

Seasonal variations in the growth of anchovy larvae (*Engraulis anchoita*) on the Argentine coastal shelf

EZEQUIEL LEONARDUZZI, DANIEL R. BROWN and RAMIRO P. SÁNCHEZ

Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Paseo Victoria Ocampo N°1, B7602HSA, Mar del Plata, Argentina. E-mail: eleonard@inidep.edu.ar

SUMMARY: Age and growth rates of the anchovy larvae (*Engraulis anchoita*) in Argentine waters were estimated by analysing daily growth increments in sagittal otoliths under light microscope. The samples were collected during 2000 on the Argentine coastal shelf using a Bongo net. A total of 251 larvae were analysed (size range 3.5 to 12.2 mm standard length). Length-at-age and standard length-otolith radius relationships were best described by linear models. We put forward the hypothesis of differential larval growth in anchovy in relation to seasonality. Mean growth rates at four days before capture were determined by back-calculation and analysed in relation to temperature. The growth rate values obtained from the linear growth models were 0.51 mm day⁻¹ (spring), 0.41 mm day⁻¹ (summer) and 0.42 mm day⁻¹ (autumn). Significant variations were detected between spring and summer and between spring and autumn. These variations do not seem to be associated with a thermal influence.

Keywords: anchovy, *Engraulis anchoita*, larval growth, otoliths, age.

RESUMEN: VARIACIONES ESTACIONALES EN EL CRECIMIENTO DE LARVAS DE ANCHOÍTA (*ENGRAULIS ANCHOITA*) EN LA ZONA COSTERA ARGENTINA. – Se determinó la edad y el crecimiento de larvas de anchoíta (*Engraulis anchoita*) mediante el conteo y medición de los incrementos diarios de los otolitos sagitta. Las larvas fueron capturadas en la Plataforma Costera Argentina durante el año 2000 por medio de una red Bongo. Se analizaron un total de 251 larvas entre 3.5 a 12.2 mm. Las relaciones talla-edad y talla -radio del otolito se representaron mediante modelos lineales para cada estación del año (primavera-verano-otoño). La mayor tasa de crecimiento, calculada como la pendiente de los modelos talla -edad, se registró en primavera (0.51 mm día⁻¹) la menor en verano (0.41 mm día⁻¹), mientras que otoño presentó una tasa de crecimiento intermedia (0.42 mm día⁻¹). Si bien no se encontraron diferencias significativas en las tasas de crecimiento entre verano y otoño, sí las hubo entre primavera y verano y entre primavera y otoño. Se calculó una tasa de crecimiento larvaria 4 días antes de la captura mediante retrocálculo y se la relacionó con la temperatura. Las variaciones en el crecimiento no parecen relacionarse con la influencia térmica.

Palabras claves: anchoíta, *Engraulis anchoita*, crecimiento larval, otolitos, edad.

INTRODUCTION

The anchovy *Engraulis anchoita* is the most abundant and widely distributed pelagic species in the south western Atlantic. The Argentine shelf is the largest in the southern hemisphere with a total area of about 1000000 km². Two stocks of anchovy have been identified on the Argentine Shelf: the Bonaerensis stock (34°S-41°S), and the Patagonian stock

(41°S-48°S) (Hansen *et al.*, 1984; Ratti, 1986). Commercially the Bonaerensis stock is the most important and biomass fluctuations from one to six millions tons have been detected (Hansen, 2004). Apart from its commercial value, the anchovy has a relevant ecological role, as it is one of the main components of the diet of other commercial species such as hake (Angelscu, 1982), and also of marine mammals (Crespo *et al.*, 1997) and sea birds (Mauco *et al.*, 2001).

TABLE 1. – Sampling data, number of larvae analysed and sea surface temperature.

Location	Cruise name	Station	Date of cruise	Range (mm)	n	Sea surface temperature (°C)
Additional 1	CC 02	summer	18-Jan	4.0-12.2	76	21.0
E.P.E.A.	CC 04	summer	03-Feb	3.7-6.0	19	21.3
E.P.E.A.	CC 09	autumn	29-Mar	4.0-11.1	30	19.3
E.P.E.A.	CC 13	autumn	10-May	3.5-9.8	48	16.9
E.P.E.A.	CC 15	autumn	20-May	4.3-5.8	7	15.0
E.P.E.A.	CC 32	spring	03-Nov	4.0-6.5	22	12.6
E.P.E.A.	CC 34	spring	17-Nov	4.2-6.8	12	13.6
Additional 2	CC 35	spring	21-Nov	6.3-11.2	24	12.6
E.P.E.A.	CC 37	spring	01-Dec	3.9-10.2	30	15.5

The reproductive activity of the Bonaerensis stock occurs throughout the whole year; however, massive spawning takes place during spring, mostly in waters shallower than 50 m (Sánchez and Ciechowski, 1995), covering an area of 100000 km². A second spawning peak occurs in autumn. The extensive distribution of the spawning sites implies that the species is subject to a broad range of environmental conditions at time of the eggs and larvae development.

Factors affecting the recruitment level are crucial during larval periods. Larval survival is related to growth and mortality (Houde, 1996), i.e. accelerated growth reduces the period during which individuals are smallest and are therefore more vulnerable to predation (Bailey and Houde, 1989). Since the study by Panella (1971), the analysis of daily growth increments in otoliths has been applied broadly to age various fish larvae and juveniles, thereby contributing to the knowledge of vital parameters (age, growth and mortality). These records of daily events during the early life history of fish, remain unaltered through time (Jones, 1992). The studies of vital parameters of larvae throughout the reproductive season therefore contribute to the recruitment knowledge of this species.

