

AGE AND GROWTH OF THE PORTHOLE SHOVELNOSE CATFISH (*Hemisorubim platyrhynchos*) IN THE PANTANAL

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ABSTRACT

The Porthole Shovelnose Catfish, *Hemisorubim platyrhynchos*, is the sixth largest pimelodidae of the Pantanal. Its age and growth were studied using pectoral fin-spines from fish collected in the Cuiabá river basin, Pantanal. The fish, which came from commercial and experimental fisheries, were all caught with hook and line. Growth-ring formation time could not be defined through the Kruskal-Wallis test on marginal increment ($H = 4.142$; $p = 0.247$). Nevertheless, decrease in the marginal increment index occurring as waters recede suggests this as the probable time when growth rings form. Estimation of the parameters of von Bertalanffy growth curve, adjusted through nonlinear regression to observed fork lengths, with L_{∞} fixed at 64 cm, were: $k = 0.222 \text{ year}^{-1}$; $t_0 = -2.149$ years. Individual life span was estimated at 11.4 years. The results suggest that fork length is a good predictor of age for individuals of this species.

Key words: porthole shovelnose catfish, age, growth, fin-spine, *Hemisorubim platyrhynchos*, Pantanal.

RESUMO

Idade e crescimento do jurupoca (*Hemisorubim platyrhynchos*) no Pantanal

O jurupoca, *Hemisorubim platyrhynchos*, é o sexto maior pimelodídeo do Pantanal. Sua idade e crescimento foram estudados a partir dos espinhos de nadadeiras peitorais de exemplares coletados no rio Cuiabá, Pantanal mato-grossense. Os exemplares provieram da pesca comercial e experimental com linha e anzol. A análise do índice de incremento marginal não permitiu que se distinguíssem a periodicidade e a época de formação dos anéis de crescimento ($H = 4,142$; $p = 0,247$). Porém, o declínio acentuado do índice de incremento marginal registrado na vazante sugere que esse seja o período de formação dos anéis. A estimativa dos parâmetros que descrevem a curva de crescimento de von Bertalanffy, ajustada por meio de regressão não-linear aos comprimentos observados e com o valor do L_{∞} fixado em 64,0 cm (comprimento furcal), foi de $k = 0,222 \text{ ano}^{-1}$ e $t_0 = -2,149$ anos. A longevidade dos indivíduos foi estimada em 11,4 anos. Os resultados indicam que o comprimento furcal é bom preditor da idade para os indivíduos dessa espécie de peixe.

Palavras-chave: idade, crescimento, *Hemisorubim platyrhynchos*, Pantanal, jurupoca.

INTRODUCTION

The genus *Hemisorubim* is a monospecific member of the Pimelodidae family. *H. platyrhynchos*, Jurupoca, inhabits the deep slow regions of large South American river basins, among them the Amazon, Maroni, Orinoco, and Paraná (Froese & Pauly, 2002). This fish is medium sized (maximum standard length = 52.5 cm; weight = 1470 g) and a predator of benthic microfauna and fish (Froese & Pauly, 2002).

The meat of *H. platyrhynchos*, which is caught mainly during the receding and flooding periods, is highly valued by riverine inhabitants of the Cuiabá river. While no estimated landing data for this basin exists, this animal is found in the fish market of Cuiabá in March, April, September, and October. In the southern Pantanal, landing data, including professional and recreational fishing results for 1999, recorded 7.8 tons. The accumulated amount of fish landed from 1994 to 1999 was 50 tons (Catella, 2001).

Despite its wide distribution, average abundance, and importance in ecosystem functioning and regional fishery, little is known about the biology of this species. We report here on the age and growth of *H. platyrhynchos*, based on a ring count on pectoral fin-spines. The purpose of this study was to determine the age, adjust the von Bertalanffy growth curve, and estimate the longevity of individuals of the species.

