REPRODUCTION OF SPECIES OF THE GENUS *Cichla* IN A RESERVOIR IN SOUTHEASTERN BRAZIL

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ABSTRACT

The reproduction of two species of *Cichla* (*Cichla* cf. *ocellaris* and *C. monoculus,* commonly known in Brazil as *tucunaré*) introduced in the Volta Grande Reservoir, southeastern Brazil, was analyzed. The period for spawning began at the end of the dry season (September) and extended until the end of the rainy season (January). The length of the first gonad maturation (L_{50}) and the length at which all fish are considered adults (L_{100}) were very similar for both species and coincide with the length of fish at one year of age. The analysis of disassociated oocytes evidenced a partitioned spawning, and that *C. monoculus* was more prolific than *C.* cf. *ocellaris*. The low fecundity, partitioned spawning, bi-parental brood care, and supplying of food for the young are related to the way of life, habitat, and reproductive behavior of these fish.

Key words: *Cichla*, reproduction, fecundity, reservoir, Brazil.

RESUMO

Reprodução de espécies de *Cichla* em um reservatório do Sudeste do Brasil

Foi analisada a reprodução das espécies de tucunarés (*Cichla* cf. *ocellaris* e *Cichla monoculus*) introduzidas no reservatório de Volta Grande, Sudeste do Brasil. A época das desovas teve início no final do período de seca (setembro) e estendeu-se até o final do período chuvoso (janeiro). O comprimento da primeira maturação gonadal (L_{50}) e o comprimento a partir do qual os peixes dessas espécies são considerados adultos (L_{100}) foram muito próximos e coincidem com os comprimentos de peixes com um ano de vida. A análise dos ovócitos dissociados evidenciou a desova parcelada, sendo *C. monoculus* mais prolífico do que *C.* cf. *ocellaris*. A baixa fecundidade, a desova parcelada, o cuidado biparental e o suprimento de alimento para os jovens estão relacionados ao modo de vida, ao *habitat* e ao comportamento reprodutivo desses peixes.

Palavras-chave: *Cichla*, reprodução, fecundidade, reservatório, Brasil.

INTRODUCTION

Increasing electricity demand requires the construction of many hydroelectric plants that, as a result of river damming, have innumerable consequences for fish populations. A unavoidable result with respect to aquatic fauna is the alteration in abundance of animal species, with excessive proliferation of some and reduction, or even elimination, of others. The impact level is mainly related to local fauna characteristics, location of the dam with respect to population distribution in the area, morphometrics of the basin, existence of other dams upstream, dam design, and operational procedures of the plant itself (Agostinho, 1994).

Introduction of species from other basins into reservoirs is a common practice. Since the 60s, significant transfer of native species from the Amazon basin into fish-rearing centers in northeastern Brazil has occurred, followed by their subsequent transfer into southeastern and southern Brazil. From these rearing centers, the species can easily reach nearby natural water bodies, which incurs high risk, especially in the case of predatory fish species (Agostinho & Julio Jr., 1996). When environments are altered, native species are especially vulnerable (Elvira & Almodóvar, 2001). An example is the the Volta Grande Reservoir where at least 15 years ago two species of piscivorous fish easily distinguished by their external coloration, *sagittae*, and meristic characters, were introduced (*Cichla* spp.).

Introduced species affect native species through competition for available resources, predation, pathogen transfer, or simply by habitat alteration. Introduction of alien species and consequent natural habitat loss were the factors responsible for most animal species extinctions during the twentieth century (Elvira & Almodóvar, 2001). Stable environments are more susceptible to the introduction of new species (specially piscivores) than relatively less stable ones; however, every natural system is unique and identical changes are rarely possible (Zaret, 1982). Exponential population growth is common among introduced predatory species, bringing with it more intraspecific competition for space and food (Bedarf *et al.*, 2001). As a consequence, biomass of the introduced species may decrease (Williams *et al.*, 1998).

The family Cichlidae is the most species-rich of all freshwater percoid fish (1,400 species), displaying great variation in reproductive behaviors (McKaye, 1984; Murray, 2001). Out of the 495 families of bony fish, about 20% exhibit parental care and only two of them, Pomacentridae and Cichlidae, include genera with transitions between kinds of parental care (Gittleman, 1981). The perciforms of the family Cichlidae generally present local sedentary populations, stable food resources, a prolonged breeding season, and parental care, attributes corresponding to an equilibrium strategy (Winemiller, 1989). Parental care occurs in many different manners, and variation exists as to which sex takes care of the brood; nevertheless, brood care by both parents is the ancestral condition in relation to single-parent brood care (Goodwin *et al.*, 1998). Parental care in animals is determined by the complexity of behavioral interactions between parents and their brood, and the amount of food destined for the brood is clearly related to the type and extent of this care (Godfray, 1995). Male fish with external fecundation generally have a high probability of being genetically related to offspring hatching at the spawning site; this is a precondition to the evolution of parental care (Blumer, 1979). Cichlids possess fins and muscles associated to control of certain movements including fanning water, an important requirement in lentic waters since it supplies eggs with a constant water flux for oxygenation and removal of debris from their surface, as well as minimizing the chance of fungi infection (Zaret, 1980; Blumer, 1986).