Previous reports on larval growth of *E. anchoita* have mainly been carried out in Brazilian waters (Castello and Vasconcellos, 1995; Kitahara and Matsuura, 1995; Ekau, 1998; Castello and Castello, 2003). The existing information on anchovy larval growth in Argentine waters is fragmented and preliminary (unpublished data), or based on experimental conditions (Sánchez, 1995). Brown and Sánchez (in press) estimated the growth of anchovy larvae collected on the Patagonian shelf, but there are no previous published works on larval growth of this species for the Bonaerensis stock. The aim of this study was to analyse the larval growth of *E. anchoita* throughout the year by analysing the microstructure of daily depositions in the sagittal otoliths for the Bonaerensis stock.

MATERIALS AND METHODS

Sampling

A total of 268 anchovy larvae were collected during nine research cruises (Table 1). These cruises were carried out by the research vessel 'Capitán Cánepa' (INIDEP) from January to December 2000. Sampling was performed at the station EPEA (Estación Permanente de Estudios Ambientales) located at 38°28'S and 57°41'W (Fig. 1). Anchovy larvae were also captured at two stations located near the EPEA (additional station 1: 38°20'S 56°50'W and additional station 2: 38°00'S 57°03'W).

A Bongo net with 300 µm mesh and a flowmeter were used. A SCANMAR sensor was mounted on the sampler to determine the depth. The maximum bottom depth was 45 m and the gear was operated obliquely, from 5 m above the bottom to the surface, at 2.5 knots for fifteen minutes. The plankton material was preserved in 96% ethanol. The sea surface temperature (SST) was measured with a SeaBird SBE1901 CTD

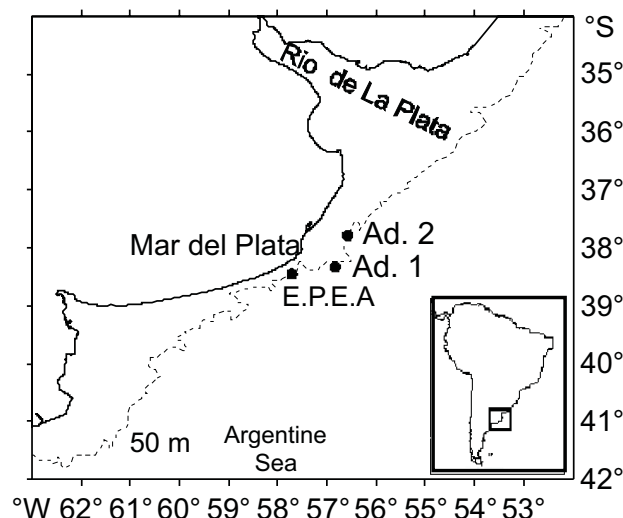


FIG. 1. – Study area and sampling sites for anchovy larvae off the Argentinean coast (SW Atlantic).

at all stations. The SST was considered because in stratified waters the anchovy larvae tend to be situated above the thermocline (Ciechowski *et al.*, 1986; Sanchez *et al.*, 1999).

Laboratory analysis

Anchovy larvae were identified according to the description given by Ciechowski (1965). For each specimen the standard length (SL) was measured using an ocular micrometer attached to a dissecting microscope. The sagittal otoliths were removed from the heads of the larvae and mounted onto glass slides and covered with Pro-texx (a transparent mounting medium) for examination by light microscopy.

Otolith increments were observed under a Zeiss Axioscop binocular microscope (1000 X) fitted with an image analysis system. Image enhancement and analysis was conducted using Kontron® software. The widths of daily increments were examined along the longest radius and counted and measured starting at the hatch check (Campana and Jones, 1992). Deposition of increments was assumed to be daily according to what is known from observations of other anchovy species, like *E. japonicus* (Tsuji and Aoyama, 1984), *E capensis* (Thomas, 1986), and *E. encrasicolus* (Cormeño *et al.*, 2003).

Data analysis

For the seasonal study of larval growth the larvae were grouped according to the season in which they were collected. Both sagittal otoliths of each larva were considered for the microstructure analysis. Differences in the number of increments and otolith radii (OR) in the right and left otoliths were tested with a t-test (Zar, 1984). The number of increments from hatch check was assumed to be the larval age. One way ANOVA was performed to analyse differences between mean hatch check of each seasonal group.

Back-calculation by counting daily increments was used to determine the temporal distribution of birth dates.

Individual growth rate (IGR) was estimated as:

$$IGR = (\text{total length} - 4 \text{ mm}) / \text{number of increments}$$

IGR values were only determined for two larval cohorts (see “Results”).

Size-at-age data of anchovy larvae were expressed as linear functions of age:

$$SL = b.t + a \tag{1}$$

where t is the number of increments in the otoliths, SL is standard length at age t, a is the y-axis intercept, and b is the slope, linear growth rate (mm day⁻¹).

These growth rates estimated as slopes were compared statistically by analysis of covariance (ANCOVA, Zar, 1984).

To analyse the seasonal effect on the width of the increments, the mean increment widths (IW) were grouped according to season (spring, autumn and summer) and plotted as a function of larval age.