MATERIALS AND METHODS

Sampling procedure and data analysis

The measurements of 207 jurupoca specimens were recorded between July 2000 and October 2001. Most of these specimens ($n = 163$) were collected monthly between July and October 2000 and in March, April, and October 2001 from the Antonio Moisés Nadaf Market, in the city of Cuiabá, Mato Grosso State. During the period of legally prohibited fishing (between November 2000 and February 2001), 44 additional specimens were collected for research purposes. All the specimens were caught with hook and line in the Cuiabá river basin, in the Pantanal. Additional information about the study area is given in Penha (2003) and Penha *et al.* (2004a).

The left pectoral fin-spine was extracted from each specimen and measurements of total length (TL – cm), fork length (FL), total weight (TW – g), and eviscerated weight (EW) were recorded. Additional details about fin-spine preparation, measurements,

ring-reading conditions, and criteria used to identify double and false marks can be found in Penha (2003) and Penha *et al.* (2004a).

To circumvent the problem created by the reabsorption of the first growth ring (Casselman, 1983), an ANOVA was performed. The analysis was conducted considering the age (number of rings) as a factor and the radius of the first ring as 0° (Rz) as a response variable. In the presence of the phenomenon of reabsorption of the first ring, individuals from older age groups should show larger first ring radii than individuals from younger age groups (Penha *et al.*, 2004b).

The Von Bertalanffy growth model (Bertalanffy, 1938) was adjusted to the age data. Growth curve parameters were used to estimate longevity of the individuals in stock by the Taylor method (Taylor, 1957). Details about data analyses can be found in Penha (2003) and Penha *et al.* (2004a).

All the statistical analyses were conducted using the SYSTAT software program (SYSTAT, 1997).

RESULTS

The results indicated that the pectoral fin-spines of *H. platyrhynchos* are suitable for counting growth rings. Of the 207 fin-spines analyzed, 195 (94%) displayed visible growth rings. In some cases, sections revealed grooves crossing the rings. In some cases, rapid growth zones were more translucent. However, even in such cases the growth rings were clearly visible. Of the total number of spines with visible rings ($n = 195$), 72% only showed simple growth rings, while 28% displayed double marks in addition to simple rings; 40% of the spines also showed false marks. Whereas double marks usually appeared between the first and second rings, false marks were common between the second and fifth rings. While 195 fin-spines contained growth rings, only in 173 (89%) of them was the number of rings repeated in at least two sections. Thus, only data from the readings of these 173 fin-spines were considered reliable and used in the subsequent analyses.

The sample used in this study included individuals with FL varying from 26 to 64 cm. The mean size (FL_{mean}) of the sampled individuals was 43.1 cm (standard error = 0.49) and the mode was 41 cm (Fig. 1a). The fin-spine sections revealed up to 7 rings, representing 7 age groups, with the age class with 3 rings predominating (Fig. 1b). The mean age

(t_{mean}) was 2.9 rings (standard error = 0.087) and the mode (t_{mode}) was 3 rings.

There was no evidence of resorption of the first growth ring of older individuals due to presence of holes in spine cores ($F = 1.537$; d.f. = 5 and 166; $p = 0.181$). Because of the limited number of observations, which would lead to a significantly imbalanced analysis and reduce the power of the F test, the ANOVA test was conducted excluding age 7. This increased the reliability of the readings taken from fin-spine rings.

Analyses of the relation between the number of rings, fin-spine size, and FL showed that the spine rings were indicators of the fish's growth. A visual analysis of the box plot between the fin radius and ring number indicated that the larger spines contained more rings (Fig. 2). Moreover, a positive relation was found between lengths of fin and fin-spine. Linear models satisfactorily described the relation between these variables (Fig. 3). The FL variation explained 94% of the variation in spine length and 74% in spine diameter, while 59% of the variation of the radius at 0° (Rz) and 60.5% of the radius at 45° were also explained by the FL variation. In short, a positive relation was found between the fin-spine ring number and the size of the individuals.

The analysis of growth data along the edge of the spines (marginal increment – MI) by a statistical test did not determine ring-formation periodicity. Owing to the low number of observations, the test was conducted on seasonal MI of individuals having 2 or 3 rings. Because the distribution of residuals did not meet the assumption of normality ($g_1 = 0.912$; $g_2 = 0.666$; $p < 0.05$) and the problem could not be solved by transforming the data, the analysis was carried out using the nonparametric Kruskal-Wallis test. This test indicated no significant differences

between the hydrological seasons considered ($H = 4.142$; $p = 0.247$).

