

Comparative ecology of the African pike, *Hepsetus odoe*, and tigerfish, *Hydrocynus forskahlii*, in the Zambezi River floodplain

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The ecology of sympatric African pike, *Hepsetus odoe* (Hepsetidae), and tiger fish, *Hydrocynus forskahlii* (Characidae), were compared during high (May–August) and falling water (September–December) conditions in the Upper Zambezi R. drainage of Zambia. Both species were common in the central and southern regions of the river and associated floodplain, and *Hydrocynus* was common in the northern region in swift flowing tributaries where *Hepsetus* was rare. *Hepsetus* inhabited vegetated environments of river backwaters, lagoons, and sluggish tributaries, whereas *Hydrocynus* occupied the open water of the main river channel almost exclusively. During the period of annual flooding, juveniles of both species coexist in flooded savanna regions. Size distributions of adult *Hydrocynus* and *Hepsetus* changed relatively little between high and low water conditions. Stomach contents analysis indicated that adult size classes of both species are almost entirely piscivorous, and both show diet shifts with changes in size. Only very small seasonal diet shifts were noted. Approximately 50% of the diet of *Hepsetus* consisted of haplochromine cichlid fishes, but also included large numbers of tilapine cichlids and mormyrids. *Hydrocynus* consumed primarily cichlid fishes, but also consumed large percentages of *Hepsetus* and small characid fishes. Small size classes of *Hepsetus* fed heavily on small mochokid catfishes (*Synodontis* spp.) and later shifted to a diet of cichlids and mormyrids, and small *Hydrocynus* preyed heavily on *Barbus* spp. (Cyprinidae), small characids, and mormyrids. Ratios of prey length–predator length averaged approximately 0.26 for *Hydrocynus* and nearly 0.40 for *Hepsetus*. The large potential for food resource competition appears not to be realized due to a very high degree of habitat partitioning between larger size classes of the two species. At the interface between river backwaters and channel habitats, *Hydrocynus* is a significant predator of *Hepsetus*, a factor that should further restrict the occurrence of the latter in open areas of the main channel.

Key words: Barotse floodplain; *Hepsetus odoe*; *Hydrocynus forskahlii*; piscivory; seasonality; Zambezi River.

INTRODUCTION

The African pike, *Hepsetus odoe* (Bloch, 1794), is the sole representative of the characiform family Hepsetidae and is widely distributed in rivers in western and central Africa between Senegal and Zimbabwe. In southern Africa, *Hepsetus* are generally restricted to swampy, lentic habitats of lagoons and river backwaters, and this has been attributed to the threat of predation by the larger tigerfish in the open waters of the main river channel (Bell-Cross & Minshull, 1988; Merron *et al.*, 1990). *Hepsetus* form an important component of the subsistence catch of local fisherman in the Upper Zambezi (Zambia), Kafue (Zambia), and Okavango Delta (Botswana) floodplains, but it is not a major part of commercial fisheries (Kelley, 1968; Merron & Bruton, 1988). The tigerfish, *Hydrocynus forskahlii* (Cuvier, 1819), is an open-water piscivore widely distributed in larger

rivers and lakes of western and southern Africa. Within this region, *Hydrocynus* is often one of the most common of the larger fish species inhabiting larger rivers (Bell-Cross & Minshull, 1988). In southern Africa, *Hydrocynus* supports important commercial and recreational fisheries in the Zambezi, Okavango/Chobe Rivers and Lake Kariba.

Jackson (1961) and others hypothesized that either predation by, or possibly competition with, larger tigerfish in the open waters of the main river channel restrict *Hepsetus* to lagoons and backwaters. For example, *Hepsetus* is common in the primary river channel of the Kafue R. where *Hydrocynus* is historically absent owing to a geographical barrier (i.e., cascades at the head of the Kafue Gorge). Despite the widespread occurrence of *Hepsetus* and *Hydrocynus* throughout western and southern Africa, relatively little work has addressed their comparative ecology and coexistence. Much of the natural history information on these species was compiled from fisheries surveys and sport anglers' reports (summarized in: Jackson, 1961; Jubb, 1961, 1967; Bell-Cross, 1972; Moriarty, 1983; Bell-Cross & Minshull, 1988). Kelley (1968) noted length frequencies, length-weight relationships, gillnet selectivity, and general diets in a survey of the Upper Zambezi fishery. Van der Waal (1985) reported reproductive biology, habitat preferences, population structure and diet data for both species in Lake Liambezi (Chobe drainage). The ecology of *H. forskahlii* in Lake Kariba (Middle Zambezi River) was investigated by Matthes (1968), Balon (1971), and Kenmuir (1973). The feeding habits of *Hydrocynus forskahlii* and *H. brevis* (Gunther, 1864) in Lake Kainji, Nigeria were summarized by Lewis (1974). Here, we report the results from an 8-month study that compares diet and habitat use by *Hepsetus odoe* and *Hydrocynus forskahlii* (Fig. 1) in the Upper Zambezi R. and its associated floodplain in western Zambia.

UPPER ZAMBEZI FLOODPLAIN ENVIRONMENT

The Upper Zambezi R. drainage of Zambia's Western Province has been described elsewhere (Winemiller, 1991; and see Jubb, 1961; Kelley, 1968; Bell-Cross & Minshull, 1988), and therefore only a brief description follows. The Upper Zambezi R. flows south from the northwestern corner of Zambia, passes through eastern Angola, and re-enters Zambia at latitude 13° S (Fig. 2). Victoria Falls marks the lower limit of the Upper Zambezi drainage. The fish fauna of the Upper Zambezi is distinct from the region below the falls, although several species occur both above and below the falls (Jubb, 1967; Balon, 1974; Bell-Cross, 1972; Bell-Cross & Minshull, 1988). The Upper Zambezi is considered a reservoir-river that exhibits seasonal inundation of a very broad, gently sloping floodplain (Jackson, 1961; Jubb, 1961). The Middle and Lower Zambezi is a sandbank-river that exhibits a rapid rise in water levels within a narrow floodplain during the rainy season. Floods are more violent and flood crests pass much more rapidly in sandbank-rivers than reservoir-rivers. According to Balon (1974), environmental conditions of the Middle Zambezi inhibit colonization by Upper Zambezi fish species.

