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ORIGINAL PAPER

Age structure, growth and survival rates of the commercial fish *Prochilodus nigricans* (bocachico) in North-eastern Ecuador

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Abstract The bocachico, *Prochilodus nigricans*, is a commercially important fish distributed throughout the central and western Amazon. Age and growth of this species in eastern Ecuador were determined by otolith and scale increment analyses. For otolith analyses, we used thin sections of the astericus, and clear visualization of annuli required the use transmitted polarized light. Accuracy and precision of age estimation were compared to select the best ageing structure. Precision indices showed that otoliths are more reliable than scales to determine the age of bocachicos. Based on marginal increments analysis, we found that annulus formation in both structures occurs once a year between August and December. Seasonal changes in growth were associated with hydrological cycle of the river. The Ecuadorian *Prochilodus* at the juvenile–adult stage grew faster (i.e., $K = 0.29$ for ages 2 and older) than conspecific populations from Bolivia and Brazil ($K = 0.5$). In addition, annual mortality rate ($A = 0.\ 56$) was lower than reported for *Prochilodus* populations elsewhere in the Amazon. We conclude that this population is presently not overexploited, but conservation and management schemes for this population will need to consider that it is an international, trans-boundary migrant.

Keywords Ecuadorian Amazon · Otoliths · Prochilodontidae · Scale analysis · von Bertalanffy growth function

Introduction

The bocachico, *Prochilodus nigricans*, is a characin fish that occupies a wide variety of habitats in Amazonian drainages of Bolivia, Brazil, Colombia, Ecuador and Perú, including rivers, shallow streams, lagoons and flooded forests (Goulding 1981; Loubens and Panfili 1995; Castro and Vari 2004). *Prochilodus* species are potamodromous and form large schools that perform complex migrations among habitats in response to abiotic and biotic factors such as seasonal river fluctuations, reproduction, food availability and predation risk (Lowe-McConnell 1987; Duque et al. 1998; Mochek and Pavlov 1998; Winemiller and Jepsen 1998). Prochilodontids are considered among the most important commercial and subsistence fishes of South American inland waters (Welcomme 1979; Goulding 1981; Mochek et al.

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1991). Loubens and Panfili (1992) reported age estimation, validation and related growth parameters for *P. nigricans* based on scale data for a Bolivian population. Others have estimated age based on sclerite numbers (Werder and Soares 1985; Montreuil and Tello 1988). Factors influencing growth of young *P. nigricans* and other floodplain fishes were reviewed by Bayley (1988).

In the Napo River basin, studies have concentrated on the biodiversity and distribution of fishes at the community level, which are fundamental information for natural resource management and conservation (e.g., Saul 1975; Ibarra and Stewart 1989; Galacatos et al. 1996, 2004). However, there have been no studies on the growth and survivorship of *P. nigricans* or any other migratory food fish in the Ecuadorian Amazon. Such knowledge about fishery resources in eastern Ecuador is critical for establishing sustainable fisheries (Barthem et al. 1995). Neotropical aquatic ecosystems, in general, are poorly understood compared to the terrestrial ecosystems, so there is an urgent need to study and understand their functional dynamics. This study contributes critical information on *P. nigricans* that can be applied to develop management plans and to guide future research.

Our purpose was to test the null hypothesis that the growth and survivorship patterns of the Ecuadorian bocachico population were similar to those of other populations within the Amazon. The following specific objectives of this research permit an evaluation of that null hypothesis. First, validation of the techniques to determine ages of bocachicos are based on sampling over an annual period to correlate annulus formation with environmental fluctuations and associated ecological processes. Second, population age structure, growth rates and survival are estimated and compared with previous estimates for bocachico populations in Bolivia and elsewhere in the Amazon.

Materials and methods

Study area

The study area is located in the western part of the upper Amazon Basin, and more specifically, in the Sucumbios and Orellana Provinces of Ecuador (see Ibarra and Stewart 1989). That area is covered primarily with humid tropical forest (Saul 1975; Canaday 1997). Detailed descriptions including information on ecological, geological and geographical characteristics as they relate to fishes of the region can be found in Saul (1975), Ibarra and Stewart (1989), and Galacatos et al. (1996). The Aguarico River, with a length of about 500 km, flows east into the Napo River, a tributary of the Amazon River. In the piedmont and river reaches just upstream from there (i.e., 250–400 m altitude), the Aguarico River has moderate lateral incisions and meandering begins. As is typical for this kind of white water river, the water is turbid because it carries silt and bottom-load sand that forms sandbanks (Sioli 1984). In the lower reaches, the riverbanks are constantly being changed by lateral erosion associated with meanders. That leads to formation of temporary channels, locally called 'chictas', and water bodies like oxbow lakes and pools (pozas) that connect seasonally to the main channel. In the lowlands, tributaries that flow into the main river are classified as black water rivers due to their dark, tea-like color, origin and chemical composition (e.g., low pH due to humic acids and tannins, Sioli 1984).

The wet and dry seasons are well defined in this tropical region (Saul 1975; Galacatos et al. 2004). The primary increase in rainfall occurs between April and July. There is, however, a short rainy season in October and November known as 'inviernillo' or little rainy season by the river inhabitants. December and January are characterised by the lowest precipitation during a typical annual cycle. Annual precipitation for the western Amazon typically ranges between 2000 and 3400 mm (Salati and Marques 1984). Average air temperatures along the Aguarico River fluctuate around 27°C with an average daily fluctuation of 10°C (Saul 1975). Water temperatures that we measured in the study area averaged from 20.5 to 24.3°C, with upstream areas having the coolest values (Silva 2000).

