

Research Article

**Age, growth and natural mortality of the Patagonian sprat
Sprattus fuegensis (Jenyns, 1842) in Chiloé inland sea, southern Chile**

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ABSTRACT. Growth parameters (L_{∞} , K , and t_0) and natural mortality of the Patagonian sprat (*Sprattus fuegensis*) Chiloé inland sea were estimated. This area corresponds to the northern limit of the species distribution in the South Pacific Ocean. A total of 1,584 otolith were analyzed between July 2005 and December 2006. A covariance analysis ruled out significant differences ($P = 0.654$) in the otolith size-fish length relationship between males and females. The otoliths showed high monthly proportion of hyaline edge type in August 2005 and from July to October 2006. The hyaline band formation from mid-winter to spring coincided with the breeding season extending from September to December. This suggests an annual periodicity of annuli formation, likely as a consequence of channeling energy into reproduction. The growth parameters were $L_{\infty} = 17.71$ cm; $K = 0.78$ yr⁻¹; and $t_0 = -0.46$ yr, while the maximum observed age was 6 years. Natural mortality given growth parameters and species maturity, was estimated at 1.0 yr⁻¹. The modal decomposition of monthly length distribution, analyzed by a statistical-numerical algorithm (MIX approach) gave similar results to those obtained from otolith readings.

Keyword: *Sprattus fuegensis*, otolith, growth, mortality, distribution, Chiloé inland sea, southern Chile.

**Edad, crecimiento y mortalidad natural de la sardina austral
Sprattus fuegensis (Jenyns, 1842) en el mar interior de Chiloé, Chile**

RESUMEN. Se estimaron los parámetros de crecimiento (L_{∞} , K , t_0) y mortalidad natural (M) de sardina austral (*Sprattus fuegensis*) en el mar interior de la isla de Chiloé. Esta zona corresponde al límite norte de la distribución de la especie en el Océano Pacífico sur. Se analizó un total de 1.584 otolitos, de ejemplares obtenidos entre julio de 2005 y diciembre de 2006. Un análisis de covarianza descartó diferencias significativas ($P = 0,654$) en la relación entre el tamaño del otolito y la longitud total entre machos y hembras. Los otolitos mostraron alta proporción mensual del tipo de borde hialino en agosto de 2005 y de julio a octubre de 2006. La formación de la banda hialina desde mediados de invierno hasta primavera, coincidió con la estación reproductiva que se extendió de septiembre a diciembre. Esto sugiere una periodicidad anual en su formación probablemente como una consecuencia de la canalización de la energía hacia la reproducción. Los parámetros de crecimiento fueron: $L_{\infty} = 17,71$ cm; $K = 0,78$ año⁻¹; $t_0 = -0,46$ años; mientras que la edad máxima observada fue de 6 años. La mortalidad natural, considerando los parámetros de crecimiento y madurez de la especie, se estimó en 1,0 año⁻¹. La descomposición modal de la distribución de longitudes mensuales, analizadas por medio de un algoritmo estadístico-numérico (enfoque MIX), mostró resultados similares a los obtenidos de las lecturas de otolitos.

Palabras clave: *Sprattus fuegensis*, otolito, crecimiento, mortalidad, distribución, mar interior de Chiloé, sur de Chile.

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INTRODUCTION

The Patagonian sprat (*Sprattus fuegensis*) is a small pelagic clupeid with a similar spatial distribution in

both the South Pacific and Atlantic Ocean. Nakamura (1986) and Whitehead (1989) describe their occurrence along the Argentinean coast from 40°S to the southern tip of the continent and around the Falkland Islands. In

Chile, this species occurs from far south in the fjords and channels to approximately 42°S in the inland sea (Radl & Culik, 1999; Aranis *et al.*, 2007; Bustos *et al.*, 2008; Leal *et al.*, 2011). According to Galleguillos *et al.* (2012), at the population level in Chile, *S. fuegensis* encompasses a single genetic stock with significant reproductive cohesion. Nevertheless, this study also identifies at least two ecological stocks, based on differences in life history traits, otolith shape, parasitic fauna and the size of individuals, which is indicative of spatial segregation. These authors also reported an important level of mixing between individuals occurring in Chiloe inland sea (41°90'S-43°50'S) and those inhabiting the southernmost areas.

