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ORIGINAL RESEARCH

Age and daily growth of juveniles *Engraulis anchoita* from southern Brazil

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ABSTRACT. The daily growth of 73 juvenile Argentine anchovies (*Engraulis anchoita*) with total lengths ranging from 37 to 86 mm collected in the southern Brazilian shelf during four research cruises in 2010 and 2011 was studied by counting and measuring daily increments in their *sagittal* otoliths. The mean somatic growth rate in length ranged from 0.20 mm day^{-1} to 0.57 mm day^{-1}. Back-calculated lengths at age in days were best fitted by the power model $L(t) = 1.89\ t^{0.70}$ ($R^2 = 0.96$). The growth showed a close relationship with metamorphosis, as observed in other species of the Genus *Engraulis*. When comparing growth results with other individuals of the same species from the Argentine shelf, some differences in growth pattern were noticed, which could be attributed to seasonality or the fact that they may constitute different stocks. All specimens hatched between February and August, mainly in June and July, coinciding with a period of high chlorophyll-*a* concentration in the study area. By applying a mixed general linear model, a slightly higher growth was detected during the first days of life in individuals hatched in April (0.51 mm day^{-1} ± 0.013) than in those born in July (0.48 mm day^{-1} ± 0.012), which could probably be attributable to thermal influence. The specimens of *E. anchoita* in this study would not have benefited from a rapid growth during the larval stages to ensure survival to the juvenile stage.

Key words: Anchovies, otolith, daily increments.

Edad y crecimiento diario de juveniles de *Engraulis anchoita* del sur de Brasil

RESUMEN. Se estudió el crecimiento diario de 73 juveniles de la anchoíta argentina (*Engraulis anchoita*) mediante el conteo y medición de los incrementos diarios en sus otolitos *sagitta*. Los especímenes fueron recolectados en la plataforma del sur de Brasil durante cuatro campañas experimentales en 2010 y 2011, con longitudes totales que variaron entre 37 y 86 mm. Los valores promedio de la tasa de crecimiento somático fluctuaron entre 0,20 mm día^{-1} y 0,57 mm día^{-1}. Se ajustó un modelo potencial a las longitudes retro-calculadas en edades previas: $L(t) = 1{,}89\ t^{0{,}70}$ ($R^2 = 0{,}96$). El crecimiento mostró una relación estrecha con la metamorfosis, como se observa en otras especies del Género *Engraulis*. El patrón de crecimiento fue similar al observado en juveniles de anchoíta de otros ecosistemas en la plataforma continental argentina. Sin embargo, se observaron algunas diferencias que podrían atribuirse a la estacionalidad o al hecho que puedan constituir diferentes stocks. El período de eclosión de todos los especímenes fue de febrero a agosto, principalmente en junio y julio, lo que coincidió con un período de alta concentración de clorofila *a* en el área de estudio. A través de la aplicación de un modelo lineal general mixto, se detectó durante los primeros días de vida un crecimiento ligeramente mayor en los individuos eclosionados en abril (0,51 mm día^{-1} ± 0,013) que en los nacidos en julio (0,48 mm día^{-1} ± 0,012); lo cual probablemente podría atribuirse a la influencia térmica. Los especímenes de *E. anchoita* de este estudio no se habrían beneficiado con un crecimiento rápido durante las fases larvarias, para garantizar la supervivencia hasta la etapa juvenil.

Palabras clave: Anchoíta, otolito, incrementos diarios.

INTRODUCTION

The Argentine anchovy (*Engraulis anchoita*) has a wide distribution, ranging from subtropical waters of Cabo Frio (22° S; Matsuura 1986) to sub-Antarctic waters in Patagonia (47° S). It is the most abundant pelagic resource in the southwestern Atlantic Ocean (Hansen 2000). In addition to its important commercial value, this species has a relevant ecological role as one of the main components of the diet of many predators such as hakes (Angelescu 1982), marine mammals (Crespo et al. 1997) and birds (Mauco et al. 2001). *Engraulis anchoita* inhabits ecosystems with different environmental conditions, from tidal fronts on the Patagonian coast to upwelling areas in southeast Brazil. Hansen et al. (1984) used back-calculated lengths at the first year of life, to determine the presence of two stocks in Argentine waters: the Bonaerense (34° S-41° S) and the Patagonian stocks (41° S-48° S). Castello and Castello (2003) analyzed growth curves of anchovy larvae from Brazil and were able to provide support for the existence of another stock in the southeastern Brazilian region (23° S-27° S). Finally, Carvalho and Castello (2013) used population parameters such as growth and size and age composition to propose that the distribution of the Bonaerense stock extended to south Brazil, with a northern limit at the latitude of Cabo Santa Marta Grande (27° S).

One of the most important tools for studying early life history in fishes are otoliths, ear bone structures that provide information on age and growth. These structures allow to study body condition, geographical area of birth, and mortality rates at individual and population levels (Campana and Jones 1992; Campana 2005). Such valuable information can be obtained through different life stages from larvae to adults (Fey and Linkowski 2006; Hüssy et al. 2010). The analysis of daily growth rings in otoliths allows for the retrospective determination of growth rates from the capture date to hatching. Back-calculation methods can then estimate daily growth during larval stages, providing insights into factors influencing survival to the juvenile stage. This allows to study the relationship between larval growth and environmental parameters in which organisms developed.

Numerous studies in fisheries biology have demonstrated that the strength of year-class recruitment is often correlated with fast growth during early life stages (Campana 1996; Kamimura et al. 2015). Cohorts of fast-growing larvae that reach larger sizes earlier in life (i.e. shorter larval stages) experience lower cumulative, stage-specific mortality, and thus have a higher probability of recruiting successfully (Houde 2008). Having survived the larval stages of highest natural mortality, small juvenile anchovies represent a crucial fraction of the population, providing valuable insights into daily growth and its relationship with survival.

