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# Spatial aspects of the reproductive and feeding biology of the striped robber, *Brycinus lateralis* (Pisces: Characidae), in the Okavango Delta, Botswana

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The Okavango Delta is a vast inland wetland system situated in northern Botswana. High rainfall is received in early summer in the southern Angolan highlands and throughout the Delta with the flood waters reaching the upper riverine floodplain between March and May where it percolates through to the lower drainage rivers between July and September. Aspects of the reproductive and feeding biology of two allopatric populations of the striped robber, *Brycinus lateralis*, a small characin species inhabiting the northern riverine floodplain and southern drainage rivers, were investigated. Both populations were similar in the biological aspects studied, with the flood cycle having little influence on the timing of reproduction, sexual maturity and dietary composition. Female fish from both populations matured sexually at 57 mm SL, breeding over a protracted period during the warm, summer months. In both populations, the sex ratio was female-dominated at 4.8:1 (riverine floodplain) and 2.2:1 (drainage rivers). The striped robber is an opportunistic micro-carnivore with immature fish feeding predominantly on *Daphnia* spp. and adults being largely insectivorous.

**Key words:** reproductive seasonality, sexual maturity, diet, characin, ontological dietary shift, flood cycle.

## INTRODUCTION

The family Characidae, restricted to subtropical and tropical African and South American freshwaters, is speciose. In Africa there are at least 18 genera and 100 species. Within southern Africa, the characid ichthyofauna is reduced and is represented by six species in five genera (Skelton 1993). Most species are small (60–180 mm maximum fork length) and in the Okavango Delta and Phongolo floodplains are harvested extensively by subsistence fishers (Merron 1991, 1993a).

The striped robber, *Brycinus lateralis* (Boulenger, 1900), is a small, ubiquitous species with an extensive distribution. In southern Africa it is found from the Zambezi system, Okavango, Cunene and Buzi Rivers in the north through to the St Lucia catchment in KwaZulu-Natal, South Africa, in the south (Balon 1971; Skelton 1993). Within the Okavango Delta, Botswana, it consistently contributes the highest or second-highest percentage of all non-cichlid species (Merron 1993a; Merron & Bruton 1995) and is an important prey species, forming a major component in the diet of various predatory fishes (Merron 1991, 1993a). The little

information that is available on the biology of this species suggests that it shoals in clear, slow-flowing or quiet, well-vegetated waters, feeding on small terrestrial and aquatic organisms (Skelton 1993). In order to contribute to an understanding of the life history of *B. lateralis* in the Okavango Delta, this study investigated several aspects of reproductive and feeding biology, such as spawning seasonality, size-at-maturity, sex ratio and feeding preferences in two populations inhabiting the riverine floodplain and drainage rivers.

## MATERIALS & METHODS

### Study area

The Okavango Delta, one of the world's few inland deltas, is situated in northern Botswana (Fig. 1). Water from the catchment area in southern Angolan highlands enters northern Botswana as the broad Okavango River. The river is approximately 150 m wide and 4 m deep at this point. Flooding is seasonal (Fig. 2) with peak flow at the panhandle of the Delta occurring between March and May (Shaw 1984; McCarthy *et al.* 2000) before slowly percolating through the perennial and

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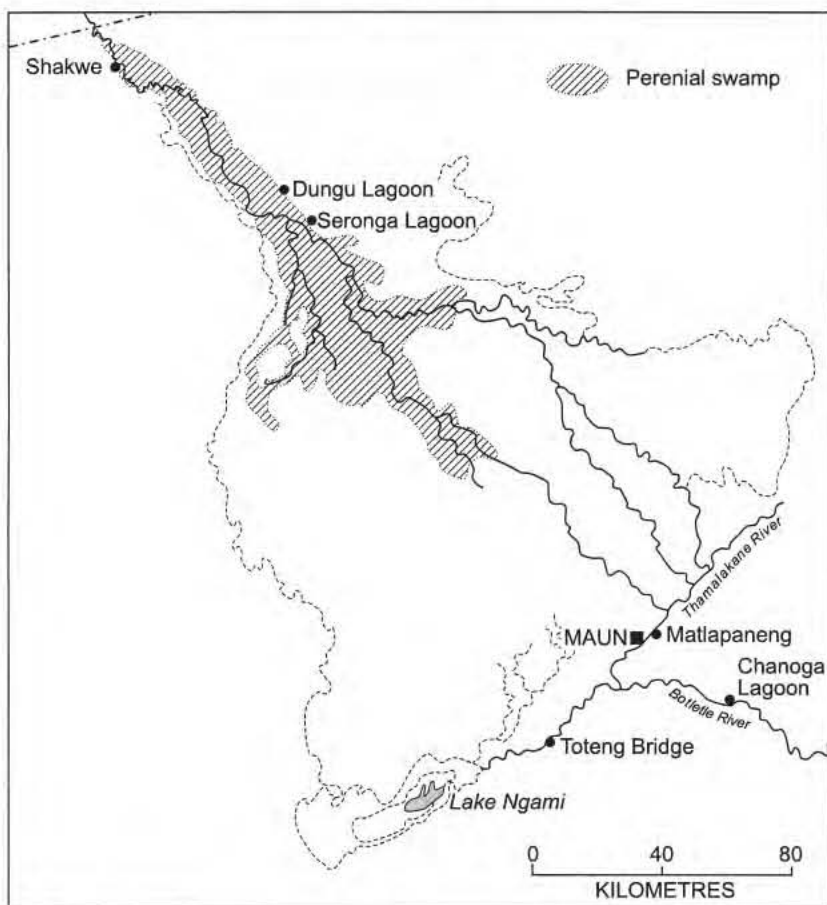


