Comparative ecology of catfishes of the Upper Zambezi River floodplain

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An 8-month survey of the Upper Zambezi River, its associated floodplain and marginal upland habitats yielded 16 catfish (Siluriformes) species, among which *Schilbe intermedius* comprised over half of the 3534 specimens. Generally catfishes were most abundant in floodplain and river channel habitats, but three species (*Clariallabes platyprosopos*, *Synodontis macrostoma*, *S. nigromaculatus*) were most abundant in the river channel, and three species (*Amphilius uranoscopus*, *Chiloglanis neumanni*, *Leptoglanis rotundiceps*) were most abundant or restricted within small tributary streams. Diet analysis revealed low pairwise dietary overlaps, but there was no statistically significant pattern of community-wide niche segregation based on prey type. The 16 catfishes fell into four size/trophic guilds: large carnivores (*Clarias gariepinus*, *C. ngamensis*), medium-sized carnivores (*C. stappersii*, *C. theodorae*, *Parauchenoglanis ngamensis*, *Clariallabes platyprosopos*, *Schilbe intermedius*), medium-sized omnivores (*Synodontis leopardinus*, *S. nigromaculatus*, *S. woosnami*, *S.* sp. cf. *woosnami*), and small omnivores (*S. macrostigma*, *S. macrostoma*, *Amphilius uranoscopus*, *Chiloglanis neumanni*, *Leptoglanis rotundiceps*). No evidence of reproductive activity was detected in any of the catfishes during the survey period of falling and low water conditions. Although catfishes are not as highly valued for food as cichlid fishes, three species are significant components of local commercial and subsistence fisheries: the two large *Clarias* by virtue of their size, and *Schilbe* by virtue of its great abundance. Abundances of the heavily exploited *Clarias gariepinus* and *C. ngamensis* stocks appear to be lower in the Upper Zambezi compared with the Okavango floodplain system.
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Key words: *Clarias*; diet; habitat; *Schilbe*; Siluriformes; *Synodontis*.

INTRODUCTION

Catfishes (Siluriformes) comprise an ecologically diverse component of most major river faunas in Africa. Catfishes occupy habitats ranging from upland streams (*Amphilius* spp.) to large river channels (e.g. *Heterobranchus longifilis* Valenciennes, 1840) to seasonal floodplain lagoons (*Clarias* spp.). Feeding niches span a wide spectrum that includes detritivores (some *Synodontis* spp.), benthic insectivores (*Leptoglanis* spp.), and piscivores [*Clarias gariepinus* (Burchell, 1822) and *C. ngamensis* (Castelnau, 1861)]. Relative to research on African lakes and rivers of other continents, few studies have examined the ecological relationships of fishes in African rivers. In recent years, ecological studies have been conducted in two regions in south-central Africa, the Okavango River and its delta in Botswana (Merron & Bruton, 1988; Merron *et al.*, 1990; Merron, 1993) and the Upper Zambezi River and its floodplain in Zambia (Winemiller, 1991; Winemiller & Kelso-Winemiller, 1991, 1993, 1994).

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TABLE I. List of siluriform families and species collected from the Upper Zambezi floodplain and marginal uplands during the 1989 survey

Family	Species	Local lozi name	*n*
Claroteidae	*Parauchenoglanis ngamensis* (Boulenger, 1911)	sibutu	13
Amphiliidae	*Amphilius uranoscopus* (Pfeffer, 1889)	—	6
	Leptoglanis rotundiceps (Hilgendorf, 1905)	—	12
Schilbeidae	*Schilbe intermedius* Rüppell, 1832	lubango	1871
Clariidae	*Clarias gariepinus* Burchell, 1822	ndombe	70
	Clarias ngamensis Castelnau, 1861	ndombe	49
	Clarias stappersii Boulenger, 1915	minga	14
	Clarias theodorae Weber, 1897	minga	188
	Clariallabes platyprosopos Jubb, 1964	minga	10
Mochokidae	*Chiloglanis neumanni* Boulenger, 1911	—	3
	Synodontis leopardinus Pellegrin, 1914	singongi	494
	Synodontis macrostoma Skelton & White, 1990	singongi	26
	Synodontis macrostigma Boulenger, 1911	singongi	14
	Synodontis nigromaculatus Boulenger, 1905	singongi	46
	Synodontis woosnami Boulenger, 1911	singongi	625
	Synodontis sp. cf. *woosnami*	singongi	93

These two river basins are interconnected by the Chobe River on the border between Botswana and Namibia, and they consequently share much of their fish faunas (van der Waal, 1985; Skelton, 1993*a*). Ecological investigations of catfishes have been complicated by the confused state of taxonomy, especially for the mochokid genus *Synodontis*. Recent work has clarified the taxonomy of some groups (summarized by Skelton, 1993*a,b*), but other groups require additional work. Here we report the findings of an 8-month investigation of the distribution, abundance, and ecology of catfishes in the Upper Zambezi River, its associated floodplain, and marginal uplands. Population size structure, habitat use, and diets are analysed in the context of resource segregation.

UPPER ZAMBEZI STUDY REGION

The study region is in Zambia's Western province (Winemiller, 1991). The Upper Zambezi River (Fig. 1) flows through the Barotse floodplain, a broad grassland that undergoes seasonal inundation. Annual rainfall averages 826 mm, nearly all of it falling between November and March. Water temperature (measured at 1200 hours) ranged from 18·0° C (7 Aug) to 28° C (23 Nov) in lagoons, and from 21° C to 27·5° C in channels. pH ranged from 5·5 in certain floodplain pools to 7·0 in the Kabompo River.

