

ORIGINAL ARTICLE

Ontogeny versus environmental forcing off the Southwest Atlantic Ocean: Nutritional condition of Fuegian sprat (*Sprattus fuegensis*) early stages

Virginia Andrea García Alonso^{1,2}  | Marina Vera Diaz^{3,4}  | Marcelo Pájaro⁴ | Fabiana Lia Capitanio^{1,2}

¹Departamento de Biodiversidad y Biología Experimental (DBBE), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

²Instituto de Biodiversidad y Biología Experimental Aplicada (IBBEA), CONICET-Universidad de Buenos Aires, Buenos Aires, Argentina

³Instituto de Investigaciones Marinas y Costeras (IIMyC), FCEyN, UNMdP-CONICET, Mar del Plata, Argentina

⁴Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina

Correspondence

Virginia Andrea García Alonso, Departamento de Biodiversidad y Biología Experimental (DBBE), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina. Email: garciaalonso.v.a@gmail.com

Funding information

Universidad de Buenos Aires, Argentina, Grant/Award Number: UBACYT 20020160100045BA 2017-2020; Consejo Nacional de Ciencia y Tecnología (CONICET)-Argentina, Grant/Award Number: PIP 11220150100109CO 2015-2017

Abstract

The Fuegian sprat, *Sprattus fuegensis*, plays a key trophic role in the Southwest Atlantic Ocean. Growth and survival of small pelagic fishes like sprat are strongly affected by environmental variability and can determine recruitment success. We estimated the nucleic acid composition and assessed with a standardized RNA/DNA index (sRD) the nutritional condition of 273 larvae, metamorphosing, and juvenile Fuegian sprat from two environmentally distinct habitats: the waters off Tierra del Fuego (TDF) and the Marine Protected Area Namuncurá/Burdwood Bank (MPAN/BB). A similar ontogenetic pattern, in which nucleic acid concentrations decreased and sRD increased with increasing standard length (SL) among larval stages was observed in both habitats. A higher percentage of preflexion larvae were under the sRD threshold for growth and optimal growth performance, with sRD values being significantly higher in TDF. Postflexion larvae in both habitats showed maximum sRD values, suggesting that both habitats are suitable nursery grounds. In contrast, metamorphosing and juvenile sprat (only captured in TDF) had consistently low nucleic acid concentrations and sRD values despite increasing SL. Environmental forcing (temperature, salinity, and station depth) was assessed over size-corrected larval sRD. The best model included a negative response to station depth, and the effect of processes associated with this factor are discussed. Although further analyses are needed to reveal underlying dynamics determining early development, these results comprise a baseline for future monitoring approaches on Fuegian sprat life traits and factors affecting their recruitment in this region.

KEYWORDS

environmental forcing, juvenile, larva, metamorphosis, MPA Namuncurá/Burdwood Bank, RNA/DNA, sprat

1 | INTRODUCTION

Small pelagic fishes (e.g., herrings, sardines, anchovies, sprats) are frequently recognized as key foundation species in many productive marine ecosystems. They occupy an intermediary position at the

“wasp-waist” level in marine food webs, controlling the energy flux from lower to higher trophic levels (Cury et al., 2000). Also, their high oil content and tendency to form large shoals make them suitable for fisheries (Stephenson & Smedbol, 2001), with small pelagic fishes representing about 20% of the total annual catch worldwide

(FAO, 2019). Recruitment variability of these fishes can, therefore, have major economic and ecological impacts.

Understanding recruitment regulation has been, and still represents, one of the most important scientific problems hindering effective management of small pelagic fish populations (Checkley et al., 2009). Small pelagic fishes often undergo complex life cycles in which small changes in the physical ocean-atmosphere system can have major repercussions on their population dynamics (Alheit & Hagen, 2001; Peck et al., 2013). Since growth and survival of early stages are known to be main determinants for successful recruitment (Cury & Roy, 1989; Houde, 1987; Leggett & Deblois, 1994), assessing environmental forcing (e.g., temperature, salinity, depth, currents, and prey abundance) on early development arises as a fundamental step in resolving recruitment dynamics of small pelagic species.

The Fuegian (Patagonian) sprat (*Sprattus fuegensis*) is a small pelagic clupeid broadly distributed along the coasts of southern South America, including both the Southeast Pacific and Southwest Atlantic Oceans (Aranis et al., 2007; Cousseau, 1982). The Southwest Atlantic Ocean is known to be one of the most productive marine ecosystems worldwide, with a vast continental shelf exhibiting high levels of chlorophyll *a* and zooplankton biomass which, in turn, sustains many species of ecological and economic relevance (Cepeda et al., 2018; Martinetto et al., 2020). This rich habitat supports highly abundant shoals of Fuegian sprat, representing one of the most important potential pelagic resources available for commercial fisheries south of latitude 47°S (Bellisio et al., 1979; Casarsa et al., 2019). *Sprattus fuegensis* also functions as a foundation species, feeding upon zooplankton and constituting the main prey for numerous harvested fishes, seabirds, and marine mammals (e.g., Belleggia et al., 2014; Scioscia et al., 2014).

