Food resource sharing and partitioning among some fishes of the Pongolo River floodplain

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The diets of 12 fish species which coexist in the Pongolo floodplain lakes were determined from an analysis of the contents of 3 691 stomachs collected over a period of 12 months. Although almost all species were found to feed on a variety of foods, with consequent dietary overlaps, quantitative analysis of the results showed that distinct preferences for specific food types considerably ameliorated the effects of such overlaps. Partitioning within the major food categories, differences in relative population sizes, spatial and temporal differences in feeding and shifts in diet following inputs of seasonally occurring foods, all tended further to reduce effective competition between species. The results are discussed in the broader context of colonization of the Pongolo system by a tropical fish community in circumstances where the principles of island biogeography may be expected to apply.

Die diëte van 12 visspesies wat in die vloedpleinmere van die Pongolorivier saamleef is deur ontleding van 3 691 maaginhoude, wat oor 'n tydperk van 12 maande ingesamel is, vasgestel. Hoewel byna al die spesies 'n verskeidenheid voedselsoorte vreet, met gevolglike oorvleuelings van hulle diëte, dui kwantitatiewe ontleding op besliste voorkeure vir spesifieke voedselsoorte, wat die gevolge van die oorvleuelings tot 'n groot mate versag. Verdeling binne die vernaamste voedselsoorte, verskille in relatiewe populasiegroottes, verskille in tye en plek van voeding, en verskuiwing in dieet na seisoenale insette, dra almal by tot 'n verdere vermindering in effektiewe kompetisie tussen spesies. Die resultate word bespreek in die breër verband van die kolonisasie van die Pongolo-sisteem deur 'n tropiese visgemeenskap onder omstandighede waar dit verwag kan word dat die beginsels van eilandbiogeografie stellig van toepassing is.

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The Pongolo River floodplain (Figure 1), located between latitude 27°15'S and the confluence of the Pongolo and Usutu Rivers, comprises some 13 000 ha of low-lying land adjacent to the Pongolo River. It includes numerous shallow depressions, the floodplain lakes, which are filled with water during floods. These lakes occupy an area estimated at 2 600 ha at their maximum retention level. The larger, deeper lakes retain water from one flood season to the next except under extreme drought conditions, thus providing a permanent refuge for a diverse aquatic flora and fauna. The likelihood of detrimental downstream effects resulting from the impending impoundment of the Pongolo River by the Jozini Dam, then under construction, prompted the initiation, in 1974, of a programme of wide-ranging studies aimed at establishing the extent to which the floodplain ecosystem depended on the natural flooding regime of the Pongolo River, particularly where this affected the floodplain resources important in the existing local socio-economic structure.

Thirty-nine primary and secondary freshwater fish species have been recorded from the study area (Bruton & Kok 1980). Attention was focused on all aspects of the biology of the 12 species listed in Table 1, which were of sufficient size and abundance to support subsistence and artisanal fishing practised in the floodplain lakes. In this paper we examine the feeding ecology of these species in the context of resource sharing and partitioning; their flood dependence and role in the overall ecology of the floodplain ecosystem are discussed elsewhere (Heeg & Breen 1982).

The Pongolo River system forms part of the Zambezi Ichthyofaunal Province, and all fish species recorded from the floodplain are thought to have entered the system from the North (Roberts 1975) where, in the lower Zambezi, they form part of a more complex community, richer in species (Bell-Cross 1982). Diamond (1975) concludes from his studies on the spread of New Guinea birds to adjacent islands, that such invasions are subject to 'assembly rules' which select for a community comprising 'permissible combinations' of coexisting species that optimally utilize the available resources of the newly invaded habitat. Resource partitioning among coexisting species is an important tenet in Diamond's hypothesis, which has its origin in the principles of island biogeography as propounded by MacArthur & Wilson (1967). Our results lend themselves to the testing of this hypothesis in an analogous aquatic situation.

Materials and Methods

Fish were collected monthly from selected floodplain lakes over the period February 1974 to December 1976. Regular, though less intensive, sampling was also done in the Pongolo River during this period. Although a variety of sampling methods was used in the programme, only catches by seine and gill nets were made with sufficient regularity to be pertinent to the investigation described here. Sampling by these methods required suitable water depth, and as this fluctuated over the period of the investigation, not every lake could be

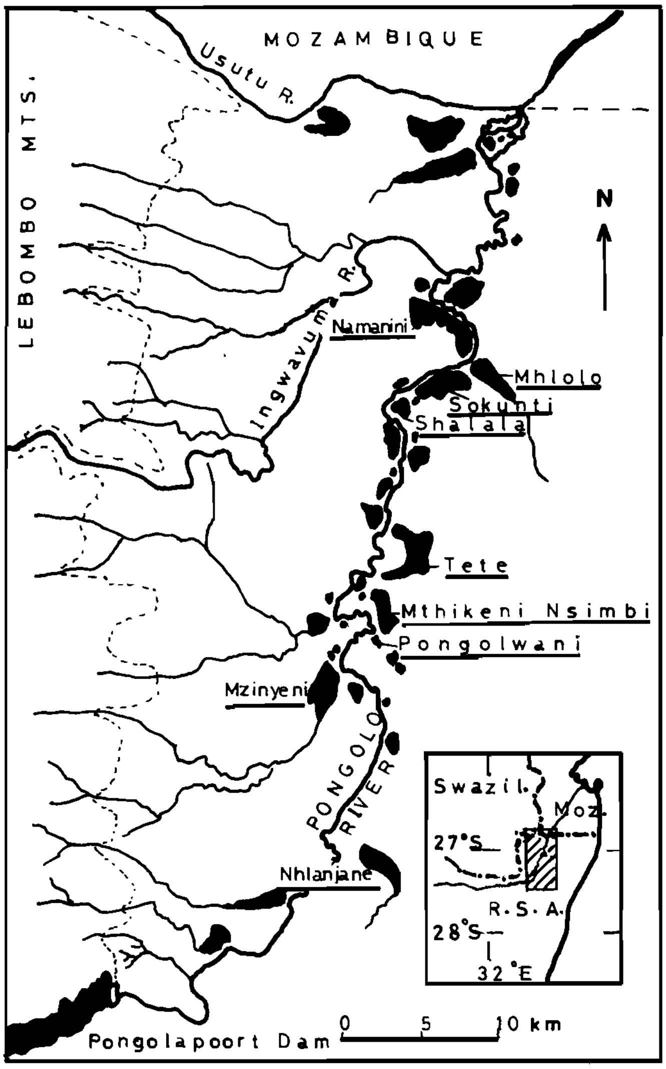

Figure 1 Map of the study area, showing geographical location (inset) and the major lakes of the Pongolo River floodplain. Only those floodplain lakes referred to in the text have been labelled; for further details see Heeg & Breen (1982).

Table 1 List of fish species studied

Order Mormyriformes (1° freshwater)
Family Mormyridae
Marcusenius macrolepidotus (Peters, 1852)
Petrocephalus catostoma (Gunther, 1866)
Order Cypriniformes (1° freshwater)
Family Characidae
Alestes imberi Peters, 1852
Hydrocynus vittatus Castelnau, 1861
Family Cyprinidae
Labeo rosae Steindachner, 1894
Order Siluriformes (1° freshwater)
Family Schilbeidae
Eutropius depressirostris (Peters, 1852)
Family Clariidae
Clarias gariepinus (Burchell, 1822)
Clarias ngamensis Castelnau, 1861
Family Mochokidae
Synodontis zambezensis Peters, 1852
Order Perciformes (2° freshwater)
Family Cichlidae
Oreochromis mossambicus (Peters, 1852)
Tilapia rendalli swierstrae Gilchrist & Thompson, 1917
Family Gobiidae
Glossogobius giuris (Hamilton-Buchanan, 1822)

sampled each month, but the monthly schedule was adhered to whenever possible.