Species of the genus Cichla, commonly known as *tucunaré* in Brazil, are basically restricted to transparent waters with high temperatures and access to lentic water habitats for feeding and/or reproduction; in these habitats, they are frequently the dominant diurnal piscivores (Winemiller, 2001). These fish, which lay their eggs on the substrate, in accordance with their reproductive strategy commonly establish a territory where eggs are laid and guarded. A couple remains together throughout the parental care period, which extends from the time of spawning until the immature individuals become totally independent (McKaye, 1977; Zaret, 1980; Winemiller *et al.*, 1997).

In species of *Cichla* reared in captivity, sexual maturity occurs between 11 and 12 months of age, with the males always being more developed than the females (Fontenele, 1950). Before mating, cichlids develop secondary sexual characteristics: post-orbital nuptial humps in the males and bright body colorations in both sexes (Fontenele, 1948; Winemiller *et al.*, 1997). The objective of the present work was to characterize the reproduction of *Cichla* cf. *ocellaris* (Bloch & Schneider, 1801) and *Cichla monoculus* (Bloch & Schneider, 1801), as well as its periodicity and fecundity in the Volta Grande Reservoir.

MATERIAL AND METHODS

The Volta Grande Reservoir, located in a tropical area (48°25' and 47°35'W, 19°57' and 20°10'S), resulted from the damming of the Rio Grande River. This river is located between the states of Minas Gerais and São Paulo in southeastern Brazil (see Fig. 1). The climate is typically tropical with a mean annual temperature of 22°C and a mean annual rainfall of 1.635 mm. There are two typical seasonal periods: a warm and rainy season from October to April, and a cool and dry season from May to September. The Volta Grande Reservoir has a flooded area of 221,7 km^2 with a water volume of 2.268 km^3 destined for electric energy production (Braga & Gomiero, 1997).

Collections were made during April and June 1997, and every month from September 1997 until August 1998. Two kinds of fishing equipment were used: simple nets with meshes of 2.0, 3.0, 4.0, 5.0, and 6.0 cm between adjacent knots, and fishing rods with natural or artificial bait. Each specific mesh set was 150 m long and 1.5 m in height, totaling 750 m.

Data for total weight (*TW*) in grams, total length (*TL*) in centimeters, sex, and gonad maturation stage were taken for each individual captured of each species. The maturation stage of each specimen was determined macroscopically, considering coloration, transparency, superficial vascularization and, for ovaries, oocyte visualization and appearance. In agreement with a previously established scale, four different maturation stages were considered: A, immature; B, in maturation; C, mature; and D, spent. The reproductive period was analyzed according to seasonal variations of the different maturation stage frequencies during collecting periods. The mean length L_{50} is of the first gonad maturation at which 50% of the individuals are adult, i.e., they have begun the reproductive cycle. The length at which all individuals are apt for reproduction is represented by L_{100}. Both L_{50} and L_{100} were estimated following Vazzoler (1996).

For the study of fecundity, in accordance with Vazzoler (1996) ovaries in stage C were extracted from the visceral cavity and weighted; their membranes were then sectioned longitudinally throughout and immersed in modified Gilson solution. The vials containing the oocytes and Gilson solution were periodically shaken and, after total disassociation, the oocytes were washed several times in 70% alcohol and kept in this solution. Fecundity was estimated according to the volumetric method (Vazzoler, 1996). Individual fecundity was estimated considering $N' = Sn/s$, where S is the volume of alcohol used to homogenize the mass of oocytes, and n is the total number of oocytes counted in a sample of s volume obtained through a Stempel pipette.

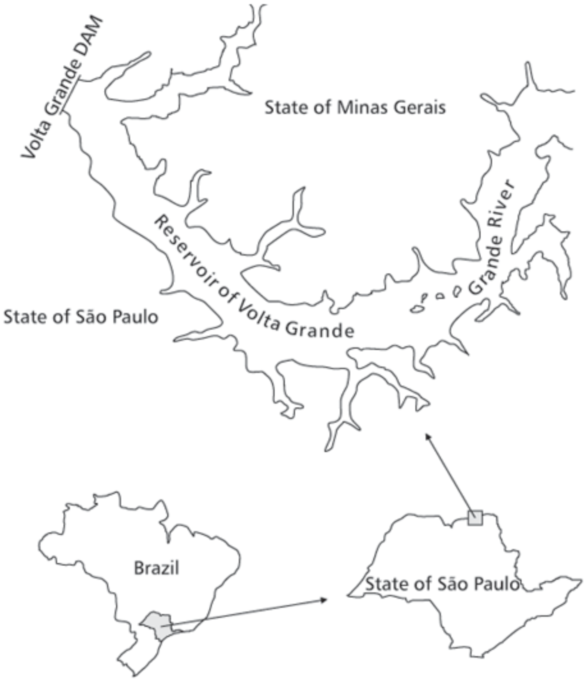

Fig. 1 — Reservoir of Volta Grande (48°25’ and 47°35’W, 19°57’ and 20°10’S).

