Food habits of tilapiine cichlids of the Upper Zambezi River and floodplain during the descending phase of the hydrologic cycle

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Habitat use and diets of five tilapiine populations of the Upper Zambezi River Basin in Zambia, south-central Africa, were examined during the 8 month descending phase of the annual hydrological cycle. All species occurred across a range of habitats, with most individuals captured from lagoons. *Tilapia rendalli*, a macrophyte feeder, was the only dietary specialist. Ontogenetic diet shifts were not observed over the size range examined (30–320 mm L_S). Algae were uncommon in tilapiine diets. *Tilapia ruweti*, the smallest tilapiine in the region, was the only species that consumed more algae (filamentous algae) than detritus. *Oreochromis andersonii*, *Oreochromis macrochir* and *Tilapia sparrmanii* had high dietary overlap and occurred in the same habitats in similar relative abundances. High overlap in habitat use and diet among tilapiines contrasted with findings from a comparable analysis of predatory haplochromine cichlids of the region that revealed strong ecological segregation and niche complementarity during the annual descending-water phase. © 2003 The Fisheries Society of the British Isles

Key words: diet; habitat; herbivore; *Oreochromis*; *Tilapia*; Zambia.

INTRODUCTION

Owing to seasonal patterns of precipitation and hydrology, tropical river fishes are exposed to continually changing availability of habitats and food resources (Lowe-McConnell, 1964, 1975; Zaret & Rand, 1971; Winemiller, 1989*a*, 1990). Relative resource scarcity frequently occurs during dry seasons when fishes are concentrated at high densities in river channels and floodplain pools. Wet-season flooding stimulates greater primary and secondary production, usually accompanied by intensified reproductive activity among fishes and other aquatic organisms (Lowe-McConnell, 1964; Winemiller, 1989*b*). In the Upper Zambezi River and Barotse Plain of south-central Africa, carnivorous haplochromine cichlids reveal a strong pattern of resource partitioning and niche complementarity during the annual period of descending water levels (Winemiller, 1991). Species that

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share habitats have extremely low dietary overlap, and those that consume similar prey categories usually occupy different habitats. Similarly, strong patterns of niche segregation were observed among piscivorous characiform fishes (Winemiller & Kelso-Winemiller, 1994), invertebrate-feeding mormyriforms (Winemiller & Adite, 1997), and omnivorous and carnivorous siluriforms (Winemiller & Kelso-Winemiller, 1996) of the Upper Zambezi and Barotse Plain.

In the present study patterns of resource use by detritivorous and algivorous fishes of the cichlid subfamily Tilapiinae from the Upper Zambezi/Barotse region were compared. Because detritus and algae (especially periphyton) are available on a year-round basis, it is hypothesized that food might not be as limiting for these tilapiines as it is for invertebrate-feeding and piscivorous cichlids. Tilapiines are known to consume a variety of food resources in addition to algae and detritus, including macrophytes, zooplankton and aquatic insects (Lowe-McConnell, 1959). In addition, not all forms of detritus are equivalent in terms of nutritional quality and dynamics that determine availability for consumers (Bowen, 1983). Thus, detritivores have the potential to partition food and habitat in response to resource limitation.

MATERIALS AND METHODS

Sampling was performed monthly in the Upper Zambezi River ($14°05'-16°05'$ S; $22°45'-23°15'$ E) drainage of Zambia's Western Province from 21 May to 9 December 1989. Regional environmental conditions are described elsewhere (Winemiller, 1991); therefore, only a brief description follows. The river undergoes seasonal flooding over a broad floodplain (Barotse Plain) *c.* 250 km long and 30 km wide in its central region. Annual regional rainfall averages 826 mm, nearly all of it falling from November to March. Flooding typically begins in the northern 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 to August. The floodplain is essentially treeless and dominated by grasses. Dominant aquatic vegetation along waterways includes *Phragmites* spp., *Potamogeton* spp., *Nymphaea* spp., *Vossia cuspidata* and *Utricularia* spp., with floating macrophytes (*e.g. Salvinia auriculata*) covering some lagoons during the dry season.

Most collections were made from the main river channel and floodplain lagoons, but additional samples were taken at irregular intervals from Zambezi tributaries (Lungwebungu, Kabompo, Luena, Luanginga and South Lueti Rivers, plus several small streams that enter the floodplain from the east). Locations of sampling stations are illustrated in Winemiller (1991), and a complete listing of collection sites and dates is archived along with voucher specimens at the Texas Natural History Collection (Texas Memorial Museum, Austin, TX, U.S.A.).