TAXONOMY

Sixteen catfish species from five families were collected within the study area (Table I). We based our field identifications primarily on descriptions in Poll (1971) and Bell-Cross & Minshull (1988). The most current summary of the ichthyology of southern Africa appears in Skelton (1993*a,b*). Following new information in Skelton & Teugels (1991), several clariid specimens that we
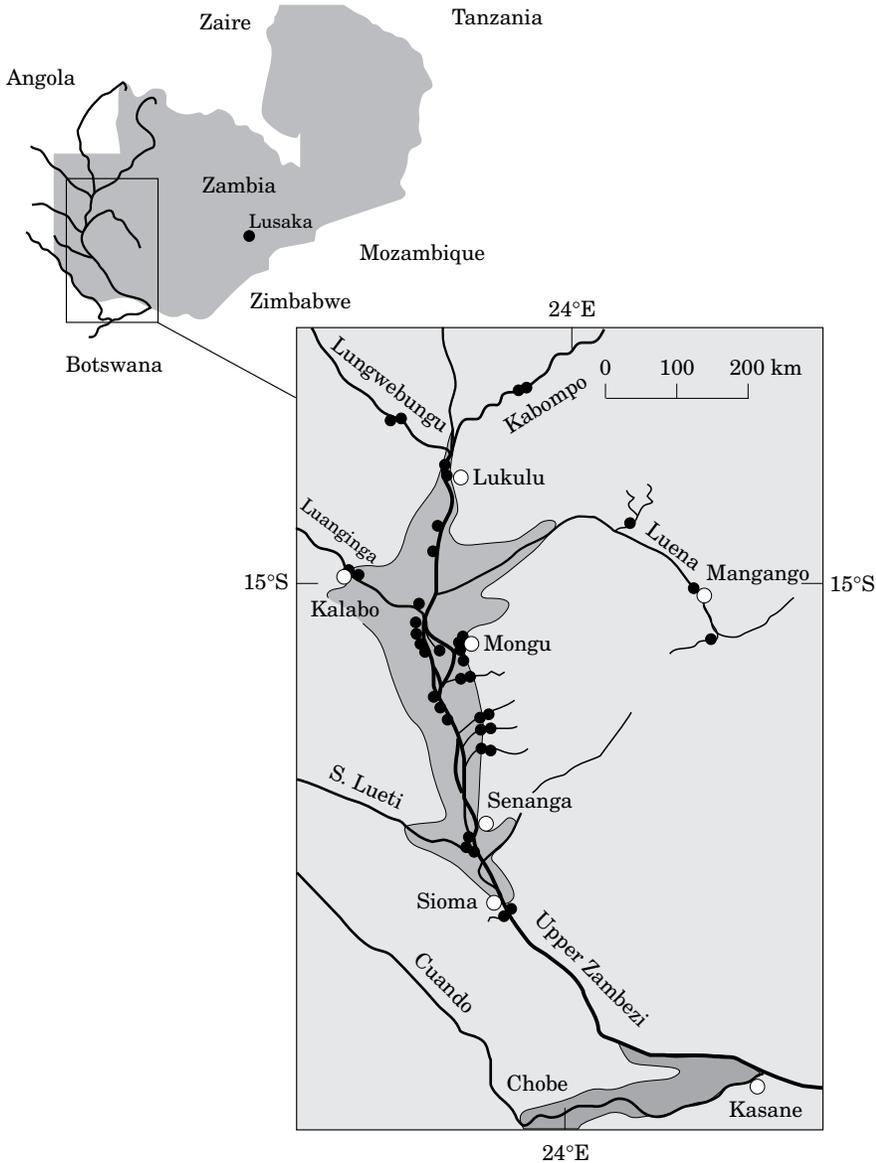
FIG. 1. Map showing the Upper Zambezi River study region in Zambia. Shaded regions represent floodplains; ●, principal collection sites.

identified tentatively as *Clarias dumerilii* Steindachner, 1866 are identified now as *Clariallabes platyprosopos* Jubb, 1965. Southern African *Schilbe mystus* (Linnaeus, 1762) are recognized now as *Schilbe intermedius* (DeVos & Skelton, 1990).

At the time of our field study, we recognized six fairly distinct morphotypes of the mockokid genus *Synodontis*, four of which are recognized species (*S. leopardinus*, *S. macrostigma*, *S. nigromaculatus*, and *S. woosnami*). One morphotype was identified tentatively as *S. nebulosus* Peters, 1852, but is

recognized now as a distinct new species, *S. macrostoma* (Skelton & White, 1990). The sixth morphotype was very similar to *S. woosnami*, but varied sufficiently from the species description to cause us to treat it as a separate unit in our study. These fish, called *S.* sp. cf. *woosnami* throughout this report probably represent a phenotypic variant of *S. woosnami* with fewer mandibular teeth (11–13) than the minima previously reported by Poll (1971) (23) and Skelton (1993*a*) (14–24). Since our survey, Skelton & White (1990) reported two additional *Synodontis* from the Okavango River basin, *S. thamalakanensis* Fowler, 1935, and a new species, *S. vanderwaali* Skelton & White, 1990. Our *S.* sp. cf. *woosnami* does not conform to Skelton & White's (1990) description for *S. thamalakanensis* or that for *S. vanderwaali*. Based on the attributes described by Skelton & White (1990) and Skelton (1993*a*), we were unable to confirm the presence of *S. thamalakanensis* or *S. vanderwaali* in the region of the Barotse floodplain.

MATERIALS AND METHODS

The field study was conducted from 21 May to 9 December 1989 on a monthly sampling schedule. Most collections were made from the floodplain region; however some samples were also taken at irregular intervals from tributary rivers and upland streams flowing into the floodplain (Fig. 1). A complete list of collection sites and dates is filed at the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas, U.S.A. Environmental conditions at each fish sampling site were recorded, including substrate composition, vegetation, water temperature, pH, and dissolved oxygen content. Several fish sampling methods were used at each site, but our primary objective was to obtain a sample at each location that reflected species' relative abundances and the size structure of populations. In general, our methods did not collect catfishes <25 mm SL. At river channel and floodplain sites, we used hook and line, castnets (2·54 cm mesh), dipnets (0·3 cm mesh), seines (30·5 × 2 m, 2·54 cm mesh and 6 × 1·5 m, 0·63 cm mesh), and overnight sets of monofilament nylon gillnets [4(2 × 50 m segments)=1(15·25 cm mesh)+2(10·22 cm mesh)+1(5·08 cm mesh)]. Small tributary streams and shallow floodplain pools were sampled only with dipnets and seines. At most sampling sites, we collected fishes from all available habitats, such as deep channel, sand bank, and emergent vegetation. Fishes were either placed in insulated boxes and examined within 18 h of capture or preserved in 15% formalin and stored for later examination.

Once each week during September–December, the commercial catch from Mukakani Village (15°27′ S, 23°7′ E) was examined in Mongu. To supplement data derived from our own field samples, catfishes from the commercial catch were measured and their stomach contents examined. In addition, two large floodplain samples from a local fisherman's 'maalelo' traps were preserved in June (15°23′ S, 23°10′ E; 1 km east of Sefula on edge of central floodplain) and July (15°18′ S, 22°53′ E, 16 km east of Mongu and 3 km east of Zambezi River on Malile canal). Maalelo are dams constructed of grass mounds or reed fences that block the return of water from the plain to lagoons and permanent channels (Kelley, 1968). Reed fish traps with funnel-type, no-exit passages are placed behind openings in the dams. Each sample was classified by one of four macrohabitats: the Zambezi River channel, marginal floodplain habitats (lagoons, sloughs, canals), large tributary rivers (e.g. Kabompo, Luanginga), and small upland tributaries (e.g. creeks entering the floodplain south of Mongu and creeks entering the upper Luena River).

Standard length (SL), gonad condition, and stomach contents were recorded for each dissected specimen. Methods for assessing gonad condition followed Winemiller (1989*a*). Stomach contents were quantified volumetrically by water displacement as described by Winemiller (1989*b*). Fish prey were identified to genus and species whenever possible,

and invertebrates were identified to order. Some of the prey categories were combined later into broader taxonomic or functional categories for quantitative comparisons. These diet categories were fish families, unidentified fish, fish scales, microcrustacea, macrocrustacea, aquatic insects, terrestrial insects, molluscs, microfauna (e.g. nematodes, protozoa), algae, seeds, and detritus/vegetation/sediment. For each recognizable prey item, prey size was recorded in 10-mm size intervals based on the anterioposterior axis (e.g. SL in fishes). For prey that were recognized but partially digested, the length of the intact organism was estimated.

