUS IN LAKE SIBAYA

The length distribution of catfish in different habitats in Lake Sibaya is given in Fig. 18. Adult catfish spawning in marginal areas have been ignored in this analysis. No catfish were caught in the limnetic zone, although they were seen there in low numbers.

Catfish inhabit marginal habitats until a length of about 200mm. At low lake level these areas include temporary marginal pools and the shores of sheltered bays, but at increasing and high lake levels extensive marginal pools are available. Small juvenile catfish ($<$50mm TL) were extremely difficult to find. They could only be secured by examining minutely plants, flotsam and detritus collected from marginal areas (Fig. 19). Juveniles in the length range 50 to 200mm inhabited dense and sparsely vegetated marginal areas, and occasionally ventured onto the open terrace edge at night. Catfish from 200-400mm TL inhabit the deeper edge of marginal pools and the shallow terrace edge.

Deeper terrace waters, sheltered bays, slopes and profundal areas are inhabited by the bulk of the adult population (350mm TL+, modal length about 560mm TL). Large adult catfish ($>$600mm TL) were more often recorded from deeper profundal habitats. Adult catfish performed diel migrations into shallow water. At low lake levels (deep edge of the terrace $<$1,5m deep) inshore migrations only took place at night whereas at increasing and high lake levels (terrace depth 2 to 3,7m deep) adults regularly ventured onto the terrace during the day as well. Foraging catfish often entered water $<$200mm deep on the terrace edge and in marginal pools during onshore migrations. Catfish from 60 to 220mm TL (and spawning adults) were collected in low numbers in the small streams entering Lake Sibaya.

The relative density of catfish in offshore habitats in Lake Sibaya is given in Table 2.

TABLE 2

The relative density of C.gariepinus (day and night catches combined) in offshore habitats in Lake Sibaya, as deduced from longline catches made during 1974 and 1975 (intermediate lake level; terrace depth $>$2m).

Habitat	Catch per unit effort (one 120 unit set laid for 6 hours)	No. of longline settings (120 unit sets)
Terrace	14,4	33
Sheltered bay	8,3	16
Steep slope	5,1	20
Gradual slope	4,4	14
Profundal	1,3	23

Catches were highest in shallow water habitats, especially on the terrace. As longlines are a passive gear relying on the fish taking a bait, their relatively high density in shallow water must reflect a tendency to feed there more often than in deeper

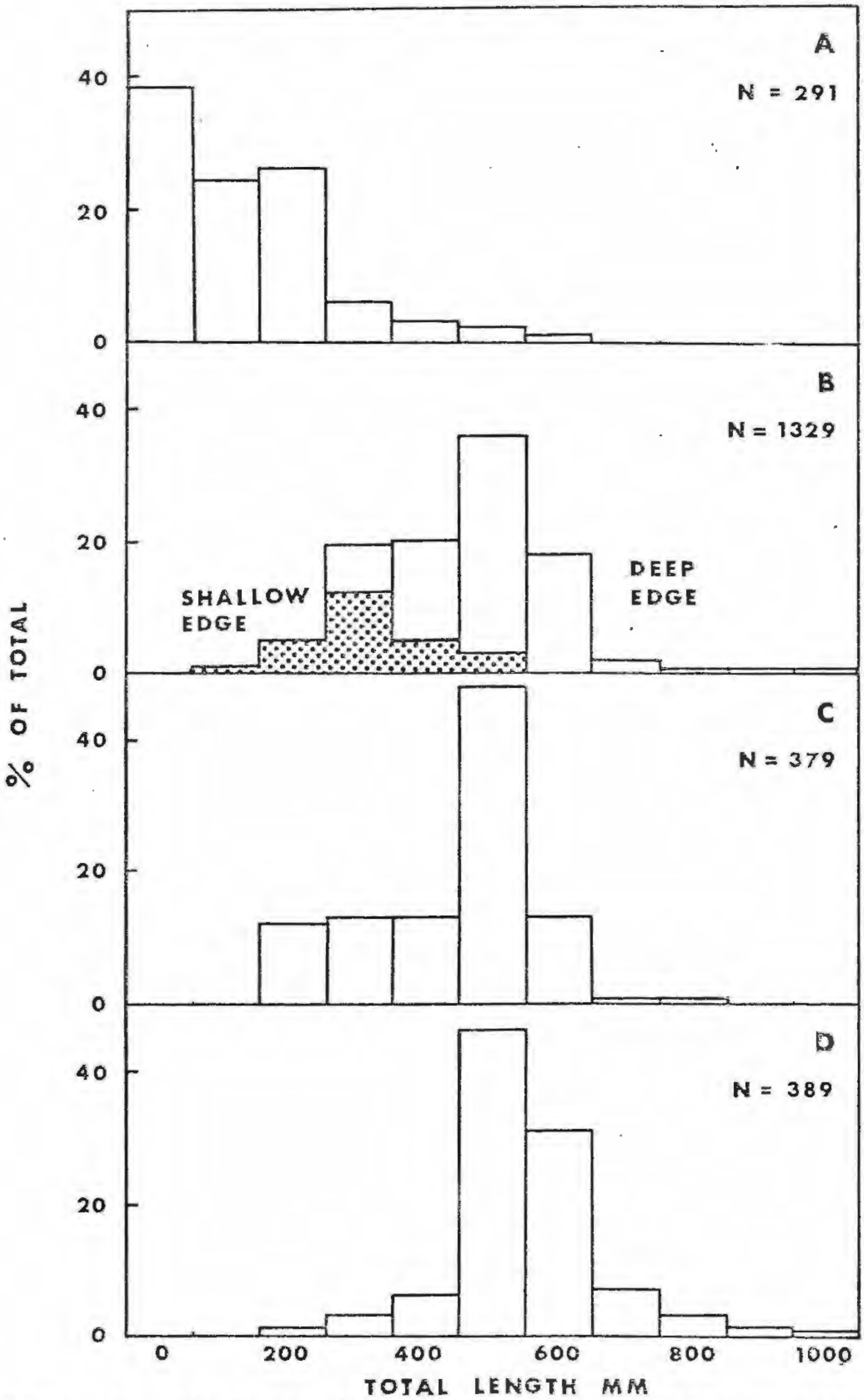


Figure 18: The length distribution of C.gariepinus in different habitats in Lake Sibaya.

A. Marginal; length mode 162mm.

B. Terrace; mode 509mm.

C. Sheltered bay and slopes; mode 499mm.

D. Profundal; mode 603mm.

Elsewhere, catfish are eurytopic and inhabit rivers, rapids, swamps, lakes and impoundments (Crass, 1964; Bell-Cross, 1976; personal observations), where they venture into shallow and deep water. Minshull (1968) caught C.gariepinus to 40m in Lake Sibaya and Gee (1969a) collected C.mossambicus from 78m in Lake Victoria.

Their occupation of shallow water during the day must, in part, be controlled by the presence of fisheagles, Haliaetus vocifer. These large raptors readily feed on catfish (Junor, 1968; Jubb, 1968; Tomkinson, 1975; my own observations) and Tomkinson found that catfish as large as 2,34kg were taken from Nyamithi pan in Ndumu Game Reserve.

Nile crocodiles Crocodylus niloticus prey heavily on C.gariepinus in Lake Sibaya (personal observations) but their effect on catfish distribution is unknown. A sample of 54 catfish heads were collected from shores where crocodiles fed regularly. The head lengths were converted to total lengths to give an idea of prey population structure. The modal length of catfish prey was 520mm, range 230mm to 670mm.

Figure 19: Accumulations of flotsam and detritus which were part of the habitat of small juvenile C.gariepinus ($<$50mm TL) in Lake Sibaya.

REPRODUCTION AND EARLY DEVELOPMENT OF CLARIAS GARIEPINUS IN LAKE SIBAYA

INTRODUCTION

Reproduction is the link in the life cycle of fishes which ensures the continuation of populations and species. For reproduction to be successful, the eggs and sperm must be brought into close approximation for fertilization. This requires accurate synchronisation of gonadal maturation in males and females, the movement of both sexes to a chosen spawning site and their mutual stimulation so that the germ cells are released at the same time.

Seasonal floods and the inundation of areas marginal to rivers and lakes are a common though variable phenomenon throughout the range of Clarias in Africa. Catfish respond to these events by ascending rivers in spate, or migrating to flooded lake shores, and depositing the eggs along the inundated margins. The chosen spawning site provides adequate food, physico-chemical conditions and protection from predators for the developing eggs and larvae.

In this chapter I describe these critical events in the life history of catfish. Catfish are shown to be annual breeders, whose gonads are developed and spent once a year, although they may remain ripe for several months. Their spawning migrations are spectacular and well-documented, but little is known of their complex pre-nuptial and courtship behaviour in Nature, which is reported in detail here for the first time. Although there is a mass gathering for spawning, there is no wasteful release of gonadal products. Fertilization takes place between isolated pairs in amplexus which ensures that the sperm comes in close contact with the eggs. Early development is rapid.

This study of breeding is based almost entirely on field observations, so the factors initiating and influencing breeding could not be examined.

METHODS

Catfish were caught for routine gonad analyses using gillnets and longlines and in shallow water during spawning runs using handnets and African fonya baskets. Monthly samples of at least 20, usually 30, catfish of each sex were collected from April 1973 to December 1976. Catfish were measured, weighed with the water drained from the buccal cavity and sexed (the male has a prominent, more pointed genital papilla). Gonads were removed, dried on absorbent paper and weighed to 0.1g. Gonosomatic indices (GSI) were calculated using the formula

$$\text{GSI} = \frac{\text{Gonad weight x 1000}}{\text{Total fish weight}}$$

Live eggs were measured to 0.1mm using a micrometer eyepiece. Gonadal maturation stages were compiled using the internationally recommended classification (Hjort, 1910). To determine fecundity, ovaries were preserved in 4% formalin until the eggs became hard (over a month), then broken open and the eggs spread out on absorbent paper. Near-dry eggs were dried to a constant weight at 60°C in an oven, and five subsamples of 500 counted, weighed, and the total number of eggs calculated by proportion for each ovary.

Field observations were recorded in a notebook or a tape recorder and then transferred to data ccards.

RESULTS

Structure of breeding population

Gonadal development starts at lengths from 200-250mm in males and females i.e. towards the end of the first year (Fig. 45). The smallest mature female examined measured 202mm TL and the smallest mature male 216mm TL. The size at first maturity was estimated for each sex by examining the gonads of 341 catfish caught in the summers of 1973/74 and 1974/75. Maturity was assumed to have been established when gonads were clearly active. The median size at first maturity (length at which 50% of the catch is mature) was 330mm in females and 340mm in males i.e. maturity was reached towards the end of the second year. The size at first maturity for other Clarias populations is compared in Table 3 . The larger size of Hardap dam catfish at first maturity requires further investigation of growth rates before any comment can be made.

The length frequency of male and female catfish caught during all spawning runs (Fig. 20) is the same as the general population (Fig. 46). However the modal size differed on different spawning runs. Catfish spawning in Mseleni stream and in small parties at Lake Sibaya Research Station were small (Fig. 21B) compared with fishes from one of the large spawning runs on Crocodile point (Fig. 21A).

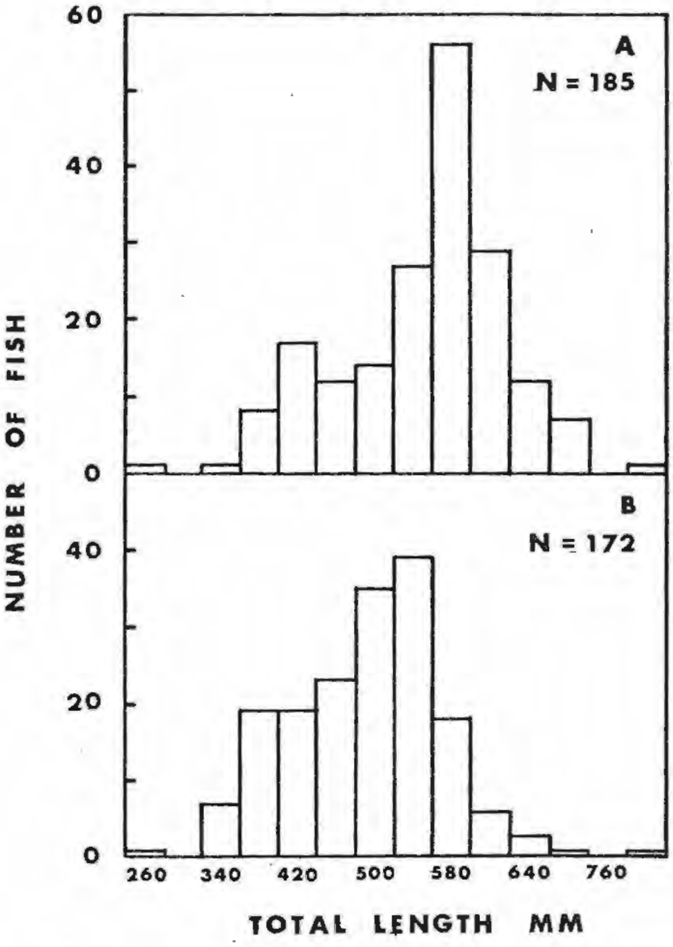


Figure 20: The length frequency of all C.gariepinus caught on spawning runs in Lake Sibaya, 1973-1976.

A. Males; mode 580mm

B. Females; mode 540mm

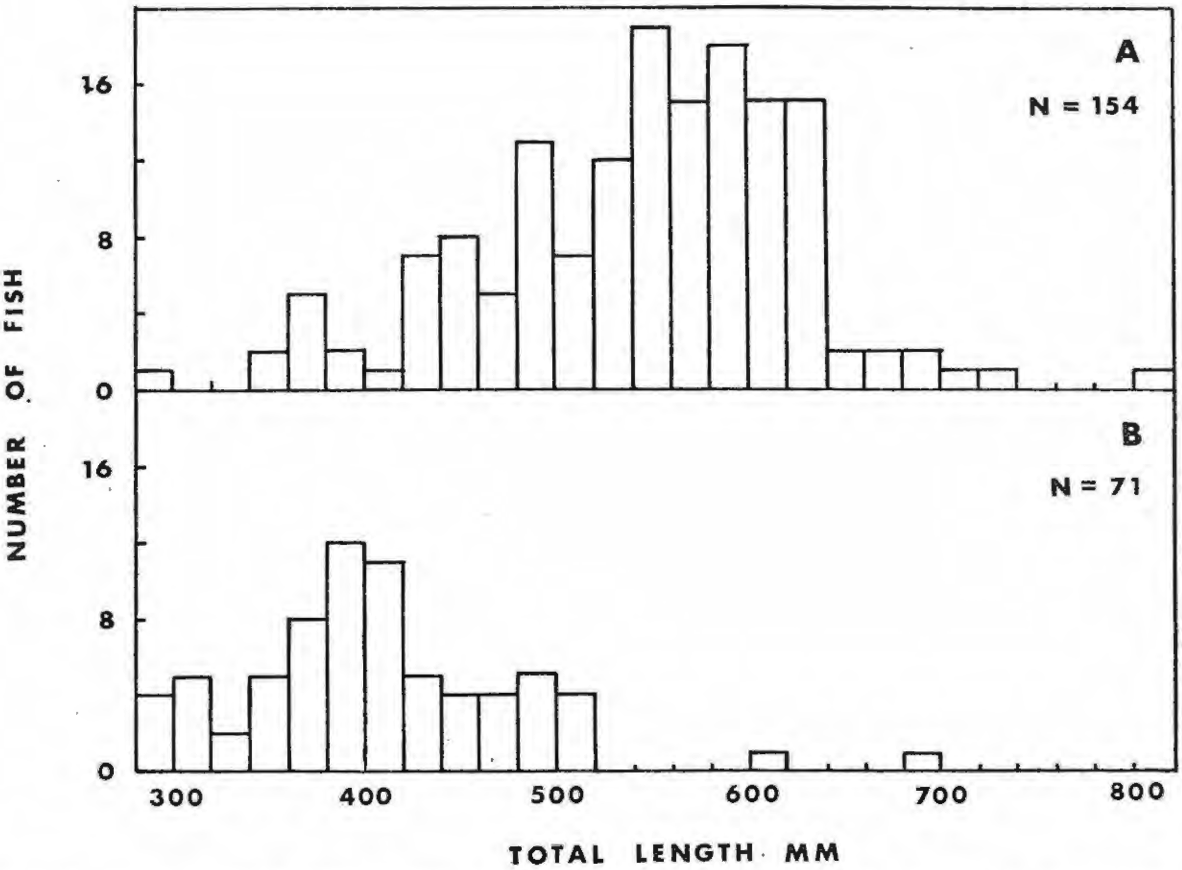


Figure 21: The length frequency of C.gariepinus caught on specific spawning runs.

A. Large group spawning on Crocodile point on 25.11.73; mode 540mm

B. Small group spawning in Mseleni stream on 27.4.75; mode 380mm

TABLE 3

Size at first maturity for different Clarias populations in Africa.

Species	TL(mm)		Place	Reference
	♂	♀		
C.gariepinus	350	350	Lake Sibaya	This paper
C.gariepinus	350-400	350-400	Elands River	Van der Waal (1972)
C.gariepinus	380	380	Rhodesia	Holl (1966)
C.gariepinus	650-750	650-750	Hardap dam	Gaigher (in press)
C.gariepinus	430-450	450-480	Vaal River	Mulder (1971)
C.gariepinus	260	260	Lower Shire River	Willoughby & Tweddle (1976)
C.mossambicus	285	260	Lake Chilwa	Kirk (1972)
C.mossambicus	300-400 (rarely 250-300)	400-440	Lake Victoria	Rinne (1975)
C.mossambicus	250-400	250-400	Lake Kyoga	Greenwood (1966)
C.mossambicus	500	500	Lake Victoria	Greenwood (1966)
C.senegalensis	320	320	Ghana	Thomas (1966)

There is no obvious morphological sexual dimorphism in C.gariepinus and no nuptial dress. All spawning catfish were uniformly black above and white below although the dorsal and anal fins of males are reddish during spawning.

Gonadal maturation

Gonadal maturation stages are given in Table 4, and monthly GSI in Fig. 22. The large ovaries of a ripe female are shown in Fig. 23. In general, gonads are in the resting stage in March, April, May and June, and begin maturing in August. Maturation is achieved by some individuals in October, and the bulk of the population is ripe from September to February, after which spent fishes which are resorbing gonads predominate. Resorbing ovaries form an amorphous red mass and vary in size from deflated near-empty sacs to fully turgid sacs from which the female had apparently shed no eggs. The range of maturation stages in the population is highest before, after and at the beginning of the breeding season, and lowest during the non-breeding season. On average, Sibaya catfish are ripe for 5 months, resting for 2-3 months, and in transitional stages for 4-5 months. In C.gariepinus in Hardap Dam the 'maturity coefficient' peaked from September to February (Gaigher, in press) and in C.batrachus the GSI peaked between June and September (Lehri, 1968).

In northern Zululand rainfall is variable but usually higher from September to March than from April to August. Typically, heavy rains fall in September to October and January to February. Gonadal maturation therefore

TABLE 4

Maturity stages of *Clarias gariepinus* from Lake Sibaya (following the International Maturity Scale modified from Hjort, 1910).

I.	IMMATURE VIRGIN	Minute gonads close under vertebral column. Testes and ovaries transparent, elongate threads, apparently empty bags. GSI ♂ & ♀ : 0.
II.	DEVELOPING VIRGIN	Sexual products have not yet begun to develop. Gonads very small, testes elongate transparent bags, ovaries transparent or translucent red. Eggs invisible to naked eye, but visible at 10X magnification. GSI ♂ : less than 1. ♀ :less than 10.
III.	DEVELOPING	Eggs distinguishable to naked eye as white granules, developing into yellow spheres. Ovaries reddish-brown, becoming oval, testes changing from transparent to pale rose colour. Rapid increase in weight of gonads is in progress. GSI ♂ : 1-2. ♀ : 10-50.
IV.	MATURING	Testes enlarged and white, ovaries enlarged, opaque and orange, eggs large. GSI ♂ 2-3. ♀ 50-70.
V.	MATURITY	Sexual products ripe: gonads have achieved their maximum weight, but the sexual products are not extruded when light pressure is applied. Eggs round, opaque, yellow, present as distinct separate bodies. Ovary wall transparent. Testes swollen, white, sometimes slightly pink, with grey proximal edging. Testes and ovaries usually approximately equal size, but one may be larger than the other by a factor of 2. GSI: ♂ 3 to 5.5 (rarely 6.5) ♀ usually 70+ in fishes smaller than 500g. ♀ Usually $\frac{80}{100}$+ in fishes larger than 500g.

TABLE 4 (contd)

VI.	RIPE	Fishes on spawning run. Ovaries distend body cavity. Sexual products extruded in response to very light pressure on the belly; weight of gonads decreases rapidly from start of spawning to its completion, and gonad sacs collapse. Brief phase with GSI variable.
VII.	SPENT	Sexual products have been discharged, but a few eggs usually remain. Ovaries deflated red sacs; eggs are re-absorbed. Testes deflated, grey-white sacs. Genital apertures inflamed. GSI ♂ : less than 1. ♀ : less than 10. In females which do not spawn, re-absorption begins with the ovary turgid, in which case the ovary wall turns red and a reddish-brown amorphous mass develops inside while the eggs are being re-absorbed.
VIII.	RECOVERING SPENT	Gonads very small, transparent or white sacs close under the vertebral column; eggs invisible to naked eye. GSI: 0-10.

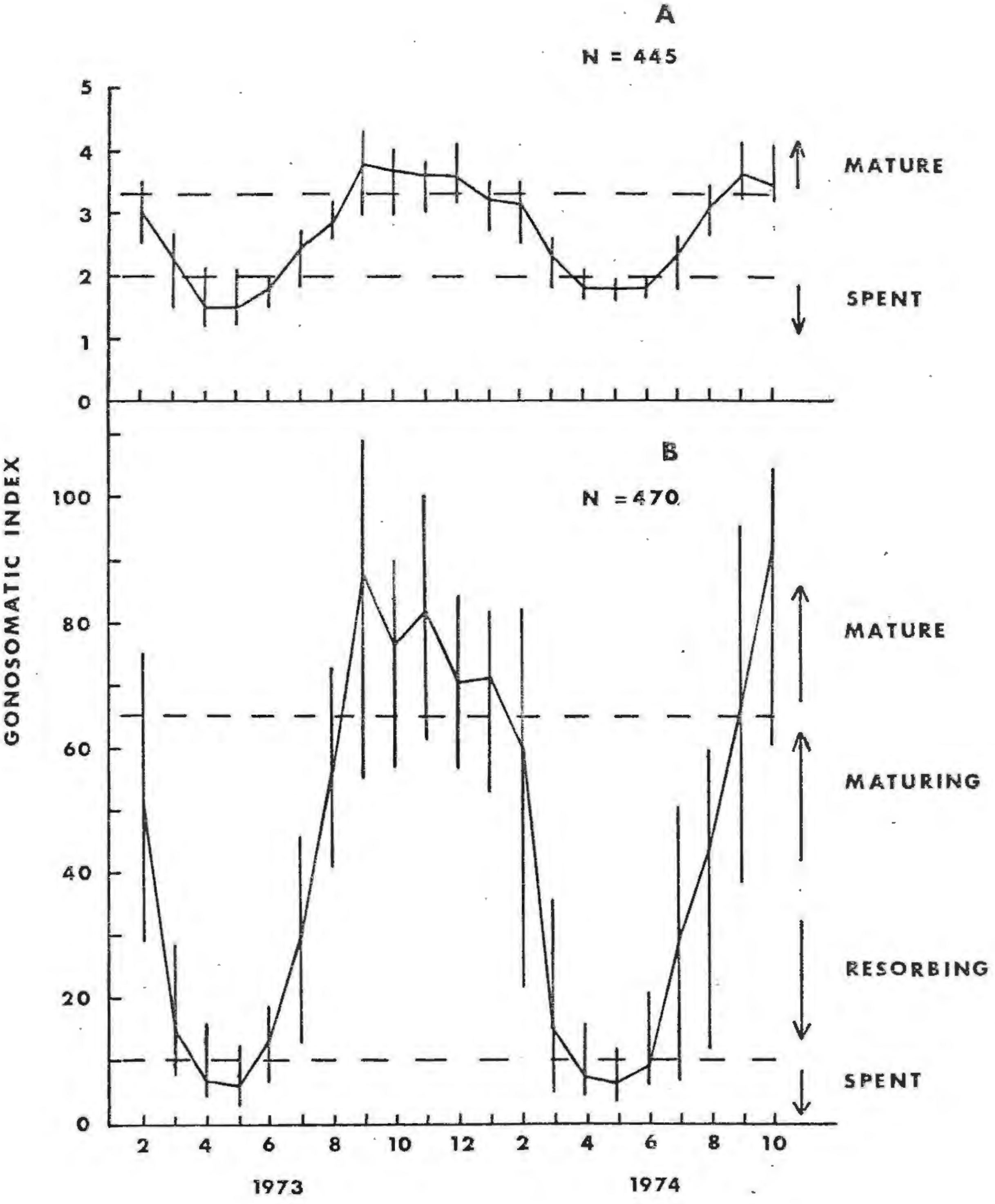


Figure 22: Monthly mean gonosomatic indices and range (vertical bars) for male (A) and female (B) C.gariepinus during 21 consecutive months in Lake Sibaya. Minimum number in each month per sex:20.

Figure 23: The large ripe ovaries of C.gariepinus (maturity stage VI; Table 4).

TABLE 5

Moon phases and rainfall during C.gariepinus spawning runs at Lake Sibaya. (Rainfall measured for the period 08h00 on day of spawning run to 08h00 the following morning at Lake Sibaya Research Station).

Moon phase	No. of spawning runs	Rainfall (mm) on spawning day	
		Mean	Range
New moon within 2 days	9	50,89	0 - 341,4
Last quarter within 2 days	6	1,35	0,1 - 35,3
First quarter within 2 days	4	65,5	3,5 - 145,4
Full moon	1	87,6	-
	20		

starts before the rainy season (Fig. 22) and most fish are ripe during the first rainy spell. Gonadal resorption corresponds with the time of cessation of late summer rains.

Male C.gariepinus have seminal vesicles on the sperm ducts which become turgid during the breeding season. Nawar (1959) has suggested that in C.lazera these vesicles serve to store spermatozoa.

The presence of intestinal fat was determined for 438 catfish for all months from January to December 1974. The highest incidence was in July to September when 54% of the sample had intestinal fat compared with less than 30% in other months. Gaigher (in press) also found that fat accumulation reaches a peak in C.gariepinus just before the gonads reach full development. It is likely that fat reserves provide readily utilizable energy for the rapid production of gonadal material.

Fecundity

Fecundity is defined here as the number of developing eggs in the ovary just prior to spawning ('absolute fecundity' of Bagenal, 1973). The fecundity of 71 ripe female C.gariepinus from Lake Sibaya in the size range 383 to 894mm TL was determined.

The fecundity of C.gariepinus in Lake Sibaya is related exponentially to total length (TL, Fig. 24) and linearly to total weight (W), as is typical in fish (Bagenal, 1973). The lines of best fit for the sample of 71 catfish are described by the expressions

$$y = 0{,}000009\ TL^{3{,}563} \quad (R^2 = 0{,}80)$$

and $$y = 45{,}177\ W + 5786{,}01 \quad (R^2 = 0{,}77)$$

where y = absolute fecundity

There is a wide scatter around the regression line in Fig.24, and the correlation with length (and weight) is not very high as shown by the regression coefficients.

According to these expressions, a 540mm female (the modal length of the breeding population) produces about 50,000 eggs, a 400mm TL female about 16,800 and a 600mm female about 70,000 eggs. The largest Sibaya female actually examined (894mm TL) produced about 163,000 eggs which is less than the projected value from the above expressions.

Similar correlations were obtained for C.gariepinus by Groenewald (1957), Mulder (1971, Vaal River catfish only), van der Waal (1972) and Gaigher (in press). Very large catfish ($<$1200mm TL) in Hardap dam, South West Africa, may produce over 800,000 eggs (Gaigher, in press). Proportionately higher fecundities are reported for C.gariepinus from Leeupan in the Transvaal (Mulder, 1971) and from the Pongola River in Zululand (Pott, 1969). Leeupan catfish in the length range 600 to 930mm TL contained 293,000 to 446,000 eggs.

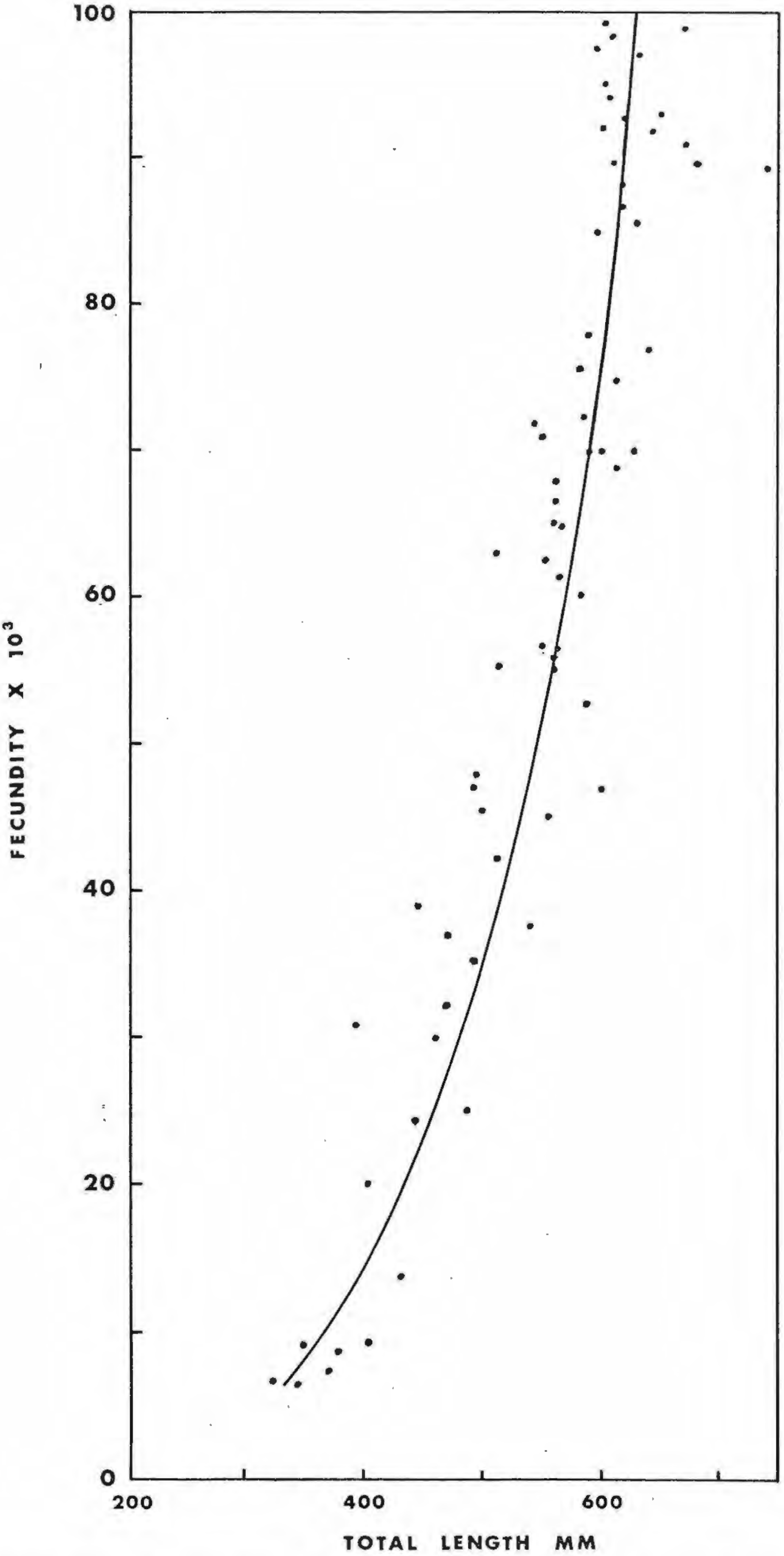


Figure 24: The relationship between absolute fecundity and total length in C.gariepinus from Lake Sibaya.

Estimates of the fecundity of other Clarias species were in the same range as C.gariepinus (10,000 to 125,000, average 38,000, for C.lazera, Nawar and Yoakim, 1962; 5000 to 192,000 for C.mossambicus, Rinne, 1975).

Weather conditions and factors initiating spawning

A summary of moon phases at the time of spawning (Table 5) and the date and brief rainfall history of 22 spawning runs in Lake Sibaya are given in Table 6. Rainfall was highly variable in relation to spawning but was on average higher on the day of, or the day preceding, a spawning run. It is notable that 8 of the 22 spawning runs took place on days during which less than 1mm of rain was recorded, but on six of these occasions heavy rain had fallen during the previous 5 days. Rain or drizzle fell during 13 of the 22 spawning runs. Spawning runs took place most often within 2 or 3 days of new moon or last quarter i.e. on relatively dark nights. On the one night during which spawning occurred at full moon, heavy rain was experienced (87,6mm). The sky was overcast on 20 of the 22 spawning runs during peak activity, and clear on the other two nights. On five occasions, all of which were associated with the first and last moon quarter, the spawning run ended abruptly when the overcast sky cleared and relatively bright conditions prevailed. The selective advantage of spawning on dark nights is obvious - the catfish would be less vulnerable to diurnal or visually-orientating predators, whereas their own breeding activities would not be affected as they apparently rely mainly on tactile and other cues. The black dorsal colouration of spawning catfish would serve as camouflage on dark nights. The lake was calm (wave height less than 100mm) on all except one of the spawning runs, when wave height reached about 300mm but the spawning site was sheltered from direct wave action.

The time lapse between heavy rain and the initiation of spawning in Sibaya catfish (usually 10-34h) was about the same as that reported elsewhere and also similar to the interval between artificial hormonal stimulation and spawning in Clarias (Table 7).

Petrichor (an oil responsible for the characteristic fresh smell after a shower of rain) has been suggested as the substance which acts as a final stimulant for spawning in inshore-migrating fish (Lake, 1967; Pott, 1969; Bowmaker, 1973; van der Waal, 1974). This explanation may hold in Lake Sibaya although it is difficult to imagine how the substance is spread from the edge of marginal pools to the main lake, a distance of over 400m in places, as there are no large inflowing rivers, and circulation in shallow pools is poor. Holl (1966) suggested that a sudden inflow of fresh, colder water may trigger the spawning migration in C.gariepinus. It is likely that no

TABLE 6

Rainfall history and duration of 22 *C.gariepinus* spawning runs in Lake Sibaya

Date	Duration and time of peak activity	Rainfall History						
		-5d	-4d	-3d	-2d	$-1d^{+}$	0*	Total****
14.12.71	1610-1745 (1700)	4.2	1.7	2.8	0	11.8	2.0**	22.5
21-22.11.73	2130-0200 (0030)	0	0	0.05	4.7	7.9	50.6	63.3
21-22.11.73	2130-0200 (0030)	0	0	0.05	4.7	7.9	50.6	63.3
22-23.11.73	2200-0130 (0030)	0	0.05	4.7	7.9	50.6	14.1	77.4
25-26.11.73	2100-1230 (2330)	7.9	50.6	14.1	20.6	0.15	0	93.4
13-14.11.74	Not recorded = ?	5.6	1.4	0.35	10.3	1.6	0	19.3
3-4 .12.74	2230-0230 (0100)	34.1	0.6	0	45.7	0	6.2	86.6
17-18.1.75	2100-0030 (2330)	10.2	0	0	0	30.8	145.4	186.4
18-19.1.75	2130-0130 (2330)	0	0	0	30.8	145.4	8.3	184.5
16-17.2.75	2200-0230 (0130)	19.9	5.5	28.8	45.8	11.6	105.0	216.6
17-18.2.75	2100- ? (0030)	5.5	28.8	45.8	11.6	105.0	3.5	200.2
27-28.2.75	2230-0030 (2330)	4.6	1.6	5.6	0	0	87.6	99.4
1.3.75	2200- ? (2330)	5.6	0	0	87.6	16.5	6.8	116.5
27-28.9.75	? (0030)	0	0	4.7	0.8	95.7	35.3	136.5
3-4.12.75	2130-0130 (2330)	0	0	0	0	0	0***	0
22-23.12.75	1800-2300 (2000)	0.6	3.9	8.1	2.9	73.4	0.1	89.0
22-23.12.75	2300-0200 (0030)	0.6	3.9	8.1	2.9	73.4	0.1	89.0
22-23.12.75	2200-0200 (2330)	0.6	3.9	8.1	2.9	73.4	0.1	89.0
29-30.1.76	2330-0200 (0030)	0	0	1.6	37.6	30.5	341.4	411.1
31.1.76- 1.2.76	0005-0200 (0100)	37.6	30.5	341.4	4.0	0	1.0	414.5
1-2.2.76	2330-0045 (0100)	30.5	341.4	4.0	0	1.0	0	376.9
25-26.2.76	2200-0400 (0230)	0	0	0	0	54.2	0	54.2
$\bar{x}$	1610-0400	7.6	21.5	21.8	14.6	36.0	39.0	140.4
Range	(1700-0230)	0-37.6	0-341.4	0-341.4	0-87.6	0-145.4	0-341.4	0-414.5

* from 08h00 on first date of spawning run to 08h00 the following morning

\+ d = one day

** 117mm rain on -11d

*** 21.7mm rain on -7d

**** Total rainfall from -5d to day of spawning run ('0')

TABLE 7

Time interval between heavy rains, or artificial hormonal stimulation, and spawning in Clarias.

Species	Time interval	Place	Reference
Natural stimulation:			
C.gariepinus	usually 10-34h	Lake Sibaya	This study
C.gariepinus	about 8h	Rhodesia	Holl (1966, 1968)
C.gariepinus	18-36h	Transvaal	van der Waal (1972)
C.gariepinus	12h	Lake Kariba	Bowmaker (1973)
C.mossambicus	18h	Lake Victoria	Greenwood (1955)
Artificial hormonal stimulation			
C.gariepinus	12-32h	Laboratory	van der Waal (1972)
C.macrocephalus	15h	Laboratory	Tonsanga *et al* (1963)

single physical or chemical factor could be isolated as stimulating the migration of fish, as migration is probably an inherent tendency reinforced by a combination of physical and chemical factors (Welcomme, 1969). Changes in water level, chemistry, temperature, clarity, flow velocity, and associated biological factors such as the appearance of flooded marginal plants, may all be important, but a final conclusion must await experimental analyses.

Date and time of spawning runs

The date and duration of all spawning runs observed are given in Table 6. The main spawning season extended from November to February (120 days) although single observations were made in September and March (Table 6). On each occasion on which a spawning run was recorded, the possibility of concurrent runs in the main basin was investigated by boat on the same night, or by questioning local inhabitants, who readily seek and club spawning catfish, the following morning. The only occasions when more than one spawning run was recorded on one night were on 22-23.12.75, when runs occurred in three places, and on 21.11.73 when runs occurred simultaneously at two sites on the western shore of the main basin (Table 6 and Fig. 25). However as the full lake shore (144km) could not be surveyed, other runs may have occurred in the various basins and arms on any night. Spawning runs occurred on consecutive nights (but in different places) on five occasions (Table 6). The shores of the main basin were inspected at night on eleven occasions from

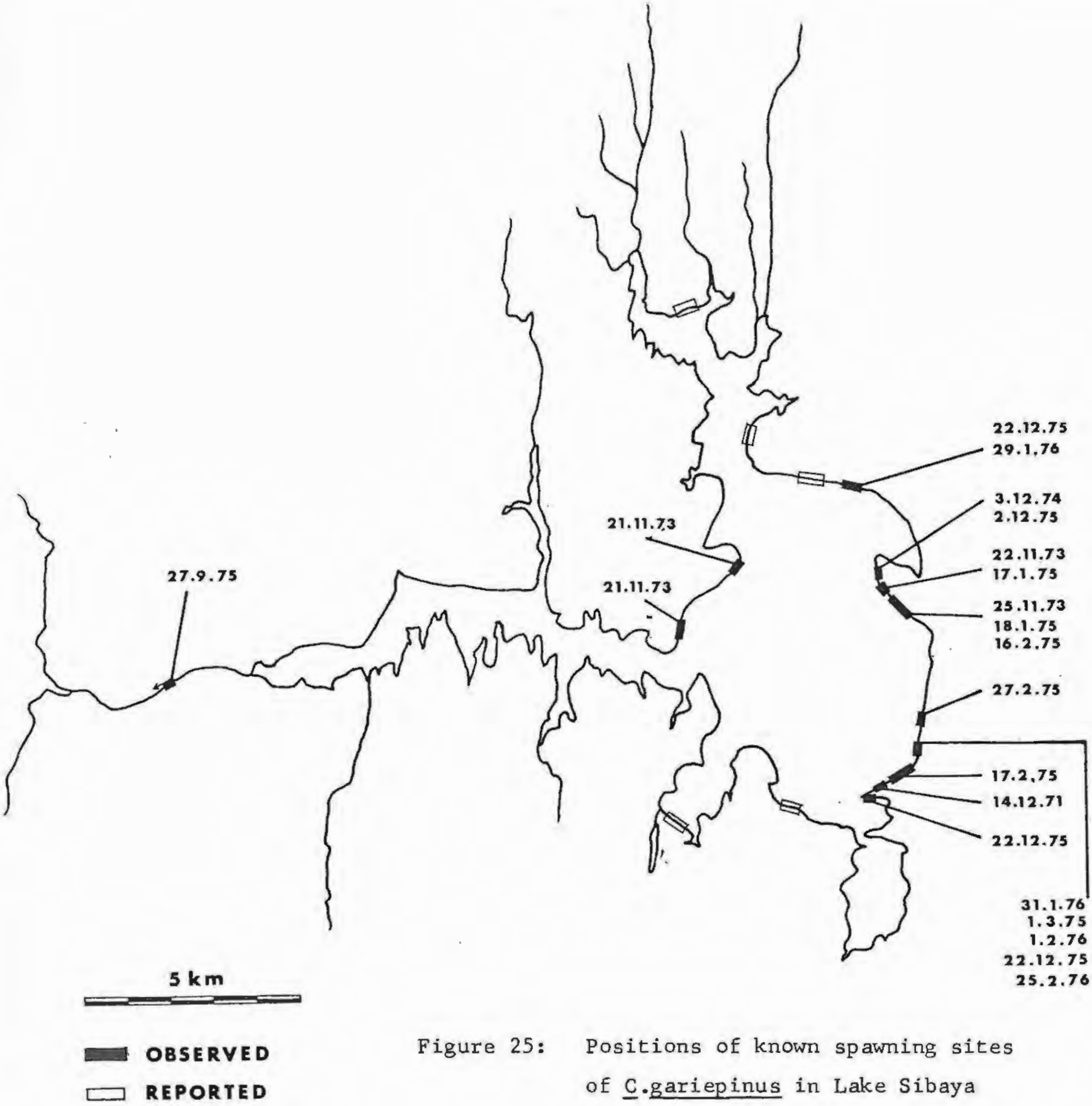


Figure 25: Positions of known spawning sites of C.gariepinus in Lake Sibaya (1973-1976).

October 1974 to February 1975 after moderate rain (>10mm), and on 8 occasions after light rain, but no runs additional to those recorded in Table 6 were found.

Twenty-one of the 22 spawning runs observed occurred at night with peak activity between 20h00 and 02h30 (Table 6) although preparatory behaviour started during the afternoon. One run took place during the afternoon (between 19h10 and 17h45, 14.12.71). During night runs spawning activity occurred as early as 18h00 and as late as 04h00 the following morning. Occasional spent fish remained in the shallows until 11h30.

All the southern African *Clarias* so far studied had southern-summer breeding seasons which coincided with high rainfall periods, with peak activity at night (Table 8). In Lake Victoria, which is situated on the equator, 'ripe' or 'ripe-running' *C.mossambicus* were caught almost throughout the year by Rinne (1975). The only months in which ripe catfish were not recorded were April, September and October, but Rinne's samples were inadequate in these months. *Clarias* populations north of the equator spawned earlier (*C.batrachus*) or later (*C.senegalensis*) than the southern populations, always in the rainy season.

TABLE 8

Breeding seasons and peak breeding times of different *Clarias* populations

Southern populations	Breeding season	Time of peak breeding activity	Place	Reference
C.gariepinus	November-February(rarely September-April)	1700-0230	Lake Sibaya	This study
C.gariepinus	October-February(rarely May)	1900-2200&0500-1100	Ponds in Transvaal	van der Waal (1972)
C.gariepinus	November-February	At night-1100	Savory dam, Rhodesia	Holl (1966, 1968)
C.gariepinus	November-March	-	Hardap dam, South West Africa	Gaigher(in press)
C.gariepinus	September-March	-	Lower Shire River, Malawi	Willoughby & Tweddle(1976)
C.mossambicus	December-March	-	Lake Victoria	Rinne(1975)
Northern populations				
C.batrachus	August-December	-	-	Lehri(1968)
C.batrachus	May-October	-	Thailand	Sidthimunka *et al* (1966)
C.senegalensis	March-April	-	Ghana	Thomas(1966)

Locality and description of spawning sites

Known spawning sites, as well as several sites reliably reported by local fishermen, are indicated in Fig. 25. Most sites were on exposed gently sloping shores. A migrating group of spawning catfish were also collected in Mseleni stream at the end of the western arm.

The nature of the spawning sites differed at different lake levels. On 14 December 1971, when extensive sandy beaches were exposed at low lake levels, a shallow ($<$ 300mm) sandy pool was used. The only plants present were less than 20 Phragmites mauritianus. To reach the pool, the catfish negotiated a narrow channel only 60mm deep. They were very vulnerable to predation by fisheagles Haliaetus vocifer and man as the spawning run took place before dusk, between 16h00 and 17h45. Large numbers of mouthbrooding Sarotherodon mossambicus were also present in the pool.

At intermediate lake levels spawning sites were typically protected by a curtain of P.mauritianus and Typha latifolia, and spawning occurred either on the lake shore amongst Juncus kraussii and Panicum meyerianum or in adjacent marginal pools ($<$ 400mm deep) densely-vegetated with grass Andropogon amplectens, rush J.kraussii and sedge Cyperus spp.

At high lake levels when extensive areas of grassland were flooded, spawning occurred on the lake edge amongst Vernonia oligocephala, Bulbostylus polystachus and Harpochloa falx. On four occasions at high lake level in 1975 and 1976 catfish spawned exclusively on a flooded lawn in the grounds of Lake Sibaya Research Station. Adjacent areas (5km on either side) had no spawning catfish on these occasions.

Catfish showed a definite preference for marginal and emergent aquatic, semi-aquatic or terrestrial plants for spawning, and were never seen to use submerged aquatics such as Myriophyllum spicatum, Potamogeton pectinatus, P.schweinfurthii or Ceratophyllum demersum, or submerged rocks and twigs.

Most, but not all, spawning sites included several square metres of grassland which had been inundated in the past 60 hours. Intensive spawning activity occurred in well-defined areas even if the adjacent topography was similar. Spawning sites varied in shore length from 30m (in the marginal pool on 14.12.71) to about 200m (on south-east shore of main basin on 17-18.2.75) but most measured between 60 and 120m long.

Spawning always took place in water less than 400mm deep on the edge of the lake or marginal pool. A typical spawning site is illustrated in Fig. 7.

Spawning congregations and migrations

In Lake Kariba, C.gariepinus accumulated in large numbers in one to two metres water depth at the mouth of the Sinamwenda river about six weeks before the first floods (Bowmaker 1970). The catfish ascended the river en masse immediately after the first flood waters reached the river-mouth. In Hardap dam, South West Africa, C.gariepinus congregated in the upper reaches of the dam several weeks prior to potamodromesis (Gaigher, in press). Van der Waal (1972) reports massive aggregations and migrations of C.gariepinus after the first heavy rains of summer in Roodeplaat and Hartebeespoort dams in the Transvaal, and smaller spawning and distributional migrations later in the season. Massive spawning runs after the first floods were also reported by Holl (1968) and Meyer (1974) in C.gariepinus, Whitehead (1959) and Spinage (1971) in C.mossambicus and Thomas (1966) in C.senegalensis. However Bell-Cross (1974) notes that breeding in C.gariepinus in the Zambezi commences in the middle of the rains. Repeated surveys using a 'Seascribe' recording echosounder, a trawl net, gillnets and diving gear revealed no unusual offshore concentrations of catfish prior to or immediately after the first rains in Lake Sibaya. Concentrations of catfish did however occur in shallow water a few hours before each spawning run. The normal density of catfish in terrace waters in the afternoon in Lake Sibaya is about one per 125m of shoreline (range 0-20 catfish). Immediately after rain, (at the site of a spawning run) the number increases to 10-20 catfish per 125m (range 0-30) and immediately before spawning to 30-60 catfish per 125m (range 20 to over 300). Rough estimates of the number of catfish on one spawning run varied from about 50 (on 2.2.76) to over 800 (2-3.12.75).

Spawning behaviour

Courtship and mating of C.gariepinus were described briefly by Holl (1966, 1968), Miller (1969) and van der Waal (1974) in the field, and in detail by van der Waal (1974) in aquaria. The only previous mention of pre-nuptial fighting is in an unpublished field note by Miller (1969): 'the fish appeared to be fighting and chasing each other just below the surface...There was almost continual movement...the one fish pursuing another and attempting to ram it in the side with the head. They did not appear to try to bite each other'.

The spawning behaviour of C.gariepinus in Lake Sibaya may be divided into four phases: aggregation, pre-nuptial aggression, courtship and mating. In riverine populations, a migratory phase may follow aggregation. In Lake Sibaya, aggregation and pre-nuptial aggression occur on the terrace, usually more than 2m from shore, whereas courtship and mating take place close inshore and in marginal pools.

Aggregation: Catfish aggregate towards dusk in loose, haphazardly swimming groups in water 1-3m deep. Some individuals lie motionless among submerged macrophytes or concealed on layers of detritus. After dark the level of activity increases, and low intensity aggressive encounters are performed, as well as loud mouth-smacking and tail-slapping at the water surface.

Aggregations before a spawning run may in part be epidiectic displays allowing catfish to 'view the field' before proceeding to pre-nuptial combat (_sensu_ Wynne-Edwards, 1962). Interestingly, small adults (300-450mm TL) rarely participated in massive spawning runs in Sibaya, or, if present, played little part in agonistic and courting behaviour. However, they formed the bulk of the groups on small spawning runs (Fig. 21).

