

Comparative ecology of *Serranochromis* species (Teleostei: Cichlidae) in the Upper Zambezi River floodplain

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The Upper Zambezi River drainage of Zambia contains six *Serranochromis* species belonging to the largemouth, piscivorous subgenus *Serranochromis* and three smallmouth, invertebrate-feeding species of the subgenus *Sargochromis*. A survey of the Barotse floodplain and associated drainages revealed that two species, *S. (S.) longimanus* (Boulenger) and *S. (S.) thumbergi* (Castelnau), were uncommon on the floodplain. *S. thumbergi* appeared to be more abundant in the Kafue, Chobe, and Kabompo rivers than the Upper Zambezi proper. Adults of the three largest species (i.e. *S. (S.) robustus* (Günther), *S. (S.) altus* (Winemiller & Kelso-Winemiller), and *S. (Sar.) giardi* (Pellegrin)) inhabit the main channel of the Zambezi River during low water, whereas most adults of the other four species (i.e., *S. (S.) macrocephalus* (Boulenger), *S. (S.) angusticeps* (Boulenger), *S. (Sar.) codringtoni* (Boulenger), and *S. (Sar.) carlottae* (Boulenger)) were collected from lagoons, canals and backwaters. Comparisons of population size structure and gonad condition during the falling water (May–August) and low water (September–December) seasons indicated that the seven common *Serranochromis* initiate spawning near the end of the low water period.

Examination of gonad condition during the pre-spawning period indicated that *Serranochromis* attain maturity at the following sizes: *S. robustus*, males (275–300 mm S.L.), females (250–275 mm); *S. macrocephalus*, both sexes (150–200 mm); *S. altus*, males (275–325 mm), females (250–300 mm); *S. angusticeps*, males (250–275 mm), females (175–225 mm); *S. giardi*, males (275–300 mm), females (225–250 mm); *S. codringtoni*, males (150 mm), females (125–150 mm); *S. carlottae*, males (150–175 mm), females (100–125 mm). Age was estimated from scale annuli comprised of closely spaced circuli that corresponded to the period of rising water (December–March). *S. robustus*, *S. altus*, *S. angusticeps*, and *S. giardi* matured at approximately 3 years, and *S. macrocephalus*, *S. codringtoni*, and *S. carlottae* matured at approximately 2 years in the Barotse floodplain. The average numbers of mature oocytes per female were as follows: *S. robustus*—1165; *S. macrocephalus*—810; *S. altus*—920; *S. angusticeps*—627; *S. codringtoni*—580; *S. carlottae*—362. Fecundity exhibited a weak positive relationship with female size. Analysis of stomach contents showed that interspecific diet overlap was low among both immature and mature size classes of *Serranochromis*. Adult size classes of *S. robustus* fed primarily on small *Synodontis* catfishes, *S. macrocephalus* fed mostly on mormyrid and cichlid fishes, *S. altus* specialized on mormyrids, and *S. angusticeps* fed primarily on small cyprinid and characid fishes. The three members of the subgenus *Sargochromis* consumed mostly invertebrates. Molluscs were the most important item in the diet of *S. giardi*, and aquatic insects and fish scales were predominant in the diet of *S. carlottae*. Larger size classes of *S. codringtoni* consumed large amounts of seeds (Graminaceae). If habitat and diet are considered together, niche separation among Upper Zambezi *Serranochromis* species appears to be nearly complete.

Key words: *Serranochromis*; *Sargochromis*; Zambezi River; Barotse floodplain; Zambia; Africa; piscivore; feeding; reproduction; seasonality; maturation; fecundity; habitat.

I. INTRODUCTION

The genus *Serranochromis* Regan contains 15 species in southern and central Africa, nine corresponding to Greenwood's (1979) piscivorous subgenus

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Serranochromis and seven corresponding to the invertebrate-feeding subgenus *Sargochromis*. The two subgenera were considered separate genera prior to revisions by Bell-Cross (1975) and Greenwood (1979). The centre of diversity for the genus is the Upper Zambezi River drainage which includes the Zambezi River above Victoria Falls, the Okavango River, and the Cuando/Chobe River. With the recent description of the piscivore *S. S. altus* (Winemiller & Kelso-Winemiller, 1991), brings the number of Upper Zambezi/Okavango *Serranochromis* species to ten. Two species, *S. (Sargochromis) greenwoodi* Bell-Cross and *S. (Sarg.) gracilis* Greenwood, seem to be restricted to the Okavango drainage (Skelton *et al.*, 1985), whereas *S. (S.) altus* currently is reported only from the Upper Zambezi and Kafue River drainages of Zambia (Winemiller & Kelso-Winemiller, 1991).

The Kafue River drainage contains eight *Serranochromis* species, all shared with the Upper Zambezi. The Chambeshi/Luapula River drainage contains four piscivorous *Serranochromis* plus two endemic invertebrate-feeders of the subgenus *Sargochromis*. Trewavas (1964) described two additional species, *S. (S.) spei* Trewavas which is restricted to extreme southeastern tributaries of the Zaire River, and *S. (S.) janus* Trewavas from the Malagarazi River, an eastern tributary of Lake Tanganyika.

Known by a variety of local names, *Serranochromis* species are sometimes referred to as 'nembwe' (i.e. the wide-ranging *S. robustus*), 'breams', 'large-mouth breams' or 'happies' (i.e. smallmouth varieties). Available evidence indicates that all members of the genus are mouth-brooders (Trewavas, 1964; Jubb, 1967). Despite the widespread distribution of the genus in south/central Africa and the importance of *Serranochromis* species in commercial and subsistence fisheries, few ecological data for the group have been published. Much of the *Serranochromis* natural history information summarized in Jackson (1961a), Jubb (1961, 1967), Bell-Cross (1972), and Bell-Cross & Minshull (1988) was derived from fisheries surveys and sports fishermen's reports. Kelley (1968) reported length frequencies, length-weight relationships, gillnet selectivity, and preliminary diet findings for five *Serranochromis* species in his survey of the Upper Zambezi fishery, and Van der Waal (1985) reported *Serranochromis* ecology in Lake Liambezi (Chobe River). Lagler *et al.* (1971) reported standing stocks and Chapman *et al.* (1971) investigated gill net selectivity and the relationship between local stocks and environmental variables for seven *Serranochromis* species in the Kafue flats. Here findings from an 8-month study of *Serranochromis* ecology in the Barotse floodplain and associated drainages of the Upper Zambezi River in Zambia are reported.

II. DESCRIPTION OF THE UPPER ZAMBEZI FLOODPLAIN ENVIRONMENT

The investigation was conducted in the Upper Zambezi River drainage of Zambia's Western Province from 21 May through 9 December 1989. The Upper Zambezi River arises on Africa's Central Plateau in Zambia's Northwestern Province and flows south through Angola before re-entering Zambia at latitude 13° S (Fig. 1). Victoria Falls on the border between Zambia and Zimbabwe marks the lower limit of the Upper Zambezi River drainage. Although many species are shared, the fish fauna of the Upper Zambezi is distinct from the region below the falls, designated the Middle Zambezi River (Jubb, 1967; Balon, 1974; Bell-Cross,

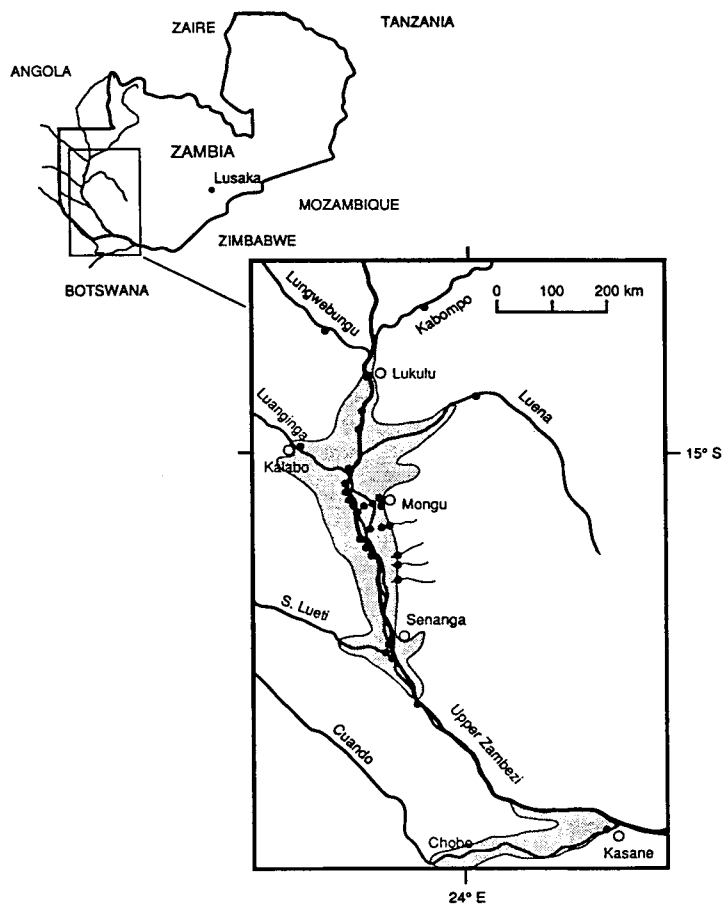


FIG. 1. Map showing the Upper Zambezi River study region in Zambia. Shaded regions represent floodplains; ●, locations of principal collection sites.