Field sampling

Bocachicos were collected monthly from January to December, 1999, along the Aguarico River basin in north-eastern Ecuador. Sampling took place in six stations located along the river course to attain a better understanding of migrations and to ensure that most age-classes were sampled each month. The six sampling sites and their altitudes were: Due (465 m), Dureno (265 m), Chiritza (250 m), Cuyabeno (220 m), Sábalo (210 m), and Yanayacu–Zancudo (210 m). These locations included a variety of habitats such as major tributaries, streams, mouths of tributaries, permanent and temporary lagoons, flooded forest, and sandy beaches. The following environmental characteristics were recorded in the area: air temperature, water temperature at the surface, pH, water velocity, and mean level of the river. Fluctuations of the river were assessed based on weekly records taken at Chiritza. In addition, the mean monthly water levels taken in 1999 were compared to those collected during the years 1981 through 1986 provided by the Ecuadorian Institute of Meteorology and Hydrology INAMHI (Fig. 1). Consequently, the year was divided into four seasons: I—rising water season (1 February–30 April), II—flood season (1 May–31 July), III—falling water season (1 August—31 October), and IV—low water season (1 November–31 January).

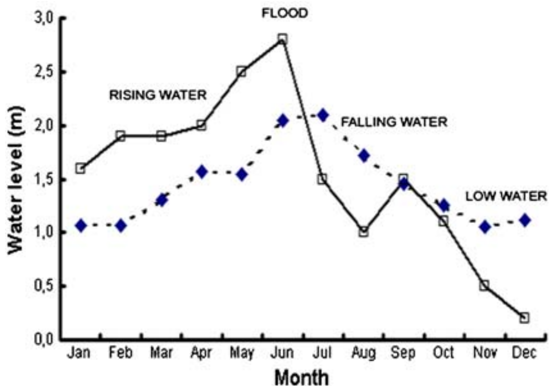

Fig. 1 Mean monthly water level relative to a base level for low-flood periods in the Aguarico River. Data for 1981–1986 (dashed line) was based on monthly records from near Due provided by Ecuadorian Institute of Meteorology and Hydrology (INAMHI). Data for the year 1999 (solid line) was based on field observations recorded at Chiritza

In all seasons, fishes were taken using three multi-filament nylon gillnets (20, 40, 50, and 70 mm stretch mesh; 2 m deep × 30–60 m long) in shallow areas of the Aguarico River, mouths of tributaries, streams, temporary lagoons, and floodplains. We set gillnets between 18:00 and 19:00 h every evening (20 nights a month) and fishes were collected every three hours until dawn (05:00–06:00).

The standard length L_S (mm) of each bocachico was taken with a measuring tape. Weights were obtained using a 1000-g scale graduated to the nearest 10 g for large fish and a 100-g scale graduated to the nearest 1 g for small fish. In addition, details of location, date, sex, gonadal stage and feeding status were recorded for each individual. Data on reproduction and feeding will be considered in a separate paper. A total of about 20 scales were removed from the left side of each fish directly beneath the dorsal fin base (above and below the lateral line) and stored in labelled envelopes. The body area for scale sampling was selected following Werder and Soares (1985). The otoliths (asteriscus and lapilli) were removed from the head (vestibular apparatus) of the fish applying the 'guillotine' and 'right-between-the-eyes' methods (Secor et al. 1991). After extraction and rinsing with water, the otoliths were air-dried and stored in labelled vials.

Laboratory methods

The selection of the best scales to examine annulus formation was based on the methods used for this species in Bolivia (Loubens and Panfili 1992). Therefore, structures with partial or total indication of regeneration (macrocentric scales) were discarded. Scales that showed no regeneration (microcentric) were washed in KOH (5%) and mounted between glass slides. The main growth marks of microcentric scales were examined, using a projecting microscope with a magnification of 20×. From the projected image, the radius of each ring and the edge of the structure were measured to the nearest mm at a constant angle (45°) on the anterior right field of the scale.

For otoliths, the standard preparation method was a double polishing technique where each lateral face (medial and distal) of the otolith was polished until it was thin enough to visualise growth marks. We prepared 240 otoliths (asterisci) for subsequent measurements. Otolith increment marks and dimensions were determined using a binocular stereo microscope at 25× magnification with polarised transmitted light connected to a Fuji video camera and a video digitiser board (Fujix Photograb 300z). The images were converted to 18-bit grey scale, enhanced with a medium sharpening filter, and interpreted using Optimas image analysis software (Media Cybernetics 1999). The Optimas system was calibrated to the nearest 0.01 mm for otolith measurements. The opaque (grey) and translucent (white) zones of the whole asteriscus were identified in the modified image. The radial distances from the nucleus to the outermost edge of each discontinuous zone (white band) and to the edge of the whole otolith were measured to the nearest 0.01 mm at a constant angle (53°). Measurements were made along a straight line originating at the nucleus to the dorsal and posterior edge of the proximal face of the asteriscus (Fig. 2).

Data analysis

All linear regressions were calculated employing the least square method. Regression models for body length versus calcified structure radius were compared using analysis of covariance (ANCOVA using the General Linear Model, GLM procedure in SAS). Non-linear regression analysis was utilised to fit the data to the von Bertalanffy model using an iterative secant method. Analysis of residuals was performed to evaluate the adequacy of the model. The Kruskal–Wallis test (non-parametric) was used to compare medians of more than two independent samples (Sokal and Rohlf 1995). Statistical significance was considered when $P < 0.05$. All statistical analyses