Three different spawning/nursery grounds of Fuegian sprat have been identified in the Southwest Atlantic Ocean (Figure 1): the Malvinas (Falkland) Islands, the Patagonian coasts (mainly waters off Tierra del Fuego), and the Marine Protected Area Namuncurá/Burdwood Bank (García Alonso et al., 2018; Sánchez et al., 1995). The latter two encompass the southernmost extension not only of Fuegian sprat, but also of clupeids worldwide (Acha et al., 1999). While major spawning occurs during spring/summer and late larvae are present during autumn in both Tierra del Fuego (TDF) and the Marine Protected Area Namuncurá/Burdwood Bank (MPAN/BB) (Acha et al., 1999; García Alonso et al., 2018), different environmental features distinguish each habitat as a result of the region's complex oceanographic conditions, affecting *S. fuegensis*' early development. Differing spawning/nursery strategies have been found, with sprat being energetically transported along the coast of TDF (Acha et al., 1999), or retained in the MPAN/BB (García Alonso et al., 2018). Also, results from previous studies of age-size relationships suggest the existence of environmentally forced variability in early growth rates. A prolonged larval phase and a lower larval growth in the MPAN/BB were detected compared with TDF (Brown & Sánchez, 2010; García Alonso et al., 2018), possibly a consequence of colder temperatures experienced during early development. Thus, these habitats offer

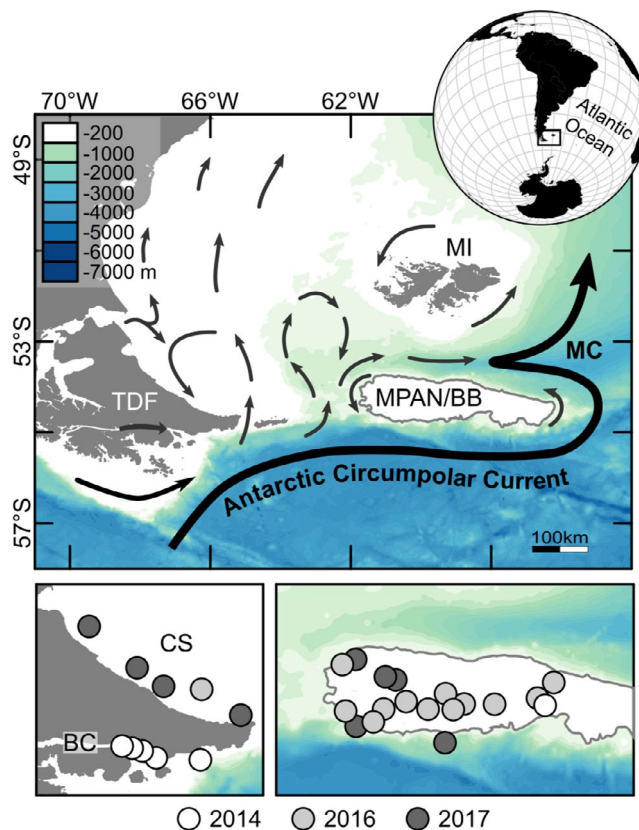


FIGURE 1 Study area and position of the stations analyzed in the Southwest Atlantic Ocean. Arrows represent main current features. Colors identify the survey in which stations were sampled. BC, Beagle Channel; CS, Continental shelf; MC, Malvinas Current; MI, Malvinas (Falkland) Islands; MPAN/BB, Marine Protected Area Namuncurá/Burdwood Bank; TDF, Tierra del Fuego. Modified from Piola and Rivas (1997). Bathymetry from ETOPO1 Global Relief Model (Amante & Eakins, 2009)

distinct natural scenarios in which to assess environmental forcing over early Fuegian sprat development.