The Upper Zambezi, or Barotse, floodplain is about 30 km wide in its central region near Mongu (Fig. 2) and approximately 250 km long in a N-S axis running between Lukulu and Ngonye Falls. The central Barotse floodplain region averages 826 mm of rainfall annually, nearly all of it falling from

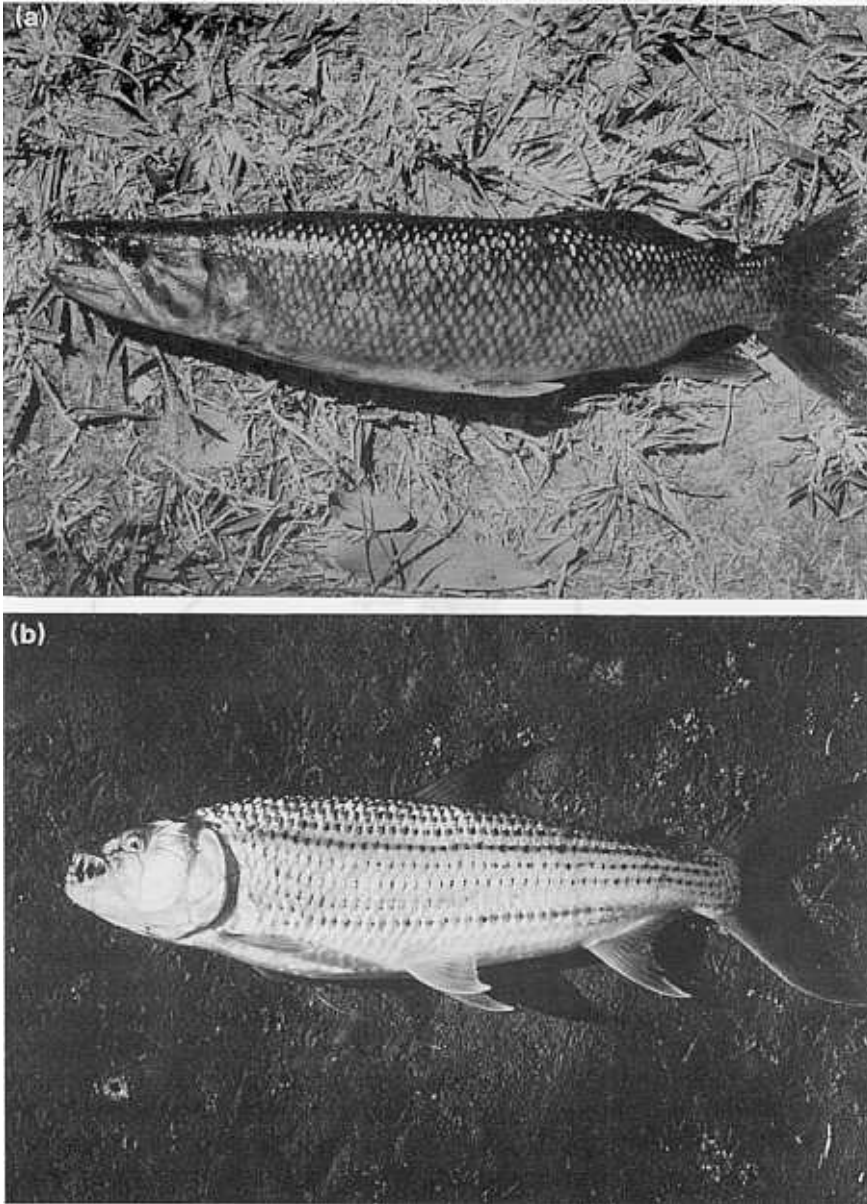


FIG. 1. Representative specimens of (a) *Hepsetus odoe* (African pike, 'mulomezi', 370 mm S.L. and (b) *Hydrocynus forskahlii* (tigerfish, 'ngweshi', 550 mm S.L.) from the Upper Zambezi R.

November through March. Rainfall was higher than average during the early flood period of 1989 and lower than average during November, 1989 (Winemiller, 1991). Flooding typically begins in the northern Barotse floodplain region during December or January, peaks in the central region in March and April, and gradually subsides in the central and lower regions during May–August.