A 15 mm bar mesh seine net, 60 m long with an effective haul depth of 2,5 m and a 4,0 m trailing purse was used to sample Mzinyeni, Tete, Sokunti and Namanini lakes (see Figure 1) over the period February 1974 to March 1975. The net was attached to 50-m warps, giving a sampling area of 3 000 m^2. Seine netting proved to be the only effective means of obtaining specimens for gut content analysis, but had to be restricted to the four lakes mentioned through lack of suitable seining beaches elsewhere. These lakes were, however, sufficiently diverse in their characteristics (Breen, Furness, Heeg & Kok 1978; Heeg, Breen, Colvin, Furness & Musil 1978) to be considered representative of the floodplain. Seining could only be carried out during the day, owing to the danger from crocodiles and hippopotami, and therefore selected to varying degrees against nocturnal species. Such selection was most marked in the case of the Mormyridae.

A fleet of multifilament (210/6 ply) nylon gill nets of stretch mesh 30, 55, 75, 105, 110, 125 and 155 mm was used to sample Nhlanjane, Pongolwane, Mthikeni-Nsimbi, Shalala and Mhlolo (Figure 1) in addition to the four lakes mentioned above, over the period April 1975 to December 1976. This increased the number of lakes sampled and allowed both day and night sampling, thus giving a better estimate of community structure. Fish caught in gill nets almost invariably regurgitated their stomach contents before the nets were meshed. The gill nets were found to select markedly against the capture of *Tilapia rendalli* and *Alestes imberi,* and to a lesser extent against *Hydrocynus vittatus.* It is perhaps significant that the gill nets selected against species essentially diurnal in their activity.

This study, being concerned with the impact of different species on food resources, required an estimate of community structure to be derived from the catch statistics, and thus needed to take cognisance of gear selectivity. The total gill net catches were accepted as the best possible estimate of the relative numbers of the species, except where clear selection against a particular species was apparent. In such cases the seine catch, corrected for the shorter sampling period, was used. To test the validity of this approach, the community structure thus derived could be compared with that derived from the total catch over the whole period by all fishing methods (i.e. seine, gill, fyke and throw nets and long lines) at all localities. Marked differences between the two assessments should then be accountable in terms of gear selectivity. Sampling frequency and the long period over which the investigation was carried out increased the likelihood of this estimate of community structure being at least realistic.

All fish caught were measured to the nearest millimetre standard length (SL) and weighed to the nearest gram on a 1,5 kg capacity beam balance or, if exceeding this, to the nearest 10 or 20 g respectively on a 10 or 25 kg spring balance. Twenty-five specimens from each seine net catch between March 1974 and March 1975 were used for the analysis of stomach contents; where the catch of a species was less than 25, all specimens were used. The entire viscera of these fish were removed in the field, preserved in 10% buffered formalin and labelled with the details of the fish. Each stomach was slit open in the laboratory, and the entire contents washed into a petri dish for microscopical examination. Individual food items were separated manually, recorded and oven dried at 70°C to constant mass. Dry mass was determined to within 0,1 mg. Where entire fish prey was found in a stomach, the standard length of such prey was measured. Plant-derived foods (algae, detritus, macrophyte fragments, etc.) could not be effectively separated for gravimetric analysis, thus only total dry mass was determined. The desirability of using reconstructed mass or volume in diet analysis is recognized, but the overall scope of the research programme and limited manpower precluded such a time-consuming approach. The large number of fish examined, totalling 3 691 stomachs, is likely to have offset the inaccuracies inherent in the method used.

The acceptability of a particular food type to a given fish species would be reflected in the frequency with which it was eaten. Frequency of occurrence in the diet was therefore expressed as the number of stomachs containing that food type. An alternative frequency measure, the number of items of a particular food type recovered from each stomach, could not be determined with any accuracy from an often-triturated and partially digest bolus. Such a measure would have yielded little additional information through being difficult to interpret (e.g. what is an 'item' of detritus?). Recovered dry mass gave a measure of the importance of a food type. Both frequency and recovered dry mass were used to establish diet overlaps and breadths. Diet overlaps between species pairs (α) were calculated using Schoener's Index (Wallace 1981):

$$\alpha_{jk} = 1 - 0{,}5\ (\Sigma\ {}_{i}\text{»fd}_{1}\ /\ P_{ij} - P_{ik}/)$$

where P_{ij} is the proportion of the i^{th} food resource present in the stomach contents of species j and P_{ik} is the proportion of that resource in species k. This index has a range from 0 (no overlap) to 1,0 (complete overlap). Values exceeding 0,5 on the Schoener scale were considered as high and indicative of competition for food resources. Diet breadths (β) were calculated as the Inverse Simpson Index:

$$\beta = \sum_{i=1} \frac{1}{(P_{ij})^2}$$

where P_{ij} is the proportion of the i^{th} resource in the diet of species j, giving a range from 1,0 (single food category) to n (n food categories in equal proportions).

Results and Discussion

The composition of the community of the larger fish species found on the floodplain, as calculated from catch statistics with due allowance for gear selectivity, is set out in Table 2. Substantial deviations in the percentage contributions from those calculated from the

Table 2 Summary of fish community structure derived from catch statistics

Species	Number caught	Mean standard length (mm)	mean mass (kg/individual)	Percentage of catch: Numerical		Percentage of catch: Biomass	
P. catastoma	1 692	77	0,010	4,1	(4,6)	0,2	(0,2)
M. macrolepidotus	2 084	147	0,046	5,0	(5,4)	1,3	(1,1)
H. vittatus	4 662*	251	0,262	11,3	(11,7)	16,1	(13,7)
A. imberi	13 829*	111	0,033	33,5	(23,2)	6,0	(3,4)
L. rosae	3 860	247	0,358	9,3	(10,5)	18,1	(16,8)
C. gariepinus	1 034	475	1,317	2,5	(4,3)	17,9	(25,4)
C. ngamensis	382	421	0,851	0,9	(1,1)	4,2	(4,2)
E. depressirostris	4 901	192	0,107	11,9	(13,4)	6,8	(6,4)
S. zambezensis	238	128	0,056	0,6	(0,8)	0,2	(0,2)
O. mossambicus	5 486	185	0,254	13,3	(19,3)	18,6	(21,9)
T. rendalli	3 022*	182	0,266	7,3	(4,3)	10,6	(5,2)
G. giuris	110	183	0,155	0,3	(0,3)	0,1	(0,1)
Total	41 300			100		100	

Numerical catch represents the gill net catches except where indicated by *, where corrected seine net catches were used;

percentages derived from the total catch by all fishing methods are shown in parenthesis for comparison; and mean standard lengths and biomasses were calculated from the total catch.

uncorrected total catch of 47 605 fish caught by all sampling methods, were only apparent for *A. imberi* (33,5% vs 23,2%). *O. mossambicus* (13,3% vs 19,3%) and *T. rendalli* (7,3% vs 4,3%).

The discrepancy in the case of *A. imberi* can be accounted for by the gill nets selecting against certain size ranges owing to stepped increases in the mesh sizes of the gill fleet. Notable here was the almost complete absence of the size range between 110 and 130 mm SL, which contributed 38% to the seine catch, as well as fish below 85 mm SL. Gill net selection against *T. rendalli* has been reported by several authors (Junor 1969; Kenmuir 1973; Mitchell 1976; van der Waal 1976). The decrease of 7% in the contribution of *O. mossambicus* is largely a compensation for the increases in *A. imberi* and *T. rendalli* following correction. When expressed in terms of mass, the discrepancies are considerably less, owing to the small size of *A. imberi*. Under the circumstances of the study, the relative contributions of the 12 species to the total catch, as given in Table 2, represent the best possible estimate of the structure of the fish community.