Oceanographic parameters such as temperature, salinity, nutrient availability, dissolved oxygen, and primary productivity play a critical role in the development and growth of fish larvae (Yamamoto et al. 2018). These parameters influence the availability of food resources, larval behaviour and overall survival rates. However, under unfavorable conditions (e.g. low prey density or high temperatures), growth is stunted, which negatively affecting survival and recruitment rates (Sardi et al. 2023). Larval growth rates can thus be significantly impacted by changes in oceanographic conditions. Optimal conditions promote faster growth and development, whereas unfavorable conditions result in reduced growth and lower survival rates (Houde 2008; Sakamoto et al. 2022). Understanding this relationship could contribute to studies of marine species recruitment and to assess the impacts of environmental changes on marine ecosystems (Heath 1992; Stevenson and Campana 1992; Govoni 2005). However, no studies have been done regarding late juvenile growth of *E. anchoita* on the Brazilian continental shelf. Up to date, daily growth studies have focused on larval stages (Castello and Vasconcellos 1995; Kitahara and Matsuura 1995; Ekau 1998; Castello and Castello 2003). Only two studies on the growth of juveniles were performed for specimens on the Argentine shelf (Brown et al. 2011, 2014). In this study, we aimed to establish the growth of juvenile *E. anchoita* in southern Brazil. In addition, growth was compared with previous studies conducted in other regions and between cohorts born at different times of the year. Finally, growth during the larval stages was analyzed by back-calculation of past sizes.

MATERIALS AND METHODS

Data collection and otolith reading

Between September and October 2010 and 2011, juvenile anchovies were collected from the southern Brazilian shelf during four scientific surveys (Figure 1; Table 1). The research vessel 'Atlantico Sul' conducted mid-water trawling operations utilizing a mid-water trawl net to sample pelagic fish species. These operations were complemented by echo integration surveys using an EK-500 scientific echo sounder to detect fish schools and assess species composition. Concurrently, the fishing vessel 'Victoria Mar' employed purse seine nets, a common method for capturing schooling pelagic fish such as anchovies. Purse seine nets encircle fish schools, with floats on the upper edge and weights on the lower edge, allowing the net to close at the bottom and effectively capture the targeted species.

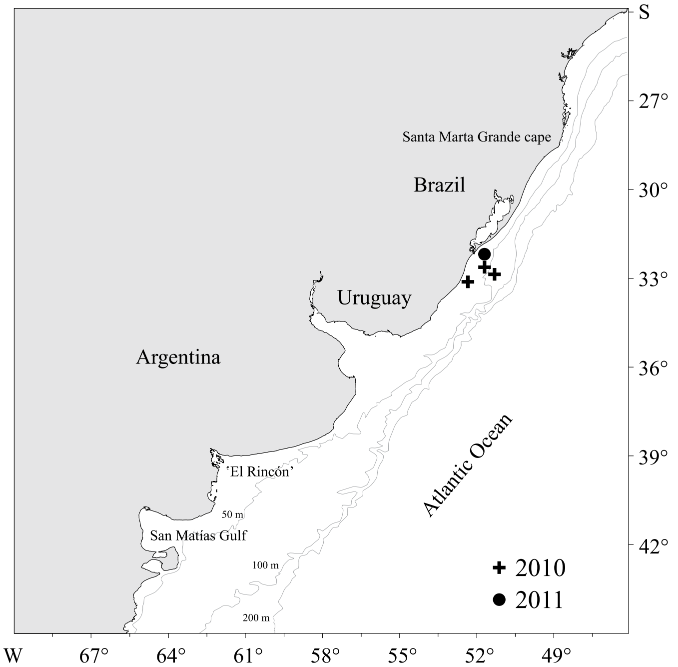

Figure 1. Sampling sites of *Engraulis anchoita* from southern Brazil in September and October 2010 and 2011.

Table 1. Basic statistical values of sizes and ages of juveniles *Engraulis anchoita* from southern Brazil in September and October 2010 and 2011. SD: standard deviation.

				Total length (mm)			Age (days)		
Year	Vessel	Catch date	N	Average ± SD	Min.	Max.	Average ± SD	Min.	Max.
2010	'Atlantico Sul'	Sep 24	14	68.4 ± 6.4	57.1	80.0	148.8 ± 30.8	108	206
		Sep 26	13	49.3 ± 9.0	37.4	63.6	94.8 ± 18.0	66	122
		Oct 10	32	52.1 ± 6.6	42.5	62.9	107.5 ± 23.1	70	145
2011	'Victoria Mar'	Sep 22	14	79.7 ± 4.3	70.9	85.7	172.6 ± 31.8	75	207

During the austral spring (September-October), the south Brazilian shelf experiences the influence of the Brazil Current along the slope, with surface temperatures typically ranging from 20-22 °C (Sasaki et al. 2024). The upwelling of nutrient-rich South Atlantic Central Water (SACW) begins along the mid and outer shelf, supporting productivity. Nearshore areas are influenced by fresher, colder Coastal Water (CW), while the offshore regions see saltier, warmer Tropical Water (TW; Sasaki et al. 2024). These dynamics create stratification that can affect juvenile anchovy distribution.

Specimens measuring less than 116 mm in total length (TL) were classified as juveniles according to Hansen (2000). A total of 90 individuals were collected for analysis. Individuals were measured to the nearest millimeter and their heads were preserved in ethanol (96%) inside plastic tubes for later analysis. The *sagittae* otoliths were then washed in the laboratory and mounted in slide glass with a transparent mounting medium. Due to their thickness, after drying the medium (48 h), otoliths were manually ground in decreasing porosity with 12, 9 and 3 µm lapping film paper. The polishing process was carried out until the entire microstructure was visible on the same plane. The identification of the daily deposition pattern in the otoliths was made following the criteria adopted by Cermeño et al. (2003, 2008) for juveniles *E. encrasicolus*, Namiki et al. (2010) for specimens *E. japonicus*, and Cerna and Plaza (2016) for juveniles *E. ringens*.