Spawning behaviour during the afternoon run on 14.12.71 was different. The catfish formed a dense shoal which swam rapidly across the terrace and back and forth along the shore. When the shoal encountered the inlet to a marginal pool, the catfish swarmed into the pool. Spawning was completed rapidly and the catfish dispersed back into the lake as individuals. Shoaling behaviour by catfish on this spawning run may have been brought about by their vulnerable situation in shallow water during the day. Interestingly, mouth brooding _Sarotherodon mossambicus_ shoaled under the same circumstances in Lake Sibaya just prior to releasing their fry (Bruton & Boltt, 1975).

Prenuptial aggression

Catfish performed several types of intraspecific aggressive actions after aggregating but before commencing courtship. These actions were observed on 22 spawning runs in clear shallow terrace waters by moonlight and using torches. Initially, aggressive actions consisted of low intensity ritualised displays, but as group activity increased, aggression took the form of high intensity displays which sometimes lead to fighting. In all cases, the aggressive actions were performed rapidly and graded almost imperceptibly into one another. They lacked the distinctness of the well-known agonistic displays of three-spined stickleback _Gasterosteus aculeatus_ (Wooton, 1972), Mozambique tilapia _Sarotherodon mossambicus_ (Neil, 1966), bicolor damselfish _Eupomacentrus partitus_ (Payne, 1976) and other fishes. Catfish participating in pre-nuptial aggression could not be sexed, but the indications were that the aggressive displays, at least the high intensity ones, were performed exclusively by males (see below). The normal sequence of aggressive actions is shown in Fig. 26.

Five types of low intensity displays were identified (Fig. 27):

(a) Approach: One catfish approaches another from the front with the median fins erect, and then turns away at the last moment.

(b) Tail-slap: sometimes in turning away or swimming past another catfish, the aggressor slaps the attacked fish on the head, body or tail with its tail.

(c) Lateral displays: catfish swim slowly past one another with their median fins erect and paired fins extended. This action often leads to circling.

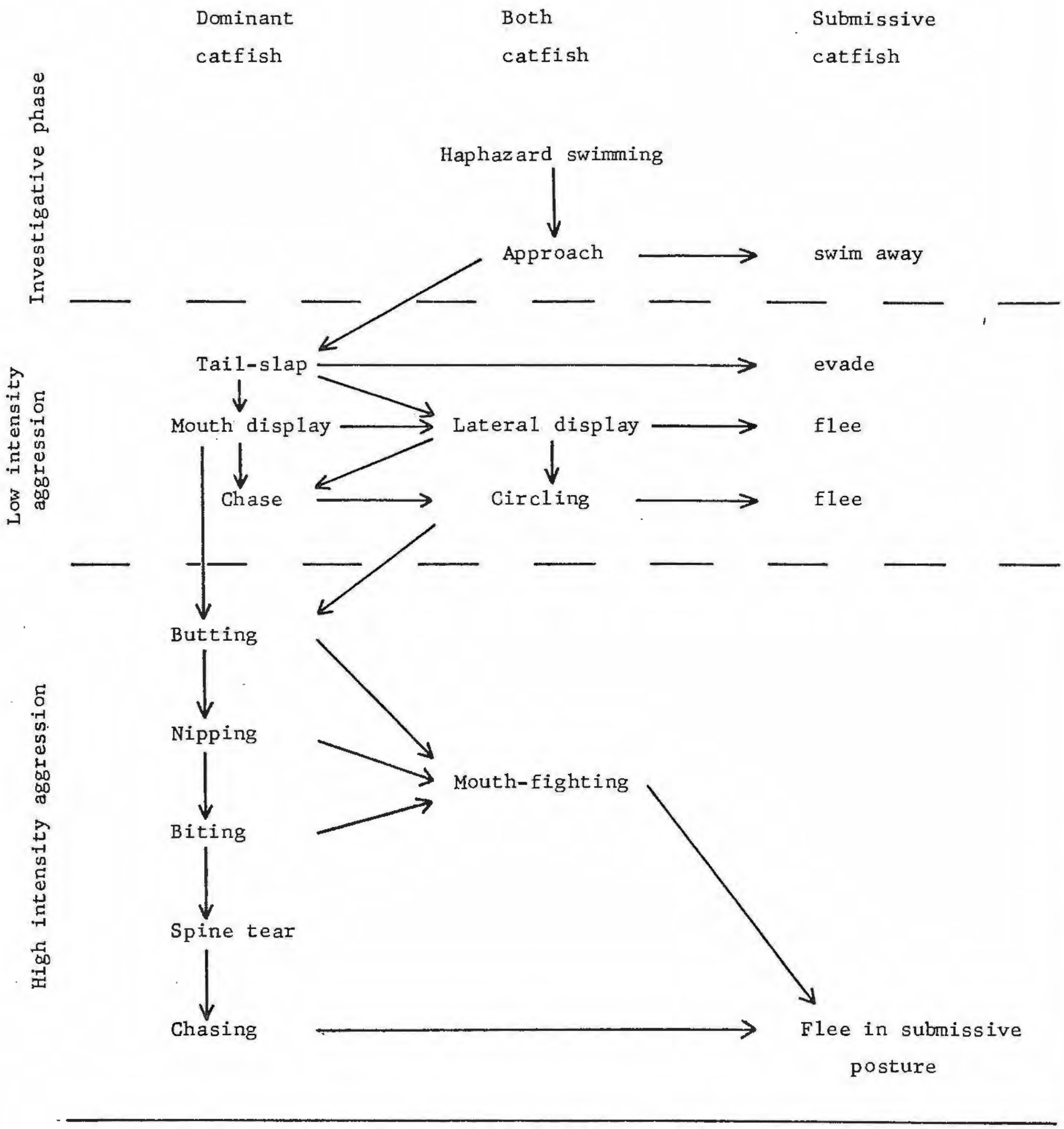


Fig. 26 : A schematic sequence of behavioural events during prenuptial aggression in C.gariepinus. The actions are probably only performed by males.

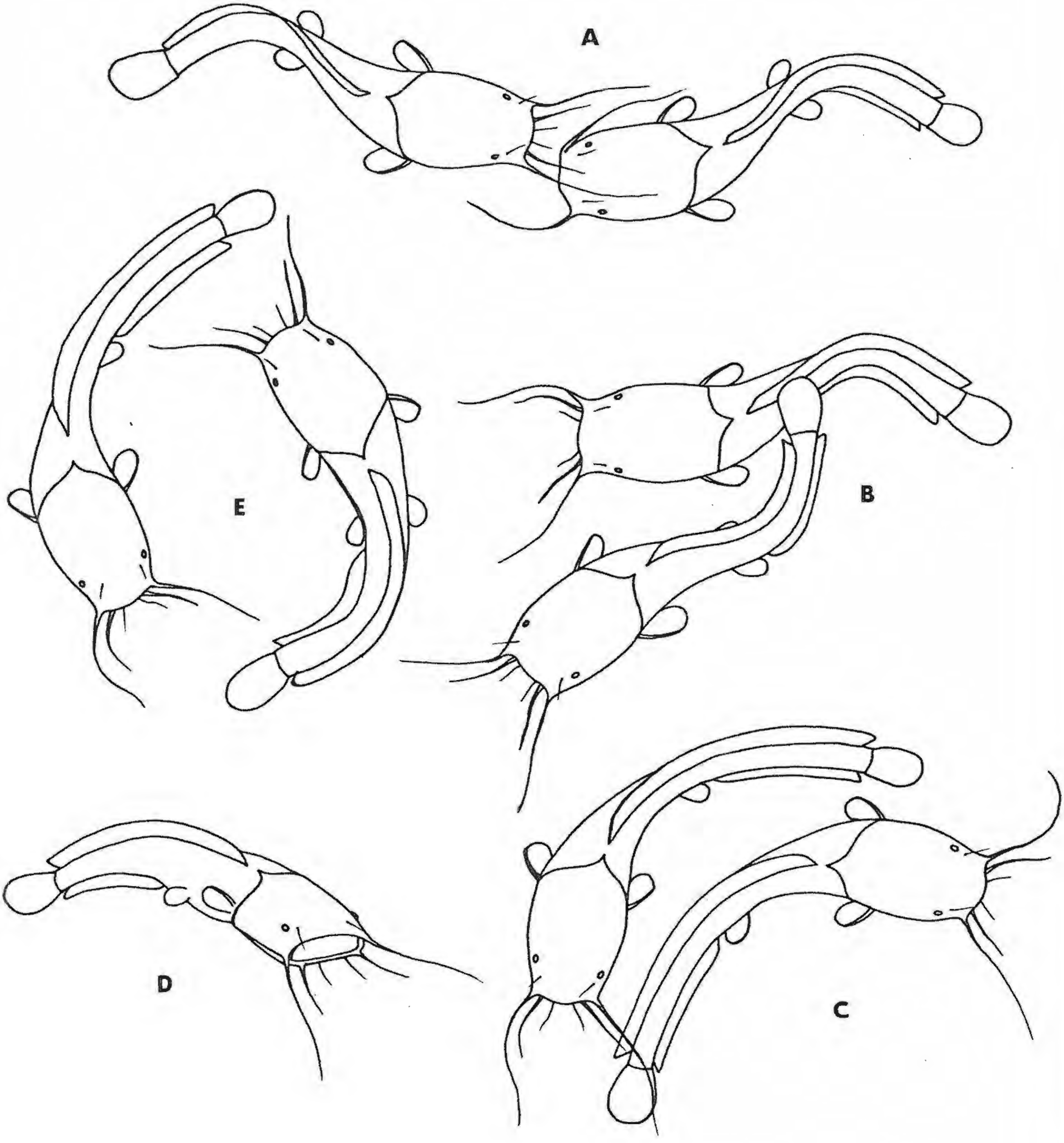


Figure 27: Low intensity pre-nuptial aggressive behaviour of *C.gariepinus*.
A: Approach; B: Tail-slap; C: Broadside display;
D: Mouth display E: Circling.

(d) Circling: two catfish circle one another, usually near the water surface. Circling may be rapid or slow.

(e) Mouth display: during some 'approaches', the aggressor opens its mouth wide, revealing a flash of white buccal skin. Intensive mouth displays take the form of a 'snarl' with the lips pulled back to reveal the mandibular and maxillary teeth bands.

High intensity displays involved direct ritualised attacks on other catfish, and in contrast to low intensity displays, body contact is common. The mouth and pectoral spines are used and injuries may be inflicted if the encounter continues for more than a few seconds. The barbels are extended forwards and the fins are erected by an aggressor, whereas an escaping submissive fish trails the barbels under the head and lowers all fins. High intensity displays constituted less than 10% of all displays observed. Six types were observed (Fig. 28).

(f) Butting: the aggressor butts another with the leading edge of the head, usually near the urogenital opening, but occasionally on the head and abdomen. The chased catfish may turn around and butt and tail-slap the aggressor, and both may circle briefly before swimming apart. The skin on the mouths of butting catfish becomes tattered.

(g) Nipping: during intensive butting, a catfish may cause slight damage with its teeth by tearing another catfish's skin.

(h) Mouth fighting: Butting catfish may approach one another from the front, briefly lock their jaws and push to and fro.

(i) Biting: Butting, in extreme cases of aggression, leads to biting in which a catfish approaches another from the side or rear and suddenly presses its open mouth against the other's skin and scrapes off a rough rectangle of skin. The wounds measure about 20x40mm (Fig. 29). The mandibular and maxillary teeth bands, which consist of many small, re-curved teeth, are used for biting. Catfish have also been seen to remove flesh by biting carcasses of other catfish, crocodiles and hippopotamus. No female catfish had bite marks whereas 52.6% of all males examined (n = 76) on spawning runs showed bite marks on the tail and abdomen. The median and paired fins of the males were also far more damaged than in females. Biting can thus be considered the pursuit of males.

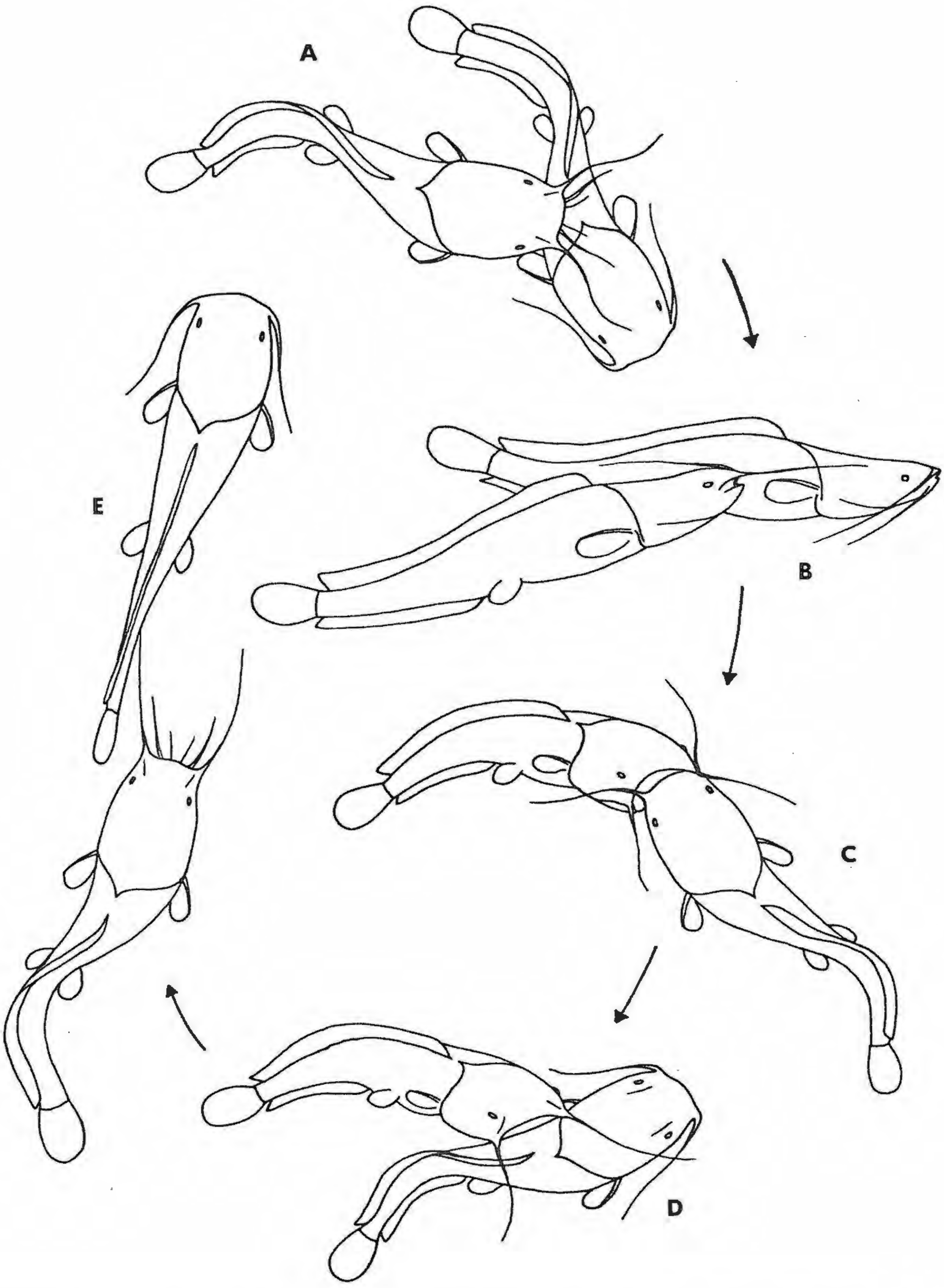


Figure 28: High intensity pre-nuptial aggressive behaviour of <u>C.gariepinus</u>.

A. Butting B. Nipping

C. Mouth-fighting D. Biting

E. Chasing

Figure 29: An extreme example of injuries caused by biting C.gariepinus.

Figure 30: A catfish injured as a result of pectoral spine tears by other C.gariepinus on a spawning run. Photo: A. Bruton.

(j) Spine tear: on rare occasions catfish wounded opponents by thrashing the locked serrated pectoral spine, thus causing skin tears and profuse bleeding (Fig.30). Twelve catfish collected with spine tears were all males.

(k) Chasing: Fights end when one catfish in an aggressive posture (barbels extended forwards, mouth open, fins erect) chases the other away. Chasing can also occur as a low intensity activity involving 2 to 5 catfish.

Mouthing, lateral displays, butting, biting and chasing are common aggressive activities in fish and occur in similar forms in Ictalurus natalis (Todd, 1971) and piranhas Serrasalmus spp. (Markl, 1972). Use of pectoral spines during intra-specific aggression may be less common, although 'spine fighting' is part of agonistic behaviour in the three-spined stickleback Gasterosteus aculeatus (Wootton, 1972).

During combat, catfish occasionally leapt out of the water, or engaged in frenzied circular swimming at the water surface. In addition, noise was created by slapping the water surface with the tail, releasing bubbles of air, or taking in air at the surface with a loud smack and then slapping the head onto the water surface. This ritualised aerial breathing behaviour was also observed in Sibaya catfish during pack-hunting and surface feeding. Mouth- and tail-slapping prior to spawning could be heard up to 300m away across the water on calm nights.

Aggressive interactions in the inshore zone usually reached a peak between 21h00 and 23h00.

Courtship (Fig. 31).

One of the primary ways of regulating population numbers (and ensuring sexual selection) is to control the number of matings, and the way this is done is to make mating conditional upon successful courtship (Wynne-Edwards, 1962). Males fight to establish which fish have the status to proceed with courtship. After a skirmish, the victor in a particular fight approaches a female and butts her lightly on the body. If the female is not receptive, it swims away or does not move. Receptive females swim towards the lake shore, followed by the male, and enter an area of inundated grassland or sedges. The following catfish in the pair (usually male) swims with the barbels extended forwards whereas the leader (female) has its barbels trailing under the head (Fig. 32). On their way to the shore, the pair may be attacked by one or more other catfish, at which the male raises his median fins and makes aggressive approaches towards the intruders (usually mouth displays, butts and nips) in an apparent attempt to chase them away.

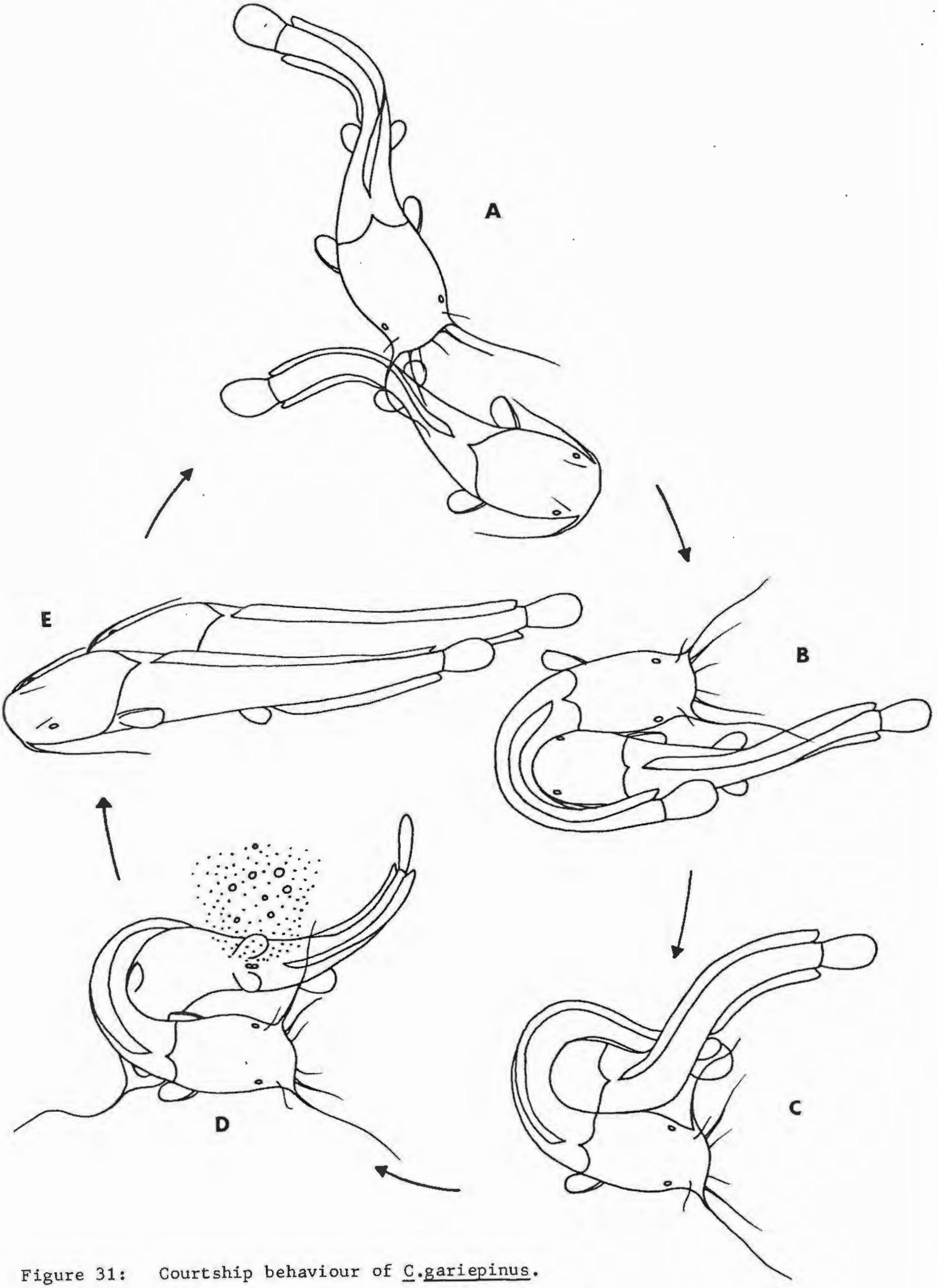


Figure 31: Courtship behaviour of C.*gariepinus*.

A. Following B. Amplexus

C. Sperm release D. Egg release

E. Resting

Figure 32: Male C.gariepinus following a female during courtship in very shallow water in Lake Sibaya. The large size difference in this case is exceptional. Photo: A. Bruton.

Figure 33: Male (curved) and female C.gariepinus in amplexus in very shallow water on a spawning run on 22.12.75. Photo: A. Bruton.

The pair wind their way through inshore vegetation for one to two minutes and may negotiate sandy spits in less than 50mm of water, using the pectoral spines as levers to 'walk' (see Johnels, 1957). Eventually the female stops or is induced to stop by light butts by the following male on her abdomen, head and tail, in water 50-300mm deep. Towards the end of following, both the male and female begin to quiver. Once they have stopped, the female butts the male near the urogenital opening and the male butts the female along the abdomen and around the head, and then adopts a U-shaped position around the female's head with the dorsal fin directed towards the female. After a few shuffling movements accompanied by continued quivering, the pair suddenly become motionless.

Mating (Figs 33, 34 and 35).

The mating posture, a form of loose amplexus, is usually held for 17-18 seconds (42 timings by stopwatch, range 15-20 secs), after which the male suddenly stiffens and arches his body (Figs 31 and 34). This action probably accompanies the release of sperm (which are invisible to the naked eye in the field). The male then moves posteriorly over the female's body, still in the U-shape, while pronounced tensioning of muscles behind the cephalic shield occurs in the female. Within one to two seconds, the female suddenly stiffens, arches her back sharply to one side in a violent movement and shovels her head under the male's body and into the substrate (Figs 31 and 35). A large cloud of eggs and gas bubbles is released from the cloaca of the female, and air also escapes from her buccal chamber through the gills. Within about two seconds of egg release the female swishes her tail vigorously from side to side, using her burrowed snout as an anchor to prevent forward movement,and thus mixes and distributes the sperm and eggs. The male lies to one side. That a pheromone may be released during mating is suggested by observations of catfish swishing their tails vigorously when swimming past an egg deposition site after the original pair have left. Mating took place on the main lake edge and on the lakeward and shoreward edges of marginal pools.

Thirty pairs of catfish were caught in amplexus using fonya baskets and in 28 of these pairs the males were longer (average length difference 118mm, range 80-214mm). In two mating pairs the females were longer by 38 and 115mm .

The pair usually rest after mating and then resume following and courtship, which may be disrupted by an intruding male. Carefully watched pairs usually mated twice, rarely five times, before being disturbed. It is doubtful whether over 50 consecutive matings could be achieved in Nature, as observed by van der Waal (1974) in a pair of <u>C.gariepinus</u> in an aquarium. The resting interval between mating increased from less than 40 secs after the first mating to over 10 mins after subsequent matings in Lake Sibaya.

Figure 34: The male contracts and begins to slide posteriorly over the female's body at sperm release. Note 'mouth bite' wounds on male from prenuptial aggression.

Figure 35: The female arches its body sharply and releases eggs and air bubbles.

As courtship and mating activity in inshore areas increased, aggressive encounters on the terrace decreased until, within 60 to 80 mins of the commencement of pre-nuptial aggression, most catfish had moved into marginal areas to court and mate. Intensive courtship and mating lasted about one hour, after which increasing numbers of catfish moved back into deeper terrace waters or rested in the shallows. By 02h00 most spawning activities had ceased and clumps of listless spent fish could be found lying in groups, usually obscured by plant cover, in water less than 500mm deep on the lake edge and in marginal pools.

Development of eggs and young

The eggs are oval, measuring 1,6 to 1,7mm on the long axis and coloured orange from respiratory pigments (Nikolsky, 1963) in the yolk. After release the eggs became attached to plant leaves and stalks by means of an adhesive disc. C.gariepinus eggs have no hard protective covering and they are not resistant to desiccation.

Eggs and larval development was followed on 30 eggs collected from the lake, and approximately 2000 eggs milked from a ripe female, and fertilized in vitro. The parent catfish in the latter case measured 555mm TL(♀) and 546mm TL (♂). The eggs and sperm were mixed in a beaker and then poured into a clean 330 x 490mm enamel tray, through which a constant stream of lake water flowed. Clean test tubes were used as extra substrates. When the larvae were 40h old, 50 were introduced into a 250mm^3 aquarium planted with Myriophyllum spicatum in sand, and 100 into a similar-sized mosquito gauze box placed in a known spawning site on the lake edge. Larvae were collected from the tray, aquarium and box populations at regular intervals and preserved to determine developmental rates. Water temperature ranges in the three containers were as follows:

Enamel tray:	19,0° to 24,0°C
Aquarium:	20,2° to 33,0°C
Gauze box:	19,3° to 32,8°C

Larvae in the tray and aquarium were fed on 'Tetramin' fish food flakes (minimum crude protein content: 45%). Those in the gauze box were not fed but they obtained sustenance from the lake, judging from their good growth.

In the tray, eggs which formed dense clumps died whereas individual eggs, or those in loose groups, survived. In the lake, eggs which fell into the sand or into detritus died.

Egg and larval development was rapid. A full description is given in Table 9 and drawings of selected developmental stages are presented in Fig. 36. The eggs hatched after 24-25h at 19,0° - 24,0°C in the enamel tray, which corresponds with hatching times for Clarias reported by all other workers except Holl (1968; Table 10).

TABLE 9

Developmental chart for C.gariepinus eggs and larvae held at 19° - 33°C in an irrigated tray and an aquarium from 23.12.75 to 5.1.76 at Lake Sibaya Research Station.

Age (hours then days)	Mean TL(mm)	Structure	Behaviour
0	1.6 - 1.7	Fertilized egg.	Adheres to substrate by means of chorionic adhesive disk
1h		Blastula visible as small red dot on pole opposite adhesive disk	Adheres to substrate
3.5h		Meroblastic cleavage produces gastrula which is tightly confined by vitelline membrane	Adheres to substrate
9.2h		Gastrulation completed by cellular overgrowth of yolk	Adheres to substrate
16h			Adheres to substrate
24-25h	3.6		Larva hatches
27h		Head and pharyngeal regions project beyond yolk anteriorly and tail projects posteriorly. Two gill slits.	Tail begins to move, sometimes detaching yolk sac from substrate.
33h	4.6	Larvae yellow, yolk greenish-orange, large olfactory sacs, notochord prominent, vertical fin fold and rudimentary intestine present	Wriggle vigorously but attached by ventral sucker on vitelline membrane
35h		No visible external sense organs. Operculum present	Larvae detached and swimming haphazardly, thigmotactic
44h	4.9	Yolk sac reduced, vascular network on branchiostegal membrane well-defined	Swim at 10-15mm/sec. When water flow reduced, activity decreases
56h	5.4	Mouth cavity and rudimentary eye formed, barbels form as buds	Very active near substrate
60h	5.6	Pigmentation prominent on head	Very active, swimming up to 200mm above substrate in an aquarium
66h	5.7	Opercula and mouth develop	
80h	6.2	Barbels longer and densely covered with sense organs, eye entire, mouth and intestine functional, mouth and perimeter of vertical fin fold lined with sense organs, yolk sac resorbed.	Begin feeding, mainly on water surface, but also on substrate. When irrigation stopped they form clumps with active movement of tails, possibly to produce a respiratory current. When inactive, form tight groups.

TABLE 9 (contd)

96h	6.3	Mouth assumes adult form	Readily eat introduced zooplankton. Strong swimmers capable of evading pippette. Feed on water surface, substrate and sides of container
107h	6.7	Head shield formed	Intraspecific aggression - butting and conflict over food. Feed in midwater on *Pseudodiaptomus hessei* (Copepoda).
120h (5days)	7.1	Vertical fin fold large, maxillary barbel reaches head length	
6 days			Feed actively throughout 24 hour period, with irregular rest periods
7 days	8.2	Caudal fin rays and pectoral fin bud appear. Barbels exceed head length	Feed on *Caridina nilotica* and dead catfish larvae; also grub in sand expelling grains through opercular opening
8 days	8.8	Pectoral fin forms	First observation of aerial breathing
9 days	9.2	Near adult body form	Readily feed on small insects, crustaceans and bread
10 days	9.5	Pectoral fin rays present	Congregate at water surface when irrigation is stopped
11 days	10.1	Dorsal fin rays form	
14 days	12.1	External morphology closely resembles that of adult	

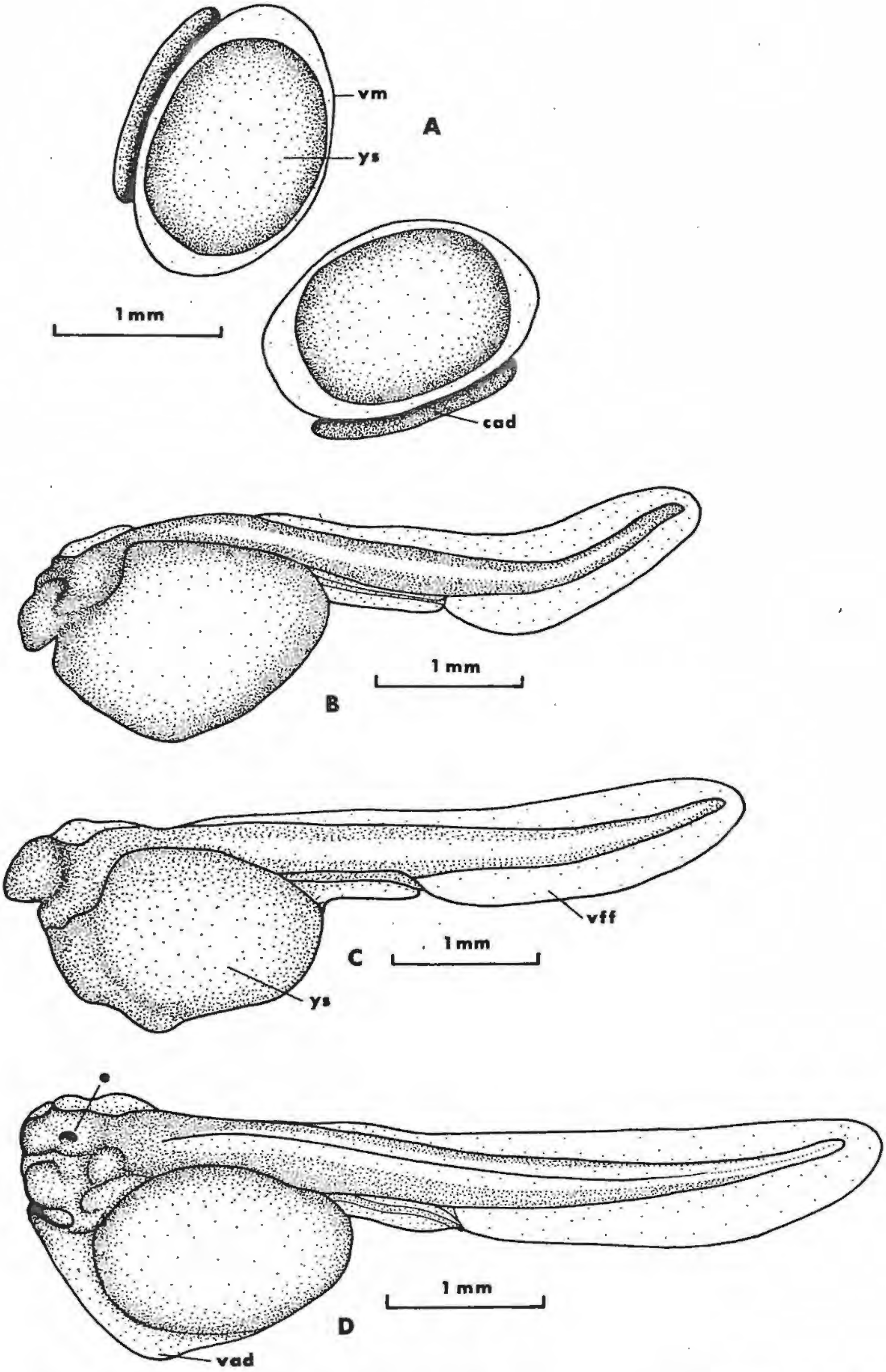


Figure 36: The early developmental stages of C.gariepinus at 19°-33°C.
A. Fertilized ova. B. 33h larva C. 44h larva
D. 56h larva vm: vitelline membrane ys: yolk sac
cad: chorionic adhesive disc vff: vertical fin fold
vad: vitelline adhesive disc.

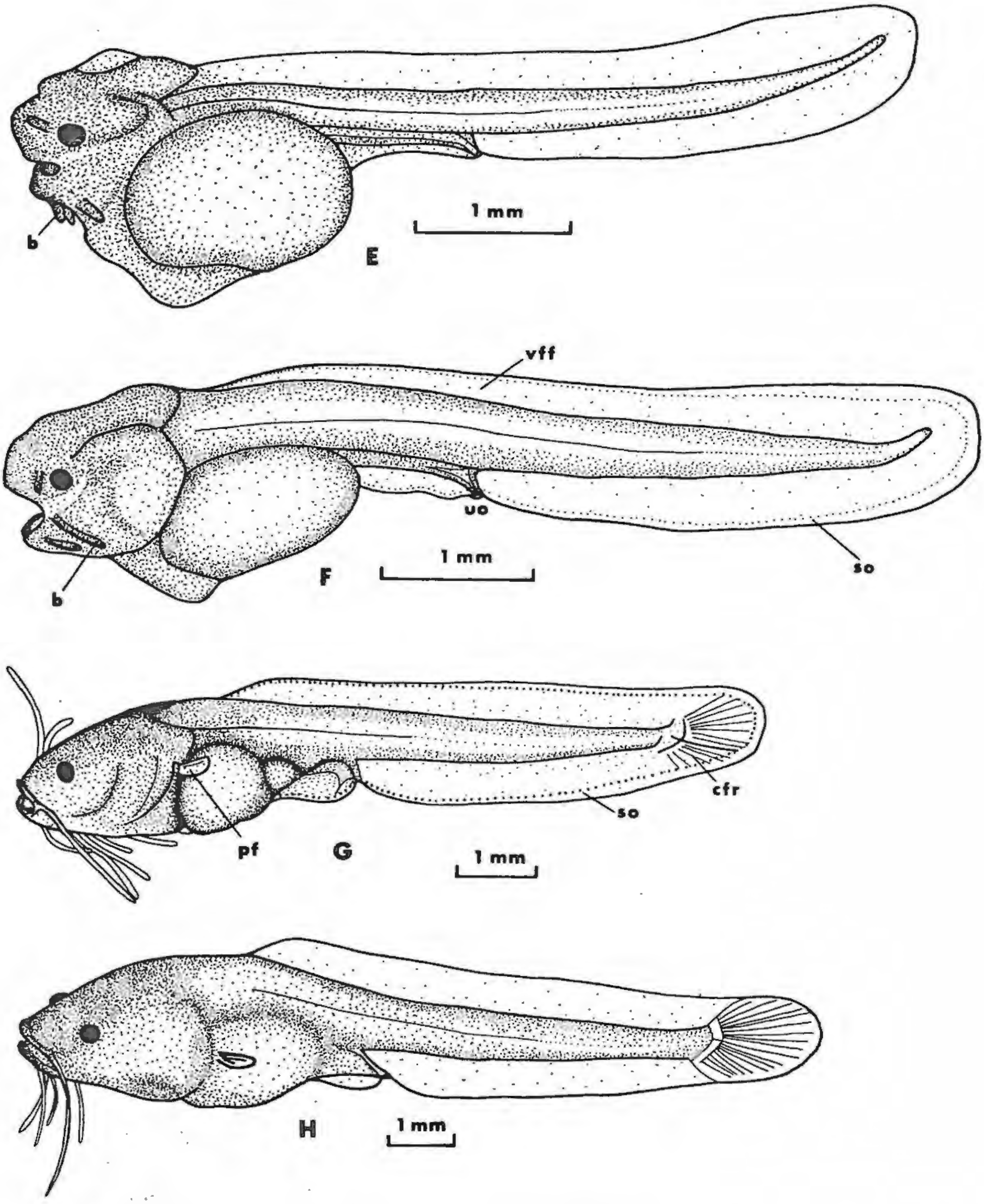


Figure 36 (contd): The early developmental stages of C.gariepinus at 19°-33°C.

E. 66h larva F. 80h larva

G. 10 day fingerling H. 14 day fingerling

b: barbel vff: vertical fin fold

uo: urogenital opening so: sensory organs

cfr: caudal fin rays pf: pectoral fin

TABLE 10

Hatching times of various Clarias species (all in captivity)

Species	Hatching Time	Temperature	Reference
C.gariepinus	24-25h	19-24°C	This study
C.gariepinus	40-48h	20-24°C	Holl (1968)
C.gariepinus	23-25h	26-27°C	van der Waal (1972)
C.mossambicus	23-25h	-	Greenwood (1955)
C.lazera	24h	-	Micha, in van der Waal (1972)
C.macrocephalus	20h	25-32°C	Sidthimunka et al (1966) and Sidthimunka (1972).

After hatching the larvae adhere to the substrate by means of the chorionic adhesive disc. They cannot swim at this stage but perform progressively more active tail-flapping movements from their attached position. After 33h some larvae became detached and gyrated in haphazard circles on the substrate, propelled by the tail. At 45h some larvae are able to swim haphazardly in midwater and by 50h the majority swam rapidly around the tray and aquarium, although the eyes were not completely formed. The circum-oral barbels and sensory buds on the perimeter of the vertical fin fold develop rapidly at this stage. These are probably the main sense organs which allow the apparently blind larvae to swim around seeking cover and eventually food. A respiratory vascular network had developed on the branchiostegal membrane after 44h. The larvae fed on protein-rich fish food in the aquarium after about 60 hours, and began searching for food on the sand, plants and side of the aquarium after 80 hours. Zooplankton were caught in midwater after 96 hours and aerial respiration began after eight days (192h). The larvae are capable of swimming into deeper water within 40 to 50 hours of hatching. In the aquarium they remained in close contact with the dense leaves and stalks of M.spicatum during the day, but at night they explored the whole aquarium.

After 14 days the average lengths in the tray, aquarium and gauze box were 12,1 (N=34); 12,2 (29) and 12,6mm (14) respectively. Larvae reached 18,2 and 22,2mm TL after three and four weeks in the aquarium (n=18) and 41mm after 70 days (N=3).

Greenwood (1955) reported a length of 12mm after 14 days and 18-20mm after 30 days in C.mossambicus, and Holl (1968) lengths of 37-48mm after 65 days, and 60-80mm long after 70 days. Van der Waal (1972) records faster growth rates for C.gariepinus larvae in breeding ponds, with lengths of 39mm after 40 days.

According to Greenwood (1966), larval C.mossambicus are remarkably hardy and can withstand considerable and rapid change in water temperature. They are also able to use atmospheric oxygen at an early age even though the supra-branchial organ is not fully developed. Oxygen tension, associated with water circulation, is probably an important feature controlling developmental rates (Greenwood, 1955). He noticed that early development was faster in C.mossambicus embryos raised in dishes with a strong current agitating the water than in those with only a slight water flow. Oxygen concentrations measured at a spawning site in Lake Sibaya using an YSI oxygen meter ranged from 65 to 82% saturation, with the lowest readings in the early morning. These values are within the range of readings obtained by Allanson & van Wyk (1969) in the main lake body.

The food of larval catfish (<20mm TL) could not be determined in the field with any accuracy due to the small sample. The six larvae examined all contained nymphal Caridina nilotica and larval Chironomidae. Catfish larvae in aquaria readily ate the copepod zooplankter Pseudodiaptomus hessei which is present but not abundant in Lake Sibaya (Hart & Allanson, 1975). A sample of 19 C.gariepinus from Sibaya measuring 20-50mm TL had fed on Grandidierella lignorum, chironomid larvae, C.nilotica, and Corophium carinata. Thereafter insects, large crustaceans and fish became increasingly important in the diet (see Table 26). Holl (1968) reported that C.gariepinus larvae fed on 'zooplankton, changing to an insectivorous diet when they reach about 30mm with Chironomid larvae forming a major item'. Larval C.mossambicus fed on Ostracoda and aquatic insects to about 30mm TL, and thereafter fish became important food (Corbet, 1959). In another African freshwater predator, Hydrocynus vittatus, the fingerlings also had an insect-eating stage intermediate between zooplankton and fish-eating stages (Kenmuir 1975).

The habitat of larval catfish is usually temporary, more so on the floodplains of rivers than on the margins of lakes. Mortalities through desiccation are likely to be high if marginal pools become isolated due to poor rains, as shown by Greenwood (1955) in C.mossambicus. The rapid developmental rates of catfish and larvae would ensure that they could move into deeper water soon after spawning so as to reduce the risk of isolation and desiccation.

Predation on spawning catfish

Africans club and spear large numbers of catfish on spawning runs at Lake Sibaya. Their yield on five spawning runs on Crocodile point ranged from 29 (when only one African was active) to 163 (by a group). Nile crocodiles, Crocodylus niloticus, were seen feeding on catfish on three spawning runs, but no bird predators appeared (probably because of our presence) except on the afternoon spawning run when 3 fish eagles H.vocifer took one catfish each.

Discussion on breeding

Stimulation of participating individuals by mass behavioural displays plays an important role in a catfish spawning run. Trophallaxis, the stimulating effect of courtship and mating, has also been reported in trout, *Salmo* spp; bream *Abramis brama*; whitefish, *Coregonus* spp. (Brown, 1957); grunion *Leuresthes tenuis* (Marshall, 1965) and many other fish. Chemical stimuli are likely to play a role. Liley (1969) showed that pheromones may induce changes in responsiveness to external stimuli in fish and increase locomotory activity during breeding. Pheromones play an important role in courtship and mating of channel catfish, *Ictalurus punctatus* (Timms & Kleerekoper, 1972), guppies *Poecilia reticulata* (Amouriq, 1965) and gobies, *Bathygobius soporator* (Tavolga, 1956). Todd *et al* (1967) and Todd (1971) found that the bullhead *Ictalurus natalis* has a 'complex chemical language' with which it communicates individual identity, status, aggression or submission, and reproductive state. As their eyesight is apparently poor, we can expect that non-visual cues, such as mechanoreception and chemical stimuli, may be important during spawning runs of *C.gariepinus* as well. This is certainly an interesting further line of research.

In some siluroids, such as *Siluris glanis* (Nikolsky, 1963), *Ictalurus* spp. (Lagler *et al*, 1962) and *C.batrachus* (Sidthimunka, 1972), nests are made and the eggs are guarded. In *C.gariepinus* no nests are made and the eggs are abandoned. Any form of territoriality would be impractical for *C.gariepinus* as the adults would be vulnerable if they remained in or near the spawning site for a long period.

There are two main strategies in connection with choice of embryonic environment, exemplified firstly by fishes which carry or escort their young to suitable areas, and secondly by those which abandon their young in these areas. An example of the first category is the maternal mouth-brooding cichlid, *Sarotherodon mossambicus*. This species creates a stable environment for embryonic development by brooding the larvae in its mouth where they are protected from external conditions. It is noteworthy, therefore, that *S.mossambicus* started breeding in Lake Sibaya at almost exactly the same time of the year (the first and second week of September) every year from 1970 - 1976 irrespective of prevailing terrace conditions (Bruton & Boltt, 1975, and recent observations). After the mouth-brooding phase, the larvae, now capable of strong swimming movements, are released in suitable marginal shallows. In contrast, *C.gariepinus*, a non-guarding, substrate spawner, must await suitable environmental conditions before spawning can take place. That *C.gariepinus* spawns under a narrow range of external conditions is shown by the observations of Holl (1968) and Gaigher (in press). Holl reports that in the summer of 1964/65, catfish spawned after the first rains on 8 December, whereas in 1965/66 the main rains were very late and no spawning runs were observed until 10 February. In Hardap dam, Gaigher found that catfish gonads were fully developed by November 1974 but spawning was delayed over 4 months until the first heavy rains in March 1975. Likewise, in Lake Sibaya catfish had mature gonads in September 1975 but the first major spawning run only took place after heavy rains on 31 January 1976, although catfish had spawned as early as September in previous Summers. Clearly, C.gariepinus only spawns when environmental conditions in marginal areas fit certain narrow criteria.

The optimal conditions for early development of C.gariepinus and C.mossambicus are unknown. Greenwood (1965) has stressed the importance of elevated oxygen tensions and water movement for larval development. Low oxygen concentrations or anaerobiosis may lead to harmful attacks by bacteria and fungi, as he found when artificially raising clariid larvae. Water movement at the spawning site may serve to keep the egg membrane free of organisms which might settle on it. In C.gariepinus and C.mossambicus, the chorionic adhesive disc allows the larva to attach itself to plants away from anaerobic substrates until swimming movements can be performed efficiently. In the wels, Siluris glanis, the larva has no adhesive disc. In order to avoid contact with the hypoxic bottom mud, the embryonic period is prolonged and the newly hatched larvae swim instantly (Balon, 1975).

Protection from predators may be another important requirement during embryonic development. In Lake Sibaya, newly inundated areas do not have a permanent well-developed (potentially predatory) fish population. This observation was verified by rotenoning six, 10m x 10m areas which had been netted off using a curtain of 5mm bar mesh netting. Three sites were chosen on recently-inundated shores where catfish spawning runs had taken place, and three in adjacent but contigious marginal areas where fish populations had become established.

The species composition of the catch (Table 11) shows that few potential predators occurred at the spawning sites at the time of sampling. Conversely, small predators (P.philander, G.giurus, C.multispinis and C.theodorae) constituted over 39% of the catch in the adjacent pool. However, this result is by no means conclusive as predation pressure in the spawning sites may be high despite the apparent paucity of predators. A few P.philander could take a very large number of larval catfish during a brief foray into marginal areas. Furthermore, all the rotenone collections were made during the day (due to the risk of crocodiles at night), and small predators may have ventured into the extreme shallows at night. P.philander, G.giurus, C.multispinis and C.theodorae all readily ate catfish larvae in aquaria, although the larvae often escaped detection when plant cover was provided. However, the question of larval protection from predation in the natural situations is still unanswered.

TABLE 11

Composition of fish populations in newly inundated catfish spawning sites, and adjacent well-vegetated marginal shallows in Lake Sibaya.

	Number of rotenone treatments in netted 10mX10m area			
	3		6	
Fish species	Spawning site		Marginal shallows	
	No.	%	No	%
P.philander*	2	0.8	718	38.3
T.sparrmanii	5	2.1	422	22.5
A.katangae	176	73.3	331	17.6
T.rendalli	6	2.5	199	10.6
B.paludinosus	19	7.9	121	6.4
S.mossambicus	26	10.8	42	2.2
C.gariepinus*	0	0	13	0.7
B.viviparus	3	1.3	13	0.7
G.giurus	3	1.3	12	0.7
C.theodorae*	0	0	2	0.2
C.multispinis*	0	0	1	0.1
Total	240	100	1877	100
Total predators*	5	2.1	746	39.7

GROWTH AND POPULATION STRUCTURE OF CLARIAS GARIEPINUS IN LAKE SIBAYA

INTRODUCTION

According to Weatherley (1972), temperature and intensity of competition for food appear to be the main growth controls in fish. In Lake Sibaya, water temperatures are relatively high (18° - 28°C in the main lake) in relation to other ecosystems inhabited by the species, and they are unlikely to explain the growth pattern reported here. The extent of interspecific competition for food is unknown, but there are no other piscine predators larger than 150mm TL in the lake. Fish-eating birds such as cormorants *Phalacrocorax* spp. feed mainly on gobies, which are unimportant in the diet of Sibaya catfish, and cichlids, which are important, but their impact is unknown. Fish eagles *Haliaetus vocifer* take adult tilapia, but there are only 3 - 5 pairs on the lake.

Intraspecific competition for food is a more likely factor controlling growth. I have already shown that catfish feed in different habitats in the lake during their ontogeny. If food availability, density or quality varies in the different habitats, growth rates may be affected. Likewise, in a given habitat, intense intraspecific competition for the available food resources may affect growth.

This chapter serves to define the growth pattern and population structure of *C.gariepinus* in Lake Sibaya. Previous studies on the growth of *C.gariepinus* by Pivnicka (1974), van der Waal and Schoonbee (1975) and Willoughby and Tweddle (1976) are also reveiwed and the size reached by catfish in southern Africa is discussed. The next two chapters outline the diet and predation strategy of catfish, and in the discussion an attempt is made to explain the given growth rate in terms of different food quality and availability in the various habitats.

METHODS

Collection and measurement

Small catfish were collected using rotenone, traps and seine nets, and large specimens using longlines, gillnets and traps. All lengths given are total lengths (TL).

