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On the biology of the catfish *Clarias senegalensis*, in a man-made lake in the Ghanaian savanna with particular reference to its feeding habits

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(Accepted 6 January 1966)

(With 1 plate and 12 figures in the text)

The present study of *Clarias senegalensis* C. & V., from a small man-made lake in the coastal savanna of Ghana, was initiated because this species has not been investigated previously and there is a need to have precise information regarding its general biology and food niche both from the theoretical and practical viewpoints. This catfish becomes sexually mature when about 32 cm in length and once a year, after the onset of the major rains in April, or early May, they ascend the feeder stream to spawn in its flood zone. Spent fish soon return to the lake after spawning but smaller immature fish do not do so until September. As with other piscivorous fish the feeding intensity is low and with one exception the stomachs of the monthly samples were on the average less than half full. The suggestion of a slight seasonal increase in the amount of food consumed from August onwards appears to be correlated with a seasonal increase in standing crop and is followed later by an increase in condition factor. *C. senegalensis* is extremely euryphagous but it subsists mainly on organisms swimming in midwater including fish such as *Tilapia*, zooplankton and insects, those living on the surface of the sediment and small organisms swimming near the surface of the sediment. Animals from these habitats have a higher forage ratio than those living under stones, in the sediment or in shallow water or in vegetation close to the shore. Vegetation, adventitious food and detritus are of little consequence to *C. senegalensis* in Nungua lake and it is suggested that the latter is not exploited because the sediments are poor in organic matter. The euryphagous habits of *C. senegalensis* are shared by other *Clarias* species and this is reflected in several anatomical adaptations concerned with feeding. Seasonal changes in the dietaries are very slight because the catfish do not exploit phytophilous species to any great extent even when they become abundant during the wet season. For this reason it is doubtful whether they are of value in controlling important vectors of diseases many of which are phytophilous. Although there is a suggestion that larger fish eat more vegetation, phytophilous species and adventitious food the evidence for ontogenetic changes in the dietaries are very slight and fish in all the size groups eat minute food organisms such as copepods and also large ones such as fish including *Tilapia*. The possibility of combining *Clarias* with *Tilapia* in fish ponds is, therefore, worthy of consideration. The factors which cause expansion and contraction of food niches are discussed.

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Introduction

No information has been published on the biology of *Clarias senegalensis*, a species which occurs commonly in West Africa (Irvine, 1947; Daget, 1954). In contrast, the feeding habits of several other species of *Clarias* have been studied in East and Southern Africa. These include *Clarias mossambicus* Peters by Graham (1929), Fryer (1959) and Corbet (1961), *Clarias carsoni* Boulenger and *Clarias alluaudi* group Boulenger by Corbet (1961) and *Clarias gariepinus* (Burchell) by Groenewald (1964). In the case of the latter three species relatively small number of fish were examined from any one habitat and the food was not analysed at generic or specific level. In consequence, the only species for which detailed information is available is *C. mossambicus*. The reproductive biology of this species has also been studied by Greenwood (1955).

In the above mentioned cases no quantitative attempt was made to correlate food with the fauna but in the present investigation this has been attempted in order to provide precise information regarding the feeding niche of a predator in a tropical ecosystem. Such information is also desirable for the purposes of fishery management in consequence of the proposals that have been made regarding the possibility of combining *Clarias* with *Tilapia* in fish ponds (Brown, 1955).

Topography of the lake

The catfish were obtained from a man-made lake situated on the grounds of the University of Ghana, Agricultural Research Station at Nungua in the Accra plains of Southern Ghana (5.41°N 0.06°W) at an altitude of approximately 21 m. It was completed in March

1954 by damming a small, intermittent stream, the Mamahuma, which drains into the Sakumo lagoon near the port of Tema. The triangular lake is about 1430 m long and 465 m broad at its base when at full capacity (Plate I). Its catchment area, of gently undulating savanna, is about 65 km² in extent. Over much of area the vegetation is characterized by somewhat uniformly distributed clumps of thicket, usually associated with *Macrotermes* mounds and lying in a matrix of tussocky grasses. The soils are of three main types including regosilic groundwater laterites, tropical grey and black earths. Such soils are rich in aluminium and iron oxides and poor in one or other of the biologically important elements including nitrogen and phosphorus (Nye & Greenland, 1960; Brammer, 1962) and in organic matter (Brammer, 1962; Thomas, 1966). Crop husbandry is little practised in the catchment area, except in the research station, and the area is used mainly for cattle ranching. The macrofauna was studied at two stations, one on the southern shore (A) and the other (B) on the northern shore near the spillway. The catfish were also collected at or near these stations.

Materials and methods

The observations on the meteorological conditions, physico-chemical factors in the lake and the bottom fauna were made during the period June 1958 to March 1960 and those on the catfish from March 1959 to February 1960. Numerous data were gathered but for the purposes of the present paper only the following need to be mentioned.

Physico-chemical factors

Rainfall

Daily readings, to the nearest 0·01 in. were taken at 0900 h. These were later converted to the nearest 0·1 cm.

Water level, volume and surface area

The water level was recorded in feet and inches by means of a gauge located at the deepest point near the dam wall. The zero value of the gauge coincided with the level of the lake at full capacity. With the aid of the water level data and a planimetric map prepared prior to the flooding it was possible to determine the approximate capacity and surface area of the lake at any time during the period of investigation.

Water temperatures

Regular measurements of the water temperature were made at Station A. A hydrothermograph was used to record the temperature at 0·5 m and a mercury thermometer reading to the nearest 0·1 °C was used to measure the surface water temperature at 0900 and 1500 h each day.

Particle size analysis

This was undertaken with the sediments from both stations using the method recommended in British Standards 1377 (1948) except that a wider range of sieves was used in confirmation with the Wentworth scale.

Organic matter

The amount of organic matter on the sediments was estimated by using the Walkley and Black modifications of the Schollenberg technique for determining carbon (Piper, 1950).

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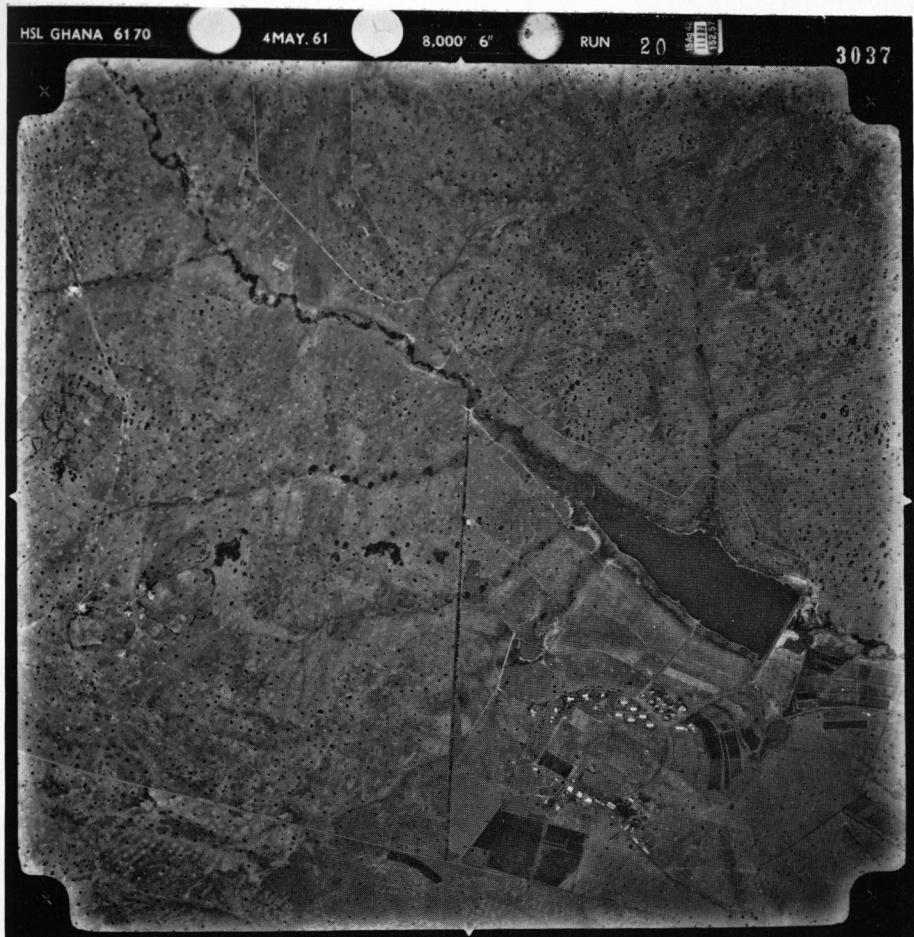


PLATE I. Aerial photograph of Nungua Lake. (Courtesy of Hunting Surveys Ltd.)

Water analysis

These were undertaken by the Government Chemist at fortnightly intervals.

Fauna

Qualitative and quantitative collections of the bottom fauna were made each month in water up to 0·9 m in depth at both stations A and B. An Ekman dredge was also used occasionally to collect samples in the deeper parts of the lake. In the present account only the quantitative samples are considered. Five of these were taken each month in water of from 20 to 90 cm in depth at both stations A and B with the aid of a Wilding square-foot sampler (Welch, 1948). It was discovered that the outer cylinder of the sampler could be worked into the silty or clay horizon of the sediments at both stations and as it acted as an almost perfect seal all the enclosed organisms with the exception of the very minute forms were recovered by draining the water and sifting the substratum to a depth of about 2 cm through standard sieves. The inner cylinder and its valve arrangement was, therefore, discarded because it did not function very satisfactorily, particularly on the gravelly substratum at station B. In addition to the bottom fauna the sampler also captured weed inhabiting and mid-water swimming forms including Hemiptera, Coleoptera and the smaller fish. Although small individuals of *Clarias*, *Tilapia* and *Hemichromis* were captured in this way the larger ones almost invariably escaped. The samples were examined in the laboratory with the aid of microscopes. The material from each square-foot sampler was identified as far as possible either on a generic or specific basis and the numbers of individuals in each taxon counted. The total number of individuals of each taxon were then added either on a monthly or annual basis and expressed as a percentage of the total number of organisms in the faunal collections.

Flora

The phanerogamic vegetation, periphyton and phytoplankton were collected and later identified in the laboratory. The extent of the distribution of phanerogamic vegetation was recorded with the aid of photographs once each month.

Catfish

Up to 20 catfish were collected each month from March 1959 to February 1960 inclusive. Except for July and August when night lines were used and in October when gill nets were put down the fish were captured by means of a seine net from 0600 to 0800 h. As the gill nets and long lines were set in the evening the fish were caught during the night and were not collected until dawn. The fishes were brought back to the laboratory as soon as possible after capture. After being given a reference number each fish was weighed to the nearest 0·5 g and its total length from the snout to the end of the caudal fin measured to the nearest mm. Each fish was dissected to determine the sex, the state of the gonads and the amount of fat deposited on the mesenteries. The catfish were said to be ripe when their gonads were showing definite signs of producing mature sperms or ova, spent when it was clear that sperms or ova had recently been shed, un-developed if there was no evidence of sperms or ova and developing when the gonads were beginning to enlarge. The number of gill rakers on the first gill arch were also counted in a representative number of fish.

Examination of food contents was made with the aid of a dissecting microscope and was confined to the stomach which is well defined in this species. Food organisms were identified to the genus and whenever possible to the species. This was facilitated by the fact that the food items are normally swallowed whole. The analysis of the food was undertaken by the following methods:

Occurrence method

This gives the percentage of the total number of fish examined containing individual food items. The number of occurrences of all food items is summed up and scaled down on a percentage basis to give the percentage composition of the diet.

A modified points scheme suggested by Hynes (1950) and described by Thomas (1962)

When using the scheme each stomach was first given a number of points proportional to its degree of fullness. A stomach was given 16 points when full, 8 points when half full and 4 points when a quarter full. The total number of points based on the degree of fullness of the stomach was then subdivided into point groups indicating the relative proportion by volume of the food item present. All the points gained by individual food items were summed up and converted to percentages to give the percentage composition of the food either on a monthly basis or for all the fish examined.

Number method

The total number of individuals of each food item are given and expressed as the percentage of the total number of organisms found in all the fish either on a monthly basis or for all the fish examined.

The forage ratio of Hess & Swartz (1941) was used to compare the composition of the bottom fauna and the food of the catfish. This is determined by the following formula, $\left(\frac{100n}{N}\right)/\left(\frac{100n^1}{N^1}\right)$, where n is the number of any given organism in the stomachs and N the total number of organisms in the stomach, n^1 = the number of the same organism in the bottom sample and N^1 is the total number of organisms in the bottom sample. The forage ratio is influenced by the availability or accessibility of the fauna and also by the degree of selection by the fish. It is, therefore, simply a means of describing the final results of all the factors which determine the extent to which each potential food is eaten by the *Clarias*. A forage ratio of <1 indicates that the fish are not selecting the organism or that it is not readily available: a ratio of 1 indicates that a particular organism occurs in the stomach with the same frequency as in the bottom samples and the fish are feeding at random. A ratio of more than 1 indicates that the fish are either selecting the organism or that it is readily available. In using the forage ratio it is assumed that the fish and fauna are being adequately sampled and that the organisms are equally available to fish and sampler. Unfortunately, these assumptions are never completely justified for the following reasons. First, sampling of the fauna and fish stomach is made difficult by the contagious distribution of most of the faunal constituents and of the fish. Second, the faunal sampling does not usually take into account the mid-water forms, the microfauna including plankton, the fish or the terrestrial food. The errors involved in determining the forage ratio in the present investigation were obviated by the dearth of food of terrestrial origin and by the fact that the sampler captured all the important constituents in the food of the catfish with the exception of the larger fast moving fish and the zooplankton.