The number of daily increments was counted and their width was measured on the otoliths along the longest axis using a digital camera attached to a transmitted light microscope (400-1,000X), connected to an image analysis software (Kontron program). Two readers participated in the reading of otoliths and discussed the microstructure analysis with each other. The otolith with the clearest microstructure was selected for increment counting and measurement. The number of increments in the other otolith of the pair was determined by direct counting. If there was at least 90% agreement between counts of both otoliths (e.g. 100 and 110 increments), the data were included in the analysis. However, if the discrepancy exceeded 10%, the sample was excluded. If only one otolith was available due to the loss of the other during extraction or polishing, such information was used. Out of a total of 90 individuals captured, the age of 73 was determined, because 17 specimens were discarded due to discrepancies in increment counts or difficulties in microstructure interpretation.

Preliminary analysis

Hatching dates were determined by subtracting the number of daily increments from the date in which each individual was caught. For ease of interpreting seasonal trends, we grouped specimen ages into 30-day intervals that roughly correspond to months.

In a preliminary analysis, we fitted a linear model to the length-at-age data using the least-squares method. Our first aim was to assess growth rates across the size range observed in our samples (37.4-85.7 mm; Table 1). The application of back-calculation techniques for estimating size-at-age requires an allometric relationship between individual lengths and otolith radii (Takasuka et al. 2008). Back-calculation methods were applied to estimate sizes at previous ages. To obtain past size estimates at previous ages and build individual growth trajectories, the methodology described by Watanabe and Kuroki (1997), Watanabe and Nakamura (1998) and Yamamoto et al. (2018) was followed. After establishing a power relationship between TL and otolith radius (OR), the i*th* otolith increment radius (OR*i*) and TL at the i*th* increment formation (TL*i*) were modelled using a power function, expressed as $\mathrm{TL}i = a\mathrm{OR}b_i$, for each individual. Values of *a* and *b* were obtained by solving the following two equations: $\mathrm{TL}_1 = a\mathrm{OR}_1{}^b$ and $\mathrm{TL}_{\mathrm{captured}} = a\mathrm{OR}_{\mathrm{captured}}{}^b$ where TL_1 = total length at first increment deposition which was fixed as 4 mm (Leonarduzzi et al. 2010); OR_1 = the measured radius of the first daily increment; $\mathrm{TL}_{\mathrm{capture}}$ = the measured total length at capture (mm); and $\mathrm{OR}_{\mathrm{captured}}$ = otolith radius at capture. Then, a potential model was fitted to the length-at-age data of the individual trajectories by the least squares method.

For each individual, growth rates were determined for each age as average values of differences between two consecutive back-calculated sizes:

$$\sum_{j=1}^{n} (TL_j(i+1) - TL_j(i))/n$$

where *n*: number of specimens at age *i*; ($TL_j(i)$, TL_j $(i+1)$: back-calculated sizes at ages *i* and *i* +1, for each individual *j*.

Growth was determined as length variation. To investigate potential differential growth during the larval stage, the back-calculation was used to estimate juvenile sizes during the first days of life. Subsequently, back-calculated sizes were compared with several growth models fitted by several authors to describe the larval growth of *E. anchoita* in the Brazilian waters (Castello and Vasconcellos 1995; Kitahara and Matsuura 1995; Ekau 1998; Castello and Castello 2003). Because larval growth is age dependent, the same age interval was considered to compare with previous studies of larval growth (1-52 days). The following linear relationship to convert the TL into standard length (SL) and compare results with the literature was used:

$$SL = 0.86\ TL - 1.03\ (n = 104;\ R^2 = 0.99)$$

Widths of increments and somatic growth rates were analyzed as average values by age for all individuals combined. For comparative purposes, data from other studies on juvenile *E. anchoita* collected in two areas of the Argentine continental shelf were used: 'El Rincón' (42 specimens) (Brown et al. 2011) and San Matías Gulf (44 specimens) (Brown et al. 2014). Since growth is strongly related to ontogeny, comparisons were made within an identical age range (0-207 daily increments).

Seasonal differences

To analyze seasonal differences in growth, growth rates of individuals born in April 2010 (austral autumn) and July (austral winter) 2010 were compared. Due to the limited number of specimens collected in 2011, they were no included in the analysis. Both months belonged to different seasons and had similar numbers of data to facilitate statistical analysis. For this purpose, growth rates were back-calculated during the larval stage. An age interval from 0 to 80 days was chosen to represent the larval stage. A mixed general linear model was fitted using the 'lme' function from the 'nlme' package in R software (R Core Team 2023) to analyze growth differences between months, ages, and the possible interaction between both variables. These models allowed modeling the correlation structure between repeated observations, taking into account the dependence between them. The transformed variable 'log(rate)' was used to improve the normal distribution of errors.

$$log(rate) \sim month + age + month \times age, random = \sim 1|individual$$

log(rate): continuous numerical variable that represents the daily growth rate; *month*: fixed factor representing the months analyzed; *age*: fixed factor representing the ages of the larvae; *month × age*: interaction between both factors. Both variables could be related because spawning intensities might differ among months; *individual* (*month*): random factor representing each individual nested within each month.

RESULTS

Total length of specimens ranged from 37.4 to 85.7 mm (Figure 2). Between 66 and 207 daily increments were counted and measured (Table 1; Figure 3). Based on the date of capture and the estimated age, the hatching period of all specimens took place from February to August with peaks occurring in June and July (Figure 4).