1972; Bell-Cross & Minshull, 1988). At 98 m, Victoria Falls is presumed to form a barrier to upstream invasion by Middle Zambezi fishes, but is not entirely effective as a barrier to downstream invasions by Upper Zambezi fishes (Balon, 1974). The Upper Zambezi has been classified as a reservoir-river that exhibits seasonal inundation of a very broad, gently sloping floodplain (Jackson, 1961*b*). In contrast the Middle Zambezi has been classified as 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. Balon (1974) argued that sandbank conditions of the Middle Zambezi constituted an unfavourable environment for colonization by Upper Zambezi fish species. The formation of Lake Kariba in the 1960s produced a new lentic habitat within the Middle Zambezi, and was followed by the establishment of several Upper Zambezi species, including four *Serranochromis* species (only *S. codringtoni* was reported from the Middle Zambezi prior to Kariba: Jackson, 1961*b*; Balon, 1974).

The Upper Zambezi, or Barotse, floodplain is about 30 km wide in its central region near Mongu (Fig. 1) and approximately 250 km from its northern limit near

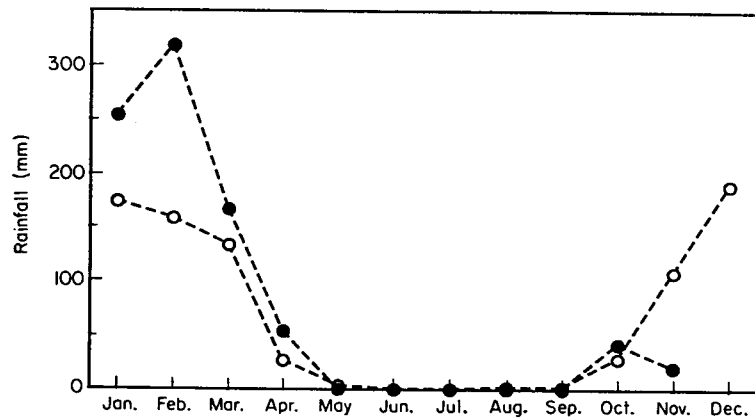


FIG. 2. Monthly rainfall averages for Mongu, Western Province, Zambia during the study period (●, 1989) compared with 10-year averages for the period 1979–1988 (○, data from Zambia Department of Climatology).

Lukulu to southern limit at the Ngonye Falls. The Barotse floodplain has been estimated to hold up to $17 \times 10^9 \text{ m}^3$ of water during the peak flood stage (Sharma & Nyumbu, 1985). The central Barotse floodplain region averages 826 mm of rainfall annually, nearly all of it falling from November through March. Rainfall was considerably higher than average during the early flood period of 1989 and lower than average during November, 1989 (Fig. 2). Rainfall exhibits a marked gradient from a high of 1400 mm annually near the Zambezi's source in the north to a low of 700 mm near the Zambia–Namibia border to the south (Handlos & Williams, 1985). As a result, the largest fraction of the annual flood waters spilling onto the Barotse floodplain are derived from northern tributaries in Angola and Northern Zambia (i.e., Kabompo, Lungwebungu, Luanginga Rivers) rather than the proximate Barotse watershed in Western Province (Handlos & Williams, 1985). Flooding typically begins in the northern Barotse floodplain region during December or January, peaks in the central region in March and April, and subsides from the central and lower regions during May–August. Annual flooding of the Chobe River swamps in Namibia and Botswana is caused mostly by Zambezi River water spilling into the Chobe which forces a temporary reverse flow of water upstream.

Water temperatures measured at 12.00 hours on the floodplain fluctuated between a low of 18°C (7 August, 2 m deep in canal) to a high of 28°C (23 November, surface in canal) during the course of the field study in 1989. Zambezi River water ranged between 21 and 27.5°C and pH from 6.3 to 6.9 over the course of the study. pH measurements ranged between a low of 5.5 in floodplain pools to a high of 7.0 in the Kabompo River. Waters of the river, tributaries, and floodplain pools were always close to full oxygen saturation and clear, but often tea-stained with organic compounds. Most of the soils of Western Province are comprised of ancient Kalahari sands, and although acidic and nutrient-poor, they support deciduous forests and scrub grasslands. Although floodplain soils are only slightly more fertile than those of the surrounding uplands, they support small-scale gardening and cattle grazing during the low water period. The Barotse floodplain is a largely treeless grassland dominated by *Phragmites* reeds, *Potamogeton* spp., *Nymphae* spp., *Vossia cuspidata* and *Utricularia* spp. along waterways. Some

lagoons become completely covered with dense mats of *Salvinia auriculata* during the dry season. Phytoplankton production is assumed to be very low in the clear, nutrient-poor waters of the Upper Zambezi River (Kelley, 1968).

III. METHODS

Most collections were made in aquatic habitats of the Upper Zambezi, or Barotse, floodplain (Fig. 1). Samples were also taken during irregular intervals from tributaries flowing onto the Barotse floodplain: South Lueti, Luanginga, Lungwebungu, Kabompo, and Luena Rivers, plus a number of small east-bank streams (Fig. 1). In addition, fishes were collected from the Zambezi River downstream from the floodplain (Ngonye Falls), the Chobe River near Kasane, Botswana (August), and the Kafue River near Kafue township (June) and the Lufupa River confluence (June, September). Chobe fishes were included in numerical analyses, whereas Kafue collections were not. A complete listing of sample sites, dates, and species taken are on file at the Texas Natural History Collection of the Texas Memorial Museum, Austin, Texas, U.S.A. Environmental conditions were recorded at each site, including quantitative measurements of water temperature, pH and dissolved oxygen. Fishes were collected using a variety of methods at each site. At most floodplain sites I used hook and line, castnet (2.54 cm mesh), dipnet (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(10.216 cm mesh), 1(5.08 cm mesh)]. Feeder streams and shallow floodplain pools were sampled with dipnet and the smaller seine (0.63 cm mesh). At most sites, attempts were made to collect all of the fish species in proportions reflecting their relative abundances at the location. Some fishes were placed in cool boxes and examined within 18 h of capture, and others were preserved in 15% formalin and stored for later examination.

The commercial fish catch brought to the Mongu Nutrition Center from the Mukakani fishing camp (15°27' S, 23°7'6" E) was examined at irregular intervals. As a supplement to data derived from captured specimens, *Serranochromis* in the commercial catch were measured and examined for stomach contents and gonad condition. In addition, two samples from local fishermen's 'maalelo' traps were preserved during the middle and late portion of the falling water period of the Barotse floodplain. Maalelo are dams constructed of grass mounds or reed fences that block the return of water from the inundated plain to lagoons and permanent channels (Kelley, 1968). Reed fish traps with funnel-type, no-exit valves are placed behind openings in the dams. Contents of three traps from a mound-type maalelo (15°23'30" S, 23°10' E; 1 km east of Sefula on edge of central floodplain) were preserved on 6 June 1989. Contents of four baskets from two fence-type maalelo (15°18' S, 22°53' E; 16 km east of Mongu and 3 km east of Zambezi River on Malile canal) were preserved on 12 July 1989.

Standard length (S.L.), condition of gonads, relative amount of visceral fat deposits, and stomach contents were recorded for all *Serranochromis* specimens. All lengths are reported as S.L. Methods for assessing gonad condition and fat contents follow Winemiller (1989a). Testes classified as smooth white and either large or medium/large were assumed to be ripe and indicative of sexual maturity. Similarly, ovaries that were opaque yellow and large or medium/large were classified as ripe. The diameter (through the longest axis) of the largest oocyte in each ovary was measured to the nearest 0.05 mm using a dissecting microscope fitted with an ocular micrometer. The number of mature oocytes in several females containing ripe ovaries were counted. Scales were removed from several individuals of each species and examined under a binocular dissecting microscope for evaluation of annulus formation. Scales were removed from the right flank about midway between the dorsal origin and the anterior lateral line. Scale annuli were fairly distinct in both immature and adult size classes and consisted of closely spaced circuli that seemed to correspond to either the late low water season (November–December) or the period of rising water (December–March). Most fishes 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.

Stomach contents were identified to the level of order for most invertebrates and quantified volumetrically by water displacement (Winemiller, 1989b). Aquatic Diptera

