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Relationship between oocyte morphology and reproductive strategy in loricariid catfishes of the Paraná River, Brazil

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Relationships between ovarian structure, oocyte structure/development, and parental care/life history strategies of six loricariid catfishes common in the upper Paraná River, Brazil were examined with analysis of catch data, relative gonad weight, histology, and microscopy. Three life history strategies were observed. *Loricariichthys platymetopon*, *Loricariichthys* sp. and *Loricaria* sp. produce several small clutches of large eggs over a protracted spawning period. Males of these species guard their eggs and larvae, which are transported as a mass on the ventral surface of the male's body. *Hypostomus ternetzi* and *Megalancistrus aculeatus* produce the largest mature eggs and the smallest clutches relative to adult mass. The spawning periods of these species are short, and males guard their broods in excavations. *Rhinelepis aspera* has high fecundity, high relative mass of mature gonads (both sexes), small mature eggs, and broadcast spawning with no parental care. This species migrates to spawn over firm substrates in channel areas during a contracted period. Mature oocytes of external bearers had the thickest zona radiata, followed by the egg scatterer, and cavity nesters. The thickness of the zona radiata probably is an adaptation to protect the developing egg from injury from abrasion. The zona granulosa appeared to be associated with production of secretions responsible for egg adhesion, and this layer was thickest in mature oocytes of the cavity nesting species, followed by the external bearers. All six species have wide distributions in the Paraná River, tributaries, floodplain lagoons, and the Itaipu Reservoir, but brood guarders tended to be most common in lentic habitats. © 2000 The Fisheries Society of the British Isles

Key words: Brazil; fecundity; gonad; oocyte; parental care; siluriform; South America.

INTRODUCTION

Catfishes of the family Loricariidae are ecologically diverse and widely distributed within South America. Loricariids are covered by bony dermal plates, and their ventrally oriented mouths are modified for scraping algae and biofilm from surfaces. Some species (e.g. *Panaque* spp.) scrape wood, and others (*Loricariichthys* spp.) use suction to ingest loose sediments that are sifted subsequently within the bucchal chamber. Also the family displays great diversity in reproductive strategies, ranging from complete absence of parental care (*Rhinelepis aspera* von Spix, in von Spix & Agassiz 1829) (Agostinho *et al.*, 1995*a*), bearers whose males transport adhesive eggs and larvae on their ventral surface (*Loricaria* and *Loricariichthys*; Taylor, 1983; Dei Tós *et al.*, 1997), and nest/brood guarders (e.g. *Hypostomus* spp.; Agostinho *et al.*, 1991; Menezes & Caramaschi, 1994).

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The present objective was to examine the relationship between life history strategy, parental care behavior, and the morphology of the gonads and mature oocytes in the loricariid fauna of the Paraná River in Brazil. Specifically, ovarian follicle development, oocyte number and diameter, mechanism of oocyte liberation, characteristics of ovarian follicle envelope, and the relative weight of gonads were examined among six common loricariid species with divergent reproductive strategies. All of these species have external fertilization and development, and it is hypothesized that eggs should reveal adaptive morphological attributes directly associated with the mode of spawning and parental care. Then species habitat affinities and distribution patterns within the Paraná basin are discussed in relation to reproductive strategies.

MATERIALS AND METHODS

STUDY AREA

The fish specimens used in this study were captured from November 1983 to March 1997 within a 380 km stretch of the Paraná River between the mouths of the Paranapanema and Iguaçu Rivers, including the Itaipu Reservoir, lagoons in the river floodplain, and tributary rivers (Fig. 1). Captures were made at 22 sites, grouped as follows according to size and water velocity: (i) Paraná River channel with sand and sedimentary rock substrates (PAR); (ii) low-gradient tributary rivers with sand substrates (Baia, Iguatemi & Ivinheima) (MDL); (iii) Itaipu Reservoir (RES); (iv) small tributary rivers of the Itaipu Reservoir (Ocoi, São Francisco Verdadeiro, São Francisco Falso & Guaçu) with rocky substrates and fast and slow flowing regions (SRT); (v) shallow floodplain lagoons (Patos, Pousada, Fechada & Guaraná) with sand–mud substrates and dense aquatic macrophytes (LAG). At its maximum level, Itaipu Reservoir has an area of 1460 km^2 and a longitudinal extension of 151 km. Water residence time averages 40 days, with a medium velocity of 0·6 m s^{-1} at the surface in the central area. Average depth is 21·5 m, and maximum depth is 170 m.

Fishes were captured in experimental gillnets according to methods described in Agostinho *et al.* (1995*a*, 1997). During each monthly survey at each site, eight monofilament gillnets measuring 20 × 2 m were set for 24 h. Gillnet mesh sizes were 3, 4, 6, 8, 10, 12, 14 and 16 cm. Species relative abundance in different habitat types was estimated as capture per unit effort (number of individuals in 1000 m^2 of gillnet per 24 h). Monthly or bimonthly sampling was conducted over the following periods at each site: Paraná River channel (September 1986–October 1988), low-gradient tributaries (September 1986–October 1988, or April 1987–February 1990), Itaipu Reservoir (November 1983–January 1989), tributaries of Itaipu (October 1985–February 1990), and floodplain lagoons (September 1986–October 1988). For statistical analysis, catch per unit effort (x) data were transformed as $\ln(x+1)$.

Following capture, fishes were transported to a temporary field laboratory where they were identified and labelled according to capture place and date. The following information was recorded for each specimen: total (L_T) and standard lengths (L_S) to the nearest 1 mm, and total weight (W_t) to the nearest 0·01 g. A ventral incision was made to expose gonads for determination of the sex and gonad development stage. Gonads were removed and weighed wet (W_g) to the nearest 0·01 g. A portion of each gonad was preserved in Bouin's solution for histological study. Depending on the size of the sample, ovarian tissue remained in this solution for a period of 12–24 h. Afterwards, ovarian tissues were transferred to 70% EtOH for preservation. The remainder of each ovary was then fixed in buffered 10% formalin and stored in 70% EtOH prior to being used for estimation of oocyte diameter and number. Fecundity data for *Rhinelepis aspera* were compared with data obtained by Agostinho (1985) from the same population. Relative gonad weights and mean oocyte diameter were almost the same (e.g. 1·35 *v.* 1·32 mm oocyte diameter), so values from Agostinho's larger sample were used. The gonadosomatic index (I_G) was computed for each captured specimens as $100 W_g \,.\, W_t^{-1}$.