A variety of sampling methods were used at each site. At river channel 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 smaller seines (0·63 cm mesh) and dipnets. At most sampling sites, an attempt was made to collect fish species in proportion to their relative abundance. Each mesohabitat (*e.g.* deep open waters, shallow vegetated areas and small streams) was sampled using the appropriate gear until an additional hour of sampling failed to produce any new species. Gillnetting was the exception, with gillnets deployed over a single night in deep habitats. Fishes were either placed in an ice chest and examined within 18 h of capture, or preserved in 15% formalin and stored for later examination.

Standard length (L_S) was recorded for each specimen; gonad state and stomach contents were examined for a size-representative sub-sample when samples were large ($n > 30$). Assessment of gonad state followed methods reported by Winemiller (1989b). Stomach contents were quantified using Winemiller's (1990) method of microscopic examination and gut volumetric estimation. Less common dietary items in stomach samples were later combined into functional categories (*e.g.* filamentous algae, microcrustacea and aquatic invertebrates). Diet diversity was estimated using Levins'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 from near 0 (specialized diet or almost no overlap) to 1·0 (even use of food resources or complete overlap).

RESULTS

Tilapia sparrmanii Smith (banded tilapia) is the most abundant and widely distributed tilapiine in the Upper Zambezi, with 891 individuals captured during field surveys (84% from lagoons, 11% from the river and 5% from streams). Total sample abundances of other tilapiines, from highest to lowest, were: 683 *Tilapia rendalli* (Boulenger) (redbreast tilapia), 225 *Oreochromis macrochir* (Boulenger) (greenhead tilapia), 50 *Oreochromis andersonii* (Castelnau) (threespot tilapia) and 34 *Tilapia ruweti* (Poll & Thys van den Audenaerde) (Okavango tilapia). Most *T. rendalli* were captured in the river channel (52%) followed by lagoons (41%) and streams (7%). *Oreochromis macrochir* was more common in lagoons (80%) than the river channel (19%) and streams (1%). Though not abundant, *O. andersonii* and *T. ruweti* were more frequently captured in lagoons (88% for both species) than the river channel and streams (3–8%).

Maximum L_S of the five populations, from largest to smallest, were: 323 mm *O. andersonii*, 276 mm *T. rendalli*, 249 mm *O. macrochir*, 125 mm *T. sparrmanii* and 53 mm *T. ruweti*. The size distributions of *O. macrochir* and *T. rendalli* had the same range, but *O. macrochir* was more strongly bimodal with relatively more large individuals (Fig. 1). Size frequency distributions were bimodal for four of the five population samples, with the small *T. ruweti* sample showing no distinct pattern (Fig. 1). With the exception of the two *Oreochromis* species, the trough between the two modes approximated the minimum size at which mature gonads were observed in dissected samples. The minimum L_S associated with mature ovaries was 80 mm for *T. sparrmanii*, 120 mm for *T. rendalli*, 200 mm for *O. macrochir* and 210 mm for *O. andersonii*. Because most of the dissected specimens were captured during the months following the reproductive season, samples were small and unreliable for computation of length at 50% maturity. The trough separating the first mode that presumably corresponds to young-of-the-year (YOY) was at 140 mm and 170 mm for *O. macrochir* and *O. andersonii*, respectively, an indication that these species may mature at age 2+ years. No *T. ruweti* specimen had mature ovaries, but most were caught during the latter portion of the descending phase of the hydrological cycle when few tilapiines were undergoing gonadal recrudescence. Juvenile size classes of all species were most frequent in samples collected during the early portion of the descending-water period (May to August), *i.e.* after floodplain breeding during the wet season.

Three species (*O. andersonii*, *O. macrochir* and *T. sparrmanii*) consumed mostly vegetative detritus (Table I). *Tilapia rendalli* consumed mostly living

(a)

(b)

(c)

(d)

