

Age and growth of the largemouth perch *Percichthys colhuapiensis* in the Negro river, Argentine Patagonia

Andrea Lopez Cazorla^{*}, Nora Sidorkewicz

Departamento de Biología, Bioquímica y Farmacia, Universidad Nacional del Sur, San Juan 670, 8000 Bahía Blanca, Argentina

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Abstract

Largemouth perch (*Percichthys colhuapiensis*) represents one of the most economically important fish species in the Argentine Patagonia. However, little research has been done on the age and growth and population dynamics of this fish, though both studies are essential to properly deal with fisheries forecasts and management. As a contribution to elaborating management programmes for *P. colhuapiensis*, we evaluated the age and growth of this species in the Negro river via scale and whole otolith reading methods. The sample consisted of 579 specimens ranging in total length (TL) from 90 to 475 mm, captured seasonally from December 1994 to December 1995. The formation of scale annuli (end of winter) and the hyaline zone on otoliths (winter) of adult fish coincided with the beginning of the spawning season (end of winter-beginning of spring). The maximum estimated age was 11 years, which indicates that this is a relatively long-lived species. Otoliths were useful for ageing specimens 1–5 years-old, but above this age whole otoliths yielded lower age estimates than scales. Isometric growth of weight with length was found for total population, juveniles, and separate sexes ($p > 0.25$ in all cases). No significant differences between the length–weight relationships of sexes were observed ($p > 0.10$). Length at first maturity was significantly higher for males ($TL_{50} = 271$ mm TL; $r = 0.88$) than for females ($TL_{50} = 243$ mm TL; $r = 0.96$) ($p < 0.01$). Largemouth perch exhibited a consistent pattern of increase in length with age, with a period of fast growth during the first 5 years, and a slow-growing phase during the rest of his life. The growth parameters based on scale data were L_{∞} : 462.1 mm, $k = 0.23$ and $t_0 = -0.94$ for total population, L_{∞} : 402.3 mm, $k = 0.33$ and $t_0 = -0.67$ for males, and L_{∞} : 548.4 mm, $k = 0.15$ and $t_0 = -1.59$ for females, whereas those based on otolith reading were L_{∞} : 537.4 mm, $k = 0.17$ and $t_0 = -1.0$ for total population, L_{∞} : 497.6 mm, $k = 0.21$ and $t_0 = -0.79$ for males, and L_{∞} : 582.0 mm, $k = 0.14$ and $t_0 = -1.53$ for females. Scales are concluded to be the best structure to age *P. colhuapiensis* because they rendered L_{∞} values closer to the maximum TL observed, high precision, easiness of collection, low processing time, and the possibility of performing non-destructive monitoring studies.

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1. Introduction

Percichthyidae is a family of freshwater fish restricted to South América and Australia (Arratia, 1982, 2003; Trnski et al., 2005). The type genus of the family is *Percichthys*, which is endemic to southern South América and covers an important part of the native fish fauna in the austral ichthyogeographic region of this continent (Arratia, 1982; Arratia et al., 1983; López-Arbarello, 2004). Of the totality of species of *Percichthys* described to date, recent studies conducted by López-Arbarello (2004) have demonstrated that only 5 are considered to be valid, namely, *Percichthys colhuapiensis*, *Percichthys trucha*

and *Percichthys laevis* in Argentina, and *Percichthys chilensis* and *Percichthys melanops* in Chile, respectively. More recently, Ruzzante et al. (2006) based on mtDNA and nuclear sequence analysis recognized only two species of *Percichthys*, *P. melanops* and *P. trucha*. However, since the cited authors did not perform morphometric analyses, we think that *P. colhuapiensis* could be probably underrepresented or absent in their samples. Furthermore, it has been demonstrated that nucleotide diversity indices (π) fail to identify many reproductively isolated lineages, especially when they have been subjected to divergent selection or other mechanisms that accelerate reproductive isolation (Hickerson et al., 2006).

Percichthys colhuapiensis, commonly known as largemouth perch, is naturally widespread in lakes and rivers in the austral central-western area of Argentina. On the other hand, both official and private enterprises have artificially introduced this

^{*} Corresponding author. Tel.: +54 291 4595100x2435; fax: +54 291 4595130.
E-mail address: acazorla@criba.edu.ar (A. Lopez Cazorla).

species to the central-western region of Argentina, thus altering its original dispersion area (Ringuelet, 1975). Nevertheless, *P. colhuapiensis* is at present strictly confined to the Argentine Patagonia (Bello and Ubeda, 1998; López-Arbarello, 2004). In the Negro river (39°–41° S; 63°–68° W), largemouth perch constitutes one of the most important fisheries resources, amounting a capture per unit effort (CPUE) of 4.7 kg in 1995 (unpublished data). Although it is quite appreciated for human consumption as well as for recreational uses, the only records about the commercial exploitation of this species were two fish farming sites located in the Negro river basin, both of which no longer exist.

The Negro river is one of the longest rivers (635 km) in the Argentine Patagonia. It is originated by the confluence of Neuquén and Limay rivers (Fig. 1), which collects the waters

of a 600 km-portion of the cordilleran border. These three water bodies constitute together the most important hydrographic system in the Argentine territory (AIC, 2006). They cover a basin area of approximately 116,000 km², which represents a territory larger than 4% of the total continental area of Argentina (AIC, 2006). The whole basin is localized in a very heterogeneous region. It is originated in high areas of the Andean Patagonia, the southern part of the Andean mountain range, and it extends either through the arid Extra Andean Patagonia or plateaus until reaching a coastal outlet. Both the climatic and geographical characteristics are therefore vastly contrasting.

Little attention has been paid to the biological aspects of *P. colhuapiensis*. The first studies are merely systematic (Mac Donagh and Thormählen, 1945; Mac Donagh, 1950, 1955).