Fig. 1. Map of the Okavango system in Botswana showing the location of all major sampling sites.

seasonal swamps, reaching the drainage rivers in the south five to six months later. Southern water levels usually peak between July and September. The sampling sites for this study were situated between Dungu and Seronga along the northern riverine floodplain and in the drainage rivers in the southern delta at and below the Matlapaneng and Toteng Bridges on the Thamalakane River.

#### *General sampling routine*

Samples were collected monthly using gillnets of various stretched-mesh sizes (24, 40 and 50 mm) and the ichthyocide rotenone between June 1980 and August 1989. Electrofishing gear could not be deployed owing to low water conductivity in the area. Immediately after capture, samples were preserved in 10% formalin and after a period of several weeks were stored in 60% propyl alcohol. In the laboratory, individual fish were measured for total, standard and fork length to the nearest

0.1 mm and all internal organs (including swimbladder but excluding the gills) removed. Sample lengths and weights were not corrected for shrinkage that occurs during long-term alcohol storage. The eviscerated specimens had all excess liquid blotted off and weighed to the nearest 0.01 g. The gonads and stomachs were separated from the viscera for reproductive and dietary analyses, respectively.

#### *Population structure and sex ratio*

Population structure was determined by measuring 367 fish from the riverine floodplain and 681 fish from the drainage rivers. As this species is sexually dimorphic, small immature fish were easily sexed.

#### *Reproductive biology*

Gonads were blotted dry and weighed to the nearest 0.001 g. Spawning seasonality was assessed



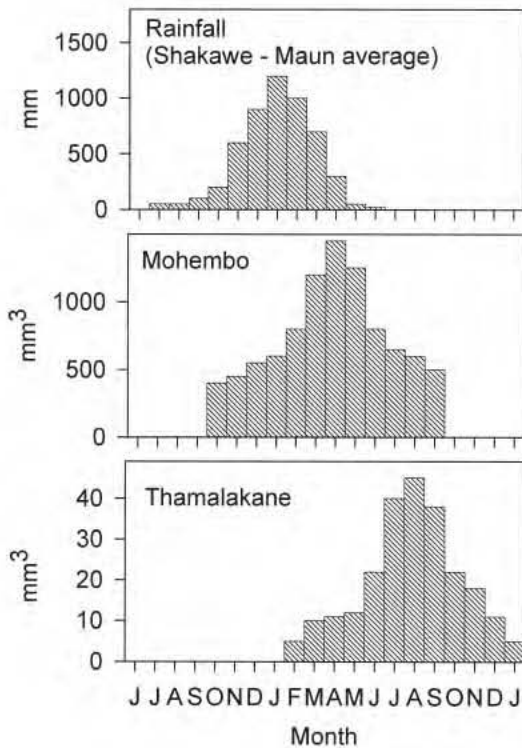


Fig. 2. Average monthly rainfall over the Okavango Delta (average of Shakawe and Maun rainfall records) together with the average monthly discharge in the Okavango measured at Mohembo and in the Thamalakane River, Maun. (Adapted from McCarthy *et al.* 2000.)

using a gonadosomatic index (GSI) (De Vlammig *et al.* 1981; West 1990) of the form

$$\text{GSI} = \frac{\text{Gonad mass}}{\text{Eviscerated mass}} \times 100.$$

In total, 71 mature specimens from the riverine floodplain and 131 mature specimens from the drainage river populations were used in the analysis.