Power relationships between SL and OR were established:

$$SL = a OR^b$$

where SL is the standard length (mm), a and b are regression parameters, and OR is the otolith radius (µm).

To analyse differences between seasons, these equations were linearised using natural logarithms and compared by ANCOVA.

In order to assess the influence of environmental temperature on larval growth, a recent growth rate 4-days before capture (G4) was calculated according to:

$$G4 = (L_c - L_4) / 4 \tag{2}$$

where L_c is the larval size (SL) at capture, and L₄ is the back-calculated larval size (SL) four days before capture.

After verifying linearity between SL and OR, the L4 values were estimated for each larva according to the biological intercept method (Campana, 1990; Campana and Jones, 1992):

$$L_4 = L_c + (OR_4 - OR_c) (L_c - L_0) (OR_c - OR_0)^{-1} \tag{3}$$

where L₀ is the larval size (SL) estimated at first increment deposition (4 mm), OR₄ is the otolith radius measured four increments (days) before capture, OR_c is the otolith radius measured at capture, and OR₀ is the otolith radius measured at first increment deposition.

The G4 values were plotted against the SL. To relate G4 to thermal influence a linear regression analysis was performed. Temperature values registered at the time of sampling were assumed to be constant during the last four days before larvae were captured.

RESULTS

Surface temperature values varied between 12.6°C and 21.3°C (winter and summer respectively, Table 1). A detailed study of the annual fluctuations in the thermal field and additional oceanographic characteristics of the study area (EPEA) have been extensively analysed by Lutz *et al.* (2006). They observed a typical annual cycle in the water column stability of temperate seas. In summer, a strong thermocline at 25 m was observed. This thermocline began to disappear in the early autumn and the water column was totally homogeneous during autumn and winter. At the beginning of spring, with the increase in the temperature, the thermocline formed again (see Fig. 2 in Lutz *et al.*, 2006).

Anchovy larval size ranged from 3.5 to 12.2 mm SL. The sagittal otoliths of *E. anchoita* were approximately round. The mean distances of the otolith nuclei (hatch check) were 6.6 µm (n = 98, SD = 0.6), 6.5 µm (n = 76, SD = 0.6) and 6.4 µm (n = 81, SD = 0.5) for larvae collected in summer, autumn and spring respectively. No differences in hatch check among seasons were detected (ANOVA, $p > 0.17$). The increments were easily identifiable under transmitted light microscopy. From 0 to 26 increments were counted and measured for the anchovy larvae and the first prominent ring was observed at a larval size around 4 mm. No differences in radii or increment number between the left and right otoliths were observed (n = 105; *t*-test, $p > 0.7$ otolith radii; n = 88; *t*-test, $p > 0.6$, increment number).

Several larval cohorts were identified by back-calculation of hatching dates (Fig. 2). All the larvae collected in spring and summer were born in a period of 30 to 40 days. Larval births were not detected in two short intervals of three days in spring and ten days in summer (Fig. 2, a and b). It was assumed that larval growth was similar for the cohorts hatched in those 30 to 40 day periods, and all the cohorts were seasonally grouped for growth analysis. However, larvae collected in autumn were born in a period of 70 days and the interval with no larval births was longer than in spring and summer (30 days). Since there may be differential growth in autumn cohorts, individual mean growth rates (IGR) were compared between two main larval groups in autumn (Fig. 2 c). The IGR values were identical (0.36 mm day⁻¹), and therefore the autumn larval cohorts were grouped together.

Length-at-age data of anchovy larvae collected during the three seasons (spring, summer and au-

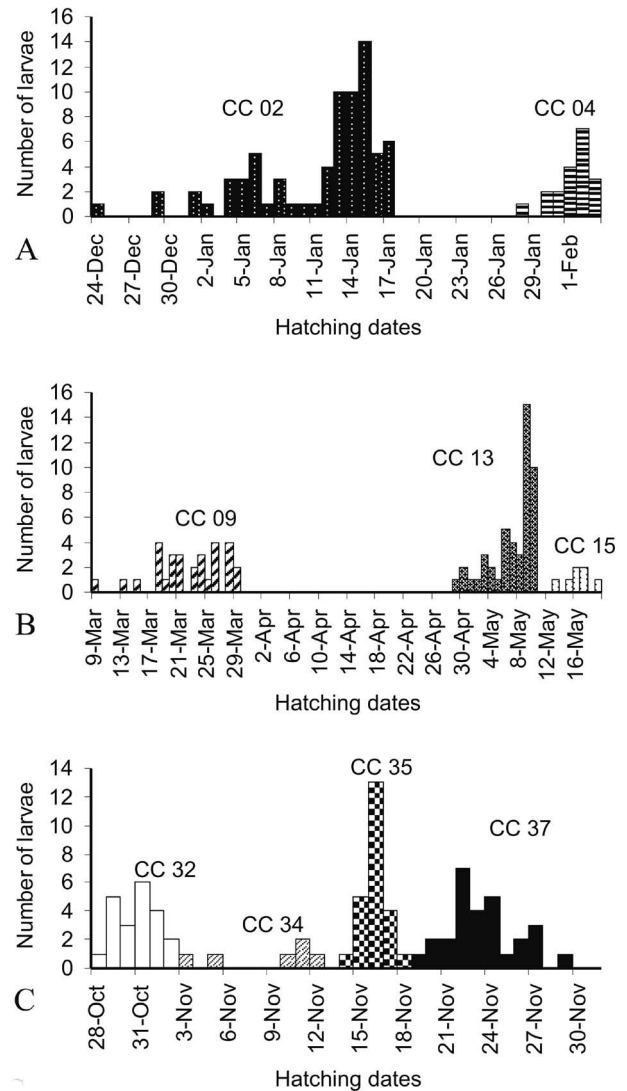


FIG. 2. – Hatching dates for different seasons: A. summer, B. autumn and C. spring (CC: cruise name).