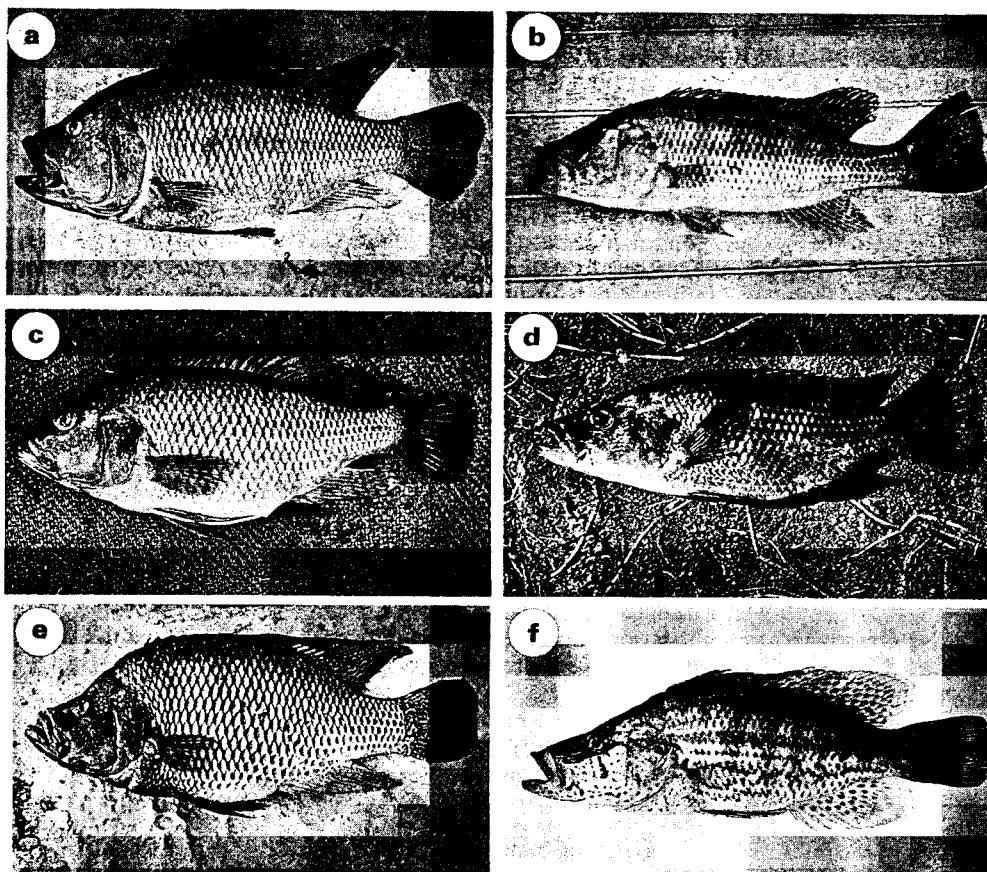


FIG. 3. Representative specimens of the *Serranochromis* subgenus *Serranochromis* from the Upper Zambezi. (a) *S. (S.) robustus* Günther, 'nembwe' (Lozi), yellow bream (422.0 mm male from Upper Zambezi River). (b) *S. (S.) thumbergi* Castelnau, 'mununga', brown-spot bream (282.0 mm from Kafue River). (c) *S. (S.) macrocephalus* Boulenger, 'njenja', purple-headed bream (340.0 mm male from Barotse floodplain). (d) *S. (S.) longimanus* Boulenger, longfin bream 172.0 mm from Barotse floodplain). (e) *S. (S.) altus* (Winemiller & Kelso-Winemiller), hump-back bream (410.0 mm male from Upper Zambezi River). (f) *S. (S.) angusticeps* Boulenger, 'mushuna', thin-faced bream (195.0 mm from Barotse floodplain).

were classified as either mosquito larvae, chironomid larvae/pupae, or other Diptera larvae/pupae, and aquatic Hemiptera were designated as either Corixidae, Gerridae, or other aquatic Hemiptera. Molluscs were classified as either snails or bivalves. Fishes from stomachs were identified to species or genus whenever possible. The other fish diet categories were unidentified fish, ctenoid scales, and cycloid scales. Diet breadths were calculated using Simpson's (1949) index, and interspecific dietary similarities were calculated using Pianka's (1973) symmetrical version of MacArthur & Levins's (1967) overlap index. Overlap values can range between 0 (no diet items shared) and 1.0 for complete diet similarity.

IV. RESULTS

In addition to the eight nominal species of *Serranochromis* reported for the Zambian Upper Zambezi drainage (Figs 3 and 4), a new species, *S. (S.) altus*, was

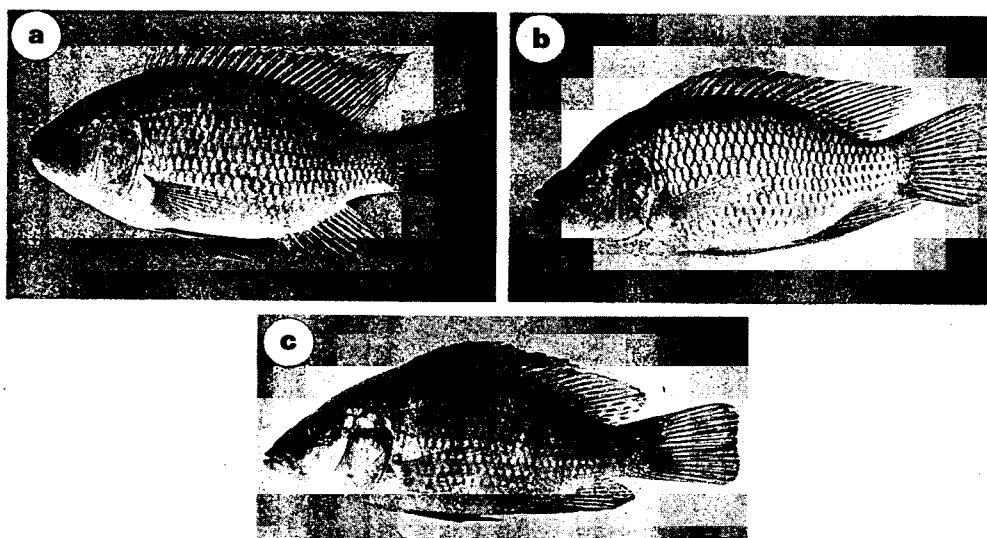


FIG. 4. Representative specimens of the *Serranochromis* subgenus *Sargochromis* from the Upper Zambezi. (a) *S. (Sarg.) giardi* Pellegrin, 'syeo', pink bream (305.0 mm from Upper Zambezi River). (b) *S. (Sarg.) carlottae* Boulenger, 'mbuma', rainbow bream (148.5 mm from Barotse floodplain). (c) *S. (Sarg.) codringtoni* Boulenger, 'syeo', green bream (120.0 mm from Barotse floodplain).

identified and found to be relatively common in the Barotse floodplain area (K. O. Winemiller and L. Kelso-Winemiller, 1991). *S. altus* is morphologically similar to *S. angusticeps*, the sympatric species with which it seems to have been confused previously. *S. longimanus* and *S. thumbergi* were rare in Upper Zambezi collections. *S. thumbergi* was absent from Barotse floodplain collections, two immatures were taken from the Kabompo River to the north, and four were taken from the Chobe River to the south. Five *S. longimanus* were captured from lagoons and backwaters in the central Barotse floodplain region, and one immature was taken from the shoreline of the Chobe River. Consequently, the analysis that follows will deal with the seven species of *Serranochromis* that were common in the Barotse floodplain region (Figs 3 and 4).

POPULATION SIZE STRUCTURE

The total numbers of individuals obtained were 425 (*S. macrocephalus*), 255 (*S. codringtoni*), 238 (*S. angusticeps*), 190 (*S. robustus*), 116 (*S. altus*), 106 (*S. giardi*) and 54 (*S. carlottae*). The seven species showed similar shifts in population size structure when the falling water period (May–August) was compared with the low water period (September–December). Collections made during the falling water period were dominated by smaller size classes that presumably contained many immature young-of-the-year fishes (Figs 5 and 6). Relatively few large size classes were captured during the falling water period, because fishes remained highly dispersed in the still greatly-expanded aquatic environment of the floodplain. After the floodplain had drained completely (September), both large and small size classes were easier to locate and much more susceptible to capture. Apparently, relative proportions of small size classes were reduced during the low water period through the combined effects of (1) predation and (2) growth in the absence of

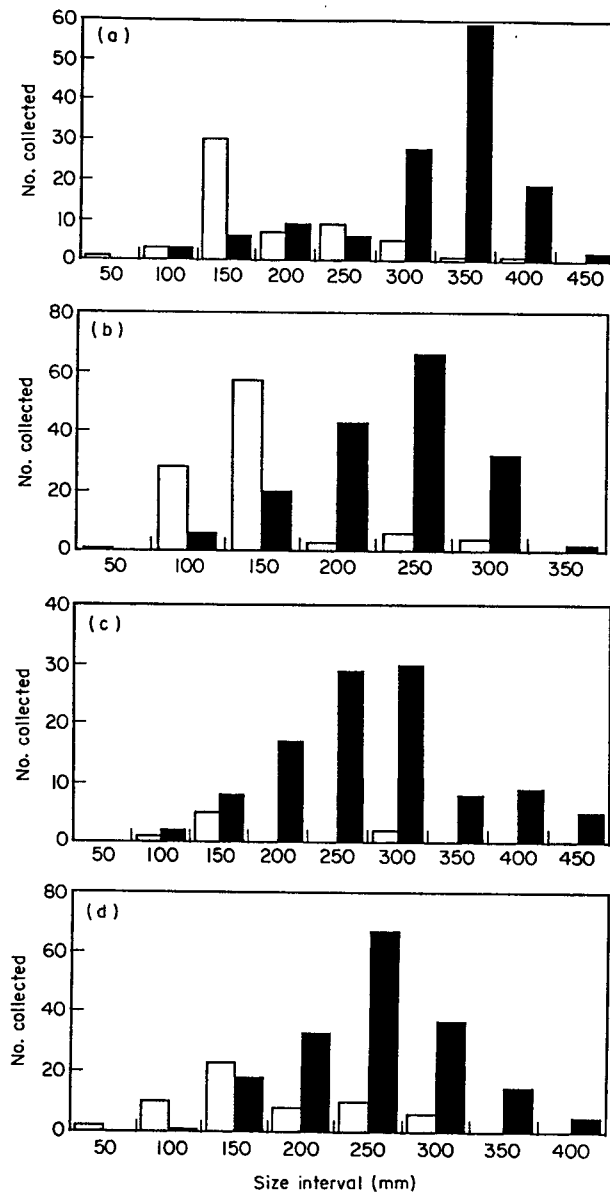


FIG. 5. Length-frequency histograms for (a) *S. (S.) robustus*, (b) *S. (S.) macrocephalus*, (c) *S. (S.) altus* and (d) *S. (S.) angusticeps* collected during the falling water season (May–August) and low water season (September–December) from the Upper Zambezi drainage in 1989. □, Falling water season; ■, low water season.

spawning activity that would add new recruits to the smallest size classes. The domination of large size classes during the low water period suggests a strongly seasonal pattern of reproduction for all seven species. The two smallest species, *S. codringtoni* and *S. carlottae*, show bimodal size distributions during the low water period (Fig. 6), suggesting that their reproductive seasons may extend well into the flood period.