In the last five years, the Patagonian sprat has become the main clupeid species of the pelagic fisheries caught in the inland sea of Chiloe Island. Since 2008, the catch in this area has been regulated through an annual TAC, and since 2009, the Fisheries Development Institute of Chile (IFOP) has performed annual stock assessments and has estimated annual allowable catches through a size-structured model. This approach, in combination with additional fisheries information, requires reliable estimates of certain aspects related to the reproduction, growth and natural mortality of this species. Regarding reproduction, Leal *et al.* (2011) indicated that *S. fuegensis* is a partial spanner, with a reproductive season mainly restricted to spring (September-December) in the inland sea area off Chiloé. This confirms what was previously reported by Shirakova (1978) for this species in Argentinean waters.

Information on the growth patterns of this species is restricted to a few studies conducted in the Atlantic Ocean. Gru & Cousseau (1982) reported significant differences in the growth parameters of *S. fuegensis* between a population occurring in Santa Cruz Province and those northward of the Falkland Islands. Hanssen (1999) found higher growth rates than previous estimates in the coastal zone and levels of natural mortality (M) between 0.59 and 0.9 yr⁻¹, depending on the method used for estimation.

Currently, there are no published studies in Chile that have addressed the growth and natural mortality patterns of this species, except for a technical report, which showed preliminarily information on growth parameters that are currently used in the stock assessment (Aranis *et al.*, 2006). Hence, there is an immediate need to know the life history traits of this species to advice in fishery regulation measure. Therefore, this study aimed to determine the age, growth parameters and natural mortality of *S. fuegensis* in Chiloé inland sea, southern Chile.

MATERIALS AND METHODS

The study area encompassed the Chiloé inland sea, southern Chile (41°90'-43°50'S) (Fig. 1). Samples were taken at random from landings of the purse-seine fishery, which often includes common sardine *Strangomera bentincki* (Norman, 1936), anchovy *Engraulis ringens* (Jenyns, 1842) and Patagonian sprat. In the laboratory, the biological sampling consisted of recording the total length (TL), total weight (TW), and sex for each fish. Furthermore, *sagitta* otoliths were extracted and stored dried in cardboard dispensers, which were carefully labeled to ensure traceability.

Age and growth

A total of 1,584 pairs of otoliths were analyzed, which corresponded to 737 males and 847 females, obtained monthly between July 2005 and December 2006. The age determination was conducted in the entire left otolith, which was immersed in liquid petrolatum (liquid lightener) and observed with reflected light under a stereoscopic microscope at 20x magnification. In addition to age, the otolith diameter (Do) and diameter-at-age (Da) in millimeters were recorded along with the edge type (*i.e.*, opaque (O) or hyaline (H)). The periodicity of the annuli formation was determined by analyzing a monthly percentage distribution of hyaline rings present in the otolith edge type (Lai *et al.*, 1996).

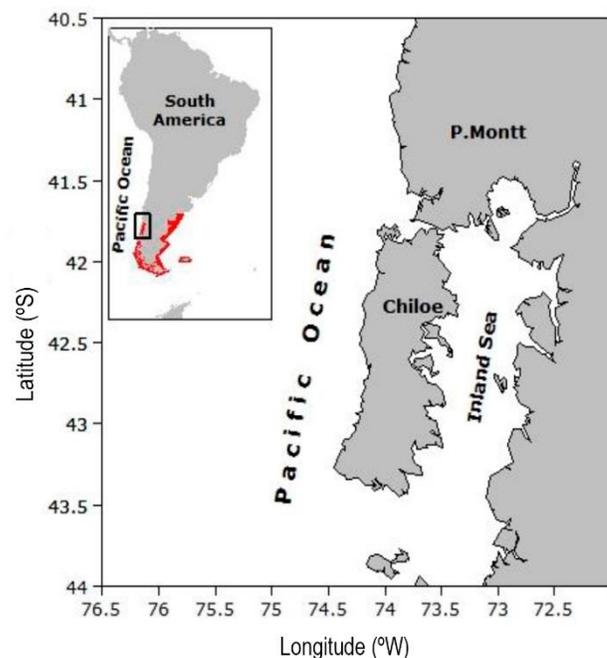


Figure 1. Study area in Chiloé inland sea, Chile. The left upper map shows in red the distribution of *S. fuegensis* in southern of South America and around the Falkland island.