tumn) were fitted in three different linear models and analysed separately (Fig. 3). ANCOVA on the linear growth rate (slope *b*) data showed significant differences between spring and summer and between spring and autumn ($p < 0.01$). Differences between summer and autumn were not detected ($p > 0.3$). The mean growth rate was more elevated in spring (0.51 mm day⁻¹) in comparison with summer and autumn (0.41 to 0.42 mm day⁻¹ respectively). The y-intercept values, which represent the larval size at first increment deposition, varied in quite a narrow range (3.6 to 3.9 mm). The lowest value of the intercept (3.6) was coincident with the highest slope in spring (0.51 mm day⁻¹) and as a consequence the slope could be artificially increased. To solve this difficulty a test of equal coefficients (Fomby *et al.*, 1984) was per-

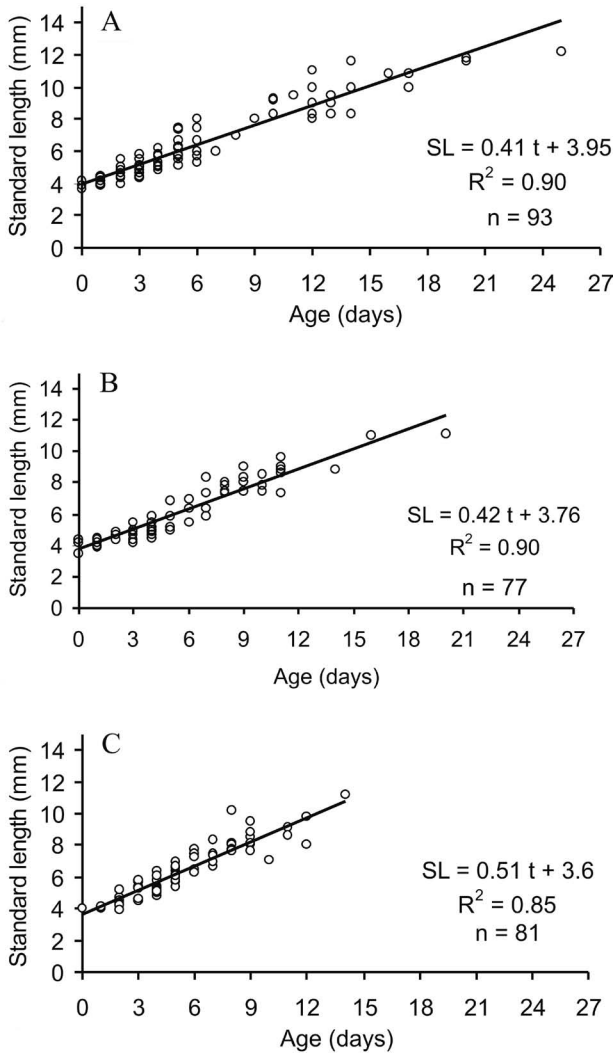


FIG. 3. – Linear relationships between anchovy larval standard length and number of daily increments in the otoliths. A) summer, B) autumn, C) spring.

formed in order to analyse differences between the three intercepts. There were no significant differences ($p > 0.35$), hence a common intercept was established (3.8 mm) and the new slopes were statistically compared. Slopes between spring and summer ($p < 0.01$), and between spring and autumn ($p < 0.01$) continued to be different, whereas slopes between autumn and summer ($p > 0.4$) were similar.

The mean daily increment width changed little over the analysed period and did not show any general tendency with respect to age (Fig. 4). The mean values were similar and ranged from 0.5 to 1.9 μm (spring); from 0.2 to 2 μm (summer); and from 0.4 to 1.9 μm (autumn).

Plots of standard length (mm) and otolith radius (μm) were fitted for the three seasons in three power models (Fig. 5). The same data range was consid-

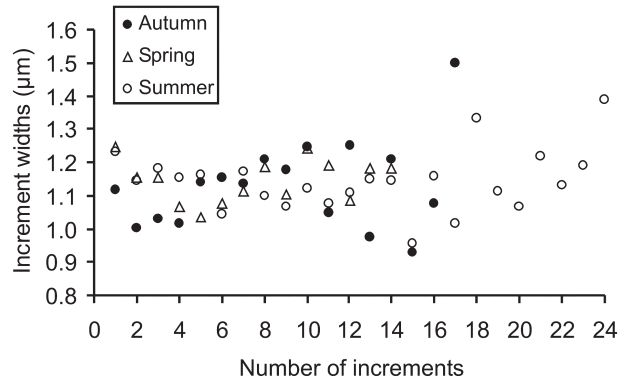


FIG. 4. – Average width of otolith increments measured in anchovy larvae captured in summer, autumn and spring.

ered when differences in slopes among seasons were analysed, because there were larger otoliths in summer and autumn in comparison with spring (Fig. 5). No significant differences in slopes were observed between seasons (ANCOVA, $p > 0.1$).