Physico-chemical environment

Figure 1 shows that the volume, surface area and depth of the lake are subject to very considerable seasonal changes. The lake fills to its capacity of 800,000 m³ after the onset of the principal rainy season from April to June, covers an area of up to 37 hectares and has a maximum depth of about 4.5 m. After the onset of the dry season the volume gradually decreases until the next major rains start the following April to June. The small

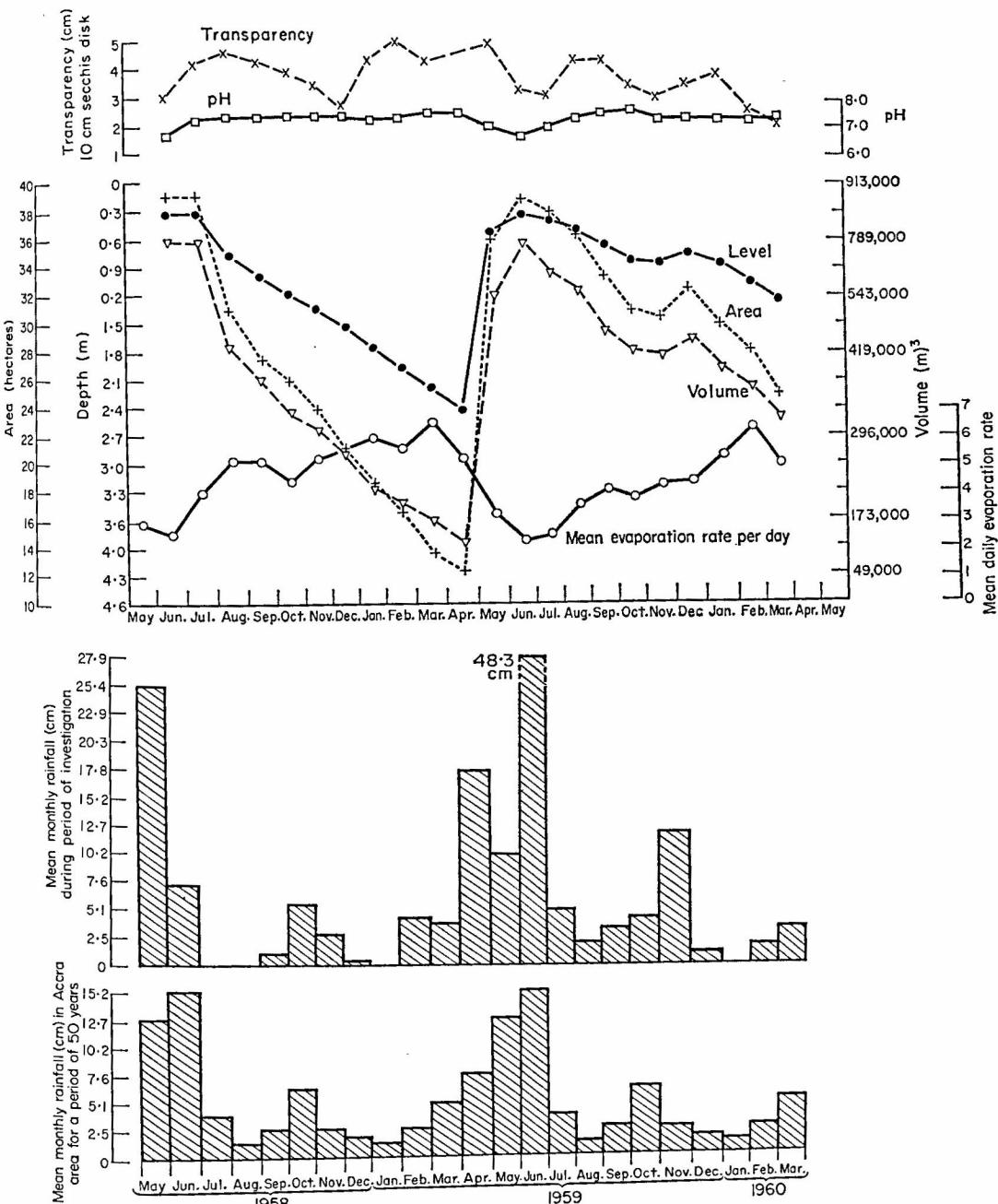


FIG. 1. Seasonal changes in rainfall, mean evaporation rate, volume, area, water level, pH and transparency as measured by a Secchi's disk at Nungua Lake.

rains in October have little influence on the lake level, presumably because much of the precipitation at this time is used up in ground water recharge and evapo-transpiration. As little water was used for irrigation and seepage losses were negligible most of the water appears to have been lost by evaporation which is about 1.95 m/year. The minimum surface areas recorded were 10.5 and 23 hectares immediately before the main rains in 1958 and 1959, respectively. It can thus be seen that the lake has a very extensive flood zone.

Seasonal changes in the volume of the lake were accompanied by chemical changes which will be reported in greater detail in a later paper. The ionic concentration reaches its maximum value towards the end of the dry season. With the advent of the wet season the water becomes much diluted as result of torrential rain and a rapid run off. At this time the conductivity may reach values as low as 35 reciprocal megohms and with the exception of nitrate all the ions decrease in concentration. Flooding also results in an increase in oxidizable organic matter most of which is allochthonous in origin. In consequence of the high water temperature decomposition of the excess oxidizable organic matter was rapid and within less than a month the high permanganate values had returned to more normal levels.

The sediments were found to contain very little organic matter; during the dry season the mean values for stations A and B, respectively, were 0.42 and 0.17. The values during the wet season were only slightly higher. The dearth of organic matter can be attributed to the following factors. First, the amount of autochthonous and allochthonous organic matter contributed by the phanerogamic aquatic and subaquatic vegetation and by the savanna catchment area is relatively small. Second, as a result of the high water temperature, the organic debris decays and breaks down quickly. In all probability most of the decomposition takes place in midwater and as a result the breakdown products go into circulation before they reach the bottom.

A detailed analysis of the water temperatures will be given in a later paper. These were higher during the dry season from November to April or May than during the wet season from April or May to October. The highest value of 34.5°C was recorded in March. During the wet season the water temperatures may fall to low levels. Thus, after almost continuous torrential rain over a period of two days in April the water temperature fell by 10°C to the lowest recorded value of 20.25°C but after about three weeks it had risen again to the more normal level of 29°C. The water is usually thermally stratified during the day except near the north-eastern shore where this is often prevented by turbulence caused by the prevailing winds. As usual in tropical water bodies the difference between the temperature of the water at the bottom and near the surface is small, rarely exceeding 3°C, and at night nocturnal mixing seems to take place.

The texture of the sediments at stations A and B, respectively, may be described as silty sand and sand according to the Revelle system of classification.

Flora

Permanent rooted vegetation is lacking at both stations A and B but after the inundation of the flood beach during the wet season a profuse growth of floating and subaquatic vegetation develops along the shore line of the lake. The subaquatic plants which are restricted to the marginal areas include *Jussiaea repens* var. *diffusa* (Forsk), *Enhydra fluctuans* Lour, *Alternanthera sessilis* (L.) various grasses and sedges. The shoots of the former

species may extend for several yards along the surface of the water and frequently intermingle with floating carpets of *Pistia stratiotes* and *Azolla africana*. The latter species is relatively rare, but during the wet season *Pistia* may undergo a population explosion and cover several hectares of the marginal areas particularly at station B. With the recession of the water after the onset of the dry season the phanerogamic vegetation gradually disappears. Among the first to go are the floating plants of *Pistia*. They are peculiarly susceptible to wind action and considerable quantities are washed on to the southern shore by the prevailing winds. Flowering plants, therefore, contribute very little by way of organic matter particularly during the dry season.

Many species of algae including representatives of the Chlorophyta, Chrysophyta, Bacillariophyceae and the Cyanophyta become seasonally abundant particularly during the dry season. The primary production is, however, confined to the surface half meter of water because of the high turbidity and tends to be higher during the dry than in the wet season. The limit of light penetration as determined by Secchi's disk varied from 21·6 to 45·7 cm.

Macrofauna

The list of species encountered has already been given (Thomas, 1966). The species per taxon pattern is characterized by the presence of a small number of species or none in those taxa normally containing many scavengers or sediment feeders. These include the Turbellaria, Hirudinea, Oligochaeta, Mollusca, Amphipoda, Decapoda, Isopoda, Ephemeroptera, Plecoptera, Trichoptera and the Corixidae and a larger number of species in the Branchiopoda, Copepoda, Coleoptera, Hemiptera, other than the Corixidae the Odonata and Diptera. It has been suggested (Thomas, 1966) that this pattern is largely attributable to the dearth of organic matter in the sediments, the rapid decomposition and the very marked seasonal fluctuations in water level. The percentage composition of the fauna, based on the combined monthly samples from stations A and B, and determined by the numerical method is illustrated graphically in Fig. 2. It can be seen from this that the dominant animals in the fauna from the numerical viewpoint are the Ostracoda, the ephemeropteran *Caenis*, the trichopteran larva *Hemiloptocerus* and *Ecnomus*, the odonatan larvae, *Brachythemis* and *Ictinogomphus*, the hemipterans *Micronecta*, *Anisops*, *Rhagovelia*, the dipteran larvae *Clinotanypus*, *Limnochironomus*, *Cryptochironomus*, *Tendipes*, *Chironomus* and other Chironomidae and the fishes *Barbus* and *Micropanchax*. As the quantitative samples were taken in a depth of 20 cm of water or more the fauna occurring in the shallow water along the margin and containing emergent vegetation during the wet season was not extensively sampled.

A full account of the qualitative and quantitative aspects of the bottom fauna and the manner in which it changes seasonally will be given in a later paper. The population density expressed in numbers per m² tends to be higher from April to June 1959 than from July 1959 to February 1960 although there is some indication of a very slight increase from August onwards to December or January followed by a decline. The biomass, on the other hand, is low from March to July 1959 but becomes progressively greater thereafter. The species diversity expressed as the ratio of the cumulative number of species over the logarithm of the cumulative number of individuals was much higher during the wet season than at other times in the year.

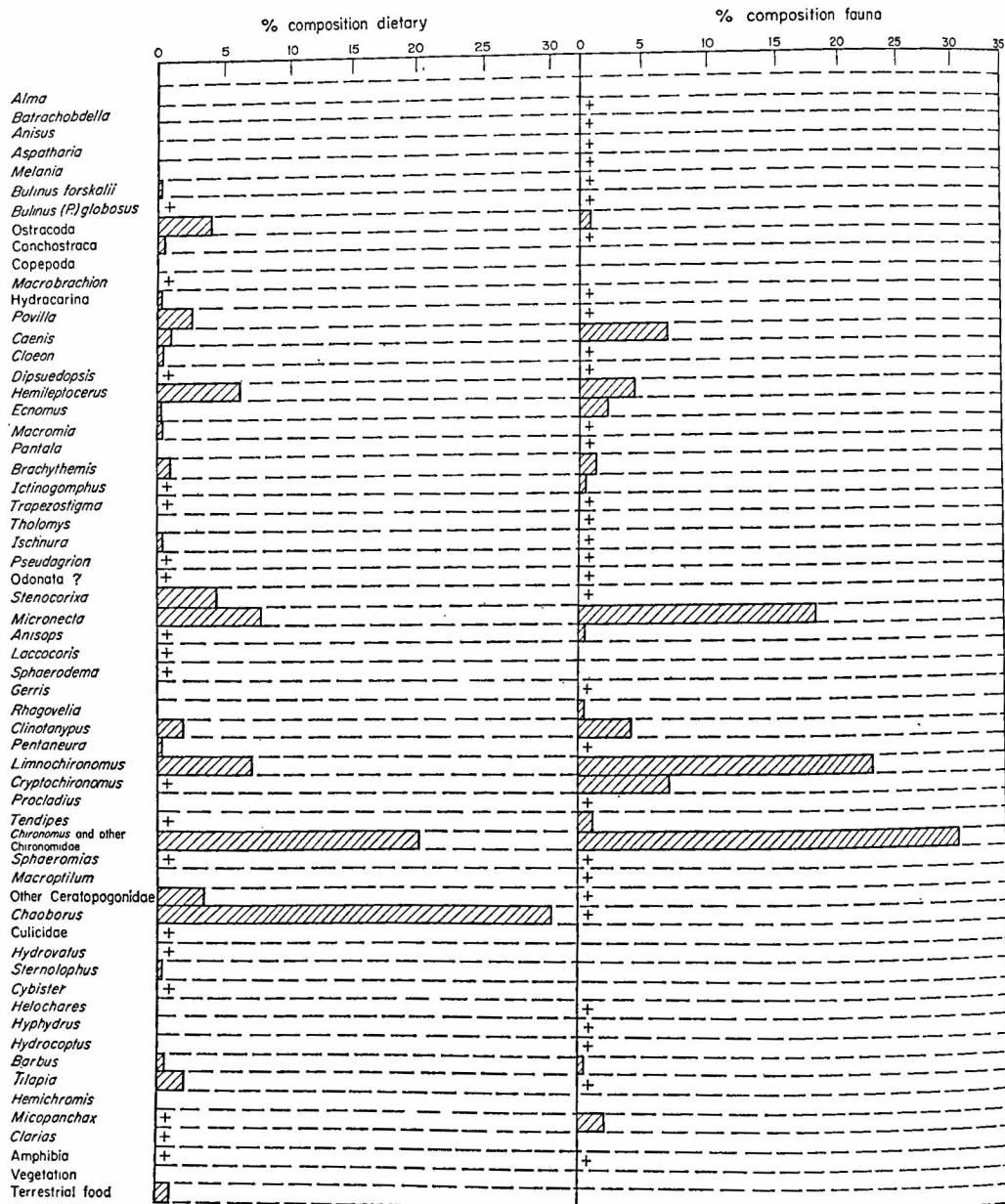


FIG. 2. The percentage composition of the fauna and of the food of all the catfish investigated (+ indicates less than 0·2%).

Observations on biology of *Clarias senegalensis* Anatomical features which may influence its feeding habits

The catfish has many anatomical features which suggest that it is adapted to a sluggish, bottom dwelling existence. These are as follows: (1) the tapering body is dorsoventrally

flattened in front and laterally compressed posteriorly. It is possible that the flattened ventral surface of the anterior region is an adaptation to allow movement on the substratum or on land when migrating. The spines on the pectoral fin may serve as levers on land although their primary function is probably to give protection; (2) the pelvic fins are small and have retained their primitive abdominal position; (3) the dorsal and anal fins have

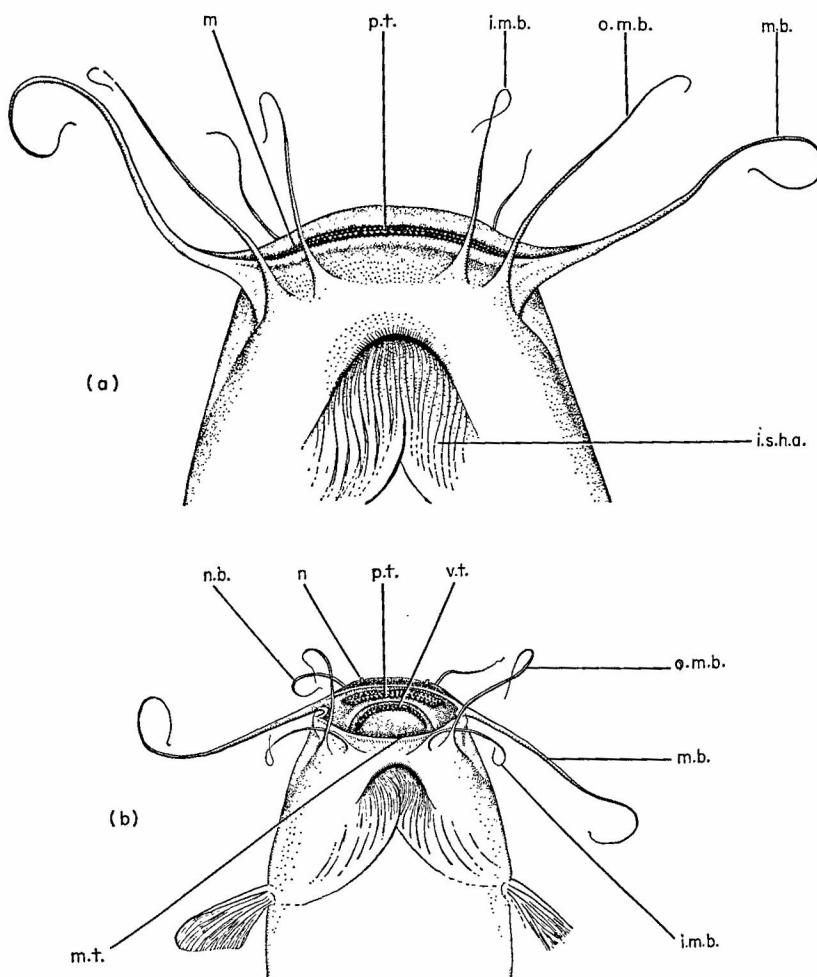


FIG. 3. (a) The head of *Clarias senegalensis*; ventral view. (b) The head of *Clarias senegalensis*; subventral view with mouth open. Key to lettering on p. 514.

become elongated so as to re-establish a continuous fin fold (Goodrich, 1930); (4) the tapering, disguised, homocercal tail; (5) the head is very large, dorsoventrally flattened and has a heavy skull; (6) the swim bladder is relatively small in size and appears to be entirely devoted to subserving the function of the Weberian ossicles rather than being a hydrostatic organ.

