

Biology of growth of *Hoplias aff. malabaricus* (Bloch, 1794) in a shallow pampean lake (Argentina)

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The trahira *Hoplias aff. malabaricus* is a top predator in pampean shallow lakes and is highly appreciated by recreational anglers and artisanal fishermen. Trahira growth from Yalca shallow lake was determined by lepidological analysis and age validated by marginal increment. When growth was fitted to the von Bertalanffy model, annual classes exhibited a bimodal pattern as a result of the presence of spring and summer annual cohorts associated with a three month spawning season, each period in turn showing different growth patterns. The trahira population-age structure at Yalca shallow lake showed a truncated profile with very low numbers of large adults and few individuals older than three to four years, thus producing an unbalanced length-structure population. Growth parameters and growth performance were similar to the corresponding parameters estimated for other shallow pampean lakes of the region, but strongly diverged from the data for those populations inhabiting subtropical and tropical environments. Such differences could be accounted for by dissimilarity in metabolic rates associated with thermal differences accompanying seasonal variability among latitudes as well as by the development of adaptive physiologic and demographic responses to cope with the high thermal amplitude and hydrologic instability observed in pampean lakes.

A traíra *Hoplias aff. malabaricus* é um predador de topo encontrado em lagoas rasas nos Pampas, muito apreciada nas pescas comerciais e esportivas. O crescimento da traíra no lago Yalca foi determinado através de análises lepidológicas, validadas a partir do incremento marginal. O crescimento foi ajustado ao modelo de von Bertalanffy, sendo que as classes de tamanho anuais apresentaram padrão bimodal devido à presença de coortes de primavera e verão, associadas à uma longa estação reprodutiva com diferentes padrões de crescimento. A estrutura etária da traíra do lago Yalca apresentou um perfil truncado, com um número pequeno de adultos de maior porte e poucos indivíduos com mais de três ou quatro anos, produzindo uma estrutura em tamanho desbalanceada. Os parâmetros e a performance de crescimento foram similares aos estimados para outros lagos rasos da região, mas fortemente divergentes de populações encontradas em ambientes tropicais e subtropicais. Tais diferenças podem estar relacionadas à diferentes taxas metabólicas associadas à variação térmica sazonal entre latitudes e ao desenvolvimento de respostas adaptativas fisiológicas e demográficas em resposta aos padrões termais altamente variáveis e instabilidade hidrológica observados nos lagos da região dos Pampas.

Key words: Age validation, Biological indices, Neotropical fish, Piscivorous fish, Trahira.

Introduction

The trahira, *Hoplias aff. malabaricus*, is a neotropical characiform fish of the Erythrinidae family with a geographical distribution ranging from Colombia to the temperate shallow lakes in Argentina, inhabiting the Atlantic slope basins within this broad latitudinal strip (09° N to 37° S). The species inhabits lentic and lotic environments and is particularly adapted to shallow vegetated bodies of water because of its wide range of tolerance to dissolved oxygen, pH, salinity, and temperature (Paiva, 1972; Rios *et al.*, 2003; Saad *et al.*, 2002). In Argentina, the trahira is distributed all along the Aymaran, Great Rivers,

Andean Cuyan, and Pampean ichthyogeographic provinces (Lopez *et al.*, 2008) with its meridional distribution boundary in the southern portion of the pampean plains (Ringuelet *et al.*, 1967; Lopez *et al.*, 1994; Rosso, 2007).

The trahira is the largest-sized predator in shallow pampean lakes (Barla *et al.*, 2003; Menni, 2004; Rosso, 2007). The species withstands artisanal and substantial recreational fishing (Lopez *et al.*, 2001; Grosman *et al.*, 2004), as is also true in other South American regions where this species is distributed (Oyakawa, 2003; Tordecilla-Petro *et al.*, 2005). Despite the prominence of trahira's presence in pampean lakes, the little information gathered on growth parameters and age