Although we found a good fit in the linear model to the length-at-age data ($L(t) = 0.32\ t + 19.8$, $R^2 = 0.83$; $p < 0.01$), the intercept value of the relationship (19.8 mm) was high due to the absence of initial larvae in our dataset. Such estimate is biologically unreasonable to represent the daily growth from larval stage to capture. Therefore, growth rates were determined using back-calculation methods.

A power relationship was fitted between total length and otolith radius for each specimen (Figure 5). According to this relationship, individual growth trajectories showed a monotonically increasing trend with decreasing speed of variation (Figure 6). Back-calculated average lengths per age at larval stages were similar to those sizes obtained in previous growth studies performed on larval populations of *E. anchoita*, on the Brazilian shelf (Figure 7).

Average estimates of width increments increased from 2.1 µm at age of 1 day to 7.4 µm at age of 78 days. Then, there was a decline in width increments until the age of 206 days, when values were around 4 µm. There was more variation in the thickness of increments in the age range of 110-206 days (Fig-

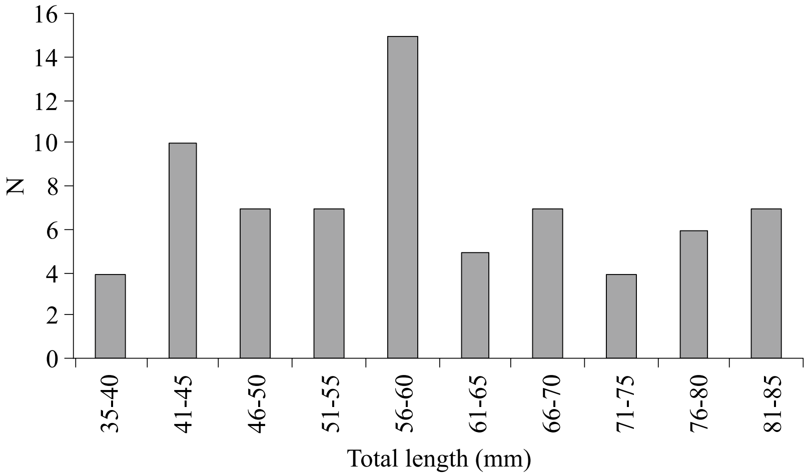

Figure 2. Total length of juvenile anchovies from southern Brazil sampled in September and October 2010 and 2011, grouped into 5-mm classes. N: number of individuals.

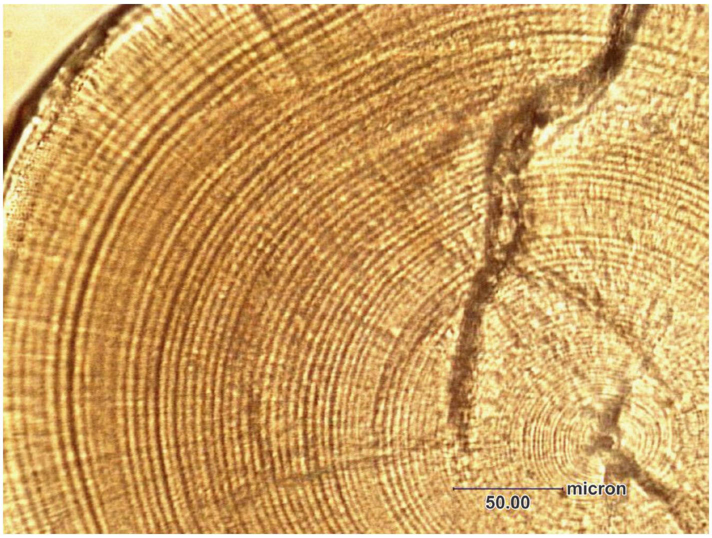

Figure 3. Microstructure of *sagitta* otolith of a juvenile *Engraulis anchoita* of 40 mm total length caught in southern Brazil. 80 daily increments were counted.

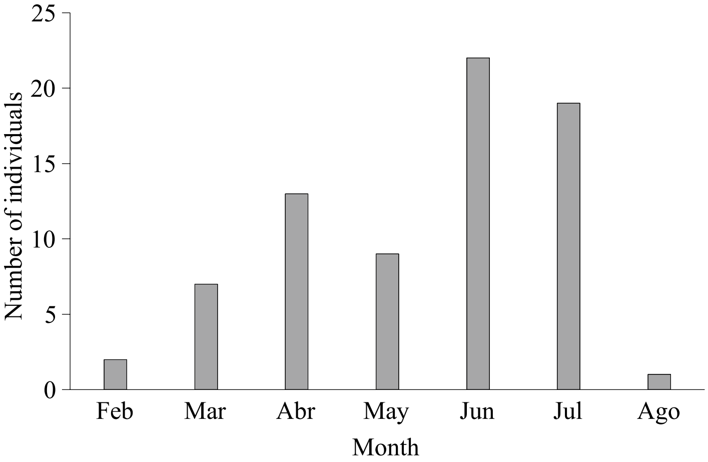

Figure 4. Hatching months of anchovy juveniles collected in southern Brazil in September and October 2010 and 2011.

ure 8). As a result, we estimated that growth rates in length decreased from 0.57 mm day^{-1} during the first days of life to 0.44 mm day^{-1} at 46 days. They then increased to 0.53 mm day^{-1} at 62 days and decreased to 0.2 mm day^{-1} at 206 days (Figure 9). For the entire age range in this study, the mean daily growth rate of specimens was 0.38 ± 0.11 mm day^{-1}.

Average daily growth rates determined for the larval period (age interval 1-80 days) were 0.51 mm day^{-1} ± 0.013 and 0.48 mm day^{-1} ± 0.012 for individuals born in April and July, respectively (Figure 10). Significant differences were detected (Mixed General Linear model, $p < 0.001$) between ages and months. No interaction was observed between month-age variables, indicating that growth rates would behave in a similar way between both months for each age (Table 2).

