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The influence of dam construction on a population of *Leporinus obtusidens* (Valenciennes, 1847) (Pisces, Anostomidae) in the Yacyretá Reservoir (Argentina)

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Abstract

A field study of age, growth and mortality of the “boga”, *Leporinus obtusidens* (Valenciennes, 1847) was carried out in the Yacyretá Reservoir, High Paraná River, Argentina. We compared age-structure, length–weight relationships and condition factor coefficients in phases previous (1990–1994) and subsequent (1995–1998) to the reservoir filling. In addition, we estimated total and natural mortality, as well as the growth and yield parameters for the whole study period. Comparisons were carried out in four sampling points within the river main channel. Fish were sampled monthly with nine gillnets ranging from 40 to 160 mm of total mesh opening (opposed knots). A scale study showed an age range comprised between 1 and 13 years, with ages 4 and 5 the most abundant before reservoir filling, whereas ages 2 and 3 were more frequent afterward. The weight–standard length relationship showed a higher growth during the second phase of reservoir filling. Maximum condition factor was registered before the spawning period (August and September), being higher after the impoundment, and particularly in the sampling site located within the reservoir. The von Bertalanffy growth coefficient, K, reached 0.12 in both sexes, while the asymptotic length, L_∞, was 578 and 547 mm, in females and males, respectively. Natural mortality according to Pauly’s equation reached 0.178 year^{-1}, and the total mortality was 0.36 year^{-1}. The Beverton and Holt yield per recruitment (Y/R) was estimated as 246.54 g, with a maximum sustainable yield of 248.00 g. This result suggests that the species had higher condition after impoundment and is fished near its maximum capacity in the reservoir.

Keywords: Age; Growth; Mortality; Yield per recruitment; Dam construction effects; *Leporinus obtusidens*; Paraná River

1. Introduction

The ichthyofauna of the Paraná River basin is comprised of approximately 600 species, dominated by Characiformes and Siluriformes (COMIP, 1994). Species of the family Anostomidae are endemic

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characiforms of South America, with a wide distribution within the continent excepting river systems of the Pacific side. Several species of this family, particularly those of the genus *Leporinus*, are an important component of commercial and recreational fisheries, with a wide acceptance of its flesh for human consumption (Braga, 1993).

The “boga”, *Leporinus obtusidens*, inhabits lentic as well as lotic environments (Ringuelet et al., 1967; Bonetto et al., 1969, 1970) and is one of the most common and abundant species collected in several experimental fishing surveys carried out in the High Paraná River (Roa and Permingeat, 1999; Bechara et al., 1999). It is a riverine species (Mastarrigo, 1950; Delfino and Baigun, 1985; Bonetto et al., 1971, 1981) that migrates upstream once a year for spawning (Oldani and Oliveros, 1984; Oldani et al., 1992; Agostinho et al., 1995). It has an omnivorous diet, with prevalence of aquatic and terrestrial plants (Hahn et al., 1998).

The high Paraná River has been severely modified since the construction and operation of two large dams, which are among the largest of the world, beginning with Itaipu (Paraguay and Brazil) in 1983 and Yacyretá in 1994. This latter dam is located in the Argentinean Province of Corrientes, on the border with Paraguay (27°28′S, 56°44′W). Reservoir establishment produces major changes in aquatic communities. This is especially apparent for populations of migratory fish species, which are reduced or eliminated, and eventually replaced by more sedentary species. Reduction in migratory fish populations following dam construction is primary due to blockage of migration routes, which prevents access of migrating shoals to spawning and nursery habitats (Agostinho, 1995; Petrere et al., 2002; Agostinho et al., 2002).

With the purpose of exploring some little known aspects of the population and fisheries biology of the boga *L. obtusidens*, we conducted a study of age structure, individual growth, mortality rates and yield per recruitment in Yacyretá Reservoir. Our first aim was to compare age–structure, length–weight relationships and condition factor in phases previous (1990–1994) and subsequent (1995–1998) to the reservoir filling. In addition, we evaluated the state of the fishery using an estimation of total and natural mortality, as well as growth and yield parameters for the whole study period.

2. Study area and sampling sites

The Paraná River is the main watercourse of the Plata Basin, and after the Amazon, represents the most important river in South America, due to its length, mean flow and basin area. This study was carried out in a reach denominated “High Paraná”, which begins at the mouth of the Iguazú River, and runs along a narrow canyon made of basaltic rocks, with abrupt margins bearing subtropical rainforest vegetation. The river flows in a southwestern direction until the city of Posadas, Argentina. Below this point, the river becomes a typical floodplain course, with an interconnected channel of loose materials (gravel and sands) and an alluvial plain that was flooded following damming. Prior to closure of the dam, this stretch was characterized by decreasing depth and a series of islands which typically were flooded at least once a year in summer. In that area, the rapids of Apipé stood out, which were channel structures below which the Yacyretá dam was built.