structure is conflicting (Ramirez, 1963; Domanico *et al.*, 1993; Domanico, 1998; Grosman *et al.*, 2004). These works also differed from studies performed in other Neotropical basins (Paiva, 1974; Moraes & Barbola, 1995; Tordecilla-Petro *et al.*, 2005), where maximum length and/or growth rate are clearly lower than the observed in pampean shallow lakes. Growth patterns have a strong influence on fish-population dynamics and thereby-along with the effect of environmental conditions, genetic characteristics, food availability, trophic interactions, and fishing practices strongly influence the ecology and management of such populations (Quist *et al.*, 2003). Growth information becomes more relevant when gathered from populations that inhabit water bodies subjected to differing climatic and environmental circumstances, since divergent populations would be expected to adapt their life-history patterns in order to cope with local or regional environmental conditions. Temperature, for example, is likely one of the strongest selective forces exerted on many fish populations because that parameter influences spawning frequency, foraging patterns and survival (Philipp, 1992). Seasonal thermal regime across divergent latitudes furthermore can be reflected in different relationships to growth, among differing species (Modde & Scalet, 1985; Conover, 1990; Galarowicz & Hall, 2003; Quist *et al.*, 2003).

In this study we attempted to analyze trahira-growth patterns and age structure in shallow Yalca Lake based on lepidological analysis and length and age composition. We also compared these results with the findings from previous studies performed in pampean lakes, as well as with other data obtained from different geographical areas in South America, with a focus on the potential influence of temperature on growth patterns.

Material and Methods

Yalca shallow lake is located in the lower Salado River basin (Fig. 1). The lake area is 1,150 hectares, but about 60% is covered by aquatic vegetation *Typha latifolia* (Linnaeus, 1753) and *Scirpus giganteus* (Kunth). The mean and maximum depths are around 1.40 m and 1.60 m, respectively, with a wide littoral area containing gentle slopes (Frenguelli, 1956). During the study, lake transparency was very low (Secchi depth = 6 cm \pm 1.08 SD), mean conductivity was 0.46 uS/cm (\pm 0.13 SD), dissolved oxygen showed high levels (7.52 mg/l \pm 1.01 SD), and pH was neutral to alkaline (7.89 \pm 0.79). As with other shallow lakes in the basin, Yalca is chemically and physically unstable (Dangavs & Dalla Salda, 1978; Thorton, 1982), with its hydrologic dynamics linked to the rainfall cycle that in turn produces alternate periods of floods and droughts, each of several years duration (Quiros *et al.*, 2002). The water body is located at a private property and has not supported fishing pressure in the last eight years.

The study period was carried out from September 2005 through July 2007 covering summer (December-March), fall (March-June), winter (June-September) and spring (September-December) seasons. Environmental measurements and fish

samples were taken at 30- to 40-day intervals. The lake's thermal patterns at 40 cm depth were obtained through hourly water-temperature recordings by an automatic thermo logger. Daily temperature averages were estimated and analyzed in order to investigate annual oscillation. Fish samples were taken in 5 permanent coastal and open-water zones plus 3 alternative sampling sites when depth restricted the use of the gear in the permanent ones (Fig. 1). Different types of fishing gears were employed: *e.g.*, fyke nets (Colautti, 1998), beach seines, a set of 5 gill nets each 25 m long (stretch mesh sizes: 20, 70, 80, 110, and 130 mm), trammel net 25 m long (60-mm inner mesh and 120-mm outer mesh) and 30 longline hooks (Mustad 4/0). All gears were set in duplicate at each sampling date. The fishing effort (12 h) extended from dusk to the following dawn for each type of passive fishing gear.

The fish were weighed (W) at a 1-g precision and their standard length (SL) and total length (TL) recorded at a 1-mm precision; gonads were weighed at a 0.1-g precision. Scales were extracted from the right side of the body behind the operculum and above the lateral line, then stored in paper envelopes.

The length-frequency distribution was made by grouping the captured fish into 10-mm length intervals. The scales to be analyzed for age determination were selected according to the following criteria: symmetry, regularity of shape, and similarity in size. Five scales per individual were chosen and submerged in an enzyme solution for 48 h; then brushed, rinsed, and fixed between two 1.5-mm-thick slides. Scales were read under a Nikon SMZ 800 stereoscopic microscope with a built-in camera and measurements obtained by means of the Image-Pro Plus software.