The mouth is a long, sub-terminal, transverse, slit (Fig. 3(a), (b)). The lateral angles of the mouth are extended anteriorly and arising from them are the long maxillary barbels. Other barbels including the inner mandibular, outer mandibular and nasal barbels also occur on the anterior head region (Fig. 4). The small eyes occur on the anterolateral

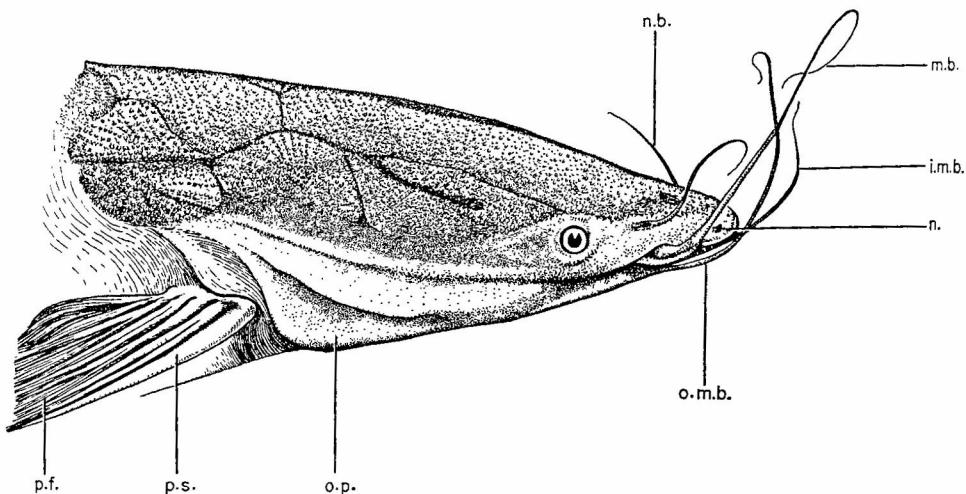


FIG. 4. The head of *Clarias senegalensis*; side view. Key to lettering on p. 514.

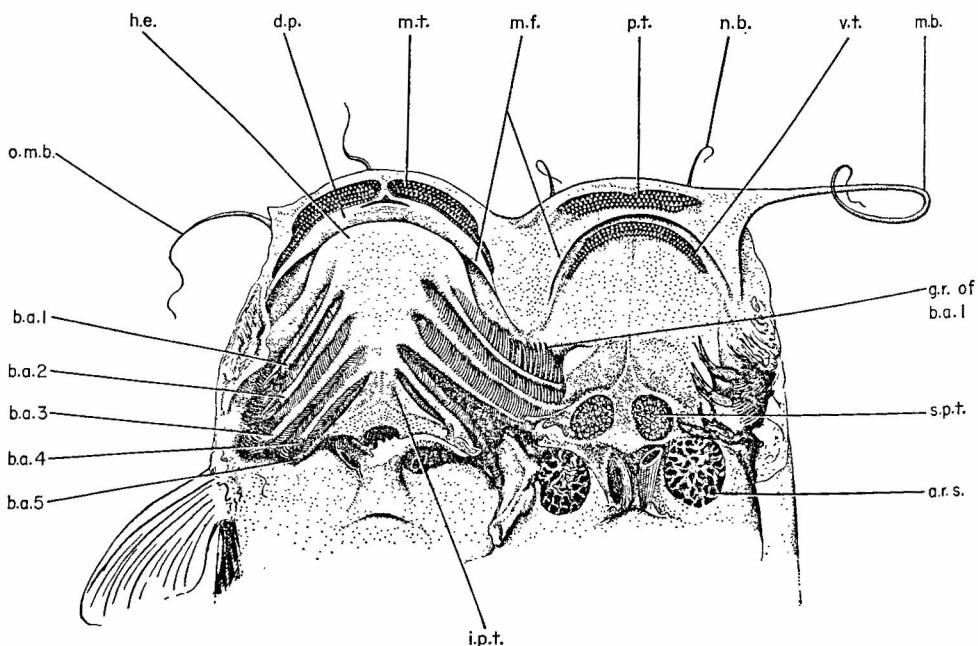


FIG. 5. The head of *Clarias senegalensis* dissected to show the buccal and pharyngeal cavities.
Key to lettering on p. 514.

aspect of the head. Both the upper and lower jaws have marginal pads bearing bands of very small backwardly directed teeth; the premaxillary in the former and the mandibular in the latter (Fig. 5). Behind the premaxillary on the roof of the mouth is a crescent shaped bony pad bearing the vomerine group of teeth. The area on the floor of the mouth opposed to the vomerine group of teeth is called the dental pad. Immediately behind the pad is an elevation in the floor of the mouth indicating the position of the hyoid arch. The large

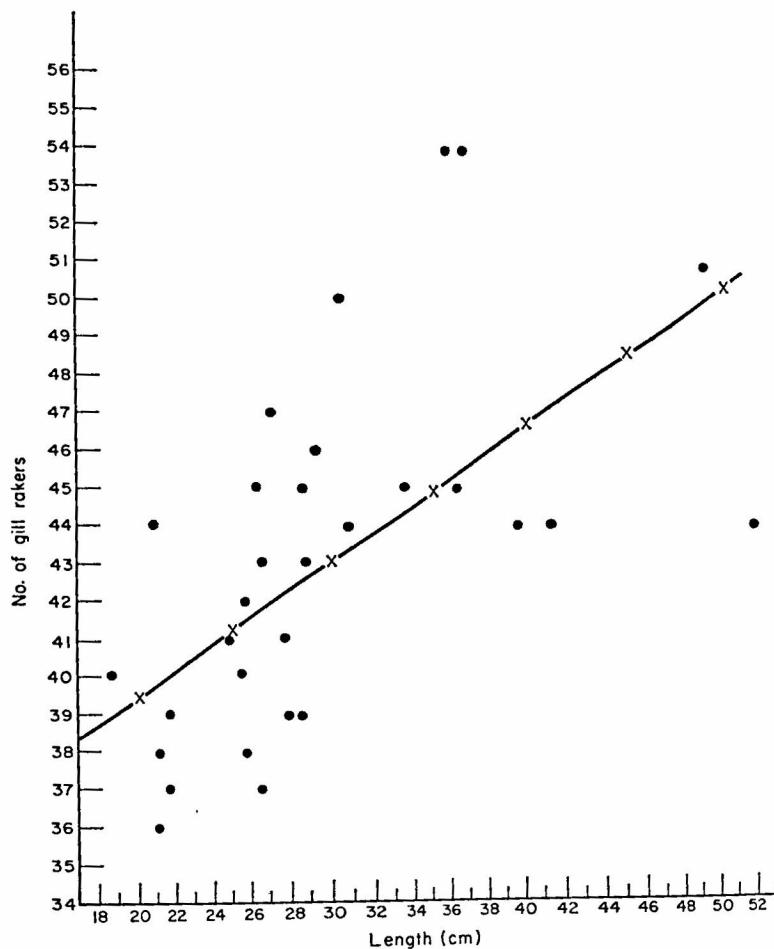


FIG. 6. Scatter diagram of length as ordinate plotted against number of gill rakers as abscissa and the regression line fitted by the method of least squares.

buccal cavity is continuous with a smaller pharynx containing inferior and superior toothed bones and five gill clefts laterally. Long gill rakers are present along the anterior borders of the five branchial arches. In addition the third and fourth arches possess gill rakers on the posterior margin which interdigitate with those from the anterior row on the succeeding arch. The number of gill rakers on the first gill arch varied from 34 to 54 in a sample of 36 fish ranging from 18.7 to 51.7 cm in length. Figure 6 shows that the number of gill

rakers tends to increase with increase in length of the fish. The regression line has the equation $y = 32.176 + 0.364x$ where y is the number of gill rakers and x is the length in cm. In order to test for the existence of some degree of association between the number of gill rakers and body length it is necessary to know whether the regression coefficient b is significantly different from the hypothetical zero value. The standard error of byx was $0.36434 + 0.0403$. As b is more than 1.96 the standard error from zero it is significantly different at more than the 5% level.

The oesophagus is short, dilatable and opens into a U-shaped stomach. The intestine is a simple, short and slightly convoluted structure which may be divided arbitrarily in duodenum, ileum and rectum. It lacks pyloric caeca.

Length frequency distribution and spawning

Figure 7 shows the length frequency distribution of fish samples taken during the period of investigation. This shows that nearly all the fish of 32 cm or more in length became ripe during the period March to April. These moved upstream to spawn in April and early

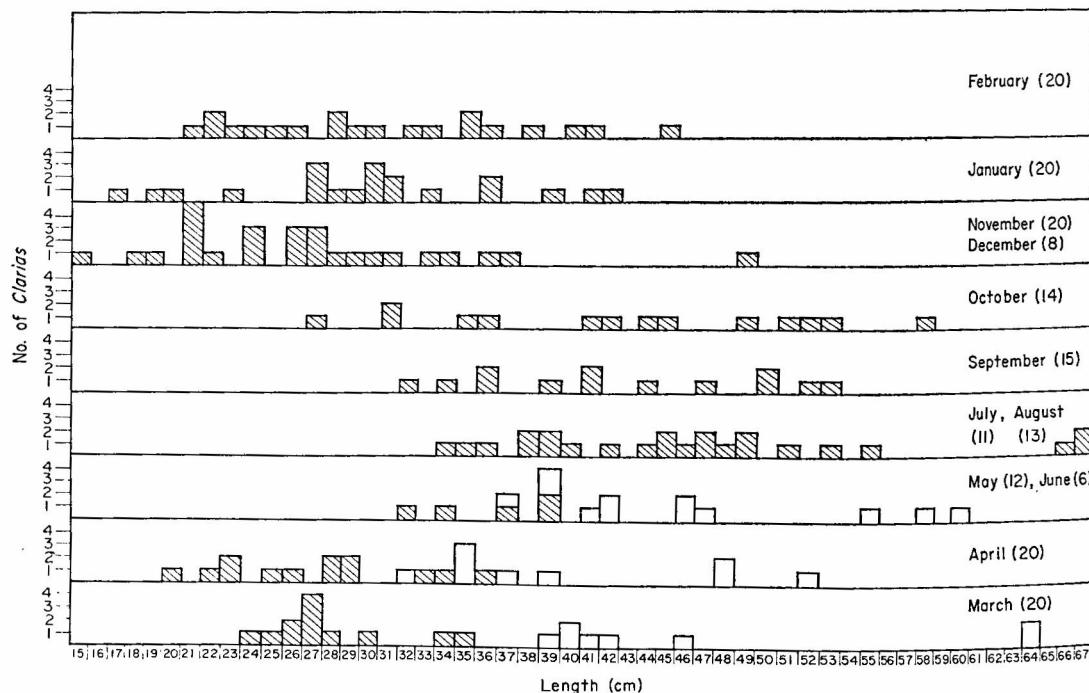


FIG. 7. The length frequency distribution of *Clarias senegalensis* taken from Nungua lake during the period of investigation. The white segments represent sexually mature fish with ripe gonads.

May. During this period the stream, which had previously consisted of a series of small, disconnected pools had flooded an extensive area in which subaquatic and aquatic vegetation including species of *Jussiaea*, *Enhydra*, *Alternanthera*, *Hydrolea*, *Basilicum* various Cyperaceae and Graminae occurred in abundance. Spawning and fry were recovered

from the flooded area during this time. It appears that spent fish return to the lake shortly after spawning. Figure 7 shows that during the period May to September no fish below 30 cm were captured in the lake because they had moved upstream. In September when the stream is drying up and the volume and surface area of the lake is decreasing these small fish return to the lake. They are accompanied by fish in the 0+ year produced from eggs laid in April and early May. Few large fish were encountered when fishing during the period November to February and it is possible that they occur in the deeper regions of the lake at this time. A small number of fish of more than 30 cm in length had developing gonads in February. It appears, therefore, that *Clarias senegalensis* spawn only once a year and that the spawning runs coincide with the onset of the major rains.

Condition factor

The condition factor of a fish is usually expressed in terms of a ponderal index K in the generalized equation $K = W10^3/L^n$ where n is the exponent determined by measuring the slope of a straight line fitted to a plot of log weight as abscissa and log length as the ordinate. In Fig. 8 the regression line has the equation: log weight = $-2.2756 + 3.0574$

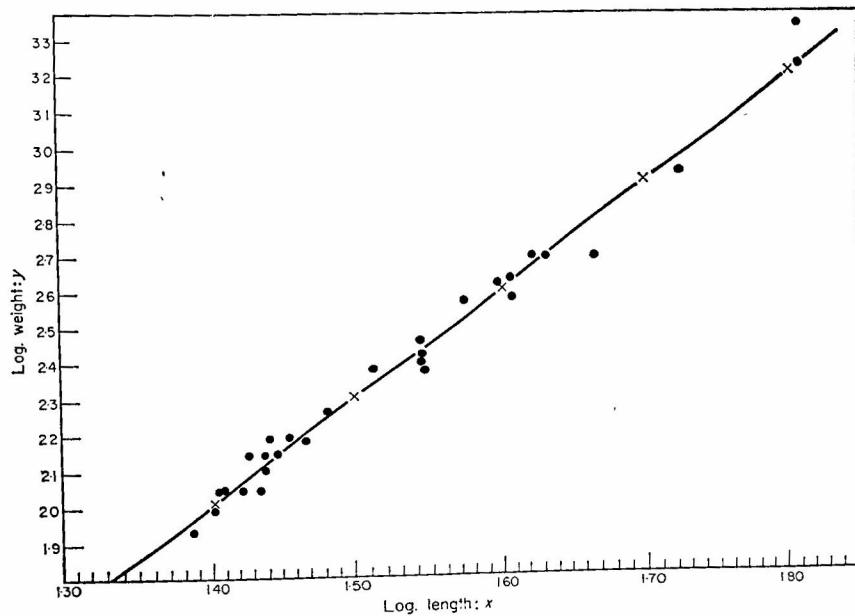


FIG. 8. Scatter diagram of log length as abscissa plotted against log weight as ordinate and the regression line plotted by the method of least squares.

