Biological traits and growth patterns of pejerrey *Odontesthes argentinensis*

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This study assesses for the first time the relationship between annual cycles of different biological indices with growth patterns of a marine pejerrey *Odontesthes argentinensis* population near its southern-distribution boundary in North Patagonia. The reproductive period is between September and November evidenced by an increase in the gonado-somatic index with a peak in October corresponding to spawning. The reproductive cycle was also coupled with metabolic processes related to energy allocation as shown by changes in the hepato-somatic index and body condition. Total length (L_T) at maturity was 270 for females and 282 mm for males, whereas fecundity was estimated at mean $\pm$ s.d. $= 9380 \pm 1797$ mature oocytes. Based on the marginal increment analysis, most of the scales showed a maximum value during summer, with a sharp decline thereafter during autumn and winter, indicating that scale rings are formed during the latter period and only once a year. Growth fitted by the von Bertalanffy model for both males and females did not show significant differences and showed a rapid growth during the first 2 years. The shorter reproductive period compared with that of the northern *O. argentinensis* populations inhabiting tropical and subtropical areas was interpreted as an adjustment to temperate environmental conditions. The larger maximum L_T and L_T at first maturity are in agreement with the counter-gradient hypothesis and could be related to the selective effects of low temperature and a shorter growing season. This latitude dependency argues strongly against the application of the same fishing regulations for different *O. argentinensis* populations as a whole and reinforces the need to assess basic biological features at a population scale to promote local sustainable fisheries management. © 2012 The Authors

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Key words: biological indices; latitudinal effects; North Patagonia; reproductive and growth patterns.

INTRODUCTION

The family Atherinopsidae comprises the new-world silversides and is represented by 108 species with a high degree of morphological similarity, but ranging widely in size, habitat, occurrence and ecology (Prodohl & Levy, 1989; Creech, 1991;

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Ivantsoff & Crowley, 1991; Nelson, 2006). Within this family, the genus *Odontesthes* is a monophyletic group encompassing 19 species that inhabit lakes, rivers, estuaries and temperate and tropical coastal areas of South America, although the marine environment is the habitat of the ancestral group (Dyer, 1993, 2006; Beheregaray & Sunnucks, 2001). These species are ecologically relevant as forage fishes and economically significant for fisheries and aquaculture (Sampaio, 2006; Somoza *et al.*, 2008; Colautti *et al.*, 2010), thus generating great interest in their biology (Bemvenuti, 2002).

The species *Odontesthes argentinensis* (Valenciennes 1835), known as the marine pejerrey, is a large-size silverside that at present is considered to be widely distributed along the Atlantic Ocean coast between Sao Paulo, Brazil (25° S), and Rawson (43° S) in Argentina (García, 1987; Dyer, 2000). As for other atherinids this fish shows a great phenotypic plasticity that allows its adaptation to different environments (Bamber & Henderson, 1988) involving a wide range of salinities. The species inhabits both estuaries and inshore waters (Cousseau, 1986), often forming local, isolated populations (Beheregaray & Levy, 2000). This geographic isolation promotes the development of differing biological features among populations, such as egg morphology, spawning period and genetic structures that reflect local environmental characteristics (Phonlor & Cousin, 1997; Beheregaray & Levy, 2000; Moresco & Bemvenuti, 2006).

Certain aspects such as feeding habits (Bemvenuti, 1987), morphometry (Bemvenuti, 2002), comparative osteology (Bemvenuti, 2005) and genetic structure (Beheregaray & Levy, 2000; Beheregaray & Sunnucks, 2001) have been studied in brazilian populations of *O. argentinensis*. The reproductive biology of this species, however, has been assessed only in a subtropical marine area of southern Brazil (32° S) (Moresco, 2006; Moresco & Bemvenuti, 2006), where environmental conditions differ greatly from those in temperate areas in North Patagonia (40° S). Other relevant population attributes such as age, growth and their related variables remain uninvestigated.

Populations of *O. argentinensis* are economically significant resources for local fisheries in southern Brazil, Uruguay and Argentina (De Buen, 1953; Chao *et al.,* 1985; Sampaio, 2006). As a shallow-water pelagic fish, the species is captured in Brazil by artisanal fishing in the Laguna dos Patos, (Moresco, 2006) and is exploited in Argentina by recreational and artisanal fisheries in Buenos Aires Province (Llompart, 2011; Llompart *et al.,* 2012) as well as on the coast of Chubut Province, where this species represents the second most fished species after *Odontesthes smitti* (Lahille 1929) (M. A. López, unpubl. data). Although in North Patagonia (San Blas Bay), Llompart *et al.* (2010) reported three silverside species inhabiting the coastal areas, including *Odontesthes platensis* (Berg 1895), *O. smitti* and *O. argentinensis* (Bemvenuti, 1993), only *O. argentinensis* is captured both by artisanal fishing during the colder months and by inshore recreational fishing during the warmer months. Despite the species significance for small-scale fisheries and wide distribution range, knowledge of its main biological features is lacking. The understanding of the biology and life cycle together with knowledge of breeding areas and fisheries stock assessments are required for defining suitable policies for fishing regulations. Therefore, local assessments have special importance to such populations distributed across broad latitudinal ranges. As *O. argentinensis* is a South Atlantic silverside that inhabits a wide latitudinal range, an appropriate knowledge of biological characteristics,

including estimations of growth patterns, is critical because of possible differences based on specific adaptations to cope with variable environmental conditions across latitudes.