Ring identification followed the criteria outlined by Ramírez

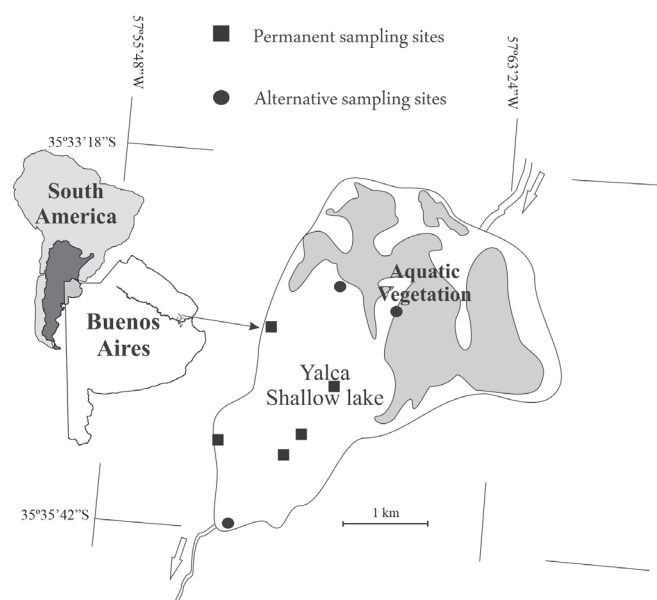


Fig. 1. Geographical location of Yalca Lake and its geographical position in south America. The sampling stations in the lake are indicated.

(1963). The total radius (TR) was measured from the focus to the most distant point of the anterior scale margin. Each successive growth radius (R1, R2, ... Rn) was measured over this axis at a 1- μ m precision. The Rn values obtained were grouped at intervals of 0.18 cm. The length of this interval had been obtained by dividing the entire range of Rn values by 45. Considering that the species has more than one spawning per reproductive season, we analyzed the R1 frequency distribution in order to verify the existence of multiple annual cohorts and then divided the data base by polymodal decomposition using this criterion, if necessary, grouping fishes with similar Rn values regardless of its maximum number of rings. The Rn-frequency distribution for pooled data and for the female- and male-subsets were decomposed into their normal components in order to obtain the mean Rn value for each growth ring and the respective standard deviations (Quinn & Deriso, 1999). The differences in the mean value between sexes at each Rn were assessed by the Student *t* test.

The average TR (ATR) was calculated for each individual and a linear model was fitted to the TL-ATR relationship in order to obtain the back-calculation equation for estimating the average fish size at each mean Rn. With the purpose of validating the age estimation, the percentage marginal increment (MI%) was calculated based on individuals from the best represented group through the following formula:

$$MI\% = \frac{(TR - Rn_{max}) \cdot 100}{TR}$$

where Rnmax is the distance along the radius from the focus to the latest ring.

A third-order Fourier-harmonic model was fitted to the mean MI%-sampling-period-pair data to obtain a description of the annulus-formation process (Rey-Pastor *et al.*, 1987; Freyre *et al.*, 2009). The mean annulus-formation period was defined as the maximum value of the model's second derivative. Differences among the estimated MI% values at different periods were assessed by means of the one-way ANOVA.

In order to analyze the relationship between the dynamics of scale marking and the physiologic processes in *H. aff. malabaricus*, we assessed yearly reproductive and condition patterns by considering female gonadosomatic index (GSI) and the relative condition factor (Kn) of the females, after Le Cren (1951), as:

$$GSI = Wg \cdot 100/W$$

where Wg represents the ovary weight and W the individual's body weight.

$$Kn = \frac{W}{W'}$$

where W' is the length-specific mean weight for a given fish within the population as predicted by the population weight-length relationship obtained from 244 pair wise data, where $\log W' = 0.00005 + 2.9904 \log Lt$

With the aim at facilitating the comparisons, the range of variation in Kn was expressed on a scale from 1 to 3 according to the equation:

$$Kn_{exp} = 4 - \left((Kn_{max} - Kn) \cdot \frac{3}{(Kn_{max} - Kn_{min})} \right)$$

where Kn_{exp} = the Kn expanded value, and Kn_{max} and Kn_{min} are the maximum and minimum mean Kn values, respectively.

For both GSI and Kn, a Fourier second-order polynomial equation was fitted to the variation in the yearly pattern.