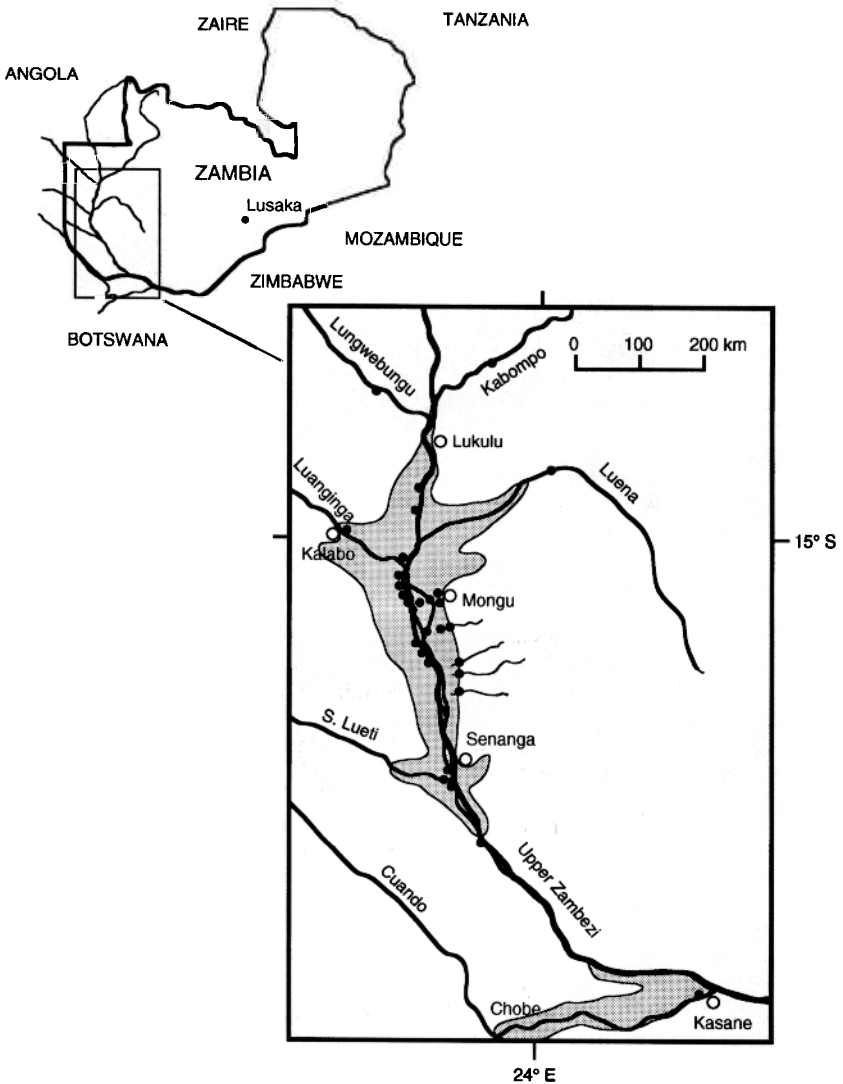


FIG. 2. Map showing the Upper Zambezi R. study region in Zambia. Shaded regions represent floodplains; ●, locations of principal collection sites.

During the 1989 field study, lagoon water temperatures (measured at 12.00 hours) fluctuated between a low of 18.0° C (7 August) to a high of 28° C (23 November). Water temperature in the river channel ranged between 21 and 27.5° C, and pH varied between 6.3 and 6.9. pH ranged between a low of 5.5 in floodplain pools to a high of 7.0 in the Kabompo R. Waters of the river, tributaries, and floodplain pools were always near full oxygen saturation, always very transparent, and often tea-stained with organic compounds. The floodplain is a largely treeless grassland dominated by *Phragmites* reeds, *Potamogeton* spp., *Nymphae* spp., *Vossia cuspidata* [(Roxb.) Griff., 1851], and *Utricularia* spp. along waterways. Some lagoons become completely covered with dense mats of *Salvinia auriculata* (Aublet, 1775) during the dry season.

MATERIALS AND METHODS

The field study was conducted from 21 May through 9 December 1989 on a monthly sampling schedule. Most collections were made from the floodplain (Fig. 2), however some samples were also taken at irregular intervals from tributaries flowing into the floodplain region. These tributaries include Lungwebungu, Kabompo, Luena, Luanginga, and South Lueti Rivers, plus several small streams east of the floodplain (Fig. 2). Fishes were also collected during September from the Zambezi R. downstream from the floodplain at Sioma (Ngonye Falls), during August from the Chobe R. near Kasane (Botswana), and during June from the Kafue R. near Kafue township, and during June and September from the Lufupa-Kafue R. confluence. Because *Hydrocynus* is absent from the Kafue R. drainage, *Hepsetus* data from the Kafue were excluded from the study. A complete listing of collection sites and dates are filed at the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas, U.S.A. Environmental conditions for each fish sampling site were recorded, including water temperature, pH, and dissolved oxygen content. A variety of sampling methods were used at each site. At Zambezi R. and floodplain sites, 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 monofilament nylon gillnets [4(2 × 50 m segments)=1(15.25 cm mesh)+2(10.22 cm mesh)+1(5.08 cm mesh)] were employed. Small tributary streams and shallow floodplain pools were sampled with dipnets and smaller seines (0.63 cm mesh). At most sampling sites, we collected from all habitats and attempted to save a sample that reflected species' relative abundances at the location. Fishes were either placed in cool 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°7'6" E) was examined in Mongu. To supplement data derived from our own field samples, *Hepsetus* and *Hydrocynus* from the commercial catch were measured and examined for stomach contents. Two large floodplain samples from a local fisherman's 'maalelo' traps were preserved in June (15°23'30" 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 R. on Malile canal). Maalelo are dams constructed of grass mounds or reed fences, which block the return of water from the plain to lagoons and permanent channels (Kelley, 1968). Reed fish traps with funnel-type, no-exit valves are placed behind openings in the dams.

Standard length (S.L.), condition of gonads, relative amount of visceral fat deposits, and stomach contents were recorded for both species. All lengths are reported as S.L. Methods used for assessing gonad condition and fat contents follow Winemiller (1989a). Scales were removed from individuals of both species representing a variety of standard lengths and examined under a binocular dissecting microscope to evaluate annulus formation. Scales were removed from the right flank about midway between the dorsal origin and anterior lateral line. Scale annuli were fairly distinct, especially in larger size classes, and consisted of closely spaced circuli that seemed to correspond to the period of rising water and spawning (December–March). Most *Hepsetus* and *Hydrocynus* caught during the low water period had formed a substantial layer of low-density circuli near the anterior scale margin beyond the most recent annulus. A detailed treatment of annulus formation on scales of *H. forskahlii* from Lake Kariba, Zambia appears in Kenmuir (1973).