Length frequency modes in juveniles

The main spawning season of C.gariepinus in Lake Sibaya extends from November to February, although some fish spawn in September and as late as March. As C.gariepinus is fast-growing, well-defined length distribution peaks can be expected in younger age-groups as a consequence of the short spawning season. Catfish up to 300mm TL mainly occupy marginal and littoral habitats in Lake Sibaya, and intensive sampling was therefore carried out monthly in these areas from October 1974 to January 1975, and from October 1975 to May 1976 to determine growth rates from length frequency modes in juveniles.

Examination of hard parts

Age determination in scaleless fishes had usually involved analysis of rings on other hard parts such as otoliths, vertebrae, cleithra, pectoral girdles and opercula (for reviews see Sinha and Jones, 1967; De Bont, 1967; Williams & Bedford, 1974). In addition, dorsal and pectoral spines have been used to age Ictalurus lacustris (Sneed, 1950; Marzolf, 1955); I.punctatus (Muncey, 1959); Pangasius pangasius (Pantulu, 1962); various Acipenseridae (Cuerrier, 1951; Probst & Cooper, 1955); Eutropius depressirostris (Gaigher, 1969); Heterobranchus longifilis (Donnelly & Caulton, 1969) and C.gariepinus (van der Waal and Schoonbee, 1975). Pectoral spines, otoliths, opercula and vertebrae were examined for possible use in age determination of catfish from Lake Sibaya.

The first fin ray of the pectoral fin is large and spinous with a central lumen filled with connective tissue and fat (Fig. 37). The proximal end of the spine forms a head which articulates directly with the glenoid joint of the pectoral girdle. Pectoral spines were removed from the glenoid joint whole, cleaned and stored in envelopes cross-referenced to date of collection and fish number. The spine retains essentially the same form throughout life but in older catfish a progressive enlargement of the lumen takes place as a result of bone re-absorption. This enlargement proceeds towards the posterior side of the lumen, so that early growth rings may be resorbed, although they usually remain visible on an antero-lateral side. To minimise this risk, a position on the spine for sectioning was chosen which gave reliable readings for all fish sizes. This position is at 5/7 from the proximal end; all spines were therefore marked off from a nomograph at 5/7 and sectioned at this site (Fig. 37C).

Spines were sectioned using a fine saw, and ground on the cut surface on silicon carbide water paper (grit sizes 100, 220, and 400) using paraffin as a lubricant. Small spines were ground manually by holding the bulb and rubbing the cut surface on firmly-fixed water paper. Larger spines were

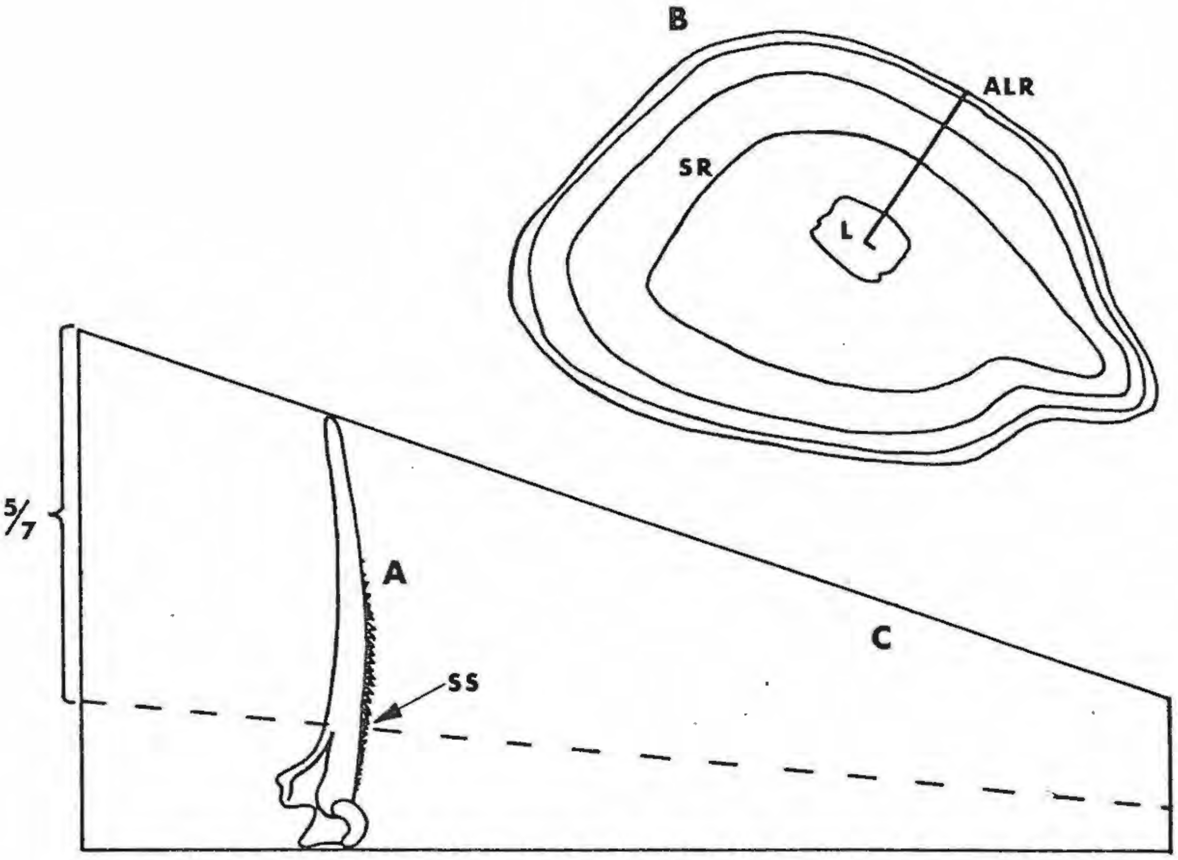


Figure 37: A. Diagram of pectoral spine of C.gariepinus (SS = sectioning site).

B. Diagrammatic cross section of pectoral spine showing lumen (L), spine ring (SR) and antero-lateral radius (ALR).

C. Nomogram of determining sectioning site at 5/7 spine length.

ground on water paper cut into discs and revolved on a sand-paper attachment to an electric drill. After polishing, a section about 2mm thick was cut, and glued onto a microscope slide with the polished side down. The other side was then ground down to a thickness of about 0.1mm, washed, labelled and examined under water or in glycerin in a black dish by reflected light. Clear subconcentric rings were usually visible. Spine sections with indistinct rings were subjected to the following procedure: boil for five minutes, decalcify in 30% HNO_3 for six minutes, stain in alizarin-red S for 40 minutes, dehydrate in 95% and 100% ethyl alcohol for 30 minutes each, clear in xylol overnight and mount in Canada balsam under a cover slip. Spine sections were examined on a Fresnel screen mounted on a compound microscope.

Spine rings took the form of clearly-defined lines of denser tissue in the bone matrix (Figs 38 and 39). Rings which did not extend from the anterior field across the lateral fields and into the posterior field were regarded as false rings, and were not used in age determination. True rings were counted on the anterior field to give the pectoral spine ring count. Spines were examined from 750 catfish collected in the summers of 1973/74 and 1974/75, of which 96% had clear rings, either before or after treatment.

Sagittal otoliths were removed by cutting the cranium just anterior to the parietal plate. The otoliths were ground to the plane of the nucleus on the convex side and etched using 1% aqueous HCl. When examined under water in a black dish by reflected light, light and dark bands were visible on 9 of the 36 otoliths examined. In addition 25 otoliths were ground to the plane of the nucleus and burned over a cool flame. When examined dry by reflected light all otoliths showed bands as well as minute rings (perhaps comparable to the growth patterns observed by Pannella, 1974, and Brothers et al, 1976). Cleaned, dry vertebrae from 15 catfish were also examined, and all showed rings which were more distinct in decalcified samples. Opercula were almost opaque when untreated, but showed bands when decalcified. On the whole, otoliths, opercula and vertebrae were more time-consuming to prepare and yielded less distinct rings than pectoral spines, which were therefore used in this study.

Back-calculation of lengths from pectoral spine rings

The antero-lateral radius of 630 pectoral spines with undamaged edges and easily-defined lumen centres was determined. There was no significant difference between the two sexes in the relationship of the spine radius to total length of the fish. This relationship is described by the formula $y = 0.131x + 2.559$ ($R^2 = 0.98$) where y = antero-lateral spine radius in mm and x = total length of fish in mm in the catfish total length range 300-700mm.

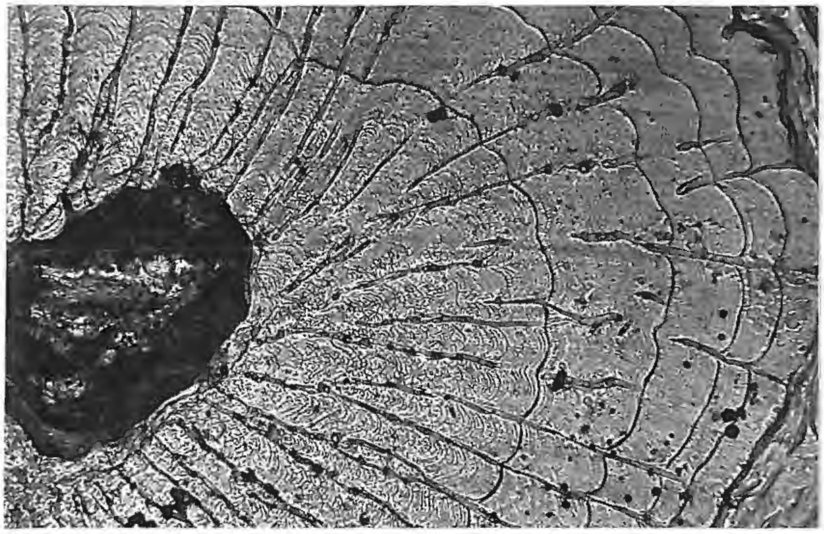


Figure 38: Lateral section of a pectoral spine of C.gariepinus showing clear spine rings and central lumen.

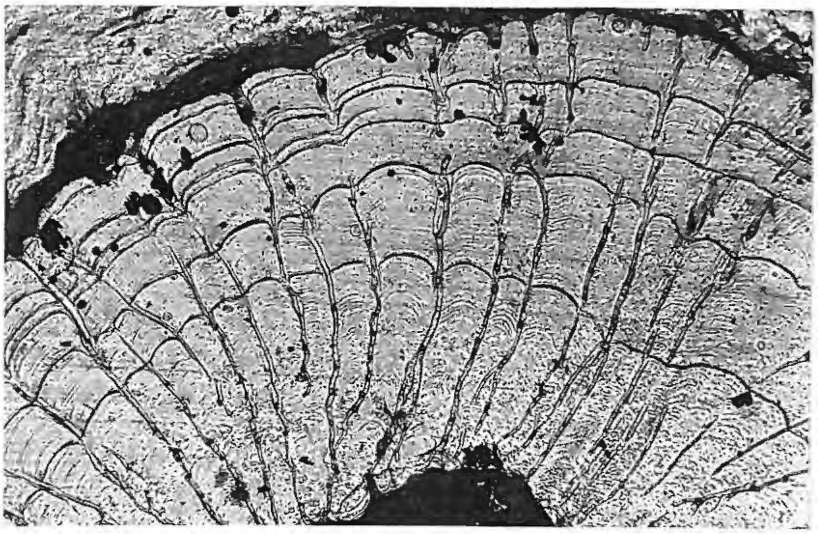


Figure 39: Anterior section of a pectoral spine showing true rings and false rings.

The regression is linear but not directly proportional and back-calculations were therefore made using Fraser's formula as suggested by Ricker (1968):

$$Ln - c = \frac{Sn}{S} (L - c)$$

where Ln = length of fish when ring 'n' was formed
L = length of fish at capture
Sn = radius of ring 'n'
S = antero-lateral radius of pectoral spine
c = intercept on length axis.

Results

Growth rate from length distribution modes

The length distribution of fingerling catfish caught monthly from December 1975 to May 1976 is given in Fig. 40. Clear modes are apparent from the catches which indicate the growth rate of fingerlings in the lake. Monthly length increments ranged between 18 and 38mm (average 24mm). The modal size after 6 months was 144mm. Collections of one year old catfish were made in the midsummers of 1974/75 and 1975/76 in marginal habitats. Length modes of yearlings were between 240 and 260mm in both years (Fig. 41). The growth curve of fingerlings obtained from Fig. 40 extrapolates to about 250mm TL at an age of one year, and confirms that catfish of this size are one year old.

Age determination from pectoral spine rings

The length distribution of male and female <u>C.gariepinus</u> for directly-read pectoral spine ring groups is given in Table 12. There is considerable overlapping in consecutive groups, but clumping is evident at each spine ring count.

Table 13 is a summary of the average back-calculated total lengths of both sexes for different spine ring counts. Catfish longer than 700mm TL were not used for these calculations as they may reflect higher growth rates than the normal population. The lengths at each spine ring count in Table 12 correspond closely with those determined from observed data in Table 13, and confirm the accuracy of the directly read lengths.

The first spine ring was formed at a modal length of 400 to 410mm, and no ring was formed at a length of 240 to 260mm at an age of about one year (Fig.41), in the bulk of fish examined. If the first spine ring is assumed to be formed towards the end of the second year, a smooth curve is obtained which produces a good fit of von Bertalanffy's growth equation (von Bertalanffy,

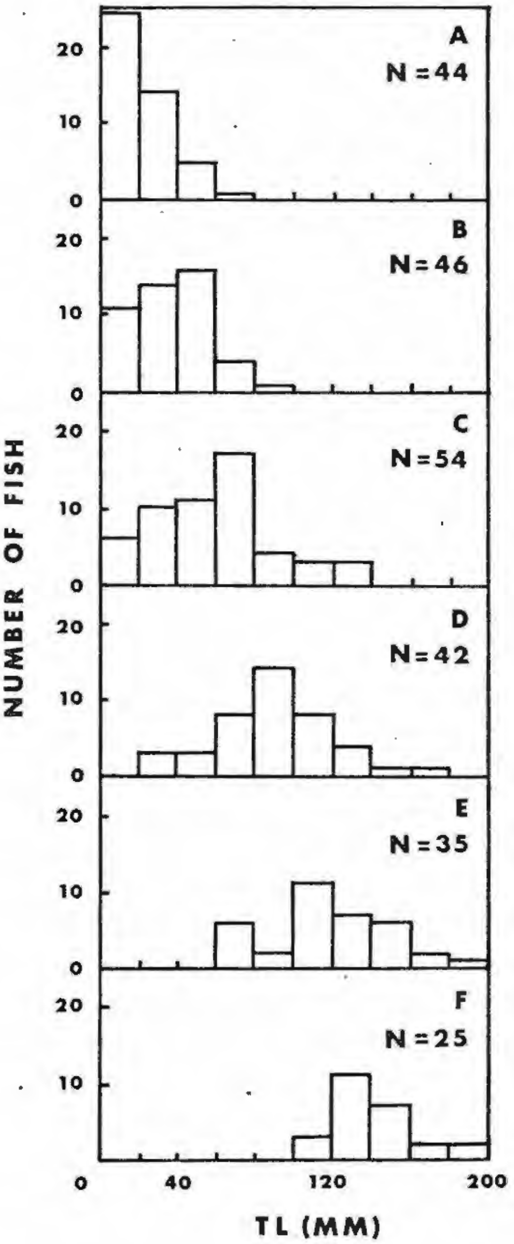


Figure 40: Length distribution of fingerling <u>C.gariepinus</u> caught in marginal shallows of Lake Sibaya, showing growth rate by movement of the length mode.

A: December, 1975; mean length 18mm
B: January, 1976; 43mm
C: February, 1976; 81mm
D: March, 1976; 102mm
E: April, 1976; 126mm
F: May, 1976; 144mm

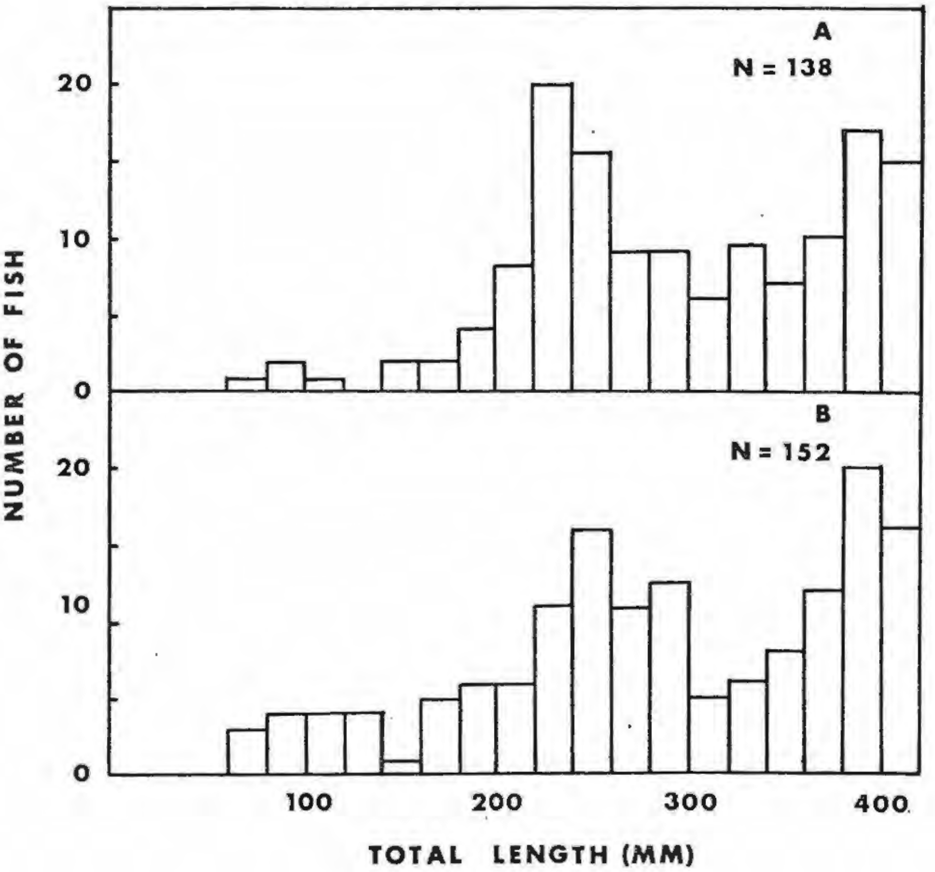


Figure 41: The length frequency of C.gariepinus caught in shallow terrace and marginal habitats in Lake Sibaya, showing length modes of one year old fish.

A: 240mm in December 1974/January 1975

B: 260mm in December 1975/January 1976

TABLE 12

Length distribution of C.gariepinus from Lake Sibaya for different pectoral spine ring counts.

	PECTORAL SPINE RING COUNT						
Total length group (mm)	1	2	3	4	5	6	7
240	2						
260	2						
280	1						
300	3						
320	5						
340	8						
360	19	6	1				
380	24	1					
400	38	1	1				
420	29	13					
440	31	11	2				
460	6	11	2				
480	3	28	3	1			
500		52	8	1			
520	1	46	12	1	2	1	
540		40	14	2	2	1	
560		24	36	2	3	1	
580		9	33	13			
600		3	19	30	3	1	
620		3	11	23	5	1	1
640				10	8	3	1
660				2	11	1	
680				3	7	2	
700				1	5	5	2
720					1	3	3
740				1		2	4
760							
780							
800							
820							1

TABLE 13

Backcalculated total lengths (mm) for male and female C.*gariepinus* from Lake Sibaya, obtained from measurements of pectoral spine rings.

No. of rings at capture	N	LENGTH AT AGE					
		II	III	IV	V	VI	VII
				MALES			
1	87	330					
2	122	368	473				
3	66	381	501	541			
4	34	387	529	553	623		
5	21	421	481	586	608	671	
6	10	382	517	551	630	635	697
No. of fish	340	340	253	131	65	31	10
Mean TL		378	500	558	620	653	697
				FEMALES			
1	78	360					
2	98	378	483				
3	54	393	496	522			
4	41	371	532	558	608		
5	19	403	512	573	616	640	
No. of fish	290	290	212	114	60	19	
Mean TL		381	506	551	612	640	

(1957). This assumption was tested by calculating von Bertalanffy's parameter, t_o (the theoretical time when length is zero) using Ricker's (1975) method in which log (L_∞ - t) is plotted against age in years. L_∞ is the final or asymptotic length obtained from a Ford-Walford plot (see below). Values of t_o close to 0 indicate a good fit to von Bertalanffy's growth model, and values approximating 1 or -1 a poor fit. The value of t_o when the first spine ring is assumed to be formed in the first, second or third years was calculated (Table 14). The calculations are shown in Tables 15, 16 and 17. As shown in Table 15, t_o closely approximated 0 when the first spine ring was laid down in the second year. This finding confirms that no spine ring is laid down in the first year. Non-formation of a pectoral spine ring in the first year may be due to rapid, uninterrupted growth of young fish in a food-rich environment.

Tweddle (1975) found in another African siluroid (Bagrus meridionalis) in Lake Malawi) that no rings were formed on the vertebrae during the first two years of life.

TABLE 14

The theoretical time when length is zero, t_o, for C.gariepinus from Lake Sibaya when pectoral spine rings are formed in the 1st, 2nd or 3rd years.

Year first ring formed	t_o	
1+	-1.02	-0.88
2+	0.033	0.077
3+	1.033	1.077

The adequacy of the von Bertalanffy growth model was also tested using Ford-Walford plots (Ford, 1933; Walford, 1946). Ford-Walford plots of length at age 'x' against length at age 'x+1' were drawn by regression analysis using the method of least squares (Fig. 42). The data points are arranged in a straight line which bisects the 45^o diagonal. This type of plot is typical of a growth curve which shows an initial period of rapid increase and then a decrease, as described by von Bertalanffy's model (Ricker, 1975). Walford (1946) pointed out that growth conforming to this pattern suggests a limiting size, the asymptotic length, which is read off a Ford-Walford plot as the intercept on the 45^o diagonal. Figures 42a and 42b give asymptotic lengths of 760mm and 674mm TL for male and female Sibaya catfish. In a sample of 1156 C.gariepinus caught in all habitats in Lake Sibaya, only 1,7% of the males and 3,2% of the females exceeded these postulated asymptotic lengths. The asymptotic lengths

TABLE 15

Calculation of t_o from von Bertalanffy's growth equation for male and female *C.gariepinus* from Lake Sibaya using Ricker's (1975) method, when the first pectoral spine is assumed to be formed in the second year. All lengths in mm.

	Males			Females		
Year	TL	L_∞ -lt	$\text{Log}_e(L_\infty$ -lt)	TL	L_∞ -lt	$\text{Log}_e(L_\infty$ -lt)
1	240	520	6.25	240	434	6.07
2	399	361	5.89	406	268	5.59
3	517	243	5.49	512	162	5.09
4	575	185	5.22	564	110	4.70
5	629	131	4.88	608	66	4.19
6	659	101	4.62	639	35	3.56
7	695	65	4.17	648	26	3.26
8	726	34	3.53			

L_∞ = 760mm

$y = 6.645 - 0.3642\ x$

($r^2 = 0.99$)

L_∞ = 674mm

$y = 6.550 - 0.4782\ x$

($r^2 = 0.99$)

where $y = \text{Log } e\ (L_\infty -lt)$

x = age in years

L_∞ = asymptotic length

lt = length at time t (years)

$$t_o = \frac{\text{y axis intercept} - \text{Log } e\ (L_\infty)}{\text{slope of plot x:y}}$$

$$= \frac{6.645 - 6.633}{0.3642}$$

$$= 0.033$$

$$t_o = \frac{6.55 - 6.513}{0.4782}$$

$$= 0.077$$

TABLE 16

Calculation of t_o from von Bertanalffy's growth equation for male and female C.gariepinus from Lake Sibaya using Ricker's (1975) method, when the first pectoral spine ring is assumed to be formed in the first year. All lengths in mm.

	MALES			FEMALES		
Year	TL	$L_\infty - t$	$\log_e(L_\infty - t)$	TL	$L_\infty - t$	$\log_e(L_\infty - t)$
1	399	366	5.90	406	267	5.59
2	517	248	5.51	512	161	5.08
3	575	190	5.25	564	109	4.69
4	629	136	4.91	608	65	4.17
5	659	106	4.66	639	34	3.53
6	695	70	4.25	648	25	3.22
7	726	39	3.66			

MALES:

$L_\infty = 765\text{mm}$

$y = 6.2814 - 0.3511x$

$(r^2 = 0.98)$

$$t_o = \frac{6.2814 - 6.6399}{0.3511}$$

$= -1.02$

FEMALES:

$L_\infty = 673\text{mm}$

$y = 6.082 - 0.4863x$

$(r^2 = 0.99)$

$$t_o = \frac{6.082 - 6.5117}{0.4863}$$

$= -0.88$

TABLE 17

Calculation of t_o from von Bertalanffy's growth equation for male and female C.gariepinus from Lake Sibaya using Ricker's (1975) method, when the first pectoral spine ring is assumed to be laid down in the third year. All lengths in mm.

	MALES			FEMALES		
Year	TL	$L_\infty - t$	$\text{Log}_e(L_\infty - t)$	TL	$L_\infty - t$	$\text{Log}_e(L_\infty - t)$
1						
2	240	520	6.25	240	434	6.07
3	399	361	5.89	406	268	5.59
4	517	243	5.49	512	162	5.09
5	575	185	5.22	564	110	4.70
6	629	131	4.88	608	66	4.19
7	659	101	4.62	639	35	3.56
8	695	65	4.17	648	26	3.26
9	726	34	3.53			

Males:

$L_\infty = 760\text{mm}$

$y = 7.0092 - 0.3642x$

$(r^2 = 098)$

$$t_o = \frac{7.0092 - 6.633}{0.3642}$$

$= 1.033$

Females:

$L_\infty = 674\text{mm}$

$y = 7.0282 - 0.4782x$

$(r^2 = 0.99)$

$$t_o = \frac{7.0282 - 6.513}{0.4782}$$

$= 1.077$

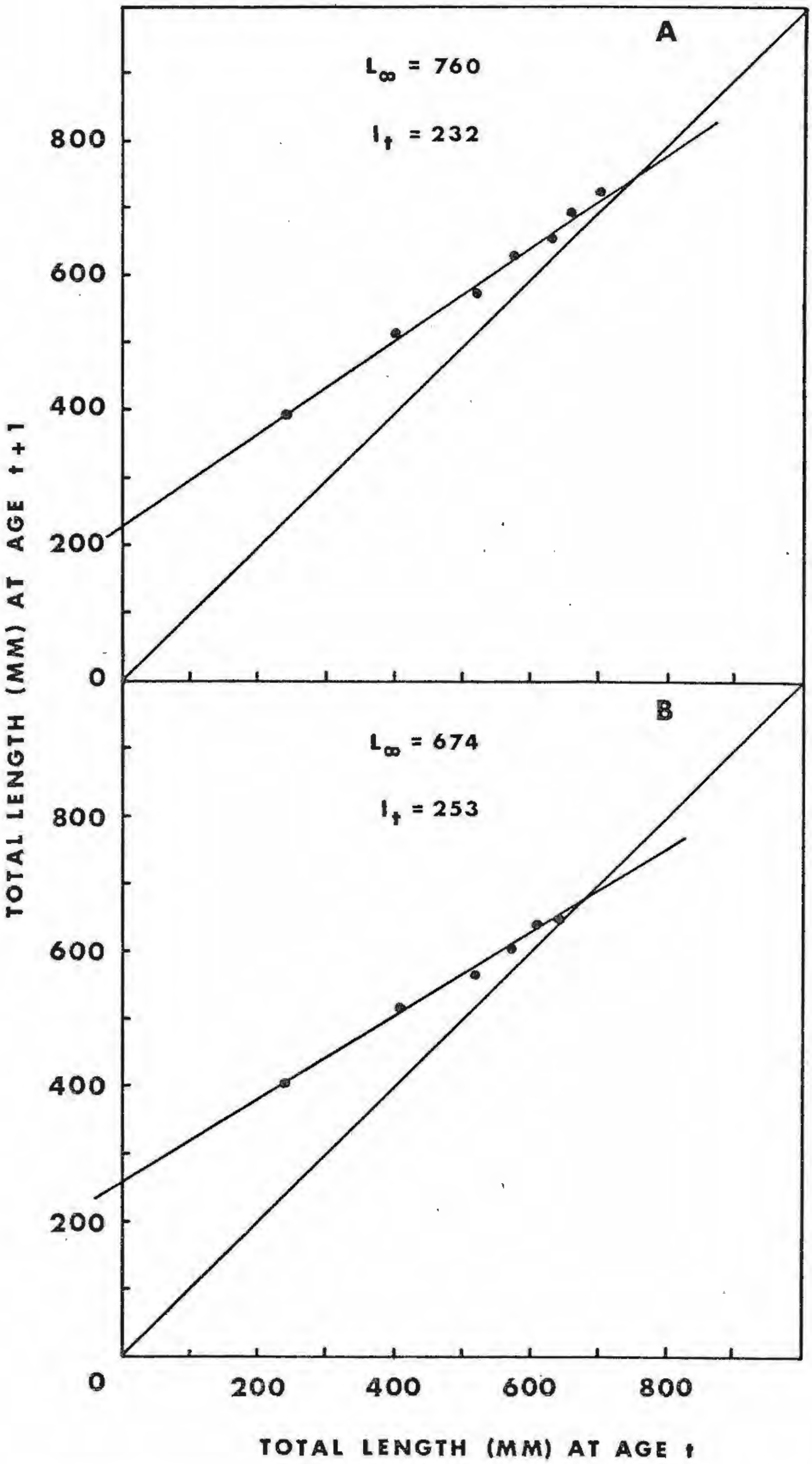


Figure 42: Ford-Walford plots for male (A) and female (B) C.gariepinus from Lake Sibaya.

L_∞ = asymptotic length (intercept on diagonal)

l_t = length at one year (intercept on y axis) obtained from the Ford-Walford plots are therefore accurate in the case of Sibaya catfish. The theoretical length at one year is read off a Ford-Walford plot as the intercept on the y-axis. Once again, the values obtained (230 - 260mm) correspond closely with observed values (Fig. 41).

Knight (1968) pointed out the danger of applying the von Bertalanffy growth model to inappropriate data. However, as demonstrated above, this model adequately described the Sibaya catfish data, provided that mean lengths at the end of each year of life were used, thus ignoring within-season changes in growth rates. Knight also criticized the use of Ford-Walford plots for determining asymptotic lengths of fishes. He is correct to emphasize that the asymptotic length is merely a descriptive summary of data, either for a population or an individual, rather than a law of Nature. In cases in which growth is nearly linear throughout life, Ford-Walford plots are of little value for predicting asymptotic lengths, as there is no intercept on the diagonal, or the intercept cannot be read off accurately. However, in populations with a growth curve which gradually reaches a plateau (as in C.gariepinus from Lake Sibaya) the asymptotic length can be read off accurately.

Description of growth

Growth rates were therefore calculated on the assumption that the first pectoral spine ring is formed at the end of the second year. Mean weight was determined from a length-weight regression based on 862 catfish, and is expressed as follows:

C.gariepinus juveniles 50-350mm TL. $W=0.000006\ TL^{3.029}$ ($R^2=0.98$, $N=218$)

C.gariepinus adult females >350mm TL. $W=0.00004\ TL^{2.705}$ ($R^2=0.90$, $N=289$)

C.gariepinus adult males >350mm TL. $W=0.00004\ TL^{2.699}$ ($R^2=0.92$, $N=355$)

where W = weight in grams TL = total length in mm.

The growth data are summarised in Table 18.

Growth in weight was nearly linear for males, but decelerated after four years in females (Fig. 43). Annual weight increments were highest in the third year for both sexes. The mean weight after one year (97g) was lower than that obtained by van der Waal and Schoonbee (about 450g, 1975) but higher than the figure given by Pivnicka (6,8g, 1974) and Willoughby and Tweddle (about 36g, 1976). The modal age was 5+ years in males and 4+ years in females (Fig. 44). Few males exceeded 8+ years and few females 7+ years.

Growth in length for males and females was similar until 3+ years, after which males grow faster (Fig. 45). In both sexes, the annual length increment was highest in the first year, and then decreased progressively. Two catfish, tagged with a FTF-69 fingerling tag and FD-67 spaghetti tag respectively, were recaught after a sufficiently long period to yield information on growth.

TABLE 18

Mean observed total lengths in mm (TL), standard error of TL (SE), annual length increment (ΔTL), mean weight ($\bar{W}$) and number of catfish in sample (N) for different year classes of male and female *C.gariepinus* in Lake Sibaya. Mean length in the 1+ year class from Fig. 41.

Males

Year	TL	SE	ΔTL	$\bar{W}$	N
1+	240		240	97	
2+	399	0.49	159	419	81
3+	517	0.41	118	843	135
4+	575	0.53	58	1123	67
5+	629	0.67	54	1431	40
6+	659	1.06	30	1623	24
7+	695	1.21	36	1873	11
8+	726	1.47	31	2107	10

Females

1+	240		240	97	
2+	406	0.48	166	455	91
3+	512	0.45	106	852	110
4+	564	0.52	52	1107	76
5+	608	0.41	44	1357	50
6+	639	0.98	31	1552	23
7+	648	2.46	9	1612	12

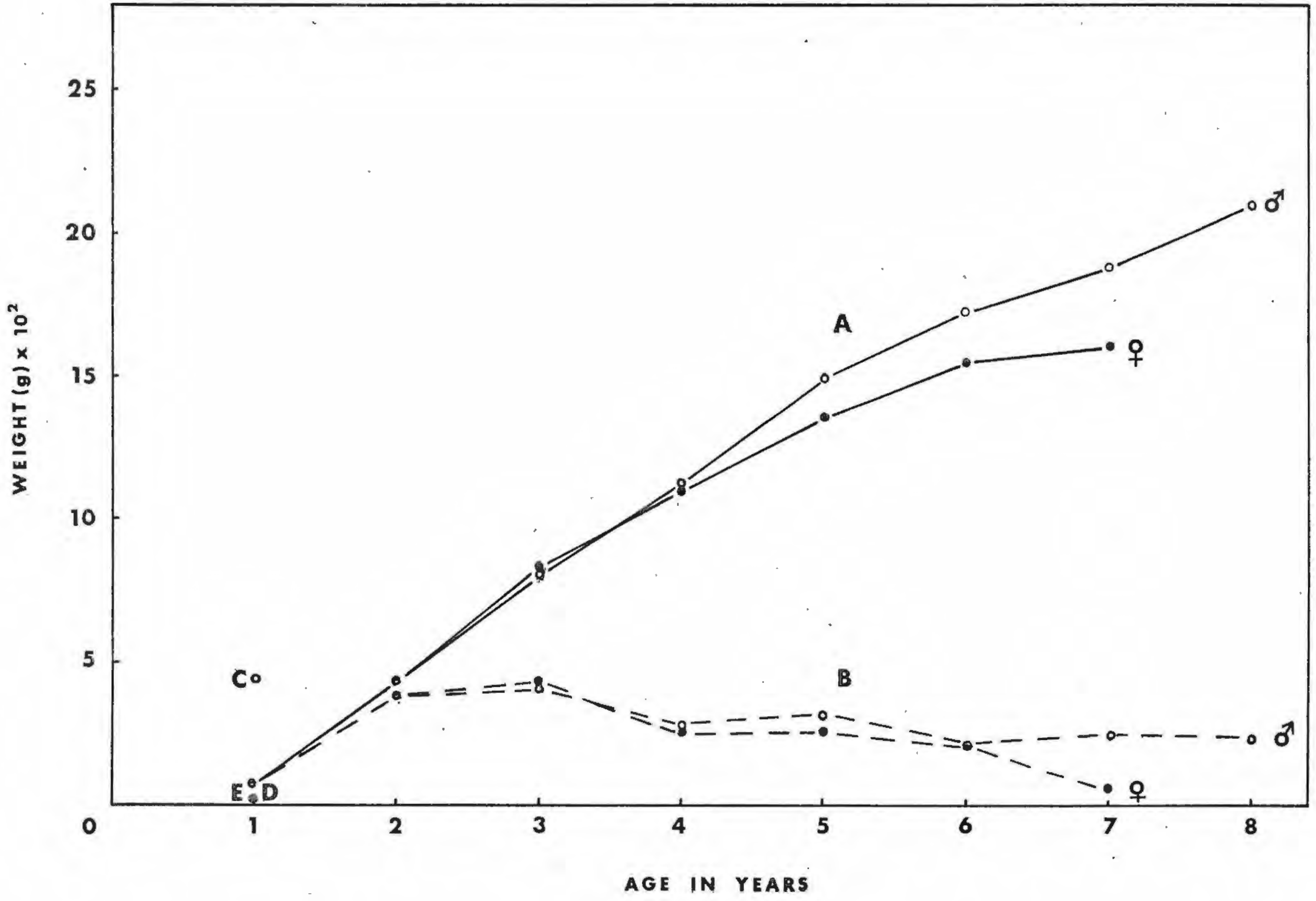


Figure 43: Growth in weight of C.gariepinus from Lake Sibaya and postulated weight after one year for other C.gariepinus populations. A. Weight increase and B. Weight increments for Sibaya catfish.
C. Weight after one year for catfish from Elands River (van der Waal & Schoonbee, 1975).
D. Weight after one year for catfish from Lower Shire River (Willoughby & Tweddle, 1976).
E. Weight after one year for catfish from Lake Kariba (Pivnicka, 1974).

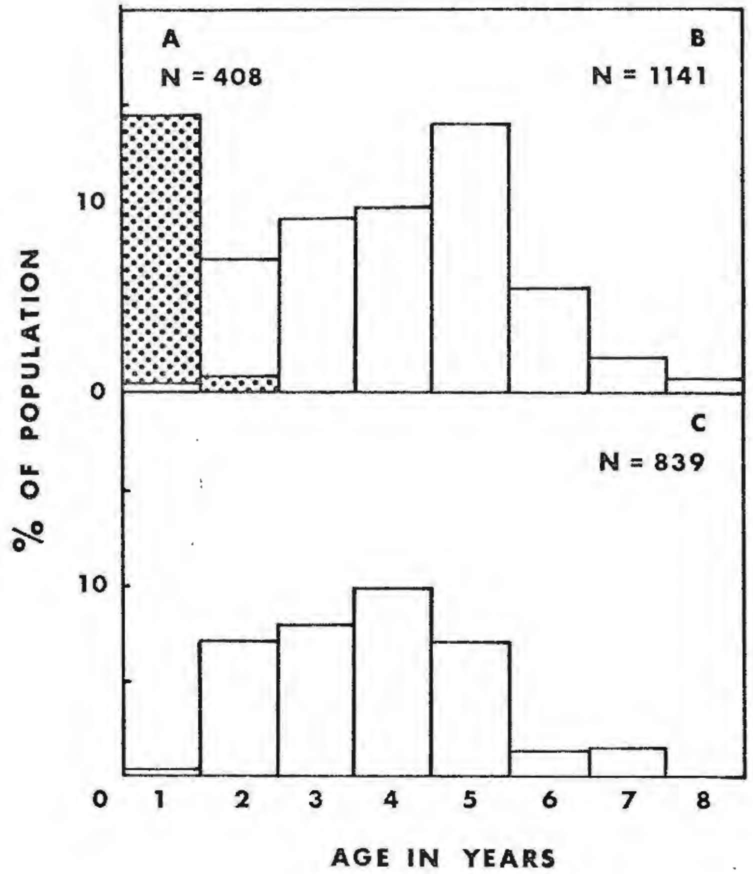


Figure 44: Age structure of C.gariepinus in Lake Sibaya based on average length-at-age data.

A. Juveniles

B. Males

C. Females

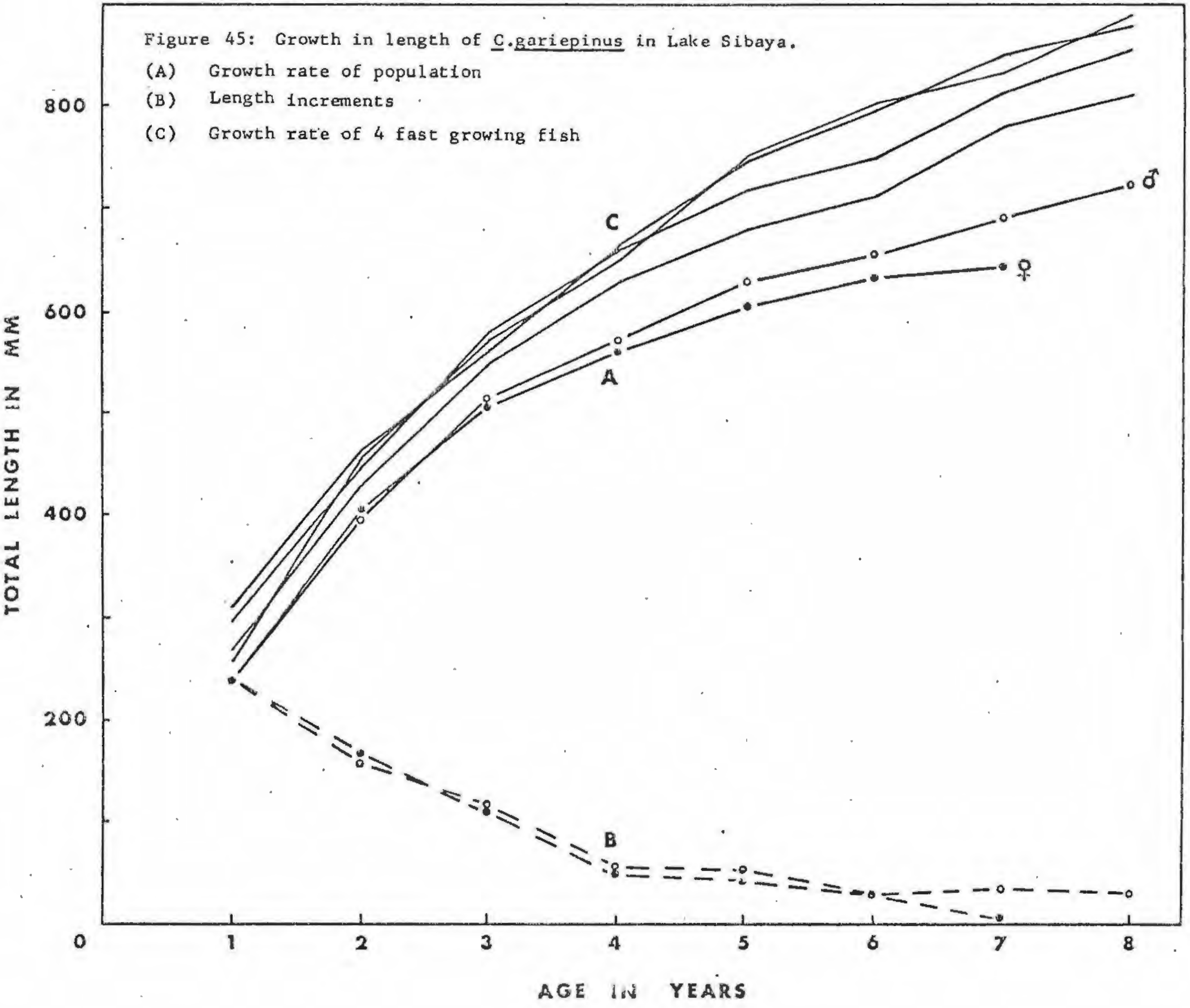


Figure 45: Growth in length of C.*gariepinus* in Lake Sibaya.

(A) Growth rate of population

(B) Length increments

(C) Growth rate of 4 fast growing fish

The first, a male which measured 666mm TL on release at an age of 6+ years, gained 60mm and lost 315g in 2,8 years. The second, a female which measured 610mm TL on release at an age of 5+ years, lost 8mm and gained 122g in 1,1 years. Both growth rates corresponded approximately to those given in Fig. 45.

Large catfish (> 700mm) are occasionally encountered in Lake Sibaya. Back calculations of growth rate from pectoral spine rings for four of these large catfish indicate that they attained a relatively high growth rate early in life which was maintained throughout life (Fig. 45). This phenomenon was also noted in aquaria where, as early as the second week, a small percentage of same-age catfish attain a larger size than the majority, and retained or increased this headstart in subsequent months.

The sizes of the largest male and female catfish caught in Lake Sibaya are given in Table 19. The largest catfish caught by Pike (1969) in Lake Sibaya weighed 6,2kg.

TABLE 19

Sizes of the largest C.gariepinus caught in Lake Sibaya

Sex	Total length (mm)	Weight (kg)
♂	1088	8,79
♂	947	5,84
♂	916	5,52
♀	1036	7,76
♀	1005	5,68
♀	951	6,18

Population structure and sex ratio

The length frequency of 408 juvenile, 839 female and 1141 males C.gariepinus caught in all habitats in Lake Sibaya is given in Fig. 46. The length mode in males was 580 - 590mm TL and in females 540 - 550mm TL. Over 1/3 of the population measured between 500 and 600mm TL. This marked clumping is explained by the sharp deceleration of growth rate between these lengths, as shown in Fig. 45 . The length distribution of both sexes is skewed to the right which indicates low catches of large fish. This result may be due in part to large fishes escaping the collecting gear, but underwater observations and the examination of over 400 spawning catfish confirmed that catfish over 650mm TL are rare in the population. Sampling methods may exert a strong influence on the supposed structure of a fish population. The length frequency of catfish caught by means of the six collection methods used in this study are given in Fig. 13 . Hand nets (including amaThonga fonya baskets)

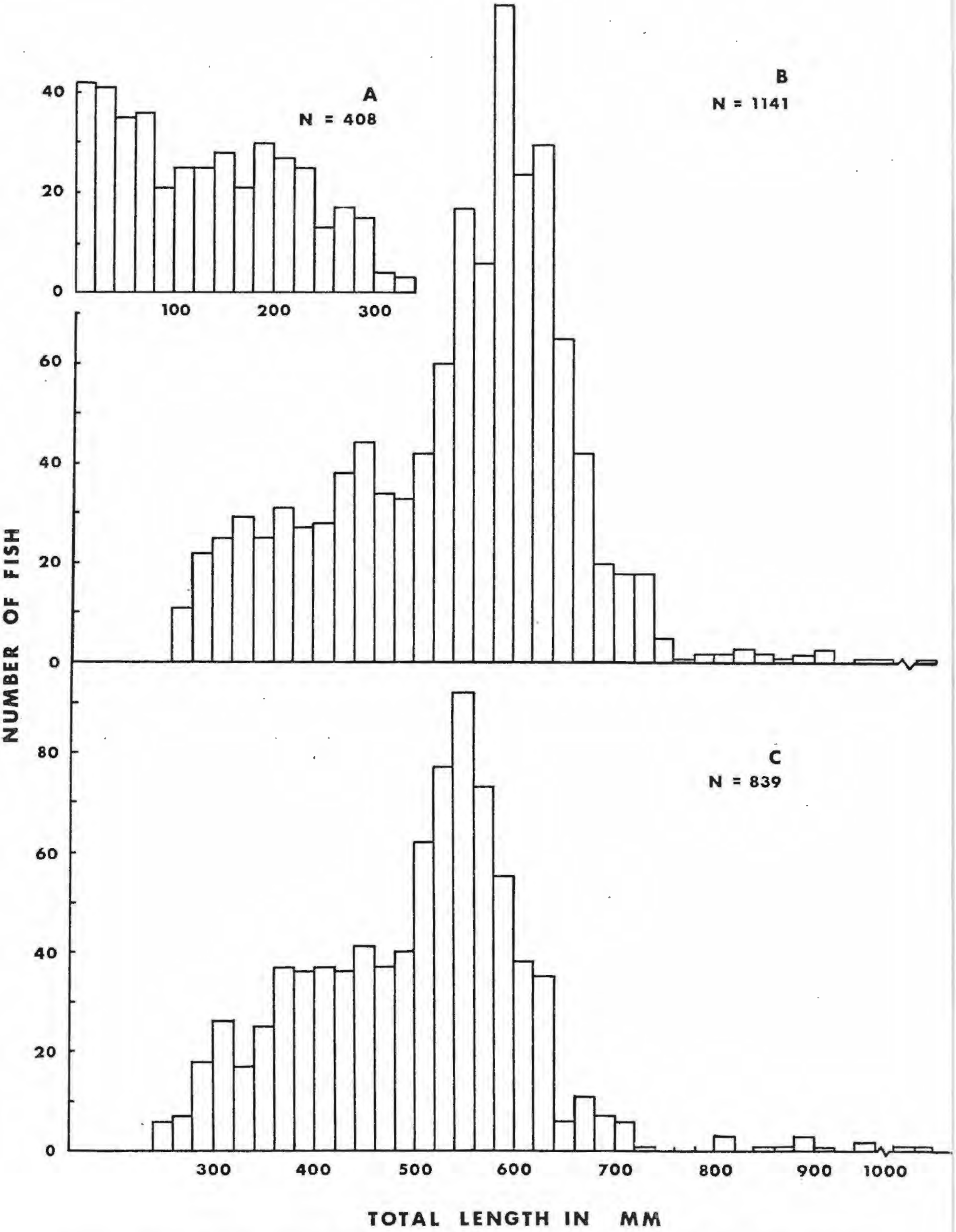


Figure 46: Total length structure of C.gariepinus from Lake Sibaya caught throughout the study period (1973-1976). A. Juveniles. B. Adult males. C. Adult females.

and rotenone, produced small catfish as well as adults on spawning runs. Valve traps, fixed lines and seine and trawl nets caught low numbers of juveniles and adults. The main methods used to sample the adult population were a fleet of gillnets (60, 80, 120 and 160mm stretch mesh multifilament nylon), and longlines. Although longlines and gillnets differ widely in their way of securing the catch, both gave similar population structures with modes between 540 and 590mm TL (Fig. 13). Their combined catches probably give an adequate representation of population structure. As both methods are efficient at catching large catfish,the low numbers of fishes >650mm TL must reflect a real trend in the population.

The overall sex ratio of 1980 C.gariepinus in Lake Sibaya was 1.36:1 in favour of males. Females exceeded males by a ratio of 1.13:1 to 500mm TL, but thereafter males were more abundant, and after 600mm TL, exceeded females by a ratio of 3,84:1. Males also exceeded females in large size groups of C.gariepinus in the Elands River (van der Waal, 1972), Pongola pans (Kok, pers.comm.), Hardap dam (Gaigher, in press) and Lower Shire River (Willoughby & Tweddle, 1976).