The aim of this study was to assess, for the first time, aspects of the annual cycle of key biological indices of *O. argentinensis* and relate them to the growth patterns for a population inhabiting a region near the southern-distribution boundary of the species; to compare the results with those from populations inhabiting lower latitudes and to highlight the relevance of such features for developing management options.

MATERIALS AND METHODS

STUDY AREA

The study was carried out in San Blas Bay off the coast of Jabalí Island (40° 33′ S; 62° 14′ W), Buenos Aires Province, at the border of the northern boundary of Patagonia (Fig. 1). This area is included in a nature reserve of multiple uses belonging to Anegada Bay, encompassing several types of coastal environments, *e.g.* marshes, tidal plains and sandy beaches (Penchaszadeh *et al.*, 2003). The bay contains small islands with banks connected by a diffuse network of channels with depths ranging from 10 to 24 m within the main channel (Lucifora, 2003). A distinctive feature of the area is the presence of the San Blas Channel, a tidal-inlet system that connects the bay with the sea. This channel is 2·5 km wide and 12 km long and has a maximum depth of 28 m (Cuadrado & Gómez, 2010, 2011). The tidal regime in San Blas Bay is predominantly mixed semi-diurnal with a maximum amplitude of 2·56 m and minimum of 1·73 m (SHN, 2009). The water temperature ranges from 6° C in winter to 20° C in summer, while the salinity varies between 32·5 and 35·0 (Borges, 2006). The climate of the region is dry (300 mm of precipitation per year), and the prevailing winds are from the north-west.

SAMPLING AND DATA COLLECTION

Samples were obtained from the coastal areas of San Blas Bay by using floating gillnets of different bar mesh sizes (15, 19, 21, 26, 32, 35 and 40 mm). The sampling was carried out monthly during a nocturnal tidal cycle between June 2008 and May 2009. In all the individuals, the total length (L_T, mm) was measured and the total mass (M_T, g) and the gonad (G_M, g) and liver (L_M, g) masses were recorded. The fish were classified according to sex and identified as juvenile (0) or adult (1) based on visual gonad analysis following Vazzoler (1996). An additional sampling was carried out during the peak reproductive period in order to conduct a fecundity study on ripe females. During the study period, the temperature of sea water was recorded daily with an automatic temperature logger (Thermochron iButton; www.maximintegrated.com).

BIOLOGICAL INDICES AND REPRODUCTION

To quantify the relative seasonal changes in the masses of the gonads and the liver, the gonado-somatic index (I_G) and hepato-somatic index (I_H) were calculated as follows: $I_G = 100 \, G_M M_T^{-1}$ and $I_H = 100 \, L_M M_T^{-1}$. The index values for each organ were averaged for each month and plotted together with S.D. to elucidate the relationship among them. In order to assess the seasonal fluctuations in fish plumpness, the relative condition factor (K_N) was used (Le Cren, 1951). This index is useful for describing variations in value around the mean condition independent of fish size and has been used as the index for assessing the condition of silverside populations as a function of trophic status and spawning periods (Baigún *et al.*, 2009). The index is calculated following the formula: $K_N = M_T M_E^{-1}$, where M_E is the length-specific mean mass predicted by the population M_T and L_T relationship, with the latter being estimated by the least-squares regression from M_T and L_T pair-wise data. In addition,
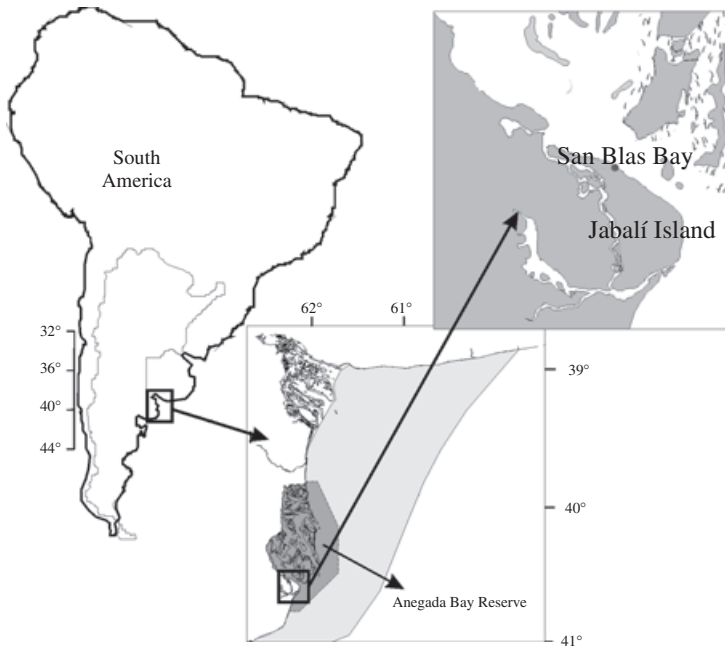
FIG. 1. Geographic location of Anegada Bay Reserve, and details of the sampling zone (San Blas Bay and Jabalí Island).