Although no differences between sessions were detected through the Kruskal-Wallis test, Fig. 4 indicates a marked drop in MI values between the flooding and receding water periods. It is therefore probable that the growth rings form during the receding period, approximately one year after cohort birth during the rising water/flooding period.

The total weight *versus* fork length relationship was described by the expression $TW = 0.001 FL^{3.457}$ ($n = 107$). The FL variation explained 97.4% of TW variation. The b value, estimated at 3.165, is significantly higher than 3 (the confidence interval for the estimated $b = 3.054$ to 3.276), indicating that the weight of *H. platyrhynchos* increases at a higher rate than that required to maintain constant body proportion.

Analyses of the residual variances and coefficients of determination indicated that the relationship between the Rz and FL of the spines could be described consistently by several models (r^2 of models: power = 0.598; exponential = 0.564; and linear = 0.589). Hence, the simplest model, i.e., the linear one, was chosen to perform the back-calculation ($FL = 13.589 + 19.846 Rz$; $n = 204$; $p < 0.001$). Fraser-Lee's equation, which was used to perform backcalculations, produced consistent results. As expected, the backcalculated lengths were shorter than those observed, the differences decreasing with age (Table 1). The mean length reached in the cohort's first year of life, shown in column FL_1 of Table 1, decreased with the age of the cohort from which it was estimated, the only exception being the most recent cohort. This fact suggests the presence of the Rosa-Lee phenomenon (Lee, 1912, *apud* Ricker, 1969).

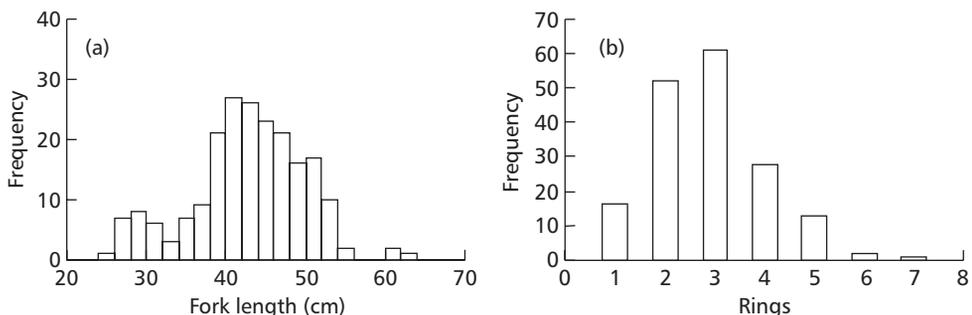


Fig. 1 — Frequency distribution of fork lengths (a) and age (number of rings) (b) of the *H. platyrhynchos* from Cuiabá river basin, Pantanal, MT.

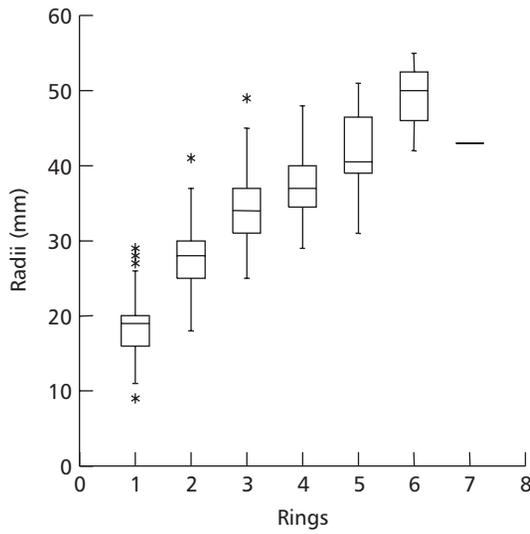


Fig. 2 — Box-plot of the correlation between the radius of the spine at 0° and the number of growth rings in the cuts.