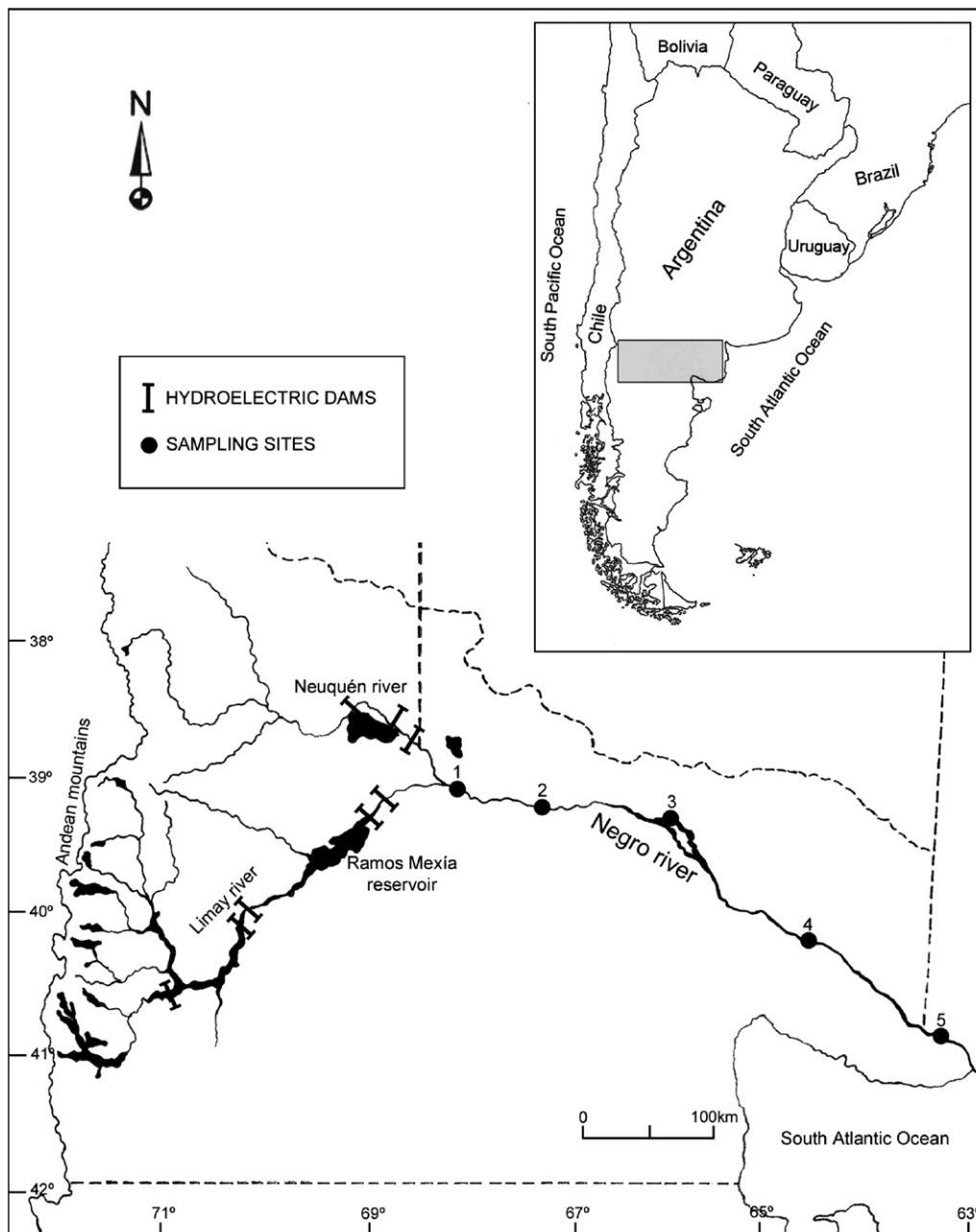


Fig. 1. Map of the Negro river basin showing sampling sites (1–5) of *Percichthys colhuapiensis*.

Later research revealed data about the diet and feeding habits of this species in different freshwater bodies (Ferriz, 1989, 2000; Lopez Cazorla and Tejera, 2003–2004). The only data about the age and growth of the largemouth perch were published by Guerrero (1984, 1989), who performed studies in different Patagonian freshwater ecosystems. Fish captured by this author ranged in size from 130 to 610 mm total length, the largest specimens being reported in lentic systems of the area. From the analysis of scales and whole otoliths, he found one marking period per year, in winter, for both type of structures, determining 8 age classes. However, he did not make comparisons between both ageing methods nor give any confirmation of the accuracy of his estimations. Some aspects of the reproductive biology of the species were afforded also in the studies of Guerrero (1989); he observed that only one spawning period, in early spring, occurs in the Patagonian populations of largemouth perch.

Percichthys colhuapiensis is found in much localized populations. Another characteristic of this species is that, in coincidence with all percichthyids, it is affected by the anthropogenic pressure caused by sport fishing and habitat modification resulting from dam construction upstream Negro river (Bello and Ubeda, 1998). In view of such alterations to the environment in the study area, it becomes a priority to make efforts towards a better understanding of the biology of *P. colhuapiensis* and its relationship with management considerations.

Studies on the age and growth of fish are crucially important contributions to research regarding population dynamics. Both topics are required when dealing with fisheries forecasts and management (Chugunova, 1963; Dwyer et al., 2003). Studies on the age structure of the population of *P. colhuapiensis* will greatly contribute to a better understanding of the biology of this species, to which particular attention – according to Bello and Ubeda (1998) – should be paid for its protection in Argentina. As a result, the aim of the present study was threefold: (i) to determine the age pattern of the population of largemouth perch *P. colhuapiensis* in the Negro river; (ii) to estimate its growth parameters via scale and whole otolith reading methods; and (iii) to compare these two ageing methods. Results will greatly contribute to elaborating management programmes for one of the most economically important fish species of the region under study.

2. Materials and methods

2.1. Identification of the material

Using the classificatory key and according to the diagnoses proposed by López-Arbarello (2004), we identified all the specimens included in this study as *P. colhuapiensis*.

2.2. Area description

The average water volume of the Negro river reaches $930 \text{ m}^3 \text{ s}^{-1}$ (AIC, 2006). The natural hydrographic regimes of its tributaries, the Neuquén and Limay rivers, are characterised by a double wave flow throughout the year, the first of which occurs during winter coincidentally with the main rainfalls of the

region whereas the second, which is more moderate, occurs usually towards the end of spring and it is produced as a result of thawing (AIC, 2006). No dams are constructed along the course of the Negro river. However, large hydroelectric dams built on the Neuquén and Limay rivers (Fig. 1) contribute to regulating its course as well as to supplying energy to a large area of the country.

The climatic and geographical characteristics are vastly contrasting along the entire basin. Large variations in thermal condition are registered between winter and summer, with an annual average temperature of 10–15 °C. Winds are predominantly dry and strong and they come from the west, south-east, and north-east. Rains are also variable. The mountain range area is very humid with annual rainfall and snowfall values of approximately 3000 mm (AIC, 2006). In the central eastern region, where the Negro river itself is located, the climate is arid and dry and rains rarely exceed the annual 200 mm (AIC, 2006).