the relative somatic condition factor (K_S) was calculated as $K_S = M_{TG}W_E^{-1}$ (Vazzoler, 1996), where M_{TG} is the total mass in g without gonads. The difference between K_N and K_S was also calculated in order to assess changes in mass linked to the reproductive cycle. Before making the K estimations, differences in the M_T and L_T relationships between the sexes were compared by means of ANCOVA, and the slopes of regressions (b) in the M_T and L_T relationships were tested for allometry ($H_o:b = 3$) through the use of the t-test described in Zar (1999).

Analysis of sexual maturation patterns as a function of L_T was fitted to a logistic model through the use of binomial maturity data: $Y = (1 + e^{-(a+bX)})^{-1}$, where Y is the proportion of adult individuals and X is the L_T class. The mean L_{T50} (size at which 50% of the population reaches maturity) is given by $-ab^{-1}$ (Mollet *et al.*, 2000). The sex ratio was estimated for the whole sampling period and the difference from 1:1 was analysed by the χ^2-test (Zar, 1999). The I_G index was applied to describe the annual gonadal cycle for each sex and to determine the length of the spawning season.

Ovaries belonging to ripe females were examined to obtain the annual fecundity (F_A). This variable was evaluated by a volumetric method (Vazzoler, 1996) that involved counting the number of mature oocytes ready to be released through the use of three replicate 2 ml samples of ovary from each female. The F_A was then calculated as the average number of oocytes in the three replicates multiplied by total volume of the female gonads. Only values $< 10\%$ of the coefficient of variation (C.V.) between replicates were considered for fecundity estimates. Finally, variations of F_A values were tested against L_T and M_T by regression analysis and the Pearson correlation coefficient was calculated.

GROWTH

Scale readings were used for determining age and growth. The scales were removed from the middle left side of the individual above the lateral line and thereafter placed in paper envelopes. The scales were selected on the basis of symmetry and similarity in size and then

individually cleaned with an enzymatic soap, brushed, rinsed and finally fixed on 10×15 cm glass plates. The scale images were obtained with a digital camera (Infinity 3) mounted on a microscope (Olympus SZ61; www.olympus.com) and the scale sizes thereafter were measured by the software Infinity Camera 5.0.2.

Scale annuli identification followed the criteria outlined by Bagenal & Tesch (1978). The total radius (R_T) was measured from the focus to the most distant point of the anterior scale margin. Each successive growth radius (R_N) was measured over this axis at a precision of 1 μm. All the scales were analysed by two independent readers. The indices of average per cent error (IAPE; Beamish & Fournier, 1981) and C.V. (Chang, 1982) were used to determine the precision of age interpretation. Differences between readers were also assessed by an age bias plot (Campana *et al.,* 1995). If C.V. exceeded 5%, a sub-set of scales that account for major disagreements were re-examined by the two readers together, in order to resolve differences in age estimates.

The R_N values were grouped according to sex at intervals of 0·1 mm and the R_N-frequency distributions obtained were decomposed into their normal components to estimate the mean R_N value for each growth annulus and the respective S.D. (Quinn & Deriso, 1999). The sex differences between same orders of R_N mean values were assessed by the *t*-test (Zar, 1999). The average R_T was calculated for each individual (R_{TA}), and a linear model was fitted to the L_T and R_{TA} relationship to obtain the back-calculation equation for estimating the average fish L_T at each mean R_N.

To determine the periodicity of annulus formation and validate the age estimation, the percent of marginal increment (M_I%) was calculated on the basis of individuals from the best represented cohorts through the following formula, $M_I\% = (T_R - R_{NL}) \, 100 \, R_T^{-1}$, where R_{NL} is the distance along the radius from the focus to the latest annuli.

A first-order Fourier harmonic model was fitted to the mean M_I% for each sampling date data pair to obtain a seasonal description of the annulus formation process (Freyre *et al.,* 2009). The mean annulus formation date was defined as the time when the model predicts the minimum M_I% value. The polynomial was fitted by means of least-squares regression and the coefficient of determination (r^2) was calculated between the average monthly M_I percentages observed against the estimated values.

The mean date of annulus formation was used to place the L_T at each annulus formation along the fish age axis and the results of reproductive analysis were used for determining the mean birth date (age-0 years). After that, the von Bertalanffy growth model was fitted by means of the generalized least-squares method by using the following formula: $L_T = L_\infty[1 - e^{-k(t-t_0)}]$, where L_T = length of a fish at moment t in mm, t = time in years, L_∞ = total asymptotic length in mm, k = growth coefficient and t_0 = hypothetical time at zero L_T.

RESULTS

The L_T values of females ranged between 161 and 441 mm, with greater lengths attained than in males (L_T from 186 to 394 mm). The M_T and L_T relationships between the sexes, however, were not significantly different (ANCOVA, d.f. = 874, $P > 0.05$); thus, the following relationship was derived for the population as a whole: $M_T = 3 \, 10^{-6} L_T^{3 \cdot 13}$ ($r^2 = 0.95$, $n = 876$, $P < 0.01$).