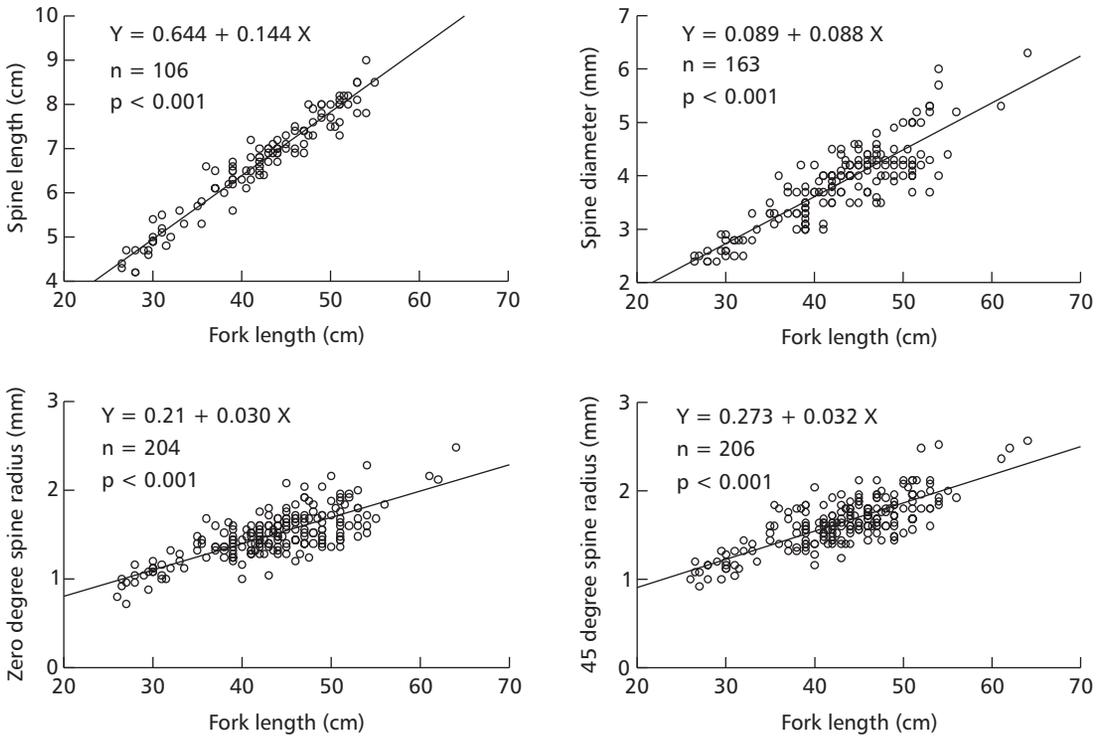


Fig. 3 — Regression between the characteristic associated with the size of the spine and the fork length of *H. platyrhynchus* from the Cuiabá river basin, Pantanal.

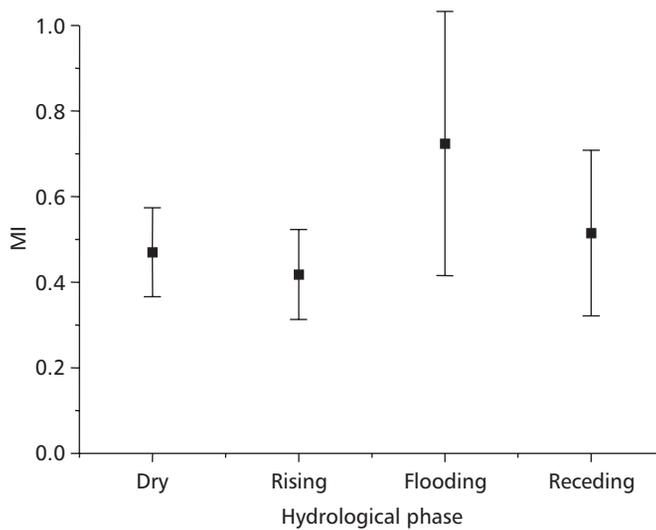


Fig. 4 — Seasonal variation of the marginal increment for *H. platyrhynchos* from Cuiabá river basin, Pantanal, MT. The values are means plus confidence interval (95%). Number of observations: dry (39), rising water (26), flooding (12), and receding water (14).