Stomach contents were quantified volumetrically by water displacement as described by Winemiller (1989b). Fish were identified to genus and species whenever possible, and invertebrates were identified to order. For the analysis, some of the prey categories that were least abundant in stomach samples were later combined into functional categories (e.g. aquatic insects). The other diet categories were unidentified fish, ctenoid scales, and cycloid scales, and detritus/substratum. Diet diversity was estimated using Levin's (1968) standardized index of niche breadth, and diet similarities were calculated using Pianka's (1973) symmetrical measure of niche overlap. For each index, values may range near 0 (specialized diet or almost no overlap) to 1.0 (even use of food resources or complete overlap).

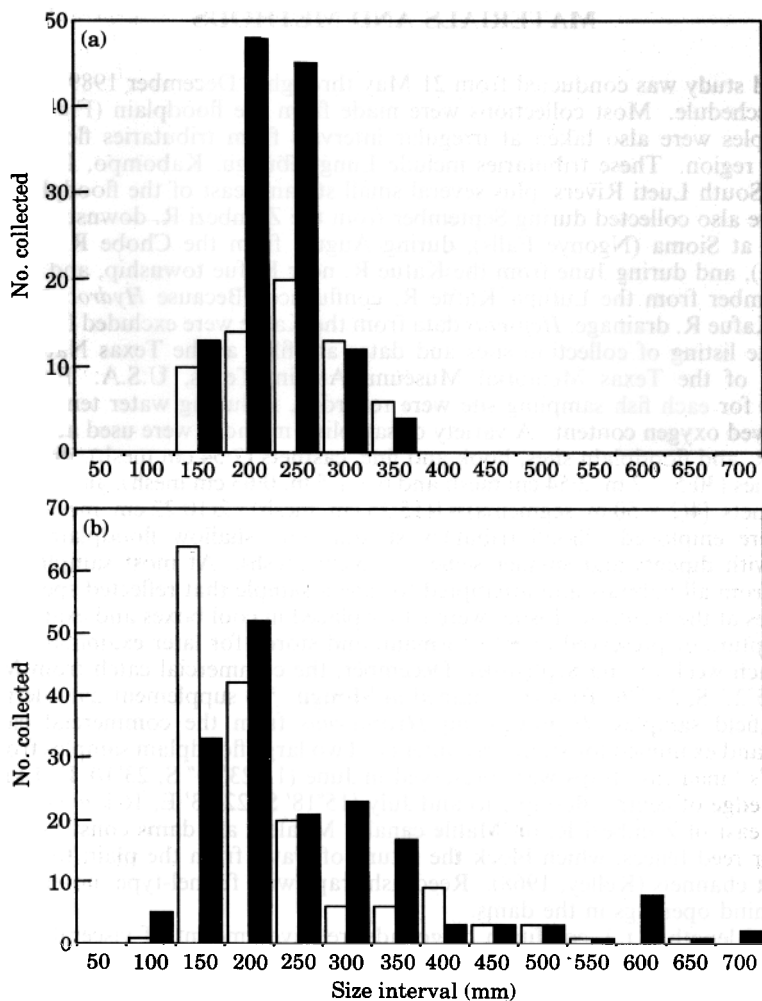


FIG. 3. Length–frequency histograms for (a) *Hepsetus* and (b) *Hydrocynus* collected during flood conditions (May–August) and low water season (September–December) from the Upper Zambezi R. drainage in 1989. □, Low water season and ■, flood conditions.

RESULTS

POPULATION SIZE STRUCTURE

The total number of individuals obtained were 185 *Hepsetus* and 354 *Hydrocynus*. Our sampling gear collected *Hepsetus* ranging in size from 110 to 350 mm s.L. and *Hydrocynus* that showed a wider distribution in s.L. from 76–660 mm (Fig. 3). During high water conditions (May–August), the bulk of *Hepsetus* were in the 200–250–300 mm size classes. As flood waters receded (September–December), the majority of *Hepsetus* remained in these intermediate size classes, but relative abundances were more evenly distributed (Fig. 3). There was no significant difference in the mean sizes of *Hepsetus* from the high water and low water samples (high mean = 203.3 mm, s.d. = 44.7, t (log-transformed s.L.) = 1.58, d.f. = 62, $P = 0.118$). Most *Hydrocynus* were in the 150–200–250 mm size intervals

TABLE I. Percentages of *Hepsetus odoe* and *Hydrocynus forskahlii* collected from the main channel of the Upper Zambezi R. and lagoons; and percentages of each species collected from the lower (Senanga and south), middle (west of Mongu), and upper (Lukulu and north) Zambezi R. and floodplain

Location	<i>Hepsetus</i>	<i>Hydrocynus</i>
River Channel	2.07	93.50
Lagoons	97.93	6.50
$\chi^2=167.5$, d.f. = $P<0.0001$		
Location	<i>Hepsetus</i>	<i>Hydrocynus</i>
Lower	20.00	12.71
Middle	80.00	82.20
Upper	0.00	5.08
$\chi^2=6.74$, d.f.=2, $P<0.05$		

throughout the year, and the size distribution was more heavily skewed toward smaller size intervals during low water conditions. *Hydrocynus* population size structure changed from a high water mean of 242.2 mm (S.D.=125.3) to a low water mean of 198.7 mm S.D.=96.7; t (log-transformed S.L.)=3.92, d.f.=155, $P<0.0001$).