Yacyretá is a plain dam located at the beginning of the fast water reach of the Paraná River. Residence time of water is between 3 and 7 days. Yacyretá Reservoir has an area of approximately 1140 km^2, a volume of 7000 hm^3, an average depth of 14 m and a maximum depth of 23 m. The operation of the first turbine began in September 1994, when the reservoir reached the bench mark of 76 m above sea level.

Fish sampling sites were located within a 130 km reach along the reservoir longitudinal gradient, beginning with the most upstream and least influenced by the dam. Sample sites included (1) the outlet of the Yabebiry Stream, a small affluent of the Paraná River at 1625 km (55°35′W, 27°18′S); (2) proximities of Puerto Nemesio Parma (Prefectura Naval Argentina), at 1570 km of the river (56°00′W, 27°20′S); (3) Puerto Valle, at 1510 km (56° 25′ W, 27° 36′ S) and (4) Puerto Jupiter, at 1478 km (56°44′W, 27°28′S).

3. Material and methods

The data analyzed in the present paper were obtained from a series of fish samplings carried out by the Regional Project on Fish Biology (CIDET-Faculty of Sciences, National University of Misiones, Argentina), in agreement with the Yacyretá Power Dam facility (EBY). Fish were collected using series of monofilament nylon gillnets with mesh sizes of 40, 50, 60, 70, 80, 120, 140 and 160 mm (opposed knots). At each sampling station, nets were deployed for 48 h, and inspected every 8 h. Samplings were carried out monthly during autumn and winter, and every 3 weeks during spring and summer.

For each individual collected, the following data were registered: gill net mesh size, total weight (TW) in grams, standard length (SL) and maximum height in mm, sex (male, female, juvenile), and state of macroscopic gonad development. Scales were obtained from 900 individuals, representing the entire range of lengths captured. Scales were taken from an area close to the insertion of the pectoral fins and were conditioned and stored in individually labeled paper bags.

In the laboratory, scales were washed with a solution of 7% sodium hypochlorite, and then brushed to eliminate soft tissues (tegument). For each individual, 10 scales were observed using a stereoscopic microscope in order to choose those in proper state for age determination, eliminating asymmetric and regenerated scales. Of the scales suitable for age determination, four to five scales were mounted between two slides. Age determination was carried out using stereoscopic microscope and a micrometric scale, the distance in millimeter between the focus and the edge of the scale (R), and between each growth mark (R_n) was determined for each individual. Scale measurements were carried out along an imaginary line at a 40° angle with the antero-lateral axis.

Growth estimates were compared with water temperature and water level of the Paraná River at Posadas. Water level data were provided by Prefectura Naval from Argentina. Daily registers were averaged for every month of the year throughout the study period ($n = 240$–248). Water temperature was measured once or twice a month, on dates and at sites corresponding to fish samplings. Registers were averaged for every month of the year using data obtained from 1990 to 1998. The marginal increment along the annual cycle was explored in relation to these environmental variables. To examine fish population structure before and after filling of the reservoir, data were classified into two periods: April 1990 to December 1994, and January 1995 to December 1998.

4. Data Analyses

Growth marks were evidenced by the interruption of growth circles on the whole scale as is usual in most temperate fishes (Payne, 1976). Only marks that comprised the whole scale were retained for subsequent analyses. Approximately 30% of the scale samples were discarded due to the presence of doubled rings or difficult interpretation. The number assigned to each age class corresponds to the number of marks. Determination of the period of the year in which the annual ring is formed was based on the monthly variation in the marginal increment of the scale (MI) according to the following expression:

$$\mathrm{MI} = \left(\frac{R - R_n}{R_n - R_{n-1}}\right) \tag{1}$$

where, R is total radius of the scale measured by micrometric ocular, R_n the distance from the focus of the scale to the ring of age n, R_{n-1} the distance from the focus of the scale to the ring of age $n-1$. Ring formation is considered to occur when the marginal increment is smallest (Heald and Griffiths, 1967). Therefore, the month corresponding to the maximum frequency of scales with the growth ring in its border is considered time of formation. To compare sizes of males and females for each age class, the unpaired t-test was used. To analyze the relationship between the scale growth (dependent variable) and relevant abiotic factors (temperature and water level; independent variables), a multiple linear regression analysis was conducted.