(log length). As n was 3.057 in this sample and 3.088 and 3.072 in other samples it is sufficiently close to 3.0 to allow the use of the usual condition factor $K = W10^3/L^3$. In the present example the length/weight relationship appears to be constant over the range of sizes involved.

Table I and Fig. 9 show the condition factor for catfish of different sizes during the

TABLE I

*Mean condition factors (C.F.) of *Clarias senegalensis* of various sizes during the period of investigation*

Length (mm)	100–200		200–300		300–400		400–500		500+		All fish	
Month	N	C.F.	N	C.F.	N	C.F.	N	C.F.	N	C.F.	N	C.F.
March 1959	—	—	9	5.774	4	6.454	5	6.218	2	7.733	20	6.217
April 1959	—	—	11	6.358	7	6.815	1	5.570	1	6.163	20	6.488
May and June 1959	—	—			9	6.393	6	5.798	3	6.456	18	6.494
July–August 1959	—	—			7	6.035	11	6.663	6	6.925	24	6.545
September 1959	—	—			5	7.282	5	6.968	5	6.746	15	6.999
October 1959	—	—	1	5.874	4	8.574	5	7.778	4	6.306	14	7.449
November and December 1959	3	7.816	18	6.711	6	6.545	1	6.505			28	6.786
January 1960	2	6.379	7	6.689	8	6.375	2	6.666			19	6.522
February 1960			10	6.481	7	6.687	3	6.302			20	6.526

N refers to the number of fish.

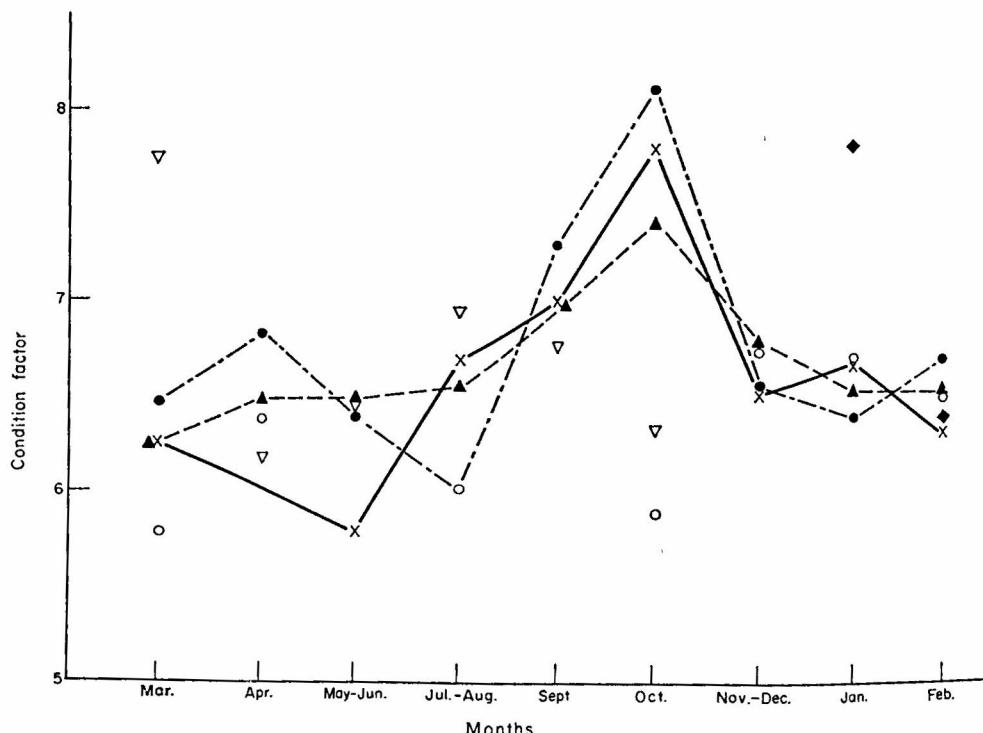


FIG. 9. The mean condition factors of *Clarias senegalensis* of different length groups during the period of investigation. Length groups: ◆, 100 to 200 mm; ○, 200 to 300 mm; ●—●, 300 to 400 mm; ×—×, 400 to 500 mm; ▽, 500 + mm; ▲—▲, combined values for all fish.

period investigated. It appears from these data that there is no consistent correlation between condition factor and length. There is, however, evidence of a seasonal change as the mean condition factors of all size groups, with the exception of those >500 mm in length, rise to a peak in September and October. It seems probable that this rise is attributable to the fact that at this time the fish are increasing proportionately more in weight because of better feeding during these and the preceding months. There is some slight decline in the mean condition factors of fish of 300 mm in March-April or May which can be attributed to the fact that some spent fish occurred in these monthly samples.

Food of the catfish

Quantity of food in the stomachs

Figure 10 shows the mean number of points per fish and the percentage of empty stomachs on a monthly basis. All the point values are comparable as the scheme used provides a measure of the relative volume of food in the stomach irrespective of the size of the fish.

It is evident that the feeding intensity is not high and with the exception of fish taken in November the stomachs are on the average less than half full and frequently empty. In this respect, the results are comparable with those obtained by Corbet (1961) and Groenewald (1964) for *Clarias mossambicus* and *Clarias gariepinus*, respectively, as 47.6% of the former species and 32.5% of the latter had empty stomachs. Two reasons can be advanced to account for the high incidence of empty stomachs. First, during some months including July, August and October the fish were left for several hours in gill nets or on long lines before they were killed and dissected. Under such conditions it is possible that the stomach contents may have been lost by regurgitation or by digestive processes. It is to be expected that the rate of digestion would be rapid at the high temperatures prevailing in the lake. As approximately the same percentage of empty stomachs were found during months when the fish were dissected immediately after capture by seine nets this cannot be the only explanation. Second, the catfish may tend to feed less frequently because they are largely piscivorous. This seems to be the most likely explanation of the high incidence of empty stomachs. Both Allen (1935) and Frost (1954) have shown that this is a characteristic feature of other piscivorous fish and the latter author found that as pike became more piscivorous with increase in size the percentage of feeding fish in the sample decreased. There are two reasons why piscivorous fish need not feed continuously. First, as stated by Allen (1935), the large size of the prey will enable them to obtain a relatively large amount of food in a short space of time and with a small expenditure of energy. Second, there is evidence (Nikolsky, 1963) that the nutritional coefficient or the ratio of weight of food consumed by the fish to increase in weight is higher for fish food than for other items in the dietaries.

Although the feeding intensity is low, the catfish seem to feed continuously throughout the year. There is, however, some slight suggestion of a seasonal trend in feeding intensity as the mean number of points per month were slightly less during the months of March to July (with the exception of May) than from August to December. The validity of this interpretation can be questioned, however, because other factors including diurnal or lunar periodicities (Macdonald, 1956) and the rate of digestion may influence the amount of food present in the stomach. Nothing appears to be known regarding such rhythms in

African catfish but if they do occur any distortion caused by them would tend to be obviated by the following facts. First, quite a large proportion of the food of the catfish is made up of organisms including *Tilapia* which cannot be expected to show any lunar periodicity. Second, the fish samples were collected at the same time of day so that the results would at least be comparable. Third, as there is little seasonal fluctuation in temperature it is unlikely that the rate of digestion will change.

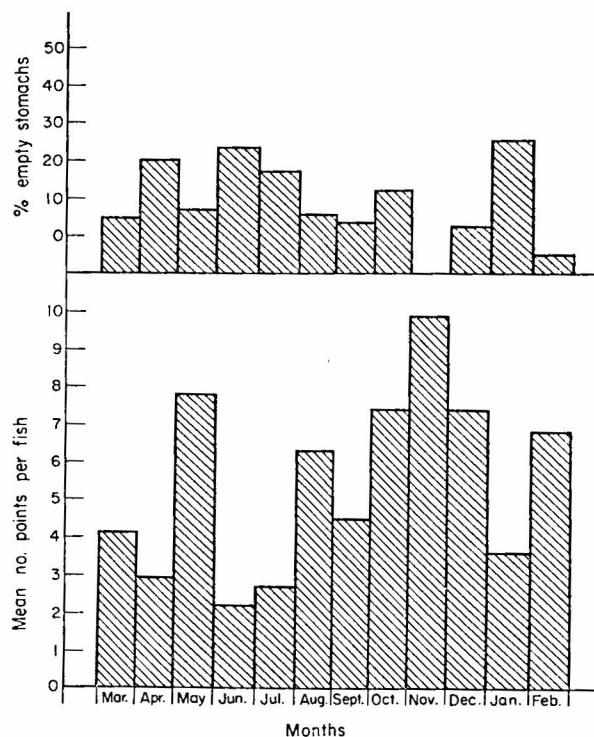


FIG. 10. The quality of food eaten expressed as the mean number of points per fish per month and also the percentage of empty stomachs encountered each month.

Percentage composition of the food

Table II gives the percentage composition as determined by the percentage occurrence method, the numerical method and the points scheme for all the fish examined. The major food items as determined by the three methods are listed below in order of importance.

Percentage occurrence method. Chironomidae including *Chironomus*, *Stenocorixa*, *Tilapia*, *Micronecta*, *Chaoborus*, *Ostracoda*, *Hemileptocerus*, other Ceratopogonidae, *Povilla*, Copepoda, *Brachythemis*, vegetation, *Barbus*, Hydracarina, *Clinotanypus*, Formicoidea, Chonchostraca, *Macromia*, *Tilapia* eggs, unidentified Pisces, Acriididae.

Numerical method. *Chaoborus*, Chironomidae including *Chironomus*, *Micronecta*, *Limnochironomus*, *Hemileptocerus*, *Stenocorixa*, *Ostracoda*, other Ceratopogonidae, *Povilla*, *Tilapia*, *Clinotanypus*, terrestrial food, *Caenis*, *Brachythemis*. (Had the copepoda been counted they would have been the most important.)

TABLE II

Percentage occurrence (P.O.) of the various food items in all the *Clarias* examined and the percentage composition of the food as assessed by different methods

		P.O.	O	N	P	N.F.
Annelida	<i>Batrachobdella</i>	—	—	—	—	+
	<i>Alma</i>	—	—	—	—	0·1
Mollusca	<i>Anisus</i>	—	—	—	—	+
	<i>Aspatharia</i>	—	—	—	—	0·1
	<i>Melania</i>	—	—	—	—	0·1
	<i>Bulinus forskalii</i>	2·2	0·7	0·2	0·5	+
	<i>Bulinus (P.) globosus</i>	1·1	0·4	+	+	+
Ostracoda		14·0	4·6	3·7	0·8	0·6
Conchostraca		3·3	1·1	0·4	0·1	+
Copepoda		9·5	3·1	—	4·1	—
Malacostraca	<i>Macrobrachion</i>	1·7	0·5	+	1·8	—
	<i>Hydracarina</i>	5·0	1·6	0·2	0·1	+
Ephemeroptera	<i>Povilla</i>	11·2	3·6	2·6	3·0	0·1
	<i>Caenis</i>	1·7	0·5	0·7	0·5	6·6
	<i>Cloeon</i>	2·8	0·9	0·3	0·1	0·3
Trichoptera	<i>Dipseudopsis</i>	1·7	0·5	+	0·2	+
	<i>Hemileptocerus</i>	13·4	4·4	6·0	7·7	4·2
	<i>Ecnomus</i>	1·7	0·5	0·2	0·1	2·0
Odonata	<i>Macromia</i>	3·3	1·1	0·3	2·3	+
	<i>Pantala</i>	—	—	—	0·2	—
	<i>Brachythemis</i>	8·4	2·7	0·7	2·0	1·1
	<i>Ictinogomphus</i>	2·2	0·7	+	0·5	0·4
	<i>Trapezostigma</i>	—	—	—	0·1	—
	<i>Ischnura</i>	2·2	0·7	0·3	0·2	+
	<i>Pseudagrion</i>	0·6	0·2	+	+	+
	Odonata?	1·7	0·5	+	0·4	0·2
	<i>Tholomys</i>	—	—	—	—	+
Hemiptera	<i>Stenocorixa</i>	31·3	12·2	4·2	8·4	+
	<i>Micronecta</i>	21·2	6·9	7·4	4·9	16·2
	<i>Anisops</i>	1·7	0·5	+	0·2	0·5
	<i>Laccocoris</i>	0·6	0·2	+	+	—
	<i>Sphaerodema</i>	1·1	0·4	+	0·1	—
	<i>Gerris</i>	—	—	—	—	+
Diptera	<i>Rhagovelia</i>	—	—	—	—	0·3
	<i>Clinotanypus</i>	5·0	1·6	1·7	0·6	4·0
	<i>Pentaneura</i>	1·7	0·5	0·3	0·1	+
	<i>Limnochironomus</i>	1·7	0·5	6·7	1·5	21·7
	<i>Cryptochironomus</i>	1·7	0·5	+	+	6·4
	<i>Procladius</i>	—	—	—	—	0·1
	<i>Tendipes</i>	0·6	0·2	+	+	1·1
	<i>Chironomus</i> and other Chironomidae	34·1	13·1	20·3	3·1	30·5
	<i>Sphaeromias</i>	1·1	0·4	+	+	0·1
	<i>Macroptilum</i>	—	—	—	—	0·1
	other Ceratopogonidae	11·7	3·8	3·2	0·6	—
	<i>Chaoborus</i>	17·3	5·9	30·2	4·0	0·5
	<i>Culicidae</i>	0·2	0·2	+	+	—

[continued]

TABLE II—*continued*

		P.O.	O	N	P	N.F.
Coleoptera	<i>Hydrovatus</i>	0·6	0·2	+	+	—
	<i>Sternolophus</i>	1·1	0·4	0·2	0·8	—
	<i>Cybister</i>	0·6	0·2	+	0·4	—
	<i>Helochares</i>	0·6	0·2	+	+	+
	<i>Hyphydrus</i>	0·6	0·2	+	+	+
	<i>Hydrocoptus</i>	0·6	0·2	+	+	+
Pisces	<i>Barbus</i>	6·1	2·0	0·5	6·2	0·3
	eggs <i>Barbus</i>	2·8	0·9	1·2	1·8	—
	<i>Tilapia</i>	27·4	9·9	1·9	25·0	—
	eggs <i>Tilapia</i>	3·3	1·1	4·4	2·2	0·5
	Cyprinodont	—	—	—	—	2·0
	<i>Clarias</i>	1·1	0·4	+	3·0	—
	<i>Hemichromis</i>	—	—	—	—	+
	Pisces ?	3·3	1·1	0·2	1·8	—
Amphibia		0·6	0·2	+	0·5	—
Terrestrial food	Araneae	1·1	0·4	+	0·1	—
	Acriidae	3·3	1·1	0·2	0·6	—
	Formicoidea	5·0	1·6	0·4	0·4	—
	Coleoptera	2·2	0·7	0·3	0·8	—
	Lepidoptera	0·6	0·2	+	0·7	—
	Hymenoptera	—	—	—	+	—
Vegetation		8·4	2·7	—	6·9	—
Empty stomachs		17·3	3·1	—	—	—
Debris		2·2	0·7	—	0·3	—

O = Occurrence method; *P* = points scheme; *N* = numerical method. The percentage composition of the fauna *N.F.* as determined by the numerical method is also given in the last column.