Food resource sharing and partitioning

The percentage frequency with which 14 identifiable food types occurred in the stomachs of the different fish species is shown in Figure 2, giving a measure of acceptability of each. *A. imberi* and *C. gariepinus* seem to be largely opportunistic in their feeding, while the remaining 10 species appear to be divided into three feeding guilds. Table 3 shows the diet overlaps between species pairs, expressed as Schoener indices, and the diet breadths of the 12 species. Each measure was derived from the recovered dry mass and from the frequency of occurrence of the different food categories shown in Figure 2.

In most instances the diet breadth based on frequency of occurrence was greater than that derived from recovered mass, indicating that in several species the range of acceptable foods exceeds that of items consumed in quantity. This difference was greatest in the two opportunistic feeders, *A. imberi* (9,45 vs 4,89) and *C. gariepinus* (7,687 vs 2,05), and was not apparent in the highly specialized mormyrids. In each guild there were some potential as well as apparently realized competitive interactions between species. Among the piscivores *H. vittatus* and *G. giuris*, both with very narrow diet breadths, overlap significantly with one another, as well as with *C. gariepinus* and *E. depressirostris*. Similarly the Schoener Index for *P. catostoma* and *M. macrolepidotus* is very high, coupled with the lowest diet breadths recorded within the community.

Unequivocal demonstration of competition for food between any two species within a community requires at least that:

(i) there is significant overlap in the diets of the species concerned,
(ii) limited alternative food sources, either as a result of stenophagy or scarcity, focuses exploitation on the common resource, and
(iii) population sizes of the species concerned are

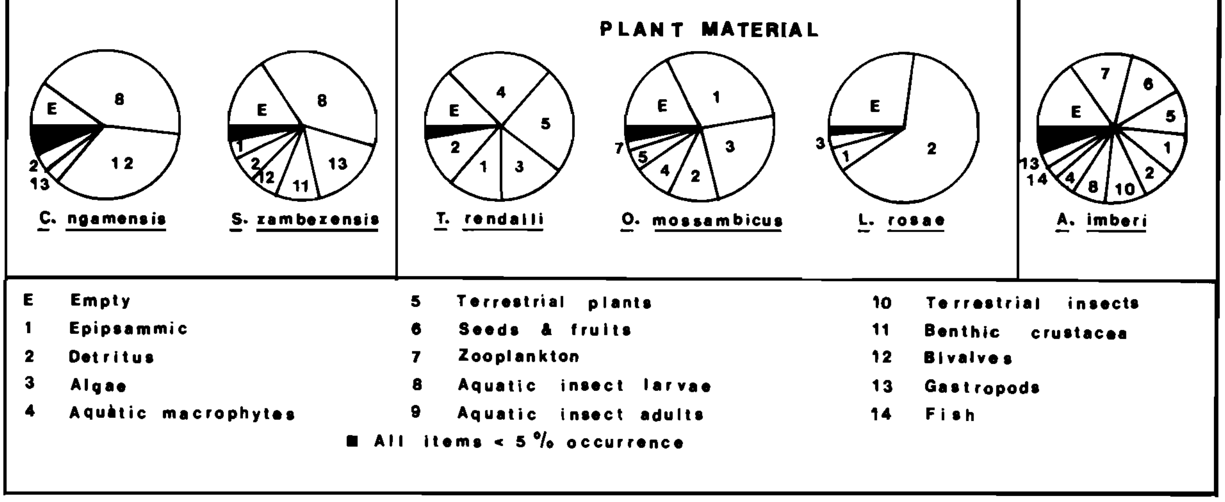

Figure 2 Frequencies of occurrence of different food items in the diets of the 12 fish species studied, based on analyses of the stomach contents of 3 691 individual fish over a period of 12 months.

Table 3 Diet overlaps between species pairs (Schoener indices) and diet breadths of species in the three guilds identified in the floodplain fish community. Entries above each diagonal are based on dry mass recovered from stomachs; those below on frequency of occurrence. Overlaps indicative of possible competition for food are shown in bold type.

Plant material

	D.B.	*A.i.*	*L.r.*	*C.g.*	*O.m.*	*T.r.*
Diet breadth	–	4,89	x	2,05	x	x
A. imberi	9,45	–	x	0,22	x	x
L. rosae	1,30	0,12	–	x	x	x
C. gariepinus	7,68	0,48	0,11	–	x	x
O. mossambicus	3,96	0,38	0,26	0,24	–	x
T. rendalli	4,69	0,40	0,25	0,20	**0,60**	–

Fish prey

	D.B.	*A.i.*	*H.v.*	*C.g.*	*E.d.*	*G.g.*
Diet breadth	–	4,89	1,06	2,05	2,51	1,02
A. imberi	9,45	–	0,08	0,22	0,24	0,07
H. vittatus	1,75	0,27	–	**0,70**	**0,61**	**0,98**
C. Gariepinus	7,68	0,48	0,44	–	**0,68**	**0,70**
E. depressirostris	4,29	0,35	**0,58**	**0,60**	–	**0,65**
G. giuris	1,47	0,19	**0,91**	0,42	0,55	–

Invertebrate prey

	D.B.	*P.c.*	*M.m.*	*A.i.*	*C.g.*	*C.n.*	*E.d.*	*S.z.*
Diet breadth	–	1,01	1,16	4,89	2,05	1,15	2,51	2,99
P. catastoma	1,01	–	**0,91**	0,05	0,03	0,03	0,07	**0,50**
M. macrolepidotus	1,03	**0,99**	-	0,05	0,03	0,04	0,07	**0,50**
A. imberi	9,45	0,09	0,10	–	0,22	0,07	0,24	0,13
C. Gariepinus	7,68	0,16	0,17	0,48	–	0,12	**0,68**	0,13
C. ngamensis	2,69	0,47	0,47	0,24	0,43	–	0,04	0,16
E.depressirostris	4,29	0,21	0,20	0,35	**0,60**	0,29	–	0,15
S. zambezensis	3,50	**0,51**	0,46	0,30	0,47	0,64	0,31	–

D.B. = Diet breadth

sufficient to make an impact on the resource for which they are competing.

Where more than two species exploit a given resource, diffuse competition (MacArthur 1972) adds a further dimension to the interactions particularly where stenophagous species are concerned. The foregoing indices can, therefore, only be regarded as indicative of the potential for competition; the impact on any resource will depend on the population sizes of all the exploiting species. By extrapolating from the dry mass of individual food categories recovered from the 3 691 stomachs examined to a community of 41 300 fish constituted as in Table 2, an estimate of the *relative* impact of each species on each category could be obtained. This is shown in Figure 3 and gives a different perspective: molluscs emerge as a distinct resource within the invertebrate feeding guild, and fruits and seeds and terrestrial insects merit separate attention. Each resource with the exception of fruits and seeds is exploited by three or more species; diffuse competition (MacArthur 1972) will therefore intensify the impact on these resources beyond the level indicated by individual interactions.

Plant feeders

Fluctuating water levels together with the seasonal growth patterns of the aquatic vegetation provide consistent inputs of allochthonous and autochthonous plant material, both living and detrital, into the floodplain lakes during a normal season (Heeg & Breen 1982; Rogers 1980). Where studied, production rates of primary producers on the floodplain have been found to be high (Furness & Breen 1980; Rogers 1981; Rogers & Breen 1980; A. Buchan, pers. comm.).