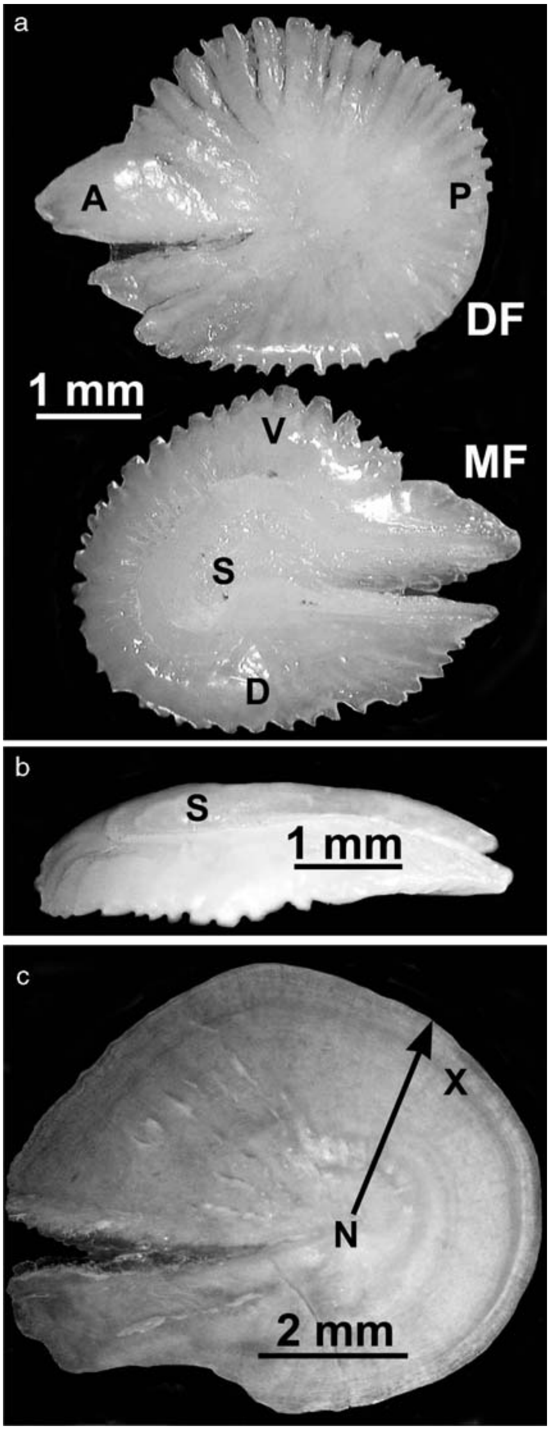

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Fig. 2 Whole and polished asteriscus extracted from *P. nigricans* captured in the Aguarico River. (**a**) Lateral view of whole otolith (female, 218 mm L_S and 203 g). (**b**) Ventral view of whole otolith (same as a). (**c**) Lateral view of polished otolith (male, age = 1, 227 mm L_S and 240 g). DF = distal face, MF = medial face, A = anterior, P = posterior, V = ventral, D = dorsal, S = sulcus, N = nucleus, X = annuli (translucent band) were made using the SAS System Version 7.0 for Windows[1].

To estimate precision of age interpretation, two readings of each structure (scales and otoliths) were made by the same interpreter. In the first count, the preparations that showed undefined growth checks were recorded as unreadable. From the structures recorded as interpretable, a randomly selected subsample ($n = 38$) was read a second time after a considerable time (60 days). The precision of age determination was computed with the following indices: (1) (P_A) percentage of agreement, (2) (A_P) average percent error, and (V) average coefficient of variation (see Appendix 1). In addition, precision of age estimations was assessed visually utilising plots of radial distances versus number of annuli (Vilizzi and Walker 1999).

Annuli indicated by check formation on scales and otoliths were indirectly validated by estimation of marginal increments over a 12-month period. Marginal increment calculations give a magnitude of the relative amount of growth that occurred since the last ring was formed. The marginal increment ratio (M_I) was estimated with the following equation of Lai et al. (1996): $M_I = [(r - r_1)/(r_1 - r_2)]$, where r is the radial distance to the edge of the structure, r_1 is the radial distance to the last formed annulus, and r_2 is the radial distance of the penultimate formed annulus. For structures with only one annulus, $r_2 = 0$. M_I was plotted against time to assess visually the marginal increment of the structures during a 12-month period.

Back-calculations of length-at-age were computed employing the Fraser-Lee equation (Everhart and Youngs 1981): $L_n = C + (r_n/r_t)(L_S - C)$ where L_n is the standard length of fish when ring n was formed; L_S is the standard length of the fish (mm) when the structure (e.g., otolith or scale) was obtained; C, the correction factor, is the intercept estimate calculated from the regression of L_S on the total structure radius; r_n is the radius of ring n (at length L_n); and r_t is the total structure radius.

Estimates of growth in length of the bocachicos were obtained using the von Bertalanffy growth function (Ricker 1975). The parameters (L_∞, K and t_0) were calculated with a non-linear estimation of the parameters employing SAS NLIN multivariate secant method[1] from the stage-explicit version of the von Bertalanffy equation developed by He and Stewart (2002, also see He et al. 2005), which was based on the general relationship of Schnute and Fournier (1980).

We estimated mortality rate for the population using age-based catch curves from the sampled individuals. The catch curve construction involved estimating size at specific age using the von Bertalanffy growth model and calculating the relative abundance of each age class in the catch. Plotting the natural logarithms of the number of fish over age (years) provides a catch curve with a slope that is equal to the instantaneous rate of annual mortality Z for those age classes that are fully recruited (King 1995). The mortality rate was calculated as (Van Den Avyle and Hayward 1999):

$$\log_e(N_t) = \log_e(N_0 - Z(t))$$

where the proportion of an age class that dies each year is $A = 1 - e^{-Z}$, and $S = e^{-Z}$ is the annual survival rate.

Results

Age determination

Of the 260 scale samples examined, 199 (77%) included scales that were interpretable. Scales were unreadable due to regeneration, absence of rings, presence of incomplete rings, extremely short radial distances between rings, and apparent resorption of rings. Based on observations of over 3600 scales, average percent of regenerated scales increased steadily as fish size increased. For example, fish from the length class below 100 mm had only 11% regenerated, while those above 300 mm had an average percent of scale regeneration greater than 45%. An annulus was identified as the region with densely packed circuli (slow growth) located between two transitional

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[1] SAS Institute, Inc. 1999. The SAS System for Windows, Release 7.0. SAS Institute, Cary, North Carolina.

regions with moderately spaced circuli that grade into regions with broadly separated circuli (rapid growth) before and after the annulus. The number of annuli observed on the scales ranged from zero to six for fishes with lengths from 89 to 405 mm. The first three annuli were broadly separated, which made them easy to discern compared to those produced later. The last few annuli of older fishes were closely spaced and, in some cases, not well defined. We identified false annuli as either incomplete checks observed only in one of the fields of the anterior part of the scale or accessory rings found in the transitional zones near the annuli.