The length-at-age data were fitted by the maximum-likelihood method to the von Bertalanffy growth model (Haddon, 2001) following formula:

$$L_t = L_{\infty} \cdot [1 - e^{-k(t-t_0)}]$$

Where:

L_t = total length or standard length of a fish at the moment *t*,
t = time in years,

L_{∞} = total or standard asymptotic length,

k = growth coefficient,

t_0 = hypothetical time at zero length.

To compare the growth among Yalca and other shallow lakes within the pampean region and/or in other South-American river basins, the published data for lengths at a given age were transformed to total lengths, when necessary, and the von Bertalanffy curve fitted. Those conversions were made by means of a linear equation obtained from SL and TL pair wise data from trahiras (N = 680) captured in several pampean shallow lakes according to the following equations:

$$SL = 0.893 \cdot TL - 6.950 \quad TL = 1.152 \cdot SL + 10.173$$

$$r^2 = 0.99$$

Then the growth performance index (ϕ') was calculated based on the following formula (Pauly & Munro, 1984):

$$\phi' = \log(K) + 2\log(L_{\infty})$$

Results

Temperature patterns were closely monitored throughout the year and showed a clear seasonal variation and wide amplitude (Fig. 2a). The annual frequency distribution of daily water temperatures was bimodal, thus suggesting the existence of two thermal states over the annual cycle (Fig. 2b).

A total of 562 trahiras were collected during the entire sampling period. The trahira-size distribution ranged between 255 and 616 mm, with individuals between 330 and 400 mm (TL) being highly represented (Fig. 3).

The decomposition of polymodal distribution allowed recognition of a first ring with a bimodal distribution (Fig. 4a), thus justifying a division of the data set into two groups. As

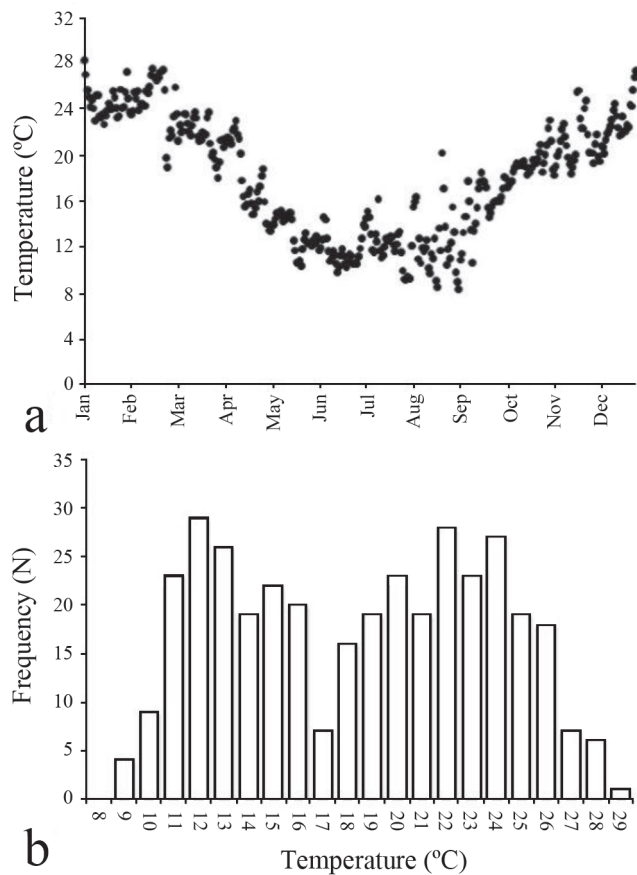


Fig. 2. Average daily water temperatures registered at Yalca Lake during an annual cycle (a), and frequency distribution of the average daily temperatures (b).

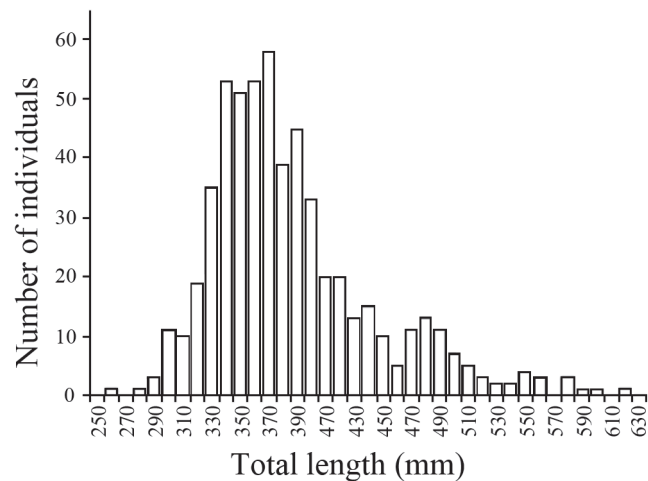


Fig. 3. Frequency distribution of total lengths of the trahira *Hoplias aff. malabaricus* captured during the entire sampling period.