The slope, b, of the M_T and L_T relationship was significantly different between the sexes and > 3 (*t*-test: $t = 5 \cdot 529 > t_{(0 \cdot 05, \, n > 100)} = 2 \cdot 32$), thus indicating positive allometric growth.

According to the reproductive cycle indicated by the female's I_G values, gonad ripening took place between September and November with a peak in October, when the seawater temperature reached 15° C. Thereafter, the I_G values strongly decreased during November, indicating that spawning mainly occurred between October and November and ended in December, when the water temperature rose to *c.* 20° C,
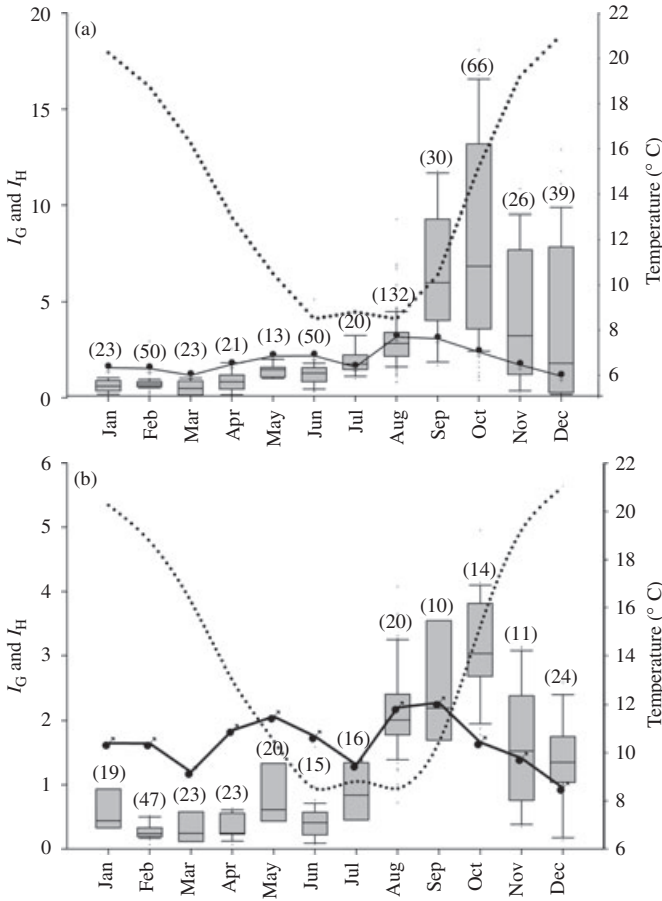
FIG. 2. Box plot of monthly values of the gonado-somatic index (I_G) (–•–, first quartile, mean and third quartile) and its respective s.d. together with hepato-somatic index (I_H) and coastal seawater temperature (⋯⋯⋯) for (a) females and (b) males. Numbers above the boxes (in parentheses) refer to the number of *Odontesthes argentinensis* analysed in each month.

indicating that births take place mainly in November. From January to August, the I_G values remained low, corresponding to the gonad resting period [Fig. 2(a)]. Accordingly, the I_H from females gave the maximum values before the I_G increased, showing first a peak during August and September and then a decrease until December [Fig. 2(a)].

In males, gonad ripening took place earlier than in females, ranging mainly from August to November [Fig. 2(b)]. Nevertheless, and similar to the situation in females, the maximum I_G was observed in October, thereafter decreasing in January and remaining low until July. In contrast, the I_H exhibited an initial peak in May, but went through a maximum during August and September before the I_G peak [Fig. 2(b)].

The value of K_N did not show variations throughout the year (Fig. 3). Upon elimination of the effect of gonad mass in females, a decrease became evident in K_S during October [Fig. 3(a)]. In males, a similar difference was also observed during
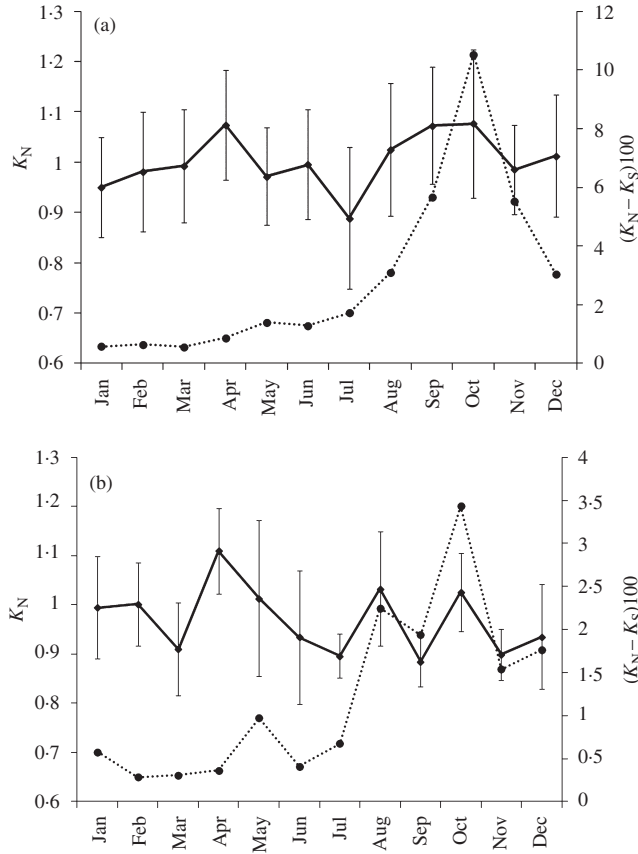
FIG. 3. Monthly variation of relative condition factor (K_N) (◆) with its respective S.D. and difference between K_N and somatic condition factor [($K_N - K_S$) 100] (●) for (a) females and (b) males.