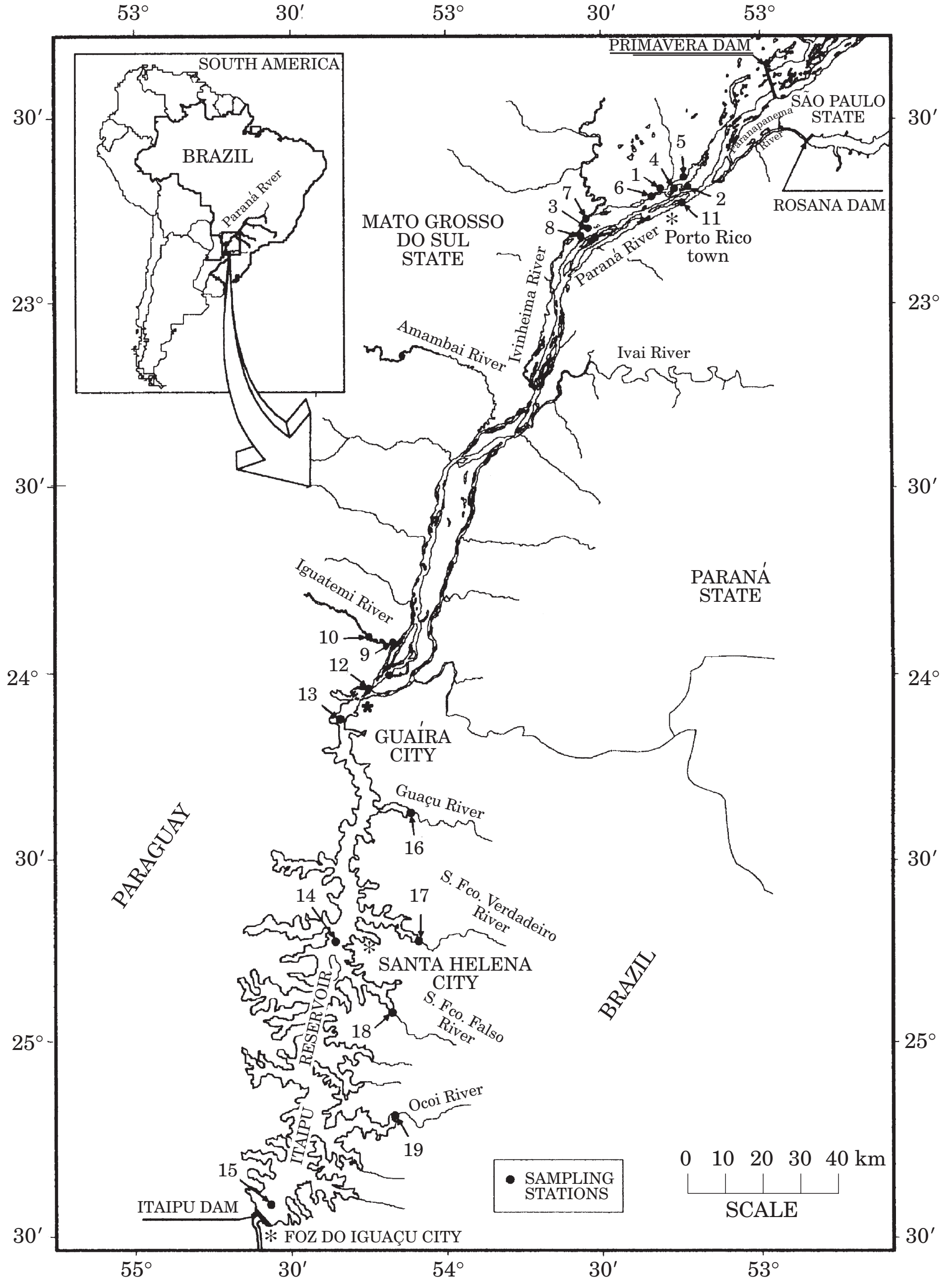

Fig. 1. Map showing 19 sampling locations (●) within a section of the Paraná River, Brazil.

Those ovaries destined for histological study were stained with haematoxylin-eosin. Stained sections were used to characterize the phases of ovarian follicle development, for measurement of the thickness of the zona radiata and granular layer, and for determination of oocyte development and spawning mode (e.g. multiple *v.* batch spawning). Only free oocytes in the ovarian cavity were measured. The occurrence of partially spent ovaries, identified by the simultaneous presence of post-ovulation follicles and vitellogenic oocytes, was used also to determine spawning mode.

Minimum length of maturity was estimated as the smallest male and female observed with gonads in the maximum state of maturation among the entire sample. Maximum fecundity was the greatest number of mature oocytes based on examination of the five females with the greatest I_G values. Mature oocytes, those of the largest diameter, were separated from the conjunctiva and counted. Oocyte diameter was measured with a dissecting microscope equipped with an ocular micrometer. Relative fecundity (number of eggs per gram of body weight) was calculated to remove the effect of body size. Relative fecundity was estimated from adjusted averages from ANCOVA (Snedecor & Cochran, 1989), where the covariate was $\ln(W_t)$ and the dependent variable was ln(number mature oocytes). This procedure permits comparisons among species independent of body size.

RESULTS

Of the six common loricariids obtained by the survey (Fig. 2), two *Loricariichthys* species were most abundant, followed by *Loricaria* sp. (Fig. 3). *Loricariichthys platymetopon* Isbrüker & Nijssen, 1979 was most common in floodplain lagoons, and was rare in Itaipu Reservoir and its tributaries. *Loricariichthys* sp. was more abundant in the tributaries of the reservoir and absent from floodplain lagoons. *Loricaria* sp. was most abundant in low gradient tributaries of the Paraná River and the reservoir. *Rhinelepis aspera* was common in Itaipu reservoir, mostly within the upper fluvial portion, and the main channel of the Paraná River and its tributaries. *Megalancistrus aculeatus* (Perugia, 1891) showed a similar pattern of distribution and abundance, but it was relatively more abundant in low-gradient tributaries of the Paraná River. *Hypostomus ternetzi* (Boulenger, 1895) was captured only in low densities from Itaipu Reservoir.