To measure the accuracy of the age determination, a second reading was performed by another independent reader (*i.e.*, reproducibility analysis). Both readings were performed by the analyst without knowing the biological data of the fish (length, weight, sex and month of capture). The reproducibility of growth ring counting was evaluated through the average percentage error (APE) (Beamish & Fournier, 1981) and the coefficient of variation (CV) (Chang, 1982). These indicators were supplemented with the use of a graphical method using the average age estimated by a reader irrespective of the pattern reader (Campana *et al.*, 1995; Campana, 2001).

The growth parameters were estimated by fitting the length-age data at capture through the von Bertalanffy growth curve (VB; Von Bertalanffy, 1938):

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where: L_t = average total length at age t , L_∞ = asymptotic length, K = growth coefficient and t_0 = hypothetical age at zero length.

The growth parameters were estimated using the Gauss-Newton algorithm and the nonlinear module of SYSTAT 7.0. A modal progression analysis was also performed to contrast with growth parameters derived from the VB model. For this purpose, the length distributions of individuals collected in 2006 were used. A total of 19,912 specimens were analyzed, whose length frequency distribution were adjusted by maximum likelihood through the mixture distribution models (MIX models) (MacDonald & Green 1988) using the algorithms of MacDonald & Pitcher (1979). The distributional sample, whose observable shape is a frequency histogram, is represented by:

$$g(l) = p_i f_i(l) + \dots + p_k + f_i(l)$$

where $g(l)$ is a function of overall probability l , p_i is the proportion of the total number of individuals that are represented in the distribution i , $f_i(l)$ is a function of the probability density function of the length l shown in the distribution i and k is the number of mixing functions.

Natural mortality

The rate of natural mortality (M) was calculated from empirical models using the growth parameters (t_0 , K , and L_∞) and maturity (L_{m50}) of this species. The growth parameters corresponded to those estimated in the present study, while the length at maturity corresponded to those reported by Leal *et al.* (2011). The average of the following four methods was finally assumed as the value of M .

Hoening (1983) relates the rate of total mortality (Z) and the maximum observed age (t_{max}). When assuming Z is equal to M , the equation has the form:

$$\ln(Z) = 1.44 - 0.982 \ln(t_{max})$$

The maximum age (t_{max}) is estimated on the assumption that this is achieved when the fish reach 95% of the asymptotic length (Pauly, 1980), where:

$$t_{max} = t_0 - \frac{1}{K} \ln\left(1 - \frac{0.95L_\infty}{L_\infty}\right) = t_0 + \frac{3}{K}$$

Rikhter & Efanov (1976) relate the rate of natural mortality (M) with the average age of maturity ($T_{m50\%}$) using the expression:

$$M = \left[\frac{1.521}{t_{m50\%}^{0.72}} \right] - 0.155$$

where $T_{m50\%}$ was calculated using the size at 50% of mature females, estimated by Leal *et al.* (2011) as follows:

$$t_{m50\%} = t_0 - \frac{1}{K} \ln\left(1 - \frac{L_{m50\%}}{L_\infty}\right)$$

Hewitt & Hoening (2005) suggest that the rate of natural mortality (M) can be estimated by:

$$M = \frac{4.22}{t_{max}}$$

Finally, the method developed by Pauly (1980) was used, which relates the rate of natural mortality, growth parameters and mean environmental temperature (T) through the following equation:

$$\log_{10}(M) = -0.0066 - 0.279 \log_{10}(L_\infty) + 0.6543 \log_{10}(K) + 0.4634 \log_{10}(T)$$

It is important to note that the annual average temperature in southern sardine habitat was assumed to be 11°C.