a result, we obtained one group containing fish with first rings closer to the scale nucleus (summer group; Fig. 4b) and another group containing fish with first rings far away from the scale nucleus (spring group; Fig. 4c). All told, we were able to detect up to four normal components in cohort 1 and

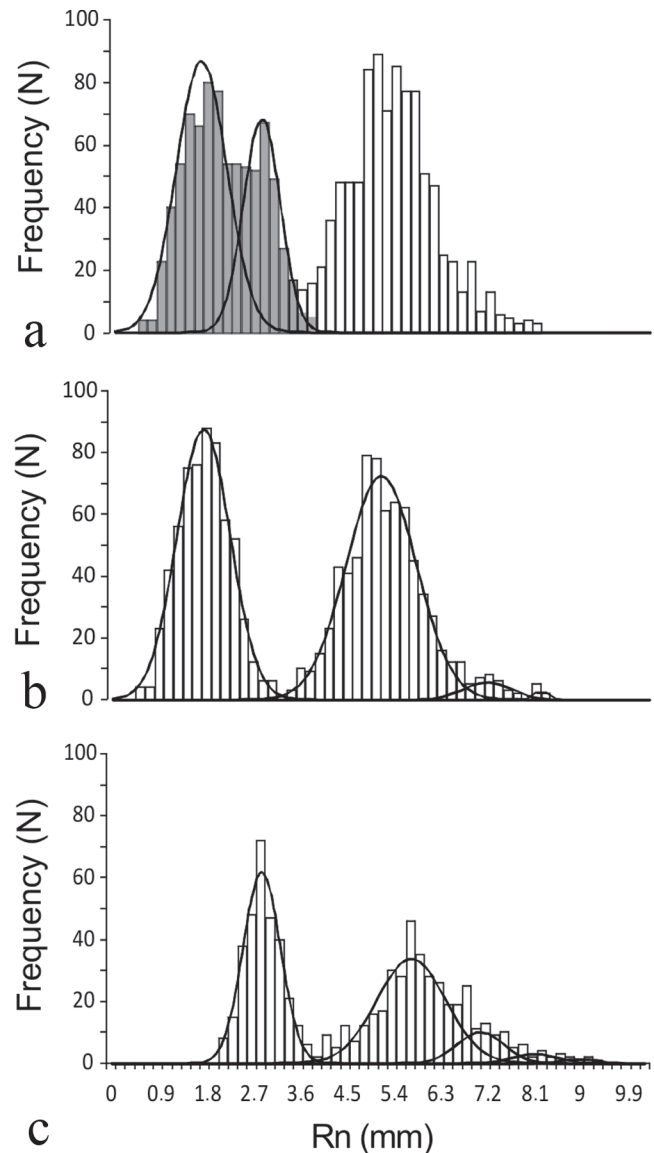


Fig. 4. Total frequency distribution of the scale radius (Rn) and decomposition of first ring measurements (shaded columns) in order to discriminate between the fish from summer and from spring groups (a). Decomposition of polymodal frequency distribution of ring measures from summer group (b) and spring group (c).

five in cohort 2. The maximum number of decomposed normal curves matched the maximum number of growth marks observed in the scales from each group.

Neither of the groups showed significant differences between the female and male Rn comparisons ($p > 0.05$), thus indicating that both sexes have similar growths and enabling a pooling of the data.

The mean value and standard deviation of each normal curve were transformed to TL values by means of the following linear model fitted by least squares to TL-ATR pair wise data:

$$TL = 54.014 \cdot ATR + 47.12 \quad r^2 = 0.7439$$

$$p < 0.001 \quad N = 190$$

The respective back-calculated lengths from this equation are shown in Table 1. Most of the individuals had scales with up to 2 rings, indicating a narrow age structure that likely reflected high mortality rates after the second year of life. For trahiras of three or more years of age, no differences were noted for the length-at-age structures between groups.