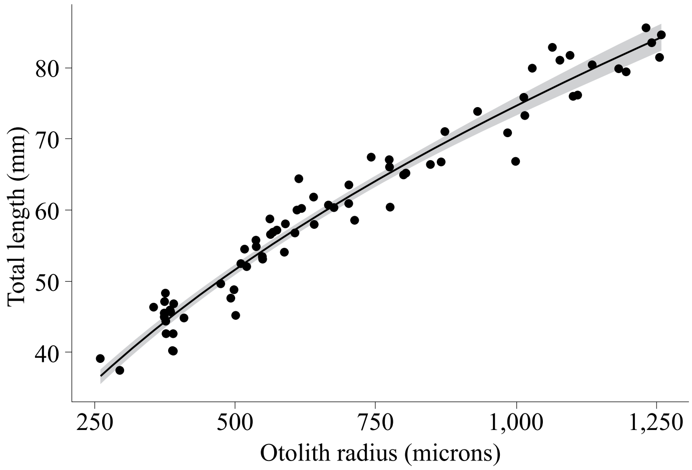

Figure 5. Power relationship between total length (TL) and otolith radius of juveniles *Engraulis anchoita* from southern Brazil. Grey shaded area represents the confidence interval of 95 % of the regression $L(t) = 1.90\ RO^{0.53}$; $R^2 = 0.95$.

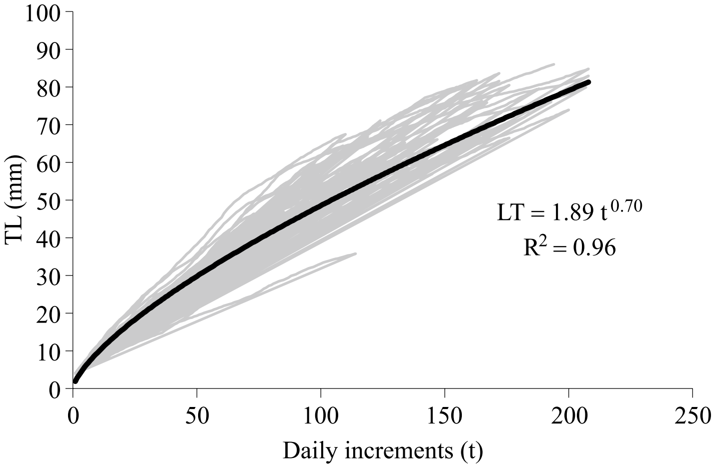

Figure 6. Individual growth trajectories of juveniles *Engraulis anchoita* from southern Brazil and the fitted allometric function. Total length (TL), daily increments: age in days.

DISCUSSION

This study is the first to use the otolith daily rings analysis technique to assess the daily growth of juveniles *E. anchoita* in the Brazilian shelf. Daily growth estimates of juveniles in this species were similar to those obtained in previous studies for the Genus *Engraulis*, such as those reported by Basilone et al. (2018), Djurovick et al. (2012), and Aldanondo et al. (2011) for juveniles *E. encrasicolus* (Table 3). Our values were lower than those obtained by Bacha and Amara (2012) and Schismenou et al. (2014) for *E. encrasicolus*. *Engraulis ringens* was the species with the highest daily growth values (Table 3). This phenomenon could be due to the highly productive upwelling ecosystem in which the species lives in the southeast Pacific Ocean (Muñoz et

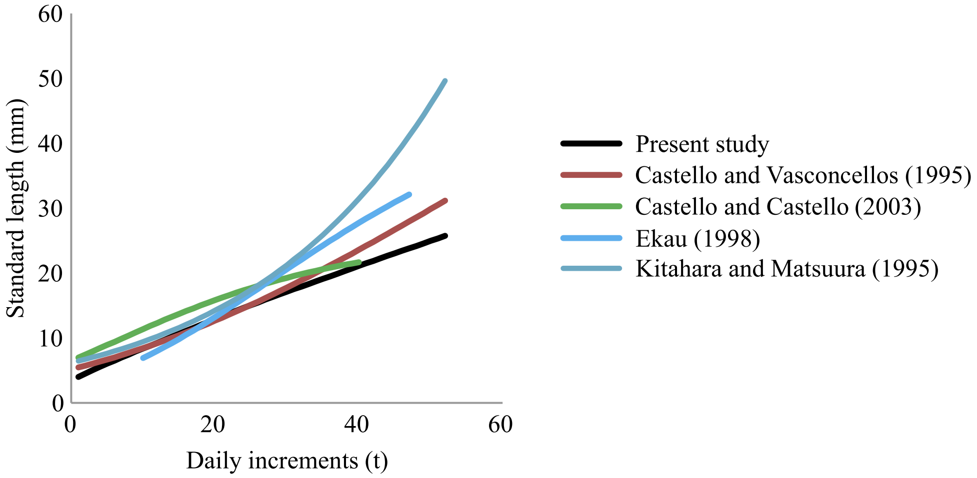

Figure 7. Comparison of mean back-calculated growth trajectory at larval period (age interval 1-52 days) of juveniles *Engraulis anchoita* from southern Brazil, with different Laird-Gompertz models fitted by several authors for anchovy larvae from the Brazilian shelf.