RESULTS

Overall, 734 males and 850 females were analyzed, with lengths ranging between 9.5 and 18.5 cm TL and a mean of 14.6 cm (standard error = 0.055).

There was a significant linear relationship ($P < 0.01$) between the diameter of the otolith (Do) and the total length for each sex and for when the data were combined. The functions were:

$$TL = 0.283 Do + 2.517 \quad r^2 = 0.86 \quad \text{for males}$$

$$TL = 0.286 Do + 2.403 \quad r^2 = 0.86 \quad \text{for females}$$

$$TL = 0.284 Do + 2.459 \quad r^2 = 0.86 \quad \text{for combined data}$$

The analysis of covariance did not show significant differences between the otolith size and the fish size relationship between sexes ($P = 0.654$); hence, the data processing was performed by combining the information for males and females.

Patagonian sprat otoliths resembled those described by the common sardine, especially in the juvenile stage; however, adult fish Patagonian sprat differed from *S.*

bentincki in the occurrence of lobes or ridges in the otolith contour, which appeared in higher proportion to the lower or ventral edge. Additionally, a distinctive feature was the occurrence of clear or translucent growth bands in both juveniles and adults. The hyaline rings appeared marked and well-defined throughout the otolith, which facilitated the reading of the otoliths (Fig. 2).

The accuracy was high for the age determination through counting otolith rings from two independent readers. Both the APE and the CV showed low values, 1.8% and 2.6%, respectively. The graphical age analysis indicated an absence of bias in readings, even reaching a 100% match in identifying the first annuli.

A high proportion of otoliths showed a monthly occurrence of hyaline edges in August 2005 and from July to October 2006, with proportions higher than 0.8, while between September 2005 and May 2006, a lower proportion was found. Although, in March 2006, this proportion increased slightly, and the overall trend suggests the formation of a hyaline band per year, which would be formed in the otolith between late winter and early spring (Fig. 3).

The growth fit through the von Bertalanffy equation using the nonlinear procedure resulted in the following parameters and their respective standard errors: $L_{\infty} = 17.71 \pm 0.233$ cm; $K = 0.78 \pm 0.07$ yr⁻¹; and $t_0 = -0.46 \pm 0.102$ yr, while the maximum observed age from the otolith reading was 6 years (Fig. 4).

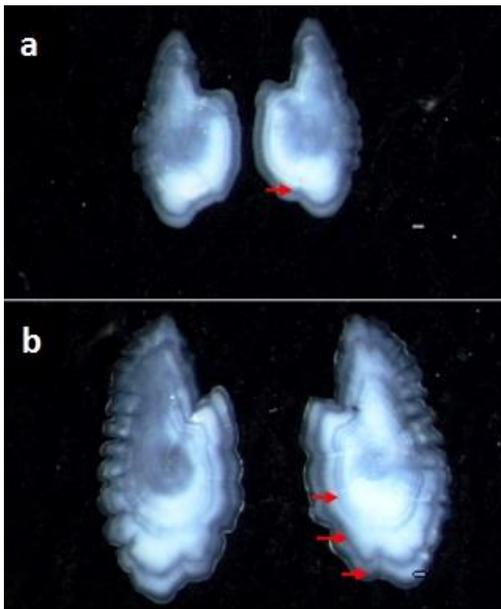


Figure 2. Left and right sagittal otoliths of *S. fuegensis* from a fish of 11.0 cm TL and 1 year old (a) and another fish of 15.5 cm TL and 3 years old (b). The red arrows indicate the hyaline rings (annuli).

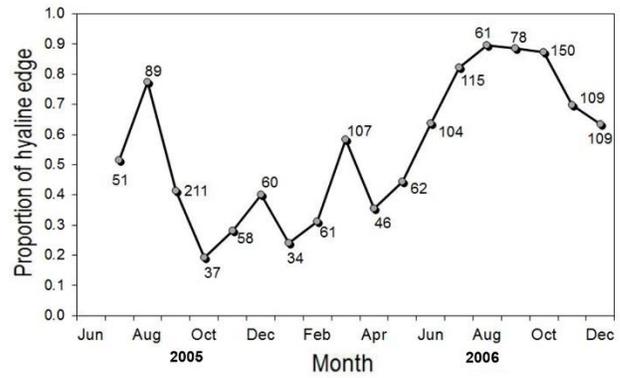


Figure 3. Monthly frequency of hyaline edge in the *S. fuegensis* otoliths between July 2005 and December 2006. The numbers on the curve indicate the monthly sample size.