Sexual maturity was determined for reproductively active female fish sampled during the breeding season. Length-at-(50%)-maturity was determined by fitting a logistic ogive to the percentage of female mature fish in 5 mm classes. Percentage sexual maturity was described by a logistic ogive of the form

$$P_L = \frac{1}{1 + e^{-(L-L_{50})/\delta}},$$

where  $P_L$  is the percentage of mature fish at length  $L$ ,  $L_{50}$  = length at sexual maturity and  $\delta$  the width

(or steepness) of the ogive. The ogive parameters were calculated by non-linear minimization of the squared residuals.

#### Feeding biology and dentition

Stomach contents were sorted and identified to the lowest possible taxon. The percentage number of individuals of each prey item (%N), the percentage frequency of occurrence (%FO) of each prey item to the diet and each prey's visual percentage volume (%V) were noted. An index of relative importance (IRI) was calculated for each prey item according to Hyslop (1980) where

$$\text{IRI} = (\%N + \%V) \times \%FO.$$

Most prey items examined in the stomachs were found to be unidentifiable due to extensive maceration. In an effort to investigate the role of maceration in the feeding biology of this species, the premaxillary, pharyngeal and mandibular tooth pads of immature (<45 mm SL) and mature (>65 mm SL) fish were examined using scanning electron microscopy. Excised tooth pads were cleaned using trypsin and prepared for scanning electron microscopy using methods described by Cross (1987).

## RESULTS

### Population structure and sex ratio

Length frequency distributions for males and females collected in the riverine floodplain, drainage rivers and the combined dataset are illustrated in Fig. 3. Modal lengths of the sexes were found to be significantly different in both populations studied ( $P < 0.05$ ), with females attaining a larger size than males.

Both the riverine floodplain and drainage river populations exhibited skewed sex ratios favouring females in the riverine floodplain (4.8:1), drainage rivers (2.2:1) and combined (2.8:1) populations, respectively. All sex ratios were found to be significantly different from unity using a Chi-square test ( $P < 0.001$ ).

### Reproductive biology

Patterns of sexual maturity were found to be similar for both populations (Fig. 4). Female maturity was initiated at 55 mm SL with the size-at-(50%)-maturity of both populations estimated at 57 mm SL. All female fish were mature by 65 mm SL.

The riverine floodplain and drainage river pop-



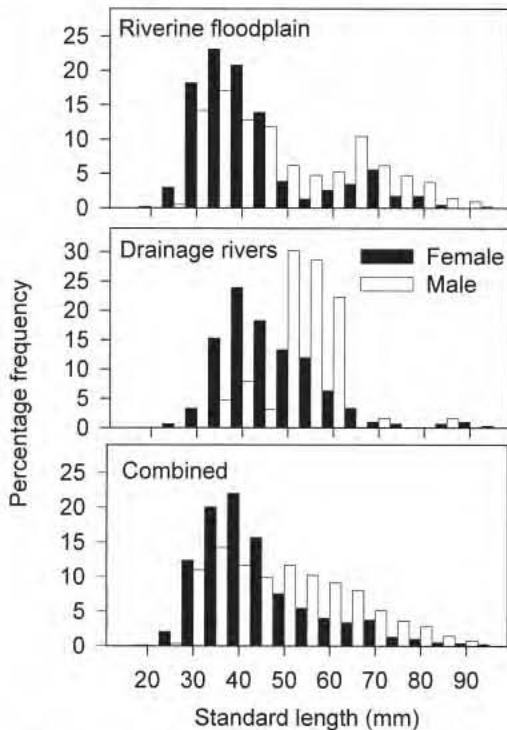


Fig. 3. Length frequency histograms of *Brycinus lateralis* sampled from the riverine floodplain, drainage river and combined populations of the Okavango Delta, Botswana, between June 1980 and August 1989.

ulations of female *B. lateralis* exhibited similar seasonal patterns in spawning activity (Fig. 5), spawning over a protracted period during the warmer months between October and March. Little correlation was noted between reproductive seasonality and the flood cycle (Fig. 6).

### Feeding biology

Stomach content analysis revealed a great diversity of food items in the diet of immature and mature *B. lateralis* in both populations. This species is an opportunistic feeder, feeding on aquatic and terrestrial micro-fauna and flora (Fig. 7; Tables 1, 2). Overall the diets of both populations of immature (<57 mm SL) and mature (>57 mm SL) fish were similar. A considerable portion of the diet of immature and mature fish was, unfortunately, unidentifiable.