It has been stated that in any stage of the life of a fish, weight varies directly with length (Ricker, 1975) according to the expression:

$$\mathrm{TW} = a \times \mathrm{SL}^b \tag{2}$$

where TW is total weight (g), SL the standard length (mm), a and b the regression constants.

Based on this equation, length–weight relationships were fitted for males and females separately and for all individuals independently of the sex. The constants a and b were calculated by functional regression, using natural log ($\ln X$) transformed data. In order to estimate the constants of these equations, data gathered from all fish captured were employed. The fitted length–weight relationships were compared between the periods before and after reservoir filling, as well as for both sexes separately, using analysis of covariance (ANCOVA) to determine if significant differences in slopes were present using the test of parallelism included in ANCOVA (Sokal and Rohlf, 1981).

In order to evaluate the statistical significance of the differences in fish condition between the two periods of study, sex and sampling sites, the Fulton condition factor (K) was used (Fulton, 1911, in Ricker, 1975). The following equation was employed:

$$K = \left(\frac{\mathrm{TW} \times 10^3}{\mathrm{SL}^3}\right). \tag{3}$$

As the condition factor can vary according to the size of the fish (Narahara et al., 1985; Gomes and Agostinho, 1997), the mean values of K were calculated for different classes of standard length ($i = 20$ mm) to detect this phenomena. The existence of differences between the condition factor for sex, sampling place and period of study was tested through factorial ANOVA. Separate one-way ANOVA's for each factor were first carried out, then two-way ANOVA's were performed for the different combinations of factors (sex-site, sex-period and site-period). This procedure had to be employed because the number of samples did not allow for a completely balanced three-way factorial design.

The von Bertalanffy equation was used to estimate growth parameters. Non linear regression was employed for estimating parameters using the Marquart algorithm (Saila et al., 1988), as implemented in the program Statgraphics (Graphics Software Systems Inc., 1990). Parameters were calculated for males, females and the whole samples according to the following formulae:

$$\mathrm{SL}_t = L_\infty(1 - e^{-k(t-t_0)}) \tag{4}$$

where SL_t is standard length at the age t; L_∞ the asymptotic length, k the coefficient of growth, t_0 the hypothetical age to which growth begins.

The equation of growth in weight was calculated deductively using the length–weight relationship and the equations previously described for growth in length. The value of the asymptotic weight (W_∞) was obtained by substituting the asymptotic length (L_∞) in the equation:

$$W_\infty = a \times L_\infty^b \tag{5}$$

where, W_∞ is the maximum total weight that individuals could potentially reach if they lived under ideal environmental conditions. The curve of growth in weight is defined by the equation:

$$W_t = W_\infty[1 - e^{-k(t-t_0)}]^b. \tag{6}$$

The distribution of frequencies in length can contribute to the interpretation of growth. The size-distribution was calculated by sex and for the period of study (before and after reservoir filling), and compared through the Kolmogorov–Smirnof test of association (Sokal and Rohlf, 1981).

For the calculation of total mortality, the equation proposed by Ssentongo and Larkin (1973) was used. These authors considered that when not having detailed information about growth and captures, it is useful to consider the relationship between the average age and the age of the first capture, or the average length and the average length of the first capture, as indicators of the coefficient of total mortality, as follows:

$$Z = \left(\left(k\left(\frac{n}{n+1}\right)\right)\ln\left[\frac{L_\infty - l_c}{L_\infty - l}\right]\right)^{-1} \tag{7}$$

where Z is total mortality; n the total number of individuals captured, l_c the smallest length captured; l the average length captured.

The determination of natural mortality (M) was calculated following the equation of Pauly (1980):

$$\log M = -0.0066 - 0.279\log L_\infty + 0.6543\log k + 0.4634\log T \tag{8}$$

where T is average water temperature, k the von Bertalanffy growth coefficient.

One of the models used to estimate the magnitude of fishery exploitation is yield per recruitment (Beverton and Holt, 1957). In this model, the age entrance to the phase of exploitation remains constant, and fishing effort is the independent variable expressed as the coefficient F of fishing mortality. The dependent variables are biomass in grams per recruit and annual yield in grams per recruit (Sparre et al., 1990). This model is convenient to analyze data from experimental fishing, where an estimate of total captures is not available but “catch per unit effort” (CPUE) is available. The equation is:

$$\frac{Y}{R} = F \exp\left[-M(T_c - T_r)\right] W_\infty \left[\left(\frac{1}{Z}\right) - \left(\frac{3S}{Z} + k\right) + \left(\frac{3S^2}{Z} + 2k\right) - \left(\frac{S^3}{Z} + 3k\right)\right] \quad (9)$$

where S is $\exp\left[-k(T_c - t_0)\right]$; k and t_0 the von Bertalanffy growth parameters, T_c the age at first capture, T_r the minimum age at which fish are harvested, W_∞ the asymptotic body weight, F the fishing mortality.