For each species, evidence of reproduction was observed most frequently in those areas where the species was captured in greatest abundance. The exception was *R. aspera* which was more abundant in the reservoir, but revealed no evidence of reproductive activity there. Reproduction by *R. aspera* apparently is restricted to the more lotic environment of the Paraná River and its tributaries. Although widely distributed, *M. aculeatus* with ripe gonads were encountered only in tributaries of the Paraná River. Some fishermen informed us that mature females of this species were captured sometimes in the upper region of the Itaipu reservoir. Although not abundant in the reservoir and its tributaries, *L. platymetopon* with mature gonads were common within samples from these locations.

Among the studied species, *M. aculeatus* attained the largest body size (maximum $L_S = 60{\cdot}7$ cm), and *Loricaria* sp. was smallest (maximum $L_S = 27{\cdot}5$ cm) (Table I). Females dominated in the largest size classes of *Loricariichthys* species and *Loricaria* (Fig. 4). *Hypostomus ternetzi* had a bimodal distribution for both sexes, with the males larger than females. Males and females of *R. aspera* and *M. aculeatus* had similar size distributions, although the largest size classes of *M. aculeatus* were dominated by males. Ratios of the smallest mature adult L_S to the maximum L_S were as follows: *M. aculeatus* 0·36, *R. aspera* 0·41, *L. platymetopon* 0·50, *Loricariichthys* sp. 0·55, *Loricaria* sp. 0·59, and *H. ternetzi* 0·60).

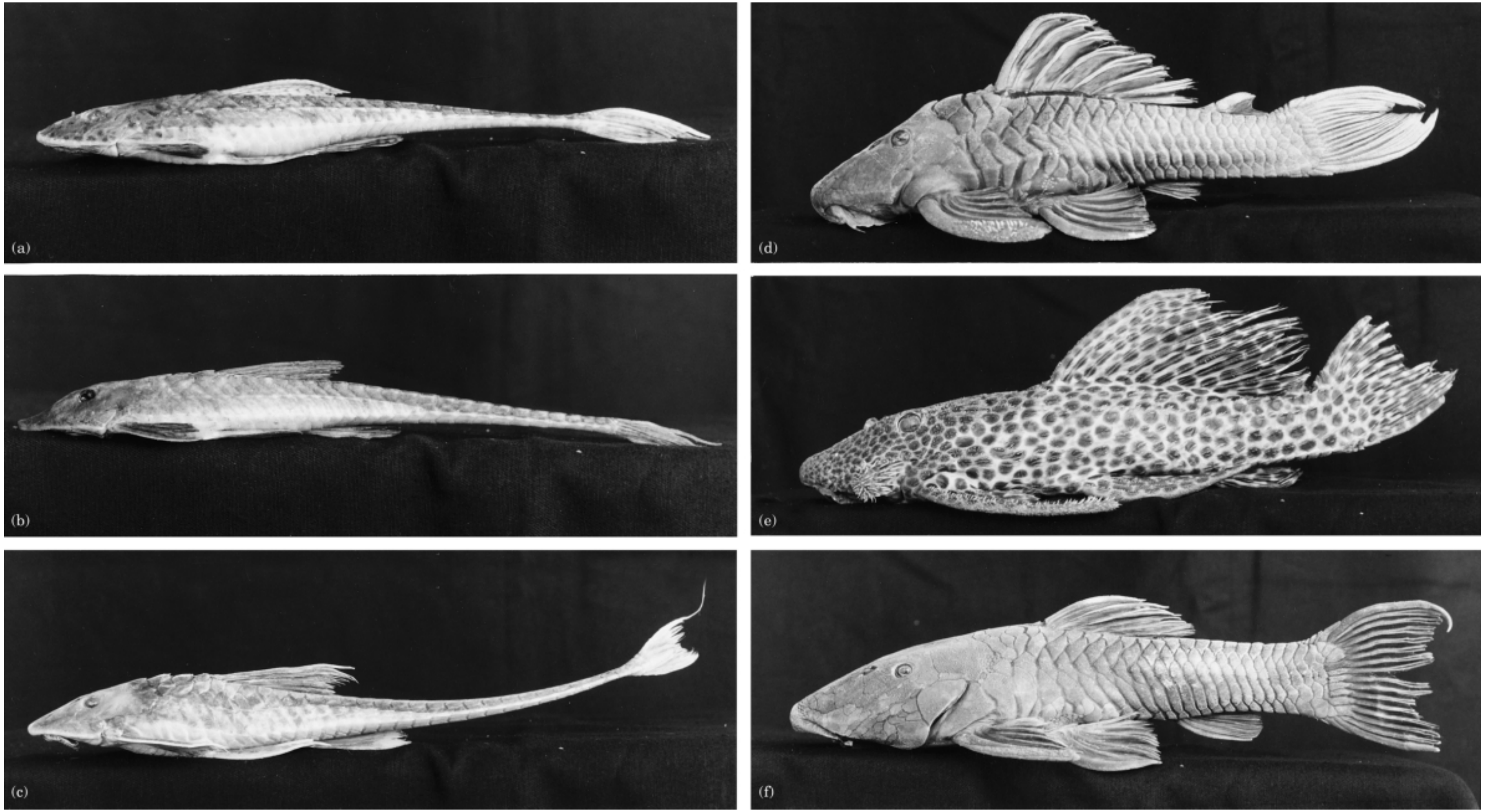

FIG. 2. The six common loricariid catfishes captured from the study region and compared for reproductive biology: (a) *Loricariichthys platymetopon* (20·9 cm L_S), (b) *Loricariichthys* sp. (20·9 cm), (c) *Loricaria* sp. (22·4 cm), (d) *Hypostomus ternetzi* (25·5 cm), (e) *Megalancistrus aculeatus* (25·0 cm); (f) *Rhinelepis aspera* (26·0 cm).