Plant and plant-derived material of both aquatic and terrestrial origin, but excluding fruits and seeds, was consumed in greater quantity than any other food type, with *O. mossambicus* and *T. rendalli* exerting the greatest pressure on this resource. While competitive interaction between these two species is suggested by the Schoener Index, this could, in this instance, be derived only from frequencies of occurrence, and therefore reflects an overlap in acceptable rather than preferred foods. Both species accept a variety of foods as indicated by their respective diet breadth indices. However, even though this was not quantified, *T. rendalli* stomachs

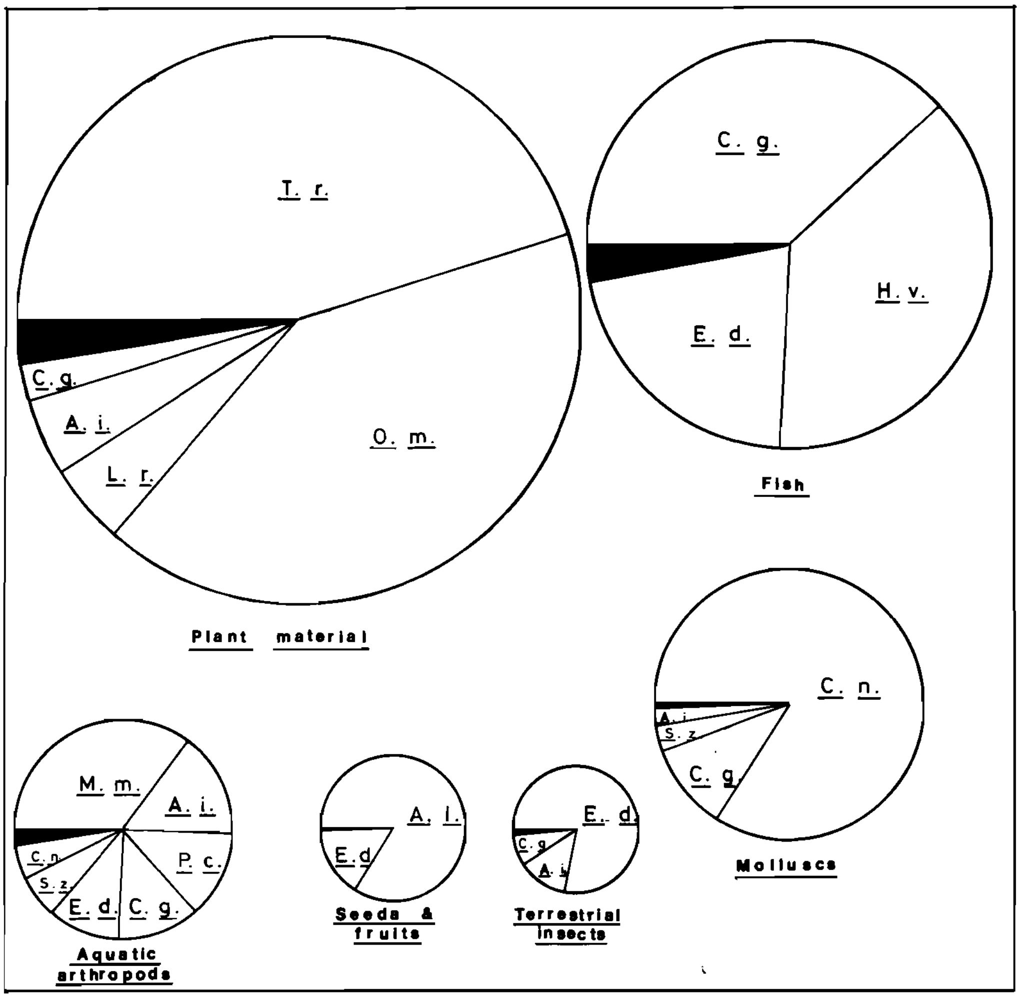

Figure 3 Impact on the six major food categories of the floodplain by the 12 fish species studied. The relative contributions of these food resources to the total consumed by the community are represented by the areas of the individual pie diagrams, derived from the total dry mass recovered from that species extrapolated to a community of 41 300 fish constituted as in Table 2.

contained largely macrophyte fragments, while those of *O. mossambicus* contained mostly algae, sand, mud and detritus. These dietary preferences have been reported by several authors (e.g. Bailey, Churchfield, Petr & Pimm 1978; Batchelor 1978; Bowen 1976; Bruton & Boltt 1975; Gaigher 1969) and indicate minimal competition between these two cichlids. The stenophagous *L. rosae* emerges as a specialist detritivore and shows little dietary overlap with any other species. Its impact on the detritus pool is probably greater than indicated in Figure 3; lacking a true stomach (Matthes 1963), only the contents of the anterior intestinal bulb were considered, and this is unlikely to have represented food intake comparable with that recovered from a species with a normal stomach. The impact of the euryphagous *A. imberi* and *C. gariepinus,* although substantial, was small relative to that of the other species and spread over all components of the resource pool.

Piscivores

The incidence of fish prey in the stomachs examined was high, exceeded in mass only by the plant material in herbivores. Although *G. giuris* and *H. vittatus* show a very high degree of dietary overlap, both being almost exlusively piscivorous, the relative population size of the former was such that its impact on the resource would be minimal (Figure 3). *H. vittatus, C. gariepinus* and *E. depressirostris,* which together accounted for 97% of fish prey taken, all show significant dietary overlaps, the effect of which would be greatest on the stenophagous *H. vittatus.* No qualitative differences were apparent in the fish components of the diets of these three species; Gobiidae occurred in all diets with approximately twice the frequency of any other species, but beyond this no pattern was apparent. Schoener Indices for the fish components of the diets, based on frequency of occurrence, were as follows:

H. vittatus / E. depressirostris : 0,79
H. vittatus / C. gariepinus : 0,77
E. depressirostris / C. gariepinus : 0,81

However, where intact prey was recovered from stomachs, size discrimination by the predators in selecting their prey was indicated, as shown in Figure 4. Division of the prey into 50 mm length classes (Table 4) allowed for statistical analysis, with the following result:

H. vittatus / E. depressirostris $\chi^2 = 8{,}7;\ 0{,}05 > P > 0{,}01$
H. vittatus / C. gariepinus $\chi^2 = 25{,}7;\ 0{,}001 > P$
E. depressirostris / C. gariepinus $\chi^2 = 4{,}3;\ P > 0{,}1$

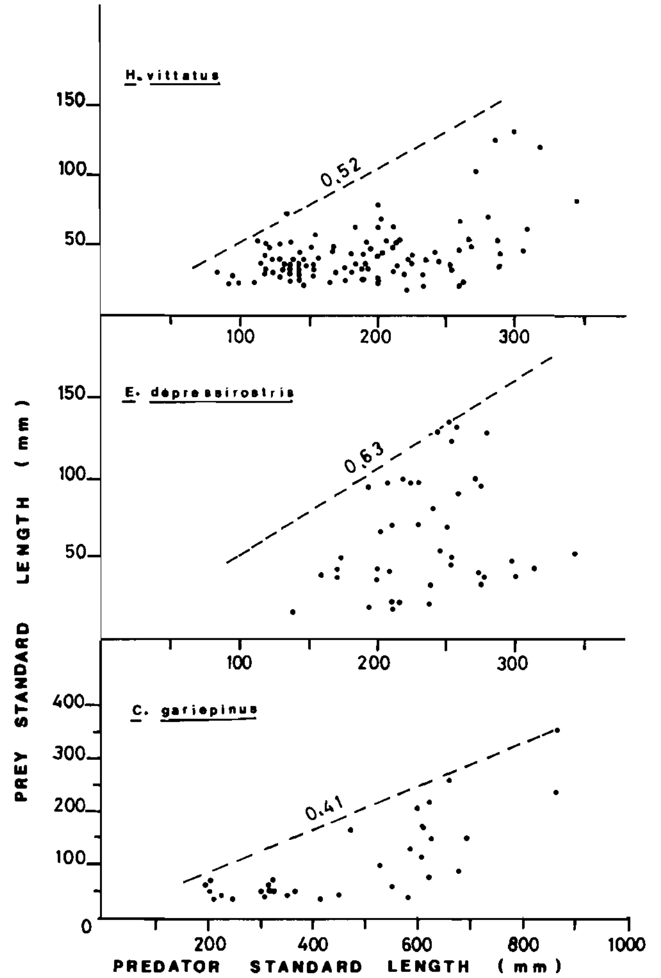

Figure 4 Relationships between predator and fish prey standard length for *H. vittatus*, *E. depressirostris* and *C. gariepinus*. Maxima of prey : predator SL ratios are indicated by the dashed regression lines, the slopes of which are given in each instance.