We examined scale annuli from 33 individual *Hepsetus* (S.L. range 113–265 mm) and 39 *Hydrocynus* (S.L. range=112–710 mm). The regression equation for *Hepsetus* was No. annuli= $1.08e^{-2L} - 1.61$ ($r^2=0.62$), and for *Hydrocynus*, No. annuli= $1.87e^{-2L} - 2.14$ ($r^2=0.94$). If we assume that scale annuli correspond to annual rings, *Hepsetus* average about 225 mm S.L. and *Hydrocynus* average 170 mm S.L. at Age I, and *Hepsetus* average 240 mm S.L. and *Hydrocynus* average 230 mm S.L. at Age II. We did not age any *Hepsetus* over Age II or 270 mm S.L., and the oldest *Hydrocynus* for which we have data were as follows: female, 11 yr, 710 mm S.L., 7.1 kg; and female, 9 yr, 650 mm, 5 kg.

HABITAT AFFINITIES

Aquatic habitats were divided into two basic categories: river (main channel of Zambezi and Chobe R.) and lagoon (permanent floodplain lagoons, canals, small tributary rivers, backwaters). No specimen of either species was collected from small tributary streams on the edge of the floodplain. Approximately 98% of the *Hepsetus* specimens that we collected inhabited lagoons (Table I), and only three fish were collected in the main river channel. Ninety-four per cent of *Hydrocynus* sampled were taken from the river channel. Of the 28 individuals captured from backwaters and permanent canals connected to the main river, at least 10 of these were young-of-the-year and most of the others appeared to be juveniles. During the low water period, *Hydrocynus* were never encountered in sloughs and lagoons of the floodplain. Most specimens of *Hydrocynus* were collected from swift currents near midwater depths with hook and line, or near swift current with gillnets set in deep water close to the bank. Both species were

TABLE II. Major diet categories by percentage volume based on cumulative data for Upper Zambezi populations of *Hepsetus odoe* (n=185) and *Hydrocynus forskahlii* (n=328)

Prey category	<i>Hepsetus</i>	<i>Hydrocynus</i>
Mormyrids	19.2	4.4
<i>Hepsetus odoe</i>	3.6	25.1
Small characids	0.4	1.0
<i>Barbus</i> spp.	3.4	4.3
<i>Clarias</i> spp.	1.9	0.1
<i>Schilbe mystus</i>	0.6	0.7
<i>Synodontis</i> spp.	2.3	5.5
Haplochromine cichlids	42.8	27.7
Unidentified cichlids	9.3	26.7
<i>Tilapia</i> spp.	11.3	0.1
Unidentified fish	50.0	4.2

common in the central (west of Mongu) and southern regions (Senanga and southward) of the floodplain (Table I). In the swift flowing waters of the Zambezi R. and its major tributaries of the northern floodplain, the dominant piscivore was *Hydrocynus*.

FEEDING HABITS

The ratios of number of empty stomachs among the total number of fish examined for stomach contents were *Hepsetus* (110/185=59.5%) and *Hydrocynus* (188/328=57.3%). Both species were almost exclusively piscivorous. The diet of *Hepsetus* primarily consisted of cichlid fishes (over 60%) and mormyrids (19%) (Table II). *Hepsetus* smaller than 150 mm S.L. consumed a larger fraction (83%) of mochokid catfishes (*Synodontis* spp.) and a smaller fraction of cichlids (5%) and mormyrids (0%) than larger fish, but later shifted to a diet that contained these latter two prey items (Table III). Larger *Hepsetus* also preyed upon conspecifics, which consisted of just over 5% of their total diet. During low water conditions, *Hepsetus* increased predatory pressure on conspecifics (10%) and mormyrids (29%). As water levels increased, cichlids comprised over 75% of the diet of *Hepsetus* (Table IV).

Hydrocynus (Table II) fed primarily on cichlids (over 50%), but also consumed large volumes of *Hepsetus* (25%) and small characid fishes (10%, especially *Micralestes acutidens*, Peters, 1852). In contrast to prey consumed by *Hepsetus*, scarcely any of the cichlids consumed by *Hydrocynus* could be positively identified as *Tilapia*. Small *Hydrocynus* preyed heavily on *Barbus* spp. (21%), small characids (30%), and mormyrids (29%). Large adult size classes changed to a diet in which cichlids and *Hepsetus* predominated (Table III). During periods of low water, the *Hydrocynus* diet consisted of one-third *Synodontis* spp., one-third cichlids, and mormyrids (17%). During high water conditions, *Hydrocynus* increased intake of cichlids (59%) and *Hepsetus* (30%), but the numbers of mormyrids and *Synodontis* ingested diminished to almost zero (Table IV).

Based on 19 prey categories and cumulative survey data for each species, diet breadths were 0.17 for *Hepsetus* and 0.20 for *Hydrocynus*. Diet breadth varied

TABLE III. Diet items by percentage volume for Upper Zambezi *Hepsetus odoe* and *Hydrocynus forskahlii* aggregated by size class, small (<150 mm S.L.), medium (151–250 mm), large (>250 mm)