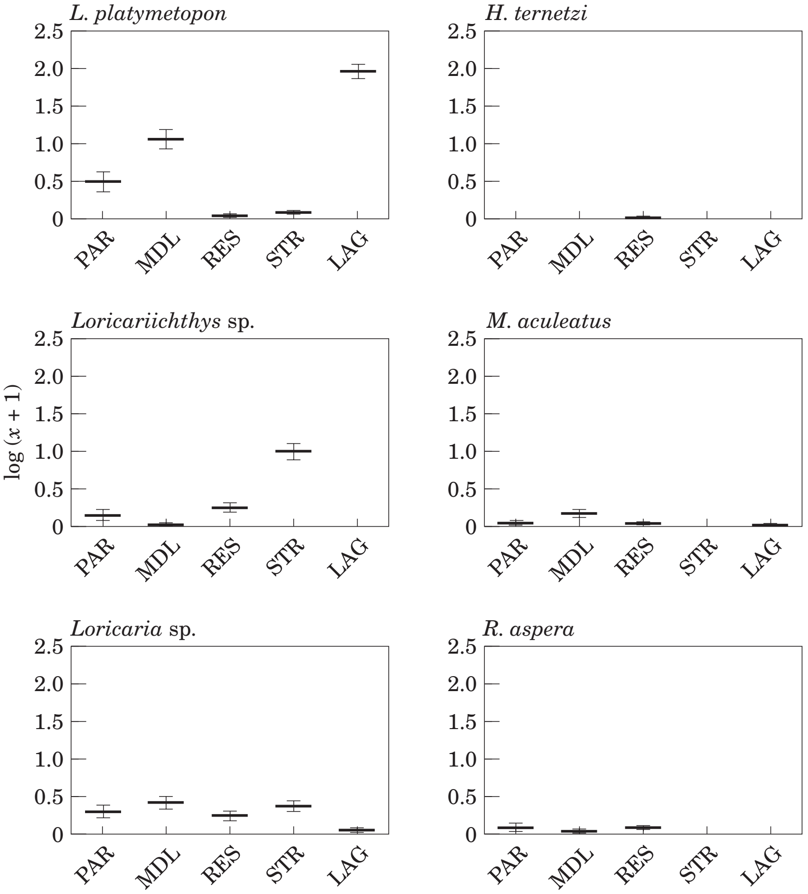

FIG. 3. Mean catch per unit effort (x), [log(x+1)] in different habitats of the Paraná River, Brazil. PAR, Paraná River channel; MDL, low-gradient tributary rivers; RES, Itaipu Reservoir; SRT, small tributary rivers of the reservoir; LAG, floodplain lagoons; vertical bars equal ± 1 S.E.

Ovarian morphology of loricariids conforms to the general pattern observed for teleosts, with paired ovaries of the cystovarian type linked in the caudal third and terminating in a short oviduct. When fully developed, ovaries occupied the entire free space within the abdominal cavity. I_G values did not vary greatly among species for females, with *Loricaria* sp. having the smallest value (11·3) and *R. aspera* the largest (16·4) (Table I). The range of values was greater among males, with the largest I_G observed in *R. aspera* (6·4) and all other species <0·8.

Direct observations of reproductive behaviour in the field revealed that *Loricariichthys* spp., *Loricaria* sp., *M. aculeatus* and *H. ternetzi* spawn adhesive eggs. *Rhinelepis aspera* spawns non-adhesive eggs, but after 10–15 min of hydration, they become adhesive (René A. F. Belmont, pers. comm.). Except for the granulosa layer of *R. aspera* which has numerous transparent or empty vesicles, cells of granulosa layer of loricariids are tall and distinctly granulated in appearance (Fig. 5). Greatest thickness of the granulosa layer was observed in *M. aculeatus* (75·52 μm) and the smallest in *R. aspera* (20·96 μm) (Fig. 5).

TABLE I. Comparison of life history traits among six common loricariid catfishes of the Paraná River in Brazil

	L. platymetopon	*Loricariichthys* sp.	*Loricaria* sp.	*H. ternetzi*	*M. aculeatus*	*R. aspera*
L_s maximum (cm) (M, F)	28·5, 33·5	26·5, 28·5	26·5, 27·5	35·7, 32·4	60·7, 57·5	47·2, 49·0
L_s maturation (cm) (M, F)	15·3, 16·5	15·9, 15·7	16·5, 16·2	19·0, 19·5	24·8, 20·5	20·0*, 20·0*
Maximum I_G (M, F)	0·58, 11·90	0·53, 14·75	0·71, 11·30	0·10, 12·44	0·32, 14·06	6·39, 16·46
Oocyte development	Synchronous in batches	Synchronous in batches	Synchronous in batches	Synchronous in batches	Synchronous in batches	Not synchronous
Spawning type	Batches	Batches	Batches	Total	Total	Total
Parental care	Male bearers	Male bearers	Male bearers	Male nest guarder	Male nest guarder	None
Maximum fecundity	1451	619	547	2802	13 022	181 200*
Relative fecundity (no. oocytes g^{-1} body weight)	9·46	5·71	7·37	1·50	1·45	39·88
Mean oocyte diameter (mm) (S.E.)	2·32 (0·189)	2·74 (0·199)	2·55 (0·119)	4·36 (0·135)	4·29 (0·118)	1·32 (0·072)
Mean zona radiata (μm) (S.E.), *n*	9·87 (0·38), 19	9·1 (0·57), 14	9·95 (0·25), 12	3·97 (0·35), 10	4·8 (0·31), 5	5·1 (0·25), 13
Mean granulosa layer (μm) (S.E.)	26·44 (0·83)	21·48 (1·65)	35·47 (2·17)	40·96 (3·77)	75·52 (3·77)	20·96 (2·36)

*Values from Agostinho (1985).