The Von Bertalanffy model was adjusted both to lengths observed by age and to the backcalculated one. The adjustment based on observed data produced an estimate of L_{∞} greater (51.3 cm) and of k smaller (0.551 year^{-1}) than the one based on backcalculated lengths ($L_{\infty} = 47.6 \text{ cm}$ and $k = 0.634 \text{ year}^{-1}$). Backcalculation use improved the quality of the adjustments (r^2 backcalculated lengths = 0.60; r^2 observed lengths = 0.52). Because the confidence intervals overlapped, they were considered statistically the same. However, the two adjustment procedures produced L_{∞} values far below that of the L_{max} observed (64 cm) and were considered unsatisfactory. Therefore, an alternative procedure was utilized, which consisted of fixing the L_{∞} as the longest length observed in the sample and then generating k and t_0 values for the set of lengths observed at a given age. Though not statistically satisfactory, this solution produced a more realistic k estimate than the previous ones ($L_{\infty} = 64 \text{ cm}$; $k = 0.222 \text{ year}^{-1}$) (Fig. 5). The last procedure produced a life expectancy estimate (longevity) of 11.4 years. Hence, the individuals of the species would take 11.4 years to reach 60.8 cm (95% of their L_{∞}).

DISCUSSION

Many hard structures have been used to determine the age of pimelodidae. Among these,

otoliths, vertebrae, and fin-spines are the structures that have produced the best results (Fenerich *et al.*, 1975; Barthem, 1990; Muñoz-Sosa, 1996; Rêgo *et al.*, 1998; Pérez Lozano, 1999; Loubens & Panfili, 2000; Alonso, 2002; Mateus & Petrere, 2004). Although few studies compare the age determined by various structures of the same sample, preliminary data indicate that age underestimations tend to result when based on pectoral fin-spines in comparison with those based on dorsal spines (Layher, 1981) and vertebrae (Clay, 1982). Even so, indirect evidence suggests that the pectoral fin-spines of *H. platyrhynchos* are appropriate structures for age determination. This evidence includes: (1) the presence of clearly visible annual growth rings, (2) discernible double and false marks of growth rings, (3) absence of evidence of resorption of the first growth rings through the appearance of a hole in the center of the spine, and (4) the presence of a positive correlation between the number of growth rings in the spine, its size, and the length of the fish. However, it should be noted that it was fairly difficult to identify the rings on the edge of the spine in individuals with more than five rings. This had been expected since, from the sixth growth mark on, identifying the edge rings tends to become increasingly difficult (Casselmann, 1983).

Analysis of the relative marginal increment by the Kruskal-Wallis test did not indicate the period

of growth ring formation of *H. platyrhynchos*. However, the sharp decline in the MI value recorded during the receding period suggests that rings probably form during this period. This pattern differs from the one normally found for Pimelodidae inhabiting river-floodplain systems. Most studies undertaken so far have founded evidence of ring formation during the dry season (Fenerich *et al.*, 1975; Reid, 1983; Reina *et al.*, 1995; Muñoz-Sosa, 1996; Resende *et al.*, 1996; Loubens & Panfili, 2000; Mateus & Petrere, 2004; Penha *et al.*, 2004). The only exceptions have been the studies of Pérez Lozano (1999) and Alonso (2002), the former studying *Calophysus macropterus* and the latter, *Brachyplatystoma flavicans* in the Amazon basin. These authors detected the formation of two annual growth rings: one in the receding and the other during the rising water period. The growth rate reduction and consequent growth ring formation have generally been associated with temperature, environmental retraction effects during the dry season, reproduction (Welcome, 1992), and migration (Brett, 1979). Thus, annual growth ring formation in the species under study here appears to be associated with migration that takes place during the receding period, when

the fish leave the flooded areas and return to the river channel (Ferraz de Lima, 1986-1987).