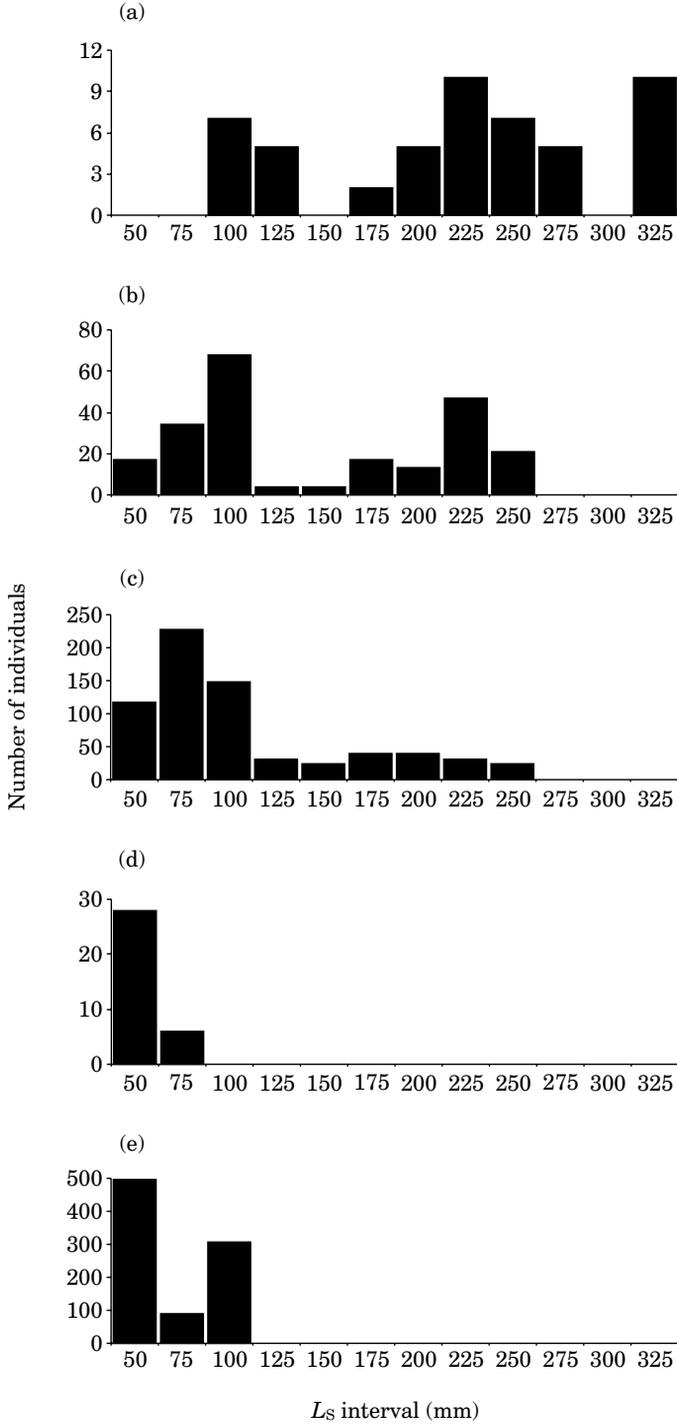(e)

Number of individuals

L_S interval (mm)

FIG. 1. Standard length distributions of tilapiine cichlid samples (a) *Oreochromis andersonii*, (b) *Oreochromis macrochir*, (c) *Tilapia rendalli*, (d) *Tilapia ruweti* and (e) *Tilapia sparrmanii* from the Upper Zambezi and Barotse Plain.

TABLE I. Volumetric proportions of major dietary categories consumed by juvenile (Juv) and adult (Ad) size classes of tilapiine cichlids of the Upper Zambezi. Volumetric proportion of sand in stomachs is not shown. B, Levins' standardized index of niche breadth. Diet items with volumetric proportions >0·30 appear in bold

Species and size class	Fine detritus	Vegetative detritus	Macrophytes	Diatoms	Unicellular algae	Filamentous algae	Aquatic inverts	B
O. andersonii Juv	0·006	**0·801**	0	0·034	0	0	0·047	0·074
O. andersonii Ad	0·028	**0·741**	0	0·023	0	0·046	0·004	0·105
O. macrochir Juv	0·086	**0·734**	0	0·107	0·007	0·013	0·005	0·112
O. macrochir Ad	0·031	**0·846**	0	0·037	0·009	0·014	0·018	0·056
T. rendalli Juv	0·013	0·080	**0·490**	0·040	0·193	0·006	0·001	0·308
T. rendalli Ad	0	0·007	**0·643**	0·003	0·001	0	0	0·125
T. ruweti	0·196	0·243	0·086	0·036	0	**0·398**	0·023	0·396
T. sparrmanii Juv	0·042	**0·354**	0·020	0·030	0·149	0·170	0·009	0·476
T. sparrmanii Ad	0·021	**0·312**	0·241	0·050	0·076	0·010	0·005	0·438