2.3. Fish sampling and data collection

Largemouth perch were obtained from five sampling stations distributed along the Negro river (Fig. 1). No samples were captured from the last part of the river, which covers a length of approximately 80 km, on account of the fact that this sector is highly influenced by marine tidal flood, thus allowing the entrance of different fish species not included in the present research. Surveys were conducted on a seasonal basis, covering an annual cycle: (1) spring (9–17/XII/94); (2) summer (6–19/III/95); (3) fall (25/V-9/VI/95); (4) winter (23/VIII-7/IX/95); and (5) spring (20/XI-4/XIII/95).

Fish sampling was carried out by using 12.5-m long gill nets, with meshes of 30, 42, 50, 60, 70, 76, and 105 mm (stretched). Nets were anchored at each of the sampling stations at sunset and they were removed at sunrise on the following day, remaining 12 h in water.

Total length (TL, mm) and total weight (W, g) were measured for each fish. The maturity stage for males and females was determined macroscopically using a 5-stage maturity key. These stages included: juvenile (J), immature (I), developing (II), spawning (III), and resting (IV).

2.4. Scale and otolith reading

Age was determined from fish scales and whole otoliths (sagitta). Scales of 567 individuals were extracted from the area above the lateral line of the left flank, between the dorsal fin and the area behind the operculum. Sagittal otoliths were extracted from 566 fish. Both structures were subsequently preserved dry. Prior to the reading, they were washed in warm water and the surrounding tissue was removed.

Of the structures processed for annual age estimation, 3 scales and 6 otoliths were considered unreadable and were rejected. All readings for each structure were undertaken twice by independent readers without prior information on length, sex, or time of capture.

Scale reading was carried out at the anterior field using binocular lenses and a microfiche reader (22.5×). The zone where

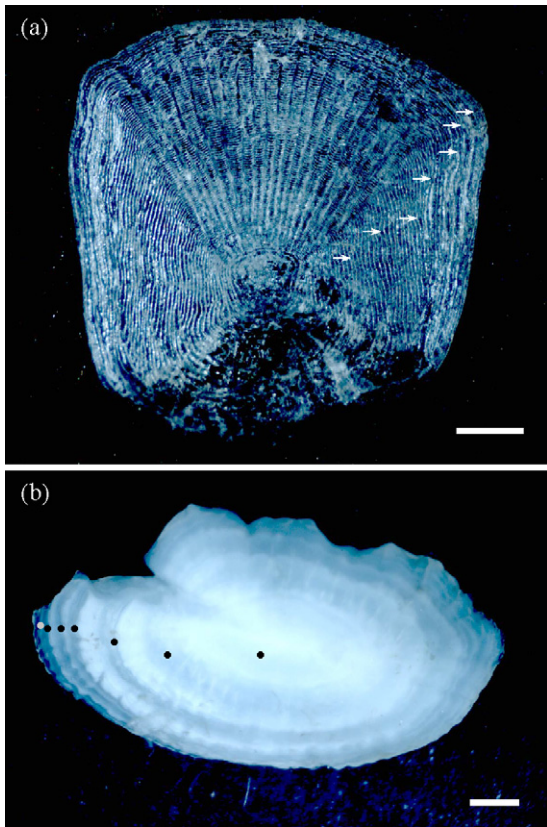


Fig. 2. Comparative appearance of a scale (a) and an otolith (b) removed from a 441-mm-TL, 1087-g male largemouth perch. Scale annuli are indicated by white arrows and hyaline bands by black and grey dots. Solid bars are 1 mm long.

growth was interrupted was labelled as a presumed annual mark (Fig. 2a). Otoliths were placed in water and examined under binocular microscope (10 \times) with reflected light against a dark background. The number of hyaline (translucent) bands was recorded over the rostrum area (Fig. 2b).

2.5. Data analysis

2.5.1. Fish

The condition factor ($K = W \text{ (g)} \times 100 / TL^3 \text{ (cm)}$) by survey and by sex, the length at first sexual maturity, and length–weight relationships were calculated. The method proposed by Hernández and Cordo (1986) was used for the determination of length at first maturity (TL_{50}). Length–weight relationships were estimated using the potential model ($W = a \times L^b$). Parameters a and b were calculated by least-squares on log-transformed data. The comparison of the estimated gradients for males and females was carried out *via* covariance analysis (ANCOVA, $p \leq 0.05$). Deviation of the allometric coefficient b from the theoretical value of isometric growth ($b = 3$) was tested by t -test (Underwood, 1997).

2.6. Ageing and growth

For scales, marking periodicity was determined by analysing these structures on a seasonal basis all throughout the year. Such

scales were divided into two groups, one including individuals with growth edge and another including individuals without it, and results were expressed as percentages. The mark itself was validated by measuring the distance from the centre to each of the first four annual marks, over 230 and 75 scales with three and four marks, respectively. The frequency of the distances from the centre to the first mark was also analysed. The fish length–scale radius (TL–R) relationship was estimated by means of regression analysis based on 319 pairs of data, which covered a size range from 90 to 432 mm TL.

For otoliths, the annual periodicity and seasonality of band formation was assessed by examining the seasonal evolution of the proportion of opaque and hyaline edges. Each specimen was assigned to a year class taking into account the number of hyaline bands counted, the date of capture, the birth date and the edge type (opaque, hyaline).

1 January was considered as the birth date to assign individual ages to age groups both for scales and otoliths. Systematic differences in estimated age (bias) within and between structures were assessed by age bias plot and the reproducibility of the age interpretation (precision) was determined by the index of average percent error (IAPE, Beamish and Fournier, 1981) and the coefficient of variation (CV) (Campana et al., 1995; Campana, 2001).

The increase in length was assumed to follow the von Bertalanffy model $L_i = L_{\infty}(1 - e^{-k(t_i - t_0)})$, where L_i is the mean length at age i ; L_{∞} the mean theoretical maximum total length; k the intrinsic growth rate, and t_0 the theoretical age at zero length. The equation parameters were estimated following the Maximum Likelihood method (Kimura, 1980; Cerrato, 1990). The length-at-age data for unknown-sex-fish were included in the curves corresponding to males (ages 0 and 1; $N = 25$ for scale data, $N = 24$ for otolith data) and females (age 0; $N = 4$ for both scale and otolith data).

3. Results

A total of 579 individuals of *P. colhuapiensis* ranging from 90 to 475 mm TL, were sampled. Of the fish examined, 160 were males, 332 females, 74 juveniles, and 13 were of undetermined sex. Juveniles were captured mostly in summer (69%), being poorly represented in the rest of the campaigns. The capture of adults of both sexes exhibited no seasonal variability.