Marginal-increment analysis indicated a defined seasonal-growth pattern characterized by a rapid increment in scale radius during the summer season that peaked at the end of that period. In contrast, the growth decreased during the fall, reaching the lowest incremental value, as estimated by the second derivative, at the start of June. This analysis further identified that the initial ring formation is followed by an essentially negligible increment between June and December (Fig. 5). Likewise, the lowest GSI values were recorded during the winter, but then increased from September on up to a peak in January, when the species reproduced. This trend was paralleled by the Kn variation, which increased probably as consequence of gonad development. As would be expected, after spawning the GSI and Kn values decreased, while the marginal growth subsequently increased between January and March.

The fitted von Bertalanffy-curve parameters indicated that the summer group exhibited a faster growth rate and had shorter asymptotic lengths than the spring group (Table 2). Those differences indicated that the maximum growth rate for the summer group took place during the first two years of life, whereas with the spring group the growth rate decreased only after the third year.

A comparison of these von Bertalanffy curves with those obtained by other authors in four pampean shallow lakes (Monte, Lobos, Chascomús, and Indio Muerto) and with those from Ciénaga Grande de Lorica (Colombia); Amanari Maranguape Dam, State of Ceará (Brazil); and Monjolinho Dam, São Paulo (Brazil), illustrated certain significant differences (Table 2, Fig. 6). The Yalca-shallow-lake growth curve was close to those obtained for the Chascomús and Indio-Muerto populations, but differed from those fitted for Monte and Lobos. The greatest divergence, however, was observed with the populations located outside the pampean

Table 1. Back-calculated mean total length (TL) and standard length (SL) at time of scale-ring formation and the respective standard deviations (SD) for each trahira group.

Summer group				
Age (Years)	Mean TL (mm)	SD (mm)	Mean SL (mm)	SD (mm)
1	141.10	74.66	112.16	54.01
2	324.52	83.31	272.68	61.58
3	433.83	71.97	368.35	51.66
4	489.7	54.03	417.30	35.96
Spring group				
1	203.47	66.49	166.75	46.86
2	358.74	82.86	302.63	61.19
3	430.50	71.18	365.43	50.97
4	486.50	69.88	414.44	49.83
5	533.21	67.59	455.32	47.82

region and at lower latitudes, where those trahira attained smaller asymptotic (maximum) sizes.

Discussion

The trahira population-age structure at Yalca shallow lake exhibited a low frequency of individuals older than three years of age, despite the use of a sampling design that employed a set of different fishing methods so as to cover the whole water body and thus sample the entire population. This characteristic age structure is nevertheless in agreement with previous analyses performed at other pampean lakes (Ramirez, 1963; Grosman *et al.*, 2004).

We were able to identify two cohorts per year, which distribution provided a reproductive period that lasted up to three months with several spawning pulses, as is shown in Fig. 5, where female GSI values are highly variable from November to January. This particular reproductive pattern of trahira has been reported by earlier studies (Paiva, 1974; Marques *et al.*, 2001; Bialezki *et al.*, 2002; Rosso, 2007). The presence of those cohorts was validated by the agreement between the maximum number of observed rings and the number of unimodal components in the ring-frequency distribution.