September and October [Fig. 3(b)], indicating that the increase in gonad mass in males took longer, but was less pronounced than for females.

Considering the 12 months sampling period, the sex ratio was 2·01:1, significantly different from parity ($\chi^2 = 99.69$, $P < 0.05$, d.f. = 1). In addition, the L_{T50} varied between the sexes, being 270 mm in females and 282 mm in males.

Thirty-two mature females between 302 and 359 mm L_T were used for fecundity analysis. The estimated mean ± S.D. F_A was 9380 ± 1797 mature oocytes per female. The mean ± S.D. number of mature oocytes g^{-1} of gonad was 206 ± 60 and the same g^{-1} of fish total body mass was 27 ± 4. A significant exponential relationship was found between F_A and L_T ($F_A = 0.072\ L_T^{2.39}$, $r^2 = 0.55$, $P < 0.05$) as well as between F_A and M_T ($F_A = 53.18\ M_T^{0.88}$, $r^2 = 0.60$, $P < 0.05$).

AGE AND GROWTH

The bias plot (Fig. 4) and simple regression analysis showed an agreement between the two readers. The values from both IAPE and C.V. indicated a good level of
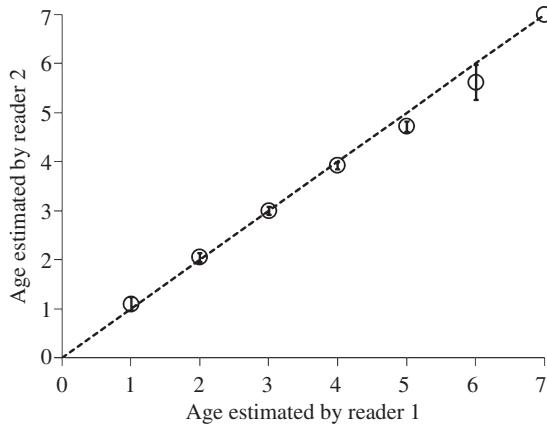
FIG. 4. Age bias graph between reader 1 and reader 2. (............), 1:1 equivalence. Observed values (○) with its respective 95% C.I.

precision for readings (Table I), suggesting that the scales of *O. argentinensis* are appropriate structures for age estimation.

Based on marginal increment analysis, most scales showed a maximum value during summer and a sharp decline during autumn and winter, indicating that marks are formed during this period and once a year. The Fourier first-order model ($r^2 = 0.7$, $P < 0.05$) showed that within an annual cycle the lowest value of edge scale occurs at the beginning of September (Fig. 5).

The polymodal decomposition of males, females and pooled-R_N frequency distributions allowed the identification of up to seven unimodal components that, based on the $M_I\%$ results, were assigned to yearly marks. The mean ring length at each age did not differ between the sexes, indicating that the growth of both males and females is similar (Table II). The linear model fitted to the L_T and R_{TA} data was used for the back-calculation as follows: $L_T = 64.83\,R_N + 8.411$ ($r^2 = 0.9$, $P < 0.01$). Table II shows the mean ring length and the respective back-calculated L_T for the whole population. The fitted von Bertalanffy curve coefficients with 95% C.I. in parentheses were L_∞ (mm) $= 422.74$ ($391.26-454.22$), k (years^{-1}) $= 0.38$ ($0.31-0.48$) and t_0 (years) $= 0.03$ ($0.08-0.15$) ($r^2 = 0.99$, $P < 0.01$). The model

TABLE I. Assessments of precision between readers

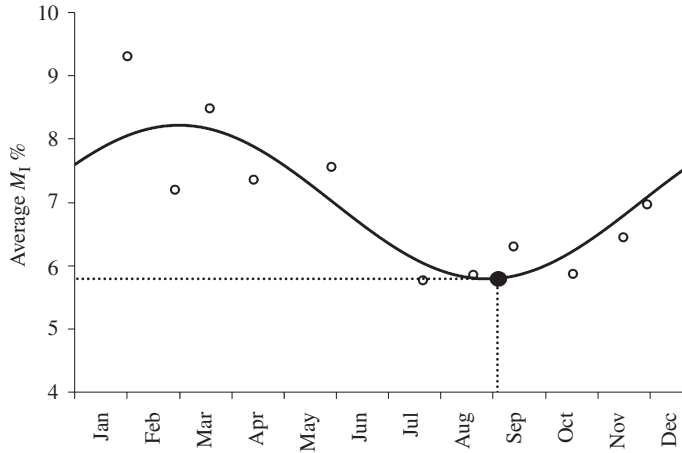| Statistic or index	Reader 1 *v.* reader 2
n	1757
r^2	0·86
P	<0·001
C.V. (%)[a]	4·6
Average per cent error[b]	2·7
Per cent agreement	81·7

[a]From Chang (1982).
[b]From Beamish & Fournier (1981).