The size reached by C.gariepinus in southern Africa

The order Siluriformes includes some of the largest freshwater fishes in the world. Among them are the wels Siluris glanis from eastern Europe and western Russia which exceeded 4m in length and 270kg (Seeley, 1886) and Amazonian catfish Arapaima gigas and Brachyplatystoma spp. which exceed 3m and 100kg (Lowe-McConnell, 1975).

Two giant catfish occur in southern Africa. The largest is the vundu Heterobranchus longifilis which is distributed from the Nile and Congo basins southwards to the Zambezi river (Jubb, 1967) and reaches 47,63kg (Bell-Cross, 1976). Vundu which exceed 30kg are fairly common (Jubb, 1967). C.gariepinus is the second largest freshwater fish in southern Africa.

The largest C.gariepinus on record was caught in the Vaal River in 1898 and measured over 2m and 56,6kg (Bennion, 1923). Another giant, which weighed 37,66kg, was caught in the Vaal river in May 1970 (Hendley and Salomon, 1972). The largest catfish recorded from the major rivers and lakes of southern Africa are summarised in Table 20, with additional records of large catfish in Table 21. Few catfish exceed 30kg. Most giant specimens have been caught in large rivers, and Hardap dam on a tributary of the Orange river in South-West Africa is the only man-made impoundment or natural lake to have contributed a catfish exceeding 20kg.

Did C.gariepinus formerly reach a greater size in southern Africa? as found by Tsepkin and Sokolov (1971) in the beluga Huso huso (L) and Russian sturgeon Acipenser güldenstädti (Brandt) in Eurasia. Unfortunately, we have very little early material with which to make comparisons, but the indications

TABLE 20

Largest recorded C.gariepinus from the major lakes and rivers of southern Africa.

River system	Locality	Weight (kg)	Total Length (mm)	Sex	Date	Reference
Vaal	-	58.8	2000+		1898	Bennion (1923)
Vaal	-	37.66			5.70	Hendley & Salomon (1972)
Zambezi	Middle reaches	30.845			1947	Bell-Cross (1976)
Fish-Orange	Hardap Dam	25.164	1482	♀	12.12 1974	Gaigher (pers.comm. 1976)
Tugela	Three miles below ferry	23.84				Crass (1964)
Tuli-Limpopo	Mshelele dam	18.16			pre-1969	Donnelly, (pers. comm. 1976)
Pongola	Near Ndumu	17.25			7.1972	Tomkinson, (pers. comm. 1976)
Usutu	Banzi pan	14.98	1250	♀	1974	Tomkinson, (pers. comm. 1976)
Limpopo	Kruger National Park	12.71			1975	Braack (pers.comm. 1976)
Closed lake, Zululand	Lake Sibaya	8.79	1088	♂	8.75	This study
Shire-Zambezi	Just north of Chiromo	8.5	1000		20.11. 1975	Willoughby, (pers. comm. 1976)
Mtilikwe-Save	Lake Kyle	8.165	-			Minshull, (pers. comm. 1976)
Hunyane-Zambezi	Lake McIlwaine	5.98	990	♂	24.4 74	Clay, (pers.comm. 1976)
Zambezi	Lake Kariba	5.125	863	♂	1.2 74	Mitchell, (pers. comm. 1976)

TABLE 21

Other large *C.gariepinus* recorded from southern Africa

River System	Locality	Weight (g)	Total Length (mm)	Sex	Date Captured	Reference
Vaal	-	31.805			1968	S.A.Angling records (1976)
Vaal	-	24.535			1964	S.A.Angling records (1976)
Vaal	-	21.922			1968	S.A.Angling records (1976)
Orange	Upstream of Barkly West	18.5			1976	Diamond Field Advertiser, 11.5.76.
Orange	Verwoerd dam	18.035	1097	♂	9.9.75	Hamman (pers.comm.,1976)
Vaal	Vaaldam	17.72			1970	S.A.Angling records (1976)
Orange	Verwoerd dam	17.02	1175	♀	12.6.75	Hamman (pers.comm.,1976)
Orange	Verwoerd dam	16.089	1150	♀	15.10.75	Hamman (pers.comm.,1976)
Tuli-Limpopo	Maleme dam	15.55	1310		6.2.76	Donnelly (pers.comm., 1976).
Pongola	Mzinyeni pan	15.0	1110	♀	1.7.74	Kok (pers.comm.,1976)
Mooi-Vaal	Boskop dam	15.0	1140	♂	25.11.74	Meyer (pers.comm.,1976)
Mooi-Vaal	Boskop dam	14.939	1280	♂	17.7.74	Meyer (pers.comm.,1976)
Orange	Verwoerd dam	14.77	1140	♀	25.9.75	Hamman (pers.comm.,1976)
Pongola	Mzinyeni pan	14.0	1095	♀	21.8.74	Kok (pers.comm.,1976)
Tuli-Limpopo	Maleme dam	13.31			28.12.72	Donnelly (pers.comm.,1976)
Orange	Verwoerd dam	12.74	1220	♂	16.10.74	Hamman (pers.comm.,1976)
Limpopo	Kruger National Park	12.71			1975	Braack (pers.comm.,1976)
Usutu	Banzi pan	12.71	1100	♀	11.72	Tomkinson (pers.comm.,1976)
Pongola	Just below Jozini dam wall	12.267	1100	♀	1968	Pott (pers.comm.,1976)
Incomati	Sabie	11.35			1975	Braack (pers.comm.,1976)
Orange	Verwoerd dam	10.48	1220	♂	18.12.74	Hamman (pers.comm.,1976)
Usutu	Adjacent to Ndumu Game Reserve	10.44	1200	♀	12.72	Tomkinson (pers.comm.,1976)
Harts-Vaal	Barberspan	10.41	1040	♂	1965	Meyer (pers.comm.,1976)
Orange	Verwoerd dam	9.164	1250	♂	25.3.75	Hamman (pers.comm.,1976)
Tuli-Limpopo	Mpomopomo dam	9.08				Donnelly (pers.comm.,1976)
Olifants-Limpopo	Loskopdam	8.579	1110	♀	2.12.75	Meyer (pers.comm.,1976)
Olifants		7.78	1100	♀	1970	Meyer (pers.comm.,1976)

are that, if the 58,6kg specimen from the Vaal is regarded as exceptional, there has been no marked decrease in the size of C.gariepinus. Several giant catfish have been caught in the last 10 years, most of which came from the Vaal and Orange Rivers (Tables 20 and 21). According to Greenwood and Jubb (pers. comm., 1976), the available Clarias fossil material from Africa, though sparse, indicates that fishes of this genus did not formerly reach a greater size than today. This conclusion is supported by Skelton (pers.comm., 1976). He examined strandloper midden beds deposited circa 1820 along the Fish River in South West Africa and found that few C.gariepinus reached 600mm and only one specimen reached 1200mm. Early travellers reported large catfish in southern Africa, but none exceed the size reached today. Thus Nicolls and Eglington (1892) report that Clarias capensis (= C.gariepinus) may weigh 'upwards of 70 lbs' (31.7kg), and Bowker (in Mitford-Barberton, 1970) wrote in 1847 'Passed the Riet River ... with large deep pools of water containing fish of an enormous size, some weighing upwards of 60lbs' (27kg; the species referred to must be C.gariepinus). Baines (1850) reported specimens of 1290mm and 12kg from the Vaal River, and 1200mm and 12 kg from the Mooi River. Other early travellers caught catfish weighing between five and 10kg (e.g. Chapman, 1868; Holub, 1881; Bryden, 1893).

The growth of other C.gariepinus populations

Pivnicka (1974) established the growth rate of C.gariepinus from Lake Kariba using rings on the vertebrae. Pivnicka assumed that vertebral rings were laid down once a year, and that the first ring was formed in the first year. An adequate sample (72) was available from only one locality. According to his back-calculated (standard) lengths, catfish were 4 years old at about 250mm and 6 years old at about 380mm. This growth rate is considerably slower than that reported here for catfish from Lake Sibaya.

Van der Waal and Schoonbee (1975) reported a different growth pattern for C.gariepinus from the Elands River, in which water temperatures ranged between 12^o - 28^oC (Schoonbee, pers.comm.). Their first year length increment was 426mm in males and 414mm in females, which is about 40% higher than that given here. Their technique relied on the use of known-age fish from production ponds some distance from the Elands River to establish the age at which the first pectoral spine ring was formed. Clarias are known to exhibit high growth rates in culture ponds e.g. C.mossambicus reached 900 and 2400g after one and two years respectively in culture ponds in Zambia (Mortimer, 1964). Van der Waal & Schoonbee's known-age fish in ponds may have grown faster than the catfish in the rivers. The first year ring in river catfish may not have been detectible, as in Sibaya, so that the mean length at the first spine ring could be the length after two years. If so, their postulated growth rate would be similar to that in Sibaya to 5+ years. However, the patterns of growth are dissimilar, as the Transvaal catfish showed no marked decline in growth rate with increasing age.

Van der Waal & Schoonbee (1975) stress that their results are based on small numbers of 6+ and older catfishes. They nevertheless state that there is no visible decline in growth rate with increasing age. Their data points for older fish are likely to be influenced by the growth histories of these individuals. I have shown that large Sibaya catfish (>700mm TL) grow faster than the general population (Fig. 45). The older Elands River catfish are also likely to be faster growing individuals in the population. Inclusion of their lengths in van der Waal and Schoonbee's growth curve gives the impression that growth rates are nearly linear but this pattern probably does not reflect that of the general population.

Willoughby and Tweddle (1976) also used vertebrae for ageing *C.gariepinus*. They based their determinations on 567 males and 468 females caught in marshes of the lower Shire River in Malawi. The pattern of growth of the Malawi catfish was very similar to that in Sibaya, but the growth rate was slightly slower. Average back calculated total lengths after one, two, three and four years were about 220, 320, 400 and 490mm respectively, i.e. 8% lower than the Sibaya figure after one year, and 14 - 22% lower in subsequent years. Males grew faster than females after 3 years, as in Lake Sibaya.

Comparison of the population structure and length-weight relationship of four *C.gariepinus* populations

In Fig. 47 the length frequency of four *C.gariepinus* populations is compared. The Pongola sample was taken by Kok (pers.comm., 1976) from shallow pans along the flood-plain of the Pongola river in north-eastern Zululand. No river catfish were included in the sample. The Elands River collection was made by van der Waal (1972) in the south-eastern Transvaal. Gaigher (pers.comm., 1976) collected his sample from Hardap dam, a large man-made impoundment on the upper reaches of the Fish River, a northern tributary of the Orange River in South West Africa. The Sibaya collection is the only one which adequately sampled juvenile catfish <200mm TL.

The length mode of the Sibaya population is 100-120mm higher than that of the Pongola and Elands River populations, whereas the modal length of Hardap dam catfish is far higher (> 700mm TL). The Pongola and Hardap populations have relatively high proportions of larger catfish (>700mm TL).

Length frequencies may overemphasize the size of fish in a population if the fish are in poor condition. Populations should therefore be compared by weight structure and length-weight relationship as well.

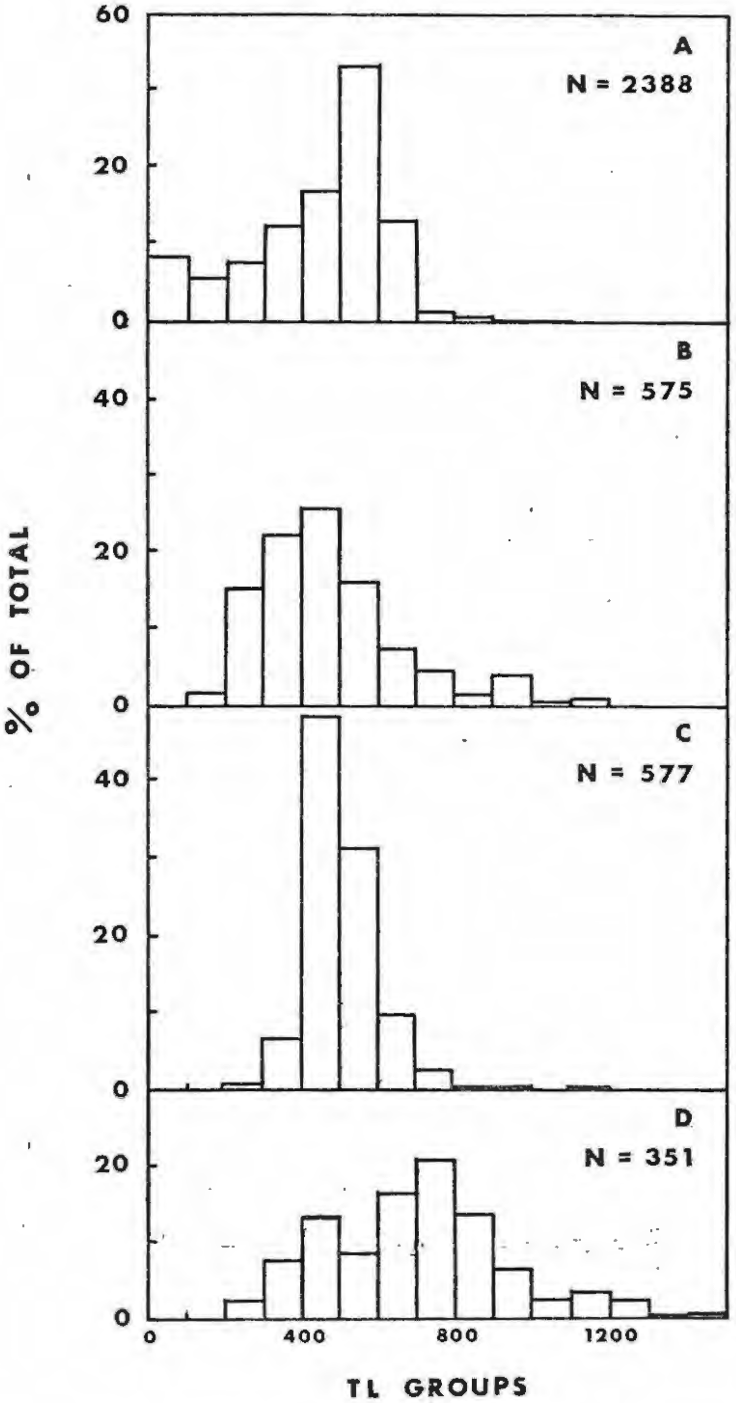


Figure 47: Length frequency of C.gariepinus from Lake Sibaya (A); Pongola pans (B, Kok, pers.comm.); Elands river (C, van der Waal, 1972) and Hardap dam (D, Gaigher, pers.comm.).

The weight structure of three catfish populations is compared in Fig. 48 (the relevant data on the Elands River population were not available to me). Although the Pongola catfish had a smaller length mode, their weight structure is similar to that of the Sibaya population. The Hardap dam population has a different weight structure with a very high component of large catfish. This trend is emphasized by the following set of figures.

	Percentage of catfish $>$2kg
Lake Sibaya	4,1
Pongola River pans	17,4
Hardap dam	62,8

(Pongola and Hardap dam figures calculated from data supplied by Kok (pers. comm., 1976) and Gaigher (pers.comm., 1976) respectively).

In Fig. 49 the length:weight relationship of juvenile catfish from the four populations is compared. There is no marked difference between the populations until a length of 350mm TL.

The length-weight relationship of adult male catfish from the four populations is compared in Fig. 50. Females were not used as ovary weight at different stages of maturation may confuse the length:weight relationship. This relationship is about the same for the four populations in the range 350-500mm TL. In larger size groups there are distinct differences which reflect differences in relative condition or 'fatness'. Large Sibaya catfish are in poor condition whereas Pongola catfish are in good condition. Hardap dam and Elands River catfish are in an intermediate position. It is important to realize that these observations are based on population parameters - comparisons of individual thin and fat fishes from the different populations would be worthless.

The excellent condition of the Pongola catfish is emphasized by the following set of figures which give the average weight at 1000mm TL for the four populations, calculated from the length:weight relationship of each population.

	C.gariepinus population	Average weight at 1000mm TL	% of D
A	Lake Sibaya	5539g	57
B	Elands River	6971g	72
C	Hardap Dam	7078g	73
D	Pongola river pans	9681g	100

In summary, the condition of C.gariepinus in Lake Sibaya is similar to that in three other populations to a length of about 500mm TL. In larger size groups Sibaya catfish are in poor condition.

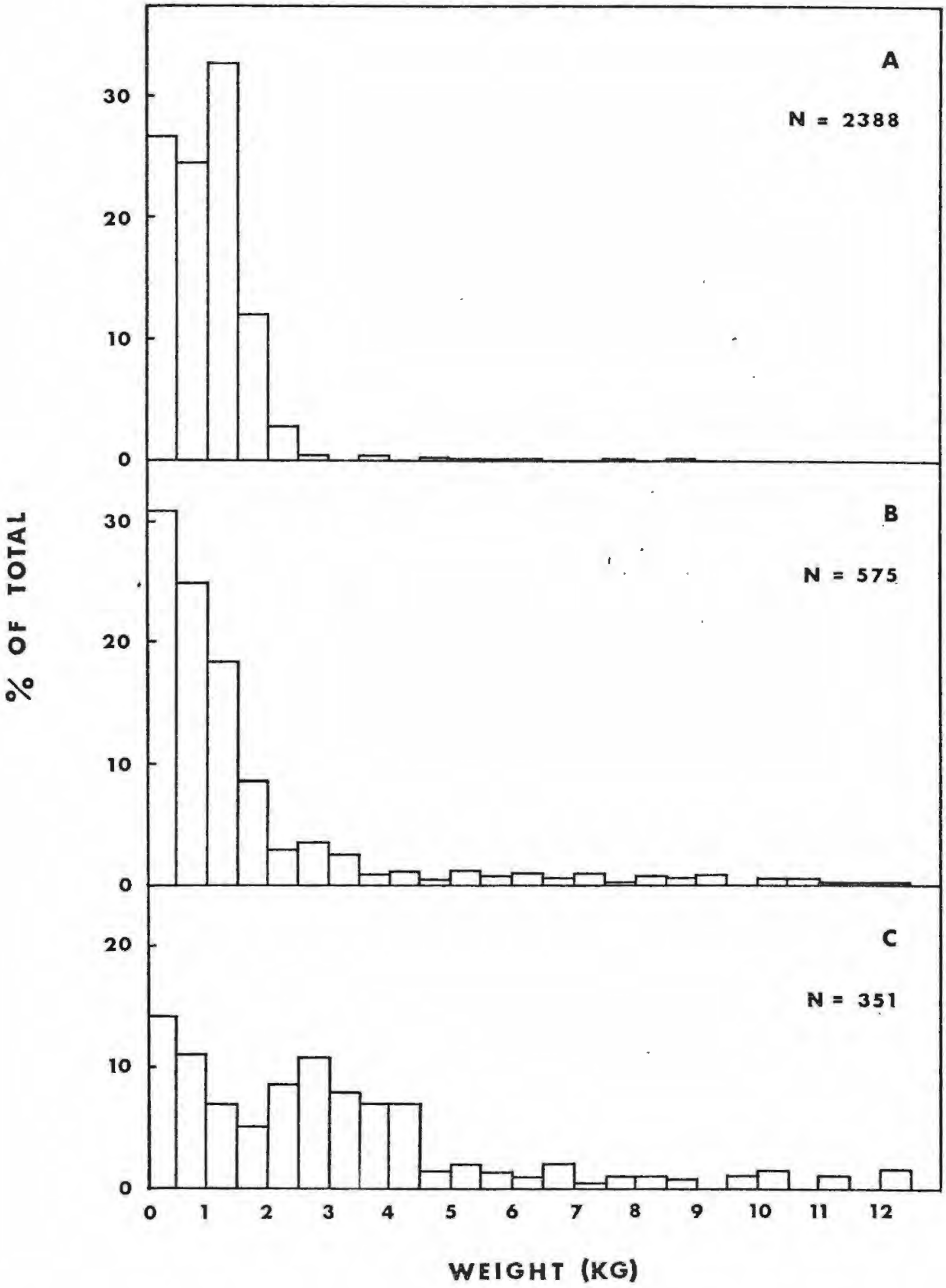


Figure 48: The weight structure of three C.gariepinus populations

A. Lake Sibaya

B. Pongola river pans (Kok, pers.comm.)

C. Hardap dam (Gaigher, pers.comm.)

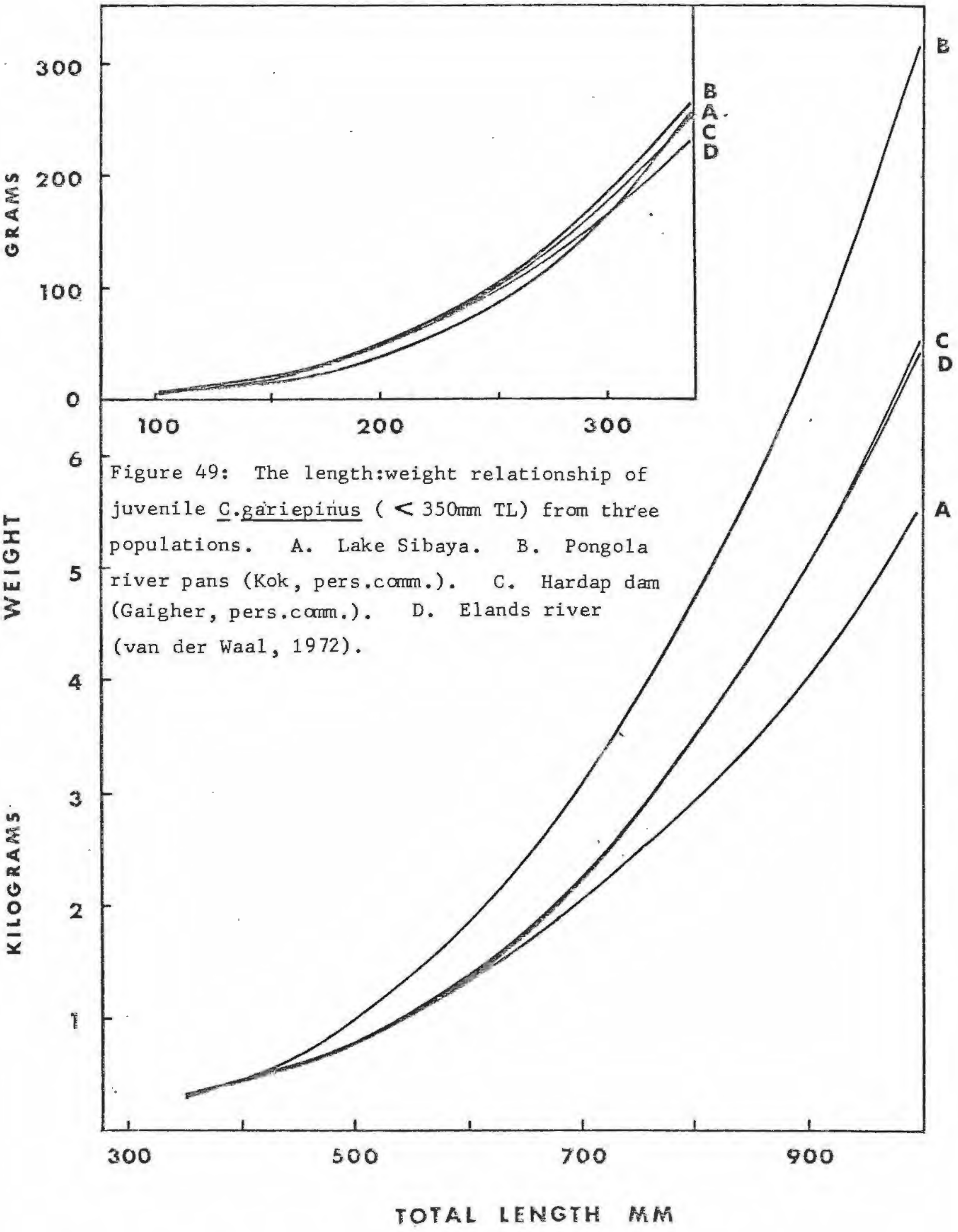


Figure 49: The length:weight relationship of juvenile C.gariepinus ($<$ 350mm TL) from three populations. A. Lake Sibaya. B. Pongola river pans (Kok, pers.comm.). C. Hardap dam (Gaigher, pers.comm.). D. Elands river (van der Waal, 1972).

Figure 50: The length:weight relationship of adult male C.gariepinus ($>$ 350mm TL) from three populations.

A. Lake Sibaya: $W = 0{,}00004\ TL^{2.699}$ (R^2=0,92, N=355)

B. Pongola river pans: $W = 0{,}000003\ TL^{3.169}$ (R^2=0,98, N=165)

C. Hardap dam: $W = 0{,}000004\ TL^{3.071}$ (R^2=0,95, N=139)

D. Elands river, (van der Waal, 1972).

FOOD AND FEEDING BEHAVIOUR OF C.GARIEPINUS IN LAKE SIBAYA

INTRODUCTION

The way in which a mesotrophic, closed lake supports an abundant population of large, primarily riverine predators, is examined in this chapter. Two strategies are possible: (a) the predator is euryphagic, feeding on a wide variety of organisms

(b) the predator is stenophagic, but its chosen food is abundant and easily caught.

Catfish are shown here to use the first strategy. Their impressive array of anatomical adaptations for feeding (reviewed in the first part of this chapter) allow catfish 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 and density of the prey. In the second part of this chapter the food preferences of catfish in Lake Sibaya are examined in detail as an example of the way in which an omnivorous predator utilises the resources of a lake which differ widely in quantity and quality. This point is emphasized by comparing the catfish's diet at different lake levels. Finally, the food preferences of other Clarias populations in Africa are compared.

The only previous study of catfish feeding in Lake Sibaya is by Minshull (1969) who examined 53 specimens. Crustacea, mainly H.orbiculare formed 44% of the food and fish, mainly small cichlids and G.giurus, 32%. Other food items were insects, mainly terrestrial forms (12%), gastropods (10%), small quantities of the alga Botryococcus braunii, and diatoms.

METHODS

Determination of feeding behaviour and food preferences

Field observations on feeding behaviour, which cover a 3½ year period from 1973 to mid-1976, were made from boats, a 7m high tower in shallow water, and using SCUBA and free-diving gear. Catfish for food analyses were collected in three stages (Table 22). 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.

TABLE 22

Catfish caught for food preference analyses in Lake Sibaya

	Time Period	Lake level range (m)	Collecting Methods	No. catfish caught (with stomach contents)	TL range (mm)
1.	1970-1972	0,92-1,71	seine net, rod and line	92	300-700
2.	Jan1974-Dec1975	1,83-3,03	longlines, gillnets handnets	469	12-1088
3.	March-Apr 1976	3,86-3,98	longlines, gillnets, handnets	123	246-836

As the collections were made at low, intermediate and high lake levels, the effect of the changing ecology of marginal areas on catfish diet 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 analyses 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. Thus, 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 after poisoning. However, newly-ingested fish, as well as long-line bait, could readily be distinguished from real prey.

Regularly serviced longlines and gillnets provided the best fish 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 items such as H.orbiculare, M.tuberculata and B.capillatus and small fish was obtained, but very small items such as G.lignorum and chironomids, and large items such as P.sidneyi and S.mossambicus, were not always removed successfully. This method was therefore not used.

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 0,01gm. 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 body parameter to dry weight.

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 by up to 60%. Reconstructed weights are regularly used in Russia (vide Popova, 1967), but rarely elsewhere. 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 (G.lignorum, C.nilotica and cichlid fry represented 28,3%, 11,0% and 7,0% of all prey) indicating that stomachs were examined before digestion of these items. Catfish ingesting only parts of prey would also bias results - only two such incidents were recorded when one leg each of P.sidneyi was taken.

Careful consideration was given to the method of expressing food preferences. At least fourteen useful methods have been suggested by various authors (Hess and Swartz 1941; Hynes, 1950; Pillay, 1952; Ivlev, 1961; Karamchandani and Desai, 1961; the workers mentioned by Windell 1968; Hellawell and Abel, 1970; Hobson, 1974). 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 determined by the frequency method. A composite analysis, combining the placings of the other three methods, was also used.

RESULTS

Anatomical adaptations to feeding

Catfish have a remarkable array of anatomical adaptations and behavioural patterns for feeding which allow them to take prey ranging in size from a minute plankter to a fish half their own length. They can thus feed on whichever prey is in greatest abundance. Euryphagy is an important adaptation to fish feeding in a variety of habitats and in fluctuating marginal areas of lakes and rivers, and the means by which it is accomplished by catfish is therefore discussed in detail here.

Gosline (1973) considers that the ancestral cypriniform fish from which the modern catfish (Siluriformes, of Rosen and Greenwood, 1970) 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 specialisations for feeding found in modern catfish have probably been tailored by two major factors (a) their benthic feeding habit (b) their predominantly nocturnal activity. Catfish also have the ability to feed in midwater and at the surface, as well as during the day.

The mouths of benthophage fishes vary widely in form from small to large, protrusible or non-protrusible, and with a large or small gape; depending on the method of food collection. The wide mouth (Fig. 51), vertical gape, long circum-oral barbels, and ability to depress the hyomandibular apparatus are anatomical features which facilitate the mode of benthic feeding practised by catfish i.e. 'sink' sucking (described below). The dorso-ventrally depressed head, and retention of pectoral fins in a high abdominal position to act as hydrofoils to counteract the lifting effect of the enlarged anal and caudal fins, are adaptations for swimming near the substrate. As shown below, the mouth and barbels, and planing surfaces, are also well-

Figure 51: C.gariepinus showing wide mouth, four pairs of circumoral barbels and small eyes. Photo: C. Bruton.

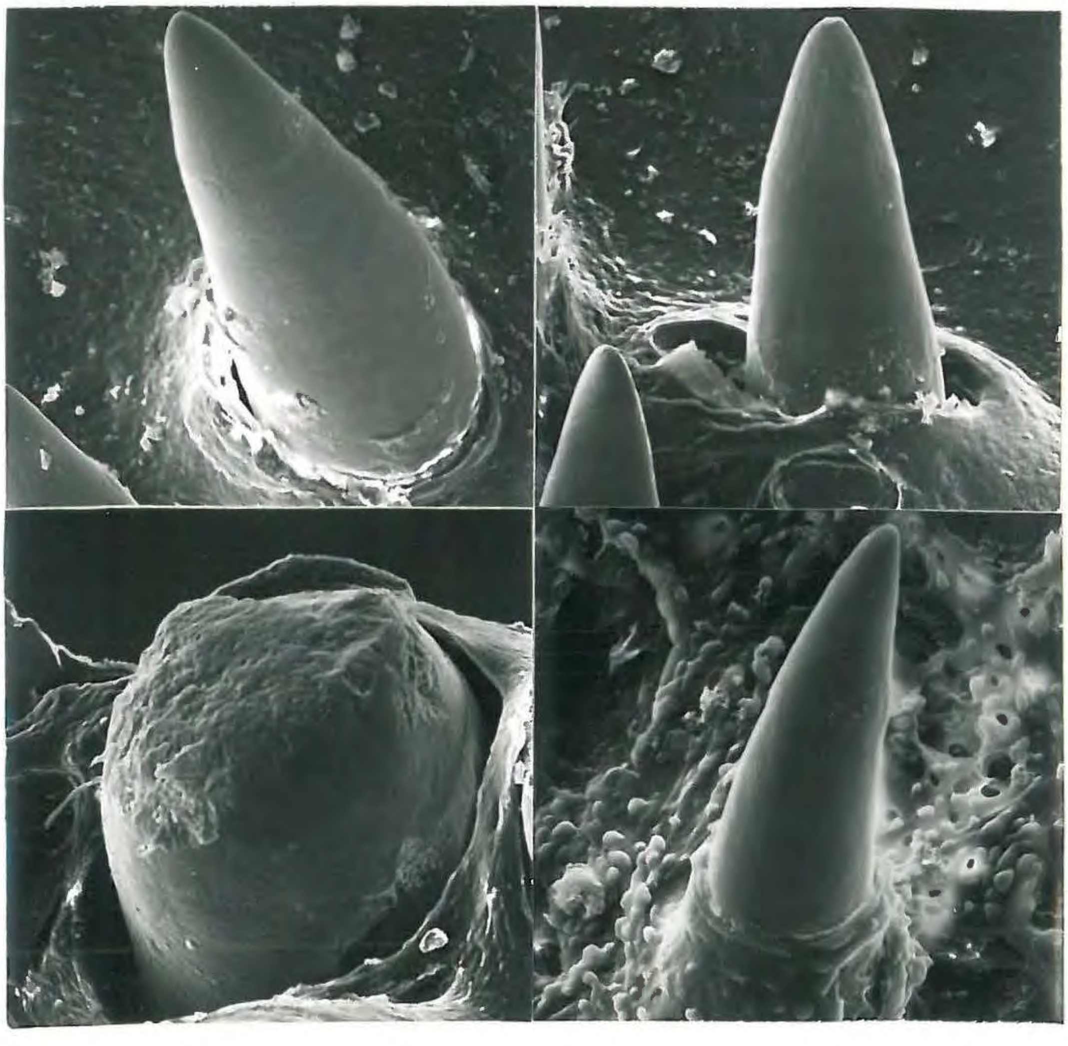


Figure 52: The teeth of C.gariepinus in Lake Sibaya. A: Maxillary; B: Mandibular; C: Vomerine; D: Pharyngeal; Magnification 150x.

adapted for certain types of surface feeding. The catfish has a wide, rounded caudal fin typical of fishes which lunge suddenly at their prey, in contrast to fast-moving predators, such as the tigerfish Hydrocynus vittatus 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 independant 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 (Angelopoulo, 1947) and the further evolution of the suck and bite method of food intake. The sensory equipment of C.gariepinus is adapted to nocturnal feeding in common with many other siluroids (e.g. Ictalurus lacustris punctatus, Bailey and Harrison, 1948; Guianaian catfish, Lowe-McConnell (1975).

C.gariepinus is equipped with four pairs of unbranched barbels of which the maxillary is the largest 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 (see chapter on 'Breeding'). Movable barbels projecting radially from the head enable catfish to scan a much larger volume of water. Upon contacting a food item, the catfish immediately turns towards the prey and lunges 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 nebulosus 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 limits the chance of escape by prey.

Catfish eyes are small and have 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 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 to100mm 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. The eyes may, however, be used to direct catfish to surface disturbances e.g. those caused by struggling insects, as catfish were immediately attracted to a disturbance even from a depth of three to four metres. The exact position of the prey was detected using the barbels. Movements of other catfish, and changes in light intensity, are doubtless also sensed visually. The role of olfaction in prey detection is unknown in C.gariepinus but likely to be important as in Ictalurus (Herrick, 1903 in Alexander, 1965). Clarias also have electric receptors although they produce no continuous electric current themselves (Lissman and Machin, 1963). In summary, long-range prey detection is probably by taste, olfaction and, to a lesser extent, sight; short-range detection is by direct contact with the prey or its eddies, usually via the barbels.

The posterior half of the body is compressed and muscular with a wide caudal peduncle and large rounded caudal fin (truncate in Kariba C.gariepinus) 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-loded swim bladder (as in C.mossambicus, Gee, 1970) connected to the oesophagus via a narrow pneumatic duct (Angelopoulo, 1947; Petrick, 1975). According to Alexander (1965) the swim bladder of Clarias 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 catfish 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. During rapid bottom foraging, the buoyant effect of air in the suprabranchial chamber is overcome by swimming forward and using the flattened head and pectoral fins as depressors. Between feeding bursts, catfish rest with the body at an angle of $20\text{-}90^{\circ}$ from the substrate when air is in the chamber, or flat on the substrate when 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.

The mouth 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 orobranchial chamber is increased by lowering the hyoid apparatus, thus creating a gaping hole in the vicinity of the food into which flows water surrounding the item (Gosline, 1973; and personal observations). This gross form of suction, a 'sink' effect, is in contrast to the more specialised '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, which feeds in a similar way to C.gariepinus, develops a negative pressure of -80cm which may be retained for 60msec, when feeding. Tanaka (1973) demonstrated in the nurse shark Ginglymostoma cirratum 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 teeth on the premaxillary and dentary bones. The vomerine (on the prevomer) 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.

Teeth are numerous, small, cardiform and backwardly directed. Maxillary, mandibular and pharyngeal teeth are conical and sharp, whereas the vomerine band has mainly granular molar-like teeth with a few conical teeth on the distal margins (Fig. 52). 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 must take place against the dentary bone or floor of the mouth cavity 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.53; and Jubb, 1967) as found in C.mossambicus (Worthington, 1933), C.lazera (Mills, 1956) and C.senegalensis (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 400mm TL do not feed on zooplankton (Munro, 1967; Schoonbee, 1969; Bowmaker, 1973, in C.gariepinus; Jackson, 1961a, in C.mossambicus) whereas large fishes do. Murray found that 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 here) and relative size or absolute volume of buccal cavity, or the habitat occupied by juveniles, were offered as explanations for a lack of filter-feeding in juveniles.

The mean width between developed gillrakers varied between $<0,1$ to 0,6mm, (Murray, 1975), thus allowing retention of plankton of greater minimum width than the above figures.

The oesophagus is short, muscular and dilatable, and opens into a distinct distendible flask-like stomach (typical of carnivores, Weatherley, 1963).

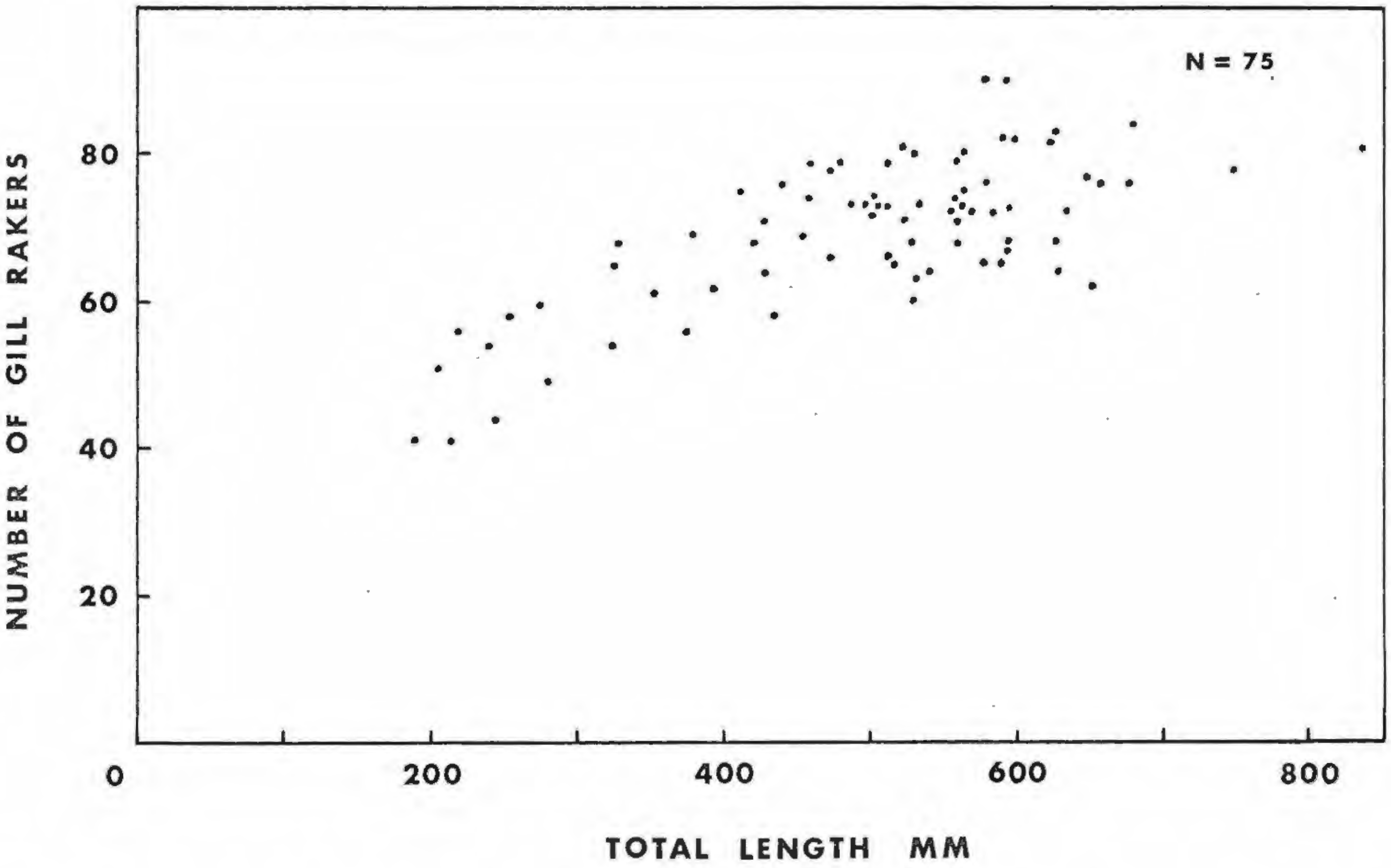


Figure 53: Scatter diagram of the number of gillrakers on the first gill arch against total length in *C.gariepinus* from Lake Sibaya.

The intestine, which is simple, thin-walled and moderately short, lacks pyloric caeca. Little mastication is performed on the prey, as considerable tumbling in the stomach facilitates digestion. Mechanical digestion was followed in C.gariepinus using the X-ray method of Molnar et al, (1967). In two experiments (X-ray exposure time 0,5secs, 65KV) prey was tumbled through 180° several times in the first three hours. In Siluris glanis, prey is turned throughout the digestion period (Molnar et al, 1967). Gastric digestion lasts about six hours (see below) after which hard parts (bones, scales, shells, carapaces) are voided into the intestine.

There are no studies on digestion in C.gariepinus but some information is available on C.mossambicus. Cockson and Bourne (1972) found protease in the stomach and intestine of C.mossambicus with maximal activity at pH4 and pH6 in each tissue. Enzyme activity in the stomach was about four times that in the intestine.

Feeding behaviour of catfish

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, Fig. 54).

(a) Individual foraging (Fig. 54A:) the normal mode of feeding in terrace and profundal habitats and plant beds. Catfish swim slowly forward, swaying the head slightly from side to side with the barbels extended forwards in a cone. When a prey is detected or flushed, the catfish darts rapidly and accurately forward. Typically, the predator-prey interaction was not prolonged. If a lunge was unsuccessful, the predator continued 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 transversed are favoured over those just unsuccessfully explored, and the locality where a 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 the 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. Ware (1973) found that prey activity, exposure, density and size were the

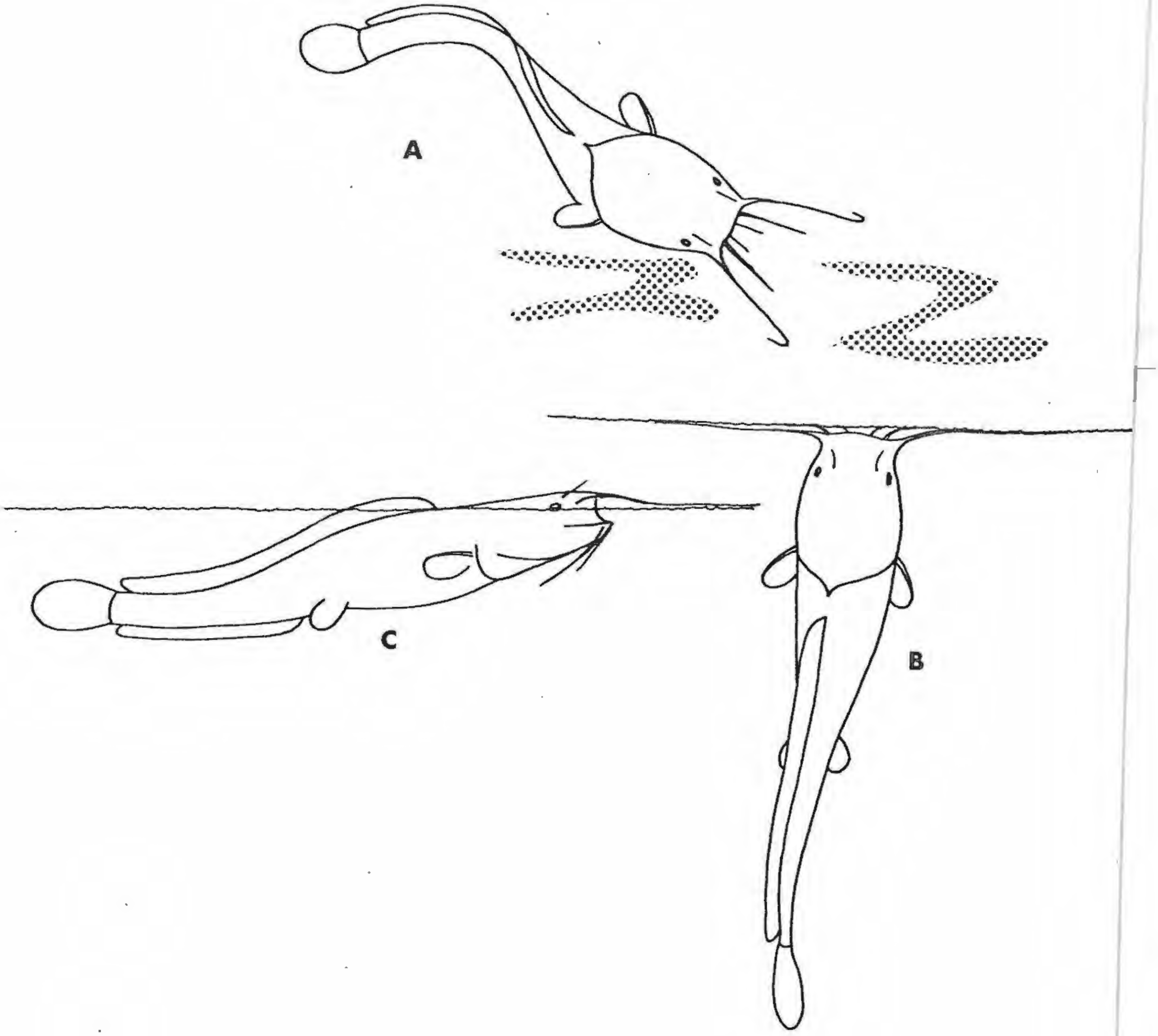


Figure 54: Feeding behaviour of C.gariepinus.

A. Individual foraging.

B. Perpendicular surface feeding.

C. Horizontal surface feeding, (sometimes performed in groups).

four major determinants of prey risk to visual fish predators on epibenthic organisms.

Organisms caught during benthic foraging include G.lignorum, Pontogeloides latipes, Cyathura carinata, Chironomidae, Bellamya capillatus, Melanoides tuberculata, Bulinus spp, Potamon sidneyi, Hymenosoma orbiculare and gobiid and cichlid fish. The catfish rarely venture further than 1m from the substrate when foraging, so that midwater fish in sheltered areas e.g. Tilapia sparrmanii, T.rendalli swierstrae, Gilchristella aestuarius, Atherina breviceps and Barbus paludinosus, are rarely taken.

When stationary, catfish erect the barbels in a cone in front of the head; any prey touching the barbels is immediately detected and grabbed (this observation has also been reported by Jubb, 1965).

(b) Individual shovelling: Where deposits of detritus such as decomposing Scirpus stems cover the substrate, catfish feed 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 odonatid nymphs, Caridina nilotica, chironomids and M.tuberculata. 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 catfish ($<$ 200mmTL) occasionally feed by positioning the body perpendicularly with the barbels spread across the water surface (Fig. 54B). 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 the tail, or, in very small catfish, by positive buoyancy and the surface tension of the water on the outspread barbels.

Larger catfish 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 when debris, molluscs, and terrestrial insects formed a scum on the water surface. Catfish, numbering up to 50 or 60, form a dense crescent-shaped group and bob up and down so that the mouth is alternately partially exposed and submerged. On rising, a strong current of water and scum is sucked into the mouth.

After three or more minutes at one place the group moved slowly to another site one to two metres distant, holding their near vertical position as they moved. Alternatively they all submerged and swam horizontally beneath the surface to another site where they reappeared and resumed the same feeding routine. This behaviour continued for about 40 minutes.

(d) Formation feeding: Co-operative hunting in catfish is further refined during formation feeding at the water surface and in shallow water.

Five observations were made of surface formation feeding (Fig.54C), all between 20h00 and 01h00 on dark nights over deep water (20-35m).

Small groups of adult catfish (estimated TL 400-600mm) swam slowly in the same direction with the mouth wide open and the upper jaw protruding slightly above the water surface. The maxillary barbels were spread out over the water surface at an angle of about 45°, and could have functioned as a uni-dimensional funnel to direct food items on the water surface into the mouth. Catfish were orientated at an angle of 20-40° from the horizontal, and kept the mouth open for up to 30 secs before suddenly snapping it closed, submerging momentarily as a group, and then resuming passive filter-feeding again, usually in a slightly different direction. Group size ranged from 3 to 13 (average 7) individuals and individual distances were about 0,5 to 3 TL. Unfortunately no surface feeding catfishes could be caught. Several sources of food are available to these fishes:

(a) flotsam, mainly flying insects caught in the surface film,
(b) neuston, especially the alga Botryococcus braunii which occasionally accumulates in large colonies, 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 0,5mm (as found in C.gariepinus; Murray, 1975).

Zooplankters are generally sparse in Lake Sibaya, and although they undergo a vertical migration at night, 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 heavy wind. White bass Roccus chrysops in Lake Mendota, Wisconsin, feed in compact shoals on aggregations of Daphnia along foam lines, roll vortices and in zones of horizontal convergence on the leeward side of shoal areas (McNaught and Hasler, 1961). Eggers (1976), on theoretical grounds, showed that schooling behaviour in planktivorous fish has selective advantage if the predators are widely spaced while feeding (as observed), or if the prey have a clumped distribution (as in the convergence zone of Langmuir spirals).

Bowmaker (1973) described identical 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'. Catfish caught in the open lake had fed mainly on plankton, especially Diaphanosoma spp. and a diaptomid spp. Jubb (pers.comm., 1976) observed vundu Heterobranchus longifilis (another southern African clariid) surface formation feeding in Lake Kariba. Their stomachs contained large quantities of plankton. During surface formation feeding, both Clarias and Heterobranchus swim with the mouth held open in a fixed position, 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 the wavyback skipjack Euthynnus affinus that the feeding mechanism is virtually dragfree when the mouth and orobranchial chamber are distended, and that the fish feeds by swimming over its food, rather than by sucking it in.