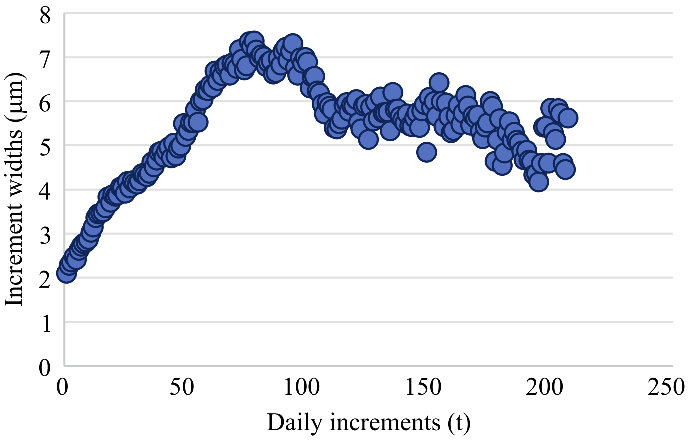

Figure 8. Mean values of the width increment by age (t) of otoliths of *Engraulis anchoita* juveniles from southern Brazil, sampled in September and October 2010 and 2011.

al. 2023). Such upwelling processes could have a strong impact on individual growth, for larvae and juveniles *E. mordax* in the northern California Current. However, comparing results of daily growth studies of anchovies with other species of the same genus is not straightforward due to different life-history traits, size ranges and sampling methods.

Lima and Castello (1995) observed that anchovy spawn along the southern Brazilian coast throughout the year, but more intensively during the winter months, when spawning would be favoured by 1) the direction of the Ekman transport to the coast, 2) the vertical stability of the water column, and 3) the high primary production rate due to the influx of nutrients from sub-Antarctic waters. Although our samples were taken only in September and October, corresponding to the hatching period, our results are consistent with the pattern described by Lima and Castello (1995).

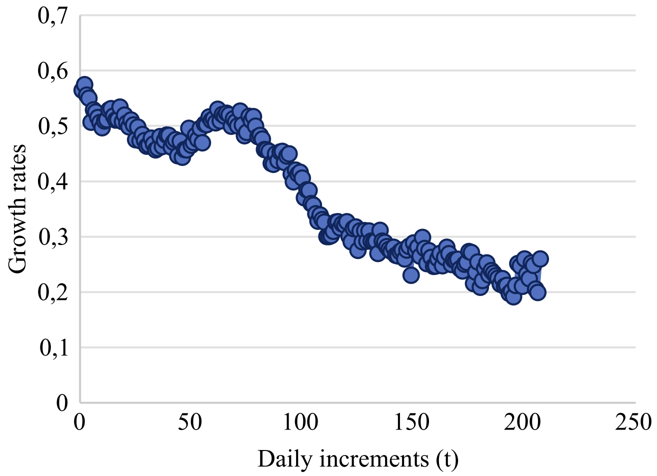

Figure 9. Mean values by age (t) of the somatic growth rate (mm day^{-1}) of juveniles *Engraulis anchoita* from southern Brazil, sampled in September and October 2010 and 2011.

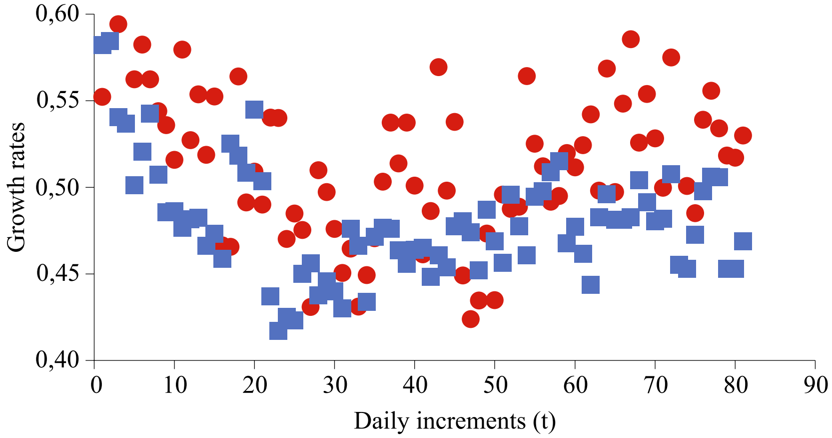

Figure 10. Average daily growth rates (mm day^{-1}) of juveniles *Engraulis anchoita* determined for the larval period. Individuals born in April (red) and July (blue). Specimens were collected in September and October 2010.

Table 2. Results of the analysis of variance corresponding to the mixed general linear model applied to daily growth of juveniles *Engraulis anchoita* collected in 2010. DF_MSM: degree of freedom of mean square of the model. DF_MSE: degree of freedom of mean square of the error.

Factor	DF_MSM	DF_MSE	F value	Probability (> F)
Intercept	1	2079	1,342.35	< 0.001
Month	1	2079	55.73	< 0.001
Age	80	2079	1.78	< 0.001
Month:Age	80	2079	0.82	0.870

Table 3. Comparison of daily growth values (mm day^{-1}) of juveniles *Engraulis anchoita* collected in southern Brazil during September and October 2010 and 2011, with other species of Genus *Engraulis*. *Different years.

Species	Size (mm)	Daily growth	Method	Area	References
Engraulis ringens	35-73 33-70	0.93 0.62	Mean absolute values	Northern Chile Southern Chile	Hernández et al. (2020)
Engraulis ringens	75-120	0.65-1.02	Back-calculated values	Northern Chile	Cerna and Plaza (2016)
Engraulis encrasicolus	43-100	0.69-0.78	Linear models	North Aegean Sea	Schismenou et al. (2014)
Engraulis encrasicolus	61-140 55-123	0.61-0.31* 0.36-0.50*	Gompertz models	Central Mediterranean Sea	Basilone et al. (2018)
Engraulis encrasicolus	25-109	0.59-0.78	Linear models	Algerian coast (SW Mediterranean)	Bacha and Amara (2012)
Engraulis encrasicolus	50-68	0.41	Linear model	Adriatic Sea	Durovic et al. (2012)
Engraulis encrasicolus	3-146	0.40-1.00	Logistic model	Bay of Biscay	Aldanondo et al. (2011)
Engraulis anchoita	7-85	0.20-0.52	Back-calculated values	Southern Brazil	This work

Throughout the 200-day period assessed in this study, the increment widths presented a dome shape, showing a trend similar to those observed for juveniles *E. encrasicolus*. This dome-shaped increment width pattern is indicative of a critical growth phase, which has been associated with physiological changes during metamorphosis, an essential stage for survival and future recruitment (Allain et al. 2003; La Mesa et al. 2009). Highest growth rates would correspond to ages of metamorphosed individuals (Brown et al. 2014). According to the power model fitted in this work, the maximum growth occurred at 78 days of age, which corresponds to a total length of 40 mm. Such value results quite similar to the estimated 42.4 mm by Brown et al. (2014), and 44 mm provided by Ciechomski (1965) for completely metamorphosed individuals.