Points scheme. *Tilapia*, *Stenocorixa*, *Hemileptocerus*, vegetation, *Barbus* sp. *Micronecta*, Copepoda, *Chaoborus*, Chironomidae including *Chironomus*, *Povilla*, *Clarias*, *Macromia*, *Tilapia* eggs, *Brachythemis*, *Macrobranchion*, unidentified Pisces, *Barbus* eggs, *Limnochironomus*.

The above analysis provides an exception to the generalization made by Hynes (1950) that for any fish with a generalized diet, provided a large number of specimens is examined, any of the commonly accepted methods of assessing the composition of the diet will give substantially the same results. The contrasts between the three estimates can be attributed to the fact that the various food items differ greatly in volume. Of the above methods the points scheme probably gives the best approximation of the relative values of food organisms in terms of biomass or energy.

Relationship of the diet to fauna

Table II and Fig. 2 give the percentage composition as determined by the numerical method for the fauna and also for all the fish examined. Similar data on a monthly basis are given in Table III. From these it appears that certain organisms have a forage ratio

TABLE III

*The percentage composition of the fauna in Nungua Lake (F.),
the percentage composition of the food of *Clarias* (C) and the forage ratio (F.R.)*

	March			April			May			June		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Annelida												
<i>Alma</i>	0·21	—	—	—	—	—	—	—	—	—	—	—
<i>Batrachobdella</i>	—	—	—	—	—	—	0·31	—	—	0·11	—	—
Mollusca												
<i>Aspatharia</i>	0·63	—	—	0·05	—	—	—	—	—	0·11	—	—
<i>Bulinus</i>	—	—	—	—	1·02	—	—	0·28	—	0·11	9·09	82·64
<i>Anisus</i>	—	—	—	—	—	—	0·15	—	—	—	—	—
<i>Melania</i>	0·63	—	—	0·30	—	—	—	—	—	—	—	—
Ostracoda	0·63	—	—	1·76	7·11	4·04	—	4·46	—	0·22	—	—
Conchostraca	0·21	—	—	—	—	—	—	—	—	0·33	—	—
Malacostraca												
<i>Macrobrachion</i>	—	—	—	—	—	—	—	—	—	—	—	—
Hydracarina	—	—	—	—	—	—	—	0·56	—	—	—	—
Ephemeroptera												
<i>Povilla</i>	—	0·30	—	—	2·03	—	—	—	—	—	—	—
<i>Caenis</i>	6·11	—	—	0·65	—	—	0·31	—	—	11·89	9·09	0·76
<i>Cloeon</i>	0·63	—	—	—	—	—	—	—	—	—	—	—
Trichoptera												
<i>Dipseudopsis</i>	—	0·30	—	—	—	—	—	—	—	—	—	—
<i>Hemileptocerus</i>	1·05	—	—	0·40	—	—	—	—	—	—	—	—
<i>Ecnomus</i>	2·32	—	—	0·45	—	—	—	—	—	—	—	—
Odonata												
<i>Macromia</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pantala</i>	—	0·30	—	—	—	—	—	—	—	—	—	—
Odonata?	—	0·30	—	0·05	—	—	1·68	0·28	0·17	—	—	—
<i>Brachythemis</i>	—	0·30	—	0·05	1·52	30·4	1·68	2·23	1·33	3·19	18·18	5·7
<i>Ischnura</i>	—	—	—	—	—	—	—	0·28	—	0·11	—	—
<i>Ictinogomphus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Trapezostigma</i>	—	—	—	—	—	—	—	—	—	0·11	—	—
<i>Pseudagrion</i>	—	—	—	—	—	—	—	—	—	0·33	—	—
<i>Tholomys</i>	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera												
<i>Laccocoris</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Stenocorixa</i>	—	0·30	—	—	5·08	—	0·31	0·56	—	—	—	—
<i>Micronecta</i>	10·32	0·61	0·06	48·64	11·68	0·24	—	50·42	—	1·10	—	—
<i>Anisops</i>	—	—	—	—	—	—	—	0·28	—	0·44	—	—
<i>Plea</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Gerris</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhagovelia</i>	—	—	—	—	—	—	—	—	—	—	—	—
Diptera												
<i>Chaoborus</i>	—	82·62	—	—	21·83	—	—	1·39	—	78·63	36·36	0·46
<i>Chironomus</i>	64·21	4·27	0·07	15·48	27·41	1·77	29·72	—	—	0·11	—	—
<i>Sphaeromias</i>	—	—	—	—	—	—	—	3·62	—	—	9·09	—
<i>Clinotanypus</i>	7·37	1·83	0·25	2·56	7·61	2·97	—	1·11	—	—	—	—
<i>Pentaneura</i>	0·21	0·91	4·33	0·10	1·02	10·2	—	0·56	—	—	—	—
<i>Ceratopogonidae</i>	—	2·44	—	—	8·12	—	—	—	—	[continued]		

TABLE III—continued

	March			April			May			June		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Diptera (contd.)												
Chironomidae?	—	—	—	—	—	—	—	—	—	—	—	—
<i>Limnochironomus</i>	3.58	—	—	23.62	—	—	57.19	—	—	2.20	—	—
<i>Cryptochironomus</i>	1.68	—	—	1.21	—	—	—	—	—	—	—	—
<i>Macroptilum</i>	1.21	—	—	0.15	—	—	—	—	—	—	—	—
<i>Tendipes</i>	—	—	—	3.77	—	—	—	—	—	—	—	—
<i>Procladius</i>	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera												
<i>Hyphydrus</i>	—	—	—	—	—	—	15	—	—	—	—	—
<i>Cybister</i>	—	—	—	—	—	—	—	—	—	—	9.09	—
Coleoptera?	—	—	—	—	—	—	—	—	—	—	—	—
<i>Synchorthus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrocoptus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrovatus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helochares</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sternolophus</i>	—	—	—	—	—	—	—	—	—	—	—	—
Gyrinidae	—	—	—	—	—	—	—	—	—	—	—	—
Pisces												
<i>Barbus</i>	—	0.61	—	—	—	—	—	—	—	0.66	—	—
<i>Tilapia</i>	—	4.88	—	0.75	5.58	7.44	—	25.63	—	0.11	9.09	82.64
Pisces?	—	—	—	—	—	—	—	0.28	—	—	—	—
<i>Clarias</i>	—	—	—	—	—	—	—	—	—	—	—	—
Cyprinodont	—	—	—	—	—	—	7.95	—	—	—	—	—
<i>Hemicromis</i>	—	—	—	—	—	—	—	—	—	—	—	—
Amphibia	—	—	—	—	—	—	—	—	—	—	—	—
Terrestrial food	—	—	—	—	—	—	—	3.0	—	—	—	—
	July			August			September			October		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Annelida												
<i>Alma</i>	—	—	—	0.38	—	—	0.93	—	—	—	—	—
<i>Batrachobdella</i>	—	—	—	—	—	—	—	—	—	—	—	—
Mollusca												
<i>Aspatharia</i>	—	—	—	—	—	—	—	—	—	0.23	—	—
<i>Bulinus</i>	0.72	63.83	86.65	—	2.53	—	—	—	—	—	—	—
<i>Anisus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Melania</i>	—	—	—	—	—	—	0.23	—	—	—	—	—
Ostracoda	—	—	—	—	11.39	—	—	18.46	—	—	2.02	—
Conchostraca	—	—	—	—	—	—	—	—	—	—	—	—
Malacostraca												
<i>Machrobrachion</i>	—	—	—	—	—	—	—	—	—	—	8.59	—
Hydracarnia	—	2.13	—	—	—	—	0.23	—	—	—	—	—
Ephemeroptera												
<i>Povilla</i>	—	—	—	1.14	—	—	1.17	28.46	24.32	—	3.03	—
<i>Caenis</i>	17.99	—	—	13.31	—	—	31.07	0.77	0.05	1.64	—	—
<i>Cloeon</i>	3.6	—	—	—	1.27	—	—	—	—	—	—	—
Trichoptera												
<i>Dipseudopsis</i>	—	—	—	—	—	—	—	—	—	0.70	0.51	0.74
<i>Hemileptocerus</i>	12.23	—	—	13.69	11.39	0.83	3.27	18.46	5.65	5.63	1.01	0.18
<i>Ecnomus</i>	0.72	—	—	1.52	—	—	8.41	—	—	3.05	—	—

[continued]

TABLE III—continued

	July			August			September			October		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Odonata												
<i>Macromia</i>	—	2·13	—	0·38	—	—	—	0·77	—	—	—	—
<i>Pantala</i>	—	—	—	—	—	—	—	—	—	—	—	—
Odonata?	—	2·13	—	—	—	—	0·23	—	—	—	—	—
<i>Brachythemis</i>	0·72	4·26	5·92	2·28	1·27	0·56	0·70	1·54	2·20	1·17	—	—
<i>Ischnura</i>	—	—	—	0·38	10·13	26·66	—	—	—	—	—	—
<i>Ictinogomphus</i>	—	—	—	1·52	2·53	1·66	2·80	0·77	0·28	0·47	—	—
<i>Trapezostigma</i>	—	—	—	—	1·27	—	—	—	—	—	—	—
<i>Pseudagrion</i>	—	—	—	0·38	—	—	0·70	0·77	1·1	—	—	—
<i>Tholomys</i>	—	—	—	—	—	—	—	—	—	—	—	—
Hemiptera												
<i>Laccocoris</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Stenocorixa</i>	—	4·26	—	—	1·27	—	—	—	—	—	3·54	—
<i>Micronecta</i>	2·16	2·12	0·99	0·76	—	—	1·17	2·31	1·97	0·70	—	—
<i>Anisops</i>	2·16	—	—	2·66	—	—	0·48	0·77	1·60	1·88	—	—
<i>Plea</i>	—	—	—	—	—	—	0·48	—	—	—	—	—
<i>Gerris</i>	—	—	—	—	—	—	5·14	—	—	—	—	—
<i>Rhagovelia</i>	—	—	—	—	—	—	—	—	—	—	—	—
Diptera												
<i>Chaoborus</i>	—	—	—	—	26·58	—	—	—	—	—	—	—
<i>Chironomus</i>	39·57	2·13	0·05	24·33	2·53	0·10	14·95	6·15	0·41	23·24	—	—
<i>Sphaeromias</i>	0·72	—	—	—	—	—	0·70	—	—	1·17	—	—
<i>Clinotanypus</i>	0·72	—	—	4·94	—	—	15·89	10·00	0·63	12·21	—	—
<i>Pentaneura</i>	—	—	—	0·38	—	—	—	—	—	—	7·07	—
Ceratopogonidae	—	2·13	—	—	—	—	—	1·54	—	—	—	—
Chironomidae?	—	—	—	—	—	—	—	—	—	38·50	60·61	1·57
<i>Limnochironomus</i>	8·63	2·13	0·25	1·52	—	—	3·27	—	—	5·87	—	—
<i>Cryptochironomus</i>	0·72	—	—	5·70	—	—	4·90	—	—	—	—	—
<i>Macrotilum</i>	3·60	—	—	—	—	—	—	—	—	—	—	—
<i>Tendipes</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Procladius</i>	—	—	—	3·04	—	—	—	—	—	—	—	—
Coleoptera												
<i>Hyphydrus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cybister</i>	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera?	—	—	—	—	1·27	—	—	—	—	—	—	—
<i>Synchorthus</i>	—	—	—	0·38	—	—	—	—	—	—	—	—
<i>Hydrocoptus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrovatus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Helochares</i>	0·72	—	—	—	—	—	—	—	—	—	—	—
<i>Sternolophus</i>	—	—	—	—	—	—	—	—	—	—	—	—
Gyrinidae	—	—	—	—	—	—	—	—	—	—	—	—
Pisces												
<i>Barbus</i>	5·04	—	—	1·52	1·27	0·84	1·17	—	—	1·41	2·02	1·43
<i>Tilapia</i>	—	2·13	—	—	13·92	—	0·70	6·15	8·80	—	—	—
Pisces?	—	6·38	—	—	—	—	—	—	—	—	—	—
<i>Clarias</i>	—	—	—	—	1·27	—	—	—	—	1·88	—	—
Cyprinodont	—	—	—	19·77	—	—	1·40	—	—	0·23	—	—
<i>Hemicromis</i>	—	—	—	—	—	—	—	—	—	—	—	—
Amphibia	—	—	—	—	1·27	—	—	—	—	—	11·62	—
Terrestrial food	—	4·26	—	—	8·84	—	—	3·08	—	[continued]		

TABLE III—continued

	November			December			January			February		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Annelida												
<i>Alma</i>	—	—	—	0·30	—	—	—	—	—	—	—	—
<i>Batrachobdella</i>	—	—	—	—	—	—	—	—	—	0·26	—	—
Mollusca												
<i>Aspatheria</i>	0·21	—	—	0·30	—	—	—	—	—	—	—	—
<i>Bulinus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Anisus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Melania</i>	—	—	—	—	—	—	—	—	—	—	—	—
Ostracoda												
Conchostraca												
Malacostraca												
<i>Machrobrachion</i>	—	0·08	—	—	—	—	—	—	—	—	—	—
Hydracaria												
Ephemeroptera												
<i>Povilla</i>	—	3·01	—	0·15	—	—	—	—	—	—	—	—
<i>Caenis</i>	3·65	8·47	2·32	12·29	—	—	2·12	0·66	0·31	0·53	—	—
<i>Cloeon</i>	—	—	—	0·15	—	—	0·71	—	—	1·60	2·83	1·77
Trichoptera												
<i>Dipseudopsis</i>	—	0·08	—	—	—	—	—	—	—	—	—	—
<i>Hemileptocerus</i>	4·51	1·74	0·39	4·20	17·86	4·25	16·27	11·84	0·73	19·95	5·03	0·25
<i>Ecnomus</i>	12·02	0·47	0·04	0·30	—	—	—	—	—	2·66	0·63	0·24
Odonata												
<i>Macromia</i>	—	0·55	—	—	—	—	—	—	—	—	—	—
<i>Pantala</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Odonata?</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Brachythemis</i>	0·43	0·08	0·19	0·60	—	—	0·94	0·11	0·12	—	1·26	—
<i>Ischnura</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ictinogomphus</i>	—	—	—	0·75	—	—	0·24	—	—	—	—	—
<i>Trapezostigma</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Pseudagrion</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Tholomys</i>	—	—	—	0·15	—	—	—	—	—	—	—	—
Hemiptera												
<i>Laccocoris</i>	—	0·08	—	—	—	—	—	—	—	—	—	—
<i>Stenocorixa</i>	—	1·34	—	—	10·71	—	—	3·83	—	—	20·44	—
<i>Micronecta</i>	—	3·48	—	3·60	9·82	2·73	7·55	0·22	0·03	8·78	15·72	1·79
<i>Anisops</i>	2·56	0·08	0·03	1·50	0·89	0·59	0·47	—	—	—	0·31	—
<i>Plea</i>	—	—	—	—	—	—	0·24	—	—	—	—	—
<i>Gerris</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Rhagovelia</i>	—	—	—	—	—	—	—	—	—	—	—	—
Diptera												
<i>Chaoborus</i>	—	51·74	—	—	2·68	—	8·25	0·44	0·05	—	33·65	—
<i>Chironomus</i>	26·61	6·57	0·25	5·25	14·29	2·72	25·71	75·11	2·92	33·24	3·14	0·09
<i>Sphaeromias</i>	—	0·08	—	0·15	—	—	0·24	—	—	—	—	—
<i>Clinotanypus</i>	6·44	—	—	1·80	2·68	1·89	3·77	0·66	0·18	0·53	—	—
<i>Pentaneura</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Ceratopogonidae</i>	—	0·63	—	—	6·25	—	—	5·81	—	—	0·63	—
<i>Chironomidae?</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Limnochironomus</i>	24·25	9·34	0·39	59·52	—	—	1·18	—	—	2·39	—	—