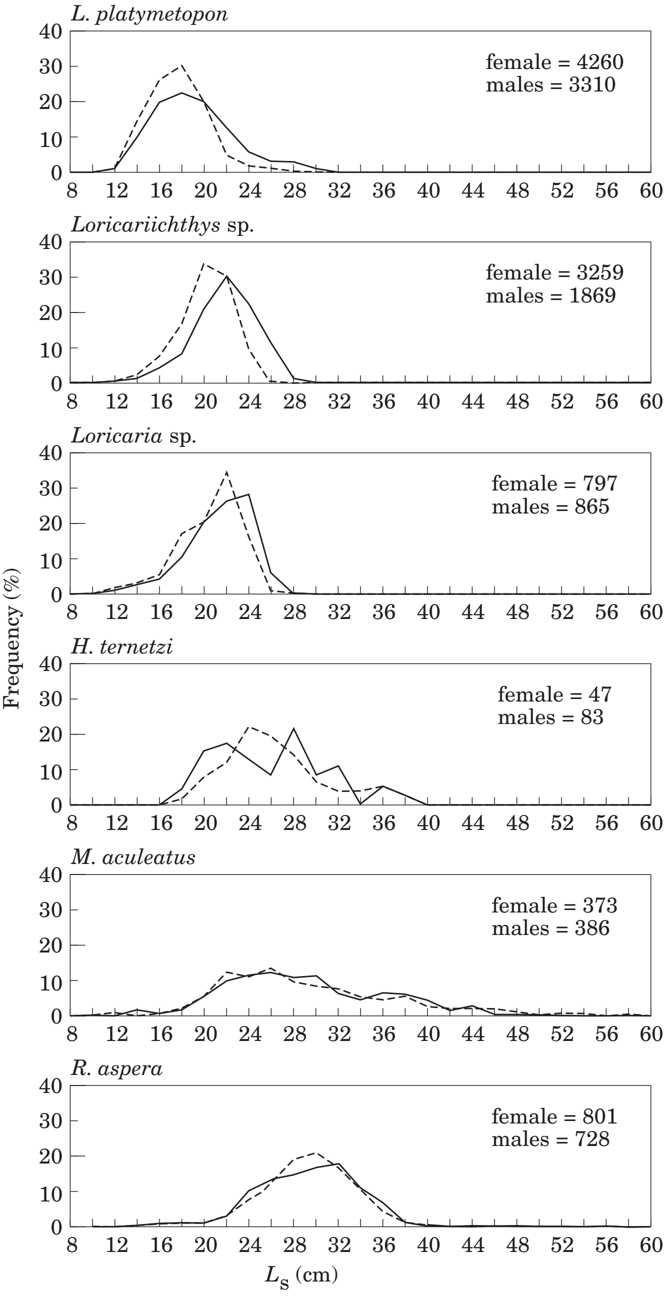

FIG. 4. Frequency distributions by L_S size classes for males (– – –) and females (——) of six loricariid species.

During the last stage of ovarian maturation in *Loricariichthys* sp., a space forms between the granular layer and the oocyte, cell height within the granular layer declines, and material from the granular layer is shed into the space (Fig. 5). This material could be responsible for the adhesive property of the eggs.

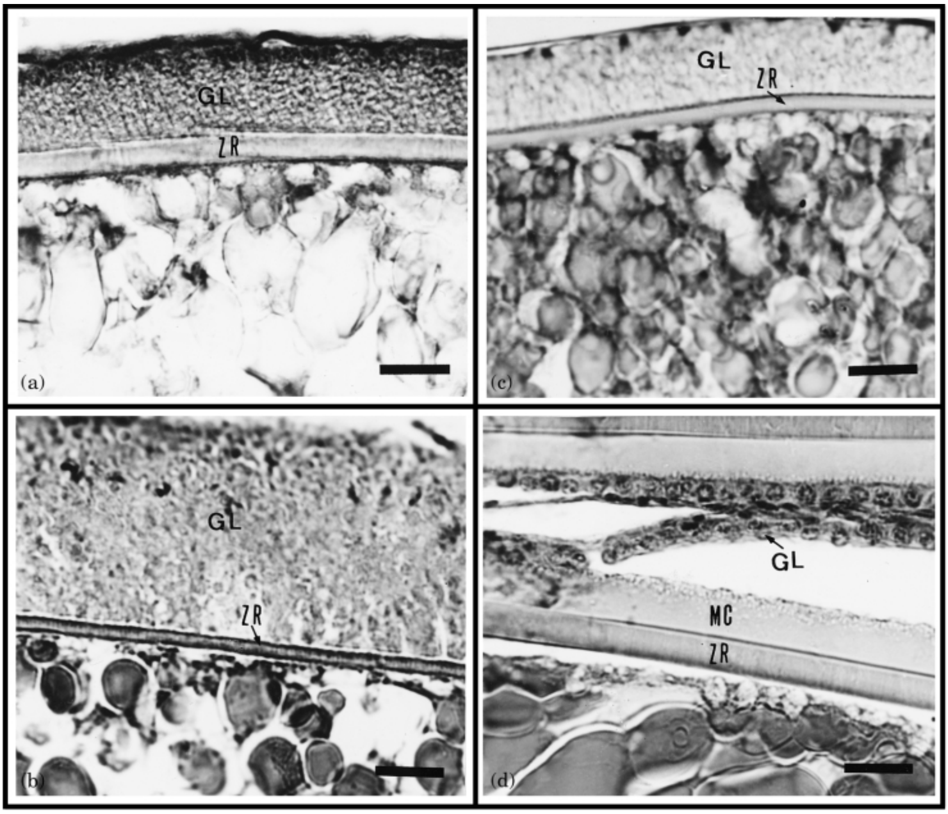

FIG. 5. Granulosa layer and zona radiata of mature oocytes within ovaries of (a) *Loricariichthys* sp.; (b) *Megalancistrus aculeatus*; (c) *Rhinelepis aspera*; (d) ripening oocyte of *Loricariichthys* sp. showing formation of the mucus (MC). GL, Granulosa layer; ZR, zona radiata; bar=20 μm).

Loricariichthys sp. and *Loricaria* sp. had the thickest zona radiata, and the thinnest zona radiata was observed in *Hypostomus ternetzi* (Table I).

Analysis of frequency distributions of oocyte diameters revealed multiple cohorts in species of the sub-family Loricariinae (*Loricariichthys* spp., *Loricaria* sp.) and two cohorts in the others (Fig. 6). Development of oocyte cohorts appears to be synchronous in the Loricariinae which suggests batch spawning. In *H. ternetzi* and *M. aculeatus*, only a single cohort of oocytes is recruited and spawned during the reproductive season. In the mature ovaries of these species, mature oocytes (>4·0 mm) are found together with pre-vitellogenic oocytes (cortical alveolus phase, diameter <1·1 mm) that remain in the ovaries after spawning, and, together with those in primary growth, form the oocyte stock for the next spawning season.