Although average sizes and weights were higher in males, the highest absolute values were registered in females (Table 1). The condition factor was highest during winter sampling for the total population (1.45 ± 0.18) and separate sexes (males: 1.47 ± 0.18 ; females: 1.45 ± 0.18). The rest of the year mean values (\pm S.D.) were lower: $1.32 (\pm 0.16)$ to $1.39 (\pm 0.23)$ for the total population; $1.35 (\pm 0.14)$ to $1.45 (\pm 0.13)$ for males; and $1.31 (\pm 0.16)$ to $1.39 (\pm 0.25)$ for females.

3.1. Ageing

From the examination of scales, clear alternating areas were observed, one of active growth on which circuli were deposited, followed by a mark indicative of growth interruption (annu-

Table 1
Average values (\pm S.D.) of size and weight corresponding to total population, juveniles, and adults of *Percichthys colhuapiensis* from the Negro river

	N	TL (mm)		W (g)	
		Mean \pm S.D.	Min.–max.	Mean \pm S.D.	Min.–Max.
Total	579	265.9 \pm 83.2	90–475	334.5 \pm 291.3	10.1–1579.0
Juveniles	74	153.0 \pm 36.2	90–251	54.4 \pm 37.5	10.1–214.0
Males	160	301.2 \pm 67.3	161–462	429.3 \pm 272.6	66.0–1360.0
Females	332	274.2 \pm 77.3	131–475	353.3 \pm 297.9	40.1–1579.0
Unsexed	13	265.5 \pm 61.4	173–375	281.2 \pm 177.6	70.0–674.0

The number of samples is also indicated (N).

lus) (Fig. 2a). One year of life was assigned to each of these interruption marks.

During the samplings conducted in summer, autumn and winter, the percentage of scales with marks of growth interruptions close to the scale border was very low (8–27%). In contrast, such percentage increase to 83% in the sampling conducted in spring,

thus indicating that marking seems to have occurred at the end of winter (Fig. 3a). The percentual distribution of the frequencies of the distance from the focus to the first annulus showed a unimodal behaviour, with a media of 1.15 ± 0.18 mm (Fig. 3b). The mean distances from the focus of the scales to each of the first four annual marks showed no overlapping, a phenomenon

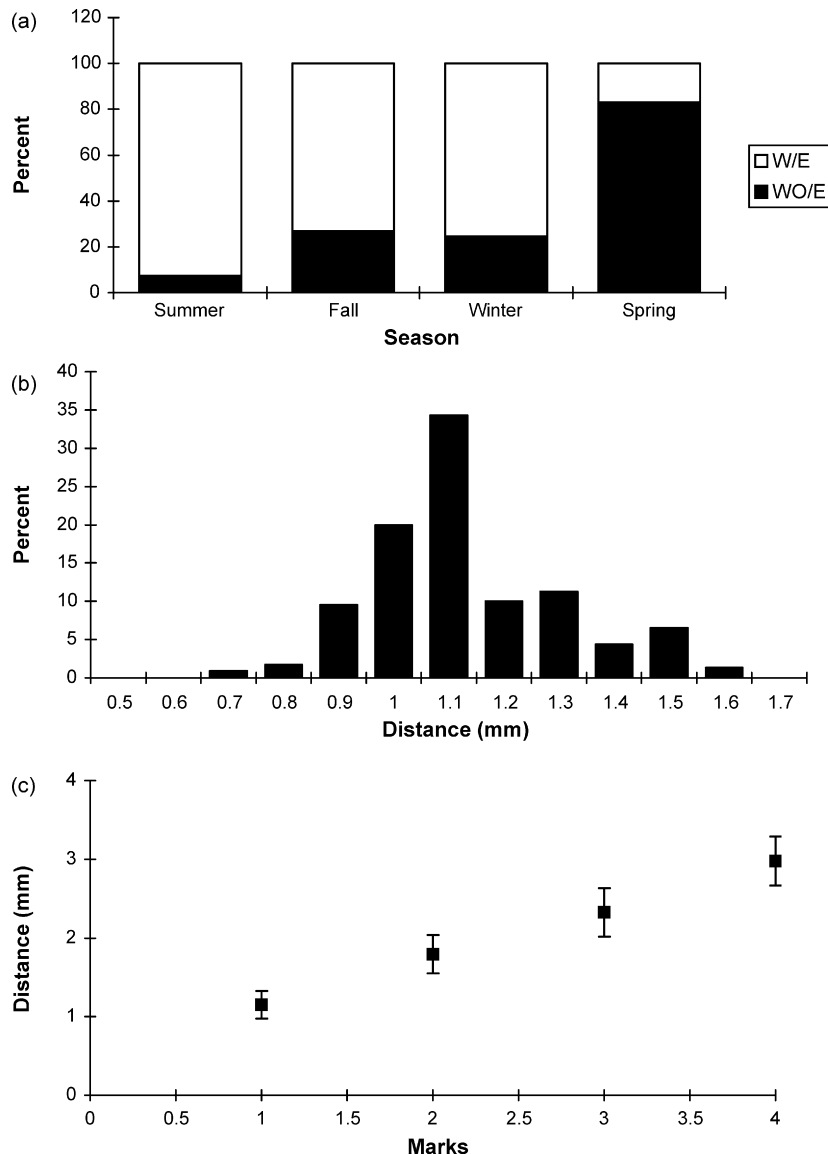


Fig. 3. (a) Seasonal distribution of *Percichthys colhuapiensis* scale edge. W/E: with edge and WO/E: without edge. (b) Frequency distribution of the distance from the focus to the first annulus in scales. (c) Mean length \pm S.D. from the focus of the scales to each of the first four annuli.

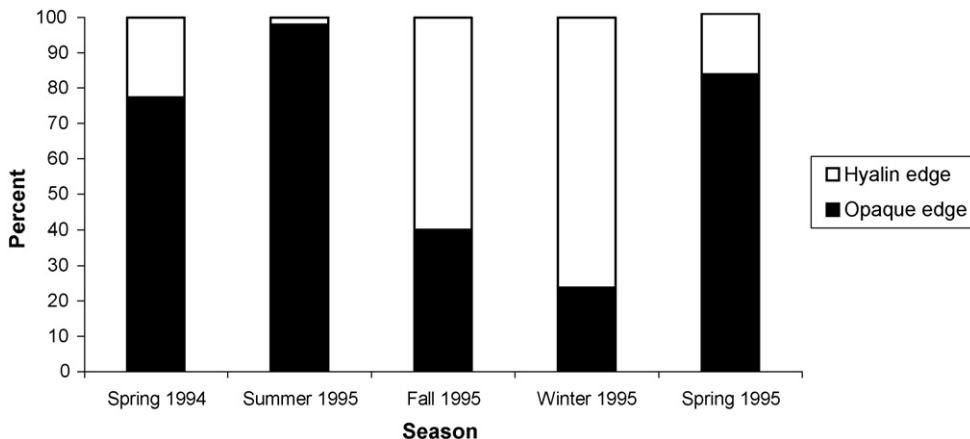


Fig. 4. Seasonal percentage of opaque and translucent edges in whole otoliths of *Percichthys colhuapiensis*.

which facilitated the determination of an annual periodicity in the marking (Fig. 3c).