In this way we estimated the total number of oocytes, *N'*, contained in the pair of disassociated ovaries. Since individual fecundity represents the number of mature oocytes and not the total number of oocytes contained in the ovaries, the formula $N = N'P/100$ was used to estimate individual fecundity, where *P* is the percentage in the ovaries of oocytes with the diameter necessary for the oocytes to initiate the maturation process, in relation to the total number of oocytes (*N'*). Once individual fecundity was established for both species of *Cichla*, we also estimated the relative fecundity in relation to length (*FRL*) and to weight (*FRW*) for both species in comparison with one another.

RESULTS

During the collecting period, 459 specimens of *C.* cf. *ocellaris* and 170 of *C. monoculus* were sampled.

The distribution of the gonad maturation stages of all exemplars captured for *C.* cf. *ocellaris* showed a prevalence of B stage (in maturation); however, C stage (mature) appeared in April, September, November, and December 1997 and in all the collections made during 1998. The D stage (spent) occurred in April, May, and July 1998. For *C. monoculus* there was also a prevalence of B stage, but the C stage occurred in all collections, except for the ones made during September 1997 and March 1998. Stage D appeared in November 1997, February 1998, and July 1998 (see Figs. 2 and 3).

Immature individuals of *C.* cf. *ocellaris* occurred from January to August 1998, while for *C. monoculus*, immatures appeared in December 1997 and from February to June 1998. For both species there was a higher frequency of immature individuals during February (see Figs. 4 and 5).

The L_{50} and L_{100} for *C.* cf. *ocellaris* were 20 and 29 cm, respectively, and for *C. monoculus* 21.5 and 25 cm, respectively. In the analysis of disassociated oocytes, 19 pairs of ovaries were used for *Cichla* cf. *ocellaris* and 38 for *C. monoculus*, divided in similar maturation groups. The ovaries corresponded to specimens collected during 1997 and 1998.

For *C.* cf. *ocellaris*, the stock batch was shown to correspond to oocytes in diameter classes of up to 306-367.2 micrometers, while developing or mature oocytes occurred from the 795.6 micrometer class until that of 2,570.4 micrometers (see Fig. 6). In *C. monoculus*, the stock batch also corresponded to oocyte diameter classes of up to 306-367.2 micrometers and developing or mature oocytes were found in all classes from 673.2 micrometers to 2,815.2 micrometers (see Fig. 7).

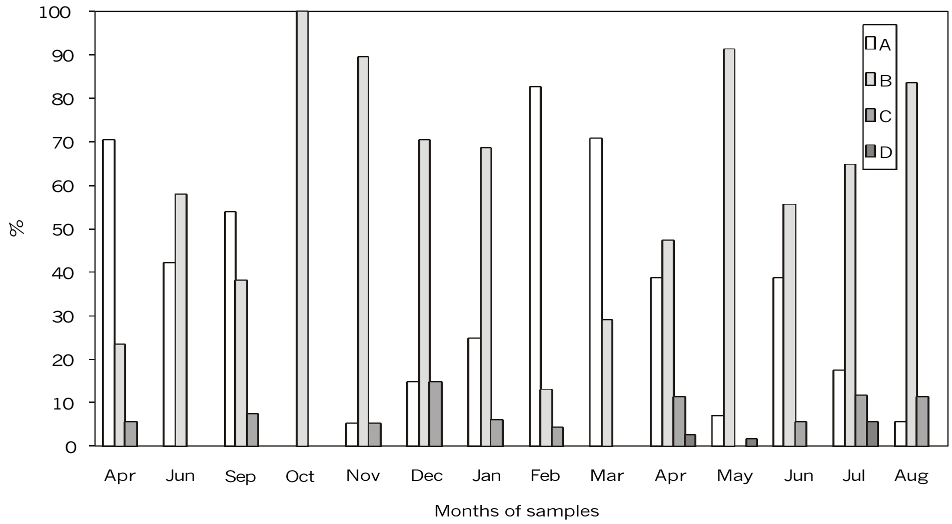

Fig. 2 — Frequency (in percentage) of the mature stages of *Cichla* cf. *ocellaris* obtained in the collections made from April 1997 to August 1998.