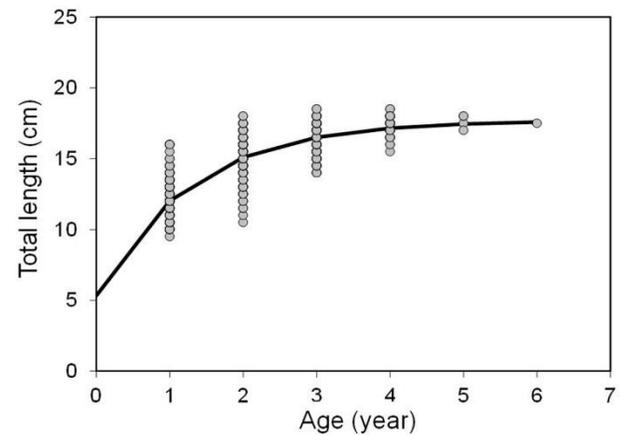


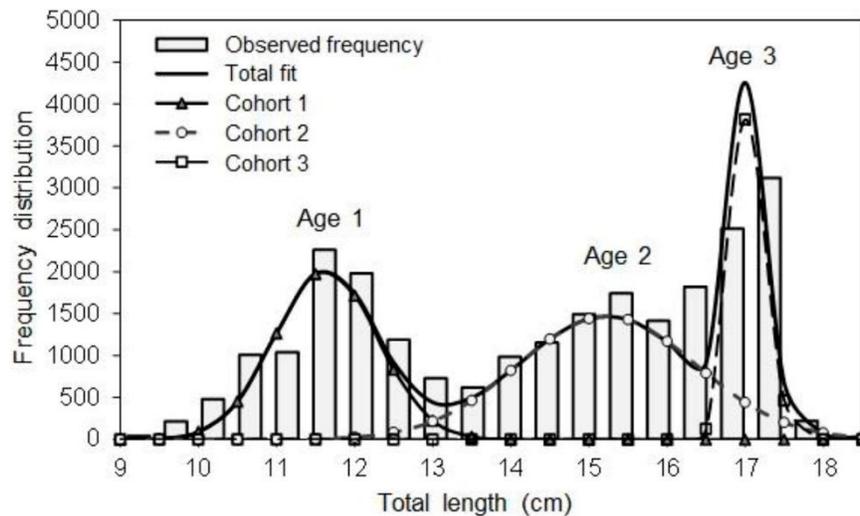
Figure 4. The von Bertalanffy growth curve fitted to observed age-at-length data of *S. fuegensis* in Chilóe inland sea.

The growth parameters obtained from the age-at-capture were compared with estimates obtained by modal progression analysis of the monthly size distributions. The identified modes through the MIX algorithm were used to construct age-at-length pairs, which were similar to those obtained from otolith readings. Thus, three major trends were identified, corresponding to 11.6, 15.2 and 17.1 cm TL (Table 1, Fig. 5). The growth parameters derived from average size by cohort and fitted through the VB model were $L_{\infty} = 18.7$ cm; $K = 0.70$ yr⁻¹; and $t_0 = -0.36$ yr. The average sizes estimated by the VB equation from modal progression analysis were similar to those obtained from the otolith readings for the first three ages (Table 1).

The natural mortality was 1.0 yr⁻¹ after averaging the results of the four methods used for estimation. The highest estimation was obtained by the approximation of Pauly (1980), 1.1 yr⁻¹, and the lowest one by the method of Rikhter & Efanov (1976), 0.94 yr⁻¹ (Table 2).

Table 1. Observed mean length and estimated mean length with the von Bertalanffy growth model for *S. fuegensis* in Chiloe inland sea.