In immature fish, *Daphnia* spp. were the most important prey consumed, contributing the most by percentage number and percentage frequency to the upper riverine floodplain (IRI = 67%) and drainage river (IRI = 89%) populations, respectively. The unidentified component of the diet was

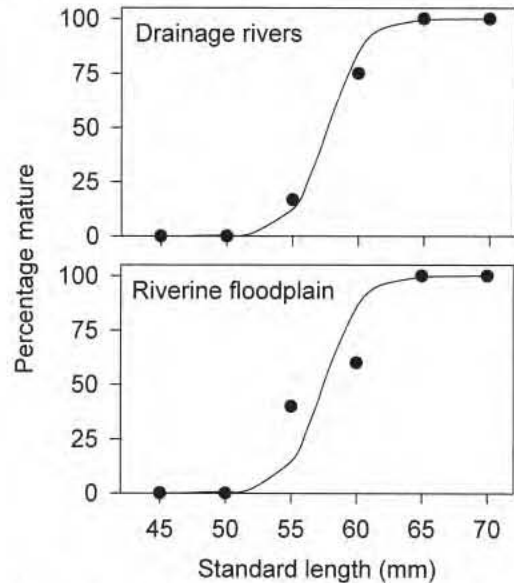


Fig. 4. Percentage of mature female *Brycinus lateralis* sampled from the riverine floodplain and drainage rivers of the Okavango Delta, Botswana, sampled between June 1980 and August 1989. Percentage maturity estimated using a logistic ogive.

large (IRI = 7–22%) and was attributable to a high level of maceration in this species. Teleost and plant matter was of minor importance in the identifiable stomach contents.

In mature fish, the most important component of the diet was unidentifiable (IRI = 47–50%). Insects from various life history stages, such as larvae, pupa and especially eggs, constituted most of the identifiable dietary components (IRI = 37%) of the riverine floodplain and drainage river populations (IRI = 42%), respectively. The most important non-insect prey in the identifiable stomach contents were *Daphnia* spp., with fish and plant matter contributing little to the relative importance index.

Most of the stomach contents were macerated by a double row of sharp tricuspid and multicuspoid teeth. No differences in tooth structure were noticed in the size range (40–70 mm SL) of fish examined. The pharyngeal pads were found to have sharp recurved teeth (Fig. 8).

### DISCUSSION

The Okavango Delta is subject to regular cycles of flooding and draining. The timing, magnitude and duration of the annual flood is not constant from year to year and is determined largely by the periodicity and amount of annual rainfall from



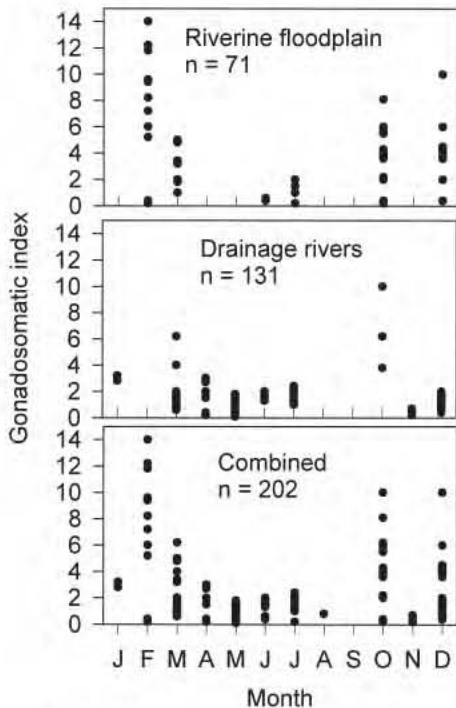


Fig. 5. Individual gonadosomatic indices of female *Brycinus lateralis* inhabiting the riverine floodplain, drainage rivers and combined populations of the Okavango Delta, Botswana, sampled between June 1980 and August 1989.

the highlands in southern Angola (Shaw 1984; McCarthy *et al.* 2000).

Floodplain fish depend on a natural, annual flood cycle for their survival. These floods periodically connect the waterbodies on the floodplain to the mainstream river and facilitate ecological functions such as the movement and spawning of most fish species (Lowe-McConnell 1975; Welcome 1979). By inundating the low-lying regions, the floodwaters also expose terrestrial plant and animal matter as food for fish and other aquatic organisms. The combination of autochthonous and allochthonous food sources allows ripening of the gonads and ensures rapid juvenile growth before the drawdown (Lowe-McConnell 1975; Welcome 1979). The inundation of shallow floodplains and the adjacent lands is also important for providing safe nursery sites for fish larvae and juveniles during their early stages of development (Bruton & Jackson 1983).