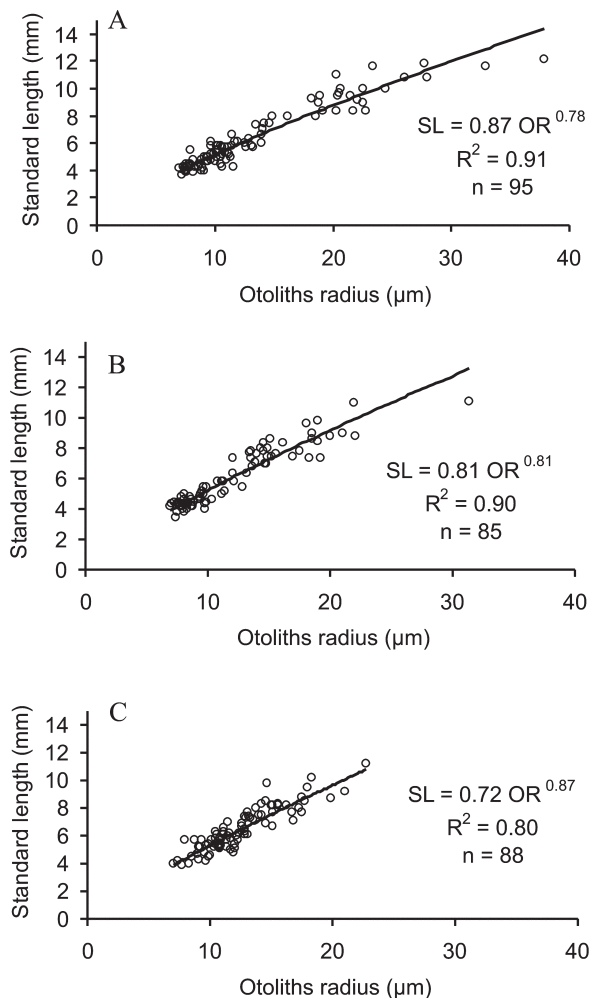


FIG. 5. – Allometric relationships between the maximum otolith radius and standard length of anchovy larvae. A) summer, B) autumn, C) spring.

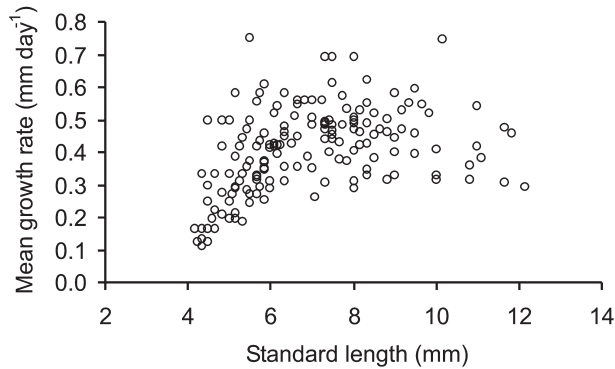


FIG. 6. – Scatter plot of the standard length and recent growth rate estimated from the last four increments of the otoliths (G4).

The values of G4 were higher in relation to larval size, mainly for smaller larvae from approximately 4 to 6 mm (Fig. 6), which shows the dependence of larval size on larval growth. To overcome this problem, before analysing G4 in relation to temperature, the larvae were grouped into two size intervals (4 to 6 and 6.1 to 12 mm). The G4 values were not related to sea surface temperature in either of the intervals (4-6 mm: $R^2=0.005$, $n=127$, $p>0.4$ and 6.1-12 mm: $R^2=0.01$, $n=105$, $p>0.1$) and high variability was observed (Fig. 7).

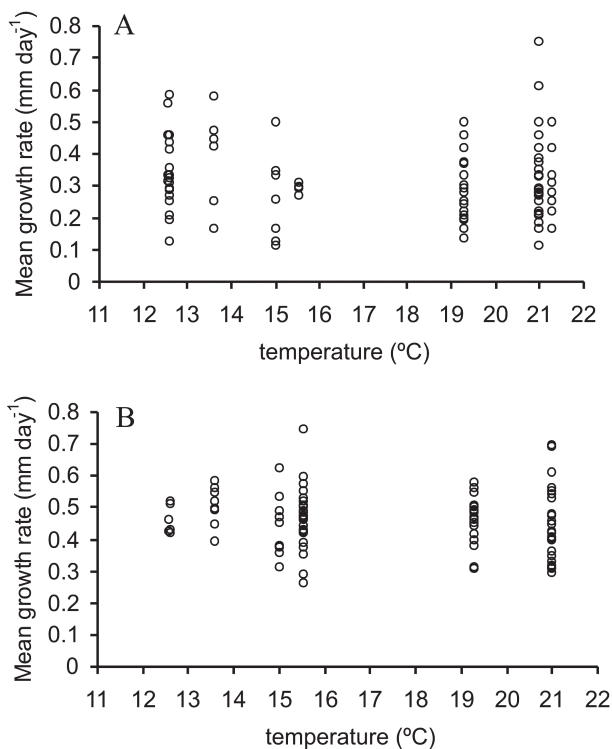


FIG. 7. – Scatter plot of recent growth rate estimated four days before capture (G4) on surface water temperature. A) size interval: 4–6 mm, B) size interval: 4.1–6 mm.