Shallow water formation feeding is performed by packs of catfish (400-800mm TL) along shallow gently-sloping sandy beaches and in sparsely-vegetated marginal pools. A tightly-knit group in a rough sickle-shape formation swim slowly inshore under the water surface with their mouths open, herding shoals of small (30-80mm TL) S.mossambicus, T.sparrmanii and P.philander. When a water depth of about 50-100mm is reached, the catfish suddenly close their mouths with a loud plop, then open their mouths again and swim forwards once more 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. Catfish under these circumstances keep their mouths open for up to 15 secs, swimming steadily inshore so that the prey are eventually encircled and form a dense, panic-stricken mass. Prey capture was apparently by chance as no grabbing or sucking movements were made by the catfish. However, many prey were captured as the open mouths formed a continuous line. When most of the prey had been eaten or dispersed, the catfish submerged and swam as a group into slightly deeper water further along the shore where formation feeding behaviour was repeated. This cycle may continue every few minutes for over an hour, although it usually terminated after 20-30 mins. The packs observed in Sibaya all numbered 15-40 individuals, but larger groups have been observed feeding in this way in the Dobi river, Botswana (Donnelly, 1966, in *C.ngamensis*, about 400 catfish) and in Nyamithi pan, Ndumu Game Reserve, Zululand (Pooley, 1972, in *C.gariepinus*, 75-100 catfish). According to Donnelly, *C.ngamensis* (from 0,5 to 1kg) were foraging upstream in column formation at the surface at a time when the river was subsiding. This behaviour occurred at about 03h00 to the accompaniment of loud noises produced every thirty secs 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 to 2,5 kg) surrounding small fish in very shallow water. Both Donnelly and Pooley report that prey were encircled in small inlets.

Similar, though less co-operative, social feeding behaviour was observed by van der Waal (pers.comm., 1976) and Bell-Cross (1974, 1976, pers.comm., 1976) in *C.gariepinus*. Van der Waal reports from Lake Liambezi in Caprivi that when the floods of the Zambezi recede young fish move back into the *Vassia* beds adjacent to river channels and here 'thousands' of *C.gariepinus* hunt in packs which chase prey fish to the surface. The panicking prey are caught amid loud clapping noises made by the catfish. The main prey were *Barbus paludinosus*, *B.haasianus*, *Nannochorax* spp. and small cichlids. *C.ngamensis* were also seen hunting in shoals for *Alestes lateralis*. Bell-Cross reports similar behaviour in *C.gariepinus* and *C.ngamensis* on floodplains in the Upper Zambezi. As the flood water recedes,small species, and juveniles of large species, moved into the main river. Packs of catfish patrolled the site and engulfed prey as they attempted to enter deeper water. The water depth at the point of capture was about 3m. The shoals of *Clarias* (with *C.gariepinus* far more numerous) numbered several hundred fishes in the range 1 to 10kg (average about 4kg). The prey numbered thousands and included mainly *Alestes lateralis*, *Micralestes acutidens*, *Nannochorax multifasciatus*, *Barbus fasciolatus*, *B.haasianus*, unidentified juvenile *Tilapia* and *Sarotherodon* spp., *Pseudocrenilabris philander* and *Ctenopoma multispinis*. Tait (1965) and Williams (1971) had previously noted heavy predation by *C.gariepinus* on small fishes, particularly *P.philander* under the same conditions in the Kafue catchment.

Discussion on social hunting

Social hunting is practised by a wide variety of animals including communal spiders and army ants (Wilson, 1972), marine fishes (review by Redakov, 1973), and birds and mammals (review by Curio, 1976). Most animals are facultative group hunters i.e. they only hunt in groups when the need arises. Others, such as wild dogs (Lawick-Goodall, 1970; for few exceptions see Kruuk, 1972) and most killer whales *Orcinus orca* (Martinez & Klinghammer, 1970) are obligate group hunters. In most cases, communal hunters herd the prey into shallow water or to the water surface where they are easier to catch or kill. For instance, I have observed marine kingfish *Caranx* spp. herding karanteen *Crenidens crenidens* and barred flagtail *Kuhlia taeniurus* into shallow water on the Zululand coast, and sharks herding mullet into the surf zone near St Lucia estuary. Van der Elst (pers.comm., 1976) observed Zambezi shark *Carcharhinus leucas* herding mullet, probably *Mugil cephalus*, and garrick *Lichia amia* surrounding *Pomatomus saltatrix* which in turn had cornered a shoal of piggies *Pomadasys olivaceum*. Hiatt & Brock (1948) observed black skipjack *Euthynnus haito* herding scads *Decapterus sanctaehelenae* and Bullis (1961) saw white tip sharks *Pterolamiops longimanus* panicking small tuna *Katsuvanus pelamis* and *Thunnus attenticus* which were then caught by the milling sharks. Greenwood (1963 a) describes how sand sharks *Carcharias taurus*, operating in shoals, herd blue-fishes *Pomatomus saltatrix* into a solid mass in shallow water before rushing in and seizing the prey. Eibl-Eibesfeldt (1962) and Redakov (1973) give several further examples. Attacks by groups of killer whales *O.orca* are characterised by a high level of group co-ordination and apparent communication between group members, and they may be among the most sophisticated predators in the world (Martinez & Klinghammer, 1970).

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

True co-operative hunting in catfish has three characteristics:

(a) the predator acting alone is less efficient in catching the prey involved than the pack

(b) the prey are herded into an area where they are spatially restricted (by removing one plane of escape as in surface feeding, or two as in shallow water feeding)

(c) the prey become disorientated by the pack of predators, and lose their normal defensive shoaling synchronisation.

Curio (1976) reviewed communal hunting in animals, and agreed with Kruuk (1972) that, at least in mammals, '<u>the</u> function of social hunting is the ability to overcome prey much larger or faster than the predators themselves'.

In some fishes, such as piranhas (Markl, 1972; Lowe-McConnell, 1975) communal hunting facilitates the overpowering of very large prey, but in most fishes its main function is the capture of prey which is normally too fast or manoevrable. Shoaling by prey is an effective defense mechanism against an individual predator (Brock & Riffenburgh, 1960; Neill & Cullen, 1974), but when more than one predator is involved the prey are easily disorientated by the diverse movements of the predators, and may lose their strict shoaling synchronisation. As a result, more individuals may momentarily stray out of the shoal and be snapped up by predators. When the pack of predators is large, the prey eventually become so disorientated and panic-stricken that they are easily caught by the predators, even if the latter merely advance with their mouths wide open.

Feeding periodicity

<u>C.gariepinus</u> is described as nocturnal by most workers, but no quantitative data have been presented, nor has their diel activity in dark profundal zones been investigated.

Evidence from gillnetting, longlining, underwater observations using SCUBA, and above water observations from a 7m tower in shallow water, indicate that catfish in Sibaya more often enter shallow terrace waters at night, and that they are active during the day and night in sheltered bay and profundal habitats. Typical standardised gillnet catches on the terrace day and night for three to six days show a repeated pattern with higher catches (hence activity) at night (Fig. 55). The ratio of day and night catches or observations using gillnets, longlines, SCUBA and the tower also indicated higher shallow water activity at night (Table 23). The higher ratios when the terraces were less than 2m deep, are explained by the very low daytime incidence of catfish in shallow water. Catfish entered terrace waters more often when the depth of the terrace exceeded 2m. Gillnet catches in sheltered bay and profundal habitats were nearly equal day and night.

Direct night observations using SCUBA, and the high incidence of full stomachs in fish collected at dawn, showed that catfish were feeding on the terrace during these onshore migrations. Feeding activity therefore followed a diurnal pattern which is modified by changes in the shallow water habitats consequent on lake level changes. In contrast, feeding in bay and profundal habitats was observed during the day and night at high and low lake level.

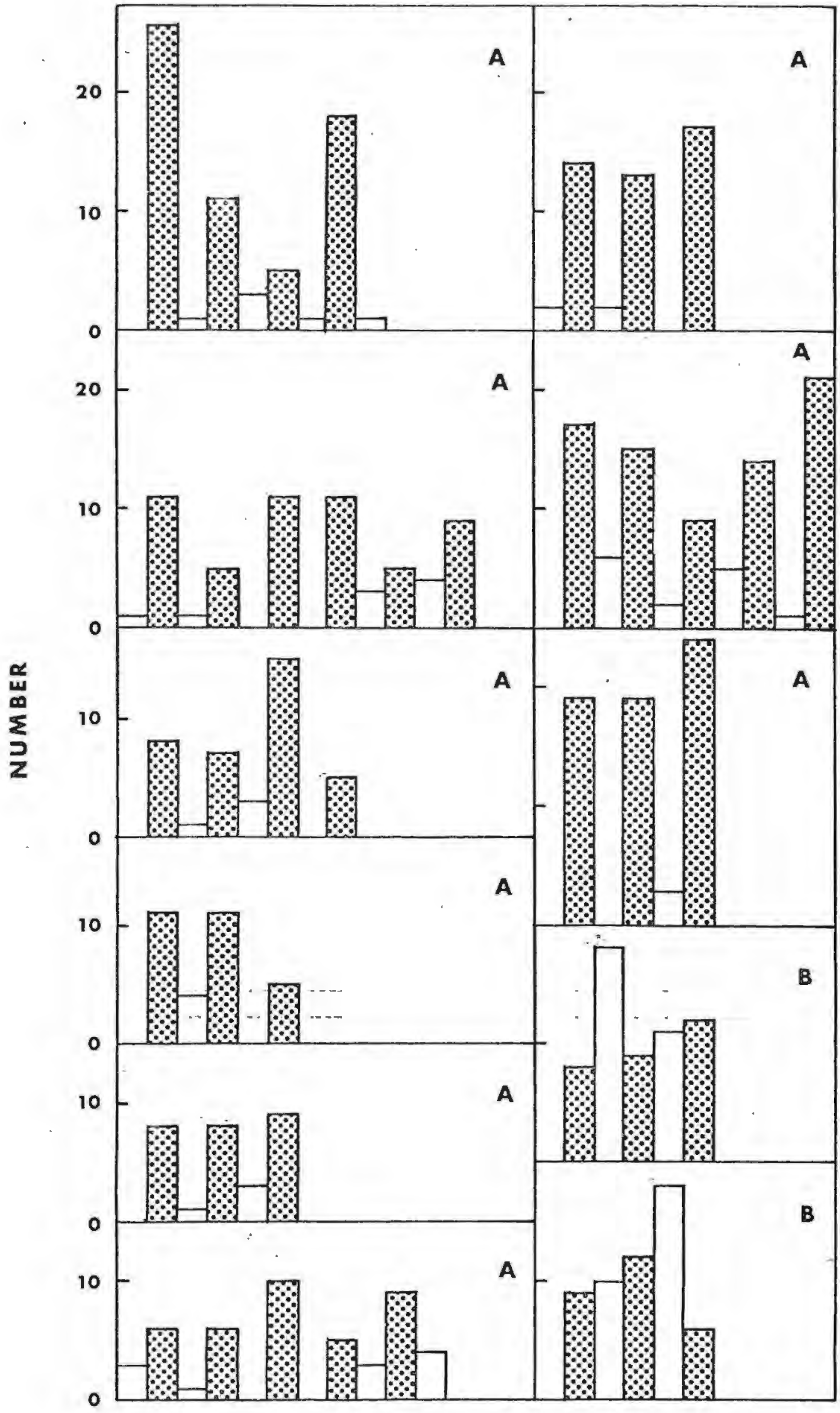


Figure 55: Day (open histograms) and night (dotted) gillnet catches of C.gariepinus in Lake Sibaya showing higher night catches on the terrace (A) and approximately equal day and night catches in sheltered bays (B).

TABLE 23

Proportion of *C.gariepinus* entering terrace day and night in Lake Sibaya.

Method	Lake level		Number of paired settings or observations
	Terrace <2m deep	Terrace >2m deep	
	day night	day night	
Catches			
Longlines and fixed lines	1 : 3	1 : 12	23
Gillnets	1 : 5	1 : 14	48
Observations			
Tower	1 : 5		17
SCUBA	1 : 5	1 : 7	18

(Gillnets: bay 1 : 1.5)

Food preferences of C.gariepinus in Lake Sibaya

The diet of catfish 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 24 for all food items, and by number and dry weight for the 17 most important prey in Table 25. In Fig. 56 these results are plotted for the four major prey classes.

The food class appearing in most stomachs was Crustacea (Table 24, 77%), followed by fish, insects and molluscs, and the most important prey species or groups were H.orbiculare, G.lignorum, C.nilotica, S.mossambicus, odonatid nymphs, chironomid larvae, P.adusta and G. giurus

The class contributing the highest number of prey organisms was Crustacea (Table 25, 66,1%) 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 odonatid nymphs.

As a class, fishes contributed the greatest proportion of total prey dry weight (Table 25, 76,2%) followed by crustaceans, insects and molluscs. The most important food species in the dry weight analysis were Sarotherodon mossambicus, Potamon 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, Atherina breviceps, Gilchristella aestuarius, Croilia mossambica, Corophium triaenonyx, Apseudes digitalis, Cyathura carinata and Pontogeloides latipes.

One incidence of cannibalism (ignored in previous analyses) was recorded - a male catfish measuring 1088mm TL (weight 8790g) contained a catfish measuring 280mm TL, weight 217g. In Barberspan, four large C.gariepinus (TL 1245mm, 1156mm, 1028mm, 610mm) had ingested four remarkably large C.gariepinus prey (TL 610mm, 381mm, 254mm, 356mm; Groenewald, 1964). Clarias mossambicus in a stream in Lake Victoria ingested small C.mossambicus and C.carsoni (TL 20mm and 60mm respectively), but in both cases the predators were also small (TL 77mm and 150mm respectively, Corbet, 1961). Small catfish killed by rotenone are readily consumed by larger catfish in Sibaya.

C.gariepinus ingested 1,75 times more B.capillatus than M.tuberculata (Table 25), although the latter species was 17 times more common in belt transects measured by SCUBA dives in Lake Sibaya (Boltt, 1969). This marked selection for the more thin-walled globose snail rather than the heavy-walled spiralled one may be related to the relative ease with which B.capillatus can be crushed. Similar selection for thin-shelled snails was found by Stein et al. (1975) in carp Cyprinus carpio.

TABLE 24

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

Number of catfish examined with stomach contents = 469

Total number of catfish examined = 683

Food species or group	Frequency of occurrence in stomachs examined	% of total no. of stomachs examined
Fish: Total	239	50.9
Sarotherodon mossambicus	91	19.4
Pseudocrenilabris philander	41	8.7
Cichlid fry	28	6.0
C.gariepinus eggs	5	1.1
Glossogobius giurus	39	8.3
Croilia mossambica	8	1.7
Aplocheilichthys spp.	41	8.7
Barbus spp.	10	2.1
Gilchristella aestuarius	6	1.3
Unidentified fish	59	12.6
Crustacea: Total	361	77.0
Hymenosoma orbiculare	231	49.3
Potamon sidneyi	30	6.4
Caridina nilotica	116	24.7
Grandidierella lignorum	122	26.0
Corophium triaenonyx	10	2.1
Afrochiltonia capensis	9	1.9
Apseudes digitalis	9	1.9
Cyathura carinata	44	9.4
Pontogeloides latipes	31	6.6
Unidentified Crustacea	35	7.5
Insecta: Total	177	37.7
Povilla adusta	67	14.3
Odonatid 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
Melanoides tuberculata	54	11.5
Bellamya capillata	28	6.0
Bulinus spp.	35	7.5
Corbicula africana	7	1.5
Arachnida	10	2.1
Plant debris	42	9.0
Diatoms	12	2.6
Sand	46	9.8

TABLE 25

The food of *C.gariepinus* at intermediate lake levels (1974-75) in Lake Sibaya - numerical and dry weight analysis of most important food items.

Number of catfish examined with stomach contents = 469
Total number of catfish examined = 683
Total number of prey found in 469 catfish = 5549

Food species or group	Numerical analysis		Dry weight analysis
	No. individual prey	Percentage of total	Percentage of total prey dry weight
Fish: Total	695	12.5	75.0
S.mossambicus	126	2.3	60.6
P.philander	44	0.8	5.3
Cichlid fry	383	6.9	2.6
G.giurus	38	0.7	4.9
Aplocheilichthys spp.	104	1.9	1.6
Crustacea: Total	3615	65.1	18.6
H.orbiculare	1302	23.5	7.1
C.nilotica	606	10.9	0.6
P.sidneyi	27	0.5	10.7
G.lignorum	1548	27.9	0.1
P.latipes	44	0.8	0.04
C.carinata	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
P.adusta	388	7.0	0.7
Terrestrial insects	79	1.4	1.7
Mollusca: Total	225	4.1	1.9
M.tuberculata	44	0.8	0.7
B.capillatus	77	1.4	1.1
Bulinus spp.	104	1.9	0.1

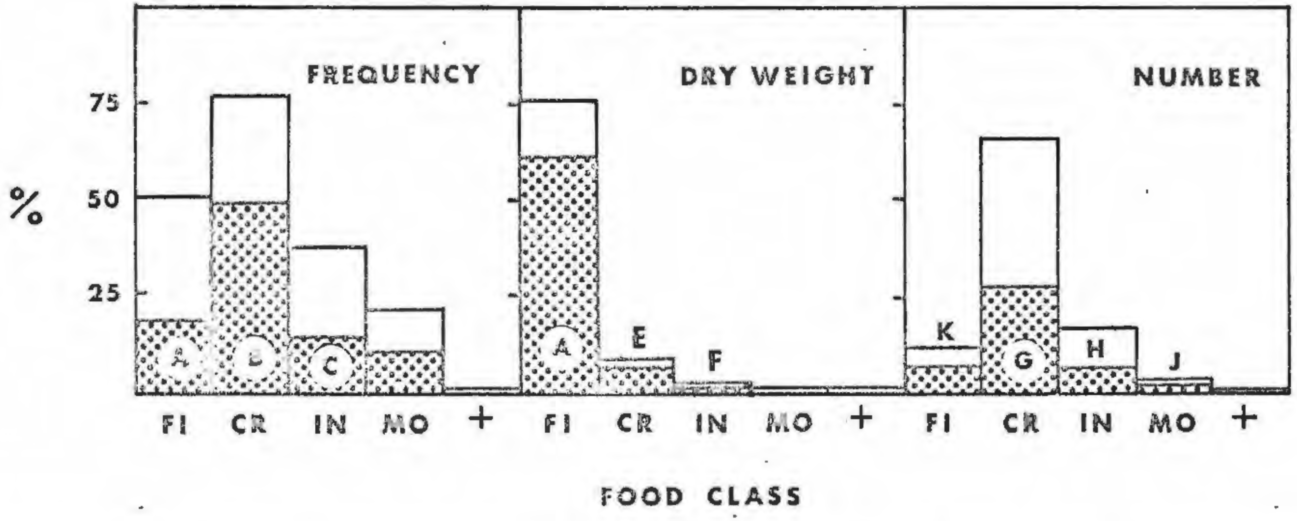


Figure 56: The percentage contribution of different prey classes to the diet of 469 C.gariepinus caught at intermediate lake level in Lake Sibaya, analysed by frequency, dry weight and number, with the dominant prey species or group shaded.

Food Classes:

FI: Fish
CR: Crustacea
IN: Insecta
MO: Mollusca
+: Other

Dominant prey:

A: S.mossambicus
B: H.orbiculare
C: Chironomid larvae
D: M.tuberculata
E: P.sidneyi
F: Odonatid nymphs
G: G.lignorum
H: P.adusta
J: Bulinus spp.
K: Cichlid fry

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 (4 stomachs) and Spirogyra (one stomach). The low standing crop of zooplankton in Lake Sibaya (5mg dry weight per m^3, Hart & Allanson, 1975) probably accounts for the dependence of C.gariepinus on benthic food items. As mentioned earlier, 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 have been caught.

The low incidence of sand in the stomach contents (9,8% of all stomachs) indicates that most prey is caught just above the substrate.

Food preferences by predator length

The food preferences of catfish in different total length groups is presented in Table 26 for prey species and groups, and in Fig. 57 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 26 . 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.

(a) 20-50mm TL: The most important prey class by all methods was Crustacea, followed by insects and molluscs. No fish were taken.

(b) 50-100mm 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 odonatid nymphs and P.adusta, and the fishes mainly of cichlid fry. C.nilotica, G.lignorum and H.orbiculare were the important Crustacea. Clarias theodorae inhabits streams and, at high lake levels, flooded marginal areas in Lake Sibaya. Eighteen stomachs contained odonatid nymphs (78% of stomachs), P.adusta (50%), Caridina nilotica (39%), Chironomid larvae (17%) and M.tuberculata (11%). They may therefore compete with small C.gariepinus for food.

(c) 100-300mm 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 100-200mm TL, cichlid fry form the bulk of the fish component, whereas in larger catfish, juvenile S.mossambicus and P.philander are more important.

(d) 300-700mm TL: Large juvenile and adult fishes, which 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

TABLE 26

Summary of feeding preferences of *C.gariepinus* in Lake Sibaya

N = number of stomachs examined with contents.

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

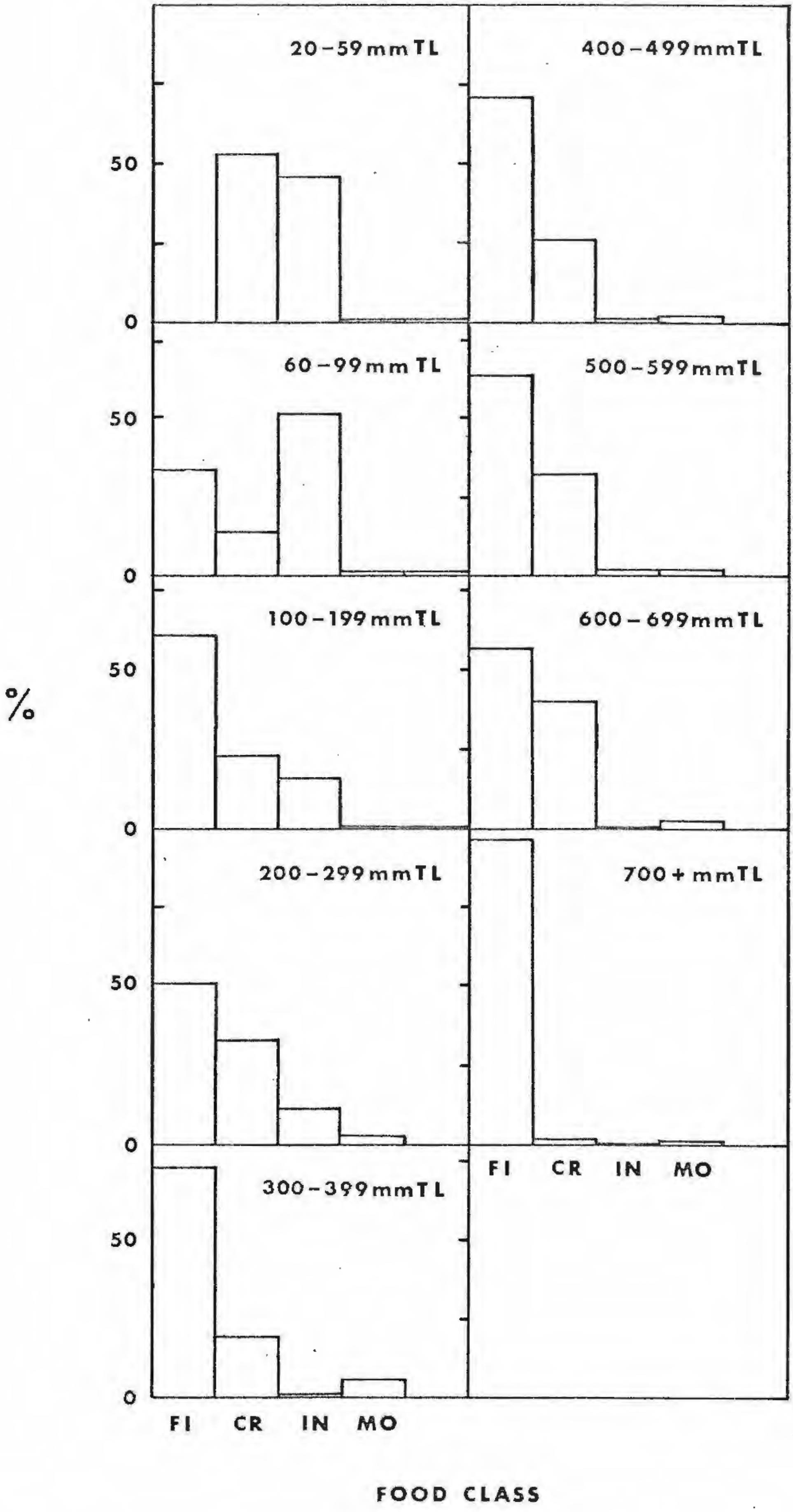


Figure 57: The percentage contribution to total prey dry weight of major prey classes for different length groups of *C.gariepinus*. Symbols as in Fig. 56.

or deep sandy areas where insects are uncommon. The relative unimportance of the molluscs Bellamya and Melanoides, which are common in the benthos, is accounted for by their small individual contribution in a dry weight analysis - the frequency method reveals that they appeared in 20% of stomachs (with contents) in this length group and the numerical method that they constituted 4% of all prey organisms.

This size group have also been observed to feed on frogs, the fruit of Ficus sycamorus and F.trichopoda, fish regurgitated by Phalacrocorax carbo, S.mossambicus fry (released by females caught in a seine net), fledgeling masked weavers Ploceus velatus and white-breasted cormorants Phalacrocorax carbo, rotting flesh on cow and crocodile carcasses and hippopotamus dung. A large group was seen feeding with crocodiles on a hippopotamus carcass in Ndumu Game Reserve 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) on young Phalacrocorax (Corbet, 1959) and on fish embryos (Greenwood, 1963b).

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

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. 58. Insects and molluscs were taken in low proportions throughout the year, with the highest insect catch in summer. Fish, mainly S.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 23,0g) than in spring and summer (2,7 and 3,2g) in catfish in the length range 300-600mm TL. Crustacea contributed more to prey weight in spring and summer than in autumn and winter, although Boltt (1969) found that H.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 small contribution to catfish diet in winter. C.nilotica and G.lignorum were taken mainly in spring and summer.

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. 59. Fish contributed the greatest proportion of prey dry weight in all habitats, whereas Crustacea occurred in most stomachs in all habitats. Insects were

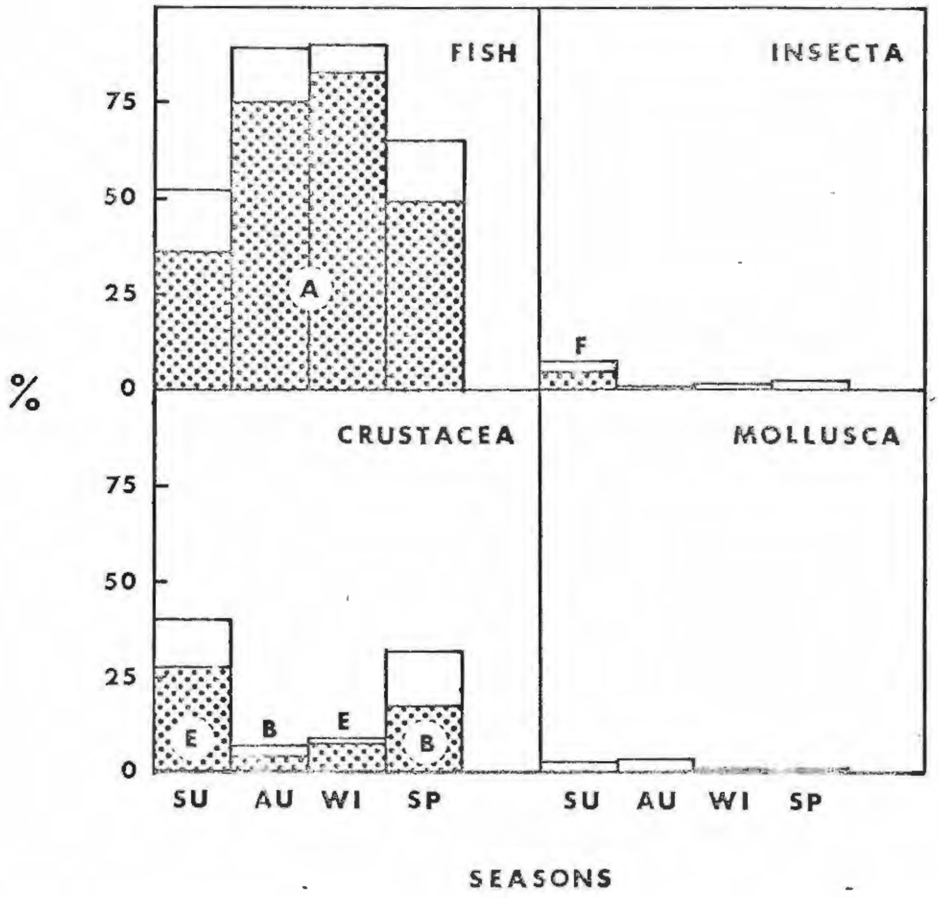


Figure 58: The percentage contribution to total prey dry weight of major prey classes of C.gariepinus in different seasons. The dominant prey species or group is shaded.

Seasons: SU: Summer

AU: Autumn

WI: Winter

SP: Spring

Other symbols as in Fig. 56.

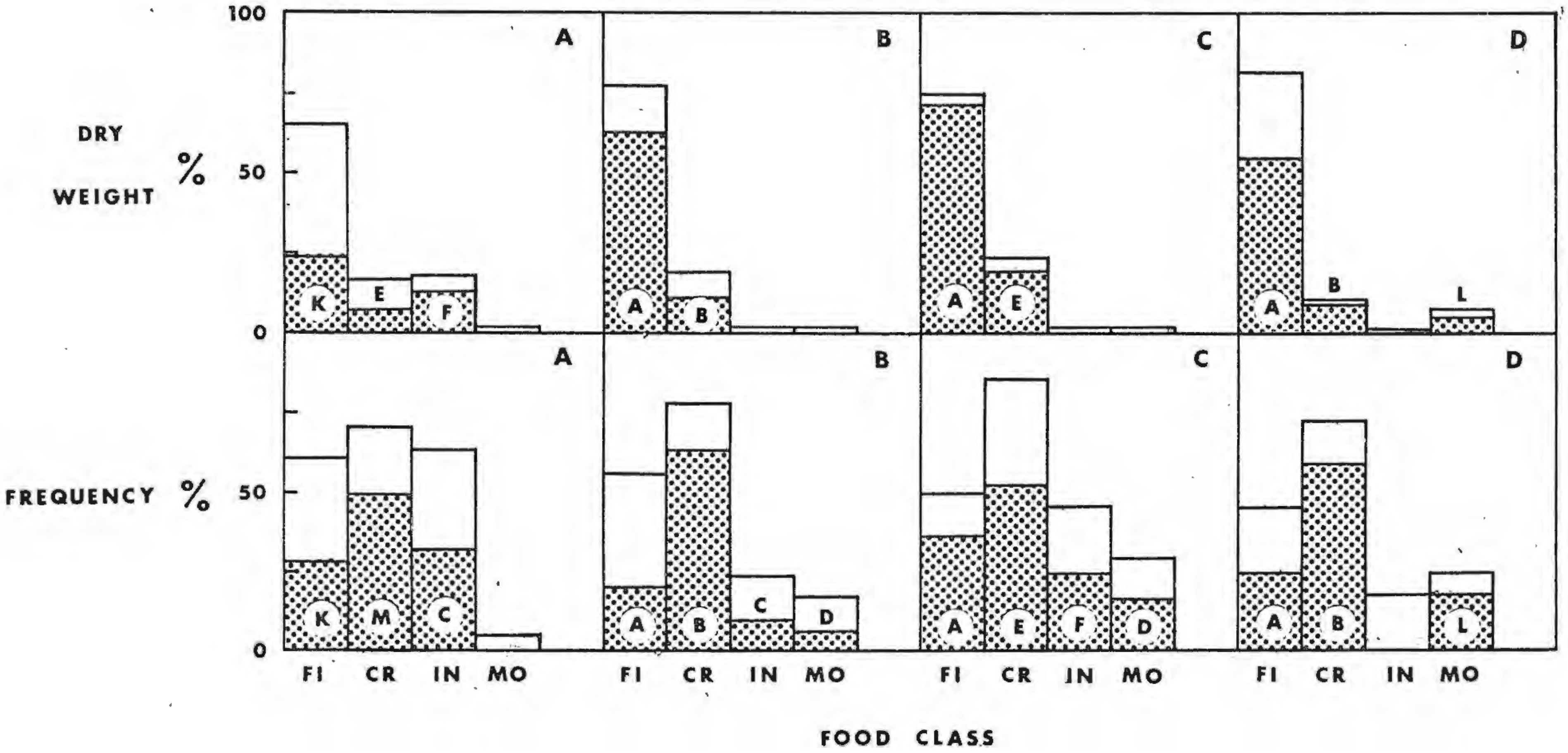


Figure 59: The percentage contribution to total prey dry weight (upper figures) and frequency of occurrence (lower figures) of major prey classes of <u>C.gariepinus</u> in different habitats. The dominant prey species or group is shaded.

Habitats

A: Marginal

B: Terrace

C: Sheltered bay and slopes

D: Profundal

Dominant prey (additional to those in Fig. 56)

K: Cichlid fry

L: <u>B.capillatus</u>

M: <u>C.nilotica</u>

N: <u>P.philander</u>

taken most often in eulittoral 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 catfish in Lake Sibaya to calculate forage ratios (*vide* Thomas, 1966) but data on prey microhabitat preferences and accessibility are presented in Table 27. Prey organisms common in the different microhabitats but rarely taken by catfish are also listed. The larvae of *P.adusta* are normally tubiculous 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* stomachs containing the larvae indicated that they were taken while out of the burrows at night, a result confirmed at Lake Sibaya. *P.adusta* is therefore included in category F. Although they build burrows in the sand, *G.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.).

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 27). A similar result is reported for *Clarias senegalensis* by Thomas (1966). Highly accessible prey was taken in preference to prey with moderate or low accessibility. Tadpoles are common in sheltered shallow water, yet they were never recorded from catfish stomachs in Lake Sibaya although Wager (1965) reports *C.gariepinus* feeding on tadpoles in an aquarium. *C.mossambicus* and *C.senegalensis* are known to eat tadpoles (Corbet, 1961; Thomas, 1966).

The composition of the diet of catfish in Sibaya does not correspond with the relative proportions of common benthic organisms reported by Boltt (1969). *H.orbiculare*, *C.nilotica* and *G.lignorum* were well-represented in the diet, but *B.capillata* , *M.tuberculata*, *Corophium triaenonyx* and *Apseudes digitalis* which are common in the benthos, were less prominent in the diet than shallow water insects such as odonatid 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 odonatid nymphs and *C.nilotica*. Both *G.lignorum* males and *P.adusta* numphs 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 detectible by a predator relying largely on mechanoreception. This possibility is investigated further in the next chapter.

Size structure of main prey

The size structure of *H.orbiculare* and *S.mossambicus* prey is given in

TABLE 27

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

	Prey microhabitat	Accessibility	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	*T.sparrmanii* *T.rendalli* *Barbus viviparus*	*Aplocheilichthys* spp.	1.6	1.9
C.	Exposed on plants or plant debris	High	Trichopteran nymphs	Odonatid nymphs Some *Bulinus* spp.	2.2	4.6
D.	Sheltering under or in association with plant debris	Moderate		Some *P.sidneyi* Some *C.nilotica*	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 1m)	High		*S.mossambicus* *P.philander* cichlid fry *P.adusta*, *G.giurus*	75.3	17.9
G.	Temporarily sheltered in substrate or living on substrate-water interface	High	*Ceratonereis keiskama*, tadpoles	*H.orbiculare*, *G.lignorum*, some *C.nilotica*, some *P.sidneyi*, *P.latipes*, *C.carinata*, *B.capillata*, *M.tuberculata*, some *Bulinus* spp.	14.5	61.8

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

Fig.60 . Catfish preyed on large benthic H.orbiculare, ignoring the planktonic zoeae. The mean size taken (8,3mm) is about the mean size of H.orbiculare in the benthos of Lake Sibaya (9mm, Forbes & Hill, 1969). S.mossambicus prey consisted mainly of fry and small juveniles, and intermediate size adults. Few S.mossambicus in the length range 80-120mm, or larger adults over 150mm, were taken. 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 intermediate size tilapia requires another explanation. Bruton and Boltt (1975) found that most young adult male S.mossambicus spent their first year in offshore waters, so that the population structure of tilapia on the terrace is bimodal and resembles that given in Fig. 60 for catfish prey. These findings indicate that C.gariepinus feeds 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. 61. The prey are grouped in three size classes - fry (10-20mm SL); juveniles (20-80mm) and small adults (120-150mm). In general, prey size increased linearly with predator length (R = 0,86) although large catfish were observed to eat some tilapia fry and small juveniles. The largest S.mossambicus found in a catfish stomach measured 185mm 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 28). Catfish from 60-400mm 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 species in a single C.mossambicus stomach.

As shown in Appendix 2, which gives six examples of diverse stomach contents, Sibaya catfish occasionally consume large numbers of one prey species. Other examples are: C.gariepinus ova (highest number in one stomach: 370), cichlid fry (94), P.adusta (59), odonatid nymphs (36), Bulinus spp. (23) and C.nilotica (20). All indicate concentrated feeding by the predator. 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 (83 taxa) or in permanently submerged beds (55 taxa, Allanson et al., 1974). These areas are inhabited mainly by juvenile catfish ($<$400mm TL) whereas areas supporting a less diverse fauna (exposed terraces, 29 taxa; deep lake sediments, 24 taxa) are inhabited by larger catfish.

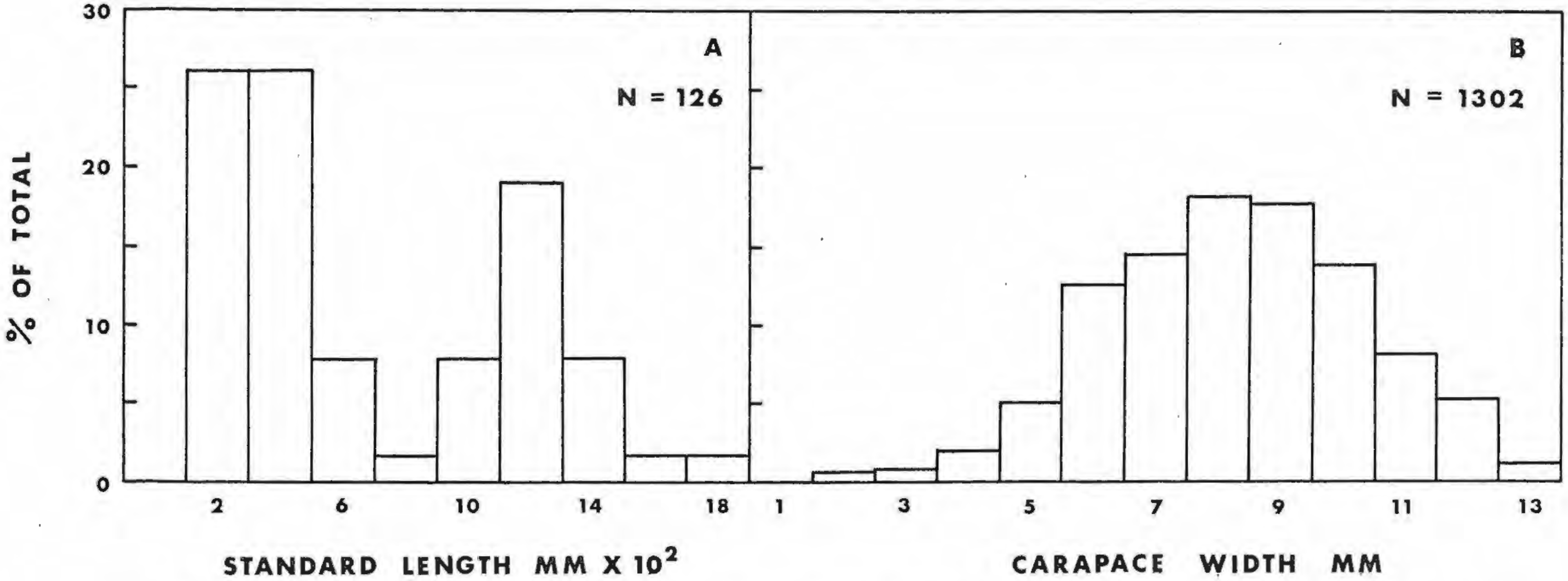


Figure 60: The size structure of S.mossambicus (A) and H.orbiculare (B) prey of C.gariepinus in Lake Sibaya.

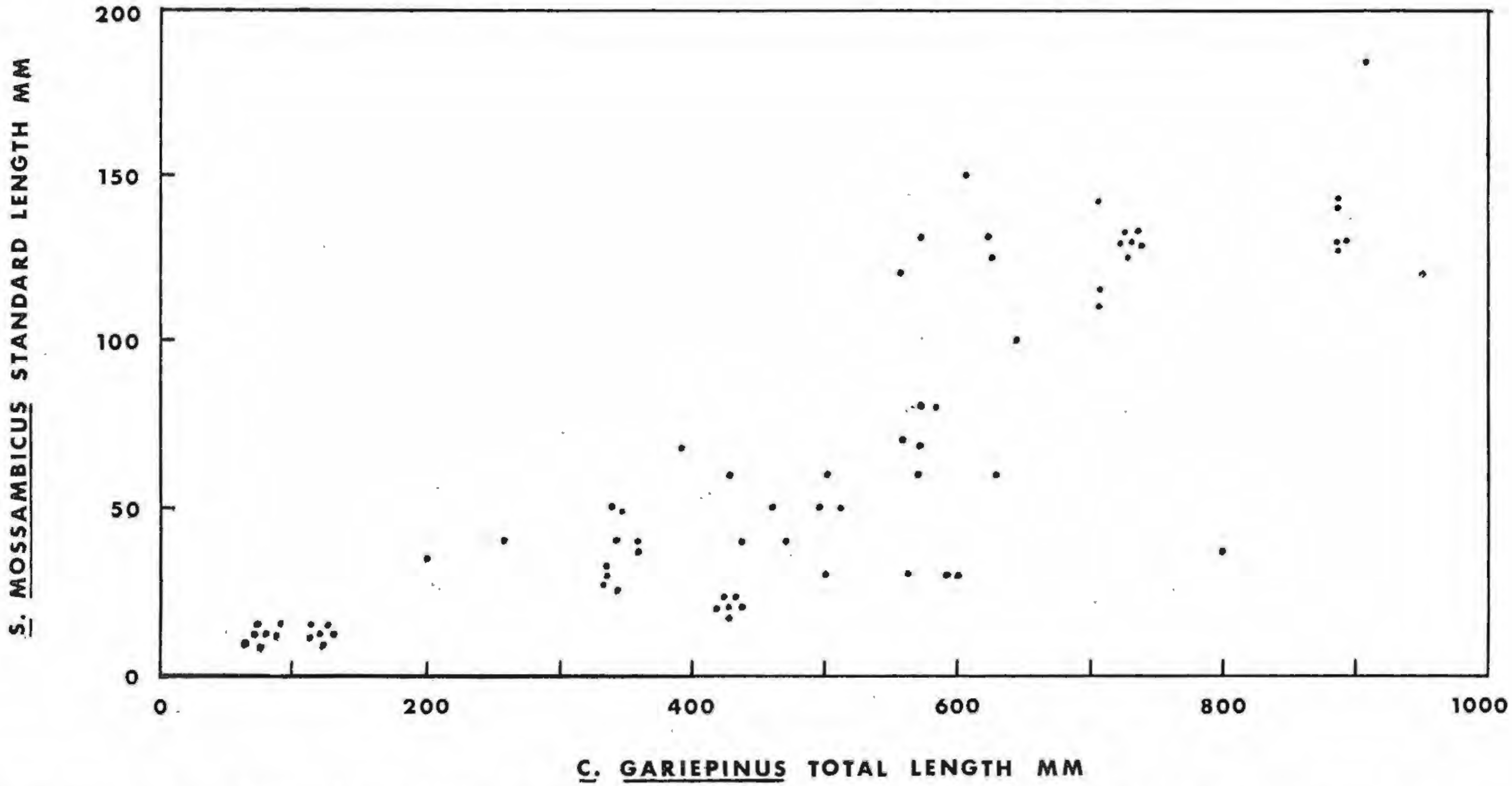


Figure 61: The relationship between total length of predator (C.gariepinus) and standard length of prey (S.mossambicus) from a sample of 71 S.mossambicus in Lake Sibaya.

TABLE 28

Number of individual prey and prey diversity in *Clarias gariepinus* stomachs from Lake Sibaya.

Catfish TL group (mm)	No. catfish stomachs examined(with contents)	Total no. individual prey	Mean no. prey per stomach	SE	Mean no. prey species per stomach	SE
0-50	19	186	9.8		2.3	0.88
60-100	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	

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. 62A). 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 catfish is not high and, with the exception of fish taken in November, stomachs are on average less than half full (Fig.62A). Small juvenile catfish ($<$ 200mm TL) had higher, more constant fullness indices. 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 catfish caught in passive gear (gillnets, traps, longlines) in Sibaya may account in part for the low fullness indices obtained. Small catfish ($<$ 200mm), which feed largely on small items had higher mean fullness indices (4,9) than medium (200-600mm TL, 3,8) or large fish ($>$600mm TL, index 2,6).

Condition factor

Condition factors also give an indication of feeding intensity, if changes in the length-weight relationship due to gonadal maturation (especially in females) are taken into account. Monthly mean condition factors for adults and juveniles are given in Fig. 62B for the period November 1973 to May 1975. Condition factors increased to normal in June 1974 and reached a peak in September, October and November. The marked increase in adult CF in early summer was not due entirely to ovary maturation as males showed the same trend. In Clarias, mature testis weight is small and has little effect on the length:weight relationship. 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.

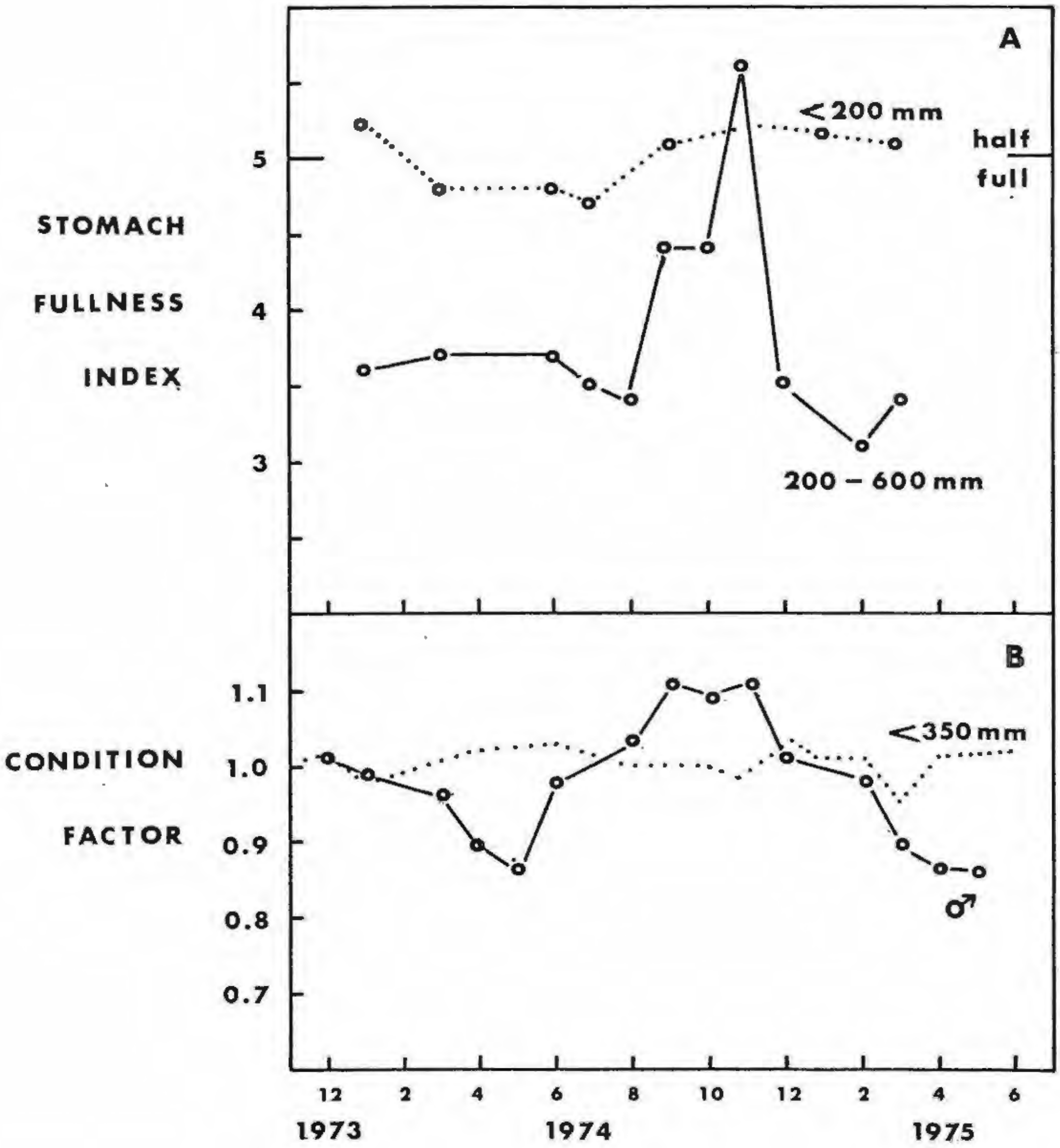


Figure 62A: Monthly stomach fullness indices of small juvenile (< 200mm TL, dotted line) and large <u>C.gariepinus</u> (200-600mm TL, solid line) from Lake Sibaya.

B: Monthly condition factors of juvenile (< 350mm TL, dotted line) and adult male (solid line) <u>C.gariepinus</u> in Lake Sibaya.

Loss of condition by adults in midyear co-incided 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 catfish 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).

Juvenile catfish which feed throughout the year in shallow water remained in good condition during the whole study period.

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 Sibaya catfish had nematodes in the stomach (Table 29). The incidence of an external parasite, Dolops ranarum was higher (33,7%), but these branchiurans cause little apparent harm to catfish. Van der Waal (1972) also found that parasites had little effect on the condition of C.gariepinus.