Reproductive activity in *B. lateralis* in the riverine floodplain followed a pattern atypical of other floodplain-dependent spawners (Lowe-McConnell 1975; Welcome 1979; Kok 1980; Merron & Mann

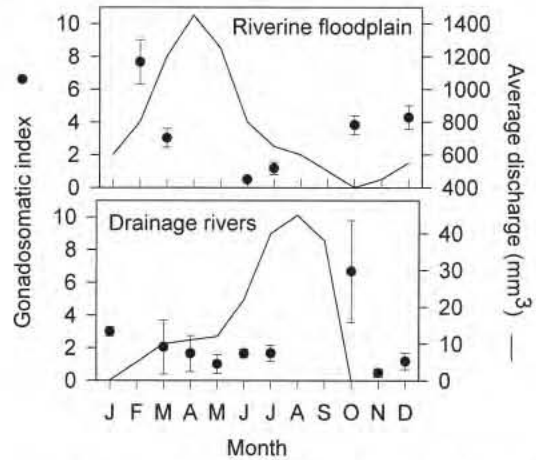


Fig. 6. Mean gonadosomatic indices ( $\pm$  standard deviation) of female *Brycinus lateralis* inhabiting the riverine floodplain and drainage rivers in the Okavango Delta, Botswana, together with the average monthly discharge in the Okavango measured at Mhembo and in the Thamalakane River, Maun. (Discharge data adapted from McCarthy *et al.* 2000.)

1995; Merron & Weldrick 1995). With the onset of the summer rains between January and February, the floodwaters rapidly inundate the Okavango River. There is a short delay before the low-lying floodplains in the Delta panhandle flood between March and April. During the warm pre-flood and peak flood periods in the riverine floodplain, with water temperatures averaging 28 °C (Merron & Mann 1995), fish were in a reproductively active state. By June, the floodwaters had percolated through to the southern drainage rivers of the Okavango Delta and the riverine floodplain population had ceased reproductive activity. The peak flood arrived at the drainage rivers in winter when the water temperature was low, averaging 10°C (Merron & Mann 1995). Reproductive activity in the drainage river population was also similar to the riverine flood population, peaking over spring and summer despite the low water levels. Considering both populations, there was a prolonged reproductive period of up to five months between October and March.

There was little noticeable difference between feeding patterns in both populations of *B. lateralis*. Immature fish (<57 mm SL) clearly preferred *Daphnia* spp., possibly attributable to their narrower gape or habitat preferences as tooth development was found to be similar over the size of animals examined. The dietary preference of mature fish (>57 mm SL), however, became more

**Table 1.** Contribution of various prey items to the diet of immature (<57 mm SL) *Brycinus lateralis* from the Okavango Delta, Botswana.

	Drainage rivers				Riverine floodplain			
	%N*	%V	%F	IRI	%N	%V	%F	IRI
<b>Arachnida</b>								
Unidentified	–	–	–	–	0.3	3.5	15	57.3
<b>Insecta</b>								
<b>DIPTERA</b>								
Chironomidae (larvae)	1.5	3.7	46.7	244.2	–	–	–	–
Chironomidae (nymph)	2.5	4.1	40	265.2	–	–	–	–
Tanytarsini	0.1	0.1	6.7	1.7	0.6	1.2	15	26.9
Unidentified	0.06	0.3	6.7	2.6	0.8	4.0	25	117.5
<b>EPHEMEROPTERA</b>								
Baetidae	–	–	–	–	0.2	0.3	5	2.3
Unidentified	0.9	2	15	43.1	0.3	0.5	5	4.1
<b>TRICHOPTERA</b>								
Unidentified	–	–	–	–	0.1	0.05	5	0.8
<b>HEMIPTERA</b>								
Ochteridae	0.06	1.3	6.7	9.3	–	–	–	–
Unidentified	0.3	3.7	13.3	52.7	–	–	–	–
<b>COLEOPTERA</b>								
Elmidae	0.06	0.2	6.7	1.7	–	–	–	–
Unidentified	–	–	–	–	0.2	4.9	10	50.6
<b>HYMENOPTERA</b>								
Formicidae	–	–	–	–	0.8	2.5	25	81.3
<b>ODONATA</b>								
Coenagrionidae (adult)	0.06	0.2	6.7	1.7	–	–	–	–
Unidentified	–	–	–	–	0.8	2.5	25	81.6
<b>ORTHOPTERA</b>								
Unidentified	–	–	–	–	0.11	0.05	5	0.8
<b>Crustacea</b>								
<i>Daphnia</i> spp.	92.7	70.9	100	16353	83.05	25.6	75	8148.7
Grit	–	–	–	–	2.1	2.7	20	95.6
Plant matter	0.2	3.7	20	76.9	0.6	3.5	30	124.2
Plant seeds	0.2	0.7	6.7	6.0	–	–	–	–
Teleosts	–	–	–	–	0.3	3.8	15	61.1
Insect remains	–	–	–	–	0.64	10	50	532
Insect eggs	0.5	0.1	13.3	8.8	7.9	5.6	10	134.9
Unidentified	0.9	11.3	100	1223.2	1.8	29.2	85	2631.6