FIG. 5. Changes of marginal increment (M_I%) during the year. Monthly observed average values (○) and estimated values by the fitted Fourier model (——). The interception at (●) refers to the date when the model assumes the lowest value.

indicates a rapid fish growth during the first 2 years, attaining up to 52% of the asymptotic length (Fig. 6).

DISCUSSION

This study represents the first attempt to describe the intra-annual changes in biological indices, some reproductive aspects and their links with growth patterns for *O. argentinensis* in the south-western Atlantic Ocean. The reproductive characteristics indicated by changes in gonad development, sex ratio, first mature size, spawning period and fecundity, coupled with changes in somatic plumpness and growth, represent key features related to this specie's life-history patterns and how they could be related to management.

TABLE II. Mean scale annuli lengths according to age for females (R_{NF}), males (R_{NM}) and statistical significance by *t*-test (P); whole population mean annuli lengths at age (R_N), S.D., sample size (n) and back-calculated total lengths (L_T) at each age

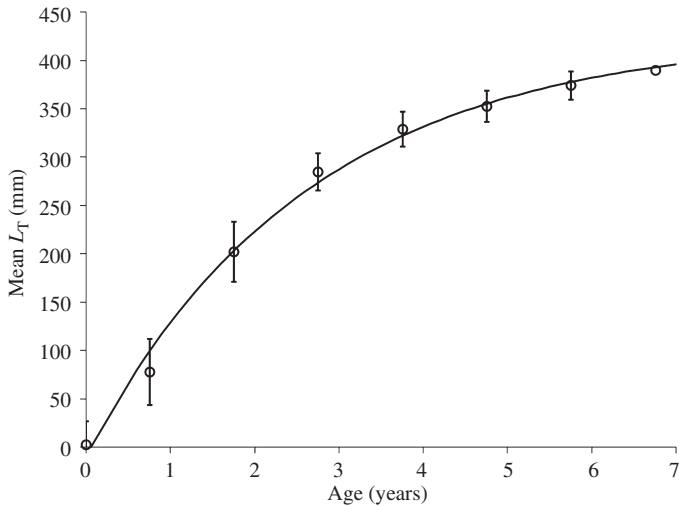| Annuli	Age	R_{NF}	R_{NM}	P	R_N	S.D.	n	L_T (mm)
1	0.75	1.05	1.07	0.06	1.08	0.24	1525.50	78.18
2	1.75	3.00	2.96	0.10	3.00	0.40	1660.73	202.67
3	2.75	4.25	4.24	0.76	4.27	0.35	1617.04	285.05
4	3.75	4.92	4.94	0.19	4.94	0.17	543.95	329.03
5	4.75	5.38	5.38	0.92	5.31	0.15	192.53	352.94
6	5.75	5.71	5.74	0.37	5.64	0.12	43.13	374.29
7	6.75	5.94	6.04	0.09	5.89	0.10	17.37	390.18

FIG. 6. Total length (L_T) at age observed values (O) with their S.D. and the fitted von Bertalanffy growth curve.

BIOLOGICAL INDICES AND REPRODUCTIVE PATTERNS

According to the results from the I_G values and the difference between the K_N and K_S indices, *O. argentinensis* populations from San Blas Bay are iteroparous and reproduce once a year, in a narrow spawning period. The dynamics of the monthly values for those indices showed that the spawning period extended to *c.* 2 months a year (*i.e.* October to November), although a few individuals remained in the mature state in December. This result differs from the findings of Moresco (2006) in subtropical areas of Brazil, where the main breeding season for *O. argentinensis* extends over 5 months (from August to December). During this period, reproduction occurred in successive batches within marine populations or even extended throughout the year in estuarine populations (Moresco, 2006). The reproductive cycles of other *Odontesthes* marine species from the Argentine coastal waters are similar to those recorded for *O. argentinensis* in the San Blas Bay exhibiting one spawning season per year lasting for 2 or 4 months as was shown by *O. smitti* in the coastal areas of Mar del Plata (38° S), spawning from July to August (Macchi, 1993), and by *O. nigricans* in the Golfo Nuevo (42° S), spawning from July to October (M. A. López, unpubl. data). These differences in reproductive strategies could be explained by the assertion of Nikolsky (1963) that species of tropical and subtropical regions are characterized by a long reproductive period during which they eliminate more than one batch of oocytes. As the southern Brazilian coastal platform has been considered a centre for radiation of *O. argentinensis* (Beheregaray & Levy, 2000), this suggests that the population of this species inhabiting the cold, temperate climate of San Blas Bay has adjusted its reproductive strategy by adopting a single spawning period during a time window encompassing only the spring months. This shorter reproductive period as compared to the northern *O. argentinensis* population is in agreement with the hypothesis of Conover (1992) who stated that in populations from higher latitudes spawning should occur during a short time window, and early

in the growing season in order to increase the likelihood of winter survival among the young-of-the-year.