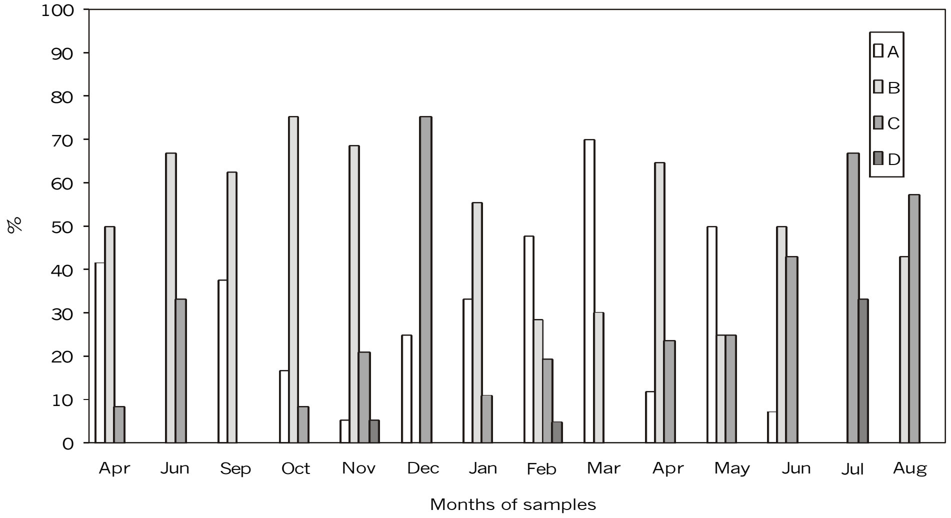

Fig. 3 — Frequency (in percentage) of the mature stages of *Cichla monoculus* obtained in the collections made from April 1997 to August 1998.

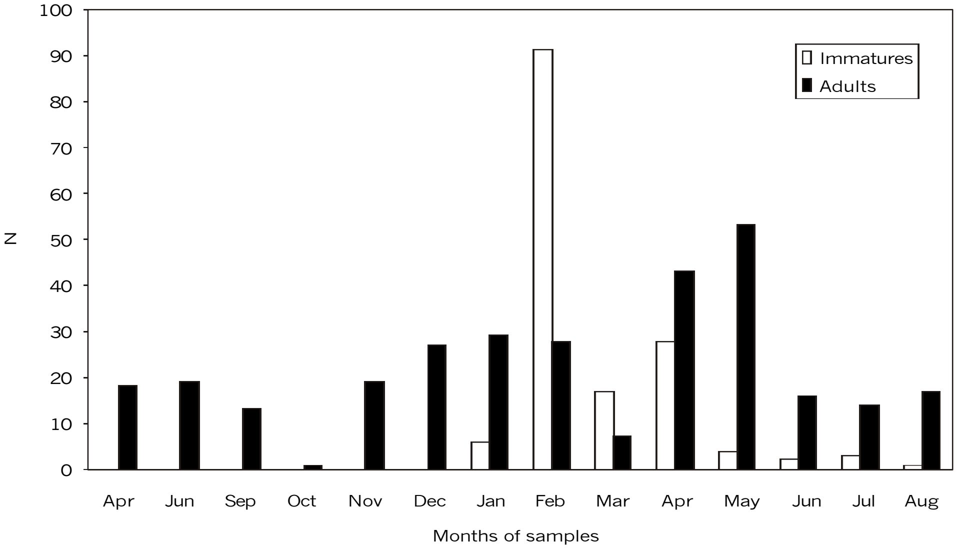

Fig. 4 — Numerical distribution of immature and adult individuals found in each collection of *Cichla* cf. *ocellaris* made from April 1997 to August 1998.

The data corresponding to total fish length (*TL*), total weight (*TW*), total number of oocytes (*N'*), number of developing and mature oocytes (*N*), fecundity in relation to length (*FRL*), and fecundity in relation to weight (*FRW*), for each pair of ovaries and for both species analyzed are summarized in Tables 1 and 2. The mean number of mature oocytes for *C.* cf. *ocellaris* was 13,769.22 with a standard error of 3,401.

For *C. monoculus* this mean was slightly higher, with 17,987.55 oocytes and a standard error of 2,522.8.