Table 4 Frequency of occurrence of prey of different lengths in stomachs of three piscivorous

	Prey size frequency			
Species	<50 mm SL	50–100 mm SL	>100 mm SL	Total
H. vittatus	72	22	4	98
E. depressirostris	21	15	6	42
C. gariepinus	11	10	11	31

H. vittatus therefore seems to select prey smaller than 50 mm SL with a significantly higher frequency than do the two siluriforms. Furthermore, *H. vittatus* is a visual diurnal predator (Munro 1967) while our field and laboratory observations on *E. depressirostris* and Bruton's (1978, 1979) studies on *C. gariepinus* point to these two species being largely nocturnal in their activities, adding a further dimension (*sensu* Schoener 1974) to the separation.

The significant dietary overlap between *C. gariepinus* and *E. depressirostris* is largely a consequence of the contribution of fish to the diets. If this component is removed, the Schoener Indices are reduced from 0,68 to 0,40 (mass) and 0,60 to 0,47 (frequency). This, together with the available alternative food sources as reflected in the diet breadths, particularly for acceptable foods, are likely to ameliorate the effects of any possible competition for fish as the principal food resource during times of stress. In addition, our laboratory observations have shown that *E. depressirostris* is predominantly a noctural mid- to surface water tactile feeder in contrast to the bottom-dwelling habit of *C. gariepinus*. This is supported by the frequency with which food items known to float on the surface, such as drowned terrestrial insects and the fruit of *Ficus sycomorus*, occurred in the diet: these items occurred in 36% of *E. depressirostris* stomachs examined, contributing 25,6% of the recovered dry mass, compared with *C. gariepinus* where their frequency of occurrence was 1,3%, constituting only 6% of the dry mass of the diet. These results suggest at least partial spatial separation of the two species.

Molluscivores

Although the dietary overlap between *C. gariepinus* and *C. ngamensis* is low, these two species are jointly responsible for the greatest impact on molluscan resources, which they shared only with *A. imberi* and *S. zambezensis*. Bivalves constituted 95% of the molluscan dry mass recovered, 99% of which was consumed by the two *Clarias* species. Clear size selection was apparent among the species utilizing this resource. *C. gariepinus* took almost exclusively the large unionid *Caelatura framesi*, which it swallowed whole, later regurgitating the intact empty shells. *C. ngamensis* selected the smaller *Corbicula africana*, which it crushed before swallowing; it also occasionally took small *C. framesi* or large *Eupera ferruginea* which it treated in the same way as *C. africana*. Apart from its more gracile skull, the morphological character distinguishing *C. ngamensis* from *C. gariepinus* is its broad vomerine plate armed with blunt teeth which, from appearances at least, suggests adaptation to a mussel-cracking habit. *S. zambezensis*, although accounting for only 0,6% of the bivalves recovered, concentrated on the very small *Eupera ferruginea* and *Pisidium* species.

Predators on aquatic arthropods

Of the seven species found to feed either wholly or partially on aquatic arthropods, only *P. catostoma*, *M. macrolepidotus* and *S. zambezensis* showed significant dietary overlaps. *P. catostoma* and *M. macrolepidotus* have particularly narrow diet breadths in terms of both acceptable and preferred foods, and show an almost complete overlap in their diets (Table 3). Diffuse competition from the other five species, including significant dietary overlap with *S. zambezensis*, should therefore intensify the apparent competitive interaction between the two mormyrids. Table 5 details the aquatic arthropod components in the diets of all seven species and shows particularly the important role of aquatic

Table 5 Composition of the aquatic arthropod component in the diets of the seven fish species shown in Figure 3 as exploiting this resource

	Insect subimagines		Insect adults		Zooplankton		Benthic crustacea		Total	
Species	Dry mass (g)	%	Dry mass (g)	%	Dry mass (g)	%	Dry mass (g)	%	Dry mass (g)	%
P. catastoma	30,8	17,3	0	0	0	0	0,2	1,9	31,0	13,2
M. macrolepidotus	78,9	44,4	6,3	34,2	0	0	0	0	85,3	36,3
A. imberi	11,0	6,2	1,5	8,2	15,6	54,9	0,2	1,9	28,3	12,0
C. gariepinus	11,5	6,5	6,0	32,6	12,5	44,0	0,5	4,8	30,5	13,0
C. ngamensis	12,1	6,8	0,3	1,6	0	0	0,4	3,9	12,8	5,4
E. depressirostris	20,5	11,5	3,6	19,6	0	0	2,6	25,0	26,7	11,3
S. zambezensis	11.6	6.5	0	0	0.1	0,4	2,8	26,9	14,5	6,2
Other	1,5	0,8	0,7	3,8	0,2	0,7	3,7	35,6	6,1	2,6
Total	177,9	100	18,4	100	28,4	100	10,4	100	235,1	
% of total aquatic arthropods	75,7		7,8		12,1		4,4		100	

subimagines of insects, which also constitute the major food of the mormyrids. Very little selectivity was shown by the species feeding on these insects. *C. ngamensis* was found to have taken largely larval Trichoptera, which were rare in other species, and *E. depressirostris* contained only odonatan nymphs. All other species contained predominantly nymphs of Ephemeroptera and Odonata and the larvae of various Diptera (mainly Chironomidae) with no clear preferences.

Although the two stenophagous mormyrid species show an almost complete dietary overlap, they are markedly different in size (Table 2), with *P. catostoma* seldom exceeding half the length attained by *M. macrolepidotus* (Jubb 1967). The mean length ratio of 1,9 between *M. macrolepidotus* and *P. catostoma* is well outside the probable limit for coexistence between two species with a qualitative diet overlap, suggested by Hutchinson (1959) as being approximately 1,3. Hutchinson's limit is based on an approximate body mass ratio of 2; the mean body mass ratio for the two species considered here was 4,6. Size differences such as these, logically imply prey size selection by the species concerned, and our subjective assessment did indeed suggest that *M. macrolepidotus* tended to take the later instars, particularly of odonatan nymphs. However, this cannot be substantiated, as no measurements were made. Hutchinson (1959) further predicted that, for two coexisting species dependent upon the same resource but separated by size, the larger of the two will breed before the smaller if impact on the resource is to be minimized. This would allow each species sole access to that part of the resource size spectrum which must be shared during growth. Such staggering of the breeding cycle was not apparent in our investigation, both species having ripe gonads by October, ripe running individuals occurring with the first floods.