Diet diversity was estimated using the standardized version of Levins' (1968) index of niche breadth and the volumetric dietary proportions (p_{ij}) for 23 aggregated resource categories. Diet similarities were calculated using Pianka's (1973) symmetrical measure of niche overlap. For both indices, values may range from near 0 (specialized diet, or almost no overlap) to 1·0 (even use of food resources, or complete overlap). For the calculation of diet overlap, we first converted volumetric dietary data to electivities (e_{ij}) based on Lawlor's (1979) method. Electivity adjusts the measure of resource use as a ratio of consumption to availability. Because sample sizes were very uneven in this dataset, raw volumes for each species first were standardized to a total volume of 1·0. The total volume of each prey item consumed by catfish species collectively was employed as the measure of its availability for the catfish assemblage. Although this method can only be used with large samples involving many species, it has the advantage of treating the fishes as the estimators of resource availability, and reduces biases from human sampling of resources, some of which may actually be more or less available to the fishes (Winemiller & Pianka, 1990). Following the rationale and protocol of Winemiller & Pianka (1990), we computed the geometric mean of the p_{ij} and e_{ij} for each prey category for each consumer. Raw diet proportions tend to inflate overlaps when consumers eat large fractions of highly available prey, whereas the use of electivities to compute overlaps can bias in the direction of low overlaps when one member of the species pair feeds on small amounts of one or more rare prey items (Winemiller & Pianka, 1990). The frequency distribution of species pairwise diet overlaps was used to estimate relative diet similarities within the Upper Zambezi catfish assemblage. To examine the likelihood that observed levels of diet overlap are higher or lower than expected based on random expectations, we also performed a computer randomization of the resource matrix (scrambled zeros method of Winemiller & Pianka, 1990) and plotted mean diet overlaps by nearest neighbour rank for observed and randomized datasets.

RESULTS

Three of the 16 species collected within the study area (*Schilbe intermedius*, *Synodontis woosnami*, *S. leopardinus*) comprised >84% of our total catfish sample of 3534 (Table I), and *Schilbe intermedius* alone accounted for over 50% of the total. Eight species had relative abundances <1% of the total (Table I). These relative abundances are biased in favour of species inhabiting the primary river floodplain, where most of our sampling effort was directed. None of the river channel and central floodplain catfishes were in spawning condition during the study period.

The 16 species spanned a wide range of adult sizes (Fig. 2), the largest being *Clarias gariepinus* and *C. ngamensis* of the river channel and marginal floodplain habitats. The two smallest species were *Chiloglanis neumanni* and *Leptoglanis rotundiceps* from upland streams. The Upper Zambezi catfish assemblage was partially size-segregated among species (Fig. 2). Whereas complete segregation between nearest neighbours was not observed, the 16 species were spread out very evenly across the spectrum of assemblage body sizes. The five clariids were the longest species, in part because they have elongated bodies.
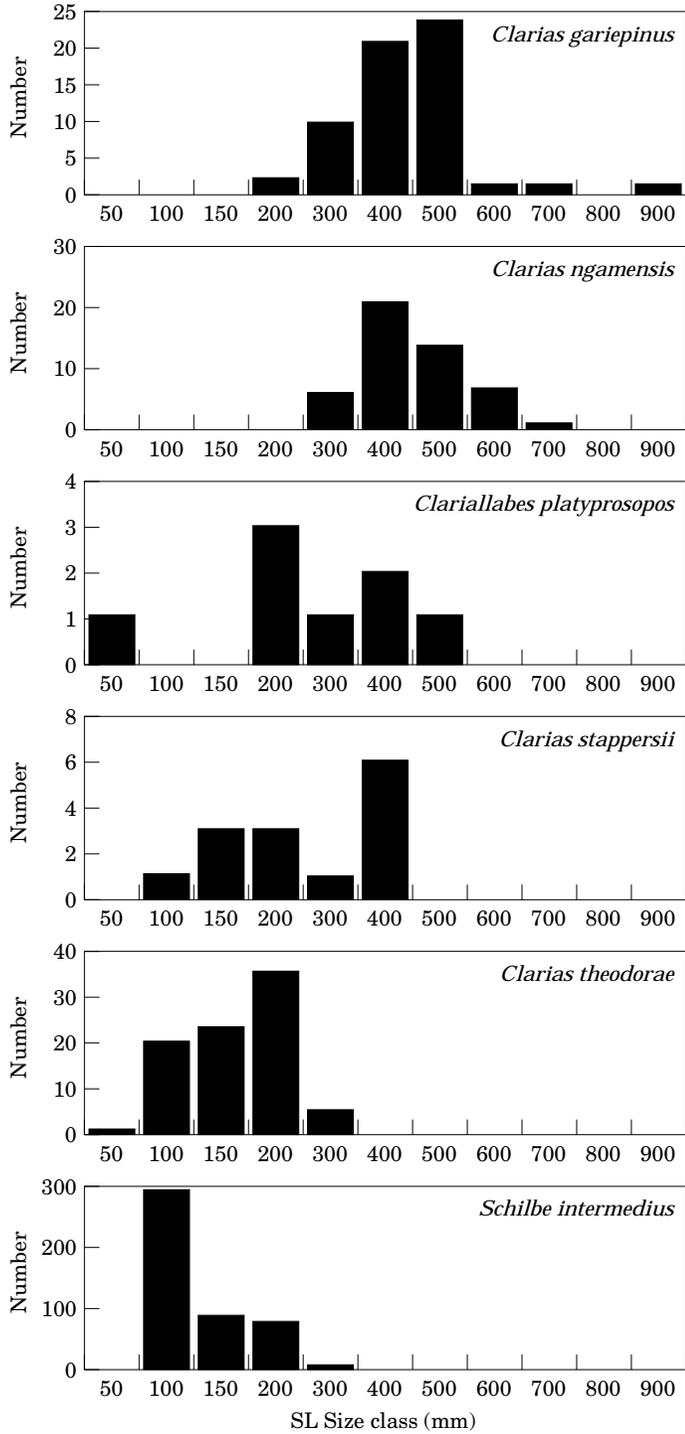
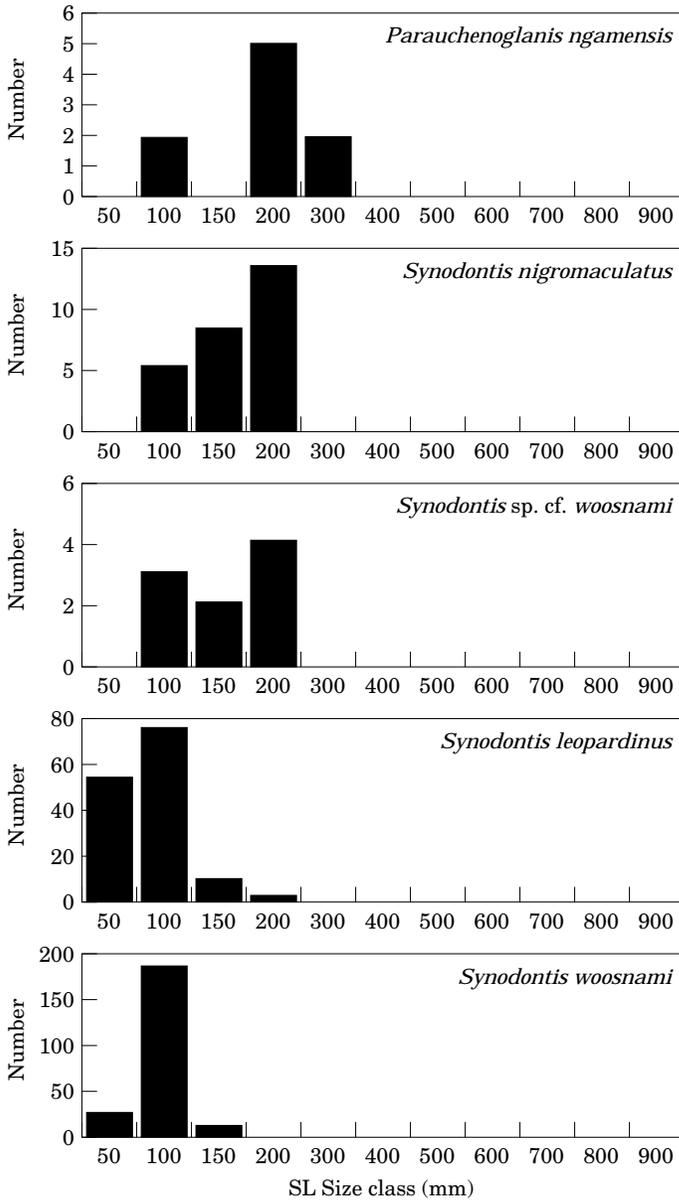FIG. 2. Standard length frequency distributions of Upper Zambezi catfishes.