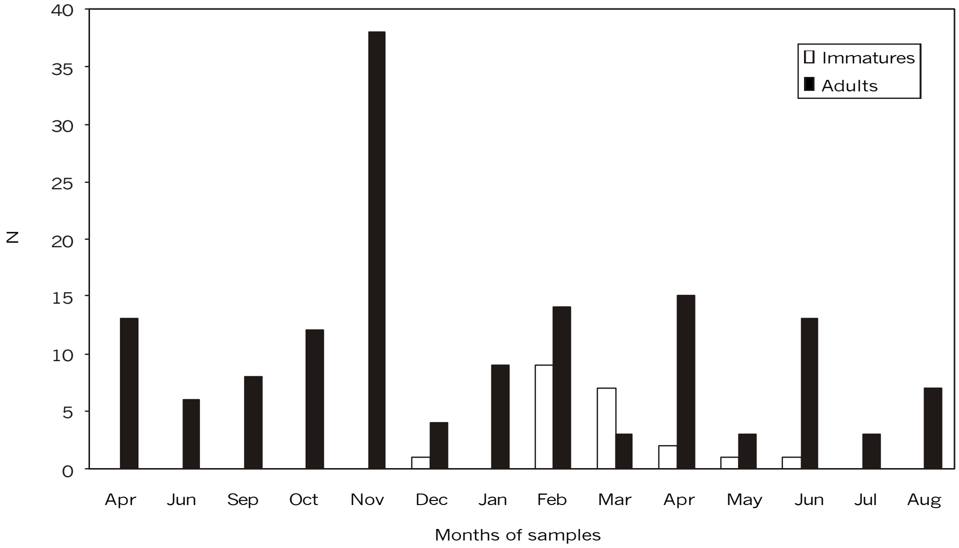

Fig. 5 — Numerical distribution of immature and adult individuals found in each collection of *Cichla monoculus* made from April 1997 to August 1998.

DISCUSSION

The maturation stages showed that C-stage individuals (mature) could be found during throughout the seasons, but reproduction occurred mainly from September to January (spring and summer). The highest frequency of immature individuals of both species occurred during summer and autumn, showing that, for these species, eggs were laid during spring and the beginning of summer, seasons that correspond to the higher incidence of rain. In tropical waters where temperatures apparently do not limit egg laying and in relatively non-seasonal environments, the seasons are imposed by environmental factors (such as competition for spawning sites or habitats) that lead to nutrient accumulation and biotic pressures (Lowe-McConnell, 1999).

From the moment the length or age of the first maturation is reached, environmental variables begin to influence the individuals so that conditions at spawning time, including its synchrony with food resources available for the larvae and young, are favorable to the survival and development of the brood (McKaye, 1984; Vazzoler, 1996).

The general pattern of higher intensity of gonad maturation for the different species of *Cichla* at various sites seems indicate the end of the dry season, with spawning occurring from the beginning of the rainy season, when the water level begins to raise (Fontenele, 1950; Lowe-McConnell, 1969; Machado-Allison, 1990; Novoa *et al.*, 1990; Magalhães *et al.*, 1996; Novoa, 1996; Jepsen *et al.*, 1997; Winemiller *et al.*, 1997; Winemiller & Jepsen, 1998; Jepsen *et al.*, 1999; Winemiller, 2001). In environments with more uniform hydrological conditions, multiple spawning may occur during the year; nevertheless it is not clear if each individual is capable of several spawnings under natural conditions. Repeated spawning during a single reproductive period constitutes an adaptation to restricted egg and larvae survival conditions (Nikolskii, 1969; Bagenal, 1971; Jepsen *et al.*, 1999). At the Volta Grande Reservoir, spring and summer also brought the best conditions for the reproduction of other fish species (Braga, 2001).

The immature individuals of *Cichla* matured during the first year of life at a length that varied according to the species and site of occurrence. In Venezuela, Winemiller *et al.* (1997), Jepsen *et al.* (1999), and Winemiller (2001) found standard first maturation lengths that varied according to the species: no less than 32.5 cm for *Cichla temensis* (Humboldt, 1833); 27 cm for *Cichla orinocensis* (Humboldt, 1833); 24.6 cm for *Cichla intermedia* (Machado, 1971); 27 cm for *C. ocellaris*; and 23 cm for *C.* cf. *monoculus*. The species of *Cichla* at the Volta Grande Reservoir presented similar lengths for the first gonad maturation. Since these lengths are related to growth, they present spatial and temporal variations according to prevailing abiotic and biotic environmental conditions in the occupied region or during the period in which the population was subjected to these conditions (Vazzoler, 1996).

Both species of *Cichla* in the study region had several batches of developing oocytes in their ovaries during the same reproductive period. Thus, these species showed partitioned spawning. The mean fecundities demonstrated that *C. monoculus* was more prolific than was *C.* cf. *ocellaris*, and fecundity values for both species were related to the length and weight of these fish. Braga & Gennari Filho (1991) reported that the presence of several modal groups, evidenced by frequency distribution of the oocyte diameters of disassociated ovaries indicated spawning of successive oocyte batches in a single reproductive season, although at different periods. The size of mature oocytes for both species corresponds to values reported by Vazzoler (1996) for a nonmigratory species with external fecundation and displaying parental care.

Multiple or partitioned spawning is characterized by the synchronic development of each oocyte batch and as the more developed batches reach complete maturation they are eliminated (Vazzoler, 1996). Since fish of the genus *Cichla* present partitioned spawning, their ovaries have oocytes of different dimensions, shapes, and colorations that indicate specific developmental stages (Fontenele, 1950; Magalhães *et al*., 1996). Jepsen *et al*. (1999), however, has hypothesized that the energy expendidure for reproduction and brood defense would probably result in single annual spawnings for most individuals.

Fecundity, a particular adaptation to variable conditions, especially mortality, varies mainly in response to food supply and is one of the basic means to adjust the reproduction rate in accordance with environmental condition fluctuation.