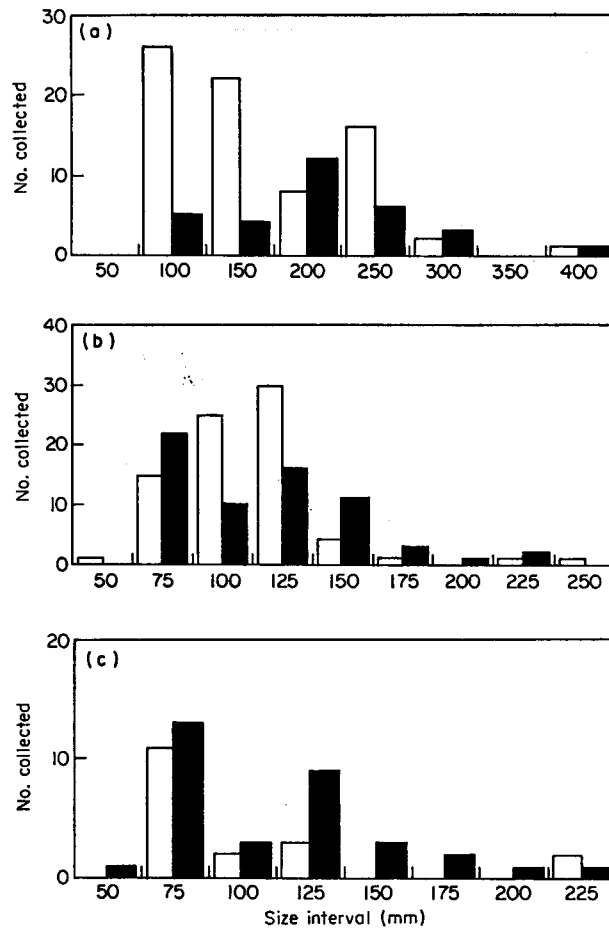


FIG. 6. Length-frequency histograms for (a) *S. (Sarg.) giardi*, (b) *S. (Sarg.) codringtoni* and (c) *S. (Sarg.) carlottae* collected during the falling water season (May–August) and low water season (September–December) from the Upper Zambezi drainage in 1989. □, Falling water season; ■, low water season.

HABITAT AFFINITIES

Aquatic habitats were divided into three basic categories: river (the main channel of the Zambezi and Chobe Rivers), lagoon (permanent floodplain lagoons, canals, small tributary rivers, backwaters), and floodplain (shallow ephemeral pools, small feeder streams on the edge of the floodplain). Large size classes of the three largest species (i.e., *S. robustus*, *S. altus*, *S. giardi*) were encountered primarily in the main river channel (Fig. 7). During the low water period, large *S. robustus* and *S. giardi* were taken frequently by hook and line and gillnet in the deepest regions near the bottom and close to high sand banks. *S. robustus* appeared to be associated with swifter currents than *S. giardi*, the latter often being taken closer to shore near the interface between swift current and slow swirling back eddies. Most *S. altus* were captured in overnight sets of gillnets above deep shoreline regions of the Zambezi River. Large *S. altus* were always taken from mid-depths or near the surface, usually beneath or adjacent to dense stands of aquatic vegetation and close to the interface between swift downstream current and slower back eddies. Large size

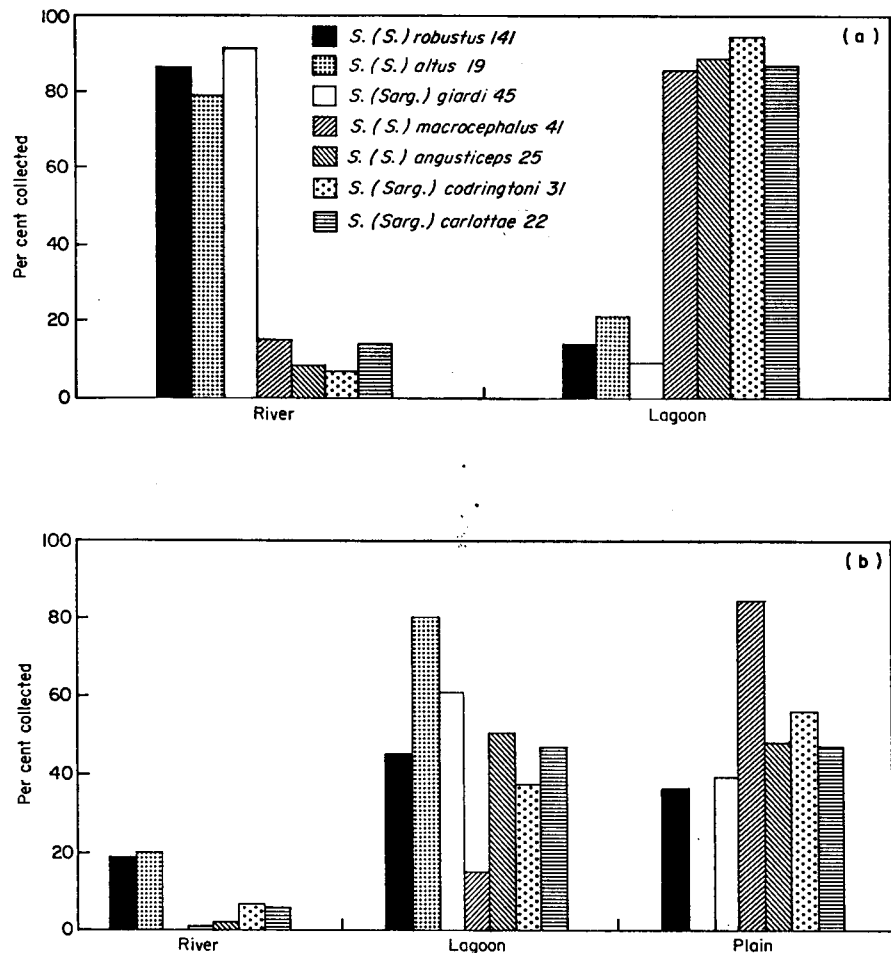


FIG. 7. Percentages of *Serranochromis* specimens collected from river (main channel of Zambezi River), lagoon (lagoons, canals, backwaters, major tributaries), and floodplain (ephemeral pools, peripheral streams) habitats. Numbers in keys are total number of specimens collected for each species; large size classes correspond to *Sargochromis* > 100 mm, *Serranochromis* > 150 mm. (a) Large size classes; (b) small size classes.

classes of *S. macrocephalus*, *S. angusticeps*, *S. codringtoni* and *S. carlottae* were captured from lagoons, slow flowing tributaries, and quiet backwaters (Fig. 7). *S. macrocephalus* and *S. codringtoni* are probably the two most abundant *Serranochromis* in the Barotse floodplain and both were taken frequently near the bottom or midwater depths in overnight sets of gillnets. *S. macrocephalus* and *S. codringtoni* were captured both near and away from aquatic vegetation, whereas *S. angusticeps* was almost always captured within or adjacent to aquatic vegetation. Large size classes of *S. carlottae* were usually captured near aquatic vegetation, submerged branches, or other cover.

Juvenile size classes of *S. robustus*, *S. altus*, and *S. giardi* were captured most frequently from the lagoon/canal habitat (Fig. 7). Few small *S. altus* were captured during field surveys. In November, a 96.0 mm *S. altus* was captured from vegetation along the edge of the main river channel using a hand net. During much of

TABLE I. Relative numbers of ripe individuals among adult size classes of *Serranochromis* examined during the falling water (June–August) and low water (September–December) seasons of 1989

Species	Minimum size of maturation (mm)	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
<i>S. altus</i>	275 (m)	—	—	—	0/9	2/7	7/7	—
	250 (f)	—	—	—	0/13	1/4	7/9	—
<i>S. angusticeps</i>	250 (m)	—	0/3	0/2	2/9	7/12	5/13	1/1
	175 (f)	—	0/9	—	1/10	3/23	24/29	1/1
<i>S. macrocephalus</i>	150 (m)	0/1	1/8	—	8/31	9/14	20/24	2/2
	150 (f)	—	0/3	—	13/22	14/19	17/22	1/1
<i>S. robustus</i>	300 (m)	—	0/1	—	3/8	6/18	11/17	—
	250 (f)	—	0/6	—	2/10	5/21	20/24	1/1
<i>S. giardi</i>	275 (m)	0/1	0/1	—	1/2	—	1/1	—
	225 (f)	—	0/3	0/2	—	—	0/1	—
<i>S. codringtoni</i>	150 (m)	—	0/1	—	—	—	0/1	—
	125 (f)	0/1	—	0/1	—	0/1	3/4	—
<i>S. carlottae</i>	150 (m)	—	0/1	—	1/2	1/1	1/1	—
	110 (f)	0/1	0/1	—	2/2	—	1/1	—

the year, dense vegetation was situated adjacent to deep water and it was difficult to sample for small fishes and juvenile *S. altus* may have been more abundant there than the records indicate. Most of the small *S. robustus* and *S. giardi* taken from seasonal aquatic habitats of the floodplain were captured in the maalelo traps during the falling water period. Juvenile size classes of the four lagoon-dwelling species were collected primarily from lagoon/canal and seasonal floodplain habitats (Fig. 7). Eighty-four per cent of the floodplain *S. macrocephalus* were taken in maalelo traps.

REPRODUCTIVE SEASONS

Except for *S. altus*, small fractions of each adult population began to show ripe gonads in September (Table I). Approximately 25% of *S. altus* adults had ripe gonads during October. Relative fractions of ripe males and females increased in all seven *Serranochromis* species between September and December. Although the field study was terminated in mid-December prior to the beginning of the new rainy season, most species appeared to be preparing for initiation of spawning prior to flooding. Several pairs of ripe male and female *S. robustus*, *S. altus*, *S. macrocephalus*, and *S. angusticeps* were taken together in stationary gillnets and single throws of the castnet. On 10 November, a 209.0 mm female *S. codringtoni* and a 374.0 mm female *S. altus* with developing zygotes in their mouths were captured. A 410.0 mm male *S. altus* with spent testes was taken along side of the mouth-brooding female in the gillnet.