For Sparre et al. (1990) the election of T_r is not decisive, since all the calculations are based on relative ages. T_r is the minimum age at which the fish can enter the fishery (Beverton and Holt, 1957), and can be calculated through the von Bertalanffy equation as the smallest fish captured. The real age at which fish enter the fishery is the age of first capture T_c, being by definition $T_r < T_c$. The value for fishing mortality is obtained by replacing the previously obtained values of natural mortality (M) and total mortality (Z) in: $Z = F + M$.

5. Results

A total of 1263 individuals of *Leporinus obtusidens* was captured, with a minimum of 31 caught in 1990 and a maximum of 521 in 1996. The average monthly distances between the last ring and the edge of the scale (MI; marginal increment) are presented in Table 1. The lowest values in MI occurred between August and September, therefore growth marks are formed once a year between the months of July and September.

Table 1
Average marginal increment (MI) in scales of *Leporinus obtusidens*

Months	MI (mm)	S.D.	n	T (°C)
January	0.0739	0.0587	45	28.3
February	0.0726	0.0686	149	27.8
March	0.0623	0.0673	79	27.2
April	0.0650	0.0761	29	25.0
May	0.0520	0.0390	21	22.0
June	0.0522	0.0369	22	19.7
July	0.0390	0.0306	71	19.3
August	0.0345	0.0410	51	20.6
September	0.0297	0.0241	15	20.7
October	0.0448	0.0504	58	23.0
November	0.0534	0.0508	99	26.0
December	0.0580	0.0440	10	29.4

S.D.: standard deviation; n: number of individuals analyzed; T (°C): averaged temperature of the water during the months of sampling (1990–1998).

Multiple regression of scale growth with temperature and water level (Fig. 1) was significant ($F_{(2,49)} = 5.0344$, $P < 0.0102$), but with a low R^2 (0.1704). The MI was positively related with each independent variable, and the overall statistical test of the regression was significant. However, the relationships for each variable considered separately were not significant.

When grouping MI data by study period (before and after reservoir filling) and season of the year, the lowest MI value during the period prior to reservoir filling was registered in winter, whereas after reservoir filling, the lowest MI value was observed during the winter-spring transition (Fig. 2). Significant differences in MI were not detected between the first and second period of study (ANOVA, $P > 0.05$). In contrast,

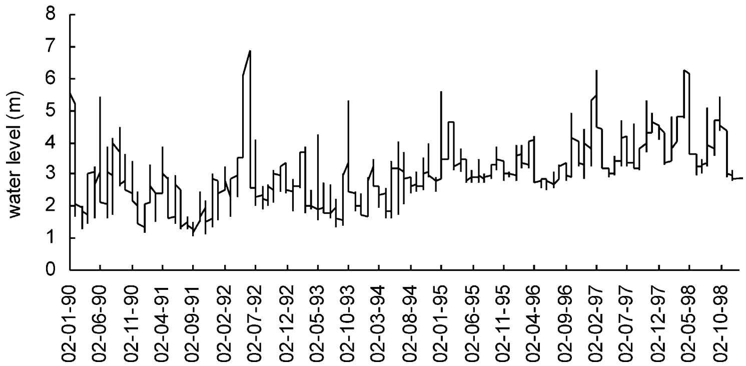

Fig. 1. Water level of the Paraná River at Posadas (Argentina). Values represent monthly averaged water levels.

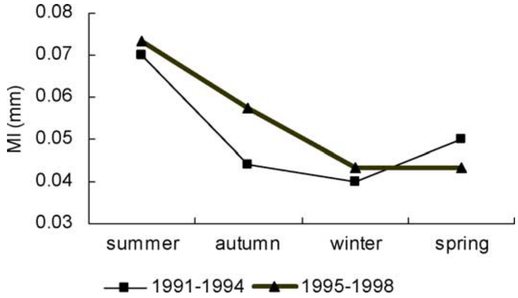

Fig. 2. Season and study period variation in the average marginal increment (MI) of *L. obtusidens*. First period: 1990–1994, second period: 1995–1998.