In the age interval of 0-78 days, width increments of Brazilian specimens were thinner than those obtained from specimens on the Argentine shelf (‘El Rincón’ and San Matías Gulf) (Figure 11). However, in the age interval of 78-100 days, width increments were similar along all regions. From 110 mm and older, daily increments in Brazilian specimens were wider than in Argentine individuals. Maximum otolith growth was observed at 78 days of age for Brazilian specimens, compared to 71 days for individuals from ‘El Rincón’ and 64 days for specimens from San Matías Gulf. Overall, the growth pattern across the entire age interval (0-200 days) was more similar between juvenile anchovies from ‘El Rincón’ and San Matías Gulf than those from the Brazilian ecosystem (Figure 11). While the general pattern of growth rate was similar across the three regions (Figure 11), growth estimates in this study were lower during the 0-70-day interval and higher between 110 and 206 days compared to the other two regions.

With respect to the average values of somatic growth, as mentioned in Results, the mean daily growth rate of specimens in this study, was

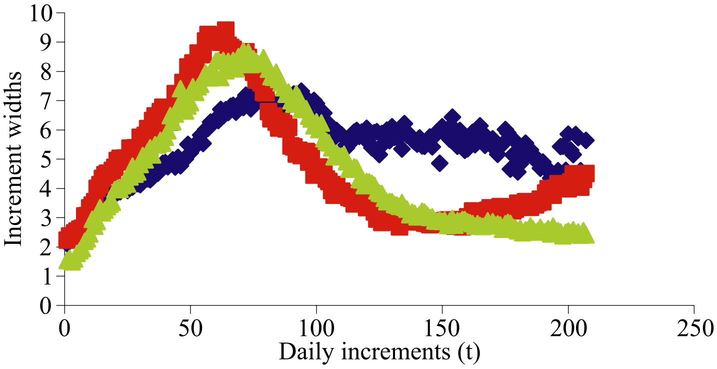

Figure 11. Mean values of otolith width increments (µ day^{-1}) of juveniles *Engraulis anchoita* from southern Brazil (blue), 'El Rincón' (green), and San Matías Gulf (red).

0.38 mm day^{-1} ± 0.11. Such estimate was identical to the one registered for specimens from the San Matías Gulf (0.38 mm day^{-1} ± 0.21) (Brown et al. 2014), and very similar to the estimates recorded for juveniles from 'El Rincón' (0.33 mm day^{-1} ± 0.18) (Brown et al. 2011).

The growth of *E. anchoita* may be affected by environmental factors, such as proximity to rivers and water column stability, among others. 'El Rincón' and San Matías Gulf are nearby locations, in comparison to the southern Brazil. Such geographic proximity could be the consequence of similar environmental conditions. Alternatively, differences in growth could be related to seasonal influences. Brown et al. (2014) mentioned that seasonality and ontogeny affect the growth of juveniles *E. anchoita*. We found that specimens from southern Brazil hatched primarily in June-July, those from the San Matías Gulf mainly hatched in April (Brown et al. 2014), and those from 'El Rincón' in March-April (Brown et al. 2011). Therefore, we could assume that the slower growth of specimens from southern Brazil during the first 70 days is caused by the influence of austral winter and cold temperatures at hatching. Conversely, juveniles from southern Brazil would benefit from austral spring and summer months at ages between 120 and 200 days, whereas in Argentina they would be going through the winter, which could also explain the faster growth of anchovies from southern Brazil at such age interval (Figure 12). Understanding seasonal and geographic variations in growth is crucial for fisheries management, since it aids in optimizing harvest timing to ensure stock sustainability.

Several studies have related the daily growth of fish larvae and juveniles to temperature and food availability (Heath 1992; Stevenson and Campana 1992; Do Souto et al. 2018, 2019). Higher surface temperatures were recorded in April in comparison to July (Figure 13 A). Faster larval growth in autumn (April) in comparison to July could be attributable to thermal influence. In contrast, chlorophyll-*a* concentration was higher in the winter (July) than in autumn (April), therefore anchovy larvae would have greater availability of food in winter months (Figure 13 B). However, chlorophyll-*a* concentration *per se* does not necessarily represent the amount of food available for fish larvae. In Mediterranean areas for example, mesozooplankton concentration (i.e. food availability) has been positively related to growth of juveniles *E. encrasicolus*, but chlorophyll-*a* showed no significant effect on growth descriptors (Schismenou et al. 2014). Furthermore, lower chlorophyll-*a* concentrations might not limit food availability. More transparent waters can facilitate efficient predation by particulate feeding species such as the European anchovy, as suggested by Aldanondo et al. (2010) for the Bay of Biscay and Basilone et al. (2017,

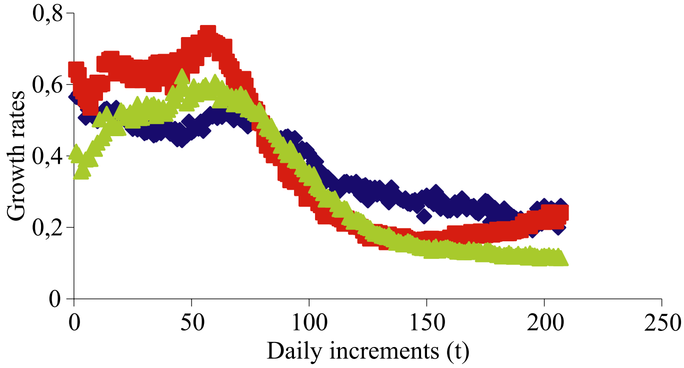

Figure 12. Mean values of somatic daily growth rates (mm day^{-1}) of juveniles *Engraulis anchoita* from southern Brazil (blue), 'El Rincón' (green) and San Matías Gulf (red).