[continued]

TABLE III—continued

	November			December			January			February		
	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.	F.	C	F.R.
Diptera (contd.)												
<i>Cryptochironomus</i>	17.60	0.08	.004	8.40	11.61	1.38	25.00	—	—	29.79	—	—
<i>Macroptilum</i>	—	—	—	0.15	—	—	—	—	—	—	—	—
<i>Tendipes</i>	—	0.08	—	—	—	—	—	—	—	—	—	—
<i>Procladius</i>	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera												
<i>Hyphydrus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Cybister</i>	—	—	—	—	—	—	—	—	—	—	—	—
Coleoptera?	—	0.08	—	—	—	—	0.24	—	—	—	—	—
<i>Synchoritus</i>	—	—	—	—	—	—	0.24	—	—	—	—	—
<i>Hydrocoptus</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hydrovatus</i>	—	—	—	—	0.89	—	—	—	—	—	—	—
<i>Helochares</i>	—	—	—	—	—	—	—	—	—	—	—	—
<i>Sternolophus</i>	—	0.32	—	—	—	—	—	—	—	—	—	—
Gyrinidae	—	—	—	0.15	—	—	—	—	—	—	—	—
Pisces												
<i>Barbus</i>	—	3.48	—	—	8.93	—	—	0.11	—	—	0.63	—
<i>Tilapia</i>	1.72	5.30	3.06	—	—	—	0.47	0.22	0.47	0.26	5.97	22.96
Pisces?	—	—	—	—	—	—	—	—	—	—	—	—
<i>Clarias</i>	—	0.08	—	—	—	—	—	—	—	—	—	—
Cyprinodont	—	—	—	0.15	—	—	5.42	—	—	—	—	—
<i>Hemichromis</i>	—	—	—	0.15	—	—	—	—	—	—	—	—
Amphibia	—	—	—	—	—	—	—	—	—	—	—	—
Terrestrial food	—	—	—	—	1.79	—	—	—	—	—	—	—

of more than one suggesting that they are being selected by the catfish or are more readily available than other food items. These include *Bulinus forskali*, Ostracoda, Conchostraca, *Povilla*, *Cloeon*, *Hemileptocerus*, *Macromia*, *Ischnura*, *Stenocorixa*, Ceratopogonidae, *Chaoborus*, *Barbus*, and *Tilapia*. Certain of these items have very high forage ratio values in the monthly data. It is probable, however, that the forage ratios of the fishes, active swimming forms such as *Stenocorixa*, the Ceratopogonidae and *Chaoborus* are exaggerated because they were not adequately sampled in the fauna. Thus many of the actively swimming forms particularly the large fish avoid the sampler whereas the other two taxa were not adequately sampled because they are more abundant in the deeper water outside the range of the sampler. In general, the catfish appear to be selecting midwater forms including *Stenocorixa* and the fishes other than the cyprinodonts, small organisms that occasionally swim near the surface of the substratum including the Ostracoda and Conchostraca, accessible species that lie on the surface of the sediments including *Bulinus forskali*, *Hemileptocerus* and *Macromia*. It is probable that *Povilla* and *Chaoborus* were preyed upon when they were swimming in midwater. The larvae of *Povilla* are normally tubicolous but swim about actively in the dark (Hartland-Rowe, 1958). The absence of silken cases from stomachs containing the larvae seems to indicate that they were taken by the fish in midwater during the night. The *Chaoborus* species at Nungua appears to be planktonic when in the first instars and mud dwelling by day and planktonic at night in the later instars.

It is interesting that *Chaoborus* occur very infrequently in the stomachs of the night-feeding benthophage *Mormyrus kannume* because the larvae undergo a vertical migration from the mud at night (Macdonald, 1956).

Certain faunal constituents including *Alma*, *Batrachobdella*, *Anisus*, *Aspatharia*, *Tholomys*, *Gerris*, *Rhagovelia* were not found in the stomachs; others including *Caenis*, *Ecnomus*, *Brachythemis*, *Ictinogomphus*, *Micronecta*, *Anisops*, *Clinotanypus*, *Limnochironomus*, *Tendipes*, *Chironomus*, other Chironomidae and *Micropanchax* have very low forage ratios. Their low accessibility can be attributed to the following factors: *Alma*, *Anisus*, *Aspatharia*, *Clinotanypus*, *Limnochironomus*, *Cryptochironomus*, *Tendipes*, *Chironomus* and other Chironomidae live buried in the mud.

Ecnomus live under algal coated stones on the wave-washed shores. Verbeke in Jacquemart (1957) found that *Ecnomus* occupied a similar microhabitat in East African lakes.

Caenis a mud or silt-dwelling ephemeropteran is cryptically coloured and lies half buried in the sediment. Aggregations of this mayfly also occur under stones or wood debris. Other workers including Frost & Smyly (1952) and Thomas (1962) have also commented on the low order of accessibility of this mayfly to the trout.

Gerris and *Rhagovelia* are agile and contagiously distributed on the surface of shallow marginal waters frequently protected by vegetation.

Culicidae larvae and *Micropanchax* live at or near the surface in shallow marginal waters and seem to have a preference for areas containing emergent vegetation. Such habitats are not normally frequented by the catfish, Jackson (1961) has found that Cyprinodonts also escape the attention of the tiger fish *Hydrocyon vittatus* in East Africa for the same reason.

Micronecta is also mainly concentrated in shallow marginal water and appears to have a particular preference for the breeding troughs of *Tilapia zilli*. The main population thus appears to be out of reach of the catfish.

It is difficult to account for the low forage ratio of the *Anisops* because *Stenocorixa* and other midwater forms have a high forage ratio. It is possible, however, that they are better protected than *Stenocorixa* because they tend to live in close proximity to vegetation rather than in the open water.

The dragonfly larvae *Brachythemis* and *Ictinogomphus* are often partly submerged in soft sediments although they do not actively burrow.

It is clear that the forage ratio of each food item is being influenced, not only by its abundance in the fauna, but also by its accessibility. This in turn is greatly affected by the habitat the food item comes from. It is instructive therefore to analyse the food on a habitat basis and this is done below.

Organisms living under stones or in the sediment. Include *Dipseudopsis*, *Ecnomus*, *Clinotanypus*, *Pentaneura*, *Limnochironomus*, *Cryptochironomus*, *Procladius*, *Tendipes*, *Chironomus*, other Chironomidae, *Sphaeromias*, *Macroptilum*, and other Ceratopogonidae fish eggs. Together these make up 8.2% of the food composition. In water of more than 1.5 m in depth the dominant organisms in the sediment are the Ceratopogonidae. The dearth of these larvae in the stomachs of the catfish indicate that they are feeding mainly in the shallow water near the shore.

Organisms living on the surface of the sediments. Include *Bulinus forskali*, *Macrobrachion*, *Caenis*, *Hemileptocerus*, *Macromia*, *Brachythemis*, *Ictinogomphus* and unidentified anisopteran dragonflies. These make up 15.7% of the food composition.

Organisms living in vegetation. Include *B. (P.) globosus*, *Cloeon*, *Pantala*, *Trapezostigma*, *Ischnura*, *Pseudagrion*, *Laccocoris*, *Sphaerodema*, *Sternolophus*, *Cybister*, *Helochares*, *Hyphydrus*, *Hydrocoptus*, other Coleoptera, and Culicidae. These make up only 1·9% of the food composition.

Organisms swimming near the surface of the sediment. These include amphibian tadpoles, *Micronecta*, Ostracoda and Conchostraca. In all these make up 6·3% of the food composition.

Organisms swimming in midwater. These include the zooplankton *Stenocorixa*, *Anisops*, fishes, *Povilla* larvae at night, *Chaoborus*, Chironomidae pupae. These make up 58·2% of the food composition. It is thus clear that *Clarias senegalensis* obtains the bulk of its food from midwater.

Aquatic organisms living on the surface of water and also of terrestrial origin. These include *Gerris*, *Rhagovelia*, Araneae, Acriiididae, etc. Together they make up only 2·6% of the food composition.

Vegetation. This makes up 6·9% of the food composition.

Organic debris from the sediment. This constitutes only 0·3% of the food composition.

Ontogenetic changes

Figure 11 shows the percentage composition of the food of fish of four size groups as determined by the points scheme and the numerical method. Only fish of more than 15 cm in length are considered and these were all obtained from the lake itself. The main feature of Fig. 11 is that it shows that the dietaries of catfish of different ages are very similar. The differences that do exist are mainly of a qualitative rather than a quantitative nature. Although fish of all sizes eat small organisms including ostracoda and copepoda and large organisms, including *Tilapia*, it seems probable that from the energy viewpoint, the latter is the most important single food item for the fish in all the size groups. It is surprising to note that the Copepoda appear to be slightly more important to the larger fish. This is not the case, however, with the smaller midwater forms including *Stenocorixa*, *Chaoborus* and the bottom living *Hemileptocerus* as these are more prominent in the food of young fish. Terrestrial organisms vegetation and phytophilous species including *Ischnura*, *Trapezostigma* and Culicidae larvae are however, more important to the larger fish.

Seasonal changes (Table III)

There is very little evidence of a well-defined seasonal change in the food. Certain phytophilous organisms including *Bulinus*, *Cloeon*, *Macromia* and *Ischnura* are only eaten during the wet season but as they never become important constituents the dietary picture as a whole changes little during the course of the year.

Discussion

Reproduction and movement

It has been shown that *Clarias senegalensis* in Nungua lake spawn once a year in the flood plains of the feeder stream after the onset of the major rains in April or May. The

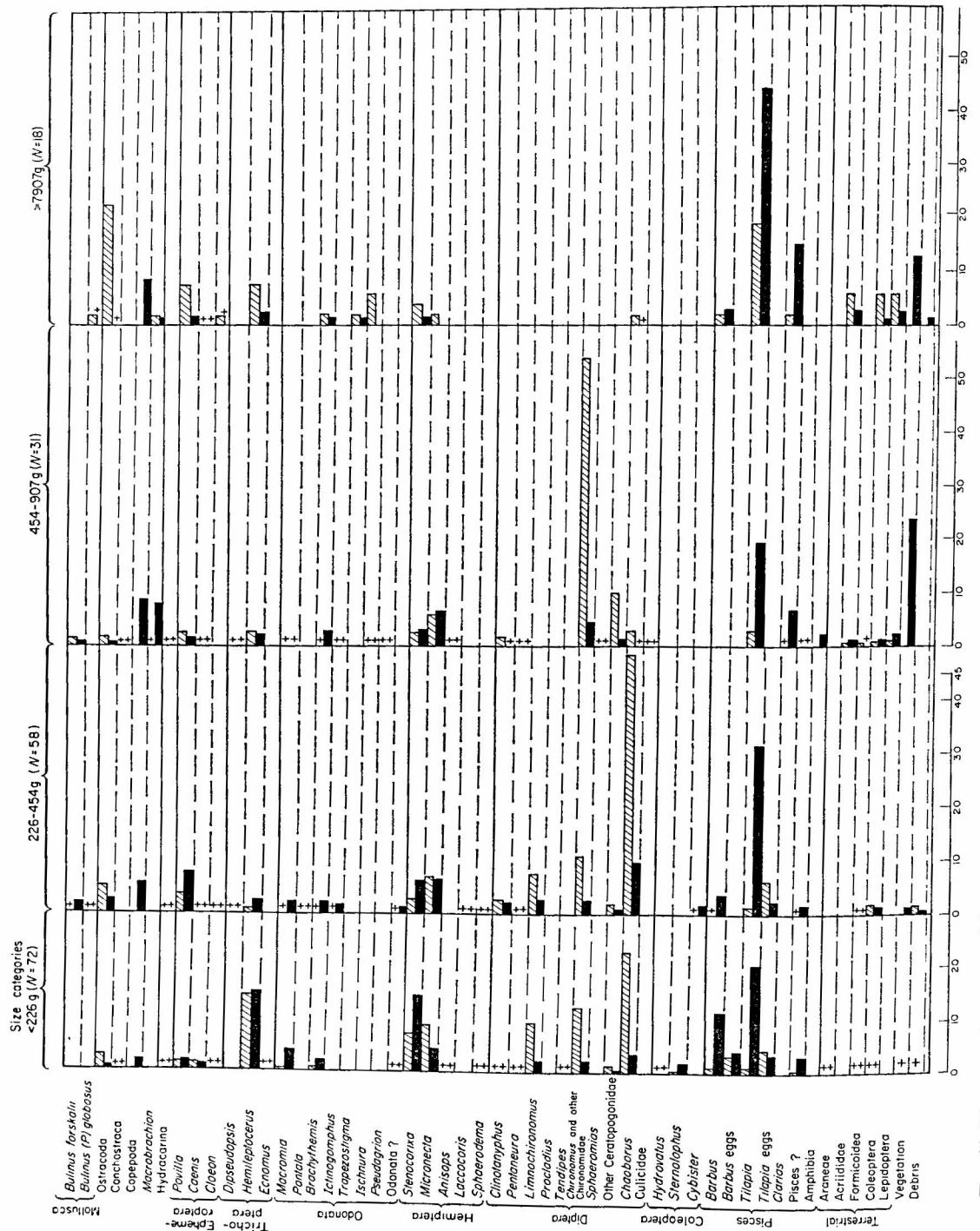


FIG. 11. The percentage composition of the food of *Clarias senegalensis* of different sizes. The black bars show the percentage composition as determined by the numerical method; the white bars the percentage composition as determined by the numerical method.

spent fish return to the lake within a few days after spawning but juveniles of 30 cm or less which also undertake an upstream migration do not do so until September by which time the water level has fallen considerably and the stream itself has become a series of isolated or semisolated pools. The present observations on *C. senegalensis* agree closely with Greenwood (1955) and Corbet (1961) for *Clarias mossambicus*. According to Corbet (1961), young *C. mossambicus* return to the lake when about 15 to 25 mm, but the young catfish apparently have the habit of returning to the stream every time it floods, until they are between 15 and 20 cm long.