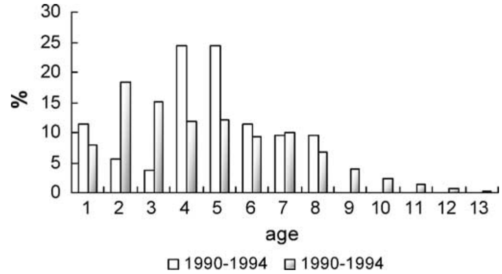

Fig. 3. Age structure of *L. obtusidens* compared by study period.

we observed significant differences among seasons of the year ($P < 0.05$). Marginal increments were larger in summer, compared to winter and spring, but no significant differences between the others seasons were found.

Age-class distribution of the sampled population showed an age range comprised between 1 and 13 years. That range extended from 1 to 8 years during the first period, but reached 13 years during the second period (Fig. 3). Prior to reservoir filling, individuals of age classes 4 and 5 were collected most frequently, whereas age classes 2 and 3 were better represented after reservoir filling (although all ages were well represented in the second period).

The average standard length discriminated for age and sex is presented in the Table 2. Females tended to reach larger sizes than males. However, statistically significant differences were only detected between sexes for age classes 3 and 7. Individuals of age class 2 were the most frequent for both sexes (14% females and 20% males).

Estimates of parameters in the length–weight regression equation discriminated for sex and study periods are presented in Table 3. No significant differences between sexes ($F = 0.74$, $P < 0.05$, d.f. = 1), or study periods ($F = 1.23$, $P < 0.05$, d.f. = 1) were found using ANCOVA. The curve for all individuals is presented in the Fig. 4.

Average condition factor (K) values in relation to standard length classes presented little variation (Fig. 5). Average K values, discriminated by period of study, sex and sampling sites are presented in Table 4. It was not possible to carry out a three-way ANOVA because the design was incomplete due to the lack of

Table 2
Age structure for males and females of *L. obtusidens*

Age	Females				Males				*t*-Test	
	n	%	SL	S.D.	*n*	%	SL	S.D.	*t*	*P*
1	17	6.2	173	31.78	31	9.2	166	28.64	0.77	0.22
2	40	14.5	191	27.25	67	19.9	192	28.74	−0.18	0.42
3	33	12.0	224	33.63	54	16.0	209	30.49	2.06	0.02*
4	31	11.3	261	37.72	42	12.5	255	34.83	0.67	0.25
5	31	11.3	301	48.89	49	14.5	289	42.25	1.07	0.14
6	27	9.8	345	49.12	32	9.5	328	41.40	1.13	0.13
7	34	12.4	378	37.37	27	8.0	363	44.59	1.35	0.05*
8	26	9.5	394	38.04	18	5.3	389	26.62	0.49	0.31
9	15	5.5	418	43.17	11	3.3	418	52.68	0.03	0.48
10	11	4.0	439	23.29	3	0.9	459	30.51	-1.06	0.18
11	6	2.2	462	33.08	2	0.6	447	48.79	0.41	0.37
12	3	1.1	488	46.52	1	0.3	449	–	–	–
13	1	0.4	476	–	–	–	–	–	–	–

n: sample size; SL: standard length (mm); S.D.: standard deviation.

Table 3
Estimators of the relationship between weight and length in *L. obtusidens*

	1990–1994			1994–1998			1990–1998		
	M	F	M + F	M	F	M + F	M	F	M + F
a	1.8×10^{-5}	1.1×10^{-5}	1.4×10^{-5}	1×10^{-5}	1.5×10^{-5}	1×10^{-5}	1.1×10^{-5}	1.4×10^{-5}	1.2×10^{-5}
b	3.02	3.11	3.08	3.14	3.08	3.12	3.12	3.09	3.11
C.I.	2.92	3.00	3.00	3.09	3.02	3.08	3.07	3.03	3.08
95%	3.13	3.23	3.15	3.18	3.14	3.15	3.16	3.14	3.15
r	0.99	0.98	0.98	0.98	0.98	0.98	0.98	0.98	0.98
n	72	68	140	502	513	1015	574	581	1155

M: males; F: females; C.I.: confidence interval of the mean; *r*: Pearson correlation coefficient; *n*: number of analyzed individuals.

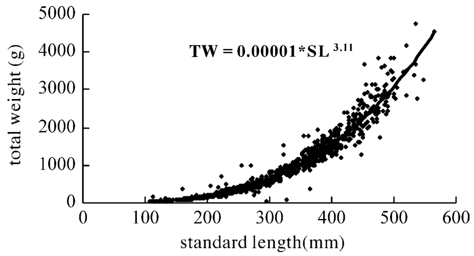

Fig. 4. Standard length–total weight relationship for all *L. obtusidens* captured between 1990–1998.