The scale radius-standard length relationship was calculated by linear regression for each sex and for the entire sample. In all cases, it was apparent that growth on the scale was linearly proportional to growth in length of the fish ($P < 0.0001$). Both sexes had similar slopes but different intercepts (ANCOVA, $F_{1,183} = 5.61$, $P < 0.02$). The regression line intercepts 12.6 for the whole sample that included 20 small individuals of undetermined sex. Intercepts of 16.3 for males and 14.7 for females were used as correction factors (C) to back-calculate length of fish at annulus formation.

For otoliths, successful readings were made on 198 (83%) of the 240 asterisci examined. Under polarised transmitted light, alternate opaque (rapid growth) and translucent (slow growth) zones appeared as white and dark bands, respectively. The digitised image converted to 18-bit grey scale showed the same zonation pattern (Fig. 2). Otoliths were rejected when preparations were exceedingly thin or not adequate to show alternate zones. The number of annuli ranged from one to seven and fish lengths from 89 to 348 mm. The distance between translucent zones decreased from the nucleus to the external margin of the asteriscus. Therefore, the last three discontinuous bands were difficult to distinguish. Alternate opaque and translucent bands in the posterior area of the otolith were concentric, which facilitated the reading of growth checks. False annuli were identified as extremely narrow dark bands (sometimes incomplete) located in any position between adjacent translucent zones (annuli).

The linear regressions of otolith radius against fish standard length for males, females and both sexes were significantly linear ($P < 0.0001$). The two sexes had similar slopes and intercept estimates (ANCOVA, $F_{1,181} = 0.13$, $P > 0.7$). The intercept values of males (–38.2), females (–30.9) and the whole sample (–32.9) of the regressions were used as correction factors to complete back-calculations of the fish length at annulus formation.

Evaluation of precision of age determination involved several approaches. A comparison of the mean radial distance of each annulus in both structures revealed that measurements in scales had larger standard deviations than otoliths (Fig. 3). This might be an indication of a better consistency of age interpretation in otoliths. The relative precision of age determination for each structure at each annulus count was estimated using percentage of agreement (P_A), the average percent error (A_P) and the average coefficient of variation (V, Table 1). The percentage of agree-

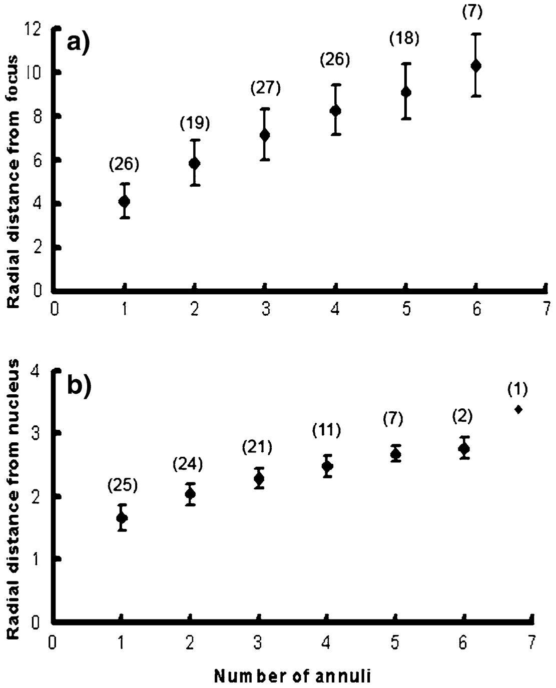

Fig. 3 Mean radial distances (mm) versus number of annuli for (**a**) scales and (**b**) otoliths of *P. nigricans* from the Aguarico River. Number of sampled individual fishes are shown in brackets; ±1 standard deviation is represented by vertical lines

Table 1 Bias and precision of annulus readings within the same interpreter on two calcified structures of *P. nigricans* taken from the Aguarico River

Structure	n	Same interpreter (two readings)		
		Percent of agreement P_A (%)	Avg. percent error A_P (%)	Mean coeff. variation V
This study				
Scales	38	70.1	20.7	0.44
Otoliths	38	80.1	3.42	0.21
Both	38	60	8.64	0.31
Loubens and Panfili (1992)				
Scales	30	83	15	0.02
Otoliths	30	50	15	0.22

Results from Loubens and Panfili (1992) are included for comparison

ment within readings by the same interpreter for otoliths (80%) was higher than for scales (70%). Agreement between independent readings for both structures was lower, with 60%. The A_P (3.42) and V (0.21) values reflected the lowest imprecision in age estimates for otoliths (Table 1). Between structures, the first annulus interpretation had the lowest P_A, which fell below 40%. This high disagreement was due to the occurrence of the first annulus in scales, but not in otoliths, of the same juvenile fishes (< 160 mm) at the onset of the falling water season.

To evaluate time of annulus formation, mean marginal increments of every structure were computed monthly with ages and sexes combined (Fig. 4). Because of the low number of fish collected in some months, marginal increment ratios (M_I) were pooled across months within each of the four periods that correspond to the hydrological cycle of the river (Fig. 4). The total absence of otolith samples in several months resulted from mistakes made during extraction, storage or preparation. For this reason, the rising water season (I) with only two otolith samples was excluded from the analysis. In scales, marginal increment ratios in the flood season (May–July) were significantly higher than those ratios in the rest of the year (Fig. 4a, Kruskal–Wallis test, $F_{3,122} = 6.2$, $P = 0.0006$). During November and December (low water season), there was a significant reduction in marginal scale growth. Annulus formation thus should take place during the low water period. The highest M_I observed in otoliths took place in the rising water period, yet the number of available samples ($n = 2$) was very low for that season. M_I values for otoliths in the falling and low water periods were significantly lower than the one in the flood season (Fig. 4b, Kruskal–Wallis test, $F_{2,88} = 30.3$, $P = 0.001$). Thus, translucent zone formation in otoliths appears to have occurred between September and December (falling water and low water seasons).