SIZE OF MATURATION

Plots of the relative numbers of individuals with ripe and unripe gonads within 25 mm size intervals were used to estimate the size of sexual maturation of *Serranochromis* species (Figs 8–10). Only fishes collected during the October–December

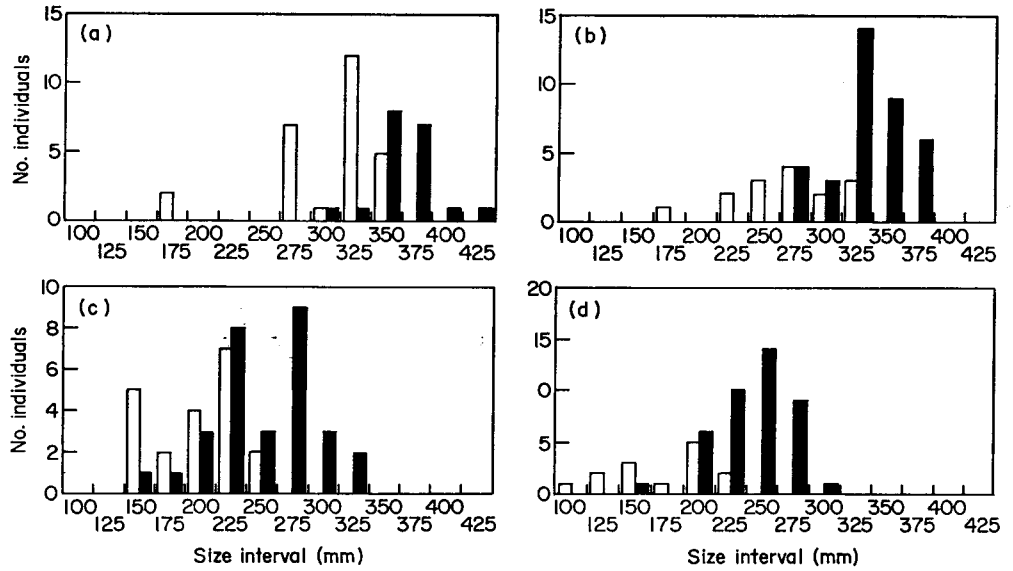


FIG. 8. Numbers of immature and ripe gonads encountered in male and female *S. robustus* and *S. macrocephalus* (plotted by s.L. interval) during the pre-spawning period, October–December 1989. □, immature; ■, mature. Male *S. robustus* (a), female *S. robustus* (b), male *S. macrocephalus* (c) and female *S. macrocephalus* (d).

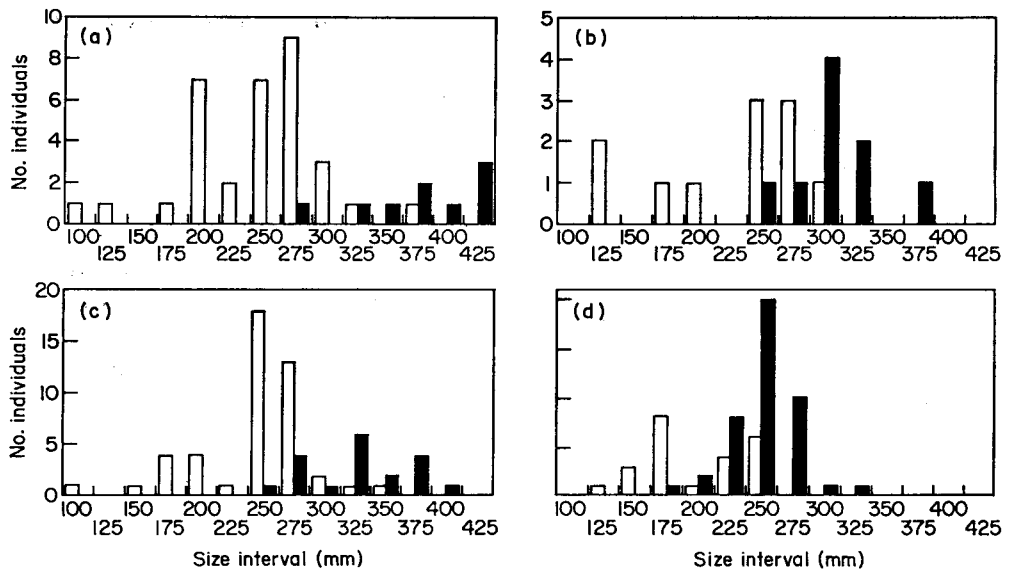


FIG. 9. Numbers of immature and ripe gonads encountered in male and female *S. altus* and *S. angusticeps* (plotted by s.L. interval) during the pre-spawning period, October–December 1989. □, immature; ■, mature. Male *S. altus* (a), female *S. altus* (b), male *S. angusticeps* (c) and female *S. angusticeps* (d).

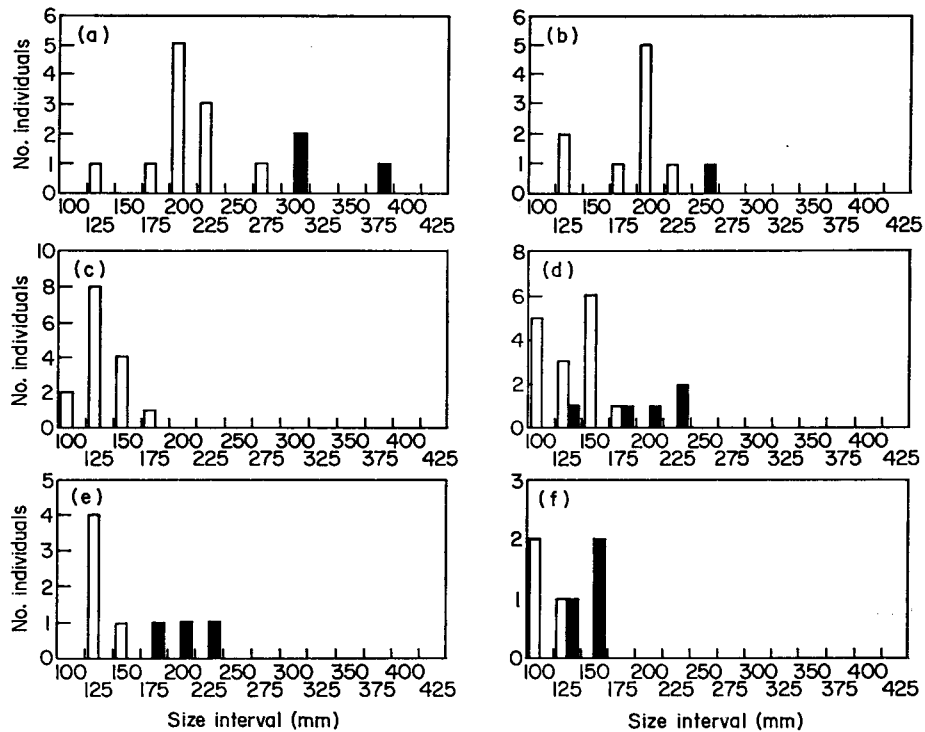


FIG. 10. Numbers of immature and ripe gonads encountered in male and female *S. giardi*, *S. carlottae* and *S. codringtoni* (plotted by s.l. interval) during the pre-spawning period, October–December 1989. □, immature; ■, mature. Male *S. giardi* (a), female *S. giardi* (b), male *S. carlottae* (c), female *S. carlottae* (d), male *S. codringtoni* (e) and female *S. codringtoni* (f).

pre-spawning period (Table I) were used for the plots. Sizes of sexual maturation were estimated as follows: *S. robustus*, males (275–300 mm), females (250–275 mm); *S. macrocephalus*, both sexes (150–200 mm); *S. altus*, males (275–325 mm), females (250–300 mm); *S. angusticeps*, males (250–275 mm), females (175–225 mm); *S. giardi*, males (275–300 mm), females (225–250 mm); *S. codringtoni*, males (150 mm), females (125–150 mm); *S. carlottae*, males (150–175 mm); females (100–125 mm). With the possible exception of *S. macrocephalus*, males matured at large sizes and attain larger maximum sizes than conspecific females. The three river-dwelling species (i.e. *S. robustus*, *S. altus*, *S. giardi*) matured at larger sizes and attained larger maximum sizes than lagoon-dwelling species. The largest fishes collected during the study were a 410.0 mm (2.1 kg) male *S. altus* and a 422.0 mm (2.2 kg) male *S. robustus* taken from the main channel of the Zambezi River near Mongu.