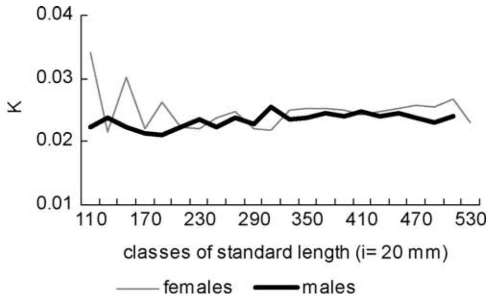

Fig. 5. Relationship of the condition factor (K) by standard length class and sex for *L. obtusidens*.

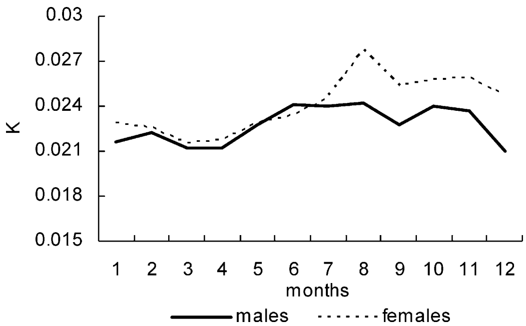

Fig. 6. Monthly variation in the average condition factor (K) between sexes for *L. obtusidens*.

data in some combinations of factors. Several separate two-way analyses were conducted instead using sex and location in one analysis and sex and period in the other. Significant differences between sex, sampling sites and period of study were observed. Highest K values occurred for females captured in Puerto Júpiter, with significant differences ($P < 0.05$) regarding the males of the same sampling point. Condition factor (K) for *L. obtusidens* reached the highest values for both sexes between August and December (Fig. 6).

Table 4
Condition factor (K) of *L. obtusidens*, for site, sex and period of study

	F (1990–1994)			*M* (1990–1994)			*F* (1995–1998)			*M* (1995–1998)		
	K	S.D.	*n*	*K*	S.D.	*n*	*K*	S.D.	*n*	*K*	S.D.	*n*
NPM	0.0232	0.006	23	0.021	0.0045	20	0.0241	0.0115	80	0.0221	0.0023	112
VLL	0.0225	0.0003	39	0.0224	0.0037	42	0.0242	0.0060	326	0.0233	0.0041	319
YBY	0.0216	0.0031	8	0.0203	0.0025	12	–	–	–	0.022	–	1
JPT	–	–	–	–	–	–	0.0268	0.0171	101	0.0233	0.0040	63

n: number individuals; S.D.: standard deviation; F: females; M: males; NPM: Nemesio Parma; VLL: Puerto Valle; YBY: Yabebiry; JPT: Puerto Júpiter.

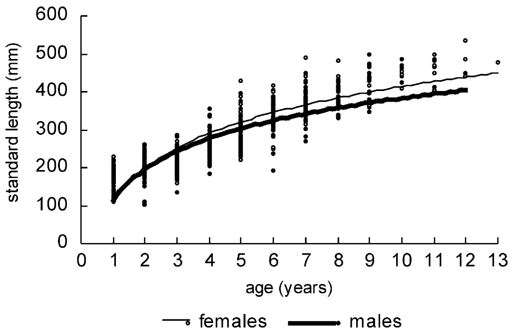

Fig. 7. Growth curve in length for males and females of *L. obtusidens*.

A significant difference in monthly mean K values was observed between sexes ($P < 0.05$), with females having higher values than males.

The fitted equations of the von Bertalanffy growth gave the following results:

$$SL = 578\{1 - e^{-0.12(t-(-1.29))}\} \quad \text{(males and females)} \qquad (10)$$

$$SL = 576\{1 - e^{-0.12(t-(-1.30))}\} \quad \text{(females only)} \qquad (11)$$

$$SL = 547\{1 - e^{-0.12(t-(-1.45))}\} \quad \text{(males only)} \qquad (12)$$

In Fig. 7, the curves of growth are presented for males and females. Although the asymptotic length is larger in females than in males, the statistical comparisons of the sizes for each age were only significantly different for age classes 3 and 7.

To obtain the total mortality, the average length at the fishery recruitment was adopted as $l_c = 165$ mm (average length to age 1), and the length at the first capture as $l = 282$ mm. With these values, the mortality rate, Z, was estimated as 0.36 year^{-1}. The value obtained for natural mortality using the equation of Pauly (1980) was: $M = 0.178$ year^{-1}.

Yield per recruit estimated by the Beverton and Holt model (using $W_\infty = 4664.19$ g and $t_c = 2$ years; $F = 0.1864$), was: $Y/R = 246.54$ g per recruit, with a maximum sustained yield (MSY) of 248 g per recruit. Therefore, it is inferred that at the present fishing effort, this species is exploited to its maximum yield in the study area.