Anadromesis is common among African freshwater fish. Thus Jackson (1962) states "Even in our present limited state of knowledge a list of such known spawning migrations is impressive". The selective advantages of anadromesis have been discussed by Jackson (1961), Fryer (1965) and Greenwood (1965). These include the provision of a mechanism for dispersion and for colonization of new water bodies, a favourable physico-chemical and biological environment for the development of the egg and the provision of food and cover from predators for the newly hatched larvae. The inundation of the flood zones of water bodies in the arid regions of tropical Africa is an annual or biannual event which provides fishes with additional space and food supply. An increase in the latter is partly attributable to an increase in allochthonous organic matter and in subaquatic and aquatic vegetation. The species diversity increases at this time and many fugitive species occur only during the wet season. It seems probable that the original stimulus for anadromesis was provided by the increase in food supply and space and that as a result of the additional selective advantages listed above it has become an obligatory feature in the life of many freshwater fishes in the arid or semiarid areas of Africa. In this connection it is noteworthy that not all migrations are concerned with reproduction as juvenile catfish also participate.

Food

Quantity of food in stomachs

Three hypotheses can be advanced to account for the fact that the stomachs contain relatively less food during March or April than during other months of the year. The first possibility that this is caused directly by temperature has already been rejected. Second, the influence of spawning may prevent the fish from feeding normally. Corbet (1961) reports that only 20% of breeding *Clarias mossambicus* examined by him from a stream contained food. In the present investigation the dearth of food cannot be attributed to the effect of spawning as mature fish of more than 30 cm in length contained on the average a greater quantity of food in the stomachs than juveniles of less than 30 cm in length. Third, it may be due to a dearth of food either in the lake or in the stream. Some support is given to this hypothesis by the fact that the weight of standing crop is low during these months. On the other hand, the population density of the fauna increases to a maximum in April at both stations.

The increase in the amount of food in the stomachs during the period August to February appears to be correlated with an increase in weight of standing crop during these months. The population density of the fauna expressed in numbers/m² is, however, low during these months. It seems probable that the increase in condition factor in September to October can be attributed to a relatively greater increase in weight than in length at this

time as a result of an increase in food intake from August onwards. An increase in condition factor following an increase in food intake has also been noted in salmonids (Allen, 1951; Ball & Jones, 1960; Thomas, 1964).

Qualitative aspects of food

Analysis based on habitat of food organisms.

It has been shown that *Clarias senegalensis* subsists mainly on organisms swimming in midwater, swimming close to the surface of the sediment or living on the surface of the sediment. Animals from these habitats have a higher forage ratio than those living under stones, in the sediment or in very shallow water or in vegetation close to the shore.

A certain amount of information is available on the food of other species of Clariidae. Thus *Clarias mossambicus* Peters has been studied by Graham (1929), Worthington (1929, 1932); Corbet (1961) and Fryer (1959), *Clarias gariepinus* (Burchell) by Groenewald (1964) *Clarias carsoni* Boulenger, *Clarias alluaudi* (group) Boulenger and *Clariallabes petricola* Greenwood by Corbet (1961). With the exception of the first three species the amount of information is limited either because very few fish were examined or else because the food was not subjected to a detailed analysis on a generic or specific basis. Despite these shortcomings an attempt is made below to compare the food of *Clarias senegalensis*, classified on a taxonomic and habitat basis with that of other species.

(a) *Organisms living under stones or buried in the sediment.* This category appears to be relatively unimportant to *C. senegalensis*, *C. mossambicus* and *C. gariepinus*. Thus few *C. mossambicus* in Lake Victoria had fed on Chironomidae larvae, burrowing Ephemeroptera, Pelecypoda (Corbet, 1961) and aquatic insects in general appear to be unimportant to *C. gariepinus* (Groenewald, 1964). Chironomidae larvae appear to be eaten more frequently by small *C. mossambicus* of 0 to 15 cm living in a stream (Corbett, 1961).

(b) *Organisms living on the surface of the sediment.* Such organisms are more important to *C. senegalensis* and *C. mossambicus* than those in category (a). In the case of *C. mossambicus* these include gastropod molluscs, anisopteran larvae such as *Ictinogomphus*, *Phyllogomphus* and the Crustacea *Cardinia* and *Potamon*.

(c) *Organisms living in vegetation.* With the onset of the wet season a considerable area of subaquatic and aquatic vegetation develops along the margin of the lake. Yet the phytophilous species that live in this are hardly exploited at all by the smaller fish and only to a slight extent by the older fish. It is for this reason mainly that there is very little seasonal change of a qualitative nature in the dietary. It also appears that phytophilous species are of little consequence to *C. mossambicus* in Lake Victoria and to *C. gariepinus*. Small *C. mossambicus* of 0 to 15 cm from a stream flowing through grassland and marginal *Echinochloa*-papyrus swamp on the other hand had consumed more phytophilous species including *Acanthagyna*, *Pantala*, *Orthetrum* and *Biomphalaria* species (Corbet, 1961). A small number of *C. alluaudi*, obtained from a floating marginal swamp of semiaquatic grass and papyrus, had also fed on phytophilous Coleoptera.

As *Clarias* species in general prefer to exploit swimming or bottom living forms, it is doubtful whether they can be very effective in the biological control of vectors of parasites of man and domestic animals many of which are phytophilous. These include *Bulinus* (*P.*) *globosus*, *Limnaea natalensis*, *Biomphalaria* and mosquito larvae. With the exception of *Biomphalaria*, all these organisms occur in patches in the lake; yet a Culicine mosquito

has been recorded only once and *B. (P) globosus* twice in the stomachs of the *Clarias*. On the other hand, *Bulinus forskali*, which can be found on the surface of the sediments, has a high forage ratio. Corbet (1961), who examined more than 615 *C. mossambicus*, found that none had eaten mosquito larvae and that *Biomphalaria* and *Bulinus* species were only rarely eaten. Out of 22 *C. alluaudi* examined by the same author, only one had eaten a vector of economic importance namely a mosquito larva. It is very probable that other fish including Cyprinodonts, *Hemichromis* and *Haplochromis* have feeding niches which make them more appropriate as agents for the biological control of economically important vectors (Hickling, 1961).

(d) *Organisms swimming near the surface of the sediment.* These form 6.3% of the food composition of *C. senegalensis*. Corixidae and Ostracoda also occur fairly frequently in the stomach contents of *C. mossambicus*.

(e) *Organisms swimming in midwater.* This is the dominant food category for *C. senegalensis*, *C. mossambicus* and *C. gariepinus*. Of the organisms in this category the most important are the fishes. Thus they are the main contents in from 71 to 95% of *C. mossambicus* in Lake Victoria (Corbet, 1961) and in Barberspan they constitute 80% of the total bulk of the food of *C. gariepinus* (Groenewald, 1964). Fish are eaten even by small catfish. Corbet (1961) showed that *C. mossambicus* becomes piscivorous when more than 3 cm in length and that fish were the dominant food items in 48% of small catfish less than 15 cm in length.

The dominant forage fishes for *C. senegalensis* at Nungua and for *C. mossambicus* in Lake Victoria are the cichlids (Graham, 1929; Corbet, 1961); mainly *Tilapia* in the former and *Haplochromis* in the latter. It is clear, therefore, that serious consideration should be given to the possibility of combining *Clarias* and *Tilapia* in fish ponds. The feeding niches of the two fish overlap very little and the presence of a predator, could prevent stunting, and thus result in the more efficient utilization of the *Tilapia heudeloti* and *Tilapia zilli* (var. *guiniensis*) which occur in the lake.

Cyprinodonts have not been recorded in the stomachs of any of the *Clarias* species. As already suggested this apparent immunity may be attributed to their relatively low accessibility as they live in shallow water close to the shore. During the wet season this is characterized by the presence of aquatic or subaquatic vegetation which provides cover from predators.

It has been shown that *C. senegalensis*, *C. mossambicus* and *C. gariepinus* can all be cannibalistic (Corbet, 1961; Groenewald, 1964). The latter author found that young catfish contributed by far the greater part of the fish eaten by *C. gariepinus* in Barberspan. The selective advantage of large fish returning to the lake after spawning and the apparent spatial segregation of fish belonging to different size groups can, therefore be appreciated. Catfish generally swallow their prey, including fish, whole but occasionally they also bite pieces of flesh out of other catfish. This behaviour can be readily observed in the laboratory and it is probable, therefore, that under field conditions individual catfish maintain a feeding territory.

Other smaller organisms swimming in midwater including chaoborid larvae or zooplankton such as Cladocera and Copepoda are also eaten by catfish including *C. senegalensis*, *C. mossambicus*, *C. alluaudi*, *C. gariepinus* and *Clariallabes petricola* (Graham, 1929; Greenwood, 1957; Corbet, 1961; Groenewald, 1964). The latter author stated that most of the individuals of *C. gariepinus* from the Juksei river had gorged themselves at

such a rate with zooplankton that not only was the whole alimentary canal filled to capacity but *Daphnia* removed from the rectum were not all digested. According to Corbet (1961), it is unusual for *C. mossambicus* to eat zooplankton.

(f) *Aquatic organisms living at the surface and also those of a terrestrial origin.* Surface living aquatic Hemiptera have not been recorded in the dietaries of any *Clarias* species. Winged mayflies, pupae and adults of Chironomidae have, on the other hand, been recorded in *C. senegalensis* in the present investigation and also in *C. mossambicus* (Corbet, 1961). Food of terrestrial origin, although eaten by larger fish to a slightly greater extent, is relatively unimportant in the dietaries of *C. senegalensis* and *C. mossambicus*. Not unexpectedly terrestrial food occurs more frequently in the stomachs of *Clarias* species living in streams (Fryer, 1959; Groenewald, 1964). Thus Groenewald (1964) found that 52% of the *C. gariepinus* from the Vaal river had fed on terrestrial invertebrates which were being selected at the expense of forage fish. It was later found that *Clarias senegalensis* fed on unusual adventitious food items including regurgitations from bird stomachs and nestling birds from a communal nesting site containing 250 nests of Cattle egrets, Long-tailed shags and darters situated in the lake. Corbet (1961) also found that *C. mossambicus* has the habit of congregating around the nesting sites of birds in Lake Victoria. According to Pitman (1957), large *Clarias* take a variety of small birds from the surface.

(g) *Vegetation.* Vegetation makes up 6% by volume of the food of *C. senegalensis*. It also occurs frequently in the stomachs of *C. mossambicus* from Lake Victoria and Lake Nyasa (Corbet, 1961; Fryer, 1959) and in *C. gariepinus* in South Africa (Groenewald, 1964). Fryer (1959) found that *C. mossambicus* had fed on seeds and according to Irvine (1947), Dr Suard in Senegal observed *Clarias* emerging from the water at night to feed on grains of millet. Both Corbet (1961) and Groenewald (1964) believe that the plant material is eaten accidentally while the fish is pursuing its prey. In some cases, however, such a large amount of vegetation occurs in the stomachs so as to make it appear that deliberate ingestion has taken place. Many other carnivores, including fishes, reptiles, amphibia and mammals, even though they possess alimentary canals of typical carnivores, are also known to ingest vegetation intentionally.

(h) *Organic debris or detritus.* As pointed out by Newell (1965) it is necessary to define the word detritus as it may be used to indicate organic debris without or with the attendant micro-organisms. In the present context the word detritus is used in the latter sense. Detritus is ingested by *C. senegalensis*, *C. gariepinus* and *C. mossambicus* (Corbet, 1961; Groenewald, 1964). The latter author, however, used the word "detritus" to include "coarse and finely divided plant material (both fresh and decomposed), droppings of water birds in addition to organic debris". It is assumed that the "clay" and "slush" ingested by *C. mossambicus* included some detritus (Corbet, 1961). As it has been shown that the barbel does not normally grub around in the sediments in search of food organisms it is not unlikely that detritus is being ingested deliberately as a source of food. This is known to be the case with other freshwater fish including *Tilapia nilotica*, *T. leucosticta* and *Catla catla* (Hickling, 1961). Detritus is rarely eaten by *C. senegalensis* at Nungua and it is possible that this is due to the fact that so little organic matter occurs in the sediments.

Anatomical structure and relationship to feeding

The catfish has various anatomical structures which are suggestive of different methods of feeding. These are discussed below in the light of the known feeding habits.

(a) *Those that suggest it is a benthophagous feeder.* These include: (i) the body form which appears to be adapted to a sluggish, bottom dwelling existence; (ii) the barbels which appear to be tactile organs for locating bottom living organisms; (iii) the small antero-laterally situated eyes. As pointed out by Nikolsky (1963), benthophagous fish use tactile and taste organs in searching for food whereas planktrophages use visual organs. In the case of gadoid species which feed on bottom fauna the barbels are longer than in those species which are piscivorous (Nikolsky, 1963). Despite these anatomical features, the catfish is clearly not a specialized benthophage and it is possible that the sensory structures on the barbels are used for locating swimming and benthic organisms, at night and also during the day, in the highly turbid water in which these species normally live.

(b) *Those that suggest it is a planktophage.* These include the large non-protractile mouth, the small teeth in the buccal cavity and the long and numerous gill rakers. When *C. gariepinus* and *C. senegalensis* are feeding on zooplankton, which is an important item in their dietaries, the gill rakers act as strainers. Corbet (1961) claims, however, that as records of *C. mossambicus* being engorged with zooplankton are rare it is unlikely that gill rakers are functional specializations for feeding on zooplankton. It is possible that gill rakers also serve as a filter for preventing the intrusion of organic debris into the branchial chamber when the catfish is feeding on it or on bottom living organisms. The fact that gill rakers continue to increase numerically as the fish increase in size seems to show that they are important adaptations in connection with feeding even in the older fish.

(c) *Those that suggest it might feed on periphyton or phanerogams.* These include the sub-terminal mouth, in the form of a transverse slit and the long mandibular and premaxillary plates which might be used in cutting vegetation.

(d) *Those that suggest it might feed on molluscs or large crustacea.* The mandibular, premaxillary and vomerine plates covered with minute, discrete teeth which might be regarded as adaptations for this purpose.

(e) *Those that suggest it may be piscivorous.* These include its large size and large oral opening. Although species of *Clarias* are piscivorous they lack the grasping mouth of highly specialized piscivores like *Esox lucius*, *Hepsetus odoe* and species of *Hydrocyon*.

Corbet (1961) has suggested that *C. mossambicus* and two other Siluroids in Lake Victoria have become piscivorous by virtue of their large size and relative freedom from benthic specializations.

Ontogenetic changes in feeding

Corbet (1961) found that young *C. mossambicus* feed mainly on ostracods and aquatic insects until they reach a size of about 3 cm after which they feed more on fishes. In the present investigation all the catfish were between 13.6 and 79.1 cm and within this size range the differences between the dietaries of the various length groups was very slight. The lack of ontogenetic change in the dietaries can be attributed to the euryphagous habits of *Clarias*. The slight differences that were noted appear to be due to the fact that the larger fish tended to select marginal areas containing vegetation and as a result tended to eat slightly more vegetation, adventitious food and phytophilous organisms. The latter category was not, however, exploited to any great extent even by the larger catfish. In the absence of marked ontogenetic differences in the dietaries the apparent spatial segregation of the catfish into different size groups would clearly have selective advantages. Ontogenetic

differences appear to be greater in the case of other species of fish including *Gasterosteus aculeatus* (Hynes, 1950), *Mormyrus kannume*, other Mormyridae and *Bagrus docmac* (Corbet, 1961). Such differences reduce the likelihood of intraspecific competition taking place and makes it easier for fish of different sizes to occupy the same habitat.