Rhinelepis aspera also revealed two oocyte cohorts, one constituting the reserve stock (previtellogenic or perinucleolar phase) and another of mature stock spawned as a single batch (Fig. 6). Oocyte development is asynchronous and cumulative, and compared with *H. ternetzi* and *M. aculeatus*, high variance in the oocyte diameter is observed during maturation in *R. aspera* (Fig. 6;

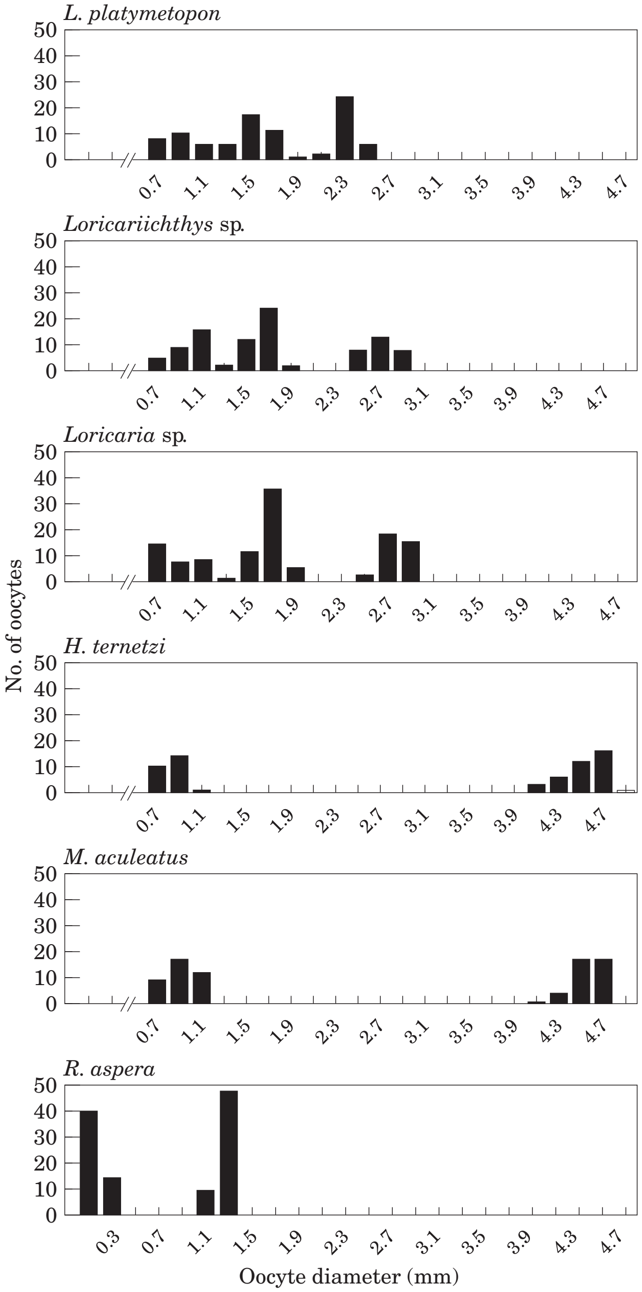

FIG. 6. Frequency histograms for oocyte diameter classes (mm) within mature ovaries by species (for each species, based on the ovary with the highest I_G).

Table I). Histology supports the model that oocyte development is asynchronous and formation of a single batch occurs by gradual accumulation of mature oocytes.

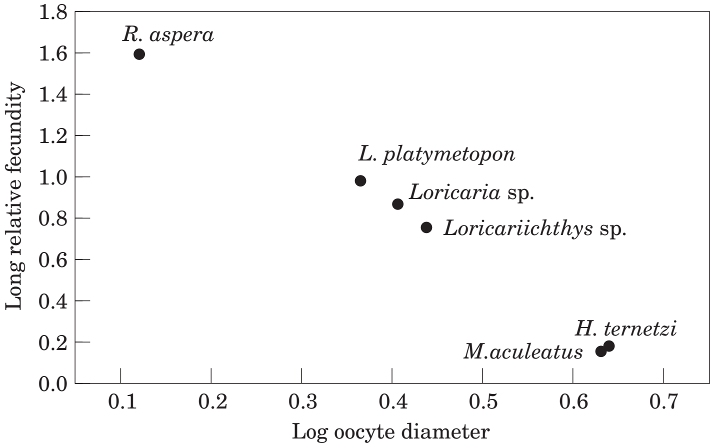

FIG. 7. Relationship between the oocyte size and fecundity for each loricariid species ($n=5$ for each species based on ovaries with highest I_G).

Species formed three groups based on maximum oocyte diameter: >4·0 mm (*Hypostomus ternetzi* and *Megalancistrus aculeatus*), 2·3–2·7 mm (*Loricariichthys* spp. and *Loricaria* sp.), and <1·3 mm (*R. aspera*) (Fig. 7). Compared across species, the number and diameter of mature oocytes were inversely related (Fig. 7). Relative fecundity was lowest in species with the largest oocytes (Table I). *R. aspera* had the smallest oocyte diameter and had the largest relative fecundity (39·9 oocytes g^{-1}). The three Loricariinae produce oocytes of medium diameter, and the number of oocytes per unit of body mass was intermediate (Table I). These species, however, spawn multiple times during the reproductive season, so total reproductive effort is much greater.

For the five species with male parental care, testes mass in relation to body mass was low (maximum I_G range=0·10–0·71), indicating a relatively low investment in semen production. The relative mass of the testes is much larger in *R. aspera* (I_F=6·39), a broadcast spawner without parental care.

DISCUSSION

Morphological, developmental, and ecological patterns among loricariid fishes follow, to some extent, patterns of phylogenetic relationship. The family Loricariidae has >600 species within six sub-families (Hypostominae, Ancistrinae, Lithogeneinae, Neoplecostominae, Hypoptopomatinae, Loricariinae) distributed from Panama to Uruguay (Burgess, 1989). Among the genera studied here, *Megalancistrus* belongs to the Ancistrinae, *Hypostomus* and *Rhinelepis* are Hypostominae, and *Loricariichthys* and *Loricaria* are Loricariinae. According to Schaefer (1987), the Hypostominae is paraphyletic. Within this phylogenetic context, reproductive behaviour appears to be associated strongly with ovarian and oocyte characteristics.