6. Discussion

The formation of growth marks in calcified structures (Weatherley and Gill, 1987) is associated with environmental factors. In tropical fish, age determination is difficult, and in some cases impossible, when there are not well defined environmental changes between seasons, such as winter-spring transitions. During those periods, variables such as temperature, photoperiod and food availability are considered decisive in the formation of annual rings (Fagade, 1974; Sparre et al., 1990). Consequently, there are few studies of growth of tropical fishes based on hard structures such as scales or otoliths (Jepsen et al., 1999). However, prior studies have associated ring formation with factors like rainy and dry seasons and food availability (Boujard et al., 1991; Fabré and Saint-Paul, 1998), water temperature (Agostinho and Marques, 1994), spawning period and temperature (Payne, 1976).

Although it is certain that *L. obtusidens* is not a typical tropical species, since it occurs in both tropical and temperate zones of South America, its growth pattern cannot be analyzed as if it was living in a temperate area neither; therefore, it is necessary to consider both aspects in the analysis. This reflection was already outlined by Fowler (1995) (in Jepsen et al., 1999), who observed that many tropical marine species share a similar growth model with fish of the temperate zone, specifically the time of annual ring formation due to growth and reproduction.

With the available data, a clearly defined relationship could not be demonstrated between the selected environmental factors (temperature and water level) and the marginal increment of the scales. However, it can be supposed that those factors would have some influence since in the first period of our study (prior to the formation of the reservoir) average values of marginal increment were smaller during winter and autumn. Based on this result, it is inferred that temperature could be an extrinsic factor associated with growth seasonality, which could also be related with low water levels that characterize subtropical winter in the Paraná River. During the second study period, corresponding to the filling of the reservoir and dam operation, smaller average marginal increment values moved to spring. In this case, it can be supposed that growth stopped, and in consequence, the formation of the annual ring would be associated with the reproduction time that corresponds to the period between the months of November and January (Hirt and Flores, persnal commmunication). The same has been observed by Barbieri and Pereira Dos Santos (1988) in *Leporinus friderici* in the Lobo Reservoir (Brazil), and also by Godoy (1975) in the Mogi Guaçu River for *L. copelandii*.

Other factors such as photoperiod, water transparency, water velocity in preferred fish habitats, and food availability should be considered to analyze the effects they have on fish physiology. Blake and Blake (1978) (in Santos and Barbieri, 1993) emphasize that diverse environmental factors influencing the formation of growth rings in tropical fishes can vary in intensity within and between years. In addition to natural oscillations of the environmental factors that control growth, in the present case damming plays an important role as an external factor, inasmuch as reservoir formation initially increases food availability and presents high water level variations (Agostinho et al., 1999).

Due to the aforementioned facts, it is difficult to determine a model or a pattern that establishes the relationship between the time of annual ring formation in tropical or subtropical fishes, and the associated extrinsic factors. Therefore, it is necessary to keep in mind the proposal made by Boujard et al. (1991), who pointed out that the intrinsic characters (genetic and physiological) of each species play a prominent role in growth. However this aspect is not up to date in studies of natural fish populations.

The age distribution of *L. obtusidens* after the filling of the reservoir indicates a stable population structure, where the age classes of 2 and 3 years were the most frequent in both sexes. Excluding this period, abundance of age classes 1, 2 and 3 were larger in 1995 than in subsequent years. This could indicate that after the filling and operation of Yacyretá Dam (June 1994), environmental conditions were favorable to the recruitment of this species. The corresponding stage of reservoir formation is characterized by high productivity resulting from the release of dissolved nutrients from decomposing organic matter, promoting increased production of all trophic levels (Agostinho et al., 1999). One supposition that may explain the dominance of younger age classes after reservoir formation is that the reservoir, during this period, resembles a natural flood area (e.g. floodplain lagoon), which is beneficial for development and protection of early age classes. However, this supposition is open to future investigations, since the definitive reservoir bench mark has not yet been reached.

Immediately after the filling of the reservoir, denominated as the period of colonization (Agostinho et al., 1999), environmental conditions favor species with dietary plasticity (Hahn et al., 1998). *L. obtusidens* is omnivorous (Hahn et al., 1998) and therefore part of the group of “plastic” or opportunistic species. After dam closing, *Limnoperna fortunei*, an Asian mollusk that recently invaded the river, became very abundant and replete stomachs of this species have been observed in *L. obtusidens*. Although Bechara et al. (1999) noted the presence of large quantities of this mollusk in stomachs of several omnivorous fish species downstream of Yacyretá Reservoir, Montalto et al. (1999) commented that *L. obtusidens* is one of the species that exercises the greatest predation pressure on *L. fortunei* in the middle Paraná River.