The relationship between fish length and scale radius (R) fitted to a linear model ($TL = 34.33 + 93.34R; r^2 = 0.95$). Taking into account the mean distance from the focus to the first mark of the scale ($R = 1.15$ mm), the mean size of fish at the time of formation of the first annulus was $TL = 141.7$ mm.

The estimated age from scales ranged from 0 to 11 years. Juveniles registered ages ranging from 0 to 3, males from 2 to 11, and females from 1 to 11. Ages 2 and 3 were the most numerous both for the total population (31% in both cases) and for the adults of each sex (males: 26 and 32% for ages 2 and 3, respectively; females: 28 and 35%, respectively). On the other hand, the highest percentage of juveniles corresponded to age 2 (58%).

Otoliths of largemouth perch showed the typical pattern of teleosts, with an alternating sequence of narrow opaque and broad hyaline bands that became progressively narrower and of similar width as the number of bands increased (Fig. 2b). An annual cycle in the seasonal evolution of the proportion of opaque and hyaline edges was observed (Fig. 4). Otoliths with opaque margins increased in spring 1994 to peak at 98% in the summer and fell down to a low value of 24% in the winter. The percentage of otoliths with opaque edge rose back up to a similar value in the spring of the second year. These data indicated only one hyaline band is formed yearly during winter, and that the opaque band is deposited during late spring–summer.

The range of otolith-based ages was 0–10. Males aged from 2 to 10 while females aged from 1 to 10. Age 3 was the most important for the total population (32%), males (42%) and females (33%). The same as with scales, 4 juvenile ages were determined (0 to 3), age 2 being the mostly represented (59%).

Age bias plots for scales and otoliths showed no systematic bias between the two age readers for each method (Fig. 5a and b). The low values of IAPE and CV obtained for both type of structures (scales: IAPE = 1.1%, CV = 1.53%; otoliths: IAPE: 1.0%, CV = 1.47%) indicated the good level of precision in our readings. However, the age bias plot of ages estimated from scales compared to ages estimated from otoliths revealed a large discrepancy in agreement between the two methods (Fig. 5c).

Otoliths tended to overage younger fish and seriously underage older fish. In the oldest fish, otoliths underestimated the age indicated in scales by more than 50%. The values of IAPE and CV between structures were 6.2 and 8.72%, respectively.

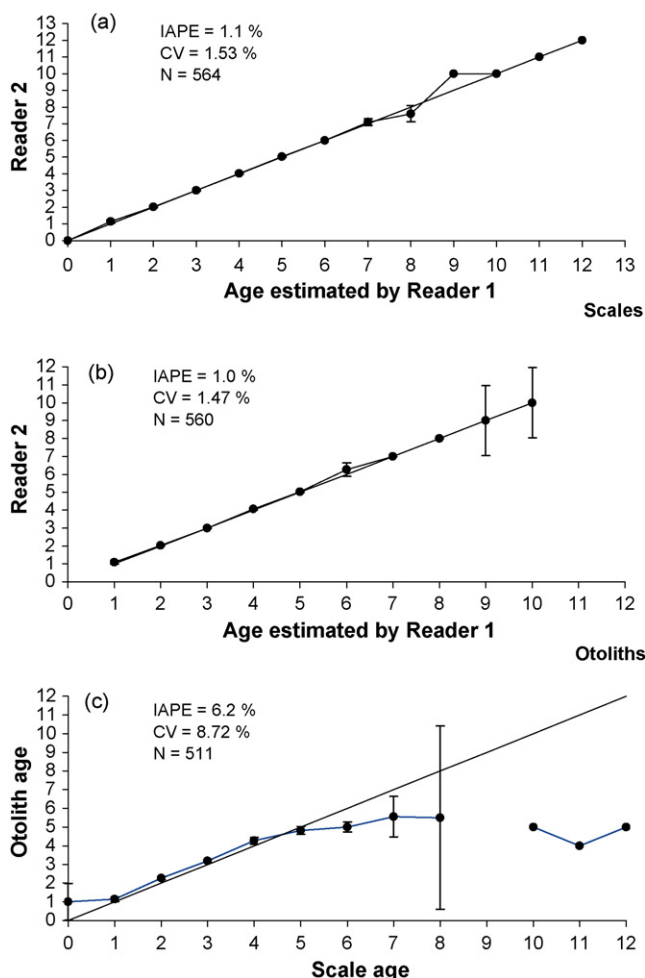


Fig. 5. Age bias plots of (a) scale age and (b) otolith age to evaluate agreement between readers; (c) scale age vs. whole otolith age to evaluate agreement between ageing structures. Solid line indicates 1:1 equivalence. Each error bar represents 95% confidence intervals. The index of average percent error (IAPE), the coefficient of variation (CV) and the sample size (N) are also indicated.