Blake (1977), Corbet (1961) and Petr (1968), all of whom have studied a variety of mormyrid species, are unanimous in their conclusion that there is very little trophic divergence within the family, and that intraspecific variations in diet often exceed interspecific differences. Apart from Petr (1968), who alludes to prey size differences but gives no measurements, prey size selection is not considered by these authors. Mormyrids generally inhabit turbid waters, and comparisons between our own day and night catches are indicative of both *P. catostoma* and *M. macrolepidotus* being active mainly at night; this precludes visual size selection. However, those mormyrid species studied have been shown to locate prey through distortions of a pulsed electric field generated by a weak electric organ situated in the tail region (Lissman 1958; Bullock 1973). That electrolocation is important to *P. catostoma* and *M. macrolepidotus* may be inferred from their absence from our catches from floodplain lakes in which the conductivity of the water exceeded 300 µS cm»fb^{1}, since high conductivities seriously impair the efficacy of the mormyrid type of electrolocation system (Bullock 1973). Lissman & Machin (1958) have shown the mormyrid *Gymnarchis niloticus* as being capable of distinguishing between two glass rods of 4 mm and 6 mm diameter encased in porous pots. If this degree of discrimination is manifest in all Mormyridae, then prey size discrimination concomitant with the size difference between *P. catostoma* and *M. macrolepidotus* is certainly feasible. Qualitative discrimination by this means is, however, far less likely, which might account for the qualitative uniformity of the diet within the family as a whole.

S. zambezensis overlaps with the two mormyrid species in being nocturnal and in diet; its size approximates that of *M. macrolepidotus.* It is a nocturnal tactile bottom feeder with a substantial diet breadth, its significant dietary overlap with the mormyrids being attributable to the importance of insect subimagines in its diet. Its mode of prey location, being dependent largely on contact with its prey, is likely to prove less effective than the remote sensing by electrolocation of the Mormyridae. This, if true, would confer a greater competitive advantage on the latter, allowing *S. zambezensis* to coexist with *P. catostoma* and *M. macrolepidotus* only by virtue of its diet breadth.

When considering the likelihood of competiton for a resource such as aquatic insects, which has been shown here to be preyed upon by several fish species, cognisance must be taken of the availability and productivity of that resource. Petr (1968) draws attention to the considerable fecundity and thus reproductive potential of insects, and concludes that, in a shallow productive lake such as Lake Volta, there would be an adequate and continuous replenishment of the aquatic insect resource to sustain several exploiting species. The Pongolo floodplain lakes are shallow with alternate inputs of allochthonous and autochthonous plant material contributing to the detritus food web (Heeg & Breen 1982; Rogers 1980), which includes many insect species, notably chironomids. Walley (1979) has studied the distribution and standing stock biomass of benthic macroinvertebrates in four of the floodplain lakes covered by our fish study, and has estimated the production of a few species. Details of the mean standing stock of aquatic insect subimagines, extracted from Walley (1979), are given in Table 6. Production estimates derived from respiration rates using the regression method of McNeil & Lawton (1970), included only one insect species, an unidentified species of *Tanypus* (Chironomidae, Tanypodidae), for which Walley (1979) arrives at a P : B ratio of 26 for the four lakes studied. This gives a turnover time of 14 days for this species, which he regards as probably being an overestimate if applied to chironomids in general, since the carnivorous Tanypodidae have a lower growth efficiency than the more common detritivorous species (Kozlovsky 1968; Welch 1968). Even at a turnover time of 14 days, the results lend some support to Petr's (1968) suggestion. It is perhaps noteworthy that the mean standing stock of insect subimagines in Mhlolo was signficantly higher than those of the other three pans studied ($0{,}001 > P$ in all instances for logarithmically transformed data to compensate for contagion *vide* Elliott 1977). No mormyrids were caught in Mhlolo during this investigation, probably owing to the high conductivity of its water (Heeg *et al.* 1978). While it would, in the absence of further supporting evidence, be premature to attribute the comparatively large insect standing stock to the absence of mormyrids from this lake, it might give some indication of their impact on the resource.

Fruits and seeds

The fruits of *Ficus sycomorus* constituted an important, though seasonal, component of the diet of *E. depressirostris,* comprising 6,3% of the total dry mass recovered from stomachs of this species. However, owing to the seasonality of the input, these fruits only occurred in the diet over a period of four months, during which time they made up 25% of the ingested food. The large gape of *E. depressirostris,* together with its largely opportunistic surface-feeding habit, equip it to successfully exploit this resource, for which it seems to have no competitors.

Seeds of terrestrial grasses, *Acacia xanthophloea* and *Nymphea lotus* featured prominently in the diet of *A. imberi,* constituting some 40% of the stomach contents recovered from this species. That the seeds were utilized

Table 6 Composition and mean standing stock biomass of aquatic insect subimagines in four floodplain lakes over the period June 1976 to June 1978 (extracted from Walley, 1979)

	Mzinyeni		Mthikeni		Namanini		Mhlolo	
	mid pan	margins	mid pan	margins	mid pan	margins	mid pan	margins
Composition (%)								
Ephemeroptera	0	14,9	3,2	18,2	2,4	50,1	0,1	20,6
Odonata	0,5	54,1	23,3	65,6	0,0	5,1	1,2	65,2
Trichoptera	82,3	0,7	28,0	1,7	12,4	0,7	5,8	0,8
Chironomidae	15,2	23,2	38,4	9,4	69,5	44,1	80,1	13,2
Other	2,0	7,1	7,1	5,1	15,7	0,0	12,8	0,2
Mean standing stock								
(mg dry mass m^{-2})	264,3	145,0	234,4	249,4	45,0	137,5	815,8	759,9
95%confidence limits	99,1	90,4	89,1	147,2	23,6	81,7	445,5	445,6
	702,1	232,4	614,2	422,6	76,9	231,0	1493,4	1295,7
Mormyridae								
Total number caught	1645		572		751		0	
% of catch	10,4		10,5		13,5		0	

Mormyrid catches from these lakes are included, in spite of the two surveys not having run concurrently, as floodplain conditions had not changed materially.

as a food source could be deduced from their recovery in a partially digested state and from the fish having bitten larger seeds into small fragments prior to ingestion. In the exploitation of this resource *A. imberi* was apparently free from competition. Marshal & van der Heiden (1977) and Munro (1967) similarly record seeds as an important dietary constituent of *A. imberi.*

Winged terrestrial insects

Several authors have reported significant proportions of terrestrial insects in the diet of *E. depressirostris* (Gaigher 1969; Groenewald 1964) and other Schilbeidae (Corbet 1961; Petr 1967; van der Waal 1976, among others). Our results similarly show this small but nonetheless important resource to be utilized largely by *E. depressirostris.* Terrestrial insects, by virtue of their hydrofuge cuticular properties and airfilled tracheal system, are readily available to surface feeders such as the Schildeidae. Gaigher (1969) found that *E. depressirostris* in the Incomati system contained more terrestrial insects than fish during summer, a time when insects were abundant, whereas in early winter fish predominated in the diet. When considered in the context of competition for, and the impact on, fish prey as discussed earlier, the importance of terrestrial insects takes on a new dimension.

Body size and food size selection

There was no overall correlation between body size and the size of food particles selected by the fishes studied; species of similar size, i.e. whose mean standard lengths differed by less than the 1,3 ratio suggested by Hutchinson (1959), fed on foods which differed both qualitatively and in particle size (e.g. *H. vittatus / L. rosae, 0. massambicus / T. rendalli / G. giuris).* Species of different sizes which fed on the same resource did show size selection in several instances, but this did not invariably correlate with body size. A clear, albeit not statistically significant ($r = 0{,}76$; $P > 0{,}1$) correlation between body size and prey size was apparent in the three siluriforms which fed on bivalves:

S. zambezensis (128 mm) – *Eupera ferruginea* (5 mm),
C. ngamensis (421 mm) – *Corbicula africana* (15 mm),
C. gariepinus (475 mm) – *Caelatura framesi* (50 mm).