The parameter b of the length–weight relationship equation is particular for each species, although generally approximates 3, in which case the growth is denominated isometric (i.e. similar growth rates for all parts of the body; Weatherley and Gill, 1987). We observed variation in the type of growth for *L. obtusidens* between the study periods. Prior reservoir formation growth was isometric, whereas growth was positive allometric following the reservoir formation. When the parameter b exceeds 3, weight increases at a faster rate than necessary to maintain constant body proportions. Therefore, it can be inferred that the new environmental conditions following the reservoir formation were highly favorable to this species. Values of the parameter b for *L. obtusidens* in Itaipú Reservoir were also greater than 3 (FUEM/NUPELIA, 1987). In contrast, Bechara et al. (1999) reported a value of $b = 3$ in the reach below the Yacyretá Reservoir.

Calculated values of Fulton’s condition factor oscillated during the year, reflecting the time and duration of the reproductive cycle (Narahara et al., 1985) or nutritional state in connection with environmental factors (Gomes and Agostinho, 1997). For *L. obtusidens*, K increased in both males and females between the months of August and December which corresponds to the reproductive period. This species reproduces between October and December in the middle Paraná River (Telichevsky de Folguera, 1981) and between November and January in the high Paraná River (Brazil) (Agostinho et al., 2003). Increased condition of individuals during this period is due to increased gonad weight and visceral fat in preparation for spawning. On the other hand, Narahara et al. (1985) reports that the decrease in the K value probably reflects a change in the use of the body reserves.

During the second period of study, highest K values were observed for individuals collected at Puerto Júpiter (reservoir region). Because the condition index can indicate changes in the quantity or quality of foods (Wooton, 1991), in addition to gonadal maturation, it is probable that the availability of nutrients that is characteristic of the period following reservoir filling could have also resulted in higher condition values (Agostinho et al., 1999).

The von Bertalanffy equation is one of the most widely used models for obtaining growth parameters, since the coefficients have physiologic meaning and therefore vary according to environmental conditions (Beverton and Holt, 1957). K values were similar between sexes, but asymptotic length was greater for females (576 mm) than males (547 mm). This fact has evolutionary implications because size of the females is related to fecundity (Agostinho et al., 2003).

Species with short life cycle and small size are generally more vulnerable to predation, resulting in a high total mortality. The opposite is true for larger-sized species. For example *Pseudoplatystoma corruscans* was observed to have a total mortality value of $Z = 0.23\ \text{year}^{-1}$ (Mateus and Petrere, 2004), and *Colossoma macropomum* had a mortality value of $Z = 0.45\ \text{year}^{-1}$ (Welcomme, 1992). The total mortality of *L. obtusidens* in Yacyretá Reservoir is intermediate ($Z = 0.36\ \text{year}^{-1}$), with half due to fishing ($F = 0.1864$) and half to natural mortality ($M = 0.178$). Even considering that boga is targeted by artisanal, subsistence and sport fisheries, its fishing mortality was low. Sample selectivity or sampling bias may be related to this, in spite of the large range of size caught. Low mortality by fishing was also reported by Braga (1999) for *Astyanax bimaculatus*, a proliferous species exploited by the commercial fishery in Barra Bonita Reservoir (Tiete River, Brazil).

The yield per recruit model (Beverton and Holt, 1957) describes yields when fishing characteristics have been the same for a long period of time, assuming that all fishes in a stock were exposed to the fishing gear since their recruitment (Sparre et al., 1990). This assumption was not completely met in this study because there were some periods without fishing. Other than that, there are some implied errors when estimating biological information from empirical models (such as that of natural mortality; Pauly, 1980) and then, using the results to enter in yield models (Pascual and Iribarne, 1993). But this practice is common when studying a tropical fishery, because there is no detailed information for most developing countries (Beverton, 1998; Pauly, 1998). Besides these limitations, the results obtained here will be very useful and fundamental to manage the boga population, because it evaluates exploitation status of this, until now, unstudied species, witch is currently being exploited at the maximum sustained yield (MSY) of 248 g per recruit.

In spite of the boga preferring lotic waters, as well as being classified as a migratory species, it successfully occupied the new reservoir environment. This species is now one of the most important for artisanal and sport fishing in the region, which was explained by relatively high yield per recruit. Based on these findings, the model applied here was useful and could also be used to model other artisanal and subsistence fisheries, but unfortunately there is no information on the size of first capture and age classes exploited for other species in Yacyretá Reservoir.

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