Parental care by loricariids has been described (von Ihering *et al.*, 1928; Breder & Rosen, 1966; Taylor, 1983; Agostinho *et al.*, 1991), and species can be classified into three groups: no parental care, which is represented uniquely by

R. aspera; external bearers in which the male transports the mass of eggs (*Loricaria* and *Loricariichthys*); and guarders in which the male cares for eggs and larvae within some kind of cavity or nest (*Hypostomus* and *Liposarcus*). The reproductive behaviour of *M. aculeatus* is not very well-known, but the structure and development of its oocytes suggest the same strategy as shown by *Hypostomus*. In addition, local fishermen described it as a brood guarder.

Because they are transported on the male's ventral surface, the eggs of *Loricaria* and *Loricariichthys* are exposed to abrasion, and these species had the thickest zona radiata. The thinnest zona radiata was observed in *Hypostomus ternetzi* which deposits its eggs in nests excavated in stream banks. *Megalancistrus aculeatus* also has a thin zona radiata, and probably deposits its eggs in protected places excavated in the substrate. *Rhinelepis aspera* sheds non-buoyant eggs in the water column and has a zona radiata of intermediate thickness.

The reproductive strategy of *R. aspera* is to produce large numbers of small eggs with no post-spawning investment in offspring. Agostinho (1985) reported that fecundity can reach 181 200 oocytes, with an average of 47 370. *Rhinelepis aspera* spawns between December and February, when it undergoes long upstream migrations to channel areas where eggs are shed into the water column. Similar to the large migratory characiform and siluriform fishes of the Paraná River [*Salminus maxillosus* Valenciennes in Cuvier and Valenciennes, 1849; *Prochilodus lineatus* Steindachner, 1882; *Pseudoplatystoma corrucans* (Agassiz, 1829)], *R. aspera* congregate and spawn only within a restricted area within the basin. Male *R. aspera* have much larger mature gonads than other loricariids, and large testes could be associated with a need to produce a large quantity of sperm for effective fertilization during broadcast spawning in the water column. Oocyte development in this species is non-synchronous and cumulative, which is different from the synchronous development of oocyte cohorts observed in most other seasonal, broadcast-spawning fishes.

Of the species studied here, *H. ternetzi* (Hypostominae) and *M. aculeatus* (Ancistrinae) produce the largest mature oocytes (4·36 and 4·29 mm, respectively) which are deposited in a single batch per reproductive season (i.e. total spawners). Other species of the genus *Hypostomus* produce large eggs (Agostinho *et al.*, 1982; Menezes & Caramaschi, 1994; Mazzoni & Caramaschi, 1997), and this genus has the largest eggs among all teleosts of the Paraná Basin (Suzuki, 1992). Spawning behaviour varies among the *Hypostomus* species. Agostinho *et al.* (1982) and Menezes & Caramaschi (1994) reported total spawning in *H. commersoni* (Valenciennes 1840) and *H. punctatus* Valenciennes, 1840, respectively. Mazzoni & Caramaschi (1997) reported that *H. luetkeni* (Steindachner, 1877) and *H. affinis* (Steindachner, 1876) are partial spawners.

Male *Hypostomus* defend offspring placed in nest cavities or holes dug in river banks. Males also clean and ventilate the developing eggs within these cavities (von Ihering *et al.*, 1928; Breder & Rosen, 1966; Agostinho *et al.*, 1991). Burgess (1989) described the reproductive behaviour of captive *H. punctatus* and confirmed that the male guards and ventilates the brood up to several weeks post hatch.

The externally-bearing Loricariinae are partial spawners that produce small clutches of large eggs. The diameter of mature oocytes from *L. platymetopon* captured from the reservoir and its tributaries (this study) was smaller (2·32 mm) than that of individuals from lagoons of the Paraná floodplain (3·20 mm) where this species is abundant also (Suzuki, 1999). The present study could not determine spawning frequency, but examination of recently spawned females suggests that these species produce at least two and possibly three or more cohorts per reproductive season. In addition to pre-vitellogenic eggs (cortical alveolus and perinucleolar) and post-ovulated follicles, ovaries revealed two oocyte cohorts in vitellogenesis (early and middle stages).

Males of the Loricariinae transport the egg mass in different ways. In *Loricariichthys* species, the egg mass has a wedge form and is partially enclosed by the broad flap extending from the lower lip (Taylor, 1983; Machado-Allison, 1990; Dei Tós *et al.*, 1997; pers. obs.). In *Loricaria* the egg mass is sheet-like with a thickness of two to three egg layers. The sheet of eggs adheres to the posterior margin of the inferior lip and continues along the abdomen (Taylor, 1983; pers. obs.). Although they perform parental care, male Loricariinae that carry their brood are usually smaller than the females, a situation that contrasts with the pattern observed within the cavity nesting Hypostominae and Ancistrinae. Captive *L. platymetopon* do not exhibit aggressive brood-defence and abandon the mass of eggs when in danger (Dei Tós *et al.*, 1997). The male reclaims the egg mass when the threat of brood predation ceases. These authors suggested that the small size of males is related to their lack of aggressiveness and feeding restrictions while egg bearing. On the other hand, fertility and the number of fertilized eggs increase with female body size, a general pattern in teleosts (Gross & Sargent, 1985).

Spawning multiple batches per year permits females to deposit their eggs with males that have lost their broods. Because males have the possibility of acquiring a new brood at any time during the reproductive season, they have the option of abandoning eggs when predators threaten their own life as well as their brood. Given the limited volume of eggs that can be transported by a single male, the production of multiple broods could facilitate higher female fitness, because eggs could be placed with the same male sequentially, or with multiple males simultaneously. Polyandry has not been confirmed in *Loricaria* species, but this mating strategy is possible for partial spawners in which the male performs all parental care. According to Gross & Sargent (1985), the male provides parental care in 61% of the loricariid species for which information is available. They concluded that the prevalence of male parental care in teleost fishes is not explained by male care promoting a greater benefit, but rather males pay a smaller future cost of parental care than do females.