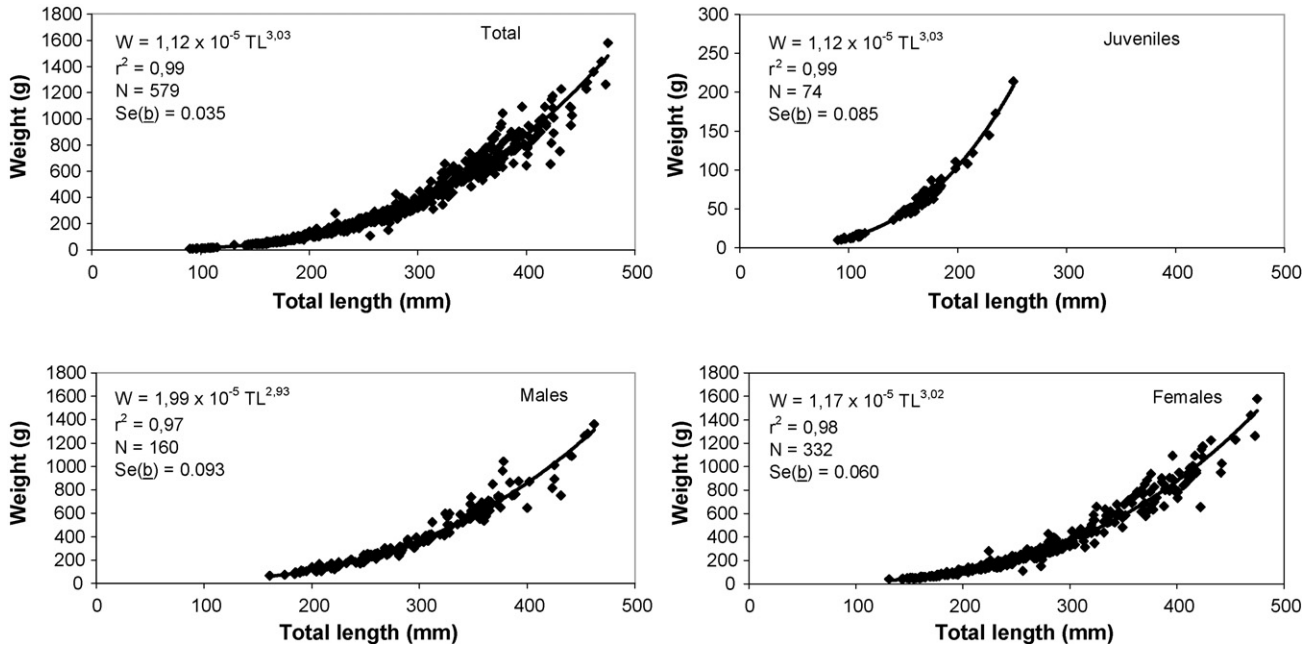


Fig. 6. Length–weight relationships in *Percichthys colhuapiensis* from the Negro river corresponding to total population, juveniles, males, and females. The determination coefficient (r^2), the sample size (N) and the standard error of the slope ($Se(b)$) are also indicated.

3.2. Length–weight relationships and growth

The length–weight relationships were found significant ($p < 0.01$) for the total population, juveniles, males, and females (Fig. 6). Isometric growth was observed in the four different groups (t -test, $p > 0.25$ in all cases). No statistical significant differences were detected between the slopes or intercepts of the regression equations of both sexes ($p > 0.10$).

A consistent pattern of increase in length with age was generally observed for both reading methods (Tables 2 and 3). The TL at age increased rapidly during the first 5 years, with similar growth rates in both sexes along this period. Beyond this age, the growth rate begun to decline, and this diminution was more pronounced in males. The growth in TL was well described by the von Bertalanffy growth equation (Table 4). Both reading methods showed that the estimated L_∞ of females was higher than that of males. Furthermore, the L_∞ based on data from scales was closer to the maximum TL observed than that based on otolith reading.

3.3. Maturity stages and length at first maturity (TL_{50})

Gonad inspection revealed a high percentage of stage II in the two sampling periods during spring. In summer, an important number of juveniles and immature individuals was observed, the adult samples exhibited gonads with post-spawning traits. In autumn, the highest percentages corresponded to immaturity and maturation stages. The campaign conducted towards the end of winter revealed the highest diversity in the maturity stages (Fig. 7). These results, summed to the high percentage of juveniles captured during summer samplings, indicate that the spawning season seems to occur between the end of winter and the beginning of spring.

Length at first maturity was significantly higher for males ($TL_{50} = 271$ mm TL; $r = 0.88$) than for females ($TL_{50} = 243$ mm TL; $r = 0.96$) ($p < 0.01$), corresponding also to different ages (males: 3 years old; females: 2 years old). The total sexual maturity was reached at 370 mm TL (age 5 years) and 330 mm TL (age 4 years) by males and females, respectively (Fig. 8a and b).

Table 2
Mean length-at-age (\pm S.D.) and sample size (N) corresponding to total population and juveniles of *Percichthys colhuapiensis* from the Negro river according to scale and otolith readings

Age	Scales		Otoliths	
	Mean TL \pm S.D. (mm)	N	Mean TL \pm S.D. (mm)	N
Total				
0	109.8 \pm 1.0	4	109.8 \pm 1.0	4
1	143.6 \pm 48.4	34	134.7 \pm 48.7	28
2	202.1 \pm 44.3	174	188.1 \pm 33.9	143
3	271.9 \pm 45.7	173	258.0 \pm 34.6	182
4	328.5 \pm 54.4	92	316.5 \pm 47.3	101
5	367.1 \pm 55.0	40	372.4 \pm 33.9	68
6	371.6 \pm 46.0	27	389.7 \pm 49.2	23
7	373.0 \pm 27.8	10	408.5 \pm 39.3	4
8	362.6 \pm 75.4	5	413.7 \pm 22.7	3
9	475.0	1	433.0	2
10	425.0	2	448.0	2
11	401.5	2		
Juveniles				
0	109.8 \pm 1.0	4	109.8 \pm 1.0	4
1	114.3 \pm 24.6	21	111.7 \pm 21.9	20
2	166.6 \pm 14.2	41	166.4 \pm 12.8	43
3	215.4 \pm 27.3	5	220.3 \pm 23.3	6

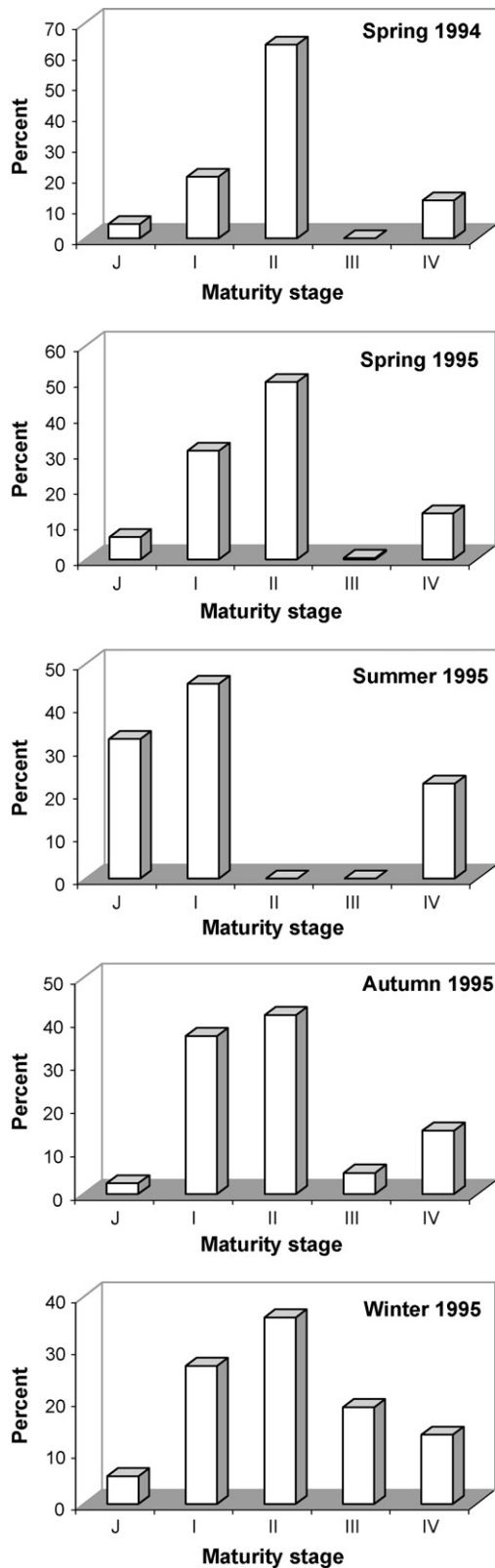


Fig. 7. Seasonal percentage of different gonad maturity stages of *Percichthys colhuapiensis* from the Negro river. J: juvenile; I: immature; II: developing; III: spawning; and IV: resting.