Prey item	<i>Hepsetus</i>			<i>Hydrocynus</i>		
	Small	Medium	Large	Small	Medium	Large
Mormyridae	0.1	31.1	11.9	28.62	19.4	2.9
<i>Hepsetus odoe</i>	0.1	0.1	5.9	0.1	0.1	27.5
Small Characidae	0.1	1.0	0.1	30.39	5.9	0.4
<i>Hemigrammocharax</i>	0	0	0	0	1.0	0
<i>Barbus</i> spp.	1.85	8.8	0.1	20.50	51.7	0.2
<i>Clarias</i> spp.	0.1	0.1	3.2	0.1	0.1	0
<i>Schilbe mystus</i>	0.1	0.4	0.8	0.1	0.7	0.7
<i>Chiloglanis</i>	0	0	0	0.42	0.1	0
<i>Synodontis</i> spp.	83.41	3.5	0.1	0.1	1.2	5.9
<i>Aplocheilichthys</i> spp.	7.41	0.1	0.1	5.64	0.1	0.1
Tilapines	4.45	11.3	11.4	0	0	0
Haplochromines	0.01	29.3	52.2	1.73	8.0	29.7
Unidentified Cichlidae	0.56	7.0	11.0	0.1	4.3	28.9
Unidentified fishes	0.01	7.6	3.4	8.2	7.8	3.9
Shrimp	0	0	0	2.2	0.1	0
Aquatic insects	0	0	0	1.67	0.1	0
Terrestrial insects	0	0	0	2.2	0.1	0
Detritus, substrate	23.20	0	0	0.45	0.1	0

TABLE IV. Major diet categories by percentage volume for *Hepsetus odoe* and *Hydrocynus forskahlii* during high and low water conditions of the Upper Zambezi River

Prey category	<i>Hepsetus</i>		<i>Hydrocynus</i>	
	High	Low	High	Low
Mormyrids	14.3	29.2	2.1	16.7
<i>Hepsetus odoe</i>	0.1	10.9	29.7	0.1
Small characids	0.6	0.1	1.1	0.9
<i>Barbus</i> spp.	0.1	10.3	3.7	7.3
<i>Clarias</i> spp.	2.9	0.1	0.1	0.1
<i>Schilbe mystus</i>	0.1	1.9	0.8	0.1
<i>Synodontis</i> spp.	1.6	3.6	0.4	33.2
Haplochromine cichlids	49.0	30.3	28.8	21.6
<i>Tilapia</i> spp.	14.2	5.3	0.1	0.1
Unidentified cichlids	13.4	1.2	29.3	12.9
Unidentified fish	4.0	7.0	3.7	6.6

by size intervals in the following manner: *Hepsetus* (<150 mm) $B=0.03$, (150–250) $B=0.23$, (>250 mm) $B=0.12$; *Hydrocynus* (<150 mm) $B=0.19$, (150–250) $B=0.12$, (>250 mm) $B=0.16$. Ontogenetic diet shifts were large for both species, particularly among smaller *Hepsetus*, and among larger *Hydrocynus*. Diet similarity was low between small *Hepsetus* and medium and large conspecifics

(0.09 and 0.01 respectively), but high between medium and large *Hepsetus* (0.81). Diet similarity was relatively high between small and medium *Hydrocynus* (0.69), but low between large-small and large-medium conspecifics (0.07 and 0.16 respectively). When we compared diet overlap between species for similar size classes, the trend was for greater diet similarity with increasing size (small=0.2, medium=0.53, large=0.73).

Diet breadths declined with water level as follows: *Hepsetus* (high water) $B=0.21$, (low water) $B=0.13$; *Hydrocynus* (high water) $B=0.21$, (low water) $B=0.16$. Interspecific diet similarity did not change with season (high water overlap=0.66, low water overlap=0.67). Between-season diet similarity was greater for *Hepsetus* (overlap=0.81) than *Hydrocynus* (overlap=0.47), indicating a greater seasonal dietary shift in *Hydrocynus*.

The length of prey in relation to the length of predator is shown in Fig. 4. For 48 *Hepsetus* with measurable prey in their stomachs, the predator length to prey length ratio ranged from 7 to 72% with a mean of 40%. For 95 *Hydrocynus* with measurable prey, the predator to prey length ratio showed a similar range, 7 to 62%, but the mean ratio was only 27%. The graph shows that, for the most part, small piscivores consumed fish from small size classes, but larger predators took a wider range of prey sizes. Overall, most of the prey items consumed by both species were ≤ 25 cm in length. The species-specific relationships between predator length and prey length were significantly different, with large size classes of *Hepsetus* tending to take larger prey than *Hydrocynus* of equivalent size (MANOVA-GLM procedure; $F=29.10$; d.f.=1, 140; $P<0.0001$).

DISCUSSION

Jackson (1961) hypothesized that many of the smaller African fish species are excluded from open waters of the principal river channels and restricted to backwaters owing to the threat of predation by *Hydrocynus* in deeper open waters. Reproductive migrations upstream and laterally onto floodplains were seen as an ecological strategy employed by larger species to reduce encounters between their offspring and the voracious piscivore *Hydrocynus*. On the other hand, *Hepsetus* is primarily a stealth or ambush predator, and it frequently utilizes dense beds of aquatic vegetation for cover (Moriarty, 1983). In the Upper Zambezi, the threat of predation by *Hydrocynus* in the river channel and by *Hepsetus* in backwater and edge habitats exerts a strong influence on community food-web structure by causing most small fishes (Cyprinodontidae, Cyprinidae, Characidae) to occupy very shallow shoreline areas or densely vegetated microhabitats. For example, the characid *Micralestes acutidens* was common in very shallow water (1–20 cm deep) over sand bars in the main channel of the Zambezi R. Small *Hydrocynus* were numerous in the deeper troughs that separated sand bars. Most of our samples of small (<10 cm) cyprinodontids, cichlids, distichodontids, mormyrids, clariids, and synodontids were captured during the daytime from dense beds of aquatic macrophytes located in lagoons and along the edge of the main river channel. Some of the mormyrids (*Petrocephalus catostomus*, Günther, 1866; *Marcusenius macrolepidotus*, Peters, 1852) are nocturnally active in quiet open waters adjacent to their vegetation refugia and frequently fall prey to the predatory catfish *Schilbe mystus*