Rineloricaria uracantha (Kner & Steindachner, 1863) are loricariines that use cavities in submerged logs as nests guarded by males until hatching (Moodie & Power, 1982). Male *R. uracantha* are significantly larger than females, and males bear bony facial bristles around the margin of the head and along the margin of dorsal surface of pectoral fin rays. Females spawn more frequently with larger males. Sexual size dimorphism is common in the genus *Hypostomus*, having been documented in *H. albopunctatus* (Regan, 1809) (Antoniutti *et al.*, 1985), *H. commersonii* Valenciennes, 1840 (Goulart & Verani, 1992), and *H. luetkeni* (Mazzoni & Caramaschi, 1997). According to Burgess (1989), when a male

Hypostomus is placed in a tank where other males are already established, they fight using their large, toothed pectoral spines.

An inverse relationship between fish fecundity and the degree of parental care has been documented repeatedly in fishes (von Ihering *et al.*, 1928; Svärdson, 1948; Nikolsky, 1963). Fishes without parental care also tend to produce the smallest eggs, often in association with high batch fecundity (Winemiller, 1989; Winemiller & Rose, 1992). The general inverse relationship between batch fecundity and egg size reported for fishes (Adebisi, 1987; Duarte & Alcaraz, 1989) is observed among the six loricariids of the Paraná. Among our six species, the non-guarder (*R. apsera*) had the smallest eggs and highest fecundity, and the cavity nesting, brood guarders had the largest eggs with lowest fecundities. Egg size of bearers was intermediate, and batch fecundity was nearly as low as that of the cavity nesting guarders.

According to the field observations, *Loricariichthys* spp., *Loricaria* sp., *M. aculeatus* and *Hypostomus* produce adhesive eggs. Burgess (1989) described how *Hypostomus* eggs deposited in excavations have a mucous secretion causing them to form a sticky ball. The eggs of *R. aspera* are non-adhesive immediately following spawning, and become adhesive subsequently. Based on induced spawning of *R. aspera* from the São Francisco basin, Sato *et al.* (1998) reported development of adhesive eggs.

Suzuki (1992) discussed the role of the granulosa cell layer for the production of material deposited on the radiata layer, which was presumed to be responsible for adhesion in loricariid eggs. Among the species examined here, only *R. aspera* lacks granules in the cytoplasm of this layer. Instead, the cytoplasm is vacuolated, a condition observed in most pimelodid catfishes (Suzuki, 1992). Evidence of liberation of material from the granulosa cells onto the surface of mature oocytes was observed during final maturation in *Loricariichthys* sp. The space between the granular layer and the oocyte proper increased simultaneously with the decrease in the height of the granulosa cells.

Loricariichthys and *Loricaria* species had the thickest zona radiata. Because their eggs are transported on the male's ventral surface, they are most likely to experience abrasion against substrates. The thinnest zona radiata was observed in *H. ternetzi* and *M. aculeatus*, the two cavity nesting brood guarders. Presumably, eggs clustered into a sticky mass within a clay-lined cavity would receive little abrasion. *Rhinelepis aspera*, the broadcast spawner, also had a thin zona radiata. The eggs of this species are transported downstream as they fall through the water column of the river channel. A certain degree of abrasion would be expected as the eggs move along the substratum before sticking to their resting place.

The most abundant species in the study area (*Loricariichthys* sp., *L. platymetopon*, *Loricaria* sp.) were externally bearing, brood guarders with partial spawning. Their high abundance suggests that this reproductive strategy is effective in this region, which formerly experienced seasonal water level fluctuations in response to seasonal rainfall, but these fluctuations now have become more frequent and variable in response to discharges from hydroelectric dams located upstream (Agostinho *et al.*, 1995*b*). The ability to replace broods rapidly might be favoured under a regime of environmental changes associated with unpredictable hydrology. Likewise, brood guarding, including cavity nesting and external bearing, should be adaptive in more stable habitats such as reservoirs (Winemiller, 1989) and other lentic habitats where the relative effect of biotic interactions on recruitment success is higher (the equilibrium strategy *sensu* Winemiller, 1992; Winemiller & Rose, 1992). Such habitats generally had highest densities of brood-guarding loricariids.

Loricariichthys sp. was most common in channel areas with swift current and rocky substrata, whereas *L. platymetopon* occurs in floodplain lagoons with mud or sand substrata. Although *Loricaria* sp. is widely distributed in the region, it is especially abundant in low-gradient tributaries of Itaipu and the Paraná. The three Loricariinae species were rare or absent in Itaipu Reservoir for the first 7 years post impoundment. After this period, *Loricariichthys* sp. became abundant and ranked among the top 10 species in the experimental fishery (Agostinho *et al.*, 1997; Benedito Cecilio *et al.*, 1997). Soon thereafter, *L. platymetopon* colonized the reservoir, but remains more common in reservoir tributaries where spawning is observed frequently.

Hypostomus ternetzi has the most limited distribution in the basin, occurring in the Itaipu Reservoir, especially its fluvial zone (Delariva, 1997). Other *Hypostomus* species occur in the basin and span a greater range of habitats. The other external brooder, *Megalancistrus aculeatus*, is broadly distributed within the reservoir and main channel of the Upper Paraná, but does not occur in small tributaries and floodplain lagoons. *Megalancistrus aculeatus* was the only loricariid captured in the channel of the Piquirí River, the first major tributary above Itaipu. According to Delariva (1997), *M. aculeatus* is most abundant in shallow areas with homogeneous substrata, whereas *H. ternetzi* prefers channel areas of greater depth with irregular bottom profiles.

The only non-guarder, *R. aspera*, was common in the reservoir, but only as adults. As noted previously, this segment of the population migrates to upstream lotic regions for seasonal spawning (Agostinho *et al.*, 1995*a*). This species' strategy of broadcasting spawning thousands of small eggs (i.e. the periodic strategy sensu Winemiller, 1992; Winemiller & Rose, 1992) should allow for periodic strong recruitment classes in habitats that vary on large spatial or temporal scales, such as river channels and fringing floodplains. Non-synchronous cumulative oocyte development observed in *R. aspera* may be an adaptation for a species that depends on environmental cues to trigger seasonal migration and spawning.

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