FIG. 2. Continued.

Capture data were analysed by species percentage frequencies in the four macrohabitats. Most species occurred in multiple macrohabitats, with the greatest percentage captured from the floodplain (Fig. 3). *Clariallabes*, *S. nigromaculatus*, and *S. macrostoma* were more common in the main river channel, although smaller percentages of these two *Synodontis* species were captured from all four macrohabitats (Fig. 3). In every species that occurred in multiple habitats, river channel specimens tended to be larger than conspecifics captured from other macrohabitats. *Schilbe* was the one exception to this rule,
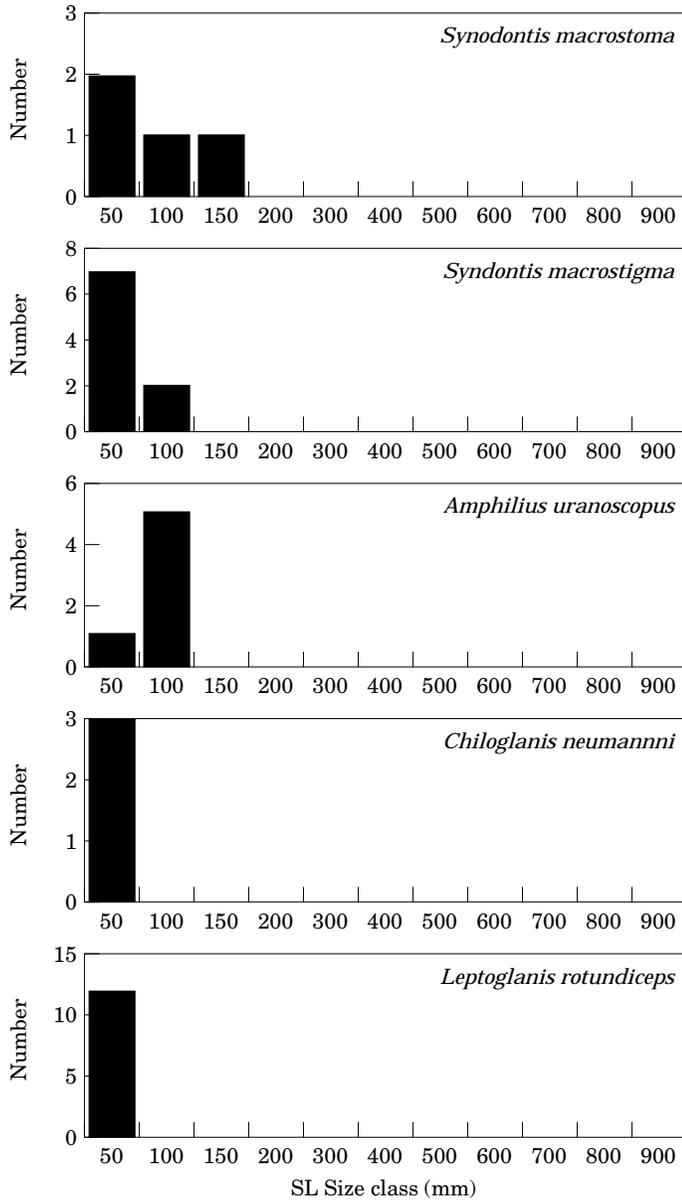
FIG. 2. Continued.