Growth

The relationships between standard length and radius for scales and otoliths were used to

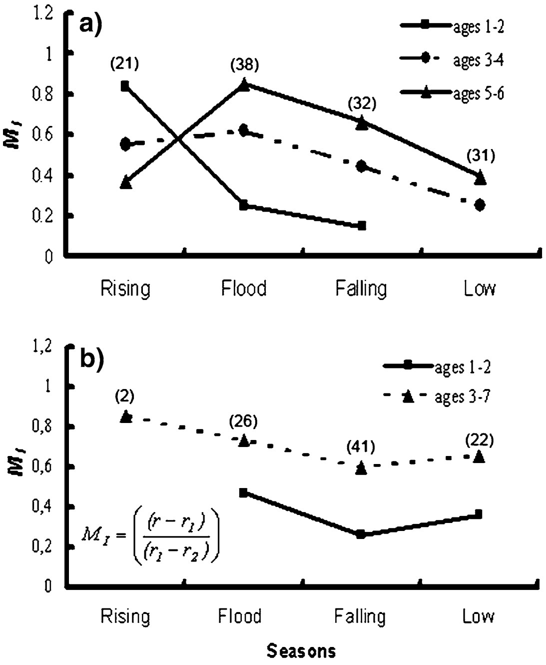

Fig. 4 Mean value of the marginal increment ratios in (**a**) scales and (**b**) otoliths of *P. nigricans* from the Aguarico River. Data were pooled by age class for the four hydrological seasons. For the equation, r is the radial distance to the edge of the structure; r_1 is the radial distance of the last formed annulus; and r_2 is the radial distance of the penultimate formed annulus

back-calculate lengths of fish at the time of annulus formation. Back-calculated lengths for *P. nigricans* were estimated for both sexes combined (Table 2). In scales, we observed that 38% of juvenile fish with a standard length ranging from 89 to 154 mm did not show any annulus. The same pattern was observed in otoliths, although yearling fish were more abundant (54%) and the size range was larger (89–197 mm). Back-calculations of standard length estimated from both ageing structures were completely different, with otoliths having much higher values than scales in all related age groups. The mean lengths back-calculated for scales were generally smaller than the observed lengths among all age groups (I–VI). In contrast, the difference between observed and back-calculated lengths at age from otoliths was similar in all age groups. The only exception was in age group I where the observed L_S was noticeably greater than the back-calculated length from otoliths.

Close agreement was found between growth increments estimated from back-calculated standard lengths for both structures. The length increment gradually decreased with increasing age, although the last increment from back-calculated lengths for scales, between ages V and VI, was higher than the previous age interval. This could be related to the small sample sizes of the oldest individuals.

The von Bertalanffy growth parameters based on otolith and scale data are given in Table 3. Residual analysis indicated homogeneous variance for various regressions, so the assumption of a linear relation was supported. We found that growth curves with parameters derived from otolith data were different from values estimated using scale data. The observed mean standard lengths at age were underestimated by the von Bertalanffy growth model based on parameters estimated from back-calculated scale data (Fig. 5). The growth curve constructed with otolith data had a lower asymptotic length and a higher von Bertalanffy growth coefficient ($L_\infty = 398$ mm, $K = 0.28$) than those found in the model based on scale data ($L_\infty = 457$ mm,

Table 2 Observed and back-calculated L_S (mm) at age for the entire population estimated from scales and otoliths in *P. nigricans*

Age (years)	n	Obs. L_S (mm)	SD	Back-calculated L_S at annulus number						
				I	II	III	IV	V	VI	VII
Scales										
0	76	116.4	16.8							
1	27	179.9	43.6	148.7						
2	19	238.9	40.1	141.5	209.8					
3	27	268.0	39.0	144.2	203.2	245.0				
4	25	302.7	38.1	153.4	209.2	254.2	286.5			
5	18	315.3	36.3	148.8	197.1	234.3	272.3	298.6		
6	7	350.9	27.7	158.2	198.6	241.9	281.1	314.3	336.0	
Total	199									
Weighted mean				149.1	203.6	243.9	280.0	306.4	336.0	
±SD				27.5	34.5	37.9	35.3	34.0	31.0	
Growth increment (mm)					54.4	40.3	36.1	26.5	29.5	
Otoliths										
0	107	124.3	23.8							
1	26	206.3	19.7	171.4						
2	23	244.0	25.1	184.3	228.3					
3	21	278.0	18.6	187.5	240.2	266.7				
4	11	303.7	24.1	179.7	233.2	265.2	286.5			
5	7	325.7	11.4	171.3	223.0	263.4	296.6	314.3		
6	2	356.5	12.0	157.5	237.4	291.7	322.2	339.5	349.1	
7	1	363.0	0.0	223.1	244.3	281.4	316.0	332.6	347.9	355.8
Total	198									
Weighted mean				182.1	234.4	273.7	305.4	328.8	348.5	355.8
±SD				20.7	7.9	12.4	16.6	13.0	0.9	0.0
Growth increment (mm)					52.3	39.3	31.7	23.4	19.7	7.3

Table 3 Summary of the estimated von Bertalanffy growth function parameters using a non-linear secant method (He and Stewart 2002)