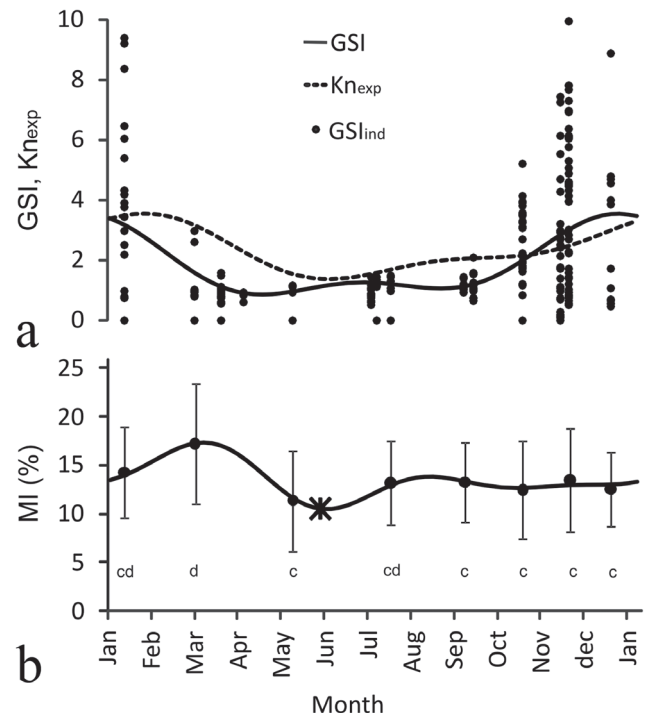


Fig. 5. Trahira annual variation of observed individual Gonadosomatic index (GSI) and its respective fitted model, and expanded condition index (Knexp) curve (a). Mean relative marginal-increment scale index (MI%) and its respective standard deviations at each sampling date with the corresponding fitted model. Asterisk in MI (%) curve indicates the mean date of ring formation. Different letters below the MI% mean values indicate significant differences ($p < 0.05$) (b).

Table 2. Parameters of the von Bertalanffy equation estimated for Yalca shallow lake and for different trahira populations. LT_{∞} : asymptotic total length; K; growth rate; t_0 : theoretical age at zero length; phi: growth performance index.

Environment	LT_{∞} (mm)	K	t_0	phi	Source
Yalca, summer group	486.54	0.57	0.54	5.1	This study
Yalca, spring group	499.69	0.47	0.13	5.1	This study
Chascomús	536.75	0.37	0.02	5	Ramirez, 1963
Indio Muerto	564.38	0.51	0.03	5.2	Grosman <i>et al.</i> , 2004
Monte	817.59	0.08	-0.76	4.7	Domanico, 1998
Lobos	792.06	0.07	-1.02	4.6	Domanico <i>et al.</i> , 1993
Cienaga Grande de Lorica	481.00	0.29	-0.50	4.8	Tordecilla-Petro <i>et al.</i> , 2005
Amanari, Maranguape Reservoir, females	388.01	0.26	-1.29	4.6	Paiva, 1974
Amanari, Maranguape Reservoir, males	452.34	0.19	-1.68	4.6	Paiva, 1974
Monjolinho Reservoir	405.00	0.24	0.10	4.6	Barbieri 1989

In Yalca shallow lake trahira growth exhibited a well defined seasonal pattern, where maximum rates took place during the warm months and almost no growth was observed when temperature dropped below 15°C. This feature has a notable effect during the first year of life because the growth period of the spring group can extend for up to 6 months, whereas that of the summer group lasted for only 3 months before the temperature started decreasing in the fall. As shown by marginal-growth analysis and the growth rate (k) derived from the von Bertalanffy curve, a fast growth was observed for the summer group; with the spring group evidencing a slower rate, though accompanied by a more extensive growth period. These results diverged from those reported by Dománico *et al.* (1993) and Dománico (1998) for the Lobos and Monte shallow-lake populations, where their analyses were made assuming the existence of only a single yearly cohort.

When the population growth at Yalca shallow lake was compared with the corresponding data from lakes located at lower latitudes, such as in Colombia (9°14'N) and Brazil (3°54'S 22°00'S), clear differences emerged in the growth parameters, probably due to differences in the thermal regime. According to Petry *et al.* (2007), the optimal temperature for growth in mass of *H. aff. malabaricus* is 21.4°C; whereas the maximum prey-consumption temperature is 30°C and ceases at some level between 18 and 14°C. The shallow lakes of the lower Salado River basin are exposed to seasonal thermal variations where the temperature ranges between 16°C and 26°C for about 220 days in a given year and drops below 16°C for the rest of the year. This thermal structure represents a notable difference from that of tropical waters, where the species live exposed to 28°C almost constantly (Paiva, 1974; Tordecilla-Petro *et al.*, 2005). Climatic effects also define consequential differences in the metabolic functioning of trahira among temperate, subtropical, and tropical regions. Thus, in the lower Salado-River basin, the thermal seasonality is such that the temperatures oscillate $\pm 5^\circ\text{C}$ around the optimal growth temperature for some 60% of the year. During the remaining days, the low temperatures

may induce “hibernation” (Ramirez, 1964; Ringuelet *et al.*, 1967) and a consequent reduction in metabolic costs.