Backcalculated lengths indicated the presence of the Rosa-Lee phenomenon in the analyzed sample. When this phenomenon is present, the mean size calculated for younger fish is smaller the older the fish from which it was estimated (Ricker, 1969; 1979). Several hypotheses have been advanced to explain this phenomenon, the main ones being: biased sampling, technical problems (incorrect use of the spine-size versus body-size correlation), size-dependent mortality (natural or by fishing) (Ricker, 1969, 1979), and spatial stratification of the different ontogenetic phases (Stanley, 1980). In the Pantanal, the Rosa-Lee phenomenon detected in this study probably results from fishing regulations, which determine, among other things, minimum catch sizes. For *H. platyrhynchos*, this is 40 cm of total length, which only fast-growing individuals can reach after two years of age (Fig. 5). Slow-growing individuals may reach this size only when they are older (3 or more rings). Fish mortality is therefore size-dependent, with fast-growing individuals caught before the others, which can explain the presence of the Rosa-Lee phenomenon in this study.

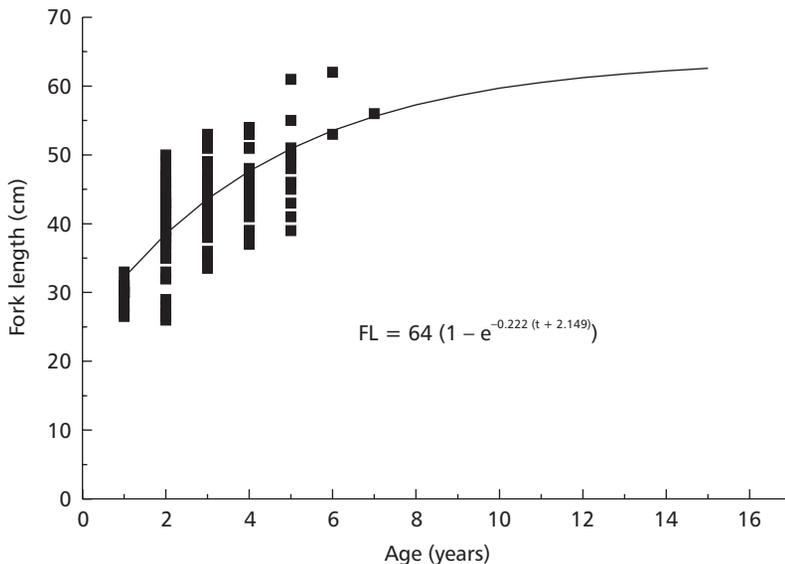


Fig. 5 — Growth curve in length for *H. platyrhynchos* from the basin of the Cuiabá river basin, Pantanal, MT. The von Bertalanffy's growth curve was adjusted to observed length in age with L_{∞} fixed at 64 cm.

TABLE 1
Mean fork length values (FL) at back-calculated ages using the Fraser-Lee equation. Highlighted values are the mean lengths of the cohorts. Age is in years.

n	FL _{obs.}	Age	FL ₁	FL ₂	FL ₃	FL ₄	FL ₅	FL ₆	FL ₇
16	29.7	1	<u>23.2</u>						
53	39.3	2	25.6	<u>35.2</u>					
60	44.4	3	24.0	34.2	<u>40.9</u>				
28	46.4	4	22.9	30.7	37.9	<u>43.4</u>			
13	48.,0	5	22.7	31.0	37.2	41.6	<u>44.7</u>		
2	57.5	6	22.5	32.2	41.3	45.7	50.1	<u>55.5</u>	
1	56.0	7	21.0	31.9	38.5	45.1	48.3	50.5	<u>51.6</u>
mean			24.1	33.6	39.6	43.0	45.6	53.9	51.6
increment			24.1	9.5	6.0	3.4	2.6	8.2	-2.2
n			173	157	104	44	16	3	1

The adjustment of the Von Bertalanffy model based on backcalculated lengths was more precise than that based on lengths observed by age. Backcalculation lessened the data noise, reducing the lengths of individuals captured along the growth period to theoretical lengths at the time of the formation of each ring. However, these estimates produced L_{∞} values far lower than the L_{\max} observed in the sample. Although the correlation between these variables depends on length variation by ages, a difference of about 20% is excessive, suggesting an inappropriate adjustment. This result cannot be attributed to the impossibility of age determination of larger individuals, since the use of a nonlinear adjustment procedure is relatively insensitive to the absence of older cohorts (Vaughan & Kanciruk, 1982). Therefore, the most sensible option was to estimate k and t_0 values, and fixing the L_{∞} parameter as the longest length recorded in the sample.