Nutrition not only affects fecundity but also the quality of what it generates (Nikolskii, 1969). According to Lowe-McConnell (1999), in fish that live under conditions of very little food supply variation (seasonally and from year to year), energy investment is more efficiently directed to greater efficiency in resource use. Such species tend to exhibit longer life cycles, retarded maturity, frequent and small spawning, often with parental brood care, territoriality, social behavior, and symbiosis with other species.

TABLE 1

Total length (*TL*), total weight (*TW*), total number of oocytes (*N'*), number of developing and mature oocytes (*N*), fecundity in relation to length (*FRL*), and fecundity in relation to weight (*FRW*) of the individuals of *Cichla* cf. *ocellaris* from which the ovaries were analyzed.

TL **(mm)**	***TW*** **(g)**	***N'***	***N***	***FRL***	***FRW***
347	680	48600	9720	28.01	14.29
352	811	48800	12200	34.65	15.04
368	770	71500	12155	33.02	15.78
379	850	21500	3655	9.64	4.3
383	1030	158200	20566	53.69	19.96
390	1088	73000	5840	14.97	5.36
390	1101	122000	12200	31.28	11.08
392	1105	91900	15623	39.85	14.13
392	1002	75100	8261	21.07	8.24
392	1106	93200	15844	40.41	14.32
398	1045	70900	16307	40.97	15.60
400	1150	125900	15108	37.77	13.13
401	1053	34500			
406	1245	120800	9664	23.8	7.76
410	1124	57600	5760	14.04	5.12
416	1102	46100	17979	43.21	16.31
476	2200	122300	28129	59.09	12.78
492	2250	142100	21315	43.32	9.47
537	2800	116800	17520	32.62	6.25

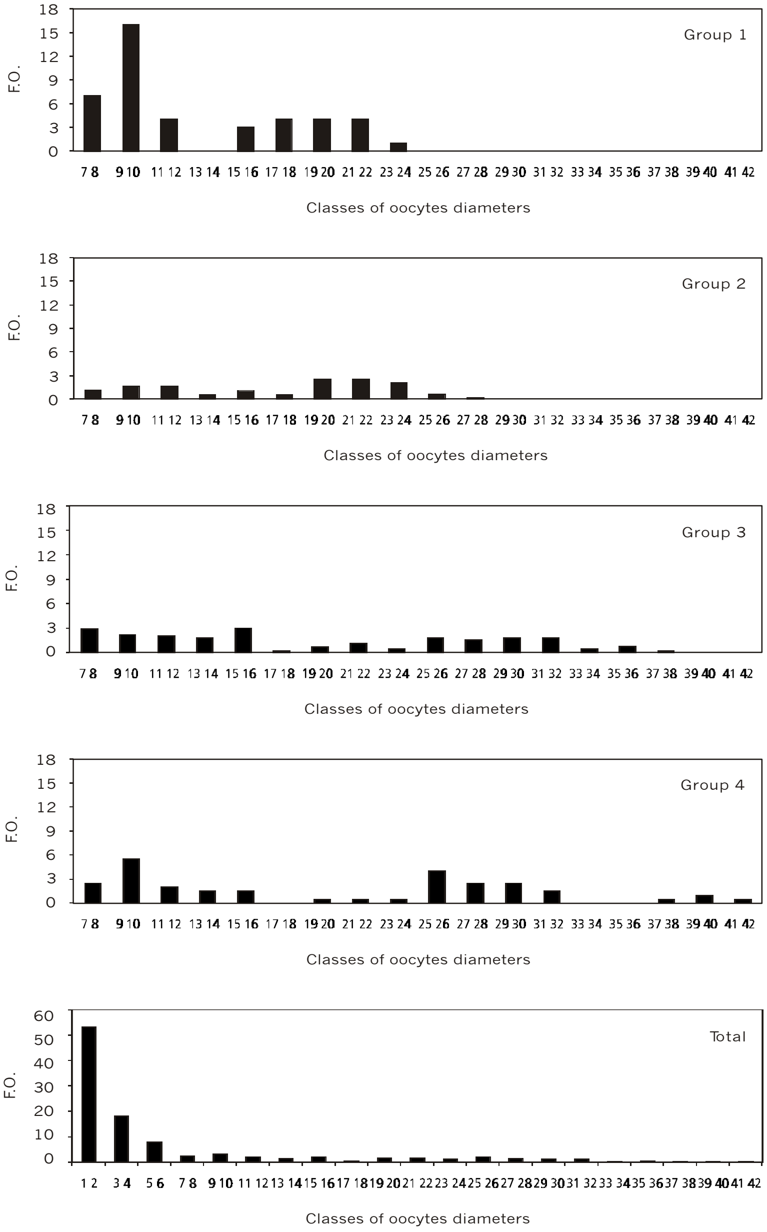

Fig. 6 — Frequency (in percentage) of the diametrical classes of oocytes in d.o.m. (division of ocular micrometer), equivalent to 61.2 micrometers, of *Cichla* cf. *ocellaris* divided into groups.