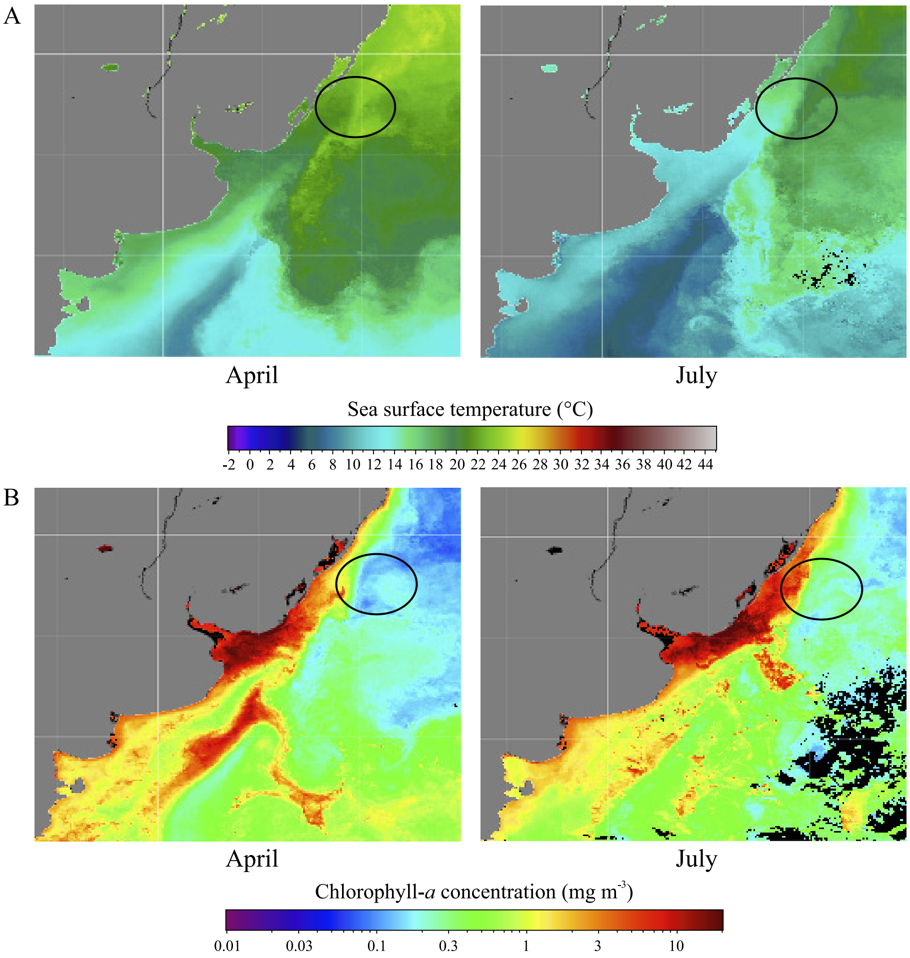

Figure 13. Satellite images of the study area during April and July 2010: surface temperature (°C) (A), and chlorophyll-*a* (mg m^{-3}) (B). Source: https://oceancolor.gsfc.nasa.gov/SeaWiFS.

2018) for the Mediterranean Sea. These findings underscore the sensitivity of juvenile anchovy growth to climatic factors, which may have significant implications for their population dynamics under future climate change scenarios.

Several earlier studies have revealed positive relationships between larval and juvenile growth and the abundance of adult marine fishes (Legget and De Blois 1994; Campana 1996; Takasuka et al. 2007). In a more recent study, Plaza et al. (2018) mention a very fast growth and early age at recruitment of anchoveta *E. ringens* in northern Chile. Slow-growing and small fish larvae remain relatively vulnerable to predation for a longer period. This is the foundation of the 'Stage-Duration' hypothesis, which implies that large size ('bigger is better') and fast growth improve survival potential (Houde 1987; Anderson 1988). The 'bigger is better' hypothesis suggests that rapid larval growth results in larger juveniles, which are less vulnerable to predation and therefore contribute positively to recruitment (Houde 2008). Therefore, it is quite common to find that juveniles exhibit greater back-calculated lengths at earlier ages compared to larvae at the same ages. This phenomenon is caused by selective size mortality as a result of slower growing of fish larvae that are not represented in the juvenile population. It has been detected by Brown et al. (2014) in juveniles *E. anchoita* from the Patagonian ecosystem and by Aldanondo et al. (2011) in juveniles *E. encrasicolus*. In the present study, back-calculated lengths fell within the observed lengths of anchovy larvae in Brazilian waters. Therefore, juvenile anchovies in this study would not have benefited from rapid growth during larval stages.

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Author contributions

Daniel R. Brown: supervision; conceptualization; methodology; validation; resources; writing-original draft. Ezequiel Leonarduzzi: formal analysis; investigation; visualisation; writing-review and editing. Claudio C. Buratti: resources; writing-review and editing; project administration. Felipe Carvalho: investigation; resources; writing-review and editing. Daniel R. Hernández: formal analysis; resources; writing-review and editing.

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