The estimated growth parameters indicate that the species presents a relatively slow growth rate. However, first-year growth is rapid. This strategy may enable predator fish, as they grow, to continue preying on juvenile cohorts of their prey (Araújo & Haimovici, 2000), which in river-floodplain systems undergo selection pressure for fast growth (Lowe-McConnell, 1999). This strategy is common to several Pimelodidae species of South American river-floodplain systems and may be one of the causes of the great abundance of these fish in rivers of the continent.

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REFERENCES

- ALONSO, J. C., 2002, *Padrão espaço-temporal da estrutura populacional e estado atual de exploração pesqueira da dourada Brachyplatystoma flavicans, Castelnau, 1855 (Siluriformes: Pimelodidae), no sistema estuário-Amazonas-Solimões*. Tese de Doutorado, Instituto Nacional de Pesquisas da Amazônia e Universidade Federal do Amazonas, 217p.
- ARAÚJO, J. N. & HAIMOVICI, M., 2000, Determinação de idades e crescimento do linguado branco *Paralichthys patagonicus* (Jordan, 1889) no sul do Brasil. *Rev. Brasil. Ocean.*, 48: 61-70.
- BARTHEM, R. B., 1990, *Ecologia e pesca da piramutaba (Brachyplatystoma vaillantii)*. Tese de Doutorado, Universidade Estadual de Campinas, Campinas.
- BERTALANFFY, L.V., 1938, A quantitative theory of organic growth (Inquiries on growth laws II). *Human Biology*, 10: 181-213.
- BRETT, J. R., 1979, Environmental factors and growth, pp. 599-677. In: W. S. Hoar, D. J. Randall & J. R. Brett (eds.), *Fish physiology*. Academic Press, London.
- CASSELMAN, J. M., 1983, Age and growth assessment of fish from their calcified structures – techniques and tools. *NOAA Technical Report NMFS*, 8: 1-17.
- CATELLA, A. C., 2001, *A pesca no Pantanal de Mato Grosso do Sul, Brasil: descrição, nível de exploração e manejo (1994-1999)*. Tese de Doutorado, Instituto Nacional de Pesquisas da Amazônia, 351p.