In contrast, among the piscivores, *E. depressirostris,* with a mean standard length which is 78% that of *H. vittatus* took larger fish prey than the latter, probably as a consequence of differences in skull architecture (see Alexander 1965, for anatomical details). *C. gariepinus,* substantially larger than *E. depressirostris* but sharing with it the basic morphological characteristics of the order Siluriformes, took larger prey, but the difference was not statistically significant. Thus, while it is possible to show trends which suggest a body size/food particle size correlation, deviations owing to anatomical and probably other differences between taxa complicate any such relationship.

Feeding ecology, biogeography and community assembly

On the coastal plain, the Pongolo River shares with both the upper and lower Zambezi the characteristics of what Jackson (1961) calls a reservoir river: extensive shallow lakes and swamps which retain floodwaters and provide refuges during seasons of low flow. West of the Lebombo Mountains, its character changes rapidly: the slope of the river course increases from 1 in 2 200 over the 150 km of coastal plain to 1 in 100 over the next 100 km, and the Effective Temperature (Bailey 1960) falls from 17,6°C (warm to very warm climate on Bailey's ten zone classification) to 14,6°C (mild climate). The Pongolo therefore provides a suitable habitat for any southward extension of the Zambezi ichthyofauna, but only over a limited range; beyond the Lebombo Mountains any fish species adapted to tropical reservoir river conditions are restricted by flow rate, temperature and physical obstacles.

River systems, bounded by their catchment watersheds and by the sea, afford little opportunity for access and egress to wholly aquatic, salt intolerant animals such as primary freshwater fishes. Tributary captures and confluences occur rarely and temporary connections via 'stepping stones' in the form of interconnections between coastal swamplands, sporadically and unpredictably. In this sense a river system is analagous to an island, the stepping stones to which are ephemeral. Lowe-McConnell (1975), in her summary of ecological correlates of freshwater fish communities in different types of tropical habitats, concludes that savanna floodplains, with their highly seasonal hydrological regimes and consequent fluctuations in resource and space availability, are characterized by immature, r-selected pioneer communities. The species which make up such communities are able to rapidly respond to the favourable conditions occasioned by seasonal floods, through their high fecundity, rapid growth and early maturation, all characteristics which MacArthur & Wilson (1967) attribute to successful colonizers. The Pongolo fish fauna would, therefore, have been drawn from a pool of species already pre-adapted to the effective utilization of available resources. However, under conditions which allow limited dispersal, the attributes which facilitated initial colonization would inevitably lead to pressure on resources as populations build up, particularly where seasonal fluctuations favour continued r-selection on a community of highly fecund organisms such as fishes. Predation becomes an important ecological factor in such communities, which normally include several non-discriminating piscivorous species (Lowe-McConnell 1975). The eventual selection of a community which optimizes resource utilization through competitive exclusion and niche compressions or shifts to give rise to a post-interactive equilibrium is therefore to be expected.

The colonization of the Pongolo system by tropical primary freshwater fishes from the more northern rivers is likely to have occurred during periods of high rainfall and temperature. Such conditions obtained in southern Africa at various times during the past 9 000 years (Tyson 1986) and appear to have been particularly favourable 6 000 years BP, when the whole of Africa experienced rainfall considerably higher than, and temperatures similar to, the present. While the time of colonization cannot, of course, be established, the inference is that the freshwater fish community has been an integral part of the Pongolo floodplain ecosystem for millennia, during which time it will have been subjected to a range of physical and biotic conditions. This, together with normal seasonal flood-related fluxes (Breen *et al.* 1978; Heeg *et al.* 1978; Heeg & Breen 1982) will have exerted continuous selection on the community over several thousand generations, and it should therefore be in an equilibrium state which is well beyond the interactive phase in Wilson's (1969) suggested sequence of equilibria. Within what is essentially a confined island habitat, such a community should show a minimum of competitive interactions in the optimal utilization of available resources; non-specific piscivory, which exploits the high fecundity within the community, is an essential component of such optimization. This is supported by our results. Specialist feeders with narrow diet breadths exploit the major food resources of the system:

macrophytes	*T. rendalli*
microphytes	*O. mossambicus*
detritus	*L. rosae*
fish	*H. vittatus*
molluscs	*C. ngamensis*
aquatic larval insects	*P. catostoma* (small?) *M. macrolepidotus* (large?)

In addition, three species emerge as generalists, their diets overlapping to varying extents with those of the specialist feeders and with one another. These species are separated along size, spatial and temporal dimensions:

small, diurnal, pelagic: *A. imberi*
medium sized, nocturnal, pelagic: *E. depressirostris*
large, nocturnal, benthic: *C. gariepinus*

A. imberi and *E. depressirostris* have refuge food resources which, although partly seasonal, contribute substantially to their diets. The remaining two species, *S. zambezensis* (invertebrate feeder) and *G. giuris* (specialist piscivore) occur in very low relative numbers. Fish prey ranked second only to plant-derived material in the food of the community and was recovered from all species examined except the Mormyridae. It constituted the major dietary component of *H. vittatus, C. gariepinus* and *E. depressirostris,* which together made up 48% of the community biomass.

Niche compressions along the dietary axis are also evident among the members of the community. These show up in differences between the ranges of acceptable and energetically profitable food items, as reflected in diet breadths calculated from frequency of occurrence and recovered mass respectively. Such differences range from being negligible in *P. catostoma* and *M. macrolepidotus,* through various other specialist feeders such as *L. rosae* (maximum possible 0,3) and *H. vittatus* (0,69) to the extreme generalists *A. imberi* (4,56) and *C. gariepinus* (5,63). Figure 5 shows the relationship between the two diet breadth measures of the ten species for which both could be calculated from our data. The clustering of the dietary specialists close to the isoline is indicative of minimal compression, and by inference these species have little possibility of niche shifts along the dietary axis. This is, however, offset by their efficient resource utilization, either in search, handling or both: mormyrids are highly efficient searchers by virtue of their electrolocating capability, *H. vittatus* is known to be a fast swimmer and efficient sight hunter and

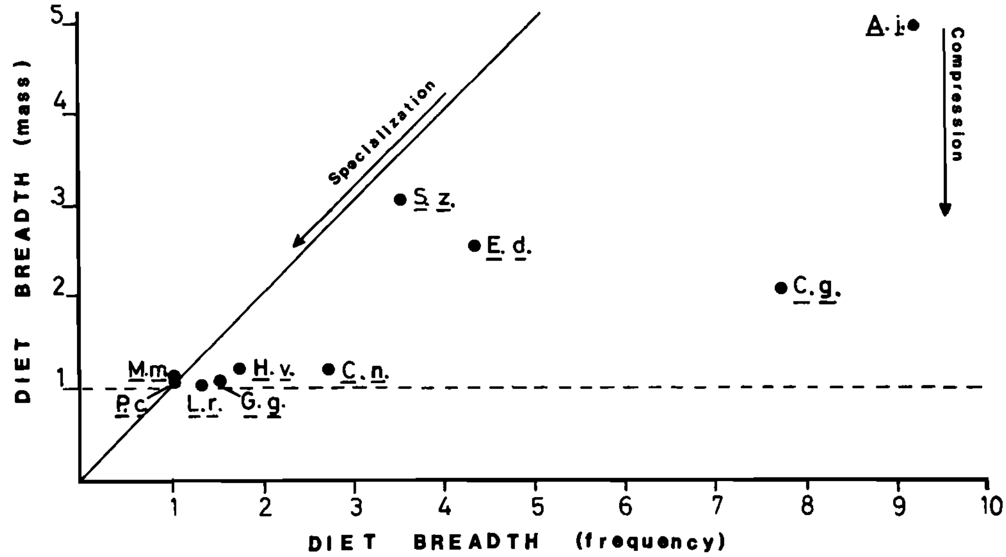

Figure 5 Relationships between diet breadths calculated from frequency of occurrence and from recovered mass of different food types for 10 of the species studied. The extent of vertical downward deviation from the isoline indicates the degree of dietary niche compression for a particular species.