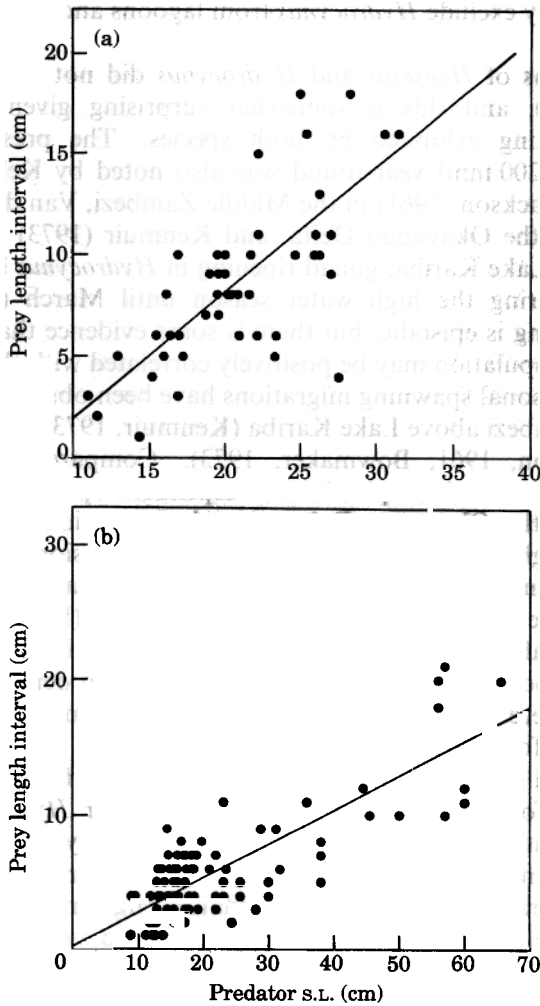


FIG. 4. Relationship of prey standard length and predator standard length for (a) *Hepsetus* and (b) *Hydrocynus* [Regressions: Prey S.L. = 0.62 (*Hepsetus* S.L.) - 4.36, $r^2=0.55$, $P<0.0001$; Prey S.L. = 0.25 (*Hydrocynus* S.L.) + 0.16, $r^2=0.64$, $P<0.0001$].

(Linnaeus, 1762) (authors' unpublished data). Bell-Cross & Minshull (1988) reported that the principal limiting factor for *Hydrocynus* distribution is water depth, yet many lagoons on the Barotse floodplain are deeper than extensive reaches of the active river channel that contain *Hydrocynus* (personal observations). Because all river channel fishes have free access to lagoons during the annual floods, we conclude that the presence of moderate or swift water current is the more critical environmental feature explaining the local distribution of *Hydrocynus*. The pursuit method of attack used by *Hydrocynus* may be poorly-suited for capturing prey in lentic habitats containing much aquatic vegetation. In contrast, the ambush habit of *Hepsetus* undoubtedly serves well in densely vegetated habitats. The combined effects of diurnal/crepuscular feeding by *Hepsetus* and nocturnal feeding by the catfish *Schilbe mystus* (Schilbeidae)

might competitively exclude *Hydrocynus* from lagoons and sluggish canals of the floodplain.

Size distributions of *Hepsetus* and *Hydrocynus* did not show large seasonal variation (Fig. 3), and this is somewhat surprising given the strategy of wet-season spawning exhibited by both species. The presence of juvenile *Hydrocynus* (150–200 mm) year-round was also noted by Kelley (1968) in the Upper Zambezi, Jackson (1961) in the Middle Zambezi, Van der Waal (1985) in a natural lake in the Okavango Delta, and Kenmuir (1973) in the man-made Lake Kariba. In Lake Kariba, gonad ripening in *Hydrocynus* begins in October and continues during the high water season until March (Kenmuir, 1973). Individual spawning is episodic, but there is some evidence that the duration of breeding by the population may be positively correlated with the duration of the annual flood. Seasonal spawning migrations have been observed in *H. forskahlii* in the Middle Zambezi above Lake Kariba (Kenmuir, 1973) and in other regions of Africa (Jackson, 1961; Bowmaker, 1973). Compared with *Hydrocynus*, spawning by *Hepsetus* is less episodic and dependent upon water level (Merron *et al.*, 1990). In the Okavango Delta, gonad maturation in *Hepsetus* largely corresponds to higher water temperatures and the recession of floodwaters that occurs during summer months between August and January, and most spawning occurs during the flood period of January–March (Merron *et al.*, 1990). *Hepsetus* is unusual among the characiform fishes in that it constructs foam nests and guards its broods. The nests are usually situated in dense vegetation at the water surface where they provide both protection from predators and a rich source of oxygen for the developing larvae.

Both species fed mostly on fish less than 25 cm S.L., a finding similar to those of Carey (1971) for *Hepsetus* and Jackson (1961) for *Hydrocynus*. However neither of those authors encountered instances where prey were greater than 50% predator length, and only in exceptional cases was the ratio greater than 40%. We observed several instances of prey–predator length ratios in excess of 50%, particularly in the case of *Hepsetus*. We observed no evidence of *H. forskahlii* consuming pieces of sheared fish flesh in the manner described for *H. brevis* by Lewis (1974). Given that (1) Upper Zambezi *Hydrocynus* are larger on average than *Hepsetus*, (2) *Hepsetus* consume larger prey than *Hydrocynus* relative to predator body length, and (3) the two species consume similar prey taxa, a potential exists for interspecific competition should resource densities decline to a point in which food becomes a limiting factor. This potential for competition appears not to be realized due to two factors: (1) segregation of habitats utilized and (2) consumption of prey taxa in different relative proportions such that diet overlap is minimized.