Scales	Parameter		ASE	ACI 95%		Otoliths	Parameter		ASE	ACI 95%	
	Symbol	Value		Lower	Upper		Symbol	Value		Lower	Upper
Males	L_∞	462.1				Males	L_∞	400.5			
	K	0.17					K	0.29			
	t_0	–1.33					t_0	–1.06			
	L_1	152.0	3.0	142.6	164.1		L_1	177.9	3.7	167.6	188.3
	L_4	276.4	1.8	270.6	282.2		L_4	305.9	2.2	299.9	312.0
	b	0.84	0.0	0.8	0.9		b	0.75	0.02	0.69	0.82
Females	L_∞	444.4				Females	L_∞	391.3			
	K	0.20					K	0.29			
	T_0	–1.07					t_0	–1.09			
	L_1	150.6	1.7	145.3	155.9		L_1	177.4	2.7	168.7	186.0
	L_4	283.3	1.0	280.1	286.5		L_4	301.3	1.6	296.1	306.1
	b	0.82	0.001	0.776	0.861		b	0.75	0.02	0.68	0.82
All	L_∞	457.5				All	L_∞	398.4			
	K	0.18					K	0.28			
	t_0	–1.18					t_0	–1.16			
	L_1	150.2	2.3	142.9	157.5		L_1	181.6	2.1	175.9	187.3
	L_4	279.7	1.4	275.3	284.2		L_4	305.3	1.2	301.9	308.6
	b	0.83	0.02	0.77	0.89		b	0.75	0.01	0.72	0.79

ASE = asymptotic standard error and ACI = asymptotic 95% confidence interval, b = slope, $L_1$and L_4 = expected lengths at age 1–4

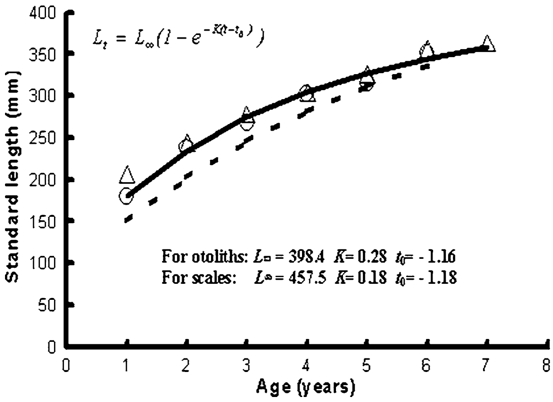

Fig. 5 von Bertalanffy growth function (VBGF) in terms of standard length for *P. nigricans* from the Aguarico River. Solid line represents the VBGF based on otoliths; dashed line represents same for scales. Observed mean standard lengths at age are represented by triangles for otoliths and open circles for scales. L_t is the standard length at age t; L_∞ is the theoretical maximum (or asymptotic) length; K is a growth coefficient; and t_0 is the theoretical age at zero length

K = 0.18). In summary, results from otolith estimations indicate that ageing structure is more reliable than scales for age and growth estimation.

Mortality

The construction of a catch curve for *P. nigricans* involved determining the ages of individuals by otolith analysis and the estimated size at age from the von Bertalanffy growth function (VBGF). We chose to use otolith data only because the forgoing results suggested more consistent and less biased estimations using that ageing structure. We used a length-age key with data from the VBGF to estimate the abundance of each age class (Fig. 6). On the basis of the assumption that all age groups have to be equally vulnerable to the same fishing gear (gillnets), fishes smaller than

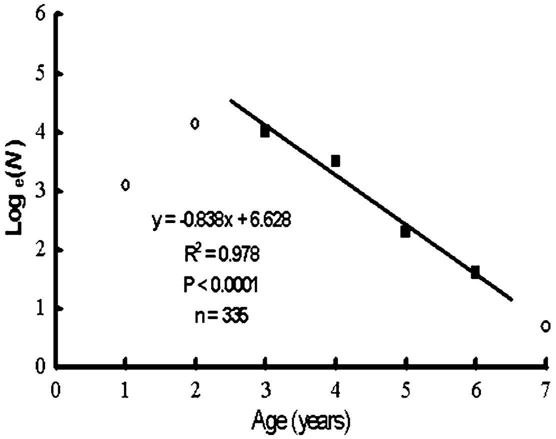

Fig. 6 Natural logarithm of the number of individuals versus age collected in the Aguarico River during 1999. The value of the slope (Z = 0.838) is the instantaneous annual mortality coefficient. The open circles for age one, two and seven were not used in the regression. The solid line is for ages three to six

180 mm were excluded from the analysis. The resulting catch curve in terms of length shows on the right side a descending portion from age three to six that was used to calculate the mortality coefficient Z (Fig. 6). This coefficient was estimated from the regression $\log_e(N)$ versus age (years) using the least squares method. The resulting slope estimate for ages three to six was $Z = 0.838$. Our value for age seven appears to conform to that relationship. The related annual survival rate was $S = 0.43$; consequently, the annual mortality was $A = 0.56$.

Discussion

Age determination

Growth marks in calcified structures (scales, bones and otoliths) of tropical fish are more difficult to interpret than those laid down on hard structures of temperate fish (Lowe-McConnell 1987). Cessation of growth and annulus formation in temperate fish is correlated with low temperatures between the onset of winter and early summer (Fabré and Saint-Paul 1998). Variation of growth in freshwater tropical fish, in contrast, is associated with seasonal water level fluctuations (Junk et al. 1997; Fabré and Saint-Paul 1998). In other words, factors influencing tropical fish growth like high population density, changes in food availability, migrations, gonad development, mortality, and predation are strongly influenced by the flood regime (Bayley 1973, 1988; Welcomme 1979; Lowe-McConnell 1987).

The results of our analysis suggest that scales of *P. nigricans* may not be suitable for age estimation or, at least, are more difficult to interpret than otoliths. Ages derived from scales were inaccurate and the precision in ageing was lower. There were difficulties in reading annuli from scales, which led to misinterpretation of the fishes growth rate and age. Scale resorption and erosion appear to be serious obstacles to obtaining reliable readings of growth checks, especially in older individuals. In addition, the spawning period seemed to coincide with the formation of pseudo-annuli found on the scales of some individuals. Back-calculated lengths at ages one to four based on scales apparently underestimated the size of the fish (Fig. 5). That apparent bias could be due to size-selective mortality or year-to-year differences in growth rate. Cordiviola de Yuan and Campana (1993) inferred that body length and scale radius grew at different rhythms in various life stages of *Prochilodus lineatus* from the Paraná River. The results for *P. nigricans* might reflect similar growth dynamics. In addition, closely spaced annuli on the edge of scales combined with possible resorption may have caused lower age estimates than otoliths. Scale regeneration was considerably higher in individuals at age three and older. High frequency of regenerated scales in Neotropical fishes is often associated with the presence of scale-eating characoid genera such as *Roeboides*, *Serrasalmus*, and *Exodon* (Sazima 1984). The first two genera are common in the Ecuadorian Amazon. This factor should be taken into consideration when sampling scales from adult fish. For this reason, we concluded that a minimum of 30 scales should be collected from each individual. In this study, accuracy and precision of age estimations derived from scale data were lower than those found by Loubens and Panfili (1992) in Bolivia. The authors of that study concluded that scales were more reliable ageing structures than otoliths.