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

During my stay at Lake Sibaya Research Station the lake level rose 3,12m Catfish were collected during an earlier study from 1970 - 72 at low lake level and during the present study at intermediate lake level (1974-1975) and high lake level (1976). The low and intermediate lake level collections were made throughout the year, whereas the high lake level collection was made in March and April (1976) only. Some food items which are only common in Lake Sibaya in summer (November to January), such as insects with aquatic larval stages, may be therefore underestimated in the diet of high lake level catfish. The three collections include catfish of all sizes above 100mm TL. Their diet is compared in Table 30 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 (personal observation).

(b) The diet at all three lake levels was dominated in terms of frequency by H.orbiculare, followed by a cichlid fish or G.lignorum.

TABLE 29

Incidence of parasites from Clarias gariepinus from Lake Sibaya

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

** per infested catfish

TABLE 30

Frequency of occurrence of major food items in *C. gariepinus* (TL 300-700mm) at three different lake levels (lake levels defined in Table 22).

N = number of stomachs examined with contents.

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

(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. These Ephemopterans burrow into submerged dead sedges and trees as nymphs, 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).

Review of feeding in large African Clarias

Five large Clarias occur commonly in Africa - C.senegalensis (west Africa), C.lazera (north), C.mossambicus (east), C.gariepinus and C.ngamensis (south). The food of C.gariepinus and C.mossambicus is well-known, but there are few studies on C.senegalensis and C.ngamensis, and only brief mention was found of the diet of C.lazera. This information is summarised in Table 31.

In most studies for which there is a reasonable sample, C.gariepinus and C.mossambicus adults feed mainly on fish (in a weight analysis) or zooplankton, with terrestrial and aquatic insects assuming importance in shallow ponds and marginal areas. Frequency or numerical analyses usually scored Crustacea higher than fishes (as in Lake Sibaya). Juveniles, which inhabit streams and shallow margins, feed mainly on insects, small fish and crustaceans. Both species filter feed, although plankton only featured prominently in the diet of C.gariepinus (possibly because no plankton-rich systems inhabited by C.mossambicus have been investigated). The habitat occupied by the catfish is a major determinant of food items taken.

Groenewald (1964) described C.gariepinus as a clumsy piscivore which 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 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 was more important in the diet of large ($>$ 400mm TL) than small C.gariepinus. Large catfish from the open waters of Lake Kariba contained mainly Cladocera and Copepoda, all with a body length $>$1mm (Bowmaker, 1973). When freshwater invades estuarine lake St Lucia in Zululand, catfish are common in the lake and feed mainly on a small gastropod Assiminea bifasciata, euryhaline fish such as Glossogobius giurus, and crabs (Whitfield, pers.comm.).

C.senegalensis in a small man-made lake in Ghana subsisted mainly on organisms swimming in midwater (including tilapia, zooplankton and insects),

TABLE 31

Review of the main foods of *Clarias* in Africa.

Clarias species	Water system	Method of stomach analysis	Predator length range (mm)	Main prey	Other important food	(with contents) number stomachs examined	Reference
C.gariepinus	Jukskei river	Frequency		Entomostracans & Chironomids	Detritus	Total 104	Groeneveld(1964)
	Barberspan	Frequency	124-228	*Clarias gariepinus*	Other fish, plankton		
	Vaal river (all Transvaal)	Frequency		Terrestrial invertebrates	Fish		
	Lake McIlwaine (Rhodesia)	Reconstructed volume	200-400	Chironomid pupae	Tanypodinae larvae, Gastropoda, terrestrial insects	102	Munro (1967)
			400-600	Chironomid pupae	Cladocera & Copepoda, Gastropoda	358	Munro (1967)
			600+	Cladocera & Copepoda	Chironomid pupae	105	Munro (1967)
	Lake Sibaya (Zululand)	Numerical	approx300-700	*H.orbiculare*	Small cichlids, *G.giurus*	53	Minshull (1969)
	Barberspan (Transvaal)	Volumetric	0-200	Fish (unspecified)	Ephemeroptera	37	Schoonbee (1969)
			200-400	Fish	Cladocera	4	Schoonbee (1969)
			400+	Cladocera	Fish	68	Schoonbee (1969)
	Shallow pools (Rhodesia)	Frequency	not given	Coleoptera (aquatic adults)	Hemiptera	Not given	Weir (1972)
	Olifants river, Transvaal	Volumetric	over 180	Fish	Filamentous algae	16	van der Waal (1972)
	Farm dam,Marble Hall	Volumetric	over 180	Grape seeds	Fish	10	van der Waal (1972)
	Farm dam, Groblersdal	Volumetric	over 180	Fish	*Nymphaea* seeds	19	van der Waal (1972)
	Lolamentes dam, Marble Hall	Volumetric	over 180	Fish	Chironomidae	13	van der Waal (1972)
	Leeupan, W.Transvaal	Volumetric	over 180	Fish	Terrestrial insects	15	van der Waal (1972)
	Kareepan,Wolmaransstad	Volumetric	over 180	Fish	Chironomidae	16	van der Waal (1972)
	Elandsriver, nr Marble Hall	Frequency	over 180	Fish	Terrestrial insects, detritus	299	van der Waal (1972)
	Lepalona dam, Olifants River	Volumetric	70-180	Chaoboridae, Chironomidae	Cladocera	15	van der Waal (1972)
	Crocodile Hill Dam, Olifants river	Volumetric	70-180	Terrestrial insects	Odonatid and Ephemeropteran nymphs	11	van der Waal (1972)
	Lake Kariba	Frequency	216-865	Cladocera	Copepoda	34	Bowmaker (1973)
	Pongola pans (Zululand)	Frequency	100-900	Fish	Aquatic insects, Gastropoda	266	Kok,pers.comm.1976
	Lake St Lucia (Zululand)	Frequency	353-462	*Assiminia bifasciata* (Gastropoda)	*Glossogobius giurus*	12	Whitfield, pers. comm. 1976
	Hardap dam (South West Africa)	Frequency	242-1482	Fish	Zooplankton	69	Gaigher(in press)
	Lake Sibaya	Frequency	21-1088	*H.orbiculare*	*S.mossambicus*, *C.lignorum*	469	This study
	Lower Shire river, Malawi	Frequency	not given	Plant detritus	Cichlid fish, humus, filamentous algae	491	Willoughby & Tweddle (1976)
	Lake Kariba (margins amongst *Salvinia molesta*)	Frequency	49-542	*P.adusta*	*Cyclaestheria* (Conchostraca), chironomid larvae	37	Mitchell (1976)
C.mossambicus	Lake Victoria	Frequency	not given	Fish	Insect larvae, molluscs, oligochaetes, prawns and zooplankton	55	Graham (1929)
	Lake Malawi (open waters)	Frequency	not given	*Haplochromis* spp.	*Tilapia* spp., small *Clarias*	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	*Haplochromis* spp.	Plants, Gastropoda, *C.nilotica* Anisopteran larvae	216	Corbet (1961)
	Victoria Nile	Frequency	100-240	Lithophilic insects	Ostracoda, chironomid larvae	5	Corbet (1961)
	Victoria Nile	Frequency	770+900	*Potamon*	*P.adusta*, *Barbus altianalis*	2	Corbet (1961)
	Uganda	Frequency	not given	*Haplochromis* spp.	Insect larvae, molluscs, plants	not given	Greenwood(1966)
	Lake Chilwa	Frequency	not given	*Barbus paludinosus*	Aquatic insects, plant detritus	not given	Kirk (1967)
	Lochinvar lagoon , Kafue river	Frequency	not given	Fish		2	Tait (1965)
C.lazera	Lake George, Uganda	Frequency	not given	*Haplochromis* spp.		not given	Greenwood(1976)
C.ngamensis	Lake Piti, Mozambique	Frequency	300-650	Chironomid larvae	*Aplocheilichthys* spp.	10	Personal observations (1970)
C.senegalensis	Nungua Lake, Ghana	Frequency	150+	Chironomid pupae	*Stenocorixa*, tilapia	178	Thomas (1966)
		Numerical	150+	*Chaoborus*	Chironomid pupae, *Micronecta* (Hemiptera)		
		Points (Thomas, 1962)	150+	Tilapia	*Stenocorixa* (Hemiptera), *Hemileptocerus* (Trichoptera)		

those swimming close to the sediment or those living on the sediment. Animals living 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 *C.ngamensis* from Lake Piti in southern Mozambique contained only chironomid larvae and *Aplocheilichthys* spp. (personal observation, 1970). This species takes mainly molluscs and chironomids in the Pongola pans in Zululand (Kok, pers.comm., 1976). Bell-Cross (1976) describes the 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. 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; personal observations, in *C.theodorae*; Jackson *et al*, 1963; Worthington, 1933; Corbet, 1961; in *C.carsoni*; Jackson, 1961a; Jubb, 1967 in *C.submarginatus*).

EXPERIMENTAL STUDY OF PREDATION BY CATFISH

INTRODUCTION

An important point to emerge from the previous chapter is that catfish feed on a wide variety of food items, but some items are preferred to others. The next step in an investigation of feeding ecology is to establish those factors which bring about a choice of prey, and to determine where in the predation process they have their influence.

Observations in the lake indicated that factors such as predator size and day-night light changes may influence the predator before prey contact. Other factors, such as the number of predators, and prey evasive behaviour, may influence predation after prey discovery. The most obvious finding was that predation is a complex process, influenced by an ever-changing matrix of events, which can only be understood if some of these variables are controlled.

Predator-prey relationships are ideally studied in natural systems in which all important variables are monitored without affecting the subjects' behaviour, but this has never been achieved. The next best solution is to glean as much as possible from observations and analyses of behaviour in the field, and then to conduct experiments in semi-natural and artificial environments in which properties of the prey, predator and environment come under control and observation. Few biologists have had this opportunity (but see Vince _et al_, 1976; and Moore & Moore 1976 a and b).

I made observations on predation using a 7m tower and SCUBA in Lake Sibaya, and then constructed enclosures to study predation under controlled conditions. No excuse is made for not reproducing natural conditions in the experiments. On the contrary, especially created situations enable one to discover certain features that cannot easily be discerned by observations in the natural environment, containing as it does an intricate complex of causes and effects. However, care was taken to use knowledge gained in the field to design the experiments so that a meaningful result could be obtained.

Observations in the enclosures showed that a full predation sequence in catfish consisted of the following chain of events (see Table 34 for a definition of the terms and for a complete flow diagram of appetitive actions):

$$\begin{tikzcd}
 & & \text{OVERLOOK} & & \text{NEGLECT} & & \text{REJECT} & \\
\text{SEARCH} \arrow[r] & \text{ENCOUNTER} \arrow[ur] \arrow[rr] & & \text{DISCOVER} \arrow[ur] \arrow[rr] & & \text{GRASP} \arrow[ur] \arrow[rr] & & \text{EAT}
\end{tikzcd}$$

The upper row are negative events leading to reduced prey risk, and may be termed negative appetitive actions. The events in the lower row are positive appetitive actions, and lead to increased prey risk. For a full appreciation of the importance of factors which influence predation, a measure of their impact on this chain of events is needed. In this investigation the frequency of each appetitive action was determined in separate experiments in which a property of the predator, prey or environment was varied. The proportion of one action leading to the next, was used as an index of prey risk.

Because of severe restrictions on the time and facilities available to one worker, the influence of only a few factors on predation could be determined, but these were selected as important ones on the basis of field observations. Likewise, risk could only be ascertained for a few catfish prey. The bulk of the experimental work was performed on the cichlid fishes S.mossambicus, T.sparrmanii and P.philander, as these are important catfish prey in Lake Sibaya. After a consideration of the interaction of tilapia and catfish in Lake Sibaya, the influence of prey density on predation efficiency was chosen as the most important component of predation to be studied. As catfish have often been described as 'opportunists' or 'indiscriminate predators', the following hypothesis was proposed and tested: 'C.gariepinus is an opportunistic predator which feeds on S.mossambicus, T.sparrmanii and P.philander in proportion to their density in the field'. The numerical importance of invertebrates in the catfish diet could not be ignored, and experiments were also conducted on some important invertebrate prey.

Many factors influence predation and it is therefore important that the researcher is aware of these factors when designing experimental studies. In the next section the literature available to me on predation by piscivorous fish is reviewed to illustrate how the findings of earlier workers have assisted in the design of the current experiments and interpretation of the results. The review also discusses recent hypotheses and concepts in relation to predation, such as 'searching image', 'area-concentrated search', and 'switching'.

After the review, the status of our knowledge on predation by Clarias and other large African fish predators on cichlids and other fishes is summarised. Thereafter, the diel movements and habitat preferences of catfish and their cichlid prey at different lake levels in Lake Sibaya are outlined. The working hypothesis is then tested using field collections and laboratory studies, and the influence of some subsidiary factors on predation is described.

Review of predation by piscivorous fish

This review relates mainly to fisheating fish, but some instances of predation on other prey, or by other predators, are discussed where an important point is emphasised. In addition, some examples of the effect of a parasitic fish 'predator' (lamprey), and fishing effort on fish populations are mentioned where the result is relevant to predation.

Analyses of predation have been conducted at two levels. Firstly, the broad effect of predation under different conditions in natural or semi-natural situations has been determined. Secondly, the factors which influence the predation process have been studied in isolation, usually in experimental situations.

(a) Studies on the effect of predation on natural and semi-natural fish communities:

Several interesting studies by early American ichthyologists have gone largely unnoticed (but see review by Errington, 1946). They showed that predation decreased the number but also increased the size, condition and species composition of prey. Hubbs and Eschmeyer (in Errington, 1946) expressed the 'biological principle' that a lake supports a constant biomass of fish; as one species decreases another increases, though they ascribed the oscillations more to competition for food than to predation. Errington (1946) emphasized that changes in fish populations are largely intercompensatory in the sense that victims of one agency (e.g. natural mortality) simply miss becoming victims of another (e.g. predation). He regarded 'intraspecific self-limiting mechanisms' as the most important agents which determine prey population levels.

Foerster & Ricker (1942) and Ricker & Foerster (1948) reported on the effect of removal of predatory fish from Cultus lake, British Columbia. Three years of persistent fishing reduced some species of predators to about one-tenth their original biomass. This resulted in a threefold increase in the survival rate of young sockeye salmon Oncorhynchus nerka and a corresponding increase in the numbers and weight of these fish migrating seaward. There was no marked change in the total production of the salmon population; production formerly used to feed the predacious fish was directed to smolt output.

Swingle's studies in the 1940's and 1950's (reviewed by Weatherley, 1972) made a valuable contribution to knowledge of predator-prey relations among fish in a semi-natural community. His interest lay in the control of excessive populations of forage fish, such as bluegills Lepomis macrochirus, by predators, mainly largemouth bass Micropterus salmoides, in ponds. He experimented with different ratios of predators and prey in an attempt to reduce the forage fish populations to a level at which the food supply per fish was sufficient for adequate growth. Swingle found that there may be considerable complexity in the relationships between predator and prey. Prey growth rate, their accessibility to the predator as juveniles, and the presence and abundance of predators at the time that young prey are available may all influence the predator's impact in the critical period during which prey are vulnerable to predators as small fish. Weatherley (1972) showed, theoretically, that a fish population in which the young were protected by virtue of their habitat for one year longer than another unprotected population, resulted in 11% better survival for the protected population.

The fish fauna of Windermere has changed markedly over the past 200 years as a result of pollution, eutrophication, angling and removal of predators (Worthington, 1950; Frost, 1954; Bagenal, 1970; Le Cren et al, 1972). During the 19th century, brown trout Salmo trutta and char Salvelinus willoughbii were dominant, but towards the end of that century conditions became more suitable for perch Perca fluviatilis and pike Esox lucius. Between 1860 and 1940 there was a progressive increase in perch and pike, and decrease in trout and char. For a period of at least 15 years after 1940 an attempt was made to alter this balance in favour of char and trout by intensive netting of perch and pike. Since pike feed on all the other important fishes, large scale removal of the predator must have reduced the predation pressure on the prey. Removal of the pike resulted in a marked increase in the number and average size of char and trout and an increase in the number of old and large perch. These results show that the feeding habits of pike have a marked effect on the survival of their prey and are a major factor in determining both the numbers present and the population structure. Later studies showed that the intensive fishery had had a very marked effect on the growth of perch (Le Cren, 1958). Significantly, the perch population has shown no tendency to return to its previous level although no perch have been removed from the North Basin since 1947 (Le Cren et al, 1972). Recent work by McCormack (1970) revealed that cannibalism by large perch is probably not responsible for the low population density, so another factor must be sought.

In a lake in Scotland in which there was no other fish food, pike longer than 200mm fed on other (smaller) pike and on frogs (the only other vertebrate prey available). By cannibalism, the pike achieved a size and growth comparable to that in waters in which they fed on other fish (Munro, 1957). Perch also use their own young as food if other fish or benthos are not available (Nikolsky, 1969). In Lebistes, infanticide is 'directly proportional to population concentration' and results in stabilisation of population numbers (Breder & Coates, 1932). According to Popova (1967) several fish predators change to mass cannibalism when a strong year class of their own species is produced, and thus decrease the severity of food competition which could result from overcrowding.

Gammon & Hasler (1965) and Schmitz & Hetfield (1965) described a nine-year experiment on the effects of introducing muskellunge, Esox masquinongy, into two small lakes in Wisconsin. Prey populations of largemouth bass, which had been stable and high before introduction of the predator, decreased in number after initially increasing in average size. Eventually they decreased in size as well, but thereafter increased in size again when the predator population declined. These trends were not shown by prey populations of smallmouth bass, which were apparently less vulnerable to the predator because of behavioural differences.

Ivanova (1969) showed that the extent of predation by pike and pike-perch on smelt and roach depended on the breeding condition and movements of the prey, there being higher predation on spent, post-reproductive or vertically-migrating fishes. The method of hunting and duration of feeding also changed in response to altered behaviour of the prey; perch hunted in shoals if the prey was clumped but individually if the prey was dispersed.

The decline of the Great lakes of North America fishery can be ascribed partly to 'predation' by sea lampreys Petromyzon marinus (reviewed by Smith, 1971). Sea lampreys co-existed with the salmonid community of Lake Ontario for at least 90 years, but were prevented from reaching the other Great Lakes by the Niagara Falls. When the Welland Canal was constructed sea lampreys gained access to the other lakes. In Lake Erie environmental conditions were unsuitable for lampreys and their predation had little effect on fish stocks. In all three upper Great Lakes invasion by the sea lamprey was followed by an acute decline in fish populations, and the lake trout Salvelinus namaycush was almost eliminated in Lakes Huron and Michigan. Initial predation was on large, cold-water species and, besides the lake trout, populations of burbot (Lota lota), rainbow trout (Salmo gairdneri) and white-fish (Coregonus clupeaformis) declined abruptly. Depletion of lake trout and burbot favoured the chubs (Coregonis spp.), which then received the full impact of lamprey predation. A close relative, the bloater (C.hoyi), became abundant and began to increase in size, but the general reduction in chubs favoured a rapid increase in the numbers of the recently established alewife (Alosa pseudoharengus). As a result, the native fish stocks of Lakes Huron and Michigan are in a state of extreme instability although the disruption in Lake Superior is less catastrophic (Smith, 1968).

Holling (1973) has suggested that the precondition for the collapse caused by lampreys was set by the harvesting of fish, which progressively reduced the 'resilience' of the population. With the added effect of a further outside disturbance (lamprey predation), the population collapsed. Increasingly efficient and intensive fishing in the Laurentian Great Lakes was also responsible for the change in species dominance from large acipenserids and coregonids to clupeids. Change of dominance from large slow-growing to small fast-growing fish species due to intensive exploitation has also been shown in Lake Tanganyika (Coulter, 1970, 1976). Here, Centropomids, especially Lates spp., correspond to the acipenserids and the clupeids consist mainly of Stolothrissa tanganicae and Limnothrissa miodon. The fish population in Lake Albert has shown the same trend, with a decline in large slow-growing species, including Lates, and their replacement by smaller species following intensification of netting (Cadwalladr & Stoneman, 1966). However the end result may differ in the relatively young Laurentian lakes compared with the older African lakes (Coulter, 1976). In the young high latitude lakes the fishes are characterised by wide ecological tolerances and flexibility of feeding habits, whereas the ichthyofauna of the older African lakes is more mature and diverse, and exhibits striking endemism. Regier & Loftus (1972) have proposed that fishes in these old tropical lakes are 'less well pre-adapted to fishing stress than those in lakes of corresponding trophic status in recently glaciated areas'. This is probably true in that the greater specialization of some tropical forms may not permit them to respond opportunistically to exploitation stresses in the same way as temperate broad-niche species. As a result, there will be less tendency towards successive replacements of substitute species under changing conditions. These comments apply more to the old Great Lakes of Africa, and their endemic fishes, and less to the younger lakes in southern Africa and elsewhere, many of which are occupied by broad-niche species such as <u>C.gariepinus</u>.

Farr (1975) studied natural populations of the guppy <u>Poecilia reticulata</u> and discovered that male sexual behaviour and degree of social cohesiveness vary drastically as a function of type of predation pressure. In populations with no predators or with various large characin and cichlid predators, the guppies live in dense aggregates along the edges of streams, and males exhibit intense sexual activity. Where the small cyprinodont <u>Rivulus hartii</u> is the sole predator, sexual activity is less intense and the guppies disperse sparsely across the entire stream. Clumping is thought to reduce predation pressure from large predators, and dispersion likewise from small predators.

A recent investigation by Kushlan (1976) gives a lucid insight into the effect of environmental conditions on the size of predator and prey populations. Seasonal water level fluctuations are the most critical environmental factor affecting fish communities of the Everglades marshes, Florida. During a 27 month period of stabilization of the natural fluctuation of water level, substantial changes occurred within the fish community. In general, the diversity of small omnivorous species, which normally dominate the community in biomass and numbers, decreased due to predation, whereas the number of species, abundance and size of large carnivorous fish increased. The overall result was a shift of the fish community to a predator-dominated system. Increased overall species richness in the community at constant high water level was the result of immigration of species which were poorly adapted for survival in fluctuating environments.

The most important finding of these field studies is that predation does more than reduce population numbers. It also changes other life history characters of the prey, including growth pattern, population structure, distribution, intensity of sexual activity, species dominance and population diversity in the community. Furthermore, the effects of predation may snowball through the ecosystem, and indirectly influence the life history of many other animals. In addition, accessibility of juveniles, movements of prey and changing dominance of prey species in response to varying environmental conditions were shown to influence predation. However, these broad causes and effects can only be fully understood if the influence of different factors on the predation process are tested in isolation, usually in experimental situations.

(b) Experimental studies on predation

Experimental investigations of the components of predation have been concerned with three main factors:

(i) properties of the predator
(ii) properties of the prey
(iii) properties of the environment.

(i) Properties of the predator: these include hunger, experience with available prey, duration of feeding on available prey, feeding periodicity and predator size.

The effect of hunger on subsequent food intake is important. Beukema (1968) found in stickleback Gasterosteus aculeatus that ingestion was proportional to the length of the deprivation period, with longer deprivations causing a doubling of the rate of eating in the first hour. The amount eaten during the second hour was equal after all deprivations (16h, 40h, 64h, 88h), with proportions in later hours smaller as deprivation was longer.

At very low hunger levels fishes may stop foraging and cease feeding to economise on energy reserves. Thus Ivlev (1961) found that pike, Esox lucius, tench, Tinca tinca and bleak, Alburnus alburnus may cease feeding altogether after long enforced starvation, and Windell (1966) that the appetite of bluegill sunfish, Lepomis gibbosus increased to a maximum after four days starvation, and then decreased, accompanied by degenerative changes in the pyloric caeca by the tenth day.

Hungry predators are generally less selective than satiated ones. Ivlev (1961) showed experimentally in carp, Cyprinus carpio, actively preying on four benthic invertebrate groups, that any selectivity present when the predator is hungry is not strongly expressed, but becomes progressively more marked as the predator becomes satiated. Thus, when the predator is hungry it eats all, or nearly all, the food objects it finds. As hunger is reduced, the predator becomes more discriminating, until at or near maximum satiation the predator eats only highly preferred items. A planktophage such as bleak, A.alburnus, on the other hand, had about the same preference at all levels of deprivation. Beukema (1968) also found in the stickleback that hunger increased the range of objects recognised and accepted as food. Similar results are reported by Nakamura (1962), Beukema (1964), Olla et al., (1970) as well as Chiszar & Windell (1973) who also found an increase in the complexity of feeding behaviour in well-fed fishes.

When presented with unlimited prey, many predators gorge themselves more than is needed for growth and metabolism. Gluttonous feeding is a regular activity of some mammalian predators (e.g. spotted hyaenas, Crocuta crocuta, Kruuk, 1972; lions Panthera leo, Schaller, 1972) and also occurs in predatory fish (Clarke et al, 1967 in Sabastoides dimidiatus; Kenmuir, 1973, in H.vittatus; Bowmaker, 1973, and my own observations in C.gariepinus). Hunger levels may also find expression through behavioural responses to prey. A fed stickleback inspects potential prey much more often than grasps it, and only at higher hunger levels will it eat it. This behaviour is economic since inspection requires much less effort than approach and capture (Tugendhat, 1960; Beukema, 1968).

Predator experience with the prey offered may influence hunting success. An important concept in this connection relates to 'searching image' (von Uexküll & Kriszat, 1934; Tinbergen 1960; (in Curio, 1976)), which Curio defines as 'a perceptual change facilitating the search for a particular object as a consequence of having seen it before'. Krebs (1973) pointed out that the term has been applied rather loosely and suggests that 'searching image' only involves selective attention for certain stimulus objects, for example camouflaged prey, which the predator has 'learnt to see', in preference to others which are overlooked and form a 'blurred' background. Beukema (1968) and Ware (1971) showed improvement in prey detection as a result of previous experience which they claimed was due to the formation of a 'searching image', in sticklebacks and rainbow trout respectively. However, another interpretation is that the fish were not learning to detect the prey but forming a stronger and stronger preference which Krebs (1973) would class as 'preference for familiar food types' and not as 'searching image'. Duration of feeding on one prey may affect selection. Thus, when given a choice between familiar and novel food, animals may select the type of food eaten previously, ignoring novel food; they are then said to have developed 'training bias'. 'Training bias' has been recorded in fishes by Ivlev (1961) and Bryan (1973), and operates against deliberate 'switching' between different prey and hence makes the diet monotonous. Switching means that the predator changes its behaviour to exert heavy predation on the prey of greatest relative abundance (Murdoch, 1969, 1971). Murdoch et al, (1975) demonstrated switching in guppies Poecilia reticulata which attacked whichever prey was most abundant when prey density was changed. Ivlev (1961) found that training heightened electivity of prey on which the fishes were trained, and usually overrides 'switching' even when a wide choice of food is given. Curio (1976) points out that a kind of 'searching image' may be involved and that the two concepts - 'searching image' and 'training bias' - cannot easily be separated.

Thomas (1974) studied the influence of discovery of a food object on the stickleback G.aculeatus. After discovery and acceptance of prey, there was a reduction in the tendency to move away from the site of eating, plus an immediate increase in the intensity of searching leading to 'area-restricted searching' (Tinbergen et al, 1967; 'area-concentrated searching' of Smith & Dawkins, 1971). After rejection of prey the opposite occurred, leading to 'area-avoided searching'. 'Area-restricted searching' also occurs in herring searching for plankton (Rosenthal & Hempel, 1970).

Predator experience in a particular area may increase searching efficiency. Beukema (1968) showed in sticklebacks that encountering efficiency (number of prey encountered per distance swum) increased with growing experience in an experimental maze, leading to highly efficient searching tracks.

The introduction of novel palatable prey typically resulted in a latent period during which risk to the new prey was low, followed by a rapid increase in risk (e.g. Beukema, 1968, in sticklebacks). According to Curio (1976), one of the causes of primary rejection may be fear. Subsequent continual stimulation from the prey would lead to habituation of fear responses, so that attack responses eventually predominate. In captive rainbow trout the 'latent' phase lasted, on average, four days (Ware, 1971, 1972). Odd (= differing from the majority) and conspicuous (= do not match their background) prey may have a higher risk than normal prey. Anchovetas Cetengraulis mysticetus swimming in well-defined sub-schools amidst countless flatiron herring Harengula thrissina were preyed upon selectively by pampano Trachinotus rhodopus (Hobson, 1968). These observations may explain partly why schooling fish characteristically shoal in groups of about the same size and appearance (Breder, 1959; Bruton & Boltt, 1975) although other factors may be equally important (Breder, 1965).

Daily feeding rhythm is another property of the predator which may affect predation. Some fish predators are known to synchronise their hunting with the main activity of their prey i.e. they are mainly nocturnal, diurnal or crepuscular (Ivanova, 1969; Reshetnikov et al, 1972; Emery, 1973; Hobson, 1974). However, this feeding pattern is by no means rigid, and 'nocturnal' feeders will readily feed in the day if no food is available at night (Starck & Davis, 1966). Hunger or other factors may therefore override feeding periodicity.

Ivlev (1961) investigated the influence of predator size on prey selection. Piscivorous fish devoured larger prey as the predator was larger, benthophages consumed prey of a certain size over a wide range of predator sizes, and planktophages had a prefered prey size dictated by the 'mesh' of the filtration apparatus. The size of zooplankton prey is also determined by gillraker gap in C.gariepinus; the mean width between developed gillrakers is 0,6mm

(Murray, 1975) and most zooplankton taken in Lake Kariba had a body width greater than 0,7mm (Bowmaker, 1973). However, Seghers (1975) showed that lake whitefish Coregonus clupeaformis are size-selective predators on Daphnia but this selection is not a function of gillrakers acting as a mechanical sieve. The plankters are taken individually and not by straining.

Frost (1954) found in Lake Windermere that pike eat larger fish species and larger individuals of a given species, as they increase in size. This trend is found in most piscivorous and many omnivorous fish (see discussion on African fish predators below). Large sticklebacks became satiated at a slower rate than smaller ones, and prey risk was thus larger as the searching fish was larger (Beukema, 1968).

(ii) Properties of the prey: these include prey size, behaviour, group size, experience with predator, novelty, appearance, catchability, distribution, density and growth rate. Other properties or strategies which have no relevance to the present discussion are omitted e.g. protective armour, chemical emissions, agonistic displays, association with protective organisms, high fecundity, mimicry (Greenwood, 1963a; Nikolsky, 1963, Thompson, 1976).

Predators may recognise prey by few or many stimuli, and in some cases by a summation of many stimuli. Stimulus-specificity is most developed in stenophagous predators and least in euryphages (Curio, 1976). Sometimes far-distance senses locate the prey generally, and accurate localization is by another sense. Sharks follow up unusual or escape movements of prey from afar using the lateral line organ, and attack following other cues (Nelson & Gruber, 1963; Banner, 1972).

Prey which has no experience with the predator concerned may display unadaptive escape reactions which lead to greater vulnerability. Thus fishes newly introduced into a large aquarium were readily taken by predators, whereas 'old residents' were not chosen and infrequently eaten (Wood, 1959). During the stocking of the new Lake Kariba with Sarotherodon macrochir, one group was accidentally released on an open beach and not among submerged vegetation. The fish, which had been bred in ponds from stock originally from the Kafue River (where no tigerfish, Hydrocynus vittatus, occur) panicked on release, and fell easy prey to endemic tigerfish. Haplochromis darlingi, which normally inhabit these areas in Lake Kariba, were easily able to avoid predation. Surviving S.macrochir eventually found refuge in adjacent plant beds (Jackson, 1961). Attacks by piscivores are also induced by struggling (Hobson & Banner, 1972), otherwise stressed (Herting & Witt, 1967) or disturbed (Potts, 1970; Markl, 1972) fishes. Popova (1967) used the term 'predator reflex' to describe learnt avoidance behaviour by prey after first encountering a predator. Naive fishes without a 'predator reflex', for example commercial fish reared artificially in ponds, are more vulnerable to predation than fishes of the same species with experience of the predator. Individuals that stray from a shoal i.e. spatially odd, expose themselves to predation. This behaviour may be induced by pack hunting predators which cause the shoal to panic (as described in the feeding chapter).

In special circumstances, behaviour of the prey may inhibit predation by a potential predator, as in the soliciting movements of cleaner wrasse Labroides dimidiatus. In addition, particular movements of the predator announce its impending departure, which prewarns the cleaner to leave (Hobson, 1971).

Neill & Cullen (1974) showed quantitatively that shoaling by fish prey decreased the success of attacks by pike and perch. The disruptive effect of shoals was shown to act for the ambush predator (pike) by interfering with the 'optimal' sequence of an attack and for the chasing predator (perch) by inducing continual switching to different targets during pursuit. Rüppell & Gösswein (1972) found that the presence of pike, or prey alarm substance, caused more intensive shoaling behaviour during the day, and dispersal at night, in the freshwater fish Leucaspius delineatus. The prey thus had different anti-predator tactics during the day and night, both presumably to reduce the rate of contact with a visual predator.

Eibl-Eibesfeldt (1962) and Redakov (1973) noted that shoals of prey may have better all-round vision and may detect prey at a greater distance, thus reducing the risk of surprise attack. Fish schools are also capable of defense movements, such as dividing in two or rapid dispersal, to confuse the predator (Baerends & Baerends-van-Roon, 1950; Redakov, 1973). Brock & Riffenburgh (1960) show that predators may find it harder to localize schooling prey than a corresponding number of isolated prey. (Interestingly, British infantry during the Battle of Waterloo found safety in masses when under severe stress; individuals breaking and running were easy prey to French horsemen! [Keegan, 1976]).

The importance of clumping by prey was investigated by Ivlev (1961). An increase in clumping caused stronger selection for preferred prey whether this increase was in one or all species of an experimental prey community. Taylor (1976) showed, theoretically, that clumping in space or time usually reduced prey risk. A possible explanation is that the synchronised appearance of a large biomass of prey swamps the predator, whose capacities of ingestion and digestion cannot take full advantage of the high prey biomass. Selection for optimum gut size in the predator would become increasingly strong if the main prey aggregated regularly. Treisman (1975) developed models to test the advantage to prey of group formation if the method of escape is by concealment or by evasive swimming. Aggregation of concealed prey is advantageous if the predator makes one kill, but not if all or a large portion of the discovered group are killed. Kill rate is lowered by group formation in evasive prey and decreased with increasing group size. Tinbergen et al, (1967) and his co-workers showed in birds that there is a correlation between camouflage and spacing out such that the distance between prey exceeds the detection distance of the predator. This correlation may also apply in certain fish prey, such as benthic molluscs.

Prey density is an important factor governing predation rates. Ivlev's (1961) experimental investigations showed that an increase in prey density led to more marked selection of preferred items, and less marked selection of previously avoided items i.e. preference was more strongly expressed. A model of optimal diet for a predator with different prey densities predicted that the number of prey types eaten would decrease as prey abundance increased, and that absolute prey abundance was a more important determinant of optimal diet than relative abundance or relative value of prey types (Estabrook & Durham, 1976). Beukema (1968) found in sticklebacks that prey density affects prey risk mainly through the progressive satiation of the predator. At high prey density, the predator becomes satiated faster, and as a consequence, prey risk is inversely proportional to prey density. In trout (Ware, 1972) the number of captures per unit time increased with prey density until an asymptote was reached, and thereafter predation rate decreased. This deceleration is explained by a progressive increase in handling time (time between initiating attack and resuming search) at the expense of searching time (Holling, 1966) and is described by Holling's (1965) so-called 'disc equation' and type-2 functional response. The same S-shaped relationship is found in many other vertebrates (Holling, 1966; Curio, 1976), which suggests that the trend is fundamental. (The elegant work of M.P. Hassell, J.R. Beddington, J.H. Lawton and others has extended Holling's findings on predator-prey relationships in insects and other animals. Their work is not reviewed here as its applicability to fish predators is at this stage little understood.)

Prey catchability is closely related to habitat diversity. Killifish, F.heteroclitus were more successful predators on amphipods and snails in salt marshes with low than high stalk density (Vince, et al, 1976). Ivlev (1961) showed experimentally that the presence of silt reduced the consumption of chironomid larvae by roach. Selection of shellfish in the same experiments was thought to be the result of reduced accessibility to roach of chironomids which are in fact the preferred prey. The diet of other predatory fishes tested did not, however, change as much when shelter was made available to the prey. Mauck & Coble (1971) found that selection by pike of several prey fishes did not alter in clear or turbid water. The intensity of predation and total food consumption of rainbow trout, S.gairdneri were inversely related to the complexity of the substrate as a number of prey were able to find cover and thus escape detection in a complex substrate (Ware, 1972). Grass carp, Ctenopharyngodon idella over a few centimetres long feed largely on plants under natural conditions (Hickling, 1966). However, Edwards (1973) has shown that they are better adapted to an omnivorous diet and eat many invertebrates when these are offered in an aquarium in the absence of cover. The low proportion of animal food in their diet may thus be due to low prey accessibility in natural systems.

A change in diet of tigerfish Hydrocynus vittatus in Lake Kariba in relation to changing density and availability of fish prey is apparent from the findings of Matthes (1968), Donnelly (1971), Bowmaker (1973), Kenmuir (1973), Begg (1974), reviewed by Mitchell (1976). During the filling period (1964/65) Micralestes acutidens were dominant prey, but after the dam had filled Alestes lateralis became dominant in the diet. In 1969/70 cichlids, which had previously been important prey, became dominant. Meanwhile, the population of introduced Tanganyika sardine Limnothrissa miodon had been expanding rapidly in the lake, and by 1970/71 this species was the main fish prey of H.vittatus. This situation persisted until the most recent survey in 1972/73 although a large proportion of the diet of inshore-feeding tigerfish still consists of cichlids, especially Haplochromis darlingi and Pseudocrenilabris philander (Mitchell, 1976). When the blossoming L.miodon population reached Sanyati Basin, an increase in the population of tigerfish in the open areas of this basin was recorded (Cochrane, 1976).

The formation of man-made lakes is an ideal opportunity in the field to study the response of predator and prey populations to changes in environmental conditions. Impoundment leads to large-scale changes in the quality and quantity of food available, and particularly to the proportion of predators. In Lakes Volta and Kainji, a decline in specialized insectivores, especially Mormyridae, occurred after closing (Petr, 1968; Lewis, 1974b)and in Lakes Kariba and Kainji an increase in piscivores was reported during the transition from fluviatile and lacustrine conditions (Coke, 1969; Lewis, 1974b). In Kariba the increase in predators, especially H.vittatus (from 15% of the catch in 1960 to 69% in 1965; Coke, 1969) was ascribed to the absence of cover for juvenile prey fishes (Bowmaker, 1970) whereas in Lake Kainji the increase in H.forskahlii probably resulted from the development of a large clupeid population (Lewis, 1974b). However, the population of H.vittatus, H.forskahlii and H.brevis in Volta lake remained low despite an abundance of the offshore pelagic fish, Pellonula and Physailia (Petr, 1974). The increase in predators typical of most new African man-made lakes has not prevented cichlids from becoming abundant, e.g. in Lakes Kariba (Balon & Coche, 1974; Mitchell, 1976), Kainji (Lewis,1974b), and Volta (Petr, 1967). The success of the cichlids may be related to their well-developed methods of protecting the young by mouth-brooding, nest-guarding and deposition of fry in relatively safe shallow littoral areas.

Physical appearance of the prey may or may not influence subsequent predation. Coble (1973) found that fantail and regular goldfish, *Carassius auratus*, and different colour goldfish were taken equally by pike *E.lucius*. However, the experimental tanks provided so little cover that the results are not surprising, and differential selection may have taken place in nature. Markl (1972) demonstrated that piranhas attack only fish shapes that exceed a ratio of length:width of 4:1, i.e. elongate species. Piranhas also do not attack small and agile species, which they by experience avoid as they are virtually uncatchable. Lemon sharks, *Negapion brevirostris*, seized fish prey illuminated by a Floy tag containing a light before unlighted but otherwise identical prey (Moeller *et al*, 1972). Lighted prey were approached in a straight line, whereas unlighted prey was circled at least once before seizure.

Prey size is an important property, and has already been discussed in connection with predator size. Rainbow trout catch larger crustaceans more often than smaller ones as larger prey are seen from a longer distance (Ware, 1972). Likewise, bluegill sunfish, *Lepomis macrochirus*, select *Daphnia magna* according to size, preferring larger ones, and this selection can be related to their higher visibility. Size selection was more marked at high prey densities (Werner & Hall, 1974). Predation by alewife, *Alosa pseudoharengus*, in small lakes in Connecticut was shown by Brooks & Dodson (1965) to result in the elimination of large zooplankton dominants (*Daphnia*, *Diaptomus*) which were replaced by smaller species, especially *Bosmina longirostris*. In *Lepomis gibbosus*, a visual predator, the reaction distance to individual plankton usually increased with increasing prey size and with increasing prey opacity (Confer & Blades, 1975). That fish predators find some prey more palatable than others was shown by Beukema (1968) in sticklebacks. Pieces of *Enchytraeus* worms were preferred to *Tubifex* forms, with *Drosophila* larvae least palatable.

Moore & Moore (1976a, 1976b) determined the factors influencing food selection by various fish predators in Severn Estuary. In flounders, *Platichthys flesus*, prey size, distribution, degree of concealment, motility and ability to escape, predator experience and speed and turbidity and temperature of the water were the major determinants (1976a). In the second study, (1976b) using four other predators, prey abundance, concealment, size, motility and ability to escape, predator hunting tactics and speed, and turbidity significantly influenced the proportion of empty stomachs and the amount of food ingested by the predator. Ware (1973) developed a model to describe the risk of aquatic prey to visual predators, with particular reference to rainbow trout. Sequential comparisons between the predicted and observed pattern of predation suggested that prey activity, exposure, density and sex were the major determinants of prey risk in benthic food chains.

(iii) Properties of the environment: these have rarely been studied in isolation but usually in combination with properties of the predator and prey: e.g. see investigations of Great Lakes; Windermere; Wisconsin lakes; Lake Tanganyika; Everglades marshes; Lake Kariba; and the effect of habitat diversity described above. An important gap in our knowledge of predation is the influence of abiotic factors such as water depth, and light, oxygen and temperature regimes. Moore & Moore's (1976a, 1976b) recent studies in this field are an important contribution.

Discussion on experimental analyses of predation:

Holling (1961) in a review of the principles of insect predation, proposed that the basic components of predation are predator and prey density, which are universally present, whereas subsidiary components, such as other properties of the predator and prey and environmental factors, may be constant or absent. The basic components determine the form of predation, whereas the subsidiary components merely alter its magnitude. In many of the studies on fish predation cited above, factors other than predator and prey density had a marked effect on prey risk. In particular, the accessibility of prey may be very important. The main factors which may influence predation by piscivorous fish are summarized in Table 32.

As noted by Thompson (1976), these factors or strategies should not be called 'adaptations' as they consist of complex aggregates of mechanisms not all of which, individually, evolved from selective pressures of predation. In particular the factor which I have called temporal asynchrony (Thompson's, 1976, term 'time-lag' is not suitable) includes several elements of the prey's life history which are only partly related to predation: i.e. diel activity, movements and exposure; habitat preferences; choice of spawning habitat; spawning season; protection of young etc. Their common feature is that the prey, especially at a vulnerable stage in its life, inhabits the same place as the predator, but at a different time. Of course, the corresponding predator strategy is to decrease temporal asynchrony, but this behaviour must not impose a significant risk on the predator.

Thompson (1976) has distinguished between coincidental and frontal prey strategies. The former are properties of the prey which were evolved partly to reduce predation risk and partly for other reasons, and may thus be practised

TABLE 32

Summary of main factors which may influence predation by piscivorous fish

Factor influencing predation	Influence on predation
Properties or strategies of predator:	
Increasing predator hunger	increases ration and decreases prey selectivity
Increasing predator experience with prey	greater predation efficiency
Increasing predator size	increase in number and size of prey taken
Efficient hunting strategy (e.g. pack-hunting, flight-inhibiting behaviour).	increases prey risk
Properties or strategies of prey:	
Prey evasive behaviour (e.g. shoaling, clumping, migrations, flight, hiding)	decreases prey risk
Temporal asynchrony (see text)	decreases prey risk
Increasing prey density	increases prey risk to asymptote after which increased proportion of handling time decreases prey risk
Increasing experience with predator	decreases prey risk
Novelty	decreases prey risk initially
Prey structure (size, colour, shape, taste)	various
Properties of the environment:	
Habitat diversity	decreases accessibility and prey risk
Changing environmental conditions favouring predator or prey	various

or present even in the absence of predators; e.g. temporal asynchrony; prey colour, taste, size and shape, and changes in prey density. Frontal strategies are performed in direct response to the threat of predation: e.g. evasive behaviour (but shoaling is also coincidental), agonistic displays and motionlessness.

In the next two sections, predation by catfish in Lake Sibaya and other African lakes, is reviewed in an attempt to define those factors and strategies which are most important in their interaction with tilapia and other prey.

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 by African fishes on speciation is not discussed (for main papers see Worthington, 1937, 1954; Jackson, 1961b; Fryer 1960, 1965; Fryer & Iles, 1972; Greenwood, 1974).

The study of fish predation by African freshwater fish has largely been confined to descriptions of food preferences, the effect of predation and the conditions under which prey are taken. There have been no experimental studies (to my knowledge) which have experimentally analysed the factors which influence prey risk, although many valuable field observations have been made on the possible effect of water depth, plant cover and other factors.

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 31. 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 1966; 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 the 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, a point emphasised by Fryer and Iles (1972) who calculated that *C.mossambicus* consumed more than 153×10^6 *Haplochromis* in the Tanzanian waters of Lake Victoria in 1958. They also show that smaller species of cichlids, especially *Haplochromis*, are more important prey of *C.mossambicus* than tilapia and other large 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. Lest I initiate another African fish predator 'ferocity' debate (see Jackson (1961b) and Fryer (1965) for main arguments), it should be added that 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 (my own observations).

Ivlev (1961) used the ratio $\frac{\text{modal size of prey}}{\text{size of predator}}$ (rapacity index) to distinguish between the ferocity of fish predators. Active predators (e.g. *Esox lucius*) had indices above 0,2 and 'peaceful' or slow predators (*Cyprinus carpio*, *Abramis brama*) 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 predation. The rapacity of fish predators can be compared using this percentage, although the values will 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 Sibaya catfish is 14 (range 5-21), although cannibalistic *C.gariepinus* in the Vaal River and Hardap dam consumed prey 25 to 58% their length (Groenewald, 1964; Gaigher, in press). 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* (>380mm; Allen, 1939), about 20 for *Hydrocynus forskahlii* and 10 for *H.brevis* (Lewis, 1974a), and 13-40 for *Bagrus docmac* (200-600mm 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 large 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 (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 characids may be major piscivores in terms of numbers of prey taken.

The impact of predation on prey behaviour is also important. Because of their active predatory tactics, *H.vittatus* elicit avoidance tactics in potential fish prey. However, *C.gariepinus* which is relatively slow-moving and readily switches to alternate invertebrate prey when fish are uncatchable, usually produce little evasive response in nearby prey (as described later).

Jackson (1961a) noted that tigerfish *H.vittatus* from the Middle Zambezi and Lakes Bangweulu and Mweru (before inundation of Lake Kariba) usually fed on fish prey less than 180-200mm TL. These prey generally sought cover in submerged vegetation and very shallow water, which tigerfish rarely enter (Donnelly, 1969; Kenmuir, 1973). Munro (1966) gives a smaller 'safe' length of 160mm for tilapia in Lake McIlwaine, Rhodesia. However, he states that *H.vittatus* larger than 400mm TL are uncommon. Donnelly (1969) confirmed that the largest tilapia recorded from 2,300 tigerfish stomachs in Lake Kariba measured 180mm TL. Larger tilapia move with relative impunity among *H.vittatus* >600mm TL whereas smaller prey inhabit mainly shallow areas. However, both Bowmaker & Caulton (pers.comm., 1977) have observed juvenile tigerfish entering very shallow water, where they may prey on cichlids. Donnelly (1969) has noted that in some Rhodesian highveld dams in which the only potential predator is *C.gariepinus*, tilapia shoals of all size groups can be found intermingled at various depths, though segregating out in warm shallow water.

According to Kenmuir (1973) the low proportion of tilapia in tigerfish stomachs in Lake Kariba (2-5%) is a result of their ability to hide from the predator. He suggests that tigerfish may restrict the areas habitable by young tilapia and thus limit population numbers. These findings indicate that the more important role of predation on tilapia by a fast-moving predator such as *H.vittatus* may be to impose a restriction on areas suitable for nurseries rather than reduce the numbers of prey directly.

Jackson's (1961b) hypothesis that spawning migrations function largely to place the eggs and young in situations in which they are relatively safe from predation, especially by H.vittatus, has been disputed by Fryer (1965) and Greenwood (1965). Fryer considers that the primary role of upstream migrations is to ensure dispersal over the whole colonizable river course, whereas Greenwood emphasizes the importance of placing the eggs and larvae in a suitable physico-chemical environment, especially in relation to oxygen requirements. Greenwood also notes the importance of cover to newly-hatched larvae and young post-larvae. Bowmaker (1973) stresses that 'ancient behavioural mechanisms' may be involved in potamodromesis.

Discussion on predation by Clarias and H.vittatus

Field observations have provided some information on the factors influencing catfish and tigerfish predation. Properties of the predator, such as size, and habitat preferences; of the prey, such as accessibility, evasive behaviour, density and size; and of the environment, especially the availability of cover, have marked effects on predation success. Important gaps include knowledge of the influence of predator hunger on prey selectivity, and the influence of predation pressure on the breeding success of prey.

The comparison between tigerfish and catfish has been useful as they appear to be complementary predators. Tigerfish are fast, attacking predators which feed mainly on obligate pelagic fishes (when these are available). Both catfish and tigerfish are vulnerable to piscivorous birds in shallow water, but this threat is reduced at night as large piscivores such as the African fish-eagle Haliaetus vocifer do not hunt after dark. Catfish, which can detect prey by mechano-reception at night, are therefore better equipped for nocturnal forays into shallow water, where cichlids can be caught. Both tigerfish and catfish are opportunistic and both will take any fish species which is abundant, especially if there is insufficient cover. In general, accessibility appears to have a more important influence on predation pressure than high prey density but this point needs confirmation.

Both types of predators respond quickly to newly available food resources, and in the case of tigerfish they may alter their habitat preferences and move from littoral to pelagic zones if pelagic fish prey become abundant. Catfish are particularly suited to feeding in the littoral zone of lakes and rivers with fluctuating shore lines as their omnivorous habits allow them to take advantage of the diversity of fish, and insects, which fluctuate in abundance according to water level and/or season. Environmental conditions may affect the success of predator populations even in the abundance of food, as in the case of Hydrocynus spp. in Volta lake (Petr, 1974).