Age	Mean length observed (cm)		Mean length estimated von Bertalanffy (cm)	
	Otolith reading	Modal progression analysis	Otolith reading	Modal progression analysis
1	12.1	11.6	12.0	11.5
2	15.2	15.2	15.1	15.2
3	16.5	17.1	16.5	17.0
4	17.3		17.2	17.9
5	17.6		17.5	18.3
6	17.5		17.6	18.5

**Figure 5.** Illustration of a MIX-based fit compared to the observed length frequency distribution of the *S. fuegensis*. The curves show three cohorts or age classes separately and the overall combined fit.**Table 2.** Natural mortality of *S. fuegensis* estimated by four empiric models.

Method	M (yr ⁻¹)
Rikhter & Efanov (1976)	0.94
Pauly (1980)	1.1
Hoening (1983)	1.0
Hewitt & Hoenig (2005)	0.98
\bar{M} (yr ⁻¹)	1.0

DISCUSSION

The ANCOVA analysis discarded the existence of a significant relationship between the total length and the diameter of the otolith between males and females, which led to a combined analysis. A similar finding has been reported for other small pelagic resources, such as common sardine and anchovy (Barría *et al.*, 1999).

The annuli (*i.e.*, macro-rings formed at an annual periodicity) appeared sharp and well defined, with little presence of false rings. Such a distinctive feature facilitated the identification, measurement and counting of hyaline rings. This finding was further supported by the existence of a high precision in age determination, with estimates of error that did not exceed 3% (APE = 1.8% and CV = 2.6%). Through a literature review, Campana (2001) indicated that in many studies, the estimation of CV has been less than 7.6%, corresponding to an APE of 5.5%. The same author stated that a CV of 5% is an acceptable standard reference for many fish with a moderate longevity (5-10 years old).

In the analysis of periodicity and in the formation of annuli, the high monthly proportion of the hyaline-edge type was formed between June and December 2006, with maximum values between July and October (>80%). Conversely, a high occurrence of opaque growth occurred between January and May. This would

Table 3. *Sprattus fuegensis* common growth parameters. Comparisons for two zones in the South Atlantic with estimates reported by other authors.

Area	Period	von Bertalanffy growth parameters			
		L_{∞}	K	t_0	Authors
Inland sea Chiloé (41°90'-43°50' S)	Jul 2005 to Dec 2006	17.7	0.78	-0.46	Present study
Argentina Coast (46°30'-51°30' S)	Feb to May 1974	14.5	0.78	0.10	Gru & Couiseau (1982)
North Malvinas (50°30'-51°30' S)	Sep 1978	20.7	0.73	0.35	Gru & Couiseau (1982)
Argentina Coast (47°20' -54°30' S)	Mar to Apr 1992	13.4	0.62	-0.35	Hansen <i>et al.</i> (1993)
Argentina Coast (50°00' -55°00' S)	Apr to May Nov to Dec 1996	14.0	1.02	-0.14	Hansen (1999)

be indicative of the formation of an annulus per year, where the hyaline band would be formed from mid-winter to spring, coinciding with the spawning season, which occurs between September and December of each year (Leal *et al.*, 2011). Such a finding suggests a potential relationship between the formation of this band and energy partitioning from growth to the formation of gametes (Cubillos & Arancibia, 1993). These results agree with those found by López-Veiga (1979) in a species of the same genus (*Sprattus sprattus*) in the waters of Galicia, Spain. It is important to note that *Sprattus fuegensis* of southern Atlantic Hansen (1999) and Gru & Couiseau (1982) did not determine the frequency of the formation of growth rings because the sampling period was less than a year.

The growth parameters of Patagonian sprat obtained from the present study resembled those obtained by Gru & Couiseau (1982) for the Santa Cruz coast in Argentina and the Falkland Islands, particularly in the growth coefficient (K) (Table 3). However, growth parameters widely differed from those reported for the same species by Hansen *et al.* (1993) and Hansen (1999), who reported sampling bias in individuals with longer lifespan. Unfortunately, there are no other studies that we can compare with our results. Regarding gender, the results are scarcely comparable because the other representatives of this genus (*i.e.*, *S. sprattus*, *S. antipodum*, *S. bassensis*, and *S. muelleri*) have much lower body sizes (Whitehead, 1989). On the coast of Chile, the growth parameters of *S. fuegensis* in the current study fall within the range of those reported for other small pelagic fish, such as sardine (Cubillos *et al.*, 2002) and anchovy (Canales & Leal, 2009).