Despite the differences in the reproductive cycles of the *O. argentinensis* populations from Argentina and Brazil, their spawning always occurs when the temperature falls below 20° C. Moreover, Streit *et al.* (2010) showed that the optimal temperature for the highest growth rate in early juveniles of this species was reached at 23° C, a value that is similar to the seawater temperature found in San Blas Bay during December and January after the spawning season has ended. This observation implies that this species could adjust its reproductive cycle in accordance with the annual temperature patterns at different latitudes. Furthermore, the photoperiod, as an environmental influence that co-varies with temperature at high latitudes, has been considered as a relevant variable in triggering the reproductive processes of many fishes in general (Bromage *et al.*, 2001; Migaud *et al.*, 2010), as well as of silversides in particular (Miranda *et al.*, 2009). Therefore, these regional differences in reproductive events observed in geographically separate populations of *O. argentinensis* should be considered as the result of interactions between environment, behaviour, physiology and genetic make-up. Accordingly, life-cycle differences among *O. argentinensis* populations over a wide range of geographical distribution could be explained by ecological divergences that, in turn, might eventually result in complete reproductive isolation (Turner, 1999; Beheregaray & Levy, 2000).

The reproductive cycle was also coupled to metabolic processes related to energy allocation as shown by the I_H. The liver performs a two-fold function of a biochemical processor and a labile reservoir of glycogen and lipids (Freyre *et al.*, 2009). The I_H in females was the highest in August and September, possibly to assist ovary development before the annual reproductive period. In comparison, the I_H in males has two peaks, each occurring just before the time of faster growth, as indicated by the I_G values. This pattern could be related to the seasonality of the male reproductive behaviour, as the males maintain an ongoing activity for nearly 4 months. Similar differences in the duration and timing of the reproductive period between the sexes of *O. argentinensis* have also been recorded in other Atherinopsidae (Miranda & Somoza, 2001).

The lack of extensive oscillations in the condition index along with the seasonal changes recorded in both the I_G and the I_H support the notion that from August to October energy intake and reserves are mainly directed at satisfying the demands of the reproductive cycle. This pattern was also clear during those months when declines in the K_S values and in the difference between K_N and K_S was more evident. In contrast, during the remaining months of the year, the species could be investing energy in growth. These observations indicate that the energy demands for reproduction necessitate a reallocation of the energy that would otherwise be used in somatic growth (Becker *et al.*, 2003).

Differences in environmental temperature appear to influence reproductive traits. Strüssmann *et al.* (1996) stated that if larvae of *O. argentinensis* are reared at a temperature between 18 and 21° C, the sex ratio becomes skewed in favour of females, whereas populations that are almost entirely males are produced at either higher or lower temperatures than that range. This observation agrees with the present finding that the highest female:male occurred within the temperature range recorded in the study area. A similar pattern in the occurrence of high female to male ratios has also been observed in other silverside populations (Moresco, 2006; Moresco

& Bemvenuti, 2006) as well as in additional species belonging to *Odontesthes* (Miranda & Somoza, 2001). The phenomenon of sex determination by temperature has also been demonstrated in many species of captive silversides and is referred to as temperature-dependent sex determination (Strüssmann *et al.*, 2010). In wild populations, however, there are several other explanations for differences in the sex ratio, such as differential mortality rates between the sexes, adaptation to overfishing and local migration for spawning (Wu *et al.*, 2001).

The mean $\pm$ S.D. F_A obtained in this study (9380 $\pm$ 1797 oocytes female^{-1} year^{-1}) was close to the values obtained by Moresco (2006) (10 014 oocytes female^{-1} year^{-1}; L_T range 212–342 mm) and by Bemvenuti (1987) (10 738 oocytes female^{-1} year^{-1}; L_T range 182–310 mm), both in the coastal areas of southern Brazil. These values suggest that, even with a limited breeding season during the favourable months of the year, the *O. argentinensis* population of San Blas Bay spawns once and the number of oocytes year^{-1} produced is similar to the figure documented for populations from more northern latitudes. These values were very high compared to those recorded for the smaller sized *Odontesthes incisa* (Jenyns 1841) (322–904 oocytes female^{-1} year^{-1}; Ciechomski, 1972). These authors also pointed out that a potential curve was the best fit for the relationship between L_T or M_T and F_A. The relative fecundity (oocytes g^{-1} of ovary) estimated for *O. argentinensis* in this study was, however, lower than that recorded by *O. smitti* (mean $\pm$ S.D. = 422 $\pm$ 123) for adult females ranging in L_T between 290 and 390 mm (Macchi, 1993), while the relative fecundity in oocytes g^{-1} of M_T (mean $\pm$ S.D. = 27 $\pm$ 4) was lower than the corresponding figure for *Odontesthes regia* (Humboldt 1821) (mean $\pm$ S.D. = 57 $\pm$ 9.6) (L_T range 140–180 mm) from the coastal areas of Perú (Alfaro *et al.*, 2006).