and large *Schilbe* (>200 mm SL) were taken from both river and floodplain habitats in about the same ratio. The three small catfishes (*Amphilius*, *Chiloglanis*, *Leptoglanis*) were restricted largely to small upland tributaries, however these samples were small (Fig. 3). A single *Chiloglanis* was captured from submerged grasses in the swift-flowing Lungwebungu River, and *Chiloglanis* appeared in stomach contents from three predators captured from the Zambezi River [*C. ngamensis*, *Clariallabes*, *Serranochromis robustus* (Günther, 1864) (Cichlidae)].
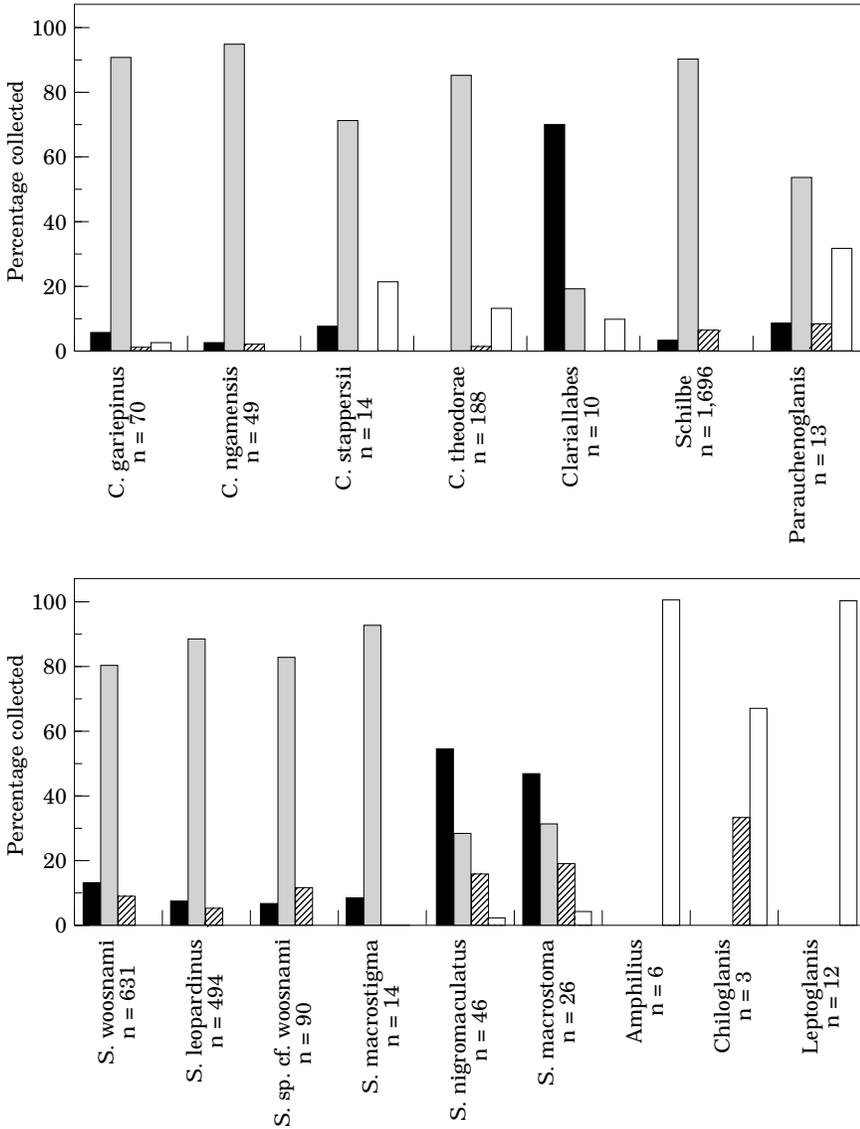
FIG. 3. Percentages of carnivorous (top) and omnivorous (bottom) catfishes collected from the river channel of Zambezi River, floodplain habitats (=sloughs, lagoons, backwaters, canals), tributary rivers, and small tributary creeks of the uplands. ■, river; ▨, floodplain; ▨, large tributaries; □, small tributaries.

Volumetric proportions of 13 diet categories consumed by 12 large and medium-sized catfishes with sample sizes >8 indicate a general separation of the fauna into two trophic groups: macrophagous carnivores (*Schilbe*, *Parauchenoglanis*, and the five clariids) and microphagous omnivores (the five *Synodontis* species) (Table II). Diets of the two largest carnivores, *C. gariepinus* and *C. ngamensis*, were very similar, with both consuming mostly perciforms (primarily Cichlidae) and siluriforms (mostly *Schilbe* and *Synodontis* species). *Clarias gariepinus* consumed more perciforms and fewer siluriforms than

TABLE II. Relative volumetric proportions of diet categories consumed by 12 catfishes of the Upper Zambezi River and floodplain showing dietary divergence between macrophagous carnivores and microphagous omnivores

Species	n	Mis. fish	Mormy.	Silurif.	Charac.	Cyprini.	Percif.	Insects	Crustac.	Mollus.	Microfa.	Seeds	Algae	Detritus	B
Schilbe (Vol.=259·1 ml)	458	0·143	**0·294**	0·124	0·009	**0·308**	0·070	0·036	0·005	0	0	0	0	0·005	0·17
Clarias gariepinus (Vol.=93·1 ml)	60	0·123	0·032	0·107	0	0·005	**0·688**	0·023	0	0	0	0	0	0·022	0·04
C. ngamensis (Vol.=104·3 ml)	49	0·063	0·034	**0·353**	0·001	0	**0·384**	0·028	0·047	0·006	0	0·001	0	0·056	0·12
C. theodorae (Vol.=91·7 ml)	85	**0·249**	0·001	0	0	0·033	**0·590**	0·053	0	0·002	0	0	0	0·010	0·08
C. stappersii (Vol.=17·8 ml)	14	0·068	0·135	**0·618**	0	0·006	**0·157**	0	0·006	0	0	0	0	0·010	0·06
Clariallabes (Vol.=10·4 ml)	8	**0·250**	0	0·077	0	**0·514**	**0·159**	0	0	0	0	0	0	0·000	0·08
Parauchenoglanis (Vol.=1·1 ml)	9	0	0	0	0	0	0	**0·732**	0·006	0·057	0	0	0	0·097	0·04
Synodontis leopardinus (Vol.=1·7 ml)	60	**0·294**	0	0	0	0	0	**0·403**	0·056	0·068	0·005	0·018	0·001	0·119	0·12
S. nigromaculatus (Vol.=13·00 ml)	26	**0·201**	0	0	0	0	0	0·029	0·003	**0·175**	0	**0·205**	0	0·106	0·21
S. woosnami (Vol.=3·89 ml)	92	0·001	0	0	0	0	0	0·144	0·037	0·012	0·002	**0·287**	0·062	**0·152**	0·17
S. sp. cf. woosnami (Vol.=0·72 ml)	9	0	0	0	0	0	0	**0·375**	0·022	0·004	0·001	**0·339**	0·001	**0·214**	0·10
S. macrostigma (Vol.=0·19 ml)	9	0	0	0	0	0	0	0·123	**0·842**	0	0·013	0·011	0·003	0·008	0·02

Dominant prey ($p_{ij} > 0.15$) are in boldface; B is Levins' niche breadth.

C. ngamensis (Table II). More than half of the diet of *Clariallabes* consisted of cypriniform prey (small *Barbus* species). *Clarias stappersii* consumed mostly siluriform prey, but this result was strongly influenced by a single individual that had consumed a single large *C. theodorae*. *Clarias theodorae* preyed heavily on perciforms, especially *Pseudocrenilabrus philander* (Weber, 1897) and immature haplochromine and tilapiine cichlids. *Parauchenoglanis* was essentially insectivorous, with aquatic Ephemeroptera, Diptera (Chironomidae), and Trichoptera dominant. *Synodontis leopardinus* was largely insectivorous, but also scavenged pieces of fish flesh and plant detritus (Table II). *Synodontis nigromaculatus* had a broad diet consisting of similar proportions of fish flesh, molluscs, and seeds, plus a lesser volume of detritus (10·6%) and aquatic insects (3%). *Synodontis woosnami* and *S.* sp. cf. *woosnami* were omnivorous, and consumed mostly seeds, detritus, and aquatic insects (Table II). *Synodontis macrostigma* consumed mostly crustacea (Cladocera, Copepoda, Eubranchipoda, Ostracoda) and aquatic insects (Chironomidae), however this small sample contained only juvenile size-classes (SL 35–60 mm). The *S. macrostoma* diet sample was small (n=4, SL range 46–106 mm), and the dominant food items were filamentous algae (60%), fine detritus (29%), and chironomid larvae (6%). Stomach contents of the small samples of *Amphilius*, *Chiloglanis*, and *Leptoglanis* (Table I) were not examined, but all are reported to feed on small benthic invertebrates and perhaps algae (Skelton, 1993a) and thus can be described as small microphagous omnivores.