\*%N = percentage number of individuals of each prey item to the diet, %FO = percentage frequency of occurrence of each prey item to the diet and %V = each prey's visual percentage volume. IRI = (%N + %V) × %FO.

insectivorous. In mature fish, insects from a wide variety of taxa constituted at least half of the diet. The insects eaten elucidate the foraging habitats of *B. lateralis* and provide additional information on this species' habitat preferences. These dietary components clearly illustrated that *B. lateralis* utilizes a wide variety of habitats, ranging from swift-flowing water (elmid beetles), slow-flowing water (chrysomelid beetles) and soft sediments (polymatrsid mayflies). The ability to occupy diverse habitats and feed on a wide variety of prey items possibly contributes to *B. lateralis*' ability to

colonize unpredictable and/or disturbed environments (cf. Balon 1971).

*B. lateralis* can be classified as a micro-carnivore consuming a variety of terrestrial and aquatic microfauna. These feeding habits are similar to other *Brycinus* species that also consume a large variety of food items, including fish, insects, fruit and plants (Bowmaker 1969; Balon 1971; Reynolds 1973; Bishai 1977a; Marshall & van der Heiden 1977; Kok 1980; Merron & Weldrick 1995). The large quantities of insects consumed also suggest that *B. lateralis* is important in importing nutrients

**Table 2.** Contribution of various prey items to the diet of mature (>57 mm SL) *Brycinus lateralis* from the Okavango Delta, Botswana.

	Drainage Rivers				Riverine floodplain			
	%N*	%V	%F	IRI	%N	%V	%F	IRI
<b>Arachnida</b>								
Sparasidae	0.2	2.0	2.3	5.1	–	–	–	–
<b>Insecta</b>								
<b>DIPTERA</b>								
Chaoboridae	0.4	1.6	2.3	4.7	–	–	–	–
Chironomidae (larvae)	6.9	1.6	11.6	99.3	–	–	–	–
Anthocoridae	–	–	–	–	0.1	1.7	2.8	5.0
Tanytarsini	6.6	1.7	16.3	135.4	0.1	0.1	2.8	0.8
Orthocladiinae	0.2	0.1	2.3	0.8	–	–	–	–
<b>EPHEMEROPTERA</b>								
Baetidae	11.5	4.4	25.6	405.4	2.1	1.81	11.1	43.4
<i>Afratalem parvum</i>	1.51	0.7	2.3	5.2	–	–	–	–
Caenidae	–	–	–	–	0.1	0.7	2.8	2.3
Polymatarsidae	–	–	–	–	0.1	0.2	2.8	0.9
<b>TRICHOPTERA</b>								
Hydroptilidae	0.2	0.1	2.3	0.8	–	–	–	–
<b>HEMIPTERA</b>								
Corixidae	0.9	0.9	4.7	8.3	–	–	–	–
<i>Micronecta</i> sp.	0.2	0.8	2.3	2.4	0.1	0.1	2.8	0.8
Ochteridae	0.2	1.9	2.3	4.9	0.1	0.008	2.8	0.4
Cicadellidae	–	–	–	–	0.1	0.4	2.8	1.6
Unidentified	0.7	0.5	4.7	5.2	0.7	1.3	5.6	10.9
<b>COLEOPTERA</b>								
Gyrinidae	0.2	2.0	2.3	5.1	0.3	5.5	5.6	32.2
<i>Oanoginis</i> sp.	–	–	–	–	0.3	1.1	5.6	7.7
Chrysomelidae	3.0	6.2	9.3	85.4	–	–	–	–
Elmidae	0.4	0.2	2.3	1.4	–	–	–	–
Unidentified	–	–	–	–	0.3	0.3	2.8	1.6
<b>HYMENOPTERA</b>								
Formicidae	0.7	0.4	7.0	7.0	–	–	–	–
<b>ODONATA</b>								
Zygoptera	–	–	–	–	0.2	1.4	2.8	4.3
Coenagrionidae	1.1	1.9	7.0	20.5	–	–	–	–
<i>Ischnura</i> sp.	0.4	0.7	4.7	5.0	0.1	1.7	2.8	5.0
Libellulidae (nymph)	0.2	0.3	2.3	1.2	–	–	–	–
<b>ORTHOPTERA</b>								
Tetrigidae	0.2	0.4	2.3	1.3	0.1	2.4	2.8	6.9
<b>Crustacea</b>								
<i>Daphnia</i> spp.	57.8	3.4	14	853.7	64	8.33	8.33	602.5
Grit	–	–	–	–	0.1	0.06	2.8	0.6
Plant matter	1.3	7.3	20.9	178.9	1.6	3.8	8.3	44.6
Plant seeds	0.4	0.2	2.3	1.5	3.1	2.6	2.8	15.9
Teleosts	–	–	–	–	0.4	4.5	8.3	40.7
Insect remains	0.9	6.6	14	104.5	–	–	–	–
Insect eggs	22	5.1	14	3185.9	26	21.7	38.9	1853.9
Unidentified	8	46.7	86.1	4704.4	3.9	31.19	75	2631.7

\*%N = percentage number of individuals of each prey item to the diet, %FO = percentage frequency of occurrence of each prey item to the diet and %V = each prey's visual percentage volume. IRI = (%N + %V) × %FO.