GROWTH

Growth represents one of the most critical parameters related to life-history patterns and therefore should be assessed with high accuracy, particularly when the results are intended to be used for the purpose of fishing management (Campana, 2001). Calcified structures in fishes exhibit periodic growth and are thus useful for age determination. Several authors (Casselman, 1983; Kimura & Lyons, 1991) have stated that age determinations are related both to the criteria applied for that estimation and to the subjectivity existing in the readers. In this study, the bias and precision observed after comparing two independent scale reading assessments suggest that scales represent reliable structures for estimating the age and growth of this species. Moreover, the growth parameters estimated for *O. argentinensis* fell within the typical values found for other Atherinopsidae characterized by a life cycle ranging from 3 to 10 years and a maximum L_T between 150 and 750 mm (Becker *et al.*, 2003).

In temperate regions, the formation of annual rings is generally linked to environmental seasonality and is especially affected by the lower temperature and the shorter photoperiod experienced by fishes in winter, both conditions that reduce growth rates (Bagenal & Tesch, 1978). Annual annuli development could also be influenced by reproduction, as has been documented in other silversides (Sverlij & Mestre Arceredillo, 1991; Creech, 1992), particularly in the South American Atherinopsidae, the members of which spawn in winter (Vila *et al.*, 1981; Bemvenuti, 1987; Macchi, 1993). Thus, a determination of the relative influence of winter or reproduction on

annual annuli formation becomes difficult (Becker *et al.*, 2003). In this study, the lowest value of $M_I\%$ that was identified as an annual mark was recorded at the beginning of September (*i.e.* the end of winter) and thus at the time when the reproductive period starts, with most of the available energy being translocated from liver to gonads.

The size-range distribution obtained for *O. argentinensis* in San Blas Bay (40° S) was similar to that found by García (1987; 36–38° S) and M. E. Ré (pers. comm.; 42° S) in other areas of the Argentine seas. In contrast, the maximum L_T in this study was higher than those reported for southern Brazil (360 mm at 32° S; Bemvenuti, 1987; Moresco, 2006; Moresco & Bemvenuti, 2006). Moreover, the L_{T50} exceeded those values found at lower latitudes, where *O. argentinensis* matured at only 230 mm L_{T50} (Bemvenuti, 1987). This discrepancy could support the hypothesis of a latitudinal shift with respect to certain life-history variables for silversides with wide distribution ranges and heterogeneous environmental conditions, where the water temperature and the length of the growing season exert strong influences on the growth patterns (Conover, 1992). Several reasons that are not mutually exclusive could explain the trade-off between growth patterns and environmental characteristics at different latitudes: (1) a size-selective mortality in winter may be more pronounced in high latitude populations, thus leading to a differential survival of individuals of faster growth, whereas a higher proportion of fish with slower growth rates could survive at lower latitudes, (2) the growth of fish populations at lower latitudes where species diversity is greater could be subject to greater restrictions because of the availability of food owing to interspecific competition, so that fish in these populations would grow at rates below their maximum physiological potential and (3) compensatory mechanisms in the form of counter-gradient variation may exist to counteract the negative effects of low temperature and a shorter growing season. This trade-off between growth rate and latitude can thus be explained as a pattern of size selection related to winter survival. In such a scenario, the larger fish contain greater reserves of stored energy (in terms of body mass and potentially oxidizable tissue stores) for surviving at higher latitudes where winters are longer and colder, with size being accordingly less essential for survival at lower latitudes (Conover & Present, 1990; Billerbeck *et al.*, 2000; Arnott *et al.*, 2007). By means of this mechanism, fish of high latitudes must have a greater growth capacity in order to offset the shortness of time available for growth (*i.e.* seasonal growth).

The yearly energy allocation, reproductive features and growth patterns detected in the *O. argentinensis* from San Blas Bay are in agreement with the hypothesis of the latitudinal counter-gradient adaptations described by Conover (1992) for Atlantic silverside *Menidia menidia* (L. 1766), an annual silverside from the northern hemisphere. Thus, *O. argentinensis*, as a species from the southern hemisphere silverside that live up to 7 years of age, could be an appropriate model for testing the multiannual cumulative results of latitudinal counter-gradient effects that, in this instance, could explain the greater L_T attained by the southern populations.

In conclusion, the findings from this study not only constitute new information on the principal biological characteristics of *O. argentinensis*, but also may have important consequences for developing management policies. Clearly, the populations inhabiting the northern areas of Patagonia show biological traits different from those of lower latitudes. As adequate fishery management policies must necessarily be strongly dependent on life-history characteristics such as natural mortality, growth and reproductive features (Beddington & Kirkwood, 2005; Hoggarth *et al.*, 2006),

this latitude dependency argues strongly against the application of the same fishing regulations for the different *O. argentinensis* populations as a whole. The results presented here reinforce the need to investigate and characterize the specific life-history patterns for any species that inhabits wide latitudinal ranges or ecosystems with differing environmental features.

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