The relationship between prey length and predator length was examined for the five most common macrophagous species (Fig. 4). The highest correlation coefficients were achieved with simple linear regression models. Except for a single 150-mm *C. theodorae* consumed by a 325-mm *C. stappersii* and a single 120-mm *Serranochromis robustus* consumed by a 420-mm *C. gariepinus*, the prey sizes consumed by the five macrophagous species were very similar (Fig. 4). Maximum prey length for *C. theodorae* was only 60 mm. The prey size distributions of the five predators showed broad overlap, but also separation of modes (Fig. 5). The three most elongate predators (*C. gariepinus*, *C. ngamensis*, *C. theodorae*) had the lowest regression slopes, and *Schilbe* and *C. stappersii* had the highest regression slopes (Fig. 4).

Synodontis nigromaculatus, *S. woosnami*, and *Schilbe* had the highest dietary niche breadths, and *S. macrostigma*, *Parauchenoglanis*, and *C. gariepinus* had lowest diet breadths (Table II). The relationship between niche breadth and consumer sample size was weak (r=0·45, d.f.=11, P>0·1). The distribution of dietary overlap values among all pairwise combinations of the 12 catfishes for which we gathered diet data shows that most species pairs had very low overlap (Fig. 6). The largest overlaps (>0·6) were for *S. woosnami* with *S.* sp. cf. *woosnami* (0·74), *Parauchenoglanis* with *S. leopardinus* (0·74), *C. gariepinus* with *C. theodorae* (0·67), *Schilbe* with *Clariallabes* (0·61), and *Parauchenoglanis* with *S.* sp. cf. *woosnami* (0·57). The assemblage randomization algorithm performed on the geometric means of dietary overlaps and electivities revealed a pattern of assemblage-wide diet segregation that was not statistically significant from random (P>0·05). Mean dietary overlaps tended to be greater than expected by chance for the first four nearest neighbours (Fig. 7).
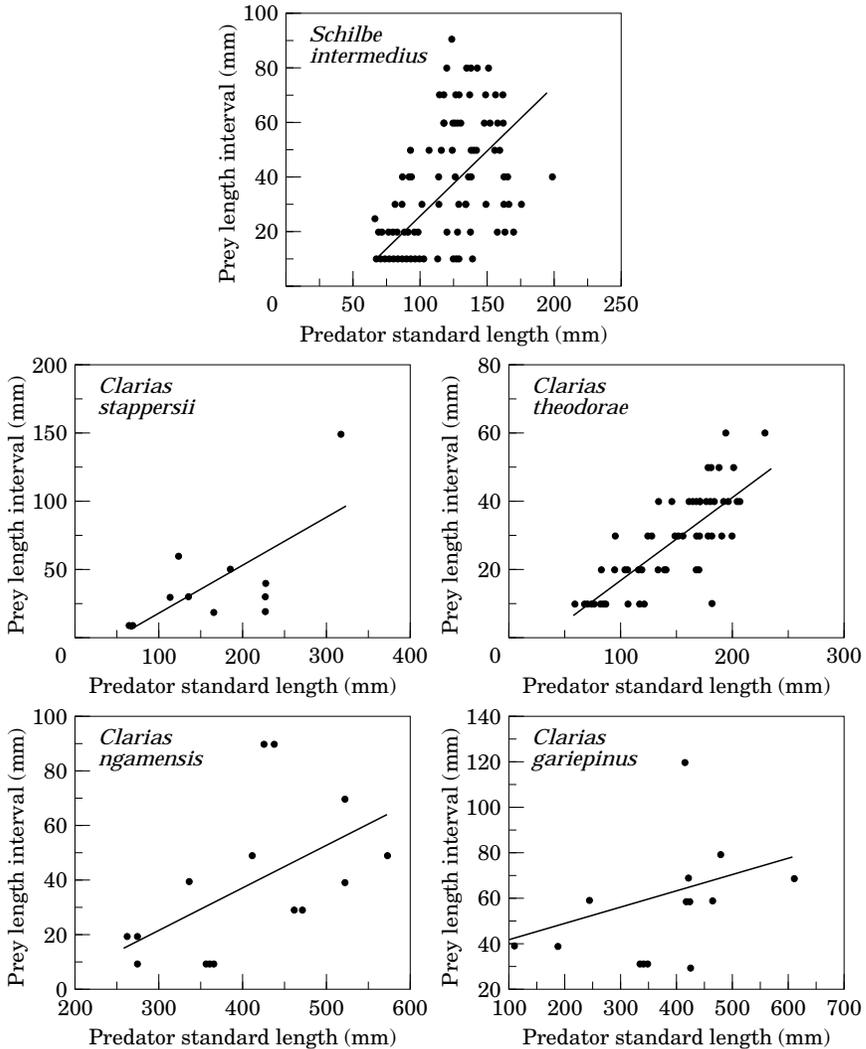
FIG. 4. Predator–prey size relationships for five common carnivorous catfishes of the Upper Zambezi based on untransformed lengths. Regression equations and coefficients were as follows: *Schilbe*, $L_{prey} = 0.46(L_{predator}) - 20.89$, $r^2 = 0.41$; *C. stappersi*, $L_{prey} = 0.35(L_{predator}) - 15.68$, $r^2 = 0.49$; *C. theodorae*, $L_{prey} = 0.24(L_{predator}) - 7.42$, $r^2 = 0.555$; *C. ngamensis*, $L_{prey} = 0.15(L_{predator}) - 23.79$, $r^2 = 0.29$; *C. gariepinus*, $L_{prey} = 0.07(L_{predator}) - 35.75$, $r^2 = 0.18$.

DISCUSSION

ABUNDANCE AND SIZE PATTERNS

Relative abundances of 16 Upper Zambezi catfishes in our ichthyofaunal survey can be compared with results from a similar survey conducted by Kelley (1968) during 1966 in the same region (Winemiller, 1966). Because of taxonomic changes and uncertainty in some of Kelley's reporting, some species had to be grouped in order to make meaningful comparisons. Siluriform abundance ranks (based on numeric abundance across all collection methods, sites, and dates)
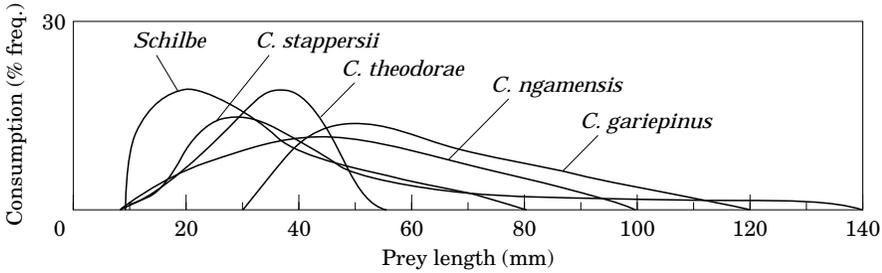
FIG. 5. Comparison of smoothed prey size distributions from stomach contents of the five macrophagous carnivorous catfishes of the Upper Zambezi. Omnivorous catfishes of all body sizes were classified as microphagus, because more than 90% of prey consumed were <10 mm.
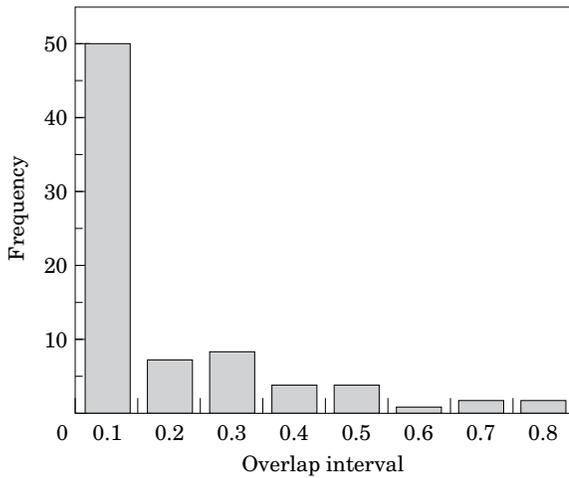