FECUNDITY

The average number of mature oocytes and average size of mature oocytes for six species is presented in Table II (no data were obtained for *S. giardi*). *S. robustus* had the highest average fecundity (no. of oocytes = 1165) and *S. carlottae* the lowest (no. of oocytes = 362). *S. robustus* had significantly higher fecundity than *S. macrocephalus* ($t = 4.17$, d.f. = 22, $P < 0.001$) and *S. angusticeps* ($t = 5.98$, d.f. = 19,

TABLE II. Mean number of mature oocytes and mean maximum oocyte diameters for ripe females of six *Serranochromis* species collected during the low water season

Species	Mean No. oocytes (s.d.)	Mean oocyte dia. (s.d.) (mm)	Mean s.l. (s.d.) (mm)	n
<i>S. altus</i>	920 (358)	3.32 (0.29)	269.5 (29.7)	7
<i>S. angusticeps</i>	627 (224)	3.57 (0.62)	246.5 (28.3)	20
<i>S. macrocephalus</i>	810 (232)	3.34 (0.63)	238.0 (24.1)	23
<i>S. robustus</i>	1165 (333)	3.76 (0.82)	323.4 (27.4)	23
<i>S. codringtoni</i>	580	3.80	178.0	1
<i>S. carlottae</i>	362 (11)	2.70 (0.42)	134.5 (19.7)	2

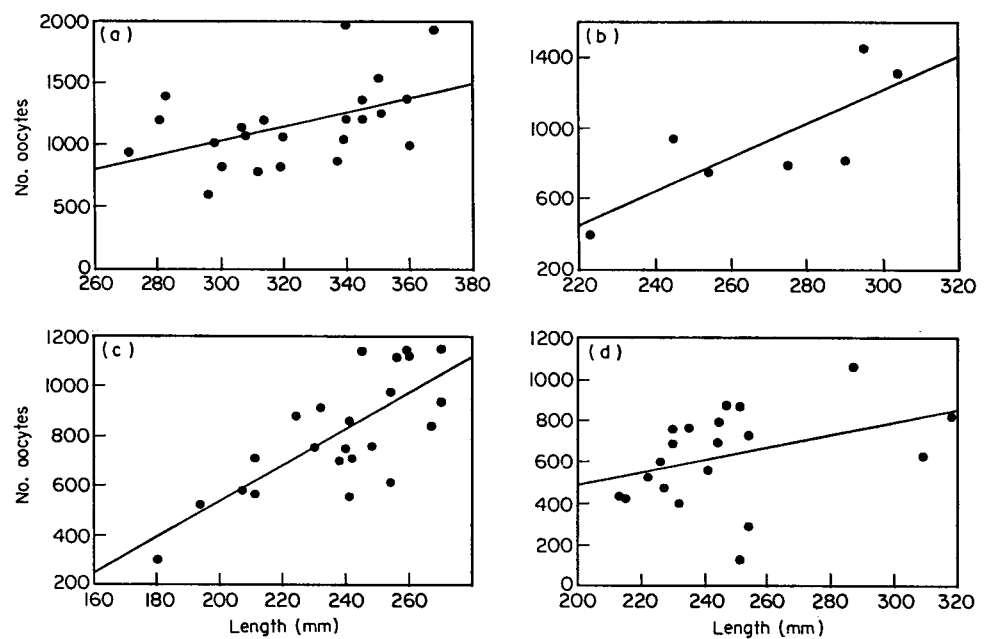


FIG. 11. Number of mature oocytes plotted against s.l. of female *Serranochromis* collected during the pre-spawning period, October–December 1989. Regressions are as follows: (a) *S. robustus*, $y = 5.8x - 717$ ($r^2 = 0.23$); (b) *S. altus*, $y = 9.6x - 1600$ ($r^2 = 0.64$); (c) *S. macrocephalus*, $y = 7.2x - 914$ ($r^2 = 0.56$); (d) *S. angusticeps*, $y = 3.0x - 122$ ($r^2 = 0.15$).

$P < 0.0001$). *S. angusticeps* had significantly lower fecundity than *S. macrocephalus* ($t = 2.78$, d.f. = 19, $P < 0.025$) and *S. altus* ($t = 2.92$, d.f. = 6, $P < 0.05$). Fecundity exhibited a weak positive relationship with female s.l. in the four species with samples > 6 (Fig. 11; $r = 0.48$, *S. robustus*; $r = 0.75$, *S. macrocephalus*; $r = 0.80$, *S. altus*; $r = 0.38$, *S. angusticeps*). Fecundity and oocyte diameter exhibited very weak negative relationships ($r = -0.10$, *S. robustus*; $r = -0.13$, *S. macrocephalus*; $r = -0.20$, *S. altus*; $r = -0.32$, *S. angusticeps*). Except for *S. altus* and *S. macrocephalus*

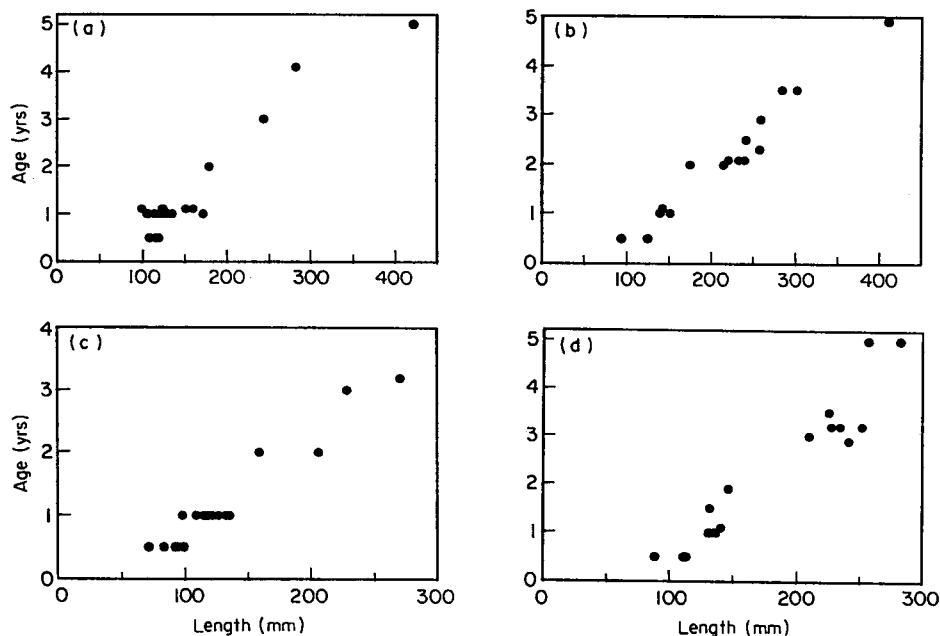


FIG. 12. Estimated ages based on scale annuli plotted against s.l. for (a) *S. robustus*, (b) *S. altus*, (c) *S. macrocephalus* and (d) *S. angusticeps*.

($t = 2.85$, d.f. = 6, $P < 0.05$), mature oocyte diameter did not differ significantly between species.

AGE-LENGTH RELATIONSHIPS

Based on the number of scale annuli and the relative width of the low-density region of circuli anterior to the last annulus, ages were estimated and plotted against length for each species (Figs 12 and 13). Multiple, faint false annuli were present on scales of many adult fishes, particularly *S. angusticeps*, *S. giardi*, *S. carlottae*, and *S. codringtoni*. Whereas annuli appeared to correspond with the transition between the low water and rising water periods in both immatures and adults, false annuli could result from multiple spawning bouts during the high water period. Combining size of maturation estimates (Figs 8–10) with age \times length relationships (Figs 12 and 13) yields estimates of the age of maturation. *S. robustus*, *S. altus*, *S. angusticeps*, and *S. giardi* matured at approximately 3 yr, and *S. macrocephalus*, *S. codringtoni*, and *S. carlottae* matured at approximately 2 yr in the Barotse floodplain. The maximum ages observed among the subset of fishes used for scale examinations were 6 yr (*S. giardi*), 5 yr (*S. robustus*, *S. altus*, *S. angusticeps*), 3 yr (*S. macrocephalus*), and 2 yr (*S. codringtoni*, *S. carlottae*).

FEEDING HABITS

The following are ratios of the number of empty stomachs encountered among the total number of fishes examined for stomach contents: *S. robustus* (100/190); *S. macrocephalus* (178/279); *S. altus* (79/114); *S. angusticeps* (182/238); *S. giardi* (48/101); *S. codringtoni* (13/162); *S. carlottae* (3/54). As a population, *S. robustus*

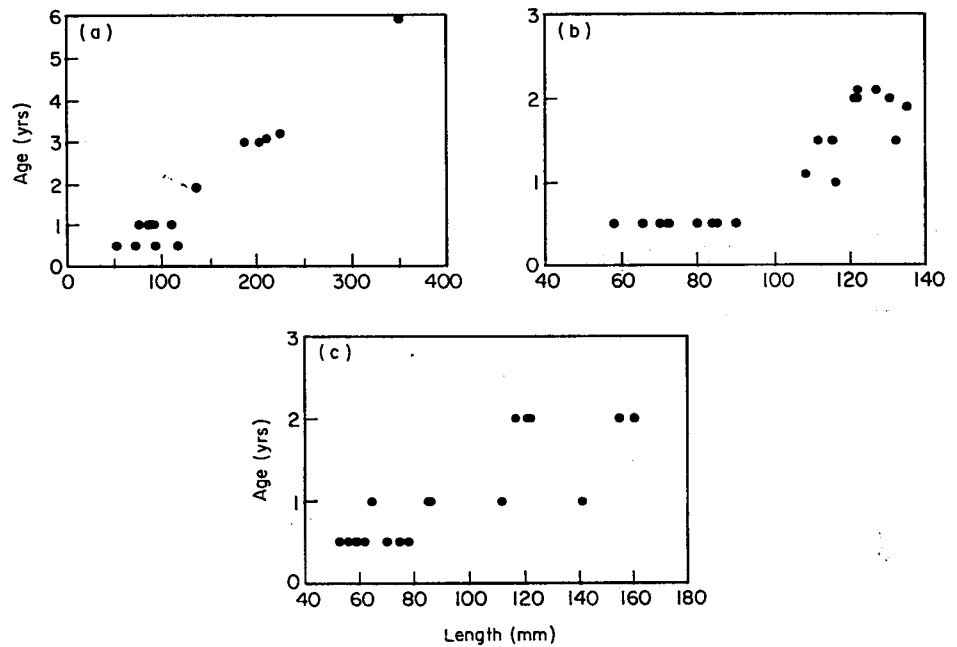


FIG. 13. Estimated ages based on scale annuli plotted against S.L. for (a) *S. giardi*, (b) *S. codringtoni* and (c) *S. carlottae*.

consumed mostly immature catfishes of the genus *Synodontis* (Mochokidae) followed by a smaller fraction (by volume) of *Barbus* species (Cyprinidae) (Fig. 14).