DISCUSSION

The study area (EPEA) corresponds to ‘Coastal Waters’ due to its proximity to the 50 m isobath, but it may sometimes be influenced by advection of ‘Middle Shelf Waters’ of subantarctic origin, and on particular occasions by fresh water from La Plata river (Carreto *et al.*, 1995). In the sector off Buenos Aires Province, there was a clear seasonal pattern in physical conditions throughout the study period. This was evident by the formation and rupture of the seasonal thermocline and changes in chlorophyll-*a*. In addition, salinity values did not suggest the influence of La Plata river waters at the EPEA station (Lutz *et al.*, 2006). For this reason, the ichthyoplankton sample collected near the EPEA was considered to be within the same water mass.

In this work the number of increments was considered as the larval age. According to other studies on Engraulid larvae, the first daily growth increment is deposited at the end of the yolk sac stage, which coincides with exogenous feeding. The corresponding age and larval length at that moment varies by an interval of 2 to 4 days depending on the *Engraulis* species (Brothers *et al.*, 1976; Regner, 1985; Palomera *et al.*, 1988; Takasuka and Aoki, 2006). As we do not have this information for *E. anchoita* we have assumed that the number of increments counted from first check to be the larval age.

The best fit of length-age data was obtained with linear models. In Brazilian waters larval growth of *E. anchoita* has been estimated using the Laird-Gompertz models for larvae ranging from 8 to 32 mm standard length (Castello and Vasconcellos, 1995; Kitahara and Matsuura, 1995). Due to the narrow range of data, a linear model was more appropriate for representing the data fit with the advantages of an easy interpretation of the data and comparison of growth rates (Campana and Jones, 1992). In this work the length-otolith radius relationships were allometric. However, linear relationships have been fitted previously between OR and SL in *E. anchoita* larvae (Castello and Vasconcellos, 1995). In agreement with this study, Takasuka and Aoki (2006), working with a large number of larvae of *E. japonicus* ($n=1140$), found a power relationship between standard length and otolith radius. The absence of a definite trend in the increment widths showed constant otolith growth during the period analysed. Furthermore, the similar hatch check among seasons indicates identical otolith sizes at larval hatching. Such constant otolith growth coincided with the constant growth rates estimated by the length-age models. It should be taken

TABLE 2. – Growth rate comparison for *Engraulis anchoita* larvae of SW Atlantic. T: temperature, TL: total length, SL: standard length, t: days. (1) This work; (2) Brown and Sánchez, in press; (3) Castello and Castello, 2003; (4) Kitahara and Matsuura, 1995; (5) Castello and Vasconcellos, 1995; (6) Ekau, 1998; * Instant growth rate obtained by deriving the Laird-Gompertz model with respect to larval sizes (10, 20 mm).

Ecosystem	T (°C)	Length (mm)		Rate (mm day ⁻¹)		Season	Model
Coastal station off Buenos Aires province (1)	14	3.9 – 11.5		0.51		spring	SL= 0.51 t + 3.6
	17	3.6 – 12.16		0.40		autumn	SL= 0.42 t + 3.7
	21	3.5 – 11.11		0.42		summer	SL= 0.40 t + 3.9
Tidal Front off Patagonia (2) *		10	20	0.53	0.56	spring	TL=4.2exp(2.345(1-(-0.036t)))
Brazilian Southeastern Bight (3)	17-24	10	19	0.5		winter	Growth rates derived from the back-calculated sizes
	22-25	7	16	0.4		spring	
Sta. Marta Grande Cape (4) *	21-22	10	20	0.41	0.78	spring	TL=6.19exp(17.08(1-(-0.0025t)))
Sta. Marta Grande Cape (5) *	17	10	20	0.44	0.61	spring	SL=5.19exp(2.95(1-(-0.019t)))
Southern Brazil (6)*	20-22	10	20	0.74	0.91	summer	TL=2.72exp(3.102(1-(-0.041t)))

into account that the increase in the increment widths with respect to age has been observed mainly in larger larvae (Folkvord *et al.*, 1997; Allain *et al.*, 2003).

Larval mean growth rates were higher for larvae collected in spring (0.51 mm day⁻¹) than those collected in summer or autumn (0.40 and 0.42 mm day⁻¹), which suggests faster larval growth during spring. This fact does not seem to be associated with the thermal influence since the highest temperatures were registered in summer. In addition, G4 was not related to SST. This indicates that other factors may influence growth. Higher food availability due to an elevated primary production during spring may be a determining factor. However, since there were no significant differences in larval growth between summer and autumn, a strict relationship between larval growth and the typical production cycles of temperate seas (high biological production during spring and a second peak of production in autumn) cannot be confirmed.

Considering that the most intensive reproductive activity of the anchovy is during spring (Sánchez, 1995), it is reasonable to believe that larvae born in spring seem to be favoured by a fast growth. These advantages could be related to the “bigger is better” and the “stage duration” hypotheses (Leggett and Deblois, 1994). The first hypothesis states that faster growing larvae achieve a larger body size at a given age as they are less vulnerable to predation. The second hypothesis explains that larvae which experience favourable feeding conditions, and therefore grow quickly, will achieve metamorphosis at earlier ages and experience lower cumulative mortality due to predation at the larval stage.