- CLAY, D., 1982, A comparison of different methods of age determination in the sharp-toothed catfish, *Clarias gariepinus*. *Journal of the Limnological Society of South Africa*, 8: 61-70.
- FENERICH, N. A., NARAHARA, M. Y. & GODINHO, H. M., 1975, Curva de crescimento e primeira maturação sexual do mandi, *Pimelodus maculatus* Lac. 1803 (Pisces, Siluroidei). *Bol. Inst. Pesca*, 4: 1-28.
- FERRAZ DE LIMA, J. A., 1986/87, A pesca no Pantanal de Mato Grosso (rio Cuiabá: importância dos peixes migradores). *Acta Amazônica*, 16/17: 87-94.
- FROESE, R. & PAULY, D. (eds.), 2002, *Fishbase*. World Wide Web electronic publication: www.fishbase.org, 15 de março de 2002.
- LAYHER, W. G., 1981, Comparison of annulus counts of pectoral and dorsal spine in flathead catfish. *Progressive Fish-Culturist*, 32: 218-219.
- LOUBENS, G. & PANFILI, J., 2000, Biologie de *Pseudoplatystoma fasciatum* et *P. tigrinum* (Teleostei: Pimelodidae) dans le bassin du Mamoré (Amazonie Bolivienne). *Ichthyol. Explor. Freshwaters*, 11: 13-34.
- LOWE-McCONNELL, R. H., 1999, *Estudos ecológicos de comunidades de peixes tropicais*. EDUSP (coleção base), São Paulo, 534p.
- MATEUS, L. A. F. & PETRERE JR., M., 2004, Age, growth and yield per recruit of pintado *Pseudoplatystoma coruscans* in Cuiabá river basin, Pantanal of Mato Grosso, Brazil. *Braz. J. Biol.*, 64(2): 257-264.
- MUÑOZ-SOSA, D. L., 1996, *Age structure and exploitation of Giant Catfish populations* (Brachyplatystoma spp.) in the Lower Caqueta River, Colômbia. Master thesis, College of Environmental Science and Forestry, State University of New York, 100p.
- PENHA, J. M. F., 2003, *Estrutura e estado de exploração dos estoques do jurupoca*, Hemisorubim platyrhynchos, e do *Jurupensém*, Sorubim cf. lima, na bacia do rio Cuiabá, Pantanal Mato-grossense. Tese de Doutorado, Universidade Federal de São Carlos, 117p.
- PENHA, J. M. F., MATEUS, L. A. F. & BARBIERI, G., 2004a, Age and growth of the Duckbill Catfish (*Sorubim cf. lima*) in the Pantanal. *Braz. J. Biol.*, 64(1): 125-134.
- PENHA, J. M. F., MATEUS, L. A. F. & PETRERE JR., M., 2004b, A procedure to improve confidence in identification of the first annulus in fin-spines of fishes. *Fisheries Management and Ecology*, 11: 135-137.
- PÉREZ LOZÁNO, A. P., 1999, *Idade e crescimento da piracatinga* Calophrys macropterus, Lichtenstein, 1819 (Pisces: pimelodidae), na Amazônia Central. Dissertação de Mestrado, Instituto Nacional de Pesquisas da Amazônia, 89p.
- RÊGO, H. V., FABRÉ, N. N. & LOZÁNO, A. P., 1998, Estruturas calcificadas de dourada (*Brachyplatystoma flavicans*) para determinação da idade. *Bol. Mus. Para. Emílio Goeldi, sér. Zool.*, 14(2): 143-173.
- REID, S., 1983, La biología de los bagres rayados *Pseudoplatystoma fasciatum* y *P. tigrinum* en la cuenca del río Apure, Venezuela. *Rev. UNELLEZ Cien. Tecnol.*, 1: 13-41.
- REINA, M. P., RAMÍREZ, H. & VALDERRAMA, B. M., 1995, Edad y crecimiento de *Paulicea luetkeni* (Steindachner, 1876) (Pisces: Pimelodidae) basado en la lectura de estructuras duras (espinas de aleta pectoral) en el Alto Río Meta (Colombia). *Boletín Científico INPA*, 3: 115-135.
- RESENDE, E. K., CATELLA, A. C., NASCIMENTO, F. L., PALMEIRA, S. S., PEREIRA, R. A. C., LIMA, M. S. & ALMEIDA V. L. L., 1996, *Biologia do curimatá* (Prochilodus lineatus), pintado (*Pseudoplatystoma coruscans*) e cachara (*Pseudoplatystoma fasciatum*) na bacia hidrográfica do rio Miranda, Pantanal do Mato Grosso do Sul, Brasil. EMBRAPA-CPAP (Boletim de Pesquisa, 02), Corumbá, 75p.
- RICKER, W. E., 1969, Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. *J. Fish. Res. Board Can.*, 26: 479-451.
- RICKER, W. E., 1979, Growth rates and models. In: W. S. Hoar, D. J. Randall & J. R. Brett (eds.), *Fish physiology Vol. VIII: bioenergetics and growth*. Academic Press, Flórida, pp. 677-743.
- SYSTAT, 1997, Version 7.0. SPSS Science, Chicago, Illinois, USA.
- TAYLOR, C. C., 1957, Cod growth and temperature. *Journal du Conseil*, 23: 366-370.
- VAUGHAN, D. S. & KANCIRUK, P., 1982, An empirical comparison of estimation procedures for the von Bertalanffy growth equation. *J. Cons. Int. Explor. Mer.*, 40: 211-219.
- WELCOMME, R. L., 1992, *Pesca fluvial*. FAO (Documento Técnico de Pesca 262), Roma, 303p.