S. robustus smaller than 200 mm consumed a larger fraction of *Barbus* (44%) and a smaller fraction of *Synodontis* (3%) than larger conspecifics (*Barbus* = 16%, *Synodontis* = 55%). *S. macrocephalus* consumed mostly nocturnal fishes of the family Mormyridae, followed by cichlids (Fig. 14). *S. macrocephalus* smaller than 150 mm consumed a greater fraction of *Barbus* (27%) and a smaller fraction of cichlids (22%) than larger conspecifics (*Barbus* = 7%, cichlids = 34%). *S. altus* larger than 150 mm specialized on mormyrid fishes of the genera *Mormyrus*, *Hippopotamyrus*, and *Marcusenius* (Fig. 14). *S. altus* smaller than 150 mm consumed large fractions of small diurnal characid fishes (36%), unidentified fishes (59%), and crustacea (6%). *Barbus* species and characids were the dominant items in the diet of *S. angusticeps* (Fig. 14). *S. angusticeps* smaller than 150 mm consumed *Barbus* in a greater proportion (57%) and fewer characids (0%) and mormyrids (0%) than larger conspecifics (*Barbus* = 45%, characids = 23.5%, mormyrids = 13%).

S. giardi fed primarily on molluscs (mostly bivalves), aquatic insects (mostly Trichoptera), and fish scales that were presumably gleaned from the sand substrate (Fig. 15). *S. giardi* smaller than 125 mm consumed a larger fraction of aquatic insects (14%) and a smaller fraction of molluscs (37%) than larger conspecifics (aquatic insects = 7%, molluscs = 42%). Small seeds were the single most important item in the diet of *S. codringtoni* (Fig. 15). *S. codringtoni* smaller than 100 mm consumed a greater fraction of aquatic insects (19.5%) and a smaller fraction of seeds (38%) and molluscs (2%) than larger conspecifics (aquatic insects = 6%,

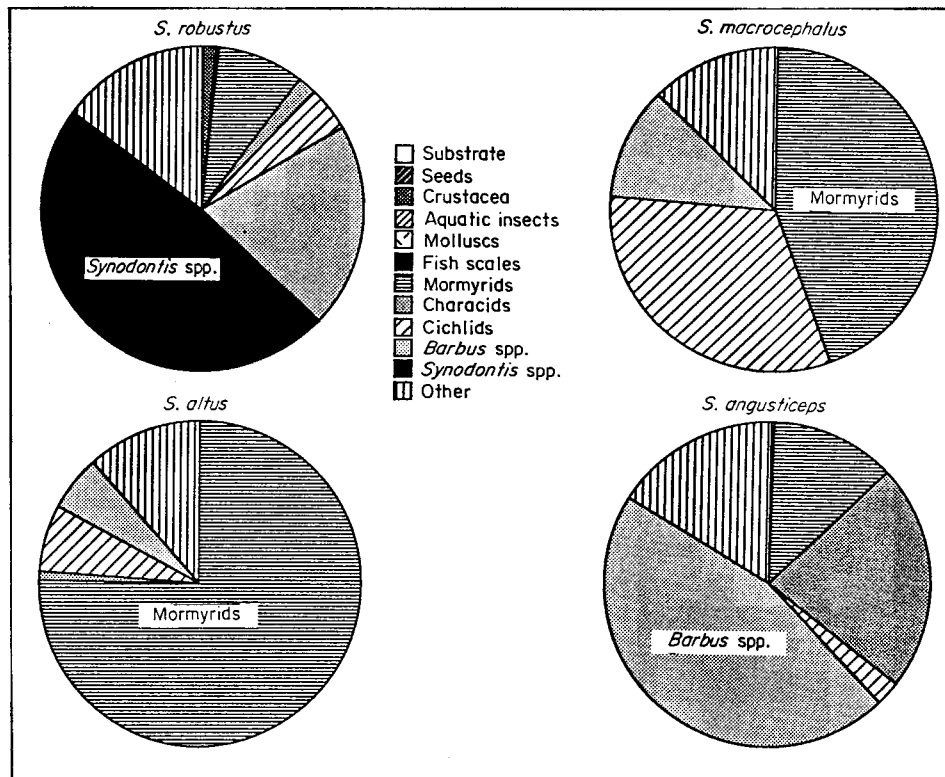


FIG. 14. Relative volumetric proportions of diet categories consumed by the four common largemouth *Serranochromis* species (subgenus *Serranochromis*) of the Upper Zambezi.

seeds = 63%, molluscs = 10%). Aquatic insects (mostly Ephemeroptera and Trichoptera) and fish scales were the most important items in the diet of *S. carlottae* (Fig. 15). *S. carlottae* smaller than 100 mm consumed greater fractions of aquatic insects (57%) and microcrustacea (13%) and a smaller fraction of scales (1%) compared with larger conspecifics (aquatic insects = 21%, crustacea = 0%, scales = 50%).

Diet breadth of small-sized *Serranochromis* (as defined above) ranged from 2.06 (*S. altus*) to 7.65 (*S. carlottae*) with an average of 5.19. Diet breadth of larger *Serranochromis* averaged 3.47 and ranged from 2.41 (*S. codringtoni*) to 4.52 (*S. macrocephalus*). Average dietary similarity was 0.12 among small-sized *Serranochromis* and 0.11 among larger fishes. Among small fishes, diet overlap was essentially zero between *S. giardi* and *S. robustus*, *S. macrocephalus*, *S. altus* and *S. angusticeps*; and between *S. angusticeps* and *S. codringtoni*. Highest dietary similarity was observed for small *S. robustus* with *S. altus* (0.54) and *S. robustus* with *S. macrocephalus* (0.33). Among large *Serranochromis*, all pairings between species of the two separate subgenera showed essentially zero diet overlap, reflecting the basic piscivore/invertebrate-feeding distinction. Highest dietary similarity was observed for large *S. giardi* with *S. carlottae* (0.51) and *S. altus* with *S. macrocephalus* (0.45).

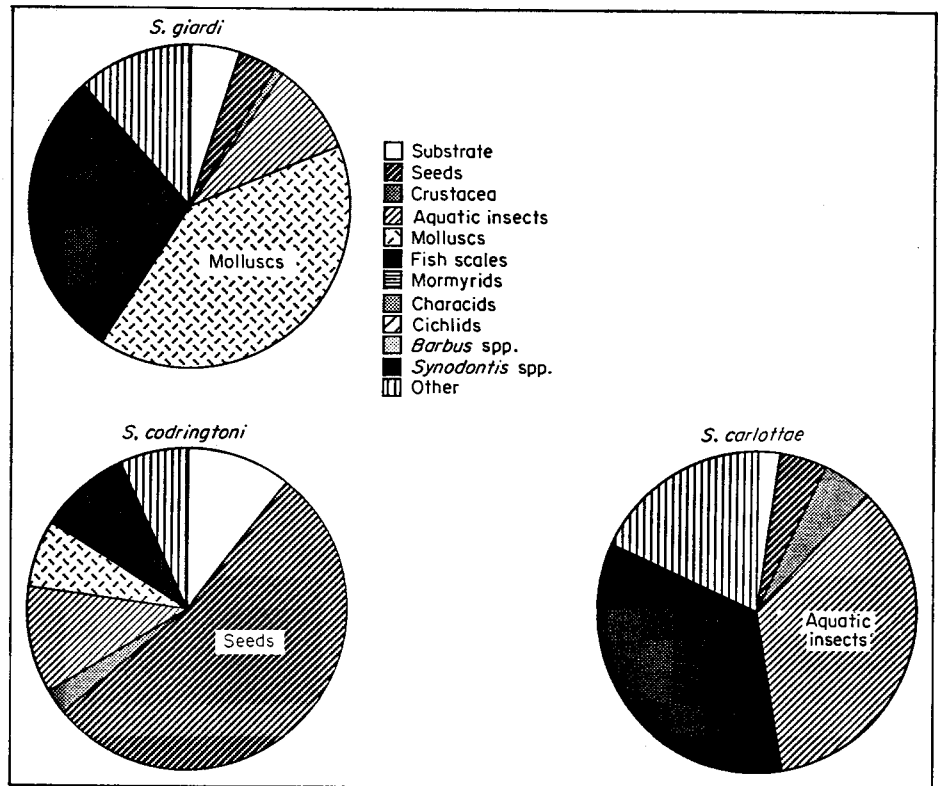


FIG. 15. Relative volumetric proportions of diet categories consumed by three smallmouth *Serranochromis* species (subgenus *Sargochromis*) of the Upper Zambezi.