Growth rate values obtained in this study were similar to the values recorded by back-calculation

methods (Castello and Castello, 2003). The rates were lower than those registered in Patagonia (Brown and Sánchez, in press), and generally lower (or at the lower limit) than those estimated for larvae collected in southern Brazil (Kitahara and Matsuura, 1995; Castello and Vasconcellos, 1995; Ekau, 1998). Several factors could simultaneously affect larval growth. Assuming that the two most important factors are primary productivity (associated with food availability) and temperature, the different values of larval growth in the ecosystems of Buenos Aires and Patagonia could be due to differential productivity, which has been observed to be higher in Patagonia than in the Buenos Aires ecosystem, where the EPEA is situated, in spring (Sánchez and Ciechomski, 1995). In contrast, the greater larval growth registered in the Brazilian ecosystem could not be associated with productivity due to the poverty of the system (Podestá, 1997); in this scenario the higher temperature could explain the faster larval growth (Table 2). Alternatively, there may be differences between stocks, as observed by Castello and Castello (2003), and therefore each of the three stocks considered would have their own characteristic larval growth. It should be noted that larvae analysed in this work were smaller in comparison with those analysed in previous studies; hence, we cannot discard the possibility that the lower growth could be attributed to ontogeny.

ACKNOWLEDGEMENTS

We are grateful to our collages from the DiPlaM-CC project, as well as to the captain and crew of the research vessel Capitan Cánepa for their help in the obtaining the biological material. We also thank An-

ibal Aubone for his advice on statistical procedures and Vivian Lutz for reading and making suggestions to improve the manuscript. Finally we kindly thank Isabel Palomera for critically reading the manuscript and two anonymous reviewers for their valuable comments.