During the height of the annual floods, fishes are dispersed throughout the Barotse floodplain and extremely difficult to sample. During the falling water period, nearly all adult *Hydrocynus* had returned to the primary river channel, and only a few small individuals remained in canals and sloughs of the floodplain (Table I). *Hepsetus* showed the opposite trend in which most individuals remain in floodplain habitats and only a small fraction of the adult population occupied the river channel during the period of lowest river discharge. All *Hepsetus* that we observed or captured from the river channel were located within 1.0–3.0 m of the edge, usually in quiet, heavily vegetated areas near backeddies or lagoon

entrances. Jackson (1961) and Bell Cross & Minshull (1988) noted that *Hepsetus* occupies the open waters of the river channel in the Kafue R. drainage (large Middle Zambezi tributary) where *Hydrocynus* is historically absent. These authors assumed that the threat of predation by *Hydrocynus* inhibits the use of river channel by *Hepsetus*. We surveyed fishes in the Kafue R. near the town of Kafue in June 1989 and near its confluence with the Lufupa R. in June and September 1989. We collected *Hepsetus* from the river channel, but always in shallow water near vegetation or other structure. The Kafue R. had very slow or negligible current compared with the swift current in the central channel of the Upper Zambezi, a factor that may contribute to the ability of *Hepsetus* to inhabit the river channel of the former.

Our diet findings were in general agreement with those from earlier studies by Kelley for both species in the Upper Zambezi and by Jackson (1961), Kenmuir (1973), Lewis (1974), and Van der Wall (1985) for *Hydrocynus* in other areas. Based on our cumulative diet data (Table II), the principal prey of *Hepsetus* were cichlids and mormyrids, whereas *Hydrocynus* consumed primarily cichlids, *Hepsetus*, and mochokid catfishes (*Synodontis* spp.). *Hepsetus* consumed a greater fraction of mormyrids and a lesser fraction of characids [*Alestes lateralis* (Boulenger, 1900), *Micralestes acutidens* (Peters, 1852)], small cyprinids (*Barbus* spp.), *Hepsetus*, and mochokid catfishes than did *Hydrocynus*. We found *Hepsetus* in stomach samples of both species but no direct evidence of predation on *Hydrocynus*. Kelley (1968) reported cannibalism by *Hydrocynus* at a volumetric percentage of 7% during the month of September (106 stomachs examined over 6 months). All available evidence suggests that both species have a low incidence of cannibalism, but that interspecific predation is asymmetrical, with *Hepsetus* suffering high levels of predation by *Hydrocynus* while the reverse appears to be absent or extremely infrequent. Virtually all of the *Hepsetus* were taken by *Hydrocynus* during the period of high and falling water (June–August) when fishes are flushed out of the flooded plains into lagoons and channels (Table IV). Kelley reported *Hepsetus* in the diet of *Hydrocynus* (20% by volume) in his November sample.

Interspecific diet overlap was slightly lower for seasonal samples (0.66) compared with that for the cumulative diet data (0.71), and this suggests that food resource partitioning may occur as environmental conditions and resource densities change with season. We observed only a small seasonal diet shift by *Hepsetus* (between-season overlap=0.81), with the primary differences being the greater consumption of mormyrids and conspecifics during the low water period (Table IV). *Hydrocynus* showed a greater seasonal diet shift (between-season overlap=0.47), and this was primarily due to a much greater consumption of mormyrids and mochokids during the low water period and a lesser consumption of *Hepsetus* and cichlids. In comparison with *Hepsetus*, *Hydrocynus* consumed more cyprinids and *Hepsetus*, and ate less mormyrids and cichlids during the high water period (Table IV). During low water, *Hydrocynus* consumed more mochokids and less mormyrids, *Hepsetus*, and *Schilbe* compared with *Hepsetus*. These seasonal diet differences could be more derived from differences in relative prey availability in the resident habitats rather than prey selection by the two piscivores. For example, *Synodontis nigromaculatus* (Boulenger, 1905) and its congeners are among the relatively few Upper Zambezi fishes that coexist with

Hydrocynus in open areas of the main river channel (see also Winemiller, 1991). Nocturnal mormyrids, *Schilbe mystus*, and *Hepsetus* are most abundant in backwater and quiet river edge habitats.

In summary, the piscivorous characiforms *Hepsetus odoe* and *Hydrocynus forskahlii* exhibit very little overlap in their use of river and aquatic floodplain habitats of the Upper Zambezi R./Barotse Plain. The absence of *Hepsetus* from the main river channel previously has been attributed to the threat of predation. Indeed, we found that *Hydrocynus* is a major predator of *Hepsetus*, especially during the period of high and falling water when the two species are most likely to come into contact with one another at the interface of aquatic floodplain and river channel environments. Both species displayed a low incidence of cannibalism, and *Hepsetus* did not appear to prey on *Hydrocynus* to any significant extent. Overall, the two species have very similar diets, especially among the largest size classes. However, diets were less similar within-seasons, and this could be due either to partitioning of food resources directly, or due to differences in prey availabilities in the different habitats occupied by the two species. The observed densities of alternative prey in river channel v. aquatic floodplain and marginal habitats suggests that food partitioning via the indirect mechanism of habitat partitioning may be the more viable explanation. The principal foraging modes of the two piscivores should favour *Hydrocynus* in open water environments, and favour *Hepsetus* in heavily vegetated and other kinds of highly structured environments. Differences in diets and habitat utilization by sympatric *Hepsetus* and *Hydrocynus* are best explained as resulting from the combined and interactive effects of predation threat, interspecific differences in foraging mode, and differential foraging efficiencies in open-water v. structured environments.

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