FIG. 6. Frequency distribution of dietary overlaps computed from 23 prey categories for 12 common Upper Zambezi catfishes. Only five of 66 pairwise overlaps were >0·50.

were as follows in our 1989 survey: *Schilbe* ranked third (12·04%), all *Synodontis* species combined ranked fifth (8·43%), all *Clarias* species combined ranked 12th (2·05%), *Parauchenoglanis* ranked 33rd (0·08%), and *Chiloglanis* ranked 37th (0·01%). In Kelley's 1966 survey, *Schilbe* ranked third (8·63%), all *Synodontis* species combined ranked fifth (8·51%), all *Clarias* species combined ranked seventh (4·05%), *Parauchenoglanis* ranked 24th (0·37%), and *Chiloglanis* ranked 31st (0·04%). The fact that these rankings are so similar is remarkable given the great potential for between-study differences in the sampling effort employed in different habitats. The same collecting methods were used during both studies, and both studies directed the majority of the effort at central floodplain habitats. Kelley did more collecting in the main Zambezi channel, whereas we surveyed small tributary streams and Kelley did not. In 1966, *Schilbe* ranked third behind the dwarf cichlid, *Pseudocrenilabrus philander* and the group *Aplocheilichthys* (Cyprinodontidae) species (the two groups combined for 32·9% of the total fish sample). In the 1989 sample, *Schilbe* followed *Pseudocrenilabrus* and the group *Barbus* (Cyprinidae) species (19·4% of the total sample).
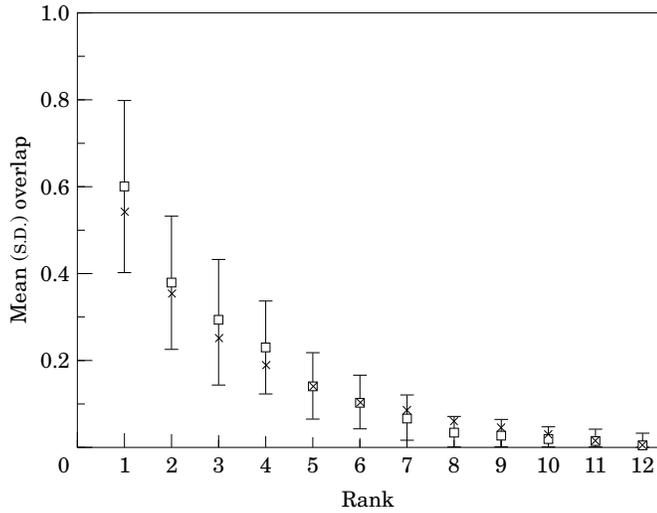
FIG. 7. Mean adjusted dietary overlaps (boxes) and standard deviations (bars) by nearest neighbour rank based on 12 common Upper Zambezi catfishes. × denotes the mean overlaps by rank based on 100 randomizations of the observed resource utilization matrix.

The relative abundances of *Schilbe* and *Synodontis* species were similar in the two studies, however *Clarias* species abundance may have declined. Whereas the group *Clarias* species declined only five rank positions, its percentage relative abundance was halved, and this may be ecologically significant. Most of Kelley's (1968) *Clarias* were adult *C. gariepinus* and *C. ngamensis*, whereas most of ours were *C. theodorae* (Kelley may have misidentified *C. theodorae* as juveniles of the two former species). It was apparent from our low water surveys of the main Zambezi River channel that the two large *Clarias* species were not abundant in the region. The two large *Clarias* were reported to be more abundant in the Kafue River to the east, and in the Lake Liambezi (Chobe River) and Okavango Delta regions to the south. In the Kafue Flats floodplain of central Zambia, *C. gariepinus* was the third most abundant species in gillnet samples, and it outnumbered *C. ngamensis* 4 : 1 (Chapman *et al.*, 1971). The two large *Clarias* dominated the ichthyofauna in regions of the floodplain that experienced aquatic hypoxia (Chapman *et al.*, 1971; Lagler *et al.*, 1971). Dissolved oxygen was measured at most of our sample sites, but we never encountered conditions of extreme aquatic hypoxia during our surveys.

In 1989, *S. woosnami* was the most abundant mochokid, followed closely by *S. leopardinus*. These species are very similar in appearance and in many of their ecological attributes (discussed further below). *Parauchenoglanis* was more abundant in Kelley's samples and *Chiloglanis* was extremely rare in both Kelley's and our samples.

Our size distributions for Upper Zambezi *C. gariepinus*, *C. ngamensis*, *Schilbe*, and *Synodontis* species are very similar to those reported earlier for the Upper Zambezi (Kelley, 1968), Lake Liambezi (van der Waal, 1985), and the Okavango Delta (Merron, 1993). For example, most *C. gariepinus* were between 400 and 600 mm SL in all four studies. The maximum size of *C. gariepinus* in our sample was 820 mm, compared with approximately 1000 mm in Kelley's Upper Zambezi

and van der Waal's Liambezi samples, and 740 mm in Merron's Okavango sample.

RESOURCE USE

Floodplain lagoons and channels were the most important habitats for catfishes of the region. Ten catfishes were much more frequently captured in floodplain habitats, three species (*Clariallabes*, *S. macrostoma*, *S. nigromaculatus*) were more abundant in the river channel (but also occurred in all four habitat categories), and three small species (*Amphilius*, *Chiloglanis*, *Leptoglanis*) were primarily inhabitants of small upland streams. Predation by the tigerfish (*Hydrocynus*) may structure river fish communities in Africa and may limit the occupation of the main river channels by other fishes (Jackson, 1961). Only certain species with morphological defences such as large spines, *Synodontis* most notably, are able to co-exist with tigerfish. In this context, it is perhaps relevant that the channel-dwelling *S. nigromaculatus* is the largest of the Upper Zambezi *Synodontis*, but *S. macrostoma*, also a channel inhabitant, is the smallest. Our few *S. macrostoma* were taken from vegetation near the river's edge. *Clariallabes* tends to be associated with swift water and coarse rocky substrates where it can hide, and some of our specimens came from such a habitat in the Ngonye Falls area. Among the three species most common in river channels, those individuals collected from other habitats tended to be juveniles. In general, all of the river and floodplain species move on to the flooded plain for spawning. Seasonal spawning migrations have been reported for several of these species in other seasonal floodplains, such as the Kafue Flats (Chapman *et al.*, 1971) and Okavango Delta (Merron & Bruton, 1988). Most of the fishes captured by the maalelo traps were juveniles spawned on the flooded plain.