REFERENCES

- Allain, G., P. Petitgas, P. Grellier and P. Lazure. – 2003. The selection process from larval to juvenile stages of anchovy (*Engraulis encrasicolus*) in the Bay of Biscay investigated by Lagrangian simulations and comparative otolith growth. *Fish. Oceanogr.*, 12(4/5): 407-418.
- Angelescu, V. – 1982. Ecología trófica de la anchoíta del Mar Argentino (Engraulidae, *Engraulis anchoita*) Parte II. Alimentación, comportamiento y relaciones tróficas en el ecosistema. *Ser. Contrib. Inst. Nac. Invest. Des. Pesq.* (INIDEP), Mar del Plata, 409: 83.
- Bailey, K.M. and E.H. Houde. – 1989. Predation on egg and larvae of marine fishes and the recruitment problem. *Adv. Mar. Biol.*, 25: 1-83.
- Brothers, E.B., C.P. Mathews and R. Lasker. – 1976. Daily growth increments in otoliths from larval and adult fishes. *Fish. Bull. U.S.* 74: 1-8.
- Brown, D.R. and Sánchez, R.P. – (in press). Larval and juvenile growth of two Patagonian small pelagic fishes *Engraulis anchoita* and *Sprattus fuegensis*. *Rev. Invest. Des. Pesq.*
- Campana, S.E. – 1990. How reliable are growth back-calculations based on otoliths? *Can. J. Fish. Aquat. Sci.*, 47: 2219-2227.
- Campana, S.E. and C.M. Jones. – 1992. Analysis of otolith microstructure data. In: D.K. Stevenson and S.E. Campana (eds.), *Otolith microstructure examination and analysis*. *Can. Spec. Publ. Fish. Aquat. Sci.*, 73-100.
- Carreto, J.I., V.A. Lutz, M.O. Carignan, A.D. Cucchi Colleoni, and S.G. De Marco. – 1995. Hydrography and chlorophyll *a* in a transect from the coast to the shelf-break in the Argentinian Sea. *Cont. Shelf Res.*, 15 (2/3): 315-336.
- Castello, L. and J.P. Castello. – 2003. Anchovy stocks (*Engraulis anchoita*) and larval growth in the SW Atlantic. *Fish. Res.*, 59 (3): 409-421.
- Castello, J.P. and M.C. Vasconcellos. – 1995. Growth rate of anchovy (*Engraulis anchoita*) larvae caught off Cape Santa Marta Grande (Brazil). *Arch. Fish. Mar. Res.*, 42(3): 263-281.
- Cermeño, P., A. Uriarte, M. de Murgía and B. Morales-Nin. – 2003. Validation of daily increment formation in otoliths of juvenile and adult European anchovy. *J. Fish Biol.*, 62: 679-691.
- Ciechomski, J.D. de. – 1965. Observaciones sobre la reproducción y desarrollo embrionario y larval de la anchoíta argentina (*Engraulis anchoita*). *Bol. Inst. Biol. Mar.*, 9: 1-29.
- Ciechomski, J.D. de, R.P. Sánchez and C.A. Lasta. – 1986. Evaluación de la biomasa de adultos desovantes, distribución vertical y variación cuantitativa de la intensidad de los desoves de anchoíta (*Engraulis anchoita*) durante la primavera de 1982. *Rev. Invest. Des. Pesq.*, 5: 30-48.
- Crespo, E.A., S.N. Pedraza, S.L. Dans, M. Koen Alonso, L.M. Reyes, N.A. García, M. Coscarella and A.C.M. Schiavini. – 1997. Direct and indirect effects of the highseas fisheries on the marine mammal populations in the northern and central patagonian coast. *J. Northw. Atl. Fish. Sci.*, 22: 189-207.
- Ekau, W. – 1998. Comparative growth analysis of *Engraulis anchoita* larvae from southern Brazil. *Arch. Fish. Mar. Res.*, 46(1): 1-17.
- Folkvord, A., K. Rukan, A. Johannessen and E. Moksness. – 1997. Early life history of herring larvae in contrasting feeding environments determined by otolith microstructure analysis. *J. Fish Biol.*, 51: 250-563.
- Fomby, T.B., R. Carter Hill and R.J. Stanley. – 1984. *Advanced econometric methods*. Springer Verlag.
- Hansen, J.E. – 2004. Anchoíta (*Engraulis anchoita*). In: R.P. Sánchez and S.I. Bezzi (eds.), *El Mar Argentino y sus recursos pesqueros. Tomo 4. Los Peces Marinos de Interés Pesqueros; Caracterización Biológica y Evaluación del Estado de Explotación*, pp. 101-115. Inst. Nac. Inv. Des. Pesq., Mar del Plata, Argentina.
- Hansen, J.E., M.B. Cousseau, and D.L. Gru. – 1984. Características poblacionales de la anchoíta (*Engraulis anchoita*) del Mar Argentino. Parte I. El largo medio al primer año de vida, crecimiento y mortalidad. *Rev. Invest. Des. Pesq.*, 4: 21-48.
- Houde, E.D. – 1996. Evaluating stage-specific survival during the early life of fish. In: Y. Watanabe, Y. Yamashita and Y. Oozeki (eds.), *Survival Strategies in Early Life Stages of Marine Resources*, pp. 51-66. A.A. Balkema, Rotterdam.
- Jones, C.M. – 1992. Development and application of the otolith increment technique. In: D.K. Stevenson and S.E. Campana (eds.), *Otolith microstructure examination and analysis*. *Can. Spec. Publ. Fish. Aquat. Sci.*, 117: 1-11.
- Kitahara, E.M. and Y. Matsuura. – 1995. Growth and mortality estimated of the southwest Atlantic anchovy *Engraulis anchoita* larvae from Cape Santa Marta Grande in southern Brazil. *Arch. Fish. Mar. Res.*, 42(3): 251-262.
- Legget, W.C. and E. Deblois. – 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the eggs and larval stages? *Neth. J. of Sea Res.*, 32(2): 119-134.
- Lutz, V.A., A. Subramanian, R.M. Negri, R.I. Silva and J.I. Carreto. – 2006. Annual variations in bio-optical properties at the 'Estación Permanente de Estudios Ambientales (EPEA)' coastal station, Argentina. *Cont. Shelf Res.*, 26: 1093-1112.
- Mauco, L., M. Favero and M.S. Bó. – 2001. Food and Feeding Biology of the Common Tern During the Nonbreeding Season in Samborombon Bay (Buenos Aires, Argentina). *Waterbirds*, 24(1): 89-96.
- Palomera, I., B. Morales-Nin and J. Leonart. – 1988. Larval growth of anchovy, *Engraulis encrasicolus*, in the Western Mediterranean Sea. *Mar. Biol.*, 99: 283-291.
- Panella, G. – 1971. Fish otoliths: Daily growth layers and periodical patterns. *Science*, 173: 1124-1127.
- Podestá, G.P. – 1997. Utilización de datos satelitarios en investigaciones oceanográficas y pesqueras en el Océano Atlántico Sudoccidental. In: E.E. Boschi (ed.), *El Mar Argentino y sus recursos pesqueros. Tomo 1. Antecedentes históricos de las exploraciones en el mar y las características ambientales*, pp. 195-222. Inst. Nac. Inv. Des. Pesq., Mar del Plata, Argentina.
- Ratti, M. – 1986. Estudio comparativo de caracteres merísticos y morfométricos de la anchoíta (*Engraulis anchoita*). *Rev. Invest. Des. Pesq.*, 5: 169-183.
- Regner, S. – 1985. Ecology of planktonic stages of the anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), in the central Adriatic. *Acta Adriat.*, 26: 1-113.
- Sánchez, R.P. – 1995. *Patrones de distribución espacio-temporal de los estadios embrionarios y larvales de la anchoíta (Engraulis anchoita Hubbs and Marini) a micro y macroescala. Su relación con la supervivencia y el reclutamiento*. Ph. D. thesis, Univ. Buenos Aires, Argentina.
- Sánchez, R.P., and J.D. Ciechomski de. – 1995. Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Sci. Mar.*, 59(3-4): 455-478.
- Sánchez, R.P., J.D. Ciechomski de, C.A. Lasta and R.A. Guerrero. – 1999. A drift study of vertical distribution and mortality of *Engraulis anchoita* eggs and larvae. *Rev. Invest. Des. Pesq.*, 12: 51-75.
- Takasuka, A. and I. Aoki. – 2006. Environmental determinants of growth rates for larval Japanese Anchovy *Engraulis japonicus*. *Fish. Oceanogr.*, 15(2): 139-149.
- Thomas, R.M. – 1986. Growth of larval pelagic fish in the South-East Atlantic from daily otolith rings in 1982/83 and 1983/84. *S. Afr. J. Mar. Sci. /Suid-Afrikaanse Tydskrif vir. Vol. 4*, pp. 61-77.
- Tsuji, S. and T. Aoyama. – 1984. Daily growth increments observed in otoliths of the larvae of Japanese Red Sea Bream *Pagrus major* (Temminck et Schlegel). *Bull. Jpn. Soc. Sci. Fish.*, 48(11): 1559-1562.
- Zar, J.H. – 1984. *Bioestadistical analysis*. Prentice Hall.

Scient. ed.: I. Palomera.

Received December 12, 2008. Accepted June 25, 2009.

Published online February 24, 2010.