The seasonal growth of the species was corroborated by an analysis of biological indices, which data demonstrated a differential energy allocation depending on the time of year (Balboni *et al.*, 2009). Certainly during the coldest season, when temperatures fall below 14°C, metabolism must necessarily decrease and prey consumption would be nil. That circumstance, however, is not critical for this species because these fish are adapted to withstand starvation periods of more than 90 days (Petry *et al.*, 2007). Nevertheless, in certain dry winters (with low water levels) temperatures can fall and remain below 5°C for several days, thus promoting massive mortalities (Freyre, 1967; Gomez, 1996; Colautti *et al.*, 1998). Those conditions at higher latitudes may furthermore create an even greater overwinter mortality with pronounced effects on the population age structure that, in turn, would need to be compensated for by larger body sizes and faster growth rates. This kind of population response (countergradient effect) has been found

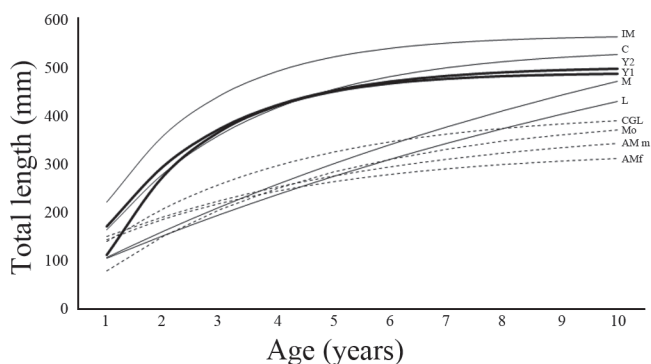


Fig. 6. Von Bertalanffy growth curves of trahira *Hoplias aff. malabaricus* obtained by several studies in South America (see Table 2 for sources information): Yalca summer group 1, Y1; Yalca spring group, Y2; Chascomús, C; Indio Muerto, IM; Monte, M; Lobos, L; Cienaga Grande de Lorica, CGL; Amanari Maranguape female, AM f; Amanari Maranguape male, AM m.

in other fish species (Conover, 1990; Conover & Present, 1990; Power & McKinley, 1997).

At lower latitudes where temperature stays over the maximum value for food conversion by the species all the time, thus generating high metabolic rates and more continuous prey consumption, the reproductive season appears to extend from October to June (Barbieri, 1989; Marques *et al.*, 2001) and is influenced by temperature and precipitation (Marques *et al.*, 2001). In pampean lakes, spawning occurs only in the late spring and early summer, at the start of the favorable season for the species. This strategy of delaying and shortening the reproductive period could be linked to maximization of growth during the part of the year when environmental conditions are better for trahira. That pattern could be considered as an adaptive physiologic and demographic response to cope with broad thermal variation and hydrologic instabilities such as those observed in pampean lakes. Such adaptations may be supported by a particularly evolutionary life history adapted to this geographic area resulting in genetic diversity divergences with other populations (Blanco *et al.*, 2010). In this sense, it is important consider also that *H. aff. malabaricus* may be a group of different species, therefore dissimilarities in behavioral and biological processes among regions could be explained in part by possible taxonomical differences.

If we consider the trahira's reproductive season in shallow pampean lakes and recognize that occasional winter mortality could reduce the reproductive stock so as to promote weak annual cohorts, such considerations would explain why pampean populations show truncated size structures with very low numbers of sizeable adults. Nevertheless, other conditions such as predator-prey relationships, food availability, and fishing practices may also act as controlling forces to regulate the trahira population structure and density in those lakes. The combined action of these influences can therefore shape age structure, thus producing unbalanced populations as was found at the Yalca and other shallow pampean lakes such as Chascomús and Indio Muerto where trahira populations have been studied (Ramirez, 1963; Grosman *et al.*, 2004).

Future efforts should be directed at gathering more sound information based on annual growth, variability in the mechanisms of recruitment, and mortality along with the relationship of these parameters to environmental variables in order to promote a more comprehensive knowledge of population structure and dynamics in pampean shallow lakes.

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