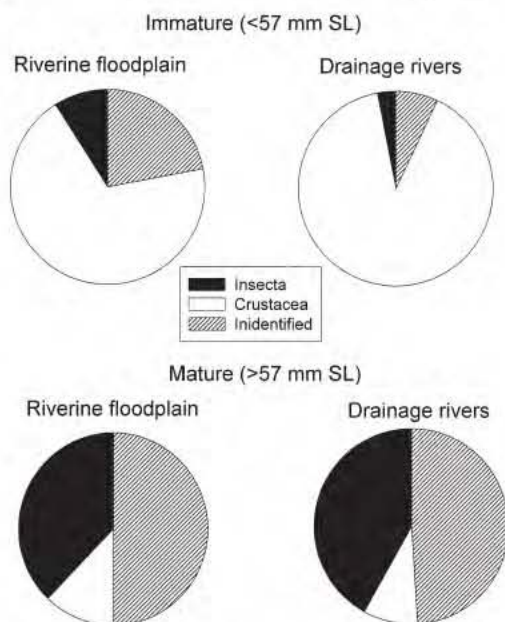


Fig. 7. Percentage relative importance of various prey groups for immature (<57 mm SL) and mature (>57 mm SL) *Brycinus lateralis* sampled from the riverine floodplain and drainage rivers in the Okavango Delta, Botswana.

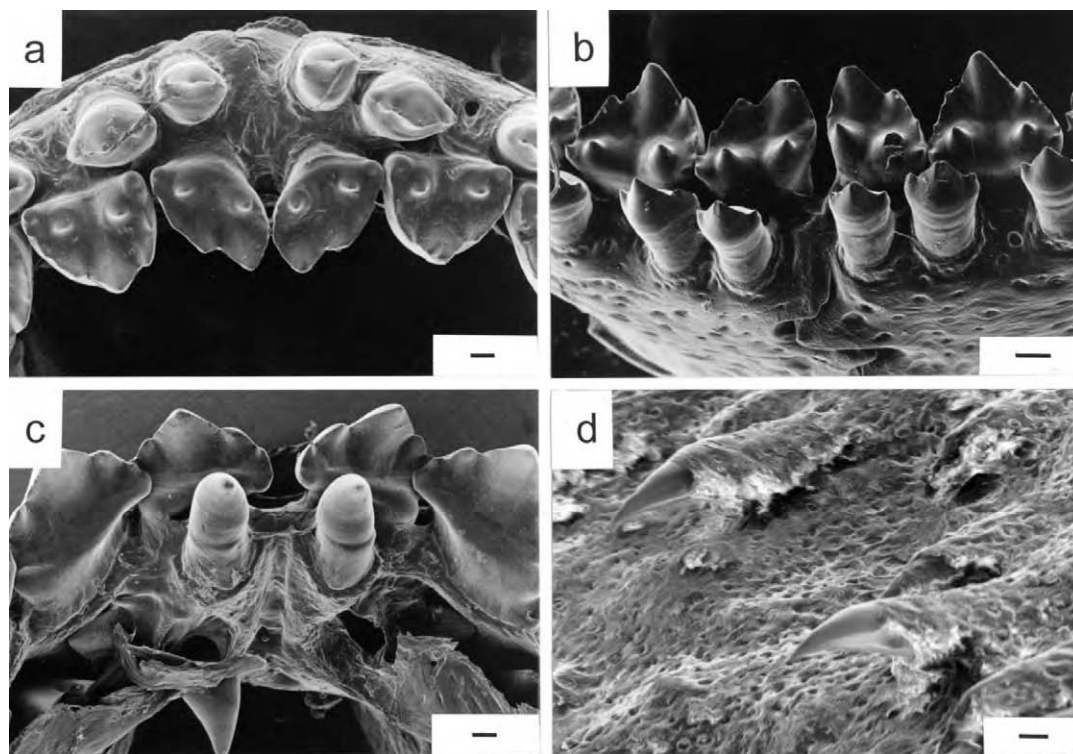
from the terrestrial to the aquatic ecosystems.