The 16 catfishes segregated into four size/trophic guilds: large carnivores (*Clarias gariepinus*, *C. ngamensis*), medium-sized carnivores (*C. stappersii*, *C. theodorae*, *Parauchenoglanis ngamensis*, *Clariallabes platyprosopos*, *Schilbe intermedius*), medium-sized omnivores (*Synodontis leopardinus*, *S. nigromaculatus*, *S. woosnami*, *S.* sp. cf. *woosnami*, *S. macrostigma*, *S. macrostoma*), and small omnivores (*Amphilius uranoscopus*, *Chiloglanis neumanni*, *Leptoglanis rotundiceps*). The two large carnivores and all but one of the medium-sized carnivores consumed mostly fishes. In our samples, *Clarias gariepinus* tended to be larger than *C. ngamensis* and tended to feed on larger prey. *Parauchenoglanis* consumed mostly aquatic insects and only about 6% molluscs (volumetrically) in our study, compared with consumption of mostly detritus, aquatic insects, and molluscs in Kelley's (1968) study. *Parauchenoglanis* samples were small in both studies.

All six *Synodontis* species were omnivores, but interspecific differences were noted. Except for one species pairing (*S. woosnami* with *S.* sp. cf. *woosnami*), all *Synodontis* differed by at least 0·25 in their proportional use of one or more of the following resource categories: fish (mostly pieces of flesh, but also including scales), aquatic insects, seeds, and detritus. Although the diet sample for specimens recorded as *S.* sp. cf. *woosnami* was small (*n*=9), their diet was very similar to that of *S. woosnami*, and this indicates that the former actually may be a morphotype (with low mandibular tooth counts) of the latter. The fish remains taken from *S. leopardinus* and *S. nigromaculatus* stomachs were never in the form

of a whole carcass, and most times consisted of small pieces of fish flesh or scales. Apparently, these relatively small-mouthed catfishes scavenge pieces of fish remains from the bottom sediments. Our small diet sample for *S. macrostigma* (*n*=9) indicated specialization on microcrustacea (84·2% by volume), and our small sample for *S. macrostoma* (*n*=4) revealed a high degree of algivory (60%). Because of the taxonomic problems and changes associated with the genus, it is difficult to compare our *Synodontis* dietary data with those from previous studies. Kelley (1968) distinguished only between the distinctive *S. nigromaculatus* and *S. woosnami* (the latter group had to contain a mixture of the remaining five congeners). Kelley's *S. nigromaculatus* sample yielded aquatic insects, fish remains, plant detritus, periphyton, and smaller amounts of seeds and molluscs. Our sample for this species contained fewer aquatic insects, no algae, and more molluscs and seeds. Van der Waal's (1985) diet sample for Liambezi *S. nigromaculatus* contained mostly fish remains, aquatic insects, and plant detritus. Based on our dietary data, Kelley's *S. woosnami* diet sample (dominated by plant detritus, aquatic insects, molluscs, fish remains, periphyton) is consistent with the view that this taxon was a conglomeration of the undocumented congeners.

Our *Schilbe* sample revealed more piscivory and less insectivory compared with the earlier Upper Zambezi sample (Kelley, 1968) and that from Lake Liambezi (van der Waal, 1985). Smaller *Schilbe* size-classes consumed greater fractions of aquatic and terrestrial insects and smaller fractions of fishes. Diets of *C. gariepinus* and *C. ngamensis* were similar to those reported by Kelley; however the latter study did not distinguish prey fish types. Our diet data for the two large carnivores agree closely with findings of van der Waal (1985) for Lake Liambezi and Chapman *et al.* (1971) for the Kafue Flats. In each case, *C. gariepinus* consumed a greater fraction of fishes, especially cichlids, and *C. ngamensis* consumed more invertebrates, including molluscs.

Merron (1993) reported pack hunting by *Clarias gariepinus* and *C. ngamensis* in the Okavango Delta of Botswana. During the low water period from October to December, Merron was able to follow large shoals moving upstream along the edge of the river channel. In the Okavango Delta, pack hunting *Clarias* fed primarily on weakly electric mormyrids, especially *Marcusenius macrolepidotus* (Peters, 1852) and *Petrocephalus catostoma* (Günther, 1866). Merron heard distinctive slurping sounds believed to result from suction feeding and aerial respiration, and most of the shoaling catfishes were observed to feed actively among the dense stands of papyrus along the channel margin. We did not observe pack hunting by *Clarias gariepinus* and *C. ngamensis* during our study. The Okavango and Upper Zambezi floodplains have very similar schedules of inundation and water recession. Because Merron observed most pack hunting during October with a gradual decline in shoaling activity through December, our surveys should have encompassed the period of peak shoaling had it occurred.

Our failure to observe shoaling in the Upper Zambezi is probably due to reduced densities of large catfishes due to commercial and artisanal fishing. From approximately May until December–January each year, fishermen harvest fishes by gillnet, harpoon, seine net, hook and line, and a variety of fish traps. According to our observations, basic fishing methods have not changed

appreciably since Kelley's (1968) survey, but the number of fishermen probably has increased. *Clarias gariepinus* and *C. ngamensis* formed a relatively small fraction of the commercial catch from the central floodplain throughout the fishing season. Whereas most of the total fish catch was obtained by gillnet and seine, many of these large catfishes were captured by harpoon. During the early portion of the falling water season a few fishermen use drifting gillnets to harvest tigerfish, *Hydrocynus vittatus* (Castelnau, 1861), and large catfishes from the main river channel. We assume that if a large catfish shoal were to form in the central Barotse floodplain, it would be located quickly and harvested by commercial seine netters and harpoon fishers.

Fish provide the major animal protein component of the Lozi diet, but catfishes are not as highly valued as cichlids. The highest prices in local markets are obtained for fresh cichlids, especially large tilapiines. The large *Clarias* are sold primarily fresh or salted and dried, and small *Clarias*, *Schilbe*, and *Synodontis* species are generally sun dried (usually without salting) and stored for several days or months before being consumed. Because they are large and tend to congregate in the river channel and permanent floodplain lagoons during the dry season, *C. gariepinus* and *C. ngamensis* may be more susceptible to exploitation (especially harpooning) than smaller catfishes. The reduction in the abundance of *Clarias*, as indicated from surveys conducted two decades apart, could have resulted from increased fishing pressure. In contrast, *Schilbe* and *Synodontis* species remain among the most abundant fishes in the region, and potentially could support exploitation above current levels.

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