The interaction of tilapia and catfish in Lake Sibaya

In Lake Sibaya, inshore terraces have high cichlid populations and form an important catfish feeding ground. The present study was therefore concentrated on the terrace. The proportion of each tilapia species on the terrace was determined by regular standardized pulls of a seine net. During trials, the efficiency of the seine net was studied underwater using SCUBA. As a result, wings, a ventral curtain and extra weights were added to improve the net's efficiency for catching all three cichlids. The total catch of S.mossambicus, T.sparrmanii and P.philander during standardised surveys at three lake levels exceeded 10400 fish. Results of the seine catches were in all cases qualitatively confirmed by day and night dives using SCUBA.

A marked increase in lake level occurred during the period of study (1973-1976) resulting in widespread changes in the terrace habitat as well as in the relative density of cichlids inhabiting the terrace. This provided an opportunity to investigate prey distribution and catfish diet under different environmental conditions and prey densities.

During a previous study (1970-73, on S.mossambicus, Bruton, 1973) water levels in Lake Sibaya were relatively low (Fig. 4), 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 shoaled and 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 & 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%) (Bruton, 1973; Bruton & Boltt, 1975). Catfish remained in slope and other offshore habitats during the day, and usually entered the terrace at night at low lake levels (Table 23). 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 had become established. The distribution and movements of S.mossambicus were quite different (personal observations, and Bowen, 1976). 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 20h00 and 0h100, but thereafter they were uncommon again.

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%). Catfish 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 24h 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 factors must now be considered. The effect of water temperature will be examined first.

Diel horizontal movements of young tilapia into shallow water along a temperature gradient have been reported by Welcomme (1964) for T.variabilis, T.esculenta and T.zilli in Lake Victoria; Coe (1967) for T.grahami in Lake Magadi; Donnelly (1969) for T.mortimeri in Lake Kariba and Caulton (1975) for T.rendalli in Lake McIlwaine. Welcomme (1964) found in Lake Victoria that shallow-sloping or temperature gradient beaches were the usual habitat of young tilapia, while haplochromids preferred steep-sloping or non-gradient shorelines. At night when temperature gradients were reversed, tilapia departed to deeper water while haplochromids encroached on the cooler shallows.

Some of the movements of tilapia 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, 1969; Josman, 1971). The upper lethal temperature is 38,2°C for small adults (80-120cm TL, Allanson & Noble, 1964) and 41,7°C for juveniles (25-35cm TL, Kemp, 1966). S.mossambicus also have a rapid rate of temperature acclimation

(1^{o}C per 150 minutes for fishes 80-120mm TL, Allanson & Noble, 1964). At temperatures below 20^{o}C metabolic rate declines and S.mossambicus becomes lethargic (Josman, 1971) and below 14^{o}C degenerative changes in kidney and blood physiology take place (Coe, 1966; Allanson, 1966; Minshull, 1967; Bok, 1968; Allanson & Cross, 1970; Allanson et al, 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^{o} and 40^{o}C, but are absent from terraces at night (or in mid winter) when water temperatures fall below 16^{o}C.

T.sparrmanii fry acclimated at $24,5^{o}$C (about the modal water temperature at Lake Sibaya) had upper temperature preferences of $32,2^{o}$C whereas adults only selected temperatures up to $30,6^{o}$C in an artificial temperature gradient (Donnelly, 1969). Pseudocrenilabris philander fry acclimated at $24,5^{o}$C had an upper preference limit of $27,2^{o}$C whereas adults only selected temperatures up to $25,5^{o}$C. At a higher acclimation temperature ($29,5^{o}$C) both adults and fry adopt a final temperature preferendum of $26,1^{o}$C (Donnelly, 1969). Both these species would thus be excluded from daytime occupation of shallow terrace waters in Lake Sibaya in summer (when temperatures regularly exceed 32^{o}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 and nutritious 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. Temperature and habitat preferenda can thus explain the broad observed pattern of distribution of these three cichlids in shallow water in Lake Sibaya.

However, certain observed movements are 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. Catfish are the main fish predators of S.mossambicus and other cichlids in Lake Sibaya and their effect must now be considered.

Catfish, like S.mossambicus, show a diel horizontal movement, 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^{o} to 35^{o}C. In captivity they forage at temperatures above 17^{o}C, but become lethargic below this temperature. 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 temperature 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 nonlethal 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 will be tolerated for brief periods. However the available information is too sparse for any definite conclusions, and no comment can therefore be made on the relative abilities of predator and prey to enter terrace waters at high or low temperatures.

Several important factors which affect the predator-prey relationship between catfish and cichlids in Lake Sibaya can now be identified. These are water depth, day-night light changes, water temperature and predator and prey density. In the next sections of this chapter the influence of nearly all these factors on the predation process is investigated. Temperature was the only factor which could not be studied at the field station.

Firstly, the working hypothesis, that catfish feed on cichlid prey in proportion to their relative abundance in the lake, is tested to assess the effect of prey density on selectivity. A series of experiments was then carried out to re-enact this field test and confirm its results. However, before the latter experiment could be performed, several preliminary investigations had to be made to determine the optimal conditions for observing catfish in captivity. These preliminary tests provided the information needed on the effect of water depth, day-night light changes, predator density and other factors on predation efficiency.

Field collection to determine the proportion of cichlids in the catfish diet 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 catfish 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 are compared in Table 33. A G-test was used to test for significant differences. The G-test has an important advantage over the Chi-square test, which has been used extensively by biologists, in that it can be applied not only to the Poisson, but also to normal, binomial and other distributions of the data (Sokal & Rohlf, 1973). In all cases the null hypothesis was that the proportions available (expected to be eaten) were not significantly different from the proportions eaten (H_o: 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 (88,3% x 36 = 31,8 in the first example in Table 33).

Ivlev's electivity index (E, 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.

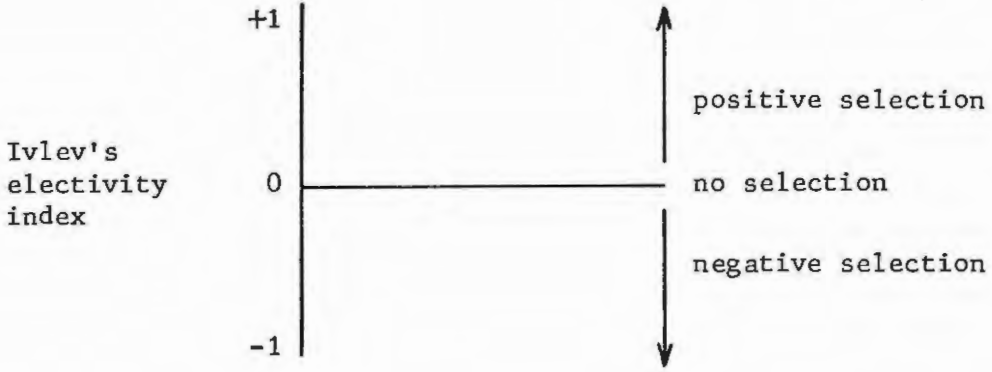
Using this index, positive selection is expressed by values from +1 to 0, absence of selection by 0, and negative selection by values from 0 to -1.

TABLE 33

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 1970-1976. 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, p.294) 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.

N = number of stomachs (with contents) examined from catfish caught on the terrace. The lake levels are defined in Table 22.

	Cichlid population sampled on the terrace using standardised seine net pulls		Cichlids in diet (number)		Modified electivity index
Low Lake Level (1970-1972)	number	% of total	Observed	Expected	
			N=92		
S.mossambicus	4570	88,3	27	31,8	-0,08
T.sparrmanii	204	3,9	3 } 9	4,2	+0,36
P.philander	388	7,5	6		+0,36
	5162		36		
			G = 4,880 P < 0,05 Significant		
Intermediate Lake Level (1974-1975)			N=275		
S.mossambicus	2009	59,1	126	101,1	+0,11
T.sparrmanii	449	13.2	2	22,6	-0,84
P.philander	942	27,7	44	47,4	-0,04
	3400		171		
			G = 39,23 P < 0,001 Significant		
High Lake Level (1976)					
S.mossambicus	273	14,8	2	9,2	-0,64
T.sparrmanii	424	23,0	15	14,3	+0,02
P.philander	1146	62,2	45	38,6	+0,08
	1843		62		
			G = 9,13 P < 0,01 Significant		



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

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 significantly different ($P < 0,05$, Table 33). 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). Dawn and dusk may be the most vulnerable time for visually-orientating prey (see discussion below).

In general, the collections showed that catfish predated on the three cichlid prey approximately in proportion to their relative abundance on the terrace, irrespective of prey species (and therefore specific avoidance tactics and habitat preferences), or changing environmental conditions. This result can be expected in an omnivorous predator if it feeds opportunistically on virtually whichever prey it detects. However, the number of encounters does not always relate closely to the number of prey eaten as shown in the next sections. Many factors may influence the predation process, and even override density effects.

Experimental analysis of predation by catfish

Introduction

In the review of factors influencing predation, several were identified as important (Table 32). As far as possible these factors were kept constant in the experiments reported below, i.e. predator hunger, experience with prey, size, prey density, prey size and experience with predator, and habitat diversity. The review of the interaction of catfish and cichlids in Lake Sibaya showed that water depth, day-night light intensity and number of predators may be factors which have a particularly marked effect on catfish predation. Their influence was therefore studied in detail to provide further clues to the understanding of the catfish-cichlid relationship. In addition, these experiments defined the optimal conditions (in terms of the three factors) under which catfish would prey on cichlids in the experimental areas. This information was used in the design of the final experiment on prey selection. Before this final experiment could be performed a series of preliminary experiments on acclimation time, the reliability of the removal method, daily food intake, stomach clearance time and feeding periodicity were carried out to establish the optimal conditions under which catfish should be kept in captivity.

Altmann (1974) discussed the important concepts of external and internal validity in experimental ethology. She noted that the primary function of research design is to maximise the validity of the conclusions, and distinguishes between internal validity, which deals with statements about the sample, and external validity, which deals with interpretations and generalisations from the sample to other situations and populations. Internal validity is an essential part of external validity. Experimental research usually emphasizes internal validity, whereas observational field situations tend to show the converse imbalance. Methods to correct this imbalance include using information from field studies to design experiments, and bringing some of the manipulations of an experiment into the natural field situation. Both methods have been attempted here in an effort to increase the external validity of the results of the preliminary and final experiments.

The reproducibility (in terms of obtaining identical results) of feeding experiments in fish is usually lower than in physiological experiments (Ivlev, 1961), as the subjects are organisms or groups of organisms each with their own peculiarities. Every attempt has been made to obtain valid results by using predator, prey and experimental situations whose properties were as constant as possible. The agreement of qualitative results in separate near-identical experiments served as the criterion of reliability of the results obtained. In this study each set of experiments was repeated at least twice, usually four times. The results were usually in close agreement. Where there was no agreement, the experimental procedure was re-examined and an unsuspected variable was usually found, isolated in further experiments and then excluded when the original experiment was repeated.

Description of experimental areas and procedures

Four Predation Experimental Areas (PEA) were designed and made. PEA I and II (Figs 63 and 64) were large outdoor pools for observations on adult catfish (TL > 350mm). PEA I was situated on the lake edge and provided a semi-natural environment for general observations on predation, and for determination of pre-experiment time and stomach clearance rate. PEA I was protected from wave-action by a 2,5m high cement bag wall, but an unexpected lake level rise eventually caused conditions to become unsuitable for quantitative observations. PEA II was therefore made to provide a closed experimental area in which water depth and food supply could be controlled and detailed observations carried out. PEA III and IV were indoor aquaria for close observations on small juvenile (<100mm TL) and large juvenile and small adult (150-400mm TL) catfish respectively. In addition, observations were made on predation in the lake using a 7m tower and SCUBA.

Predation Experimental Area I (PEA I, Fig.63): 10 x 10m enclosure on lake edge surrounded by 1m high fence on a cement foundation. Fence lined with 10mm bar mesh netting to prevent the escape of small fish. Water depth 200mm to 700mm as lake level increased. Sandy bottom. A hide, 2,15m above ground

Figure 63A: Predation experimental area I(PEA I), showing central hide, red lights and above water cords dividing observation area into 36 equal squares.

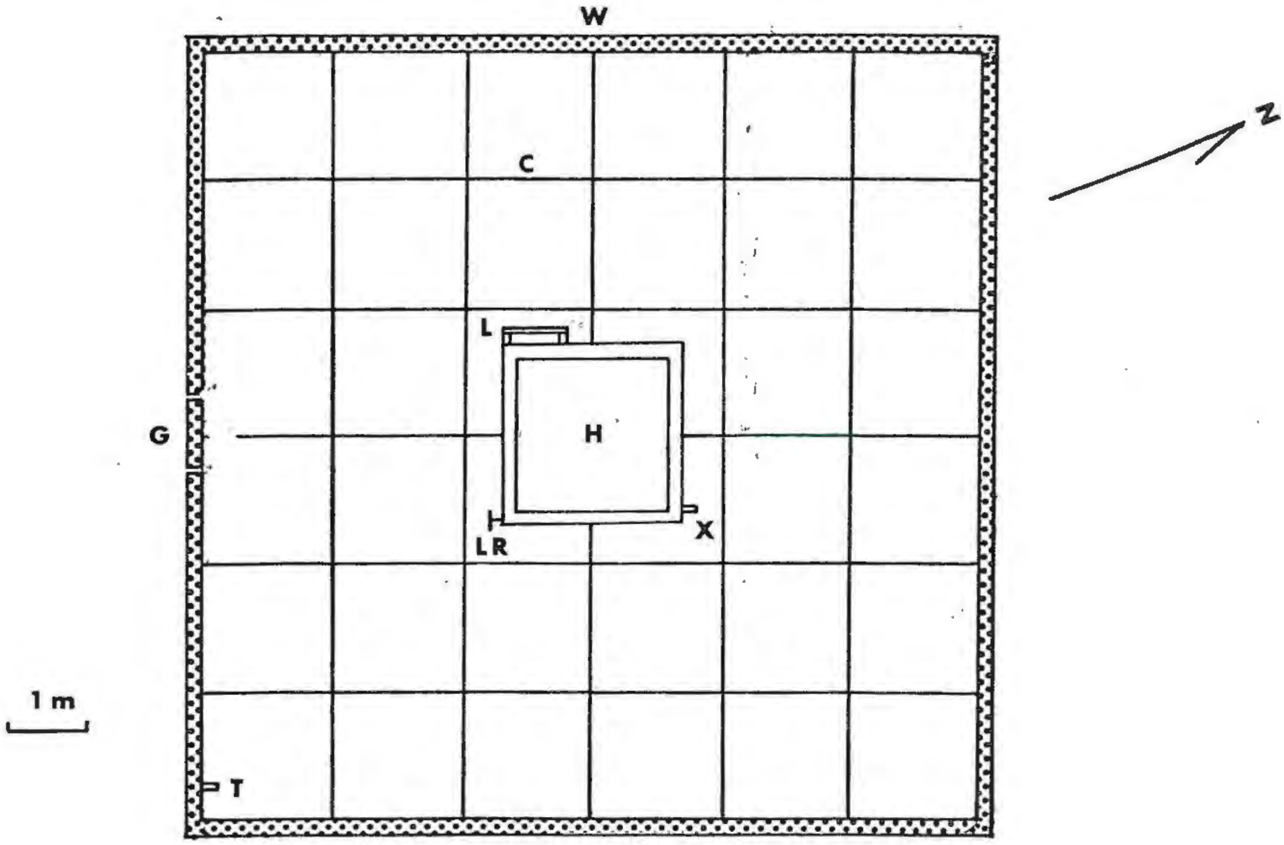


Figure 63B: Plan of predation experimental area I. W: perimeter wall. C: above water cord. L: ladder. H: hide.

X: Luxmeter. LR: water level recorder. G: gate. T: thermometer. The positions of the red lights are not shown (see Fig. 63A).

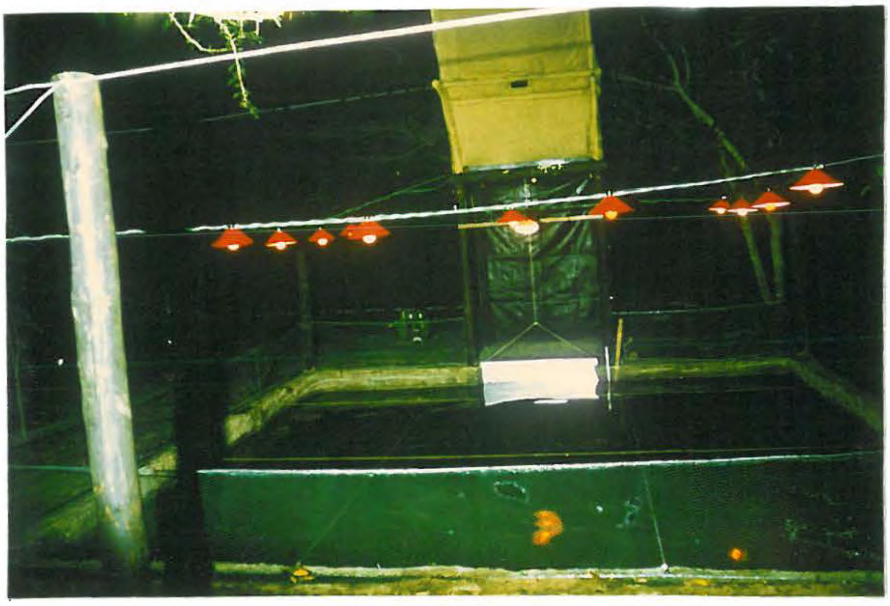


Figure 64A: Predation experimental area II (PEA II) showing hide on one side, observation slit, red lights, main observation area, trapdoor enclosing the small enclosure and the above water cords dividing the observation area into 9 equal squares.

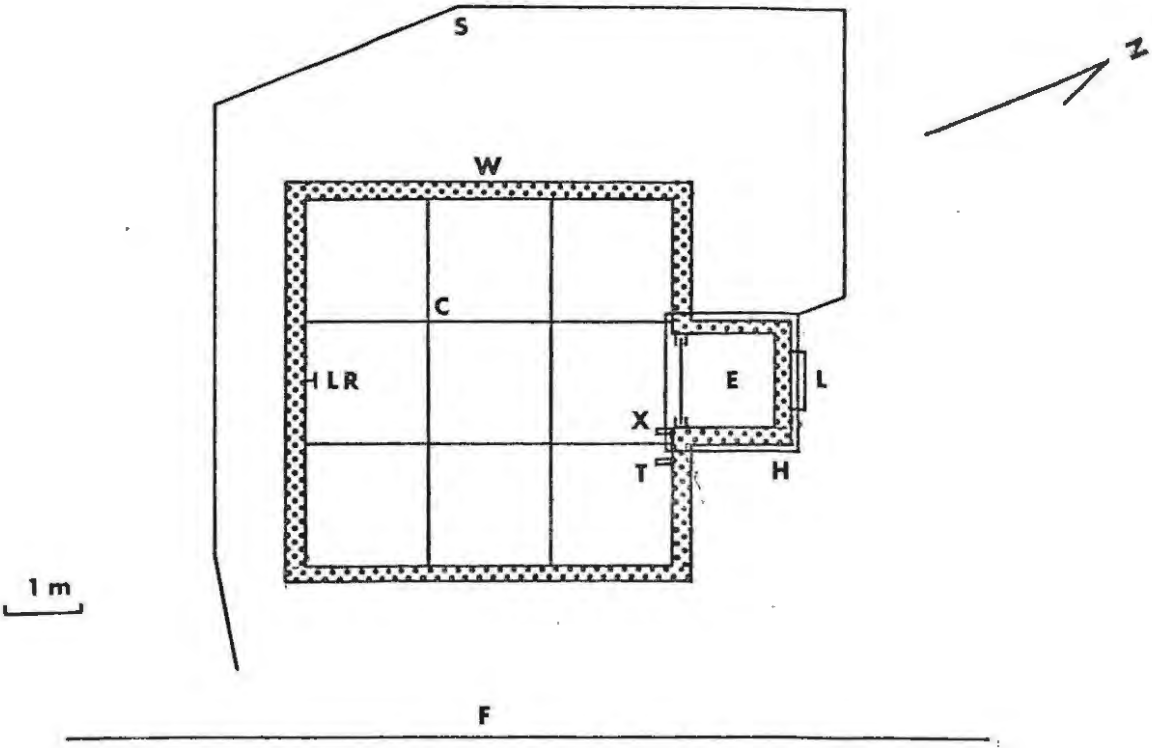


Figure 64B: Plan of predation experimental area II. S: black sheeting screen. E: small enclosure. F: reed fence. Other symbols as in Fig. 63B.

level had 1,9m hessian walls with observation slits on all sides. Entrance to the hide was via a gate in the fence, and a ladder. The hide was fitted with a red weatherproof reading lamp, and bench which housed delicate instruments and electrical sockets.

PEA I was divided into 36 equal sized 1,67 x 1,67m squares marked off above water level with tightly-strung cord. The four middle squares were reduced in size by a covered tank (abandoned evaporation tank). Numbers assigned to the squares were attached to the adjacent fence, overhead lamp shades or walls of the hide, and could easily be read off as fish passed from one square to the next. There were no underwater obstructions between squares, so the fish swam in a continuum bordered by the fence, and with the covered tank and hide supports in the middle. A water level plate and maximum-minimum thermometer within the enclosure were read routinely from outside the fence, and a Hydrobios lux meter (unshaded) and thermometer (shaded) in midwater below the hide were read remotely from the hide. The enclosure was illuminated for night observations by 13 x 60W red bulbs with red shades, operated from the hide; four in each quarter and one under the hide floor. Additional night observations were carried out using a light with a red filter. Red lights were used to simulate night conditions but allow observation of the predators and prey. Under red light the cichlid prey behaved in the same way as at night i.e. they were dispersed and did not shoal, except on bright nights when some shoaling took place. Catfish did not change their behaviour when the lights were switched on or off. During observations, one to two persons remained in the hide for long periods and outside disturbances were minimal. Prey were caught in the adjacent lake and introduced into PEA I with a minimum of disturbance and were recaught using a small seine net when the cords of the above water grid had been unclipped. Catfish were collected using handnets from holding tanks in which their food supply was controlled - their state of deprivation was therefore known.

Predation Experimental Area II (PEA II, Fig. 64): Cement pool 4,8 x 4,8 x 0,6m deep, with a 1,2 x 1,3m enclosure on the northern wall separated from the main pool by a vertically rising aluminium door, with a mesh window allowing water circulation. The door could be operated from the hide. Sandy bottom divided by cords of the above water grid into nine 1,6 x 1,6m squares clearly marked with numbers on the fence and lamps, and with no underwater divisions or obstructions. The hide stood 2,56m above sand level over the enclosure with the side facing the experimental area inclined so that a comfortable sitting position gave unimpeded vision through a narrow slit of the whole pool without the observer moving. The observer sat on a bench provided with weatherproof reading lamps and a tape recorder, light switch, thermister circuit and Hydrobios luxmeter. Water level could be read off a level plate on the opposite wall. The whole experimental area was surrounded by a 2m high black plastic sheeting wall and reed fence to reduce outside interference. Entrance to the hide was via a ladder behind the black screen without any disturbance to the experimental area. Water was added to the enclosure by gravity feed from the research station's water supply (untreated lake water) and removed using petrol-driven pumps.

The pool was illuminated for night observations by 10 x 60W red bulbs with red shades, three along each side, one in the middle and one under the hide floor. Prey could be recaught using small seine nets when the above water grid had been unclipped. Catfish were quietly herded back into the enclosure where they could easily be recaught using handnets. The enclosure remained closed and empty of fish during experiments. A closable ventral peephole allowed viewing of the enclosure from the observer position in the hide.

PEA III All glass aquarium. 1500 x 780 x 810mm deep, with sandy bottom, enclosed in a black plastic hide. The observer sits outside the hide and looks through a slit.

PEA IV All glass aquarium 250 x 250 x 250mm with sandy bottom, enclosed in a small table hide with observation slit.

Description of predatory behaviour

It is a basic tenet of this investigation that the intricate processes of predation which occur under natural conditions are composed of simple elements; that these elements can be identified and their interactions studied in artificial enclosures. Feeding behaviour in the experimental areas included individual foraging and foraging in groups but not social pack-hunting or surface feeding. The amount of feeding activity was measured both by the number of food items eaten and by the number of appetitive activities. The appetitive activities used are defined in Table 34.

A flow diagram of appetitive actions is also given in Table 34. The full sequence was not always followed. Often, in predators habituated to a prey which under the circumstances was difficult to catch, encounters and discoveries led to 'overlooks' or 'neglects', and not to 'grasps'. The responses 'encounter', 'discover' and 'grasp' may be repeated several times on a chased, elusive prey. Unpalatable prey may be grasped and then rejected. The extent to which the full sequence was followed was a measure of prey risk. Thus prey risk is highest at 'eat' and lowest at 'searching movement'.

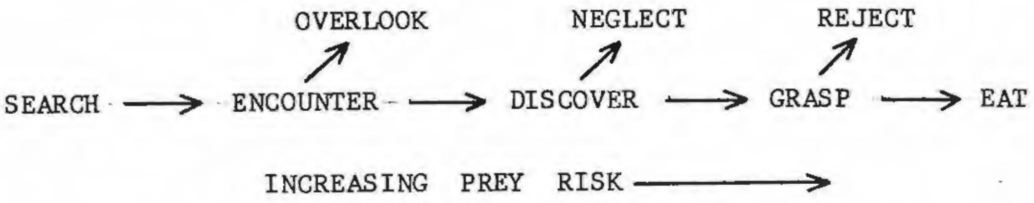
In the experiments on invertebrate prey, prey risk was measured by determining the percentage of one appetitive action which led to the next.

TABLE 34

Definition of catfish appetitive actions counted during the predation experiments

Positive appetitive actions	Description
search	- catfish passes its whole body under above-water cord
encounter*	- catfish passes its whole body into same square as prey
discover	- catfish makes orientated response towards prey
grasp	- catfish makes successful suck-snap lunge at prey
eat	- prey swallowed
Negative appetitive actions	
overlook	- catfish does not attack an encountered prey
neglect	- catfish does not grasp an attacked prey
reject	- catfish does not eat a grasped prey

Flow diagram of appetitive behaviour in <u>C.gariepinus</u>



* As the size of the squares in PEA I and PEA II (1.6 to 1.67m square) was approximately equal to the maximum reaction area of a 570mm <u>C.gariepinus</u> for cichlid prey (personal observations), an 'encounter' was scored every time a catfish had the opportunity to discover a prey. The 'maximum reaction area' is the area within which a catfish can detect strong capture-eliciting stimuli from prey.

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'

In one experiment, prey risk was also scored by weighting successive positive appetitive actions using an arbitrary, increasing multiplication factor, as follows:

Positive appetitive action	Multiplication factor
Search	x1
Encounter	x2
Discover	x3
Grasp	x4
Eat	x5

The value obtained, the risk index, emphasizes the greater risk of appetitive actions late in the predation sequence.

Records were not kept for individual catfish, but combined for all experimental fish. Changes of searching behaviour, from individual foraging (described in the feeding chapter) to rapid searching and frenzied feeding were recorded. Other activities, which could easily be distinguished from searching behaviour, included comfort movements (scraping body against sand or wall), displacement activities (e.g. grubbing in sand when there is no benthic prey available), fright movements (rapid swimming in response to an outside disturbance), agonistic behaviour (chasing of one catfish by another or mouth displays during a feeding frenzy - no butting or biting was observed), escape (rare attempts to jump out of the PEA), aerial breathing (regular gulps of air at water surface) and polarised swimming (only observed when the pool was being refilled between experiments. Catfish orientated themselves into the current near the water inlet).

Between experiments the catfish swam freely in the PEA. One hour before each experiment they were gently herded into the enclosure, and the prey introduced. The prey therefore had one hour to become familiar with the PEA in the absence of predators.

Pre-experiment time:

The time taken by catfish to become familiar with the PEAs and behave normally was determined in PEA I. Abnormal behaviour involved mainly escape movements in the squares abutting on the lake, and normal behaviour mainly search swimming throughout PEA I. The proportion of time spent in non-escape squares was therefore a reflection of acclimation. Observations were made on two groups of catfish each over three days. The square occupied by each catfish was noted continuously for half an hour every three hours. During the first 12h, escape squares were occupied for 60-95% of the time. This proportion dropped to 20-40% in the second 12h, and 15 to 35% in the third 12h. After 36h escape squares were occupied no more often than other squares in PEA I. The catfish therefore behaved normally towards the end of the second day. All catfish were kept for at least 5 days in PEA I before transference to PEA II. Escape movements in PEA II usually ceased after one or two hours.

Reliability of removal method:

A basic premise of some of the experiments was that all prey lost from PEA II had been captured by the catfish. Loss of prey by other sources had to be discounted. Two control experiments were conducted in which a known number of prey were introduced into PEA II for 2 days each 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, although catfish may have consumed dead prey before they had been noted.

Flying insects falling on the water surface in PEA I and II may have formed an additional food source for experimental catfish. However, this occurred rarely and the amount of food provided was negligible.

Normal ration:

The amount of food given to catfish between and during experiments should approximate that eaten in the wild. The normal ration of catfish in Lake Sibaya was therefore determined.

The normal ration (or average stomach contents) of 350 catfish (300 to 600mm TL) caught throughout the year 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 black bullheads <u>Ictalurus</u> <u>melas</u>, and Swenson & Smith (1976), values of 0,5 to 4,1% and 0,5 to 3,5% body weight in walleye, <u>Stizostedion</u> <u>vitreum</u> <u>vitreum</u> and sauger, <u>S.canadense</u>). Full catfish stomachs weighed 5% 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 24h, 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.

Qualitative estimate of stomach clearance time

Another parameter needed for proper experimental design was the rate of stomach clearance and the time between meals.

Thirty catfish (500-580mm TL) were retained in a large empty tank for 48h to clear their stomachs. The catfish were then force-fed two 50-60mm TL S.mossambicus each and transferred to PEA I in which the temperature ranged between 23,5° and 27,8°C. Force-feeding was rapid and easy, and samples of catfish could be recaught in the enclosure without causing panic to the rest. Groups of six catfish were caught and sacrificed at two-hour intervals and the proportion of prey remaining undigested in the stomach determined qualitatively. The prey were half digested after 4h and most digestion was completed after 6h. Despite the obvious limitations of this simple experiment, the results indicate that a catfish can clear its stomach between dusk and dawn, and thus take in two meals overnight. The experiments were not conducted using T.sparrmanii and P.philander but their structure and size is so similar to that of juvenile S.mossambicus that gastric evacuation rates would be about the same. Elliott (1972) found that rates of stomach clearance in brown trout Salmo trutta were not significantly different for food organisms of different size groups of the same taxon, or for mixed meals.

Feeding periodicity

Diel feeding periodicity in PEA II was established by continuous observation of the number of searching movements per unit time. Two experiments were conducted in PEA II, the first over 60h using 6 catfish, and the second over 48h using 4 catfish. The catfish had been fed the normal ration for a week preceeding the experiments. Readings were taken by workers in relays, and I am grateful for the assistance of Mrs C. Bruton, Mr A. Bruton, Mrs G. Bruton and the KwaZulu Nature Conservation Officers, Mr S. Mgubane and Mr E. Ndhlovu. Most observations were made by the author.

In both experiments, there was a marked searching periodicity, with peaks at dusk and dawn, and more searching at night than during the day (Figs 65 and 66). Abundant tilapia food was introduced at 09h00 on the final day of experiment 2 when the catfish would normally show low intensity appetitive behaviour. There was an immediate large increase in searching movements indicating that hunger can override diel feeding periodicity. This observation was confirmed in many subsequent experiments; hungry and well-fed catfish could always be induced to search strongly if abundant food was introduced.

The experiments show that, under conditions of fluctuating light intensity and water temperature, but in the absence of food, catfish display a diel rhythm in searching intensity which did not decline in amplitude up to 60h; this rhythm was interrupted by the introduction of food. The validity of this observation in relation to the field situation can be questioned. However, observations cited in the feeding chapter, show that there is increased shallow water searching activity by catfish at night in Lake Sibaya. Although the amplitude of searching periodicity as found in PEA II cannot be related directly

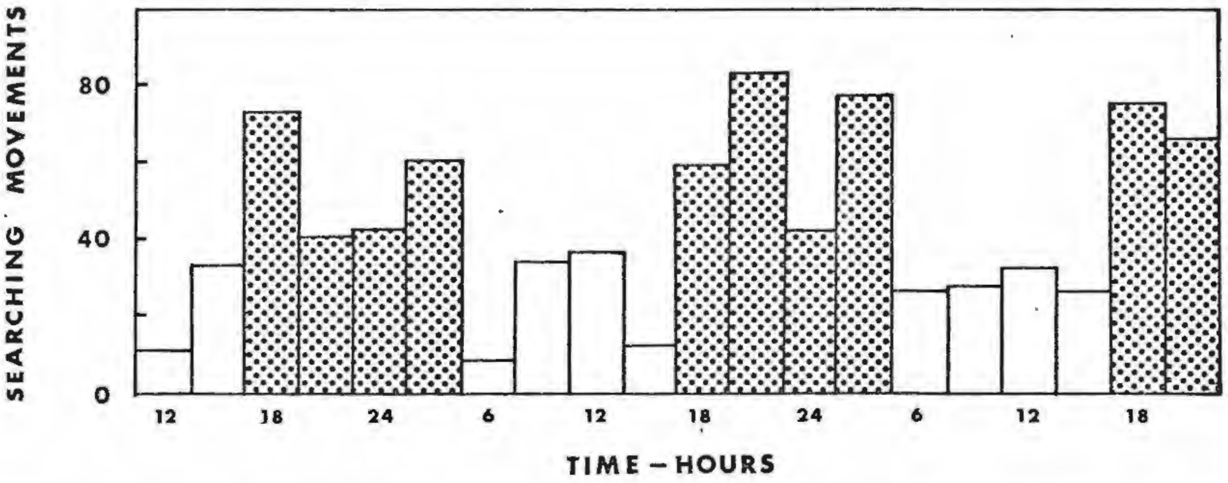


Figure 65: The number of searching movements per catfish performed by six C.gariepinus in the absence of food during 60 hours continual observation in PEA II. Each histogram representa a 3 hour period starting 12h00, 18h00, etc.
Open histograms: day Shaded histograms: night

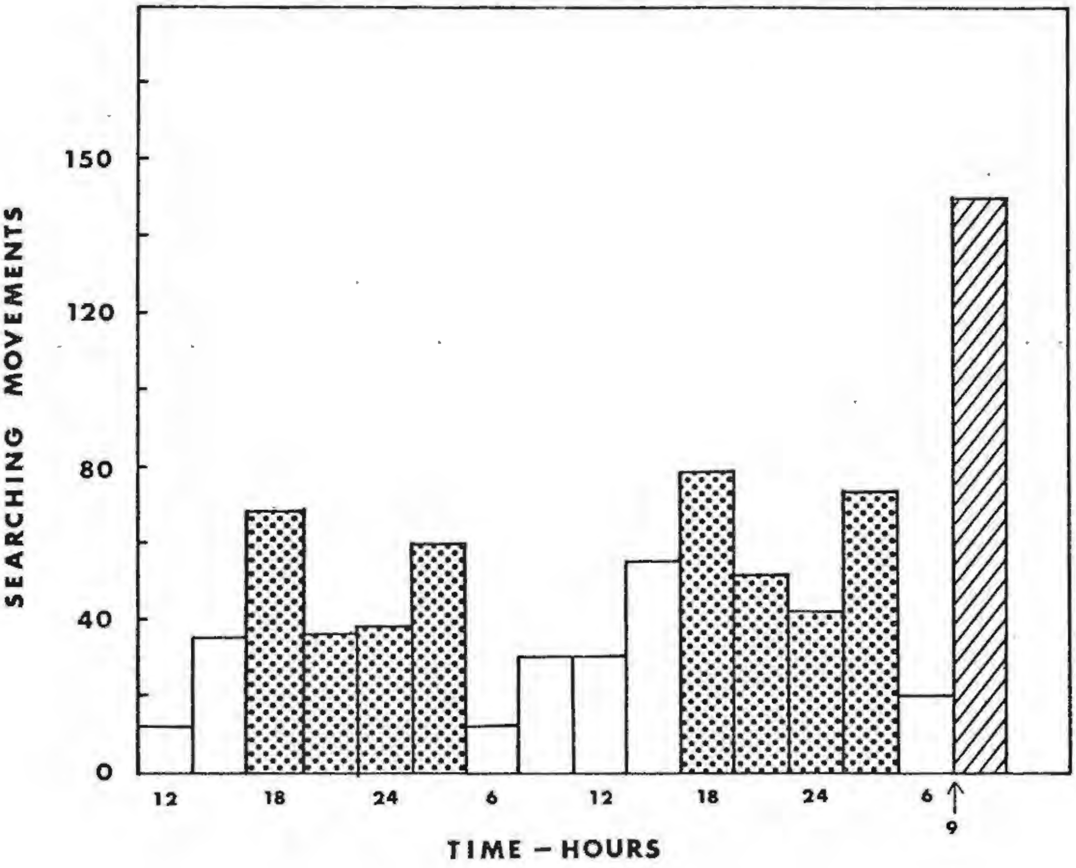


Figure 66: The number of searching movements per catfish performed by 4 C.gariepinus in the absence of food during 48 hours continual observation in PEA II. Food was introduced at 09h00 on the last day, resulting in increased searching activity.

to the field situation, it is likely that the rhythm of appetitive behaviour is the same.

Experimental analysis of the dependance of prey risk on different factors

In the following three series of experiments, the effect of water depth, light intensity and predator number on prey risk was assessed. Eight catfish (484-690mm TL) were used in different combinations, four in the first two series of experiments and up to six in the study on the effect of predator number. The catfish were fed the normal daily ration of 5% body weight fresh juvenile S.mossambicus from Lake Sibaya, and starved for 24h before each experiment. Each experiment lasted one hour so that little digestion took place. Prey (S.mossambicus, 50-70mm TL) were introduced into PEA II at a density of 30 per catfish (except in the experiment on predator number). During each experiment the catfish were watched continuously. A commentary on their behaviour was dictated into a tape recorder using symbols and abbreviations, and separate appetitive activities were scored on hand-operated counters. At the end of each experiment the number of prey eaten was determined. The observations and counts were transferred onto blank data sheets and then analysed.

The dependance of prey risk on water depth in PEA III:

Sixteen one hour experiments were performed, four each at water depths of 100, 200, 300 and 400mm. The observations were made using red lights on bright nights (150-250 lux). Water temperatures ranged between 20,3° and 24,5°C. The number of each appetitive activity at the different depths is given in Table 35 and Fig. 67. G-tests were made on each replicate for each appetitive activity to test for significant differences between experiments at each depth.

The number of each appetitive action was higher in shallow water (100 and 200mm) than in deeper water (300mm and 400mm). Values within these water depth groups were not significantly different from one another, whereas the values were always significantly different between the water depth groups. The catfish therefore predated more intensely and more efficiently on the S.mossambicus prey in 100 and 200mm depth than in 300 and 400mm depth. Less than one prey was eaten per catfish per hour in deeper water (300 and 400mm) whereas nearly three times this amount was eaten in shallower water (100 and 200mm). Swimming speed was about 1,5 times higher in shallower than in deeper water.

If the number of searching movements is higher for a given experiment, the number of other appetitive actions has a greater chance of being higher as well. Therefore, if the experiments are comparable, the number of searching movements should be about the same, or observed differences should have some explanation relevant to the questions being asked. Does the higher number of searching

TABLE 35

The number of appetitive actions (as defined in Table 34) performed by four catfish (484-690mm TL) in response to 120 *S.mossambicus* prey (50-70mm TL) at different water depths in PEA II. Each experiment with four catfish lasted one hour and was repeated four times at each water depth. The null hypothesis, that there was no significant difference between each column of replicates at each water depth, was tested using the G-test which compares observed values (those given) with expected values (average between replicate pairs; Sokal & Rohlf, 1973, p.294). The G-statistic given in each case is for six degrees of freedom, as there were eight classes of data in each test. The number of prey eaten and the swimming speed in body lengths/min per predator for each water depth are also given.

Appetitive action	Number of appetitive actions and mean for four replicate experiments at each water depth			
	100mm	200mm	300mm	400mm
Search	103	68	68	53
	91	92	71	62
	87	78	45	58
	95	81	42	56
	G = 8,812		G = 24,246	G = 6,122
	$P > 0,2$		$P < 0,001$	$P > 0,3$
	Not significant		Significant	Not significant
Mean per replicate	94	79,8	56,5	57,3
Encounter	71	64	38	42
	60	47	43	33
	48	57	32	40
	79	48	28	27
	G = 10,356		G = 19,316	G = 2,424
	$P > 0,1$		$P < 0,01$	$P > 0,8$
	Not significant		Significant	Not significant
Mean per replicate	64,5	54	35,3	35,5
Discover	61	43	20	13
	50	59	24	11
	38	41	18	17
	69	51	23	11
	G = 6,696		G = 43,894	G = 10,798
	$P > 0,3$		$P < 0,001$	$P < 0,05$
	Not significant		Significant	Significant
Mean per replicate	54,5	48,5	21,3	13,0
Grasp	26	18	3	1
	32	19	4	0
	21	14	3	3
	24	14	4	1
	G = 8,882		G = 36,128	Values too low to test
	$P > 0,1$		$P < 0,001$	
	Not significant		Significant	
Mean per replicate	25,8	16,3	3,5	1,25
Eat	22	13	2	0
	14	9	3	0
	16	8	2	0
	25	13	2	0
	G = 10,012		G = 27,098	Values too low to test
	$P > 0,1$		$P < 0,001$	
	Not significant		Significant	
Mean per replicate	19,3	10,8	2,5	0
Prey eaten per catfish per hour	4,8	2,7	0,5	0
Swimming speed (body lengths/min)	1,1	0,93	0,66	0,67

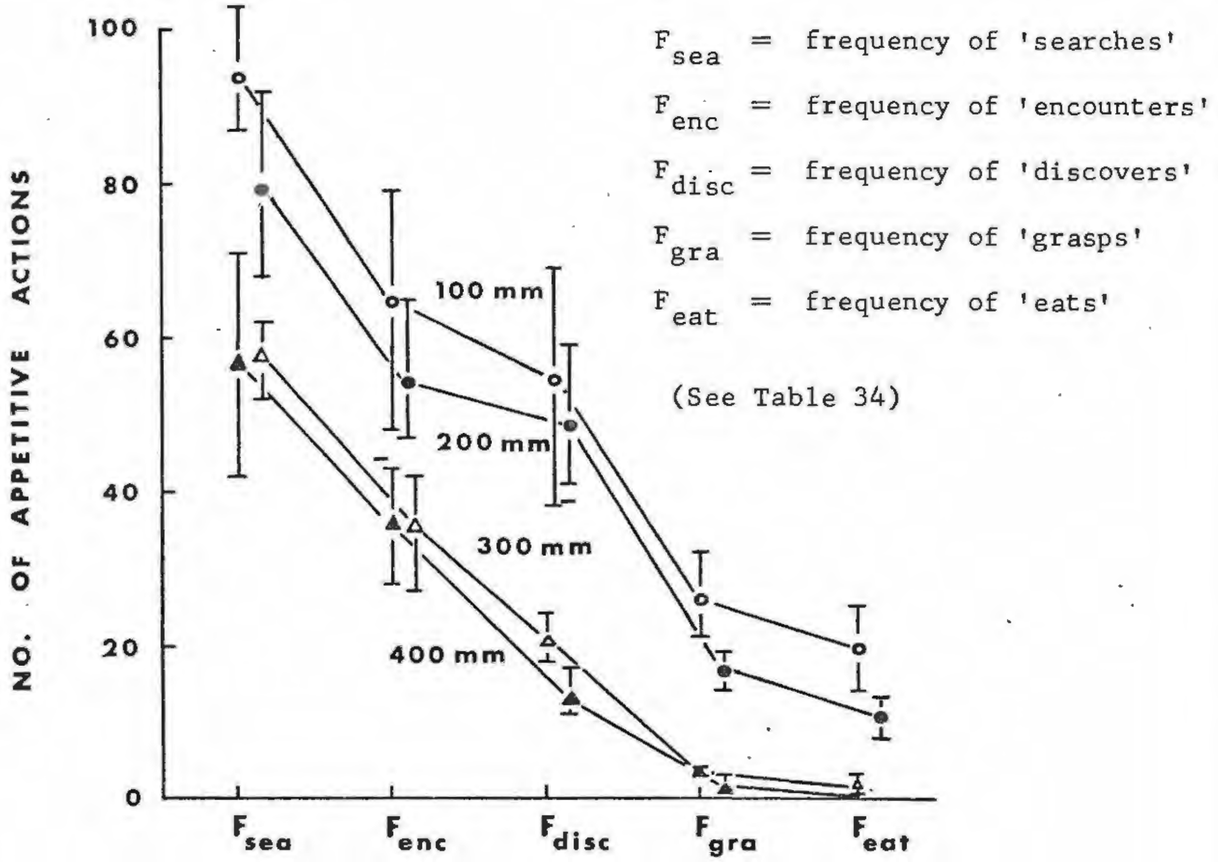


Figure 67: The number of appetitive actions performed by four C.gariepinus in response to S.mossambicus prey at four different water depths during 16 one-hour experiments in PEA II.

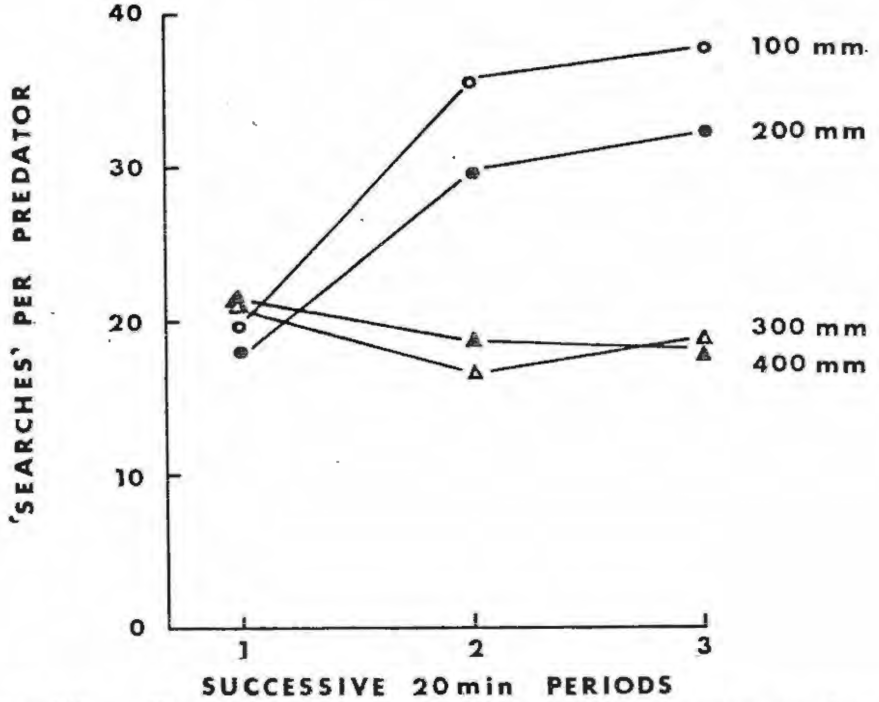


Figure 68: The number of searching movements per predator in different water depths for successive 20 minute periods during 16 one-hour experiments in PEA II. Abbreviations as in Fig. 67.

movements in shallow water (100 and 200mm) relate to the catfish's greater ability to catch prey at these depths? The answer is yes, as each link in the predation sequence is dependant for its frequency on the frequency of the other links in the chain. Thus, if 'encounters' often lead to 'discovers' and 'grasps' to 'eats', the catfish searches more intensely, and discovers more prey, with a snowballing effect. If encounters rarely lead to 'discovers' and 'discovers' rarely to 'grasps', the catfish become habituated to the 'uncatchability' of the prey, and tend to become inactive until conditions change to their (the predator's) advantage. Higher predation efficiency at 100 and 200mm depth is related to the predator's method of foraging. Catfish swim with a cone of barbels extended forwards at angles of about 30° from horizontal. The average size catfish used in this study (570mm TL) formed a circumoral cone about 130mm in vertical diameter. Thus, in water 100mm deep the cone would stretch from the sand to the water surface, and prey could only escape to either side of the catfish; one dimension of escape is removed. In 200mm depth the cone would extend within about 70mm of the water surface. Breder (1965) showed that the width of the vortex produced by a swimming fish is equal to about 0,4 TL. The cichlid prey used would have a vortex about 24mm wide of which the lower 12mm could be detected by the catfish. The 'non-detection' zone above the cone of barbels in water 200mm deep would thus be only 50-70mm; this escape route is therefore also restricted. In water 300 and 400mm deep, cichlid prey readily escape over the cone of barbels. These suppositions were repeatedly confirmed by direct observation in PEA II.

Higher prey risk in shallow water was due to the accumulative effect of imitative hunting and mutual stimulation in catfish. This effect is best analysed for different 20min periods as the experiment progressed. In Fig.68 the number of searching movements is plotted for the first, second and third 20min periods of each set of one hour experiments. During the first 20mins the amount of searching was approximately the same at all depths (18-21 searching movements per catfish), whereas searching was more intense in shallower water during the second and third 20min periods. In shallower water the number of searching movements leading to successful encounters and discoveries gradually increased as catfish reacted to one another's successful 'grasps' and 'eats' by rushing to the site of capture. In deeper water, searching movements and encounters rarely led to discoveries, probably because the prey were more readily able to escape as explained above. As a result, there was little imitative hunting and prey risk remained low.

The dependence of prey risk on day-night changes in light intensity

Twelve one-hour experiments were performed, four each on dark nights (with red lights, light reading under water in PEA II $<$100 lux), bright nights (with red lights, 150-250 lux) and during the day (8000-10,500 lux) at a constant water depth of 200mm. Water temperatures ranged between 20,6° and 24,2°C. The number of each appetitive activity at each light intensity is given in Table 36 and Fig. 69.