Table 3

Mean length-at-age (\pm S.D.) and sample size (N) corresponding to males and females of *Percichthys colhuapiensis* according to scale and otolith readings

Age	Scales		Otoliths	
	Mean TL \pm S.D. (mm)	N	Mean TL \pm S.D. (mm)	N
Males				
2	235.0 \pm 41.9	41	206.9 \pm 25.5	19
3	284.0 \pm 48.5	51	265.1 \pm 34.9	66
4	336.3 \pm 45.9	28	332.8 \pm 37.8	30
5	367.1 \pm 47.2	18	363.1 \pm 28.9	29
6	359.6 \pm 46.6	12	390.1 \pm 42.2	7
7	379.8 \pm 36.3	5	413.7 \pm 46.5	3
8	368.7 \pm 59.7	3	431.0	1
9			425.0	1
10	377.0	1	423.0	1
11	348.0	1		
Females				
1	191.3 \pm 40.5	12	192.4 \pm 50.3	8
2	203.2 \pm 42.7	92	195.3 \pm 37.7	81
3	269.1 \pm 42.9	117	255.8 \pm 33.6	110
4	325.1 \pm 57.8	64	309.6 \pm 49.4	71
5	367.1 \pm 61.7	22	379.4 \pm 36.0	39
6	381.3 \pm 44.7	15	389.5 \pm 53.3	16
7	366.2 \pm 17.5	5	393.0	1
8	353.5	2	405.0	2
9	475.0	1	441.0	1
10	473.0	1	473.0	1
11	455.0	1		

4. Discussion

A major problem in the ageing procedures is to select the most suitable and accurate structure to determine the age of fishes. Although scales have been widely used for ageing as they can be easily collected, processed and read, their use has been criticised mainly because the ages of older fish are frequently underestimated (Beamish and McFarlane, 1987; Carlander, 1987). Otolith age determinations have been considered to be more accurate than scale age determinations because the former have a higher priority in the utilization of calcium (Carlander, 1987) and unlike scales, they continue to grow as the fish ages (Beamish and McFarlane, 1987; Casselman, 1990). In the present study, the estimated value of IAPE between structures (6.2%) showed a reasonable agreement between the two methods, indicating that both scales and otoliths seem to be reliable for age determination.

Table 4

Growth parameters for total population and separate sexes of *Percichthys colhuapiensis* from the Negro river

	L_{∞}	k	t_0	N
Scales				
Total	462.1	0.23	-0.94	564
Males	402.3	0.33	-0.67	184
Females	548.4	0.15	-1.59	336
Otoliths				
Total	537.4	0.17	-1.00	560
Males	497.6	0.21	-0.79	181
Females	582.0	0.14	-1.53	334

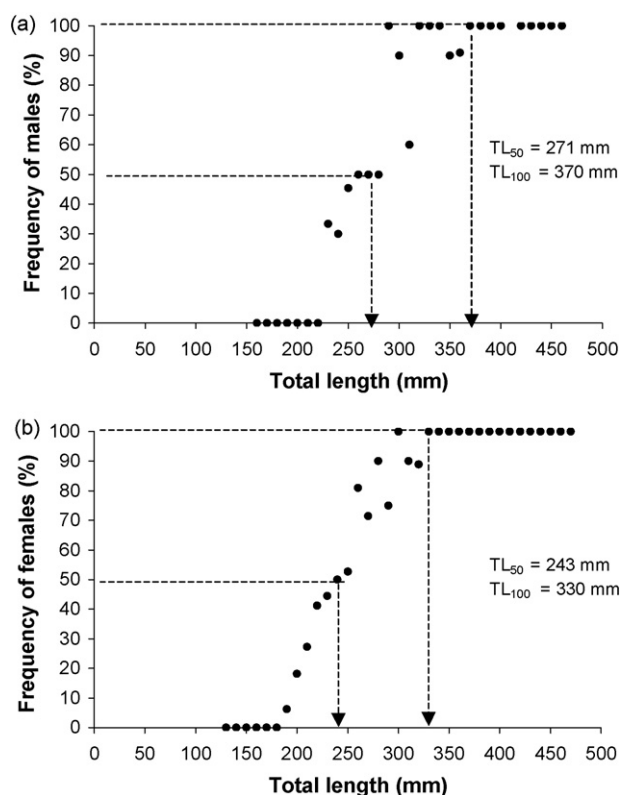


Fig. 8. Mean total lengths of males (a) and females (b) *Percichthys colhuapiensis* when 50% (TL₅₀) and 100% (TL₁₀₀) of individuals reached sexual maturity.

in *P. colhuapiensis*. Whole otoliths, however, were appropriate for ageing specimens 1–5 years-old, but above this age whole otoliths yielded lower age estimates than scales. Consequently, if whole otoliths are used to estimate ages, *P. colhuapiensis* longevity is underestimated.