Our otolith preparations using the double polishing technique, polarised light and Optimas image analysis system might have enhanced the visual clarity of annuli compared to observations by Loubens and Panfili (1992). We also tried several other otolith preparation methods, but none of them provided clearly visible annuli (Silva 2000). Thin preparations of whole asterisci showed narrow translucent bands alternating with wider opaque bands; however, when viewed under polarised transmitted light, the clarity of these bands depended especially on the orientation and thickness of the preparations. Age estimates derived from whole otoliths were relatively unbiased and precise. The imprecision of otolith-derived estimates was lower than the values reported by Loubens and Panfili (1992) for readings by the same lector (Table 1). In addition, our otolith-based longevity estimate was notably higher than that for the Bolivian population (maximum seven vs. five annuli). Ages based on otoliths were reasonably accurate for young individuals, but ages of older specimens became less accurate as growth became asymptotic. The better precision and accuracy in ageing using otoliths led us to conclude that these structures are more reliable than scales for use in age determination. However, using otoliths as ageing structures may have some disadvantages such as sacrificing individuals and problems in extracting and processing these structures. Furthermore, preparation of otoliths is more time-consuming and may require expensive optical equipment that is sometimes difficult to obtain in tropical developing countries.

The analysis of marginal increment ratios (M_I) for both ageing structures to indirectly assess the periodicity of annulus deposition indicated that checks were formed annually. Annuli in scales and otoliths were formed between September and December, and the decreases in M_I during this time (falling and low water seasons) were apparent for all age groups. Marginal increment analysis in scales of *P. nigricans* from Bolivia (Loubens and Panfili 1992) also supports the above findings. Furthermore, annulus formation coincided with the annual upstream migration. Variation in timing of annulus formation among age groups may be the result of differences in growth rates (physiological rhythms). In addition, this apparent variability may be associated with the limited number of monthly samples and the age interpretation method. In summary, we infer that annulus formation in this species may be a response to a composite of factors such as migration and food availability correlated with the flood pulse.

Growth

Our results suggest that back-calculated lengths from scale-based data may be biased. In contrast, back-calculated length-at-age from otolith data showed close agreement with observed length (Table 2). Those doing back-calculations of length-at-age from scales might need to consider the possibility that scales grow at a different pace than body length, as suggested by Cordiviola de Yuan and Campana (1993). However, a body size-scale radius non-linear relationship was not apparent in the Ecuadorian bocachicos.

Growth estimates from scale data underestimated mean standard length at a given age compared to empirical observations (Fig. 5). Also, K and L_∞ values estimated from scales were inconsistent with the biology of the fish. L_∞ was noticeably higher than the maximum observed length, whereas the growth coefficient (K) of *P. nigricans* was even lower than the range (0.28–0.61 year^{-1}) estimated from various species of *Prochilodus* elsewhere in South America (Petrere et al. 1991). In contrast, the resulting L_∞ computed from otolith-based data was consistent with observed maximum standard length, and the coefficient K (0.29) fell within the range estimated by Petrere et al. (1991) for five other populations of *Prochilodus*.

A comparison of the growth performance between the bocachicos from Ecuador and other areas suggests that *P. nigricans* in the Aguarico River grew at a different rate than in Bolivia and the central Amazon. We thus reject our null hypothesis that grow patterns in Ecuador are similar to those elsewhere in the Amazon basin. Growth parameters for *P. nigricans* in Bolivia and the central Amazon ranged from $K = 0.45$ to 0.58 and $L_\infty = 350$–680 mm (Loubens and Panfili 1995; Ruffino and Issac 1995). It may be possible that fish at the young of the year and yearling stages grew faster in Bolivia and Brazil because of better conditions. For example, the annual flooding pulse in the central Amazon lasts longer than in the upper reaches near the Andes, allowing the fish to exploit food resources like periphyton for a longer time (Bailey 1988). A large K in the Bolivian and Brazilian bocachicos during the juvenile–adult stage shows a rapid decrease in growth that may be related to diet change from phytoplankton to detritus and to an early age at first reproduction (1.5 years). In other words, rapid early growth can lead to a subsequent compensatory effect and a high K value in some fishes (He and Stewart 2002). The Ecuadorian population of *P. nigricans*, in contrast, may experience moderate young of the year and yearling growth because of a relatively shorter inundation period and energy demands of upstream migration. As larvae, they probably drift to nursery habitats in Peru or beyond and then migrate back upstream to Ecuador at an age of about 6 months (Silva

2000). A slow decrease of the juvenile–adult growth (i.e., low K for ages 2 and higher) may correspond to delayed age at first reproduction (2–3 years) and, subsequently, a relatively lower mortality. *Prochilodus* in the Napo Basin also may have lower fishing pressures than populations in Bolivia and Brazil (see Mortality below).