The estimated growth parameters acquired through modal decomposition of the length frequencies were similar to those obtained by reading otoliths, except for the mean length obtained at age 3. This difference may be because the MIX model only reproduces the first three ages, unlike the otolith reading that allowed determination up to 6 years. The similarity, especially

in mean length at ages 1 and 2, indicates that age determinations obtained from otoliths are reliable. These results are also comparable to the estimations reported by Cubillos & Arancibia (1993) for sardine and anchovy off Talcahuano using the ELEFAN program.

The estimation of natural mortality obtained in the present study was close to the upper limit of the range reported for the species in the Atlantic ocean (0.59 to 0.93 yr⁻¹) and coincided with that reported by Cubillos *et al.* (2002) for the common sardine (1.0 yr⁻¹). The apparent similarity of these results may be linked to the proximity in the estimation of growth parameters between different studies. Thus, the Patagonian sprat shows a pattern of growth and natural mortality characteristic of small pelagic fishes and can be classified as a fast-growing species with a short lifespan.

It is important to note that growth models also showed a common problem associated with almost all growth studies in small pelagic fishes, where the model fit depended on reliable estimations of t_0 , which should be close to zero. This was also described by Canales & Leal (2009) for anchovy of north-central Chile. These authors corrected the parameter t_0 using the approach reported by Lopez-Veiga (1979), which used the length at hatching as a deterministic t_0 value to fit the VB model. However, an alternative approach to increase reliability in VB would be to expand the range of age-at-length data by including pre-recruits and recruits from age zero in the analysis. This would more accurately represent the growth patterns for the lower portion of the VB curve, associated with young-of-the-year fish.

The results of this study represent a contribution to understanding the life history traits of the Patagonian sprat in Chilean waters. However, future studies need to address new issues, such as age validation and growth patterns of pre-recruits, to obtain a better picture and improve the understanding of the production and mortality rates of this species.