Several environmental factors are known to be related to the annulus formation on hard parts of fish, the most common ones being, among others, temperature, salinity, light, and food supply (Simkiss, 1974; Morales-Nin, 2000). In otoliths, zone formation has also been linked to changes in calcium metabolism during periods of increased reproductive activity in many fish species (Simkiss, 1974; Beckman and Wilson, 1995). Kalish (1989, 1991) reported that there is a strong relationship between Sr and other ions of the endolymph and otolith composition. Since the chemistry of the endolymph is likely to be determined by a fish's reproductive status, blood chemistry, seasonal temperature cycle, and other factors, the relationship between Sr/Ca ratios and environmental conditions in a fish's aquatic environment is difficult to interpret in spite of the apparently simple univariate correlations that have been commonly reported. Therefore, zone formation suggests a complex control by a combination of endogenous and exogenous factors, which vary at different ages and between sexes (Morales-Nin et al., 1998). In largemouth perch, the hyaline band formation on otoliths was observed to occur once a year, during winter (August–September), when water and air temperatures are lowest. A similar situation was evident for scales, where the formation of only one annulus per year, at the end of winter, was verified. Our results slightly

disagree with Guerrero (1984, 1989) in the time of band formation on otoliths and scales, which could be attributed to varying conditions provided by the different environments studied. He hypothesised that the deposition of calcium on otoliths occurred once a year during spring–summer and that the hyaline (translucent) zone of the annual ring was formed during autumn–winter (Guerrero, 1984). For scales, he found that this species also only formed one annulus per year, between June and July (beginning of winter) (Guerrero, 1989). Spawning seems to be also related to the band formation on both otoliths and scales of adult largemouth perch since the reproductive period was observed to occur between the end of winter and the beginning of spring. The same spawning season was found by Guerrero (1989) for the population of *P. colhuapiensis* from Ramos Mexía reservoir. A single spawning period in spring has also been reported in other percichthyids (Bath and O'Connor, 1982; Appleford et al., 1998; Rowland, 1998b) at the same time of band formation in some cases, both for scales (Bath and O'Connor, 1982) and otoliths (Rowland, 1998a,b).

The maximum estimated age of 11 years found for *P. colhuapiensis* in this study extends the estimated life span of the species from a maximum of 8 years in previous reports (Guerrero, 1984, 1989), and indicates that it can be considered a relatively long-lived species. Unfortunately, data about the maximum age attained by largemouth perch in captivity, or results of monitoring studies in fish farming sites are not available. Longevity, notwithstanding, has been well documented in other percichthyids, as indicated by the maximum ages reported in several studies conducted on other genera and species of the family, namely, 9 years for *Morone americana* (Bath and O'Connor, 1982), 10 years for *P. trucha* (Dománico and Guerrero, 1990), 21 years for *Maccullochella peelii* (Gooley, 1992), 22 years for *Macquaria novemaculeata* (Harris, 1985), and 26 years for *Macquaria ambigua* (Mallen-Cooper and Stuart, 2003).

Females of the largemouth perch reach 50% maturity at a smaller size as well as at a younger age than males (243 and 271 mm TL, respectively), thus indicating that they become part of the spawning stock before males (ages 2 and 3, respectively). Problems would then arise in ageing specimens of this species longer than 300 mm TL. In effect, the banding pattern in otoliths and scales may change after sexual maturity because of differences in the relative rate of deposition of minerals like calcium and protein, which are probably due to the distinct way males and females channel surplus energy into growth and reproduction. Such differences in the microstructure of scales and otoliths for males and females will determine that differences in appearance will exist with the scales and otoliths of both sexes before and after sexual maturity. Interestingly, the departure in agreement in age determination between scales and whole otoliths also occurred after total sexual maturity, i.e. after age 5 years.

Percichthys colhuapiensis exhibited a consistent pattern of generalized increase in length with age, with a period of fast growth during the first 5 years, and a slow-growing phase during the rest of his life. The high variation of TL at age, however, makes TL a poor predictor of age for this species. The length ranges registered in this study are similar to those reported by Guerrero (1984) for the species in the same riverine system.

However, he observed larger fish (maximum TL: 610 mm) in the largemouth perch population from Ramos Mexía reservoir (Fig. 1) on the Limay river (Guerrero, 1989). On account of the fact that the sampling methodology that he used was similar to ours, the differences in fish size observed in the latter case could perhaps be explained by environmental traits, since the Ramos Mexía reservoir constitute a lentic system that could provide more stable conditions to allow the fish attaining greater sizes than the riverine system.

Males' largemouth perch are larger and heavier than females during the first 5 years of life, i.e. during the period of fast-growing, although this relationship is then reverted. This may account for the lower values of L_{∞} and the higher growth rate observed in the von Bertalanffy equations of males. Similar results were reported by Guerrero (1984), who observed the same tendency after age 7 years. The sexual dimorphism characterised by larger females is common among fish, which, from the adaptive point of view, results in reproductive advantages since larger females yield larger eggs, higher quantities of eggs, and/or a higher survivorship of larvae (Roff, 1983; Beckman et al., 1989; Pough et al., 1996).

Largemouth perch in the Negro river exhibited isometric growth of weight with length in all the groups, i.e. juveniles, males, females and when all individuals were pooled together. In spite of the differences in weight between males and females for a given length, the absence of significant differences in length–weight relationships of both sexes could be attributed to the low number of adult fish larger than 370 mm collected in the samples. Unfortunately, no references from other studies are available regarding this species. However, the absence of differences between sexes has also been reported for other genera of the family Percichthyidae, as was the case of *Macquaria ambigua* (Anderson et al., 1992) and *Maccullochella peelii peelii* (Rowland, 1998a).

The length–weight relationship, as indicated by Wootton (1990), can be obtained from length and weigh measurements of the same fishes throughout their lives or from a sample of fish taken at a particular time. This relationship is a practical index of the condition of fish, and may vary over the year according several exogenous and endogenous factors such as food availability, feeding rate, health, sex, gonad development, spawning period and preservation techniques (Bagenal and Tesch, 1978). Subsequently, if these length–weight relationships were obtained throughout a complete annual cycle as in the present study, then the simulated parameters would be more appropriate. Mayrat (1970) has suggested that the parameter b is characteristic of each species and generally does not change significantly throughout the year. The value of b obtained in the present study for the total population (3.03) was equal to that reported by Guerrero (1984) in the Limay and Neuquén rivers, and very similar to the mean value obtained by the same author for the period 1982–1985 in the Ramos Mexía reservoir ($b = 3.022$) (Guerrero, 1989).

The present study constitutes a comprehensive first look at corroborating and validating age determination in *P. colhuapiensis* by using whole otoliths and scales. From the results, it can be concluded that whole otoliths are appropriate for ageing large-

mouth perch 1 to 5 years old, but beyond this age, scales should be used to age this species. Scales marks were consistent along the entire range of ages of largemouth perch, which led to high confidence and precision. As mentioned above, scales have also other advantages over otoliths not only regarding the easiness of collection and the low processing time required, but also for the possibility of performing non-destructive monitoring studies that allow population pursuit under natural conditions.

It is clear that *P. colhuapiensis* is a relatively long-lived species which approaches its maximum size gradually, and that it starts to reproduce at age of 3 years. The implications of slow growth are numerous. The most prominent is that population turnover and its response to recovery plans could be lower than expected. Thus, fishery regulations of this species should aim not only to prevent growth overfishing, but also to protect the oldest population components and of those occupying shallow water, where the most suitable conditions for growth in terms of water temperature and food availability are found (Wootton, 1990).

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