V. DISCUSSION

The relative abundance rankings of *Serranochromis* species collected from the Barotse floodplain in the present study were nearly identical to those obtained by Kelley (1968). *S. macrocephalus* was most abundant, followed by *S. codringtoni*, *S. angusticeps*, *S. robustus*, *S. altus*, *S. giardi* and *S. carlottae*. Kelley (1968) either did not collect or did not recognize *S. altus*, a species morphologically similar to *S. angusticeps* (Fig. 3) but found primarily in the river channel rather than lagoons. Kelley collected more *S. giardi* than *S. robustus*, with most of the former consisting of immatures taken from maalelo traps. All of Kelley's larger fishes were captured with gillnets and seines, methods that are relatively ineffective in sampling fishes in the deeper and swifter regions of the main river channel. Most of the large *S. robustus* from the present study were taken close to the bottom of the main river channel in moderate and sometimes swift current using hook and line. The current study found *S. robustus* to be the most abundant *Serranochromis* in the main channel of the river. Densities of *S. giardi* in the main river channel of the central floodplain region appeared to decline rapidly during the late portion of the falling-water season (July–August). During this time, much of the local hook and line fishing activity appeared to be directed at *S. giardi*. Men and boys of all ages gathered around steep banks of the main river channel where they placed lines

baited with snail flesh into slow, swirling currents. During the month of July, fishermen generally could catch from 10 to 20 large *S. giardi* within 1 or 2 h. By September, only a few young boys were observed fishing using this method along the main river channel in the central floodplain region, and by November all fishing activity of this kind seemed to have stopped. During the course of the low water period attempts to capture *S. giardi* from the central floodplain region yielded progressively fewer and mostly smaller *S. giardi*. Hook and line fishing by central floodplain fishermen would therefore appear to significantly reduce the adult population of *S. giardi* in its preferred habitat, deep shoreline regions. In contrast, *S. robustus* inhabits regions of swifter current, further from shore making it relatively inaccessible to gillnets and hook and line fishing as currently practised by the local Lozi fishermen. In addition, relatively intense fishing effort seems to have been directed at *S. giardi*, since syeo is much preferred over nembwe (*S. robustus*) in local markets.

The highly-seasonal population dynamics of most Barotse floodplain fishes appears to counteract the negative impact of intense fishing activity during the falling and low water periods (July–December). As floodwaters rise during January through April, most fishes leave the confines of permanent channels and colonize the submerged plain. Most, if not all, *Serranochromis* species probably initiate spawning just prior to the initiation of flooding. I obtained direct evidence that at least some *S. codringtoni* and *S. altus* began spawning in November of 1989, and Kelley (1986) suggested that *S. macrocephalus* might have spawned as early as October in 1966. Fish populations attain their highest densities near the end of the low water period, a factor that probably facilitates location of suitable mates for courtship. Mouth-brooding females can then transport their offspring to the flooded plain where they are later released into an environment of relatively low predator densities. Presumably, low predation pressure is a primary factor selecting for wet season reproduction, since larval food resources probably do not reach peak abundance until the falling water period in this sandy, nutrient-poor environment (Kelley, 1968). Fish densities are sufficiently low during the annual flood, such that fishing is abandoned as an unproductive and unprofitable venture. During the low water period, the main river channel of the central floodplain region becomes the focus of intensive gillnet, seine and hook and line fishing, yet many of the lagoons and backwaters of the vast floodplain are relatively unexploited. Though unsanctioned by the Zambian government, the Lozi institution of traditional village fishing rights (Gluckman, 1968; Mainga, 1973) continues to exert major influence over regional patterns of fish harvest, reducing the probability of over-exploitation on a massive scale. As a result, fairly large numbers of old fishes probably survive each year to reproduce during the floods and to colonize lagoons and stretches of the main river that were heavily exploited during the previous year's low water season.

When habitat affinities and food habits are considered simultaneously, Upper Zambezi *Serranochromis* exhibit nearly complete ecological separation during the low water season. Adults of the three largest species inhabited the main channel of the Zambezi River and exhibited almost no dietary overlap (i.e., average overlap among *S. robustus*, *S. altus* and *S. giardi* was 0.028). Immature *S. robustus* feed on a variety of aquatic insects and small fishes, especially *Barbus* species, in shallow backwater and along the river margin. Adult *S. robustus* were the only fishes

observed to specialize on small *Synodontis* catfishes in the main river channel. *Synodontis* catfishes possess strong, serrated pectoral spines and heads covered by dense bone tissue that deter predators (Lowe McConnell, 1975). The massive jaws, numerous blunt jaw teeth, and massive pharyngeal plates of *S. robustus* apparently enable it to crush the bony head and locked pectoral spines of *Synodontis*. Only a few small *Synodontis* were ever found in stomachs of other Upper Zambezi fishes [*Hydrocynus vittatus* Cuvier (Characidae) and *Clarias* species (Clariidae)]. Cormorants [*Phalacrocorax africanus*, *P. carbo* (Phalacrocoracidae)] were commonly observed feeding on *Synodontis* of all sizes. *S. altus* specialized on nocturnal mormyrid fishes and appeared to be a crepuscular or nocturnal feeder. The only two individuals captured with hook and line were taken at dusk along the edge of the river channel. Large *S. altus* was always captured in gillnets placed next to dense shoreline vegetation adjacent to deep, flowing water. *S. giardi* were taken in environments similar to those preferred by *S. altus*, although the presence of aquatic vegetation seemed to be less important. *S. giardi* fed primarily off the sand substrate on small bivalves and aquatic Trichoptera larvae. The coarse, rounded pharyngeal teeth and massive pharyngeal plates of *S. giardi* are specialized for crushing mollusc shells (Jubb, 1967).

Jackson (1961c) argued that intense predation by tigerfish, *Hydrocynus vittatus*, limits the number of species that inhabit open regions of main river channels in southern and central Africa. Kelley (1968) suggested that only *Synodontis* species, armed with locking pectoral and dorsal spines, coexist with *Hydrocynus* in the main channel of the Upper Zambezi River. Kelley noted *Tilapia* species (*Tilapia*, *Oreochromis*) inhabiting protected shoreline regions of the river, and he observed much higher fish diversity in lagoons. Based on the current study, large size classes of *S. robustus*, *S. altus*, *S. giardi*, plus the herbivorous/detritivorous cichlids *Tilapia rendalli* (Boulenger), *Oreochromis andersonii* (Castelnau), and *O. macrochir* (Boulenger) co-existed in the main river with *Hydrocynus* (most individuals of the herbivorous cichlids were, however, taken in lagoons). Adult size classes of these tall-bodied cichlids appear to be beyond the size range of fishes that large *Hydrocynus vittatus* can swallow whole (Jackson, 1961c; Lewis, 1974).

The four lagoon/backwater-dwelling *Serranochromis* also showed little diet similarity among large size classes (i.e., average overlap among *S. macrocephalus*, *S. angusticeps*, *S. codringtoni* and *S. carlottae* was 0.080). The high relative abundances of *S. macrocephalus*, *S. angusticeps* and *S. codringtoni* are undoubtedly a reflection of greater abundance of lagoon and backwater habitats on the Barotse floodplain relative to primary river channel. *S. macrocephalus* consumed mostly nocturnal mormyrids, especially *Marcusenius macrolepidotus* (Peters), followed by small cichlids. *S. macrocephalus* is probably a crepuscular/diurnal benthic predator of lagoons. Of the total *S. macrocephalus* captured in gillnets from the Kafue flats by Chapman *et al.* (1971) 73% were from bottom sets (given equal numbers of top sets). In contrast, Chapman and co-workers took nearly equal numbers of *S. angusticeps* in top and bottom gillnet sets in the Kafue flats. On several occasions during the present study adult and immature *S. angusticeps* were observed lurking amid vegetation in clear backwaters of the Barotse floodplain. Immature *S. angusticeps* appear to be leaf-mimics, and both immatures and adults possess eye stripes and profuse small red or brown spots on the face and lips that tend to obscure visual detection of the eye (Fig. 3). *S. angusticeps* fed primarily on

small, diurnal *Barbus* species and characids. Based on these data plus a limited number of hook and line captures, I presume that *S. angusticeps* frequently forages by ambushing passing midwater fishes from concealment amid aquatic vegetation.

The convex, gently-sloping forehead and slightly subterminal jaws of *S. codringtoni* suggest a benthic foraging habit. Based on only five individuals, Kelley (1968) found *S. codringtoni* feeding exclusively on snails during October. In the current study, seeds were the most important food item (63% by volume) of large *S. codringtoni* with snails comprising 6% of the diet ($n=72$). Fairly large fractions of chironomid larvae (17%), substrate particles (12%), plus a smaller fraction of ostracods (4%) in the diet of small *S. codringtoni* indicate a digging foraging mode. Whereas a sand substrate seemed to be a critical habitat component for *S. codringtoni*, *S. carlottae* were never captured very far from aquatic vegetation. *S. carlottae* fed mostly on scales and aquatic insects, with adults taking a larger fraction of scales (50%) and small fishes taking a larger fraction of aquatic insects (57%). It is unclear whether *S. carlottae* remove scales from other fishes or pick up scales that are already lying on the substrate. Most of the scales were ctenoid, leaving open the possibility that some are taken during intraspecific aggressive encounters. Ephemeroptera, Odonata, and Trichoptera immatures were the predominant insects groups consumed by *S. carlottae*.

In conclusion, the seven common *Serranochromis* species of the Barotse floodplain comprise a small but important part of the commercial and subsistence fisheries. During the 1989 fishing season, only the highly sought syeo, *S. giardi*, appeared to be negatively impacted to a significant extent in the central floodplain region. Most, and possibly all, species of *Serranochromis* initiate reproduction just prior to the annual flood. Fishes disperse during the flood and repopulate overexploited localities of the plain as floodwaters slowly subside. The Upper Zambezi is the centre of species diversity for the genus, and *Serranochromis* appear to have evolved very distinct ecological niches: (i) river-dwelling, epibenthic, diurnal piscivore (*S. robustus*); (ii) river-dwelling, crepuscular piscivore (*S. altus*); (iii) river-dwelling, molluscivore (*S. giardi*); (iv) lagoon-dwelling, diurnal, ambush piscivore (*S. angusticeps*); (v) lagoon-dwelling, epibenthic, crepuscular piscivore (*S. macrocephalus*); (vi) lagoon-dwelling, omnivorous digger (*S. codringtoni*), and (vii) lagoon-dwelling, diurnal insectivore (*S. carlottae*).

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