The number of 'searches' at all light intensities was just not significantly different, although higher values were recorded at night than during the day. The numbers of 'encounters' and 'discovers' were not significantly different on bright and dark nights, but significantly different between night and day. On dark nights, there were significantly more 'grasps' and 'eats' than on bright nights, whereas very low numbers of these activities were recorded during the day. No fish were eaten during the day experiments, and twice as many on dark compared with bright nights. The swimming speed, which is mainly a reflection of searching activity, was about the same at all light intensities.

Higher discovering, grasping and eating efficiency at night is explained by the relative abilities of the prey and predator at different light intensities. The cichlid prey apparently orientate mainly by visual cues (although the lateral line organ is doubtless also important). During the dark night experiments the prey dispersed and did not shoal, whereas occasional shoals were formed on bright nights. The prey always shoaled during the day. Shoaling confers many advantages on the prey. In particular, the predator rarely approaches shoaling prey close enough to effect a discovery as the prey are apparently able to detect the predator from a longer distance at high light intensity. At night, low light intensities favour the catfish which more often approach the prey within detection distance by means of mechanoreception. Fryer (1960) also observed that fish prey (young Sarotherodon variabilis and Lebistes spp.) readily escaped Clarias mossambicus by day in an aquarium, but fell easy prey to the catfish at night.

As in the previous experiments, the number of searching movements during the first 20mins was about the same at different light intensities, but increased thereafter (Fig. 70) as a consequence of imitative hunting. Searching intensity was higher on a bright than on a dark night, but the success of subsequent encounters was higher on a dark night.

The dependence of prey risk on the number of predators in PEA II

Twelve one-hour experiments were performed, two each with 1, 2, 3, 4, 5 and 6 predators. The number of prey was constant at 120 in all experiments. Water depth was constant at 200mm and water temperatures ranged between 20,3° and 23,8°C. The experiments were conducted on bright nights (150-250 lux)

TABLE 36

The number of appetitive actions (as defined in Table 34) performed by four catfish (484-690mm TL) in response to 120 S.mossambicus prey (50-70mm TL) at different light intensities during the day and night in PEA II. Each experiment with four catfish lasted one hour and was repeated four times at each light intensity. All other conditions the same as in Table 35. The G-statistic given in each case is for six degrees of freedom.

Appetitive action	Number of appetitive actions and mean for four replicate experiments at each light intensity			
	Dark night (< 100 lux)		Bright night (150-250 lux)	Day (8000-10 lux)
Search	78		87	72
	71		83	62
	65		83	68
	78		87	62
		G = 4,106		G = 10,168
		$P > 0,5$		$P > 0,1$
		Not significant		Not significant
Mean per replicate	73		85	66
Encounter	41		56	43
	49		61	37
	43		63	36
	55		52	44
		G = 7,514		G = 15,768
		$P > 0,2$		$P < 0,02$
		Not significant		Significant
Mean per replicate	47		58	40
Discover	39		51	14
	47		48	11
	40		54	12
	50		55	11
		G = 3,94		G = 108,342
		$P > 0,5$		$P < 0,001$
		Not significant		Significant
Mean per replicate	44		52	12
Grasp	27		19	1
	31		14	1
	29		15	1
	25		20	1
		G = 13,068		Values too low to test
		$P < 0,05$		
Mean per replicate	28	Significant	17	1
Eat	18		14	0
	25		10	0
	24		9	0
	25		11	0
		G = 19,808		Values too low to test
		$P < 0,01$		
		Significant		
Mean per replicate	23		11	0
Prey eaten per catfish per hour	5,8		2,8	0
Swimming speed (body lengths/min)	0,85		1,00	0,77

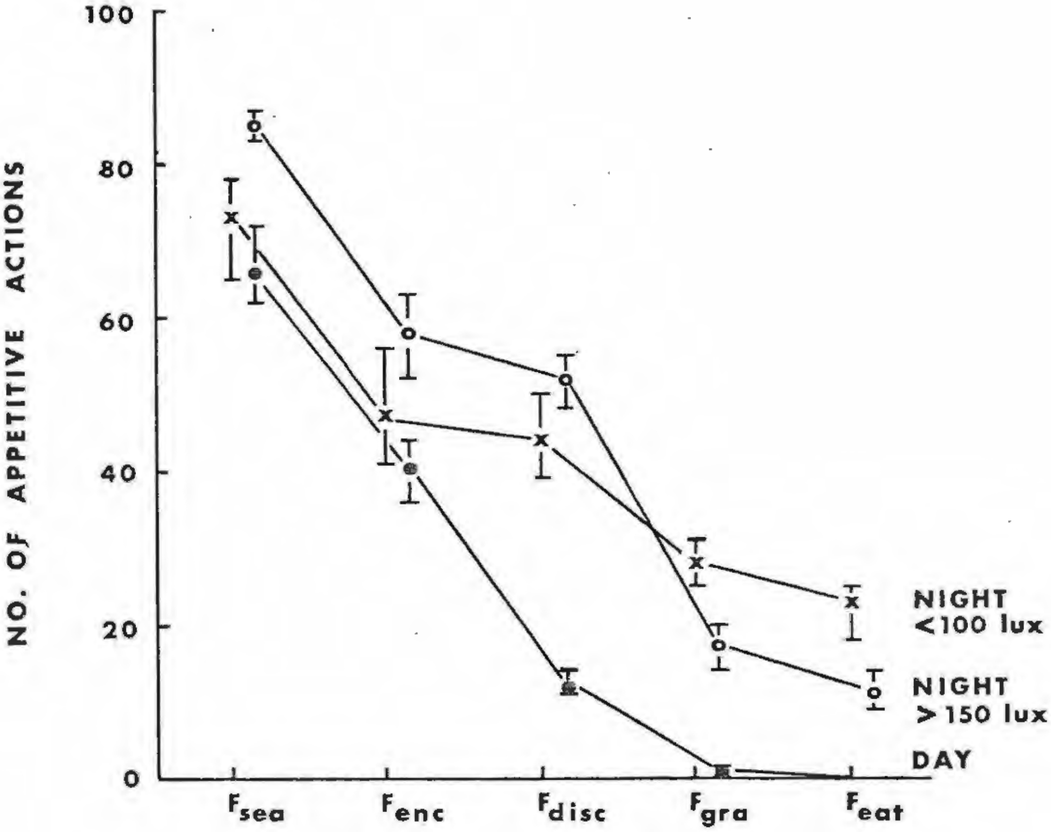


Figure 69: The number of appetitive actions performed by four catfish in response to S.mossambicus prey at different light intensities during 12 one-hour experiments in PEA II. Abbreviations as in Fig. 67.

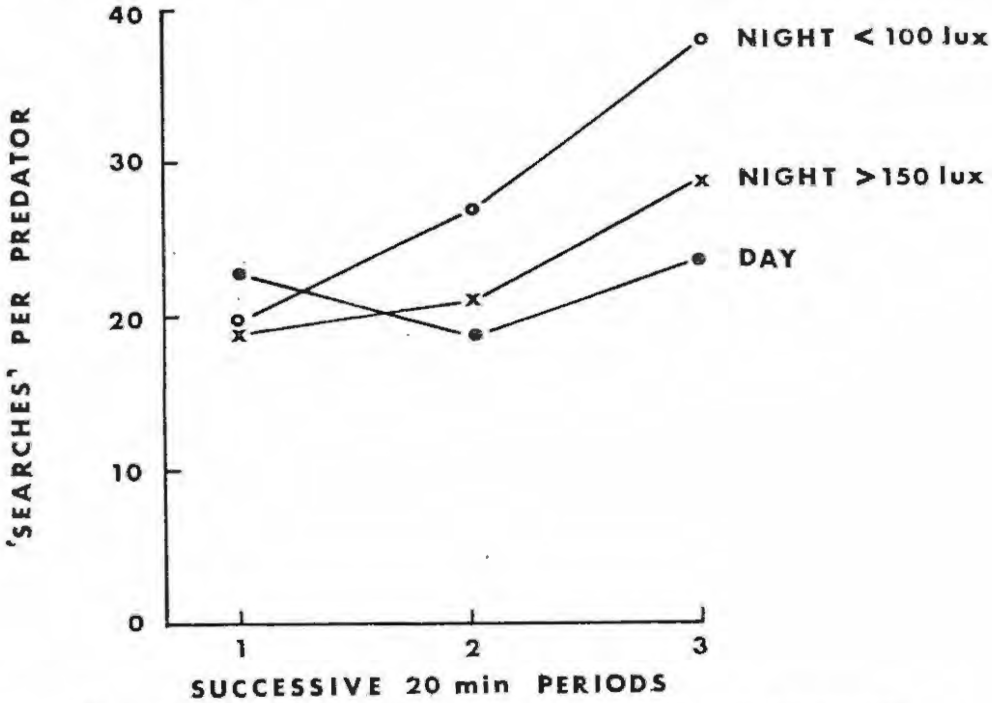


Figure 70: The number of searching movements per predator at different light intensities for successive 20 minute periods during 12 one-hour experiments in PEA II. Abbreviations as in Fig. 67.

under red lights. The number of appetitive actions per catfish for each catfish group size is given in Table 37 and Fig. 71.

The number of 'searches' and 'encounters' per predator were not significantly different for different numbers of predators. However, the number of 'discovers' was significantly different, when the columns for 1 and 5 and 2 and 6 predators, are compared. Discovering efficiency was therefore higher when a group of five or six predators is present, compared with only one or two. The number of 'grasps' and 'eats' were too low for statistical testing, but in both cases higher values were obtained per predator for larger predator group sizes. The number of prey eaten and the swimming speed per catfish was about five times higher for the largest catfish group size compared with the smallest.

Prey risk was also calculated using the 'risk index', as explained earlier. The graph of risk index (Fig. 72) shows clearly that the number of 'discovers', 'grasps' and 'eats' was markedly higher per predator when 4, 5 or 6 predators were present as opposed to 1, 2 or 3.

Increased prey risk as a consequence of increased predator density is a direct result of imitative hunting. During the first 20 mins of each experiment the number of searching movements was about the same, but thereafter searching intensity increased (Fig. 73) as the number of successful 'encounters' and 'discovers' increased in experiments with higher numbers of predators. At high rates of discovery the prey became scattered, disorientated and more vulnerable. Imitative hunting reached such a high level when 5 and 6 predators were present in PEA II that there was a drop in prey risk as catfish spent proportionately more time swimming to the sites of other successful encounters. They thus scored highly on 'searches', 'encounters' and 'discovers' but less on 'grasps' and 'eats'. The predators did not form organised shoals in PEA II.

In the wild, large groups of catfish gather at sites with abundant prey where imitative hunting leads to ritualized pack-hunting, as described earlier. The presence of a large group apparently increases the efficiency of predation. In PEA II, optimal predation efficiency was achieved by a group of 4 or 5 catfish. Imitative hunting has also been reported in other fish predators, such as piranhas (Markl, 1972).

Selection by catfish of cichlid prey at different relative densities in PEA II

Field collections indicated that catfish mostly take cichlid prey in the proportions in which they occurred in the lake. This finding was tested in PEA II using optimal conditions for high predation as defined in previous experiments i.e. water depth 200mm, four catfish in each experiment. Three cichlids, S.mossambicus, T.sparrmanii and P.philander, were presented in different proportions out of a total of about 100 prey. Three sets of 2

TABLE 37

The number of appetitive actions (as defined in Table 34) per catfish performed by one to six catfish (484-690mm TL) in response to 120 *S.mossambicus* prey (50-70mm TL) in PEA II. Each experiment lasted one hour and was repeated three times for each number of catfish. All other conditions the same as in Table 35. The G-statistic given in each case is for four degrees of freedom.

Appetitive action	Number of appetitive actions per catfish and mean for one to six catfish in three replicate experiments					
	1	2	3	4	5	6
Search	34	30,5	29,3	27,5	28,6	28,8
	35	26,5	32,3	25,5	26,2	26,5
	31	29	29	29	27,6	26,7
	G = 1,524 P >0,95 Not significant					
Mean per replicate	33,3	28,7	30,2	27,3	27,5	27,3
Encounter	18	17	21,3	18,8	19,4	16,8
	24	22	19	16,8	16,2	16
	22	19	21	19,5	16,4	18,5
	G = 1,956 P >0,70 Not significant					
Mean per replicate	21,3	19,3	20,4	18,4	17,3	17,1
Discover	5	5,5	12,7	8,8	16,6	11,8
	7	6	13	10,3	15	16,3
	4	6,5	11,7	10	16,4	15,5
	G = 0,702 P >0,9 Not significant		G = 7,074 P >0,1 Not significant	G = 1,158 P >0,8 Not significant	G = 4,88 P = 0,30 Not significant	G = 0,892 P >0,9 Not significant
	Columns 1 and 5 compared: G = 17,635 p < 0,001 Significant Columns 2 and 6 compared: G = 11,082 p < 0,01 Significant.					
Mean per replicate	5.3	6	12,5	9,7	16,0	14,5
Grasp	2	3,5	5	7	7,8	6,2
	1	2	3,7	5,3	6,2	4,8
	1	2,5	4,7	6,8	6,8	5,7
	Values too low to test			G = 0,112 P >0,99 Not significant		G = 0,454 P >0,98 Not significant
Mean per replicate	1,3	2,7	4,5	6,4	6,9	5,6
Eat	1	1	2,7	3,3	3,6	3,0
	0	1	2	3,5	3,8	4,5
	1	1	2	4,3	5,0	3,2
	Values too low to test					
Mean per replicate	0,7	1	2,2	3,7	4,1	3,6
Prey eaten per predator per hour	0,5	0,75	1,68	2,78	3,1	2,68
Swimming speed per predator (body lengths/min)	0,29	0,50	0,80	0,96	1,20	1,44

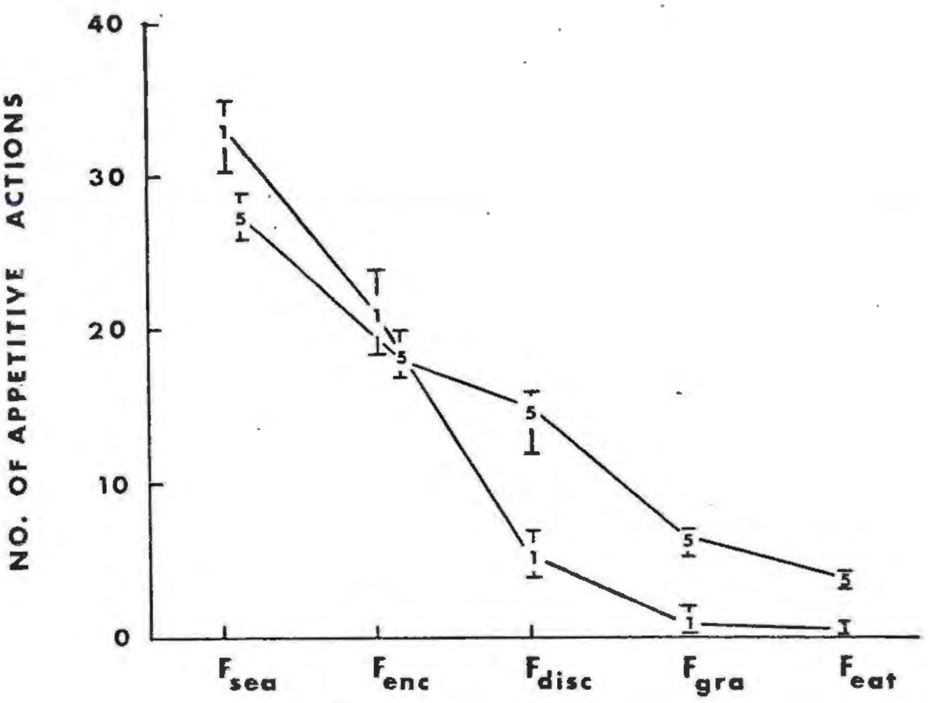


Figure 71: The number of appetitive actions per predator performed by one and five C.gariepinus in response to S.mossambicus prey during 15 one-hour experiments in PEA II. The number of appetitive actions for 2, 3, 4 and 6 predators are intermediate between the given graphs. Abbreviations as in Fig. 67.

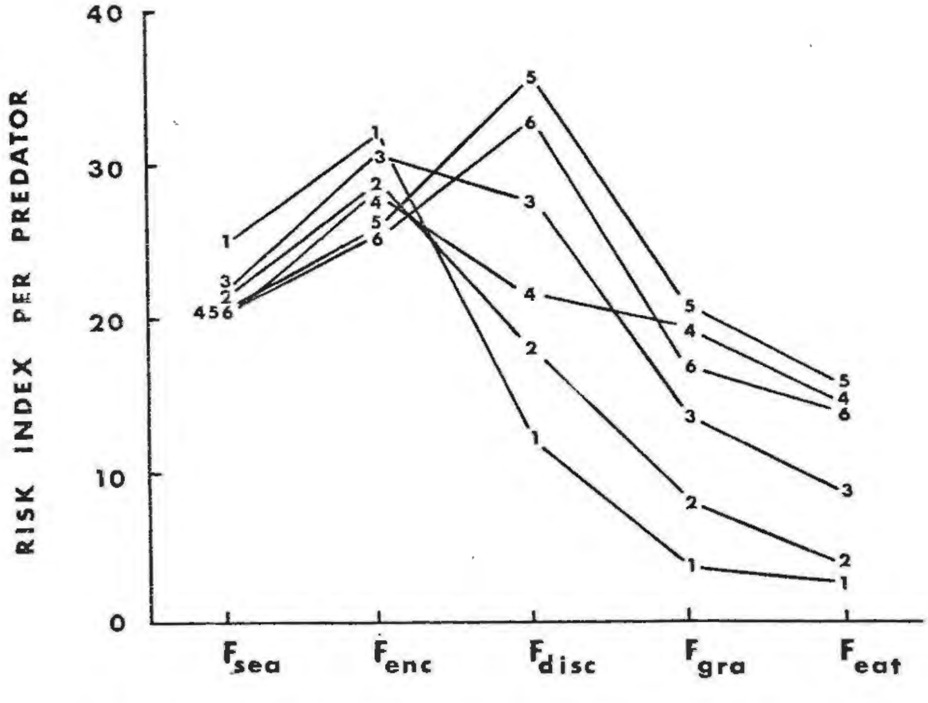


Figure 72: The risk of S.mossambicus prey at different levels of the predation sequence to predation by one to six catfish in PEA II. Abbreviations as in Fig. 67. Risk index explained on page 174.

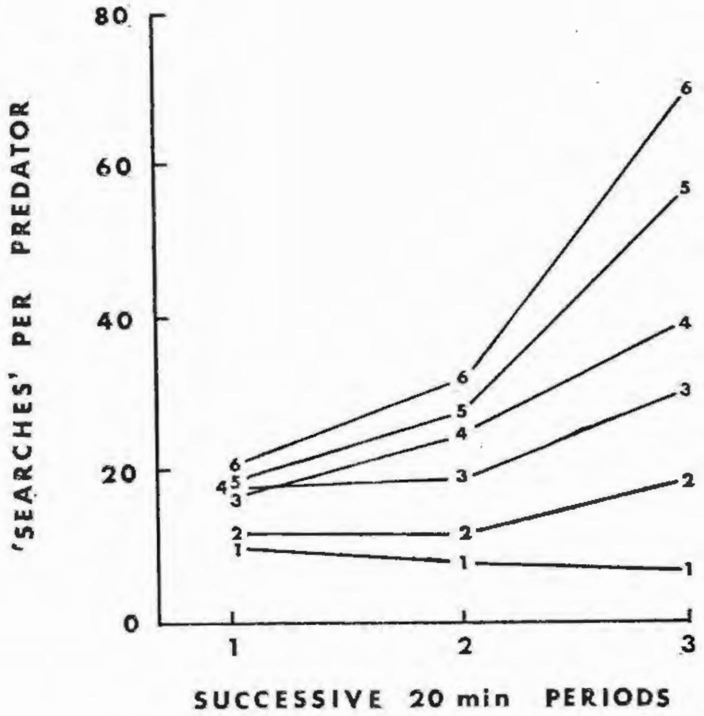


Figure 73: The number of searching movements per predator for different numbers of predators in successive 20 minute periods during 15 one-hour experiments in PEA II.

experiments were conducted (Table 38). 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 density. 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 PEA II one hour before each experiment in the absence of predators. The predators were kept in the small enclosure during the hour preceeding experimentation but swam freely in PEA II during and between experiments. Each experiment lasted three days (72h) starting at 09h00. By the end of the experiment about 1/3 of all prey had been eaten.

An important criticism of experiments of this kind is that prey density and proportions are altered as soon as 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 PEA II. However, catfish soon learnt to associate the pipe with prey 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 to 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.

The number of each prey species offered and eaten in the three sets of experiments is given in Table 38. G-tests were used to test for significant differences, and Ivlev's electivity index was calculated using observed and expected values, as explained above.

In the first set, in which prey were equally common, the observed and expected frequencies were not significantly different ($P > 0,5$) and Ivlev's 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 ($P > 0,2$). Selectivity was therefore approximately neutral even when the proportions of different prey species differed by a factor of 3.

TABLE 38

Selection of *S.mossambicus*, *T.sparrmanii* and *P.philander* by *C.gariepinus* in PEA II when the prey are offered in different proportions. Three sets of experiments were conducted, each replicated twice. Each experiment was conducted in 200mm deep water using about 100 prey and 4 catfish, and lasted 3 days (72h). Water temperatures ranged between 20,3° and 24,3°C. All other conditions the same as in Table 35. The G-statistic given in each case is for two degrees of freedom.

SET 1:

	PREY INTRODUCED			PREY EATEN (NUMBER)		MODIFIED ELECTIVITY INDEX
	Each replicate	Total	% of Total	Observed	Expected	
S.mossambicus	34	68	33,3	19	18,3	+0,02
T.sparrmanii	34	68	33,3	15	18,3	-0,10
P.philander	34	68	33,3	21	18,3	+0,07
	102	204		55		

$G = 1{,}240$

$P > 0{,}5$

Not significant

SET 2:

S.mossambicus	60	120	66,7	46	40	+0,07
T.sparrmanii	20	40	22,2	9	13,3	-0,19
P.philander	10	20	11,1	5	6,6	-0,14
	90	180		60		

$G = 3{,}05$

$P > 0{,}20$

Not significant

SET 3:

S.mossambicus	10	20	11,1	6	6,4	-0,04
T.sparrmanii	20	40	22,2	6	12,8	-0,37
P.philander	60	120	66,7	46	38,6	+0,09
	90	180		58		

$G = 6{,}27$

$P < 0{,}05$

Significant

In the third set, in which P.philander was most abundant, the observed and expected frequencies were just not significantly different ($P < 0{,}05$), but Ivlev's 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 ($P > 0{,}2$). 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 38. 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 PEA II, and as a result the number of 'encounters' leading to 'discovers' and the number of 'discovers' leading to 'grasps' was lower than for the other species. T.sparrmanii was also negatively selected at intermediate lake level (Table 33) possibly as a result of their habit of living above the substrate (as discussed earlier).

Predation by catfish on some invertebrates

The main experiments were conducted on the cichlid prey of catfish because of their important contribution to prey weight. However, invertebrate prey is taken in far greater numbers by catfish, and experiments were performed on some invertebrate prey so that general comments on predation on all prey types could be made. Prey risk was measured in these experiments by determining the proportion of one appetitive activity which led to the next, as explained earlier.

Predation on H.orbiculare in PEA III

Experiments using crown crabs as prey were unsuccessful as the predators ate over 94% of all crabs offered. Crabs were eaten within minutes of introduction into the large aquarium, PEA III, without a sandy layer, and up to 30 crabs (the maximum which could be collected from the lake at one time) were eaten within 15mins by one predator with sand present. Some observations were made. Day-night changes in light intensity had no effect on predation efficiency. All 30 crabs were eaten within 15min on dark nights (< 50 lux, with a single red light) and during the day (9000-10000 lux, 2 replicates each) by a single 264mm TL catfish. Equal predation efficiency during the day and night may be due to the catfish's use of mechanoreception for detecting crown crabs.

Water depth in the aquarium also had no marked effect on predation efficiency on crown crabs - all 30 crabs were eaten within 15mins at depths of 100, 200, 300 and 400mm (2 replicates at each depth) by the single predator. Prey risk was expected to be higher in shallow water, as with fish prey. In fact, 53 to 81% of the flushed crabs did escape from early encounters with the predator in deeper water by swimming over the cone of barbels, but they were all eventually caught in the small enclosure. Crown crabs have repeatedly been seen evading capture by catfish in Lake Sibaya by swimming over the cone of barbels.

Predation on small crustaceans in PEA IV

In the feeding chapter catfish were 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 in the small aquarium, PEA IV, which allowed close observation of feeding by two small catfish (85 and 88mm TL) on small items. (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: G.lignorum (6-7mm TL), C.carinata (10-11mm) and A.digitalis (3-4mm). The prey were delivered individually in a random order from a pipette through a glass tube fixed in position over the aquarium, with the 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. Definitions of 'discover', 'grasp', and 'eat' are the same as before. 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 6h,

the catfish were fed 15 small crustaceans each. All experiments were conducted in a dark room. The results are given in Fig. 74.

P_{disc} was high for all prey, indicating high vulnerability for 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 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, 6h-starved catfish were allowed to forage for buried prey. When flushed, the three prey species behaved differently. G.lignorum swam strongly upwards to about 30mm 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 circum-oral 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.

Some epifaunal benthos was also introduced into PEA IV. Twenty each of P.latipes, small C.nilotica ($<$ 7mm TL); small H.orbiculare (carapace width $<$ 4mm) and P.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 M.spicatum fronds or by burrowing respectively. Molluscs, including small B.capillata , M.tuberculata, Corbicula africana and Bulinus spp. were always neglected on discovery in PEA IV (20 introductions each).

Predation on epifaunal benthos in PEA II

Observations were also made on predation by 24h-starved adult catfish (484mm to 690mm TL) on B.capillata (20-25mm TL), M.tuberculata (TL 25-31mm) and P.sidneyi (carapace width 30-40mm) collected in the lake using SCUBA. Thirty each of the molluscs and 10 crabs were introduced into PEA II in separate experiments, and subjected to predation by four catfish during the day. Eleven one-hour experiments were conducted, 5 on B.capillata , 3 on M.tuberculata and 3 on P.sidneyi. The results, plotted as the proportion of one appetitive action leading to the next, are given in Fig. 75.

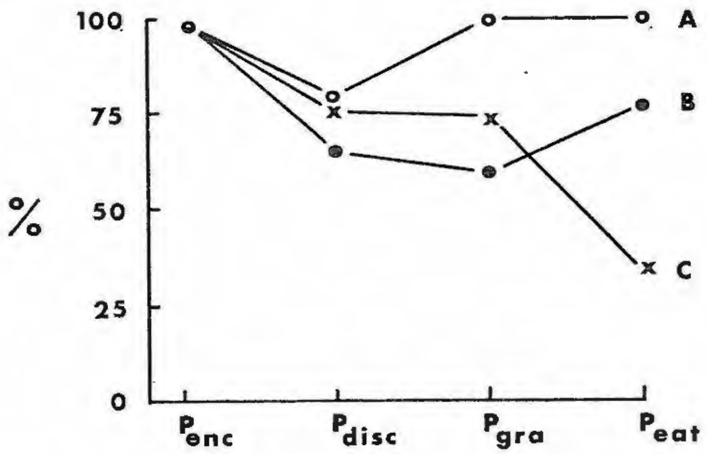


Figure 74: The proportion of different appetitive actions performed by one catfish in response to small invertebrate prey in PEA IV.

A. *G.lignorum* B. *C.carinata*

C. *A.digitalis* N = number of searching movements

Abbreviations as on page 174.

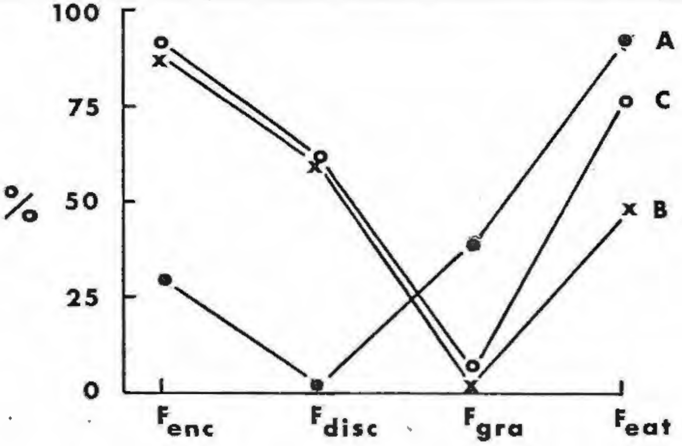


Figure 75: The proportion of different appetitive actions performed by four catfish in response to large invertebrate prey in PEA II.

A. <u>P</u>.<u>sidneyi</u> B. <u>M</u>.<u>tuberculata</u>

C. <u>B</u>.<u>capillata</u> N = number of searching movements

Abbreviations as on page 174.

The encountering efficiency on both snail prey was high as the prey were spread evenly throughout PEA II 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 56h instead of 24h. The snails were not a preferred prey of catfish 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 the grasped crabs eaten. Catfish readily fed on recently killed shore crabs, but rejected rotting crabs.

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.

Further observations on predation by catfish

Feeding intensity and social 'breathing'

Imitative hunting, in which one catfish is attracted to another by the latter's directed attentions to a prey, has already been mentioned as a factor increasing 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. Catfish markedly smaller than the group modal size were usually repulsed, and swam submissively away. If the food resource was large and could not be eaten by the catfish present within about 5mins, aggression gradually became less intense and co-ordinated feeding behaviour ensued, sometimes leading to 'social hunting' as described in the chapter on 'Feeding'.

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 (570mm TL) in PEA II rose for air about 1-6 times an hour (14 hours observation at different times of the day). However, with groups of catfish, 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. These rises appeared 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 secs was therefore counted. As shown in Table 39 which is based on 16h observations concurrent with other experiments, the total number of rises and imitative rises per hour was higher in the presence of food.

TABLE 39

Imitative aerial 'breathing' in four C.gariepinus in PEA II in the presence and absence of S.mossambicus prey (50-70mm TL) (an imitative rise was counted every time an initial rise was followed by other rises within 30secs.)

		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

Imitative aerial 'breathing' often caused previously stationary catfish to start searching behaviour, and frequent imitative rises resulted in increased searching intensity. A solitary catfish searched at a speed of 0,29 body lengths/min, whereas a group of 4 in the absence of food and with moderate social 'breathing' (17 rises an hour) searched at 1,11 body lengths/min. In the presence of abundant food, and with intensive social breathing, searching speed sometimes exceeded 19 body lengths/min in PEA II, a 17-fold increase. 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. This behaviour may have originated from the catfish's habit of eating floating insects, and the faeces and fledgelings of birds on the water surface. Loud ritualised aerial 'breathing', as well as head and tail slapping on the water surface, also apparently function as social signals during spawning migrations (see chapter on 'Breeding'). Social aerial respiration has also been reported in young gars (Lepisosteus spp., Hill, 1972).

'Area concentrated searching'

'Area-concentrated searching' by catfish was repeatedly observed from the 7m 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 PEA II and aquaria showed that, on discovering prey, the barbels were spread to form a wider circum-oral cone and thus sample a larger volume of water. Searching efficiency was thus increased after initial contact with prey by slowing forward movement, turning more often and increasing the dimension of the search path. In a broader sense, 'area-concentrated feeding' is carried out on the terrace, in permanently sheltered weedbeds and in flooded marginal areas where the diversity of potential prey animals is highest (Allanson _et al_, 1974).

Searching image and switching

Catfish may form a 'mechanoreceptive' searching image of prey, perhaps associated with the vortices produced, but insufficient data are available to prove this point. The incidence of large numbers of a single prey in a catfish stomach (see 'Feeding' chapter and Appendix 1) is probably due to area-concentrated searching, and need not involve a 'searching image' although Curio (1976) has ventured that these runs probably involve a certain degree of 'single-mindedness' in feeding fish.

Catfish have been shown to exert heavy predation on whichever cichlid prey has greatest relative abundance i.e. to show 'switching behaviour' (Murdoch, 1969, 1971). The ability to switch from one dominant prey to another has obvious selective advantage to a predator inhabiting a lake in which the diversity of food in the margins fluctuates widely. However, they retain their ability to feed on a wide variety of other novel prey if this prey is readily accessible. An euryphagous predator would not benefit if novelty inhibited switching and only recently taken prey was ingested. This would prevent the predator from exploiting the full range of food available.

Social dominance in PEA II

Dominance and territoriality were noted in PEA II. In particular, two intermediate size catfish (540 and 580mm TL) regularly rested between searching movements in squares 3 and 9 respectively (the corner squares near the hide) and challenged entering catfish with mouth and lateral displays and tail-slaps, sometimes leading to chasing. This behaviour only persisted when feeding intensity in PEA II was low. When feeding and imitative aerial 'breathing' intensities were high, the territorial individuals ranged over the whole PEA and other catfish were allowed to enter their squares unchallenged. Territoriality in catfish may be an artifact of the experimental situation as this behaviour has not been observed in the wild.

Predation strategy

Observations on catfish in Lake Sibaya and in the experimental enclosures showed that catfish 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 to virtually ignore tilapia throughout the day. However, occasional attacks were made, as if the catfish were testing the prey's vulnerability from time to time. At dusk, predation efficiency increased and more discoveries led to grasps. These successful or near-successful attacks resulted in further attempts, the success of which increased as conditions for the predator improved i.e. light intensity decreased. Foraging success also affected the amount of subsequent searching in rainbow trout Salmo gairdneri. Ware (1972) found that substrate-orientated search began to wane in trout which did not exceed an average of 0,058 captures sec^{-1}.

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.

In both diel rhythmicity experiments reported earlier, searching intensity by the catfish reached a peak at dusk and dawn. The advantage of crepuscular feeding is not well understood, for it occurs in mechanoreceptive predators, such as Clarias, as well as in visual fish predators (Hobson, 1968, 1972). Camouflage and detection advantages conferred on the predator but not the prey by the fading light may be important factors.

Catfish change their dorsal and lateral body cover 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-orientating 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 always white, which effects camouflage through counter-shading when lighted from above. Catfish are not always well camouflaged - many individuals which swim from deeper waters onto the terrace retain their dark colouration and would appear to be conspicuous to bird predators, as observed from the tower.

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, and by resting in midwater. Both perching and motionlessness 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 H.orbiculare by trailing the mandibular barbels along the sand, in a manner similar to that of marine goatfish Pseudopeneus spp. (personal observations). 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 circum-oral cone of barbels are usually detected and caught. Catfish feeding was simulated using an oval net and thin wire ticklers pushed by a diver. Highest catches of crown crabs were made by moving slowly and 'feeding' 10-20mm above sand with a thin layer of detritus on the deep edge of the terrace. The crabs were flushed before making direct contact with the 'catfish', probably by the bow pressure wave.

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 optimise predation by temporal synchrony with a temporarily vulnerable prey, such as appetitive male G.lignorum venturing out of their burrows at night. In a broader sense, the hatching 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 A.digitalis, which is not a preferred prey, the value is even lower (12,3%). However, these results are biassed 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%) was nevertheless close to values obtained for other predators such as praying mantids (15%, Mittelstaedt, 1957; [in Nybergh, 1971]); cuttlefish (10%, Messenger, 1968) and largemouth bass (10%, Nybergh, 1971). Underwater observations confirmed that catfish were far more efficient at detecting and capturing invertebrate prey.

MacArthur (1972) proposed an 'optimal foraging model' to describe the maximisation of food intake by a predator. On locating a food item, a predator has to decide whether to pursue or to search again for a better item and pursue it instead. Since either choice ends with the predator ready to start a new search, the better decision is that which promises a higher yield per unit time. Hence, a predator should elect to pursue an item only if it could not expect to locate and catch a better prey during the time of pursuit. To support his model MacArthur (1972, p.62) points to observations on great blue herons Ardea herodias. In productive Florida waters, herons selected a much narrower range of food sizes than they ate in the unproductive lakes of the Adirondacks. The observations reported here show that MacArthur's optimal foraging model applies equally well to C.gariepinus. During the day catfish ignore fish prey and feed mainly on invertebrates, which are relatively easy to catch. At night, or in packs in shallow water, pursuit of fish prey is worthwhile as the catfish has a greater chance of success in a short time. The greater biomass (and presumably nutrient value) of fish prey is probably an important factor which induces the predator to pursue fish whenever conditions are suitable. This point is discussed in greater detail in the next chapter.

Discussion on predation by C.gariepinus

These preliminary studies on catfish predation do not reject 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. An increased number of predators in the experimental area resulted in a higher predation rate per predator, as well as a higher total predation rate. Furthermore, collections of stomach contents showed that invertebrates, which are far more abundant than fishes in the lake, were numerically more important in the diet. Subsidiary factors, such as properties of the environment, may affect the magnitude of predation, as suggested by Holling (1961). In this study the effect of light intensity and water depth on predation intensity (or efficiency) was demonstrated. Other environmental factors, such as plant cover, visibility, habitat diversity and water temperature may also affect predation efficiency.

This study, and the others reviewed, 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 apparati 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 (1969a) for Lates niloticus in three lakes in East Africa; Jackson et al, (1963) for Bagrus meridionalis in Lake Malawi, and Chilvers & Gee (1974) for B.docmac in Lake Victoria. Their studies applied mainly to predation on haplochromids and not on tilapia, 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. Thus, 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 Sibaya catfish 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. However, 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 generalisation and specialisation 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), catfish are stenophagous, at least as adults. 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.

Increased lake level, and concomitant flooding of extensive marginal areas, probably had a profound effect on predator-prey relationships in Lake Sibaya. This effect cannot be defined in detail, but there are several obvious sequelae. As mentioned above, the diversity of invertebrate prey in marginal areas increased, and provided an abundant alternate source of food to catfish. (The annual summer rains would have the same effect, but on a smaller scale). Flooded marginal areas also provided a habitat for certain fishes which usually inhabit offshore plant beds. The findings in this chapter show that the increased abundance of one of these fishes in marginal areas (P.philander) caused catfish to switch to this species as their major fish prey. Another plant bed dweller (T.sparrmanii) retained its importance in the catfish's diet at high lake level. Catfish were shown in this chapter to hunt more efficiently for fishes in shallow water in PEA II. The external validity of this finding should be examined carefully. Although shallow areas are more extensive at high lake level, they are, in general, more vegetated than at low lake level. What effect does plant cover have on predation efficiency in shallow water? Vince et al (1976) found that dense plant cover hindered predation by killifish, Fundulus heteroclitus on invertebrate prey. The same may apply to catfish in Lake Sibaya, but we cannot be sure. Catfish hunt more efficiently in groups, and especially in packs, but communal hunting is also likely to be more efficient in barren shallow areas than among plants. Another finding presented here is that catfish predate more efficiently at night than during the day. Clearly the advantage of more extensive shallow water habitats must be weighed against the density and accessibility of prey in these areas at night. There are still more questions than answers, but it seems more likely that flooded, well-vegetated marginal areas will interfere with predation efficiency, rather than aid it, although these areas do offer a greater variety of prey.

Thomas (1966) discussed the environmental factors which may have led to euryphagy in large African Clarias. According to Thomas, factors which would restrict the food niche of catfish do not usually affect them strongly. These include interspecific competition, predation pressure, constant food supply at a low density and harsh physico-chemical conditions. The impact of predation pressure and interspecific competition are buffered by the catfish's large size, well-protected head, pectoral spines and piscivorous habits. 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 would 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. The intensity of competition for food, and predation pressure, are unknown for Sibaya catfish, and their effect on food niche volume cannot be assessed at this stage. The other three factors - variation and diversity in the food supply and changing physico-chemical conditions - are important aspects of the ecology of catfish in Lake Sibaya. I agree with Thomas that these factors are likely to increase the breadth of the food niche.

GENERAL DISCUSSION

It is a truism that the more one knows, the more one needs to know. Despite the findings reported here on catfish predation, and previous fairly extensive studies on their main fish prey, S.mossambicus, we are still far from understanding the nature of their interaction. Nevertheless, it is profitable at this stage to bring together the information at hand and integrate it as far as possible. In the process we will reveal the gaps in our knowledge.

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 rapidly for two or three years and reaching maturity at 250 to 300mm TL, Sibaya tilapia reach maturity after one year at 100-120mm TL. Thereafter growth rates decelerate and individual fishes rarely exceed 200mm TL. Bowen (1976) investigated the reason for this minituarization 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 1m 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) on a related cichlid, Tilapia rendalli suggests that temperature may be the overriding factor dictating the movements and feeding cycles of tilapias. 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) and Kemp (1966) 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. *S.mossambicus* reaches 432mm and 1543g in Inyamithi pan, 60km north-west of Lake Sibaya (Coke, pers.comm., 1973) and commonly exceeds 350mm 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 (1961) and Donnelly (1969) 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 no risk to terrace populations of tilapia. As the lake level increased, the factors inhibiting catfish occupation of the terrace during the day (possibly risk of predation by fisheagles H.vocifer and man) diminished in importance and greater numbers of catfish ventured onto the terrace. Meanwhile, as the terraces deepened, water temperatures were moderated and daily maxima did not approach those achieved 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, as I have shown that catfish 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 catfish is an important factor excluding S.mossambicus from terrace waters at high lake level. Bowen (1976, p.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-adaptation of the prey was to feed in terrace waters for as short a time as possible. However, 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. Nevertheless, tilapia perform several frontal tactics, including perching, shoaling, hanging motionless in midwater, and dispersing, which are successful against a relatively slow-moving, mechanoreceptive bottom-feeding predator. They also use coincidental tactics, such as diel movements, as explained above. The alternative procedure for the prey is to adjust its fecundity and growth patterns so as to minimise 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 expendible 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 tilapia 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. 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 stunting 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. 'Testing' attacks are also a common feature of many mammal predators e.g. wolves (Mech, 1970), hyaenas, (Kruuk, 1972) and lions (Schaller, 1972). From the tower I often observed catfish swimming slowly after a shoal of tilapia, 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 bluegill sunfish *Lepomis gibbosus* and largemouth bass *Micropterus salmoides*, due to injury, parasitism or starvation, resulted in a significant increase in their vulnerability to predation by bowfish, *Amia calva*. Use of testing attacks implies no conservationist instinct on the part of the predator, but simply that a completely healthy prey is more difficult to catch than an unhealthy or enfeebled one. 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).

Why should adults be less subject to predation by catfish in Sibaya? Firstly, *S.mossambicus* larger than 150mm 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% their own length (as discussed in the 'Feeding' chapter) and a 560mm predator (the modal length on the terrace, Fig. 18) would normally take prey less than 110mm TL. On several occasions while diving I observed catfish longer than 500mm 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 tilapia to abandon their nests. No attempt was made to catch the tilapia.

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 300mm 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 summary, the role of C.gariepinus as a predator on S.mossambicus is three-fold:

(a) to enhance species fitness by removing enfeebled individuals from the juvenile population i.e. act as a 'cleanser'

(b) to restrict the distribution of the prey under certain conditions when prey vulnerability is relatively high, such as at high lake level i.e. act as a 'restricter',

(c) to dampen fluctuations in the abundance of cichlid species under certain conditions. This role was shown in the predation experiments where catfish fed on the cichlid population with greatest relative abundance. However, 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 may be different for different prey or in other systems. For instance, catfish 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) sheatfish Siluris 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, sheatfish act as 'cleansers'. 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 maximise its own food supply while at the same time minimising the possibility that the prey population will be able to maintain itself and serve as food in the future. From experiments with Daphnia 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. 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 has missed the point, for she 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). This dissertation was not a study on energetics, but it is nevertheless informative to compare the approximate energy content of the main prey classes eaten by C.gariepinus in Lake Sibaya.

Prey energy content was calculated from the total prey dry weight of 469 catfish collected at intermediate lake level. Values of energy content for fish prey were taken from Caulton (1976) who calculated that average condition Tilapia rendalli from Lake McIlwaine in Rhodesia have an energy content of 4,79 kJ/g. Meakins (1976) gives a lower value of 4,30 kJ/g for Tilapia nilotica from Lake George, Uganda. Energy values for the invertebrate classes were taken from Odum (1971) and Thayer et al, (1972).

The contribution of each prey class to total prey number, weight, and energy content is given in Table 40. Although fish only contributed 12,5% by number of the prey eaten, their yield in terms of dry weight and energy content was far higher than for any other class. In addition, the average energy content per fish prey was over 14 x higher than that for other individual prey items. Clearly, fishes are the most valuable prey for fuelling metabolic processes and catfish can afford to expend considerable energy on their capture.

TABLE 40

Comparison of the contribution of different prey classes to the diet of 469 *Clarias gariepinus* caught at intermediate lake level in Lake Sibaya. Energy contents of prey organisms from Caulton (1976, fish); Thayer *et al* (1973, Crustacea and Mollusca) and Odum (1971, Insecta).

Prey class	% of total prey number	% of total prey dry weight	% of total prey kJ	Average kJ per prey item
Fish	12,5	75,0	76,5	22,88
Crustacea	65,1	18,6	16,5	0,95
Insecta	16,8	4,5	5,2	1,16
Mollusca	4,1	1,9	1,7	1,56

Figure 76: The shape of *C.gariepinus* in poor and good condition.

Top: Catfish from Lake Sibaya. Male, 1088mm TL 8,79kg. Photo: C. Bruton.

Bottom: Catfish from Verwoerd dam. Female, 1275mm TL, 24,584kg. Photo: K. Coetzee.

Juvenile catfish do not show the same rate of absolute weight increase as the fish-eating adults, but their percentage increase in weight is nevertheless high, despite their invertebrate diet. This may be achieved by more efficient protein utilisation by juveniles than adults. Gerking (1952) found that juvenile (10g) longear sunfish *Lepomis megalotis*, utilised 33% of absorbed protein for growth, whereas old fish (105g) utilised only 5% for growth.

Fish prey also provide more protein than invertebrate prey, as well as the correct amino acid balance, as intimated by the higher conversion efficiencies which are obtained when fish eat others of their kind (Lagler *et al*, 1962). Phillips (1972) has shown that the most efficient dietary protein provides the exact qualitative and quantitative amino acid requirements of the fish. Love (1970) and others determined the ten essential amino acids, and Dupree & Halver (1970) confirmed that these are essential for normal growth in another siluriform, the channel catfish *Ictalurus punctatus*. Imam *et al* (1970) determined the growth rate and condition of *Clarias lazera* on test diets of (a) minced fresh forage fish, (b) rice bran and (c) fresh vegetables. Diet (a) provided abundant protein and the correct amino acid requirements, and resulted in a better growth rate and healthier condition.

There is some circumstantial evidence that *C.gariepinus* grows larger in systems where abundant fish food is available to adults. In three large lakes in southern Africa where catfish would be expected to reach a large size but do not exceed 11kg (Lakes Kariba, McIlwaine and Barberspan, Table 21) the adults feed on plankton (Munro, 1967; Bowmaker, 1973; Schoonbee, 1969). On the other hand, catfish reach a large size (over 17kg) in the Vaal river, Verwoerd dam, Hardap dam and Pongola river (Table 20) where large adults have an adequate supply of fish food (Groenewald, 1964; Hamman, Kok and Gaigher, pers.comm., 1976). Similarly, Martin (1966) found in Algonquin Park lake trout *Salvelinus namaycush* that those feeding on plankton grew more slowly and did not reach as great a size as fish-feeders in the same population.

Large adult catfish ($>$ 600mm TL) in Lake Sibaya feed on fish, but their 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. The striking difference in shape of large catfish from Lake Sibaya and from the Verwoerd dam on the Orange River, where catfish are in good condition, is shown in Fig. 76.

There are several reasons why the quality of food available to large and small catfish in Sibaya is different. Large adults feed mainly in deeper terrace and offshore waters (Fig. 18), and their diet consists of a greater proportion of larger *S.mossambicus* (Fig. 61). 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 that for juveniles, as 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 12m in Lake Sibaya (Bruton & Boltt, 1975) and no other large prey are regularly taken by catfish in deeper water. G.giurus, P.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 H.orbiculare among the profundal benthos contributes significantly to the catfish diet. B.capillata, M.tuberculata, C.nilotica and the various infaunal microcrustacea may be too small, unpalatable and/or sparse to support a larger 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 small final size of older 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. These areas also provide abundant 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 migrations are apparently controlled by predation risk and other factors. Both species are food-limited in the larger size groups, and their final size and condition is lower than in other populations of the same species. The predator acts partly as 'cleanser', 'restricter' and 'regulator' of the prey population under different environmental conditions, whereas the prey contributes either good or poor quality food to the predator, depending on the ontogenetic stage. Both species are numerically abundant, and their success is largely a result of their ability to utilise food resources as they become available in the fluctuating littoral zone of Lake Sibaya.

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APPENDIX 1

CHECKLIST OF THE FISHES OF LAKE SIBAYA

(Common names from Jackson, 1975)

CLUPEIDAE	
Gilchristella aestuarius (Gilchrist & Thompson, 1916)	estuarine round-herring
MORMYRIDAE	
Marcusenius macrolepidotus (Peters, 1852)	bulldog
CYPRINIDAE	
Barbus paludinosus Peters, 1852	Straightfin barb
Barbus viviparus Weber, 1897	bowstripe barb
Labeo molybdinus du Plessis, 1963	leaden labeo
CLARIIDAE	
Clarias gariepinus (Burchell, 1822)	sharptooth catfish
Clarias theodorae Weber, 1897	snake catfish
CYPRINODONTIDAE	
Aplocheilichthys katangae (Boulenger, 1912)	striped topminnow
Aplocheilichthys myaposae (Boulenger, 1908)	Natal topminnow
ATHERINIDAE	
Hepsetia breviceps (Cuvier in C. & V., 1835)	Cape silverside
CICHLIDAE	
Pseudocrenilabris philander (Weber, 1897)	southern mouthbrooder
Sarotherodon mossambicus (Peters, 1852)	Mozambique tilapia
Tilapia rendalli swierstrae Gilchrist & Thompson, 1917	southern redbreast tilapia
Tilapia sparrmanii Smith, 1840	banded tilapia
GOBIIDAE	
Croilia mossambica Smith, 1955	burrowing goby
Glossogobius giurus (Hamilton-Buchanan, 1822)	tank goby
Silhouettea sibayi Farquharson, 1970	Sibayi goby
ANABANTIDAE	
Ctenopoma multispinis Peters, 1844	manyspined climbing perch

APPENDIX 2

Six cases of a catholic diet in *C.gariepinus* from Lake Sibaya.

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

Figure 2: Map of Lake Sibaya.
Bathymetry modified from Hill, (1975).