aquatic macrophyte tissues, especially grasses and sedges, and *T. ruweti* consumed mostly filamentous algae. Mean $L_S \pm$ S.D. for samples of dissected 'juvenile' (*i.e.* YOY) and 'adult' (*i.e.* age 1+ years) size classes were as follows: *O. andersonii* juveniles $94 \cdot 0 \pm 11 \cdot 1$ mm ($n = 5$); *O. andersonii* adults $244 \cdot 3 \pm 47 \cdot 6$ mm ($n = 16$); *O. macrochir* juveniles $74 \cdot 6 \pm 16 \cdot 2$ mm ($n = 29$); *O. macrochir* adults $204 \cdot 6 \pm 26 \cdot 7$ mm ($n = 24$); *T. rendalli* juveniles $66 \cdot 9 \pm 21 \cdot 1$ mm ($n = 68$); *T. rendalli* adults $215 \cdot 5 \pm 33 \cdot 0$ mm ($n = 19$); *T. ruweti* all $42 \cdot 1 \pm 7 \cdot 0$ mm ($n = 11$); *T. sparrmanii* juveniles $42 \cdot 7 \pm 12 \cdot 2$ mm ($n = 34$); and *T. sparrmanii* adults $103 \pm 8 \cdot 2$ mm ($n = 56$). Comparison of volumetric proportions consumed by juvenile and adult size classes yielded little evidence of ontogenetic diet shifts. Dietary overlap between juvenile and adult conspecifics was 0·82 for *T. sparrmanii*, 0·92 for *T. rendalli* and 0·99 for the two *Oreochromis* species. Diet breadth was low for both size classes of the *Oreochromis* species and adult *T. rendalli*. Moderate diet breadth was obtained for juvenile *T. rendalli*, *T. ruweti* and both size classes of *T. sparrmanii* (Table I). These latter groups consumed variable amounts of detritus, macrophytes and algae.

For both juvenile and adult size classes, dietary overlap was high among *O. andersonii*, *O. macrochir* and *T. sparrmanii*, with values ranging from 0·67 to 0·99. For both size classes, *T. rendalli* had low dietary overlap with all other tilapiine species except for *T. sparrmanii* (values ranged from 0·01 to 0·92). Overlap between *T. rendalli* and *T. sparrmanii* was 0·40 and 0·71 for juveniles and adults, respectively. Dietary overlap was intermediate between *T. ruweti* and other tilapiine species except for *T. rendalli* (0·44–0·53).

DISCUSSION

High habitat and dietary overlap observed among Upper Zambezi tilapiines during the protracted period of floodwater withdrawal contrasts sharply with the strong patterns of resource partitioning documented for carnivorous haplochromine cichlids (*Serranochromis* and *Sargochromis* species) of this region (Winemiller, 1991). During the falling-water period, carnivorous haplochromines displayed strong niche complementarity in relation to habitat and dietary overlap. Although these findings represent indirect evidence, such patterns suggest that, at some scale, interspecific competition for limited resources influences these haplochromine populations. By a similar process of inference, it might be concluded that food resources are not limiting for tilapiine species that show high levels of overlap in diet and habitat use (Lowe-McConnell, 1959). Detritus and algae seem to be abundant in all aquatic habitats throughout the year; however, the nutritional content of detritus and composition, nutritional quality and quantity of algae could vary in time and space. Bowen (1979, 1980, 1981) documented variation in the nutritional quality of detritus consumed by tilapiines and concluded that amino acid content strongly influences individual growth.

It is possible that algae and detritus were limiting for these populations during the period of study, but that the dietary categories used in the present study were too broad to reveal fine-scale patterns of food resource segregation. Based on microscopic examination of stomach contents, detritus was divided into two categories: fine particulate and amorphous material and coarse

vegetative detritus. Although it is possible that fishes could further subdivide detritus, *e.g.* by feeding in different microhabitats or selecting different particle sizes, this was not apparent from microscopic examination of stomach contents. Detritus consumed by Upper Zambezi tilapiines probably derives from multiple sources, including a variety of terrestrial and aquatic macrophytes, periphyton, phytoplankton and faeces. The nutritional content of detritus varies accordingly (Bowen, 1979, 1980), but it is not known how well fishes can perceive and selectively ingest detritus on this basis. *Oreochromis* species and *T. sparrmanii* consumed mostly vegetative detritus and very small fractions of fine detritus. In contrast, *T. ruweti* consumed nearly equal proportions of the two categories. The macrophyte feeder *T. rendalli* consumed comparatively little detritus of either type.