Mortality

Few annual mortality estimates have been recorded for *Prochilodus* in the Amazon basin and other regions of South America. Previous estimates of total annual mortality were $A = 0.87$ for *P. nigricans* in the central Amazon (Ruffino and Issac 1995), $A = 0.78$ for *Prochilodus magdalenae* in Colombia (Valderrama et al. 1993), and $A = 0.77$ for *P. platensis* in Bolivia (Payne and Harvey 1989). Those values are all noticeably higher than that calculated in this study ($A = 0.56$), so we also reject our null hypothesis that mortality patterns in Ecuador are similar to those elsewhere in the Amazon. These differences suggest that exploitation of migratory characoids could be more intense in the other Neotropical regions that have been studied. For instance in Brazil, *P. nigricans* accounted for approximately 50% of the commercial and subsistence catch in the Araguaia and Tocantins basins in 1988 (Petrere and Juras 1995). In Porto Velho, Rondonia, this one species represented 32% in 1986 and 23% in 1989 of the total commercial catch (Boischio 1992). In addition, *P. nigricans* in Manaus contributed approximately 12% of the total fish sold in that market (Junk 1985).

Generally, values of the instantaneous annual mortality in younger individuals are quite high and difficult to quantify (Welcomme 1979). Our estimate from the catch curve was based on samples from size-selective fishing gear (i.e., gillnets). Thus, we deleted ages zero to two because they were under-represented in the samples (Fig. 6). Instantaneous mortality rate would be lower if estimated for ages two to seven (Silva 2000), but that alternative value would not change our general conclusion that total annual mortality for *P. nigricans* in the Aguarico River is lower than in other Amazon regions.

We conclude that fishing mortality will not have a notable detrimental effect on the local population in the immediate future for several reasons: (a) human population density in the Aguarico basin is relatively low; (b) exploitation of migratory fish in the region is seasonal and mostly for subsistence; (c) gillnets, the most effective gear, selectively exclude younger and smaller individuals; and (d) access to this area and the resource is limited due a lack of roads and consequently high operational costs (i.e., gasoline for boats). In addition, part of the headwaters and lower reaches of the Aguarico River lie within the boundaries of two important conservation units (Cayambe-Coca Ecological Reserve upstream and Cuyabeno Faunal Reserve downstream). Finally, when juveniles are in downstream nursery areas (in Perú, for example), they may be too small to be of commercial interest.

Implications for management and conservation

Fish is the one of most important animal protein sources for human communities inhabiting the rivers of the Amazon basin (Batista et al. 1998). In addition, migratory food fishes like *Prochilodus* often dominate local and regional fisheries. For instance, *P. platensis* from Bolivia makes up to 65–70% of the total commercial catch sold in La Paz (Payne and Harvey 1989). In Ecuador, however, low priority has been given to studies on the biology of food fishes, fishing activities and the rate of commercialisation of these resources. Vaca (1991) reported that there are no historical records of fish exploitation in the Napo River basin, and 15 years later that situation has not changed noticeably. One of the reasons for this absence of information could be the lack of large fish markets (Barthem et al. 1995). That situation contrasts noticeably with research and monitoring activities in other Amazonian countries, and with marine fisheries on the Pacific coast of Ecuador. All these factors point to the need for expanding research on food fishes in the Ecuadorian Amazon region.

In eastern Ecuador, the strong negative factors that might undermine this important biological resource are human colonisation, deforestation, irrational forms of agriculture, and oil exploitation. The last mentioned factor, apparently the most serious problem at present, is an activity that originated the other environmental disturbances in north-eastern Ecuador. Activities like deforestation lead to erosion and increased sediment loads that could interfere with reproductive success. Perhaps, the most serious disturbances correlated with oil exploitation and agriculture is water pollution. Pollution in the Napo basin waters in the last decades has been alarming; in addition to oil spills (e.g., Kimerling et al. 1993), pesticides and residual water discharges from oil palm plantations are added to produce a more critical situation.

This study suggests that the present exploitation of *P. nigricans* in the Aguarico basin does not compromise integrity and abundance of the population. Fisheries activities in the area are mainly for subsistence and are important sources of nutrition for the local communities. However, we observed illegal fishing activities such as use of dynamite in portions of the river near towns that, eventually, could result in significant depletion of the fish populations. It is important to note that most of our observations were made within the boundaries of the Cuyabeno Ecological Reserve where commercial fishing is banned. The bocachico is just one example of many commercially exploited fishes in eastern Ecuador that are international, trans-boundary migrants having various life-stages dependent on habitats in other countries (e.g., Barthem and Goulding 1997). Thus, if a fishery developed on the lower Napo River in Perú that used fine-meshed seines, it could seriously deplete migrating schools of young fishes before they reach Ecuador. Conservation and management of such resources for sustainable harvests ultimately will require international agreements based on a solid foundation of ecological understanding.

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Appendix 1

Indices to estimate precision of age determination for *P.nigricans*

Equations used to estimate precision of age determination were as follows:

1. Percentage of agreement was calculated with the formula (Loubens and Panfili 1992):

$$P_A = \frac{N_I}{N_T} * 100\%, \quad (1)$$

where N_I is the number of identical determinations between readings; and N_T is the total number of determinations

2. The average percent error (A_P) was expressed with Beamish and Fournier's (1981) formula assuming that N fish are aged R times as follows (Lai et al. 1996):

$$X_j = \frac{1}{R}\sum_{j=1}^{R} X_{ij}, \quad (2)$$

where X_j is the average age calculated for the *jth* fish; X_{ij} is the *ith* age determination of the *jth* fish; and R is the number of readings. Next, the average error A_E in determining the age of the *jth* fish is a fraction of the average of the age estimates:

$$A_{E_j} = \frac{1}{R}\sum_{i=1}^{R} \frac{|X_{ij} - X_j|}{X_j} \quad (3)$$

Thus, the index of the average precent error for N fish is determine by the formula:

$$A_P = \frac{1}{N}\left(\sum_{j=1}^{N} AE_j\right) * 100\%. \tag{4}$$

3. The coefficient of variation (V_j) of the age of the *jth* fish for each observation was estimated with the equations of Chang (Lai et al. 1996):

$$V_j = \frac{1}{X_j}\sqrt{\frac{(X_{ij} - X_j)^2}{R(R-I)}}. \tag{5}$$

Therefore, the average V for all fish (N) aged is

$$V = \frac{\sum_{j=1}^{N} V_j}{N}. \tag{6}$$

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