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REFERENCES

- Aranis, A., R. Meléndez, G. Pequeño & F. Cerna. 2007. *Sprattus fuegensis* en aguas interiores de Chiloé, Chile (Osteichthyes: Clupeiformes: Clupeidae). *Gayana*, 71(1): 102-113.
- Aranis, A., L. Caballero, F. Cerna, A. Gómez, A. López & C. Bernal. 2006. Monitoreo de la pesquería de pequeños pelágicos en aguas interiores de la X Región, Año 2004. Informe Final, Proyecto FIP 2004-39: 96 pp.
- Barría, P., G. Böhm, A. Aranis, R. Gili, M. Donoso & S. Rosales. 1999. Evaluación indirecta y análisis de la variabilidad del crecimiento de sardina común y anchoveta en la zona centro-sur. Informe Final, Proyecto FIP 97-10: 115 pp.
- Beamish, R.J. & E.A. Fournie. 1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.*, 38: 982-983.
- Bustos, C., M. Landaeta & F. Balbontín. 2008. Efectos ambientales sobre la variabilidad espacial del ictioplancton de Chile austral durante noviembre de 2005. *Rev. Chil. Hist. Nat.*, 81: 205-219.
- Campana, S.E. 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish Biol.*, 59: 197-242.
- Campana, S., M. Annad & J. McMillan. 1995. Graphical and statistical methods for determining the consistency of age determinations. *T. Am. Fish. Soc.*, 124: 131-138.
- Canales, T.M. & E. Leal. 2009. Parámetros de historia de vida de la anchoveta *Engraulis ringens* Jenyns, 1842, distribuida en la zona centro norte de Chile. *Rev. Biol. Mar. Oceanogr.*, 44(1): 173-179.
- Chang, W. 1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.*, 39: 1208-1210.
- Cubillos, L. & H. Arancibia. 1993. On the seasonal growth of common sardine (*Strangomera bentincki*) and anchovy (*Engraulis ringens*) off Talcahuano, Chile. *Rev. Biol. Mar.*, 28(1):43-49.
- Cubillos, L., D. Bucarey & M. Canales. 2002. Monthly abundance estimation for common sardine *Strangomera bentincki* and anchovy *Engraulis ringens* in the central southern area off Chile (34-40°S). *Fish. Res.*, 57: 117-130.
- Galleguillos, R., S. Ferrada, C. Canales, C. Hernández, M. Oliva, M.T. González, L. Cubillos, E. Niklitschek & P. Toledo. 2012. Determinación de unidades poblacionales de sardina austral entre la X y XII regiones de Chile. Informe Final, Proyecto FIP 2010-17: 221 pp.
- Gru, D. & M. Cousseau. 1982. Estudio de edad y crecimiento de la sardina fueguina (*Sprattus fuegensis*) en las costas de la provincia de Santa Cruz e Islas Malvinas. *Rev. Invest. Des. Pesq.*, 3: 51-58.
- Hansen, J.E. 1999. Estimación de parámetros poblacionales del efectivo de sardina fueguina (*Sprattus fuegensis*) de la costa continental argentina. INIDEP, Informe Técnico, 27: 1-18.
- Hansen, J.E., A. Mediolas, A. Remeslo, R. Sanchez & V. Sushin. 1993. Campaña de investigación científica llevada a cabo por el B.I.P. "Dmitry Stefanov" en la ZEE de la República Argentina (21 marzo-14 abril, 1992). Informe Final, 93 pp.
- Hewitt, D. & J.M. Hoenig. 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish. Bull.*, 103: 433-437.
- Hoening, J.M. 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.*, 82: 898-903.
- Lai, H.L., V. Gallucci, D. Gunderson & R. Donnelly. 1996. Age determination in fisheries: methods and applications to stock assessment. In: V. Gallucci, S. Saila, D. Gustafson & B. Rothschild (eds.). Stock assessment. Quantitative methods and applications for small-scale fisheries. Lewis Publishers of CRC Press, Florida, pp. 82-178.
- Leal, E., T.M. Canales, A. Aranis & M. González. 2011. Actividad reproductiva y longitud de madurez de sardina austral *Sprattus fuegensis*, en el mar interior de Chiloé, Chile. *Rev. Biol. Mar. Oceanogr.*, 46(1): 43-51.
- López-Veiga, E.C. 1979. Fitting von Bertalanffy growth curves in short-lived fish species. A new approach. *Invest. Pesq.*, 43: 179-186.
- McDonald, P.D. & P.E. Green. 1988. User's guide to program MIX: an interactive program for fitting mixtures of distributions. Icthus Data Systems, Hamilton, Ontario, 75 pp.
- McDonald, P.D. & T.J. Pitcher. 1979. Age groups from size-frequency data: a versatile and efficient method for analyzing distribution mixtures. *J. Fish. Res. Bd. Can.*, 36: 987-1001.

- Nakamura, I. 1986. Important fishes trawled off Patagonia, JAMARC, Tokyo, 369 pp.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM, 39(2): 175-192.
- Radl, A. & B. Culik. 1999. Foraging behaviour and reproductive success in Magellanic penguins (*Spheniscus magellanicus*): a comparative study of two colonies in southern Chile. Mar. Biol., 133: 381-393.
- Ricker, V.A. & V.N. Efanov. 1976. On one of the approaches to estimation of natural mortality of fish populations. ICNAF Res. Doc., 76/VI/8: 1-12.
- Shirakova, E.N. 1978. Contribution to the biology of Tierra del Fuego sprat *Sprattus fuegensis* (Jenyns, 1842). Biol. Sea, 3: 78-84.
- Von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Human Biol., 10: 181-213.
- Whitehead, P.J. 1989. Clupeoid fishes of the world. An annotated and illustrated catalogue of the herrings, sardines, pilchards, sprats, anchovies and wolfherrings. Part 1. Chirocentridae, Clupeidae and Pristigasteridae. FAO Fish. Synop., 125(7): 1-303.

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