Niche size

An extended food niche or euryphagy appears to be common in freshwater fish. Thus Hartley (1948), who studied a community of freshwater fish in Britain, was impressed by the flexibility in the feeding habits of coarse fish and states that "Here is no orderly hierarchy of specialists each fulfilling its part but rather a loose assemblage in which members are distinguished by no more than the varying proportions on which they draw on the constituents of a common stock". The community described by Corbet (1961) from Lake Victoria is somewhat similar as among the non-cichlids there were only two stenophagous or monophagous species namely *Labeo victorianus* and *Garra johnstoni*. In contrast, several examples of monophagous or stenophagous fish occur among the cichlids from Lake Nyasa (Fryer, 1959). When compared with other fish the catfish appears to be one of the most euryphagous and it is interesting to speculate why this should be the case.

Some of the environmental factors which tend to cause an enlargement of the food niche are given in Fig. 12(a). In this context the niche volume describes the functional status of a species in the ecosystem when it is being subjected to the environmental factors which influence it. The food niche refers to what the species eats. Certain environment factors including interspecific competition, predation pressure and physico-chemical factors may restrict the food niche indirectly by reducing the niche volume. These factors do not operate strongly against the catfish because it is buffered against them in the following ways: first its large size, large well-protected head, pectoral spines and piscivorous habits would tend to reduce the impact of predation pressure and interspecific competition; second, although it is subjected to changing physico-chemical conditions as a result of seasonal migration or seasonal and more long term changes in water level its physiological versatility enables it to survive. Thus it can survive drought either by moving overland to another water body or by burying itself in the sediment (Johnels, 1957). Movement overland is assisted by the presence of pectoral spines and the accessory respiratory structure. The latter also makes it possible for the barbel to survive in water containing little or no oxygen. The size of the food niche can also be influenced directly by the food supply. It might be expected that the following characteristics in the latter might cause expansion of the food niche. First, if the food is in short supply and intraspecific competition is taking place. Second, if the species diversity (sometimes expressed as the ratio of the cumulative number of species and the logarithm of the number of individuals counted) is high. Third, if the food items vary spatially or temporally either because the catfish feed in different places as a result of migratory movements or because of seasonal changes in the flora and fauna following seasonal changes in water level. It is difficult to know whether intra-specific competition for food is taking place or not under field conditions but if the other environmental factors are weak it might develop into a potent force. The other two characteristics seem to apply to Nungua lake. The species diversity is high (Thomas, unpublished results) as in many other tropical ecosystems (Klopfer, 1962; Mayr, 1963) and the food supply certainly varies a great deal seasonally (Thomas, 1966).

If, on the other hand, one or more of the environmental factors including interspecific competition, predation pressure or physico-chemical factors act strongly and constantly, it is to be expected that the niche volume and hence the food niche would become more restricted resulting in stenophagy or monophagy. Three examples can be given of these

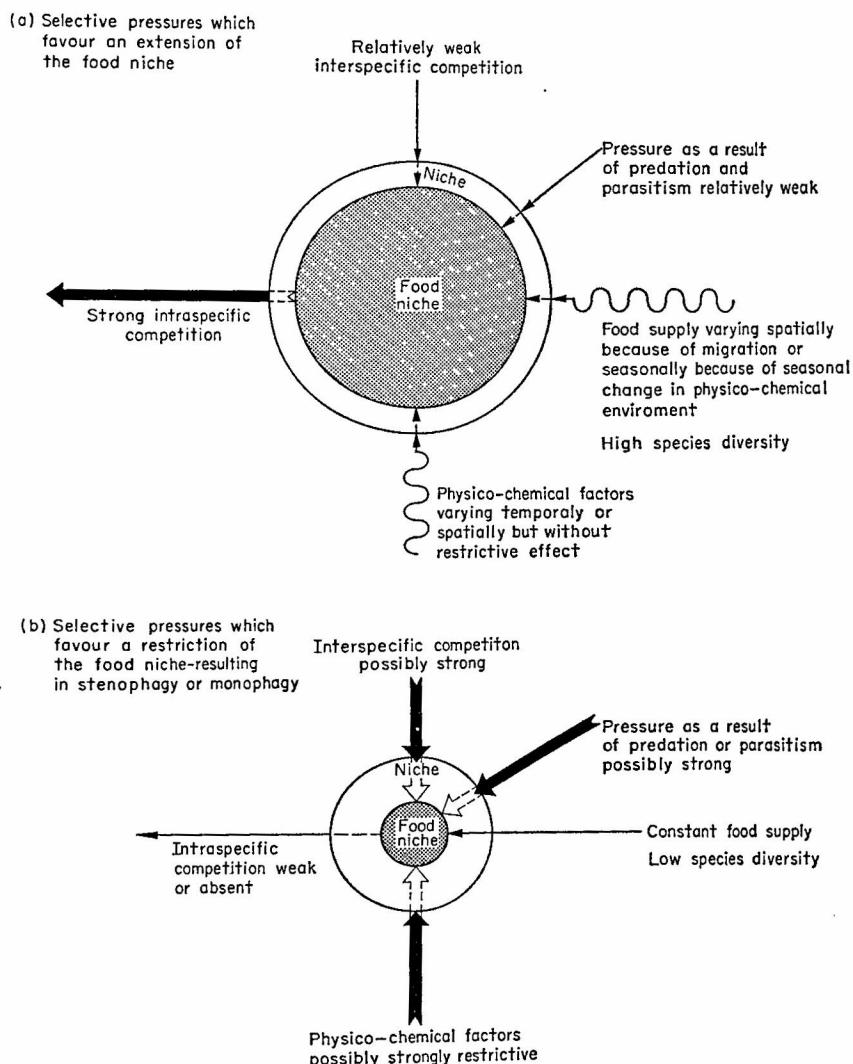


FIG. 12. Diagram to show the selective pressures which favour an enlargement or reduction of the food niche.

factors operating strongly. First, predation appears to be a potent force in the case of the small stenophagous fish studied by Fryer (1959) in Lake Nyasa. It is possible that this restricts their niche size by confining them to the cover provided by rocks. Second, Cook (1961) found that the moth *Panaxia dominula* was stenophagous at the edge of its range

where many factors including the climate were restrictive whereas at the centre of its range it was euryphagous. Third, parasites are usually monophagous because of their specificity to a particular physico-chemical environment. Direct causes which would favour a restriction of the food niche include a stable food supply, weak or non-existent intraspecific competition and a low species diversity in the fauna. The first two conditions appear to hold in cases where extreme stenophagy or monophagy have been reported. In the case of the stenophagous or monophagous fish studied by Fryer (1959) and Corbet (1961), intraspecific competition did not appear to be taking place and there was a constant food supply in the form of epilithic or epiphytic algae. Stenophagous or monophagous organisms show a tendency towards anatomical, behavioural and physiological specialization connected with their method of feeding.

It has been suggested by Klopfer (1962) and Mayr (1963) that niche size tends to be smaller in tropical areas. The latter author has suggested that the rarity or short duration of weather induced catastrophes in the tropics permits contraction in niche size but it is clear from the present discussion that other environmental factors may also influence niche size.

Very little evidence has been produced to show that niche size is in fact relatively small in the tropics. Klopfer (1962) has advanced the following indirect items of evidence, from ornithological data, in support of this hypothesis.

(a) The ratio of trophic characters such as bill lengths is greater for sympatric species living in temperate regions than for those living in tropical regions and as a result the exclusive portion of the niche is much reduced in the latter. It must be pointed out, however, that even if there is a reduction in the exclusive portion of niches in the tropics this does not imply that the niches themselves are smaller.

(b) Klopfer argues that with a decrease in niche size there should be increased specialization or behavioural stereotypy and hence a reduction in the number of individuals in a given area. In the case of passerines it appears that there is a smaller number of territorial males per unit area in the tropics than in the temperate region. These observations appear to lend some indirect support for the above hypothesis. On the other hand, there was no significant difference between population densities of non-passerines from temperate regions and those from tropical regions.

(c) A comparison of the frequency distribution of the bill lengths of non-passerines in tropical regions with those from temperate regions indicate that the former have the greater diversity and hence the greatest number of specialized individuals. A similar trend, though less well-marked, appears to hold for the passerines.

The evidence produced by Klopfer (1962) is, therefore, not only indirect but inconclusive. His argument that the behaviour of tropical species is more stereotyped is clearly very difficult to prove because of the inherent difficulty in comparing the behaviour of two species in a quantitative manner.

It is easier to give a quantitative expression to the food niche. As already pointed out there is some direct evidence (Fryer, 1959; Corbet, 1961) that the food niches of some tropical species are very reduced. It seems probable that the conditions conducive to stenophagy outlined in Fig. 12(b) are more likely to occur in regions of climatic stability such as the wet tropical forests, old and stable lakes and the oceans particularly those in the tropical zone.

On the other hand, the food niches of some tropical species including those of *Clarias*

and other freshwater fish have become very extensive. Mayr (1963) has also commented on this and states, in connection with niche size, that the existence of a large number of unspecialized species in the tropics is a particularly puzzling aspect of this problem. The extension of the food niche in the tropics would be favoured by the conditions mentioned in Fig. 12(a). These are more likely to appertain in areas in the temperate and tropical regions of the world where major seasonal changes or more long term changes in climate occur. In the savanna areas which cover much of tropical Africa major seasonal changes are caused by seasonality in the rainfall pattern.

It may be suggested that speciation occurs more readily among fish taxa containing species with narrow niche requirements than amongst those with more extended niches because populations of species with narrow niches would become more readily isolated. This trend appears to be shown in the case of the fish species described by Fryer (1959) from Lake Nyasa. Many of these species had very restricted food niches and it seems probable that they evolved from stenophagous species. In contrast the highly euryphagous species of *Clarias* (*Heterobranchiodes*) have shown little evidence of rapid speciation either temporally or spatially. The genus *Clarias* is known to have occurred in the Pliocene both in Africa and Asia (Romer, 1945) and present day species of this genus show a continuous distribution of the clinal type. It has been pointed out by Jackson (1962) that as a result it is difficult to determine where the range of one species ends and where the other begins. *Clarias (H.) gariepinus* (Burchell) merges almost imperceptibly into *C. (H.) mossambicus* Peters which again further north can scarcely be distinguished from *C. (H.) lazera*. Mills (1956) has remarked on the similarity between *C. (H.) lazera* and *C. (H.) senegalensis*. It is clear that the taxonomy of this genus requires revision.

Summary

The catfish, *Clarias senegalensis*, which were studied over a period of one year, were obtained from a small, shallow, man-made lake fed by an intermittent stream at Nungua in the coastal savanna near Accra, Ghana. The lake fills to capacity after the onset of the major rains in April or June and thereafter decreases in volume until about the same time the following year. Flooding is accompanied by dilution, a decrease in primary production by phytoplankton, a short term decrease in water temperature and by an increase in the amount of oxidizable organic matter and in aquatic and subaquatic vegetation along the shore line. The flood beach is extensive and the vegetation disappears in the dry season.

The fauna is characterized by a dearth of species in those taxa which contain sediment feeders or scavengers and by a large number of species in the Coleoptera, Hemiptera, other than Corixidae, Odonata and Diptera. More species, particularly those that were phytophilous, were encountered during the wet than in the dry season. The population density reached its peak after the onset of the wet season whereas the biomass was at its lowest before and during the wet season, but increased progressively thereafter.

Most of the catfish were captured with a seine net and their weight, length, state of gonads and the number of gill rakers in the anterior arch determined. The percentage composition of the food was estimated by the percentage occurrence method, the number method and the points scheme. A comparison was made between the fauna and the food by using the forage ratio.

The catfish become sexually mature after achieving a length of about 32 cm and

spawn in the flood zone of the feeder stream once a year after the onset of the major rains in April. Spent fish soon return to the lake after spawning but smaller immature fish do not seem to do so until September. The reasons for anadromesis are discussed.

In common with other piscivorous fish, the feeding intensity is low and except for one, monthly sample the stomachs are on the average less than half full. The slight seasonal increase in the amount of food consumed appears to be correlated with a seasonal increase in the standing crop and that in condition factor with a greater deposition of fat and a relatively greater increase in length than in breadth following a greater intake of food. The length weight relationship was constant over the size range involved and " n " in the generalized equation $K = W10^3L^n$ was near enough to three to justify the use of the normal condition factor $K = W10^3L^3$.

The three methods used to estimate the percentage composition of the food gave different results because the food organisms varied a great deal in size.

Although the catfish is very euryphagous, it subsists mainly on organisms swimming in midwater including fish such as *Tilapia*, zooplankton and insects, those swimming close to the surface of the sediment and those living on its surface. Animals from these habitats have a higher forage ratio than those living under stones, in the sediment or in shallow water or in vegetation close to the shore. Vegetation, adventitious food and detritus are not important in the dietary of *C. senegalensis* in Nungua lake. It is suggested that the detritus is not exploited because the bottom sediments are poor in organic matter. Species of *Clarias* share many common features in their dietaries. All are euryphagous and this is reflected in anatomical structures which appear to be adaptations for feeding on benthic organisms, vegetation or periphyton, molluscs or crustacea, vegetation and zooplankton. The fact that the gill rakers of *C. senegalensis* increase in number as the fish increases in size suggests that they are important feeding adaptations even in older fish.

Only slight ontogenetic and seasonal changes occur in the dietaries. The latter trend can be attributed to the fact that the catfish does not exploit phytophilous species to any great extent even when they become abundant in the wet season. There is a suggestion that the larger fish eat slightly more vegetation, phytophilous species and adventitious food than the smaller fish but they all eat Copepoda and fish including *Tilapia*. The possibility of combining *Clarias* with *Tilapia* in fish ponds is, therefore, worthy of consideration but as it does not utilize phytophilous species to any great extent it is doubtful whether it could be important in controlling important vectors such as species of *Bulinus*, *Biomphalaria*, *Limnaea* and mosquito larvae.

The factors that favour expansion and contraction of food niches are discussed. The need to obtain more information about the relative sizes of niches in tropical and temperate regions is stressed and it is pointed out that there is no reason to suppose that conditions favour the reduction of the niche and of the food niche in particular in all tropical ecosystems.

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Key to lettering of figures

a.r.s., accessory respiratory structure; b.a. 1-5, branchial arches 1-5; d.p., dental pad; g.l., gill lamellae; g.r., gill rakers; h.e., hyoid elevation; i.m.b., inner mandibular barbel; i.p.t., inferior pharyngeal teeth; i.s.h.a., infold of skin near hyoid arch; m., mouth; m.b. maxillary barbel; m.f., membranous flap; m.t., mandibular teeth; n., nostril; n.b., nasal barbel; o., oesophagus; o.m.b., outer mandibular barbel; op., operculum; p.f., pectoral fin; p.s., pectoral spine; p.t., premaxillary teeth; s.p.t., superior pharyngeal teeth; v.t., vomerine teeth.