Tropical fresh waters include numerous fish species that present multiple spawning, so there must be an evolutionary advantage in producing several oocyte batches. This might be relate to the dangers inherent in water levels fluctuations to which the first batch is exposed, which is complicated by the fact that many of these fish move only locally to spawn. The many tropical fish species that guard their eggs and young tend to have smaller clutch sizes than species that leave their eggs unprotected. Fecundity also shows an adaptative variation reflecting life conditions within the population, among populations, and among species.

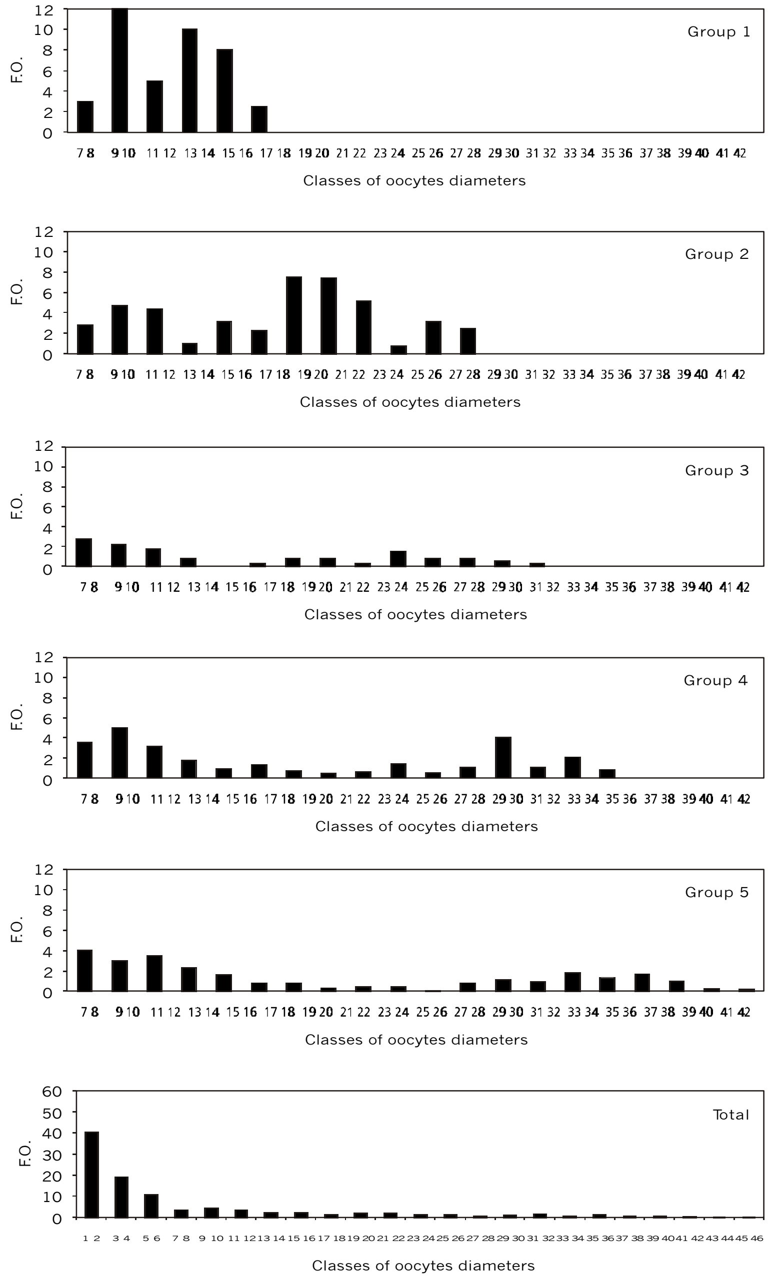

Fig. 7 — Frequency (in percentage) of the diametrical classes of oocytes in d.o.m. (division of ocular micrometer), equivalent to 61.2 micrometers, of *Cichla monoculus* divided into groups.

In addition, it increases with fish growth, and the point of decline in older fish is a characteristic specific to the population and the species (Nikolskii, 1969). Fecundity generally increases proportionally to fish weight, or its cubic length, so the bigger the female, the higher number of oocytes produced (Galvani & Coleman, 1998; Lowe-McConnell, 1999).

TABLE 2

Total length (*TL*), total weight (*TW*), total number of oocytes (*N'*), number of developing and mature oocytes (*N*), fecundity in relation to length (*FRL*), and fecundity in relation to weight (*FRW*) of the individuals of *Cichla monoculus* from which the ovaries were analyzed.