L. rosae, morphologically adapted for gathering loose particulate matter from the substratum, is also likely to prove an efficient utilizer of high cellulose foods, as has been shown for other cyprinids (Cockson & Bourn 1973; Prejs & Blaszczyk 1977; Sehgal 1969). These adaptations must confer a considerable measure of resistance to competitive exclusion on the species concerned. In contrast, the generalists show marked compression concomitant with their dietary plasticity. *C. gariepinus* feeds on a variety of food types covering a size range from zooplankton to fish larger than 100 mm SL, and is thus able to exploit these resources wherever and whenever this becomes energetically profitable. Such plasticity, which also permits seasonal shifts like those which have been shown for *E. depressirostris,* allows for coexistence with the more specifically efficient specialists wherever resources occur in sufficient variety.

While the above strongly suggests that competition has been an important factor underlying the assembly of the community, neither the species concerned, nor the selection pressures, are unique to the Pongolo system. The centre of dispersal, from which the fauna of the Zambezi ichthyofaunal province is likely to have been derived, is the tropical Zaire drainage basin (Bell-Cross 1972, 1982; Bowmaker, Jackson & Jubb 1978; Roberts 1975). Bell-Cross (1972, 1982), on the basis of evidence of past geological events and a detailed analysis of the distribution of fish species in the Zambezi and adjacent river systems, suggests that at least two Plio-Pleistocence dispersal routes were necessary to account for the present distribution of the fauna. He proposes the existence, at the end of the Tertiary, of two principal drainage basins in what is now the Zambezi catchment: a western end-Tertiary basin of internal drainage (WETBID), comprising the upper Zambezi, Cunene, Okavango and plateau Kafue Rivers, and an eastern basin (EETBID), comprising the lower Zambezi below the Cahora Basa gorge, lower Kafue, Luangwa and Shire Rivers. WETBID is thought to have acquired its fish fauna through capture of a tributary of the Kasai, whereas the EETBID fauna was derived from that of the Lualaba via the pre-rifting Malagarasi and proto-Luangwa. Subsequent connection between the upper and lower Zambezi via the Victoria Falls and middle Zambezi allowed for downstream but not upstream migrations. The fauna of the lower Zambezi, which constitutes the species pool from which the fauna of the East Coast rivers, including the Pongolo, is likely to have originated (Bowmaker *et al.* 1978; Jubb 1967; Roberts 1975), is therefore itself the product of at least two separate invasions of the southward spreading tropical Zaire basin fauna. Any assembly rules (*sensu* Diamond 1975) based on species interactions can therefore be expected to be manifest in the lower Zambezi as well. Six of the species covered by our study (*P. catostoma, M. macrolepidotus, H. vittatus, C. gariepinus, C. ngamensis* and *T. rendalli*) coexist in the upper and lower Zambezi, as well as the Limpopo and Pongolo systems. A further four species shared only by the lower Zambezi, Limpopo and Pongolo are represented in the upper Zambezi either by closely related congenerics (*A. imberi / A. lateralis, S. zambezensis / S. nigromaculatus, O. mossambicus / O. andersoni*) or by very similar species (*E. depressirostris /Schilbe mystus,* the only difference between which appears to be the presence of a small adipose fin in the former). *L. rosae,* known only from rivers south of the Zambezi, is represented in that system by the closely related *L. altivelis,* of which it might well be a sub-species (Bell-Cross 1982). These species pairs are not known to coexist anywhere within their ranges (Bell-Cross 1982). Such absolute incompatibility in a continuous system known to permit downstream migrations would, according to Diamond (1975), be indicative of ecological similarity which precludes the species concerned from inhabiting the same space, and of recent speciation. The Pongolo species therefore constitute a permissible combination which apparently resists at least the inclusion of allopatrically evolved, closely related congenerics.

The number of freshwater fish species in the East Coast rivers decreases from 75 in the lower Zambezi through 50 in the Limpopo (Bell-Cross 1982) to 42 in the Pongolo (Bruton & Kok 1980). This north-south subtraction of 44%, which continues south of the Pongolo, cannot be attributed to any single factor: temperature, access distance and nature and size of habitat may all have exercised a filtering effect on the southward extending fishes. At present the temperature regime of the coastal plain between the Zambezi and Pongolo rivers is fairly uniform, lying mainly between the 18 and 19°C Effective Temperature isolines (Stuckenberg 1969), thus placing it in Bailey's (1960) 'very warm' temperature zone. The absence of sharp temperature gradients suggests a minimal temperature effect on distribution. Access to the Pongolo would have been essentially the same for all northern invading species, although some of the larger species such as *Heterobranchus longifilis* and *Mormyrops deliciosis* are likely to have been filtered out by shallow connecting waters between systems. Compared with the lower Zambezi, which includes some 600 km of river course and adjacent floodplain downstream of the Cahora Basa gorge, the Pongolo is a small system, retaining its reservoir river characteristics over only 150 km of its course. Floodplain lakes, which are of primary importance to many of the species in providing a refuge during low flow conditions as well as a productive feeding and spawning habitat, become fewer north of the Pongolo-Usutu confluence as the river diverges from the Lebombo Mountains. This further restricts the extent of utilizable habitat. There are also few tributaries with floodplain characteristics. Reduced habitat area and diversity have, on both empirical and theoretical grounds, been shown to lead to a reduction in the number of species on offshore islands, favouring those immigrants with the longest extinction time, i.e. those which are least prone to environmental stress, including competition and predation (MacArthur & Wilson 1967). Indirect evidence for the exclusion of species is manifest in the absence from the Pongolo of lower Zambezi and Limpopo species which occur in systems to the east and south of it: *Alestes lateralis,* an upper Zambezi species which is found in some tributaries of the lower Zambezi from which *A. imberi* is absent, has been recorded from the mFolozi system near Mtubatuba, *Clarias theodorae*, of which there is one doubtful record from the Pongolo, occurs in swamps surrounding Lake Sibaya and in the mFolozi system, the cichlids *Oreochromis placidus* and *Serranochromis (Serranochromis) meridianus* have been recorded from Lake Mgobezelini near Sodwana, and, *Ctenopoma multispinis* and *C. ctenotis*, swamp-living climbing perches adapted for air breathing and overland locomotion, have been found in various Zululand coastal lakes (Bruton & Kok 1980).

The Pongolo system is located between the source of these species and their southern distribution limits outlined above, which suggests that it once formed part of their invasion routes. Since climatic conditions do not differ materially between these habitats, biotic factors, including competition and predation, are likely to have been important in eliminating these and possibly other species from the Pongolo, thus contributing to the subtraction.

While our investigation leads to the conclusion that the species studied have been assembled under selection for minimal competition for food resources, this may not apply to all species which occur on the floodplain. This study has focused on the upper end of the size spectrum where the food items selected are, for the most part, large and therefore tend to be scarcer and more widely dispersed (MacArthur 1972). Eight further species which fall into this size range have not been included: four *Anquilla* species were rarely caught and the remaining four species were largely confined to the main river course. Included among the latter, *Labeo rubropunctatus,* which did occasionally occur in our catches on the floodplain, appeared from limited observations to feed almost exclusively on periphyton, thus separating it from its detritivorous congeneric, *L. rosae*. The remaining species recorded from the system were all so small as to evade capture by the methods employed. Of these, 10 are confined to the river course while a further 12 occur commonly in the floodplain pans. The latter includes seven coexisting small *Barbus* species, which should provide an interesting future study.

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