The stomach contents in most specimens were found to be macerated and often in advanced stages of digestion, possibly due to well-developed teeth and rasped pharyngeal pads. The tricuspid and multicuspid teeth are sharp and well suited for prey capture and maceration. Enzymatic activity is probably strong in other species of *Brycinus* (Bowmaker 1969; Marshall & van der Heiden 1977), which makes prey identification in many stomachs almost impossible. Exposure of the prey to digestive enzymes was certainly aided by the teeth that during the process of maceration pierced the hard insect cuticles and exposed underlying tissue.

The delay in flooding between the riverine floodplain and drainage rivers provides a unique opportunity to investigate the role of the flood cycle in regulating biological patterns of various fish species. Many authors have speculated on the role of the flood cycle in regulating reproductive activity in other *Brycinus* species (Reynolds 1973; Bishai 1977b; Marshall & van der Heiden 1977; Kok 1980; Bénech & Peñáz 1995; Merron & Weldrick 1995). Flooding has been suggested as a stimulant to initiate spawning, despite the flooding events

occurring during the warm summer period in most floodplain systems. As a consequence, and unfortunately, the interaction between dominant environmental cues responsible for the initiation of spawning could be confused. Several studies have noticed the migratory habits of other *Brycinus* species, including *B. lateralis* during flooding events (Bénech & Peñáz 1995; van der Waal 1996), posing the question 'is *B. lateralis* a flood-dependent spawner?'

Two patterns of reproduction have been recorded in other fish species inhabiting the Okavango Delta (Merron *et al.* 1990; Merron 1991; Merron 1993b; Merron & Mann 1995). These fish species either exhibit marked potadromesis, migrating up the rivers before moving onto the floodplain to spawn or remain in the river or merely move onto the floodplain to spawn. Species that are flood dependent include the catfishes *Clarias gariepinus* and *C. ngamensis* (Merron 1993b) and *Schilbe intermedius* (Merron & Mann 1995). By contrast, those fish species found to reproduce independently of the annual flood are the three-spot tilapia, *Oreochromis andersonii*, tigerfish, *Hydrocynus vittatus* (Merron 1991), and African pike, *Hepsetus odoe* (Merron *et al.* 1990). Fish species that are flood dependent tend to be highly mobile, moving around the floodplain to forage and reproduce. The species that are flood independent are relatively resident and, due to their reproductive style, would gain little advantage from large-scale movements. For example, tilapias of the genus *Oreochromis* are maternal mouthbrooders (Trevawas 1983) while *Hepsetus odoe* constructs a bubble-nest to protect its larvae (Merron *et al.* 1990). *B. lateralis* falls in the latter category, with spawning activity correlated with the increase of photoperiod and water temperature during the summer months rather than to the flood cycle. Similar unpublished results from controlled flooding experiments on the Phongolo floodplain, South Africa, have also shown that *B. imberii* is not a flood-dependent spawner (Kok 1980; Stallard *et al.* 1986; Merron & Weldrick 1995). *B. imberii* was subsequently described as a facultative flood-dependent spawner, where reproductive activity is not dependent on flooding events. In this species, water temperature and not the increase in water levels, was considered the primary cue responsible for gonadal recrudescence. If flooding did occur during the period of reproductive activity, fish would migrate laterally onto the floodplain and spawn. The inundated vegetation



**Fig. 8.** Scanning electron micrographs illustrating the tooth structure of *Brycinus lateralis*. **a, b**, premaxilla with an anterior row of tricuspid teeth and a posterior row of multicuspids teeth; **c**, mandibular with anterior tricuspid teeth and a pair of posterior caniniform teeth; **d**, the pharyngeal toothpad with sharp recurved teeth. Scale bars: a,b,c = 100  $\mu$ m; d = 10  $\mu$ m.

would also provide a nursery area for the juveniles, offering increased refugia from predators and an increased source of food. The life history of *B. imberi* on the Phongolo floodplain is also similar in many respects to that of *B. lateralis* in that it is relatively resident in a variety of habitats and consumes a wide variety of prey items (Kok 1980, Merron & Weldrick 1995).

The two populations of *B. lateralis*, although isolated from one another, exhibited remarkable similarities in aspects of their feeding and reproductive biologies. Both populations appeared not to be directly dependent on the flood cycle for spawning activity and had the ability to colonize a wide variety of habitats and feed on almost any available food source that was of a suitable size. The differential flood regime of the Okavango Delta is, therefore, an ideal candidate for further studies of the dynamics of floodplain systems and how it affects the reproductive biology of small fish species. We have little doubt that additional hypotheses will be formulated and tested regarding the importance of the flood regime to various

aspects of the life histories, not only of fish but other invertebrate and vertebrate species in the future.

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