TL (mm)	*TW* (g)	*N'*	*N*	*FRL*	*FRW*
261	531	38600	18914	72.46	35.61
310	414	19100	15089	48.67	36.44
304	374	23600	14160	46.57	37.86
326	481	88300	17660	54.17	36.71
331	497	28900	19363	58.49	38.95
333	553	39600	14652	44	26.49
342	494	102000	15300	44.73	30.97
350	605	33700	26623	76.06	44
358	671	117800	29450	82.26	43.88
360	758	181000	10860	30.16	14.32
363	692	65900	15816	43.57	22.85
366	666	53900	8624	23.56	12.94
368	745	41300	12803	34.79	17.18
372	785	140400	30888	83.03	39.34
380	843	107900	32370	85.18	38.39
380	766	93100	12103	31.85	15.8
382	735	104800	25152	65.84	34.22
386	634	78600	15720	40.72	24.79
386	711	109400	26256	68.02	36.92
386	863	72500	12325	31.93	14.28
389	906	70300	15466	39.75	17.07
392	839	151700	39442	100.61	47.01
393	917	142300	12807	32.58	13.96
393	773	29200	12556	31.94	16.24
395	1037	73000	13870	35.11	13.37
395	941	70400	15488	39.21	16.45
396	1044	42300	10998	27.77	10.53
396	830	89100	8019	20.25	9.66
398	1070	88000	11440	28.74	10.69
401	877	49500	6930	17.28	7.9
404	792	132800	30544	75.6	38.56
406	1044	78500	9420	23.2	9.02
416	1166	100200	16032	38.53	13.74
416	1112	112000	21280	51.15	19.13
417	1134	135500	8130	19.49	7.16
451	1305	175600	19316	42.82	14.8
459	1572	109300	27325	59.53	17.38
477	1680	94800	30336	63.59	18.05

The mean number of mature oocytes for *C.* cf. *ocellaris*, as well as for *C. monoculus*, was higher than 12,000, a value very similar to that presented by *C. ocellaris* (Sawaya & Maranhão, 1946; Novoa *et al*., 1990; Novoa, 1996; Lowe-McConnell, 1999) and *C. temensis* (Fontenele, 1950). Nevertheless, it differed from those of *C. temensis, C. intermedia, C. orinocensis* (Winemiller, 2001), and *C. ocellaris* (Fontenele, 1950). These differences are probably due to low sampling or to reduced specimen size.

A few days before spawning, peacock-bass males show nuchal humps and both male and female individuals present red irises and bright body colors. The nuchal hump that some male ciclids develop during the reproductive season might aid in sex recognition (Barlow, 1998) or function as a lipid storage site (Fontenele, 1948); the bright colors might be aposematic for egg and larvae defense or for mutual recognition between a couple (Schroder & Zaret, 1979).

The males delimitate a territory from which they banish any other male, then the couples form and perform all reproductive behaviors. Peacock-basses are egg, embryo, and larva "keepers" and generally display elaborate behaviors and territoriality (Vazzoler, 1996). The couple seeks a resistant structure like a rock, submersed tree trunk, or any other sort of compact substrate to deposit their eggs (Fontenele, 1950; Lowe-McConnell, 1999; Winemiller, 2001), and the male is more active within the cleaning process (Fontenele, 1950). In many cases, several species might aggregate for nest building at lakeshore sites (Winemiller *et al*., 1997). In addition to the structure for depositing the eggs, peacock-basses dig their nests in the substrate with their nose; the nests, numbering from two to four, might be circular or oval, depending on the substrate (Fontenele, 1950; Braga, 1952). The eggs are adherent and are laid in the chosen resistant structure; after eclosion, the couple transfers the larvae to one of the previously dug accessory nests (Fontenele, 1950). The larvae have four pairs of adhesive organs on their heads that secrete the mucus which facilitates their adherence to the nest bottom (Fontenele, 1952). The kind and site of the spawning represent an adaptation against predators and favoring food supply for the young (Nikolskii, 1969). In addition, the large number of nests built serves to confuse predators, since only one nest is used to deposit the larvae (Braga, 1952). The reason why these ciclids reproduce in lentic waters is the zooplankton supply available for the larvae; this food source is generally more abundant in lakes (Zaret, 1980).

After a few days, the larvae become free swimmers and the couple accompanies the school. Chemical (pheromones) as well as visual signals may be involved in keeping the young next to their parents. Predator pressure seems to be an important factor in the evolution of some forms of parental care of eggs and the young, e.g., participation of both parents in guarding the young after they become free swimmers is very important (Lowe-McConnell, 1999). Generally, in ciclids displaying brood care by both parents, the males are larger than the females and a division of labor exists: females guard the eggs and larvae while males patrol and repel any possible predators (Barlow, 1974). The benefits of bi-parental brood care include collaboration in the division of labor necessary to repel predators and presence of the remaining parent when the other dies or abandons the brood (Annett *et al*., 1999). All of the aspects of *Cichla* species reproduction show relationships between the way of life, habitat, and strategies. The low fecundity, partitioned spawning, bi-parental brood care, and food supply for larvae and young in lentic environments are intimately associated within the complex reproductive behavior of these fish.

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