Initially, algae were categorized as diatoms, desmids, unicellular green, filamentous green and filamentous blue-green algae. Because the amount of algae consumed by Upper Zambezi tilapiines was quite low (Table I), the five categories were subsequently aggregated into two categories (unicellular and filamentous). Since algae were relatively unimportant in diets, aggregation of algal categories should not have significantly biased niche overlap values. Presumably, algae provide a richer food resource than detritus, yet relatively little algivory was observed among Upper Zambezi tilapiines. *Tilapia ruweti* and juvenile *T. sparrmanii* were the only forms that fed on significant amounts of filamentous algae (periphyton). Diatoms comprised a small portion (*c.* 10%) of the diet of juvenile *O. macrochir*, and desmids and other unicellular green algae comprised nearly 20% of the diet of juvenile *T. rendalli* and 15% of the diet of juvenile *T. sparrmanii*. Kelley (1968) reported higher percentages of periphyton consumption by all tilapiine species, but his methods of estimation and analysis were not reported, and sample sizes were small ($n = 13$–40). High dietary overlap among tilapiines has been demonstrated independently in the central region of the Upper Zambezi floodplain (Kelley, 1968, present study) and once in the Kafue floodplain in central Zambia (Chapman *et al.*, 1971).

Upper Zambezi tilapiines consumed only traces of animal material (*e.g.* protozoa, nematodes, rotifers, microcrustacea, larval insects and chitin fragments). Lowe-McConnell (1959), referencing the work of Le Roux (1956) in South African ponds, reported that *O. andersonii*, *Oreochromis mossambicus* (Peters), *T. rendalli* and *T. sparrmanii* all preferred zooplankton at total lengths <50 mm. Smallest individuals in Upper Zambezi samples were 28–40 mm L_S, except for *O. andersonii* (minimum 80 mm L_S). Greatest percentages of invertebrate prey in stomachs were *c.* 5% for juvenile *O. andersonii* and *c.* 2% for all size classes of *T. ruweti*, the smallest species.

Niche complementarity (an inverse relationship between overlap in foods consumed and overlap in habitats occupied) was not apparent during the 8 month field study. All five species occur in river channel and floodplain habitats of the Upper Zambezi, although *O. andersonii* and *T. ruweti* were less abundant overall, and less common in channel samples than lagoon samples. *Tilapia rendalli* was the only species captured more frequently in the channel than lagoons, but this difference was not statistically significant (ANOVA, $P > 0.05$). Only *T. rendalli* had a diet distinct from other tilapiines. Patterns of dietary and habitat overlap were not greatly influenced by body size or season

(early *v.* late falling-water phase). Fishes of all sizes were often captured in the same habitats, and dietary overlap between small and large size classes was high. Most of the smallest individuals were captured during the early falling-water period (May to August), yet no seasonal or size effect on diet was observed. In Lake Sibaya, South Africa, juvenile *O. mossambicus* reduced use of littoral habitats and fed more on phytoplankton and less on detritus in response to higher lake levels and the presence of predatory *Clarias gariepinus* (Burchell) in the littoral zone (Bowen & Allanson, 1982). Stable isotope analysis performed on samples from an exotic population of *Oreochromis aureus* (Steindachner) in Florida indicated that some individuals fed predominantly on detritus and others fed on phytoplankton (Gu *et al.*, 1997). Comparatively little intraspecific dietary variation was observed from analysis of stomach contents in the present study.

Even though tilapiines have the ability to feed on a variety of plant and animal foods, ontogenetic shifts did not occur over the range of sizes examined in the Upper Zambezi. In this system, ecological patterns of tilapiines seem to be established early in life (*c.* 30 mm L_S). The size at maturity reported here for *O. andersonii* corresponds closely to that reported by Dudley (1974) for Kafue populations (measured as fork length). Maximum L_S in Upper Zambezi samples appear to be similar to the maxima reported by Chapman *et al.* (1971) for Kafue populations of *O. andersonii*, *O. macrochir* and *T. rendalli*, and to the approximate species maxima reported by Skelton (1993). The largest *O. andersonii* (323 mm L_S) from the Upper Zambezi was almost equal to the largest individual from the Okavango Delta, Botswana (322 mm L_S, estimated at 11 years) examined by Booth *et al.* (1995). Tilapiine fishes, *T. rendalli* in particular, are among the most commercially valuable fishes in Zambia. Exploitation of tilapiines is heavy during the falling-water phase of the annual hydrological cycle. High similarity in diet and habitat use among Upper Zambezi tilapiines suggests that interspecific competition may not be great, at least during the protracted falling-water period when fish densities are highest and resources should be most limiting. Thus natural and fishing mortality might be regulating these populations below their environmental carrying capacities. Detailed studies of variation in food resource quality and analyses of fish condition and growth are needed to evaluate this hypothesis.

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