Examination of life traits reveals important information about early development. Nucleic acid-based indices have been widely used as proxies of growth and physiological status (Bulow, 1970; Ferron & Leggett, 1994), with RNA/DNA ratios frequently studied in clupeids species (e.g., Do Souto et al., 2019; Kanstinger & Peck, 2009; Voss et al., 2006). This biochemical index measures cell synthetic capacity, which strongly correlates with nutritional status in individuals. Higher RNA/DNA ratios indicate better nutritional condition, allowing for faster growth and increasing survival probability. Intrinsic biological attributes such as age, size, developmental stage, and disease state can determine metabolic activity and thus influence the RNA/DNA ratio. A common pattern of increasing RNA/DNA ratio with size has been registered for numerous species (Chícharo & Chícharo, 2008) including the Baltic sprat *Sprattus sprattus* (Voss et al., 2006). Besides ontogenetic constraints, several environmental features also modulate RNA/DNA ratios. Temperature has been identified as one of the main factors due to its direct effect over the metabolic rate (Buckley, 1984) along with food availability

(Catalán et al., 2006; Chícharo & Chícharo, 2008). Other oceanographic factors such as salinity plumes (and associated water stratification) located in nearshore shallow regions have also shown to favor better conditions, providing abundant food supply, and/or retaining larvae and their prey (Chícharo et al., 2003; Sabatés et al., 2001; Teodósio et al., 2017). Despite the multiple variables involved in this proxy's modulation, the RNA/DNA ratio emerges as a powerful tool to monitor physiological state in the field and to determine favorable conditions for early development and recruitment when age/stage-specific comparisons are performed.

The environmental controls over Fuegian sprat growth dynamics and survival success in the Southwest Atlantic Ocean are at present not well understood. Given that this open-sea MPA is subject to harsh climatic conditions, collecting ichthyoplankton samples is a challenging task. This logistic constrain, coupled with the fact that sprat are difficult to rear in the laboratory (Leal et al., 2017), hinders direct experimental investigation of factors affecting growth. Therefore, employing *in situ* proxies such as the RNA/DNA index in distinct habitats can provide relevant information on the relation between Fuegian sprat development and physical characteristics of the environment. The main objectives of this study were to (i) analyze *S. fuegensis* nucleic acid content and RNA/DNA ratios through early development in both habitats and (ii) assess the role of environmental forcing (temperature, salinity, and station depth as a proxy) in predicting variability of this life-trait. We hypothesize that nutritional condition will increase across ontogenetic stages and will be higher in the TDF system, associated with higher temperatures, lower salinities, and shallower depths. This knowledge is important not only for sustainable fisheries strategies in TDF and ecosystem-based management policies in the MPAN/BB, but also serves as baseline data upon which to assess possible effects of climate variability on recruitment.

2 | MATERIALS & METHODS

2.1 | Study area

The MPAN/BB and TDF (Figure 1) are both under the prevailing influence of intense westerly winds and high tidal variability. Water in both habitats has a sub-Antarctic origin formed mainly by the northernmost jets of the Antarctic Circumpolar Current and partially fed by the Cape Horn Current (Piola et al., 2018). However, distinctive circulation regimes and physical characteristics prevail in each habitat.

The MPAN/BB is a shallow seamount delimited by the 200 m isobath. It is surrounded by steep flanks descending to depths of more than 3000 m. A broad anticyclonic current flows around its perimeter acting as a retentive structure for water masses. Intense upwelling and mixing occur over the bank, entraining deep nutrient-rich waters into the photic layer (Matano et al., 2019). The water column within the bank is overall strongly mixed, resulting in weak temperature and salinity stratification throughout the year. Seasonal

variation of water temperature over the bank is slight, with values ranging between 4°C in winter and 8°C in summer. Salinity has a modal value of 34.12 (Guerrero et al., 1999). In this habitat, both early and late larvae are found throughout the entire extension of the MPAN/BB (García Alonso et al., 2018).

In general, TDF waters are fresher and warmer compared with the MPAN/BB. Sub-Antarctic waters are strongly diluted near the continent (salinities <33.00), a result of strong precipitation in the Southeast Pacific Ocean, continental run-off and glacial melting (Balestrini et al., 1998). Two different coastal regions, the Beagle Channel (BC) and the continental shelf (CS), are included in this system. The BC, a 180 km strait with depths of 30 to 300 m, extends in an east-west orientation along the southern margin of TDF and connects the Pacific to the Atlantic Ocean. Water in the BC is fresher and colder than in the CS (Antezana, 1999; Balestrini et al., 1998). In the latter, depths do not surpass the 200 m and the mass-heat exchange with the atmosphere is stronger, with mean temperatures around 9°C (Antezana, 1999). Advectively connected, both regions exhibit different intensities of water stratification during spring/summer (Balestrini et al., 1998; Piola et al., 2018), and constitute a sole spawning nursery ground. Major spawning and early development of Fuegian sprat occur within the BC. As they grow, they are transported to the northern CS, where late larvae and early juveniles are mainly found (Acha et al., 1999).

2.2 | Sample collection and preparation

Fuegian sprat were collected at 28 sampling stations during three oceanographic surveys conducted by the ARA "Puerto Deseado" oceanographic vessel (Figure 1), one in spring (November) of 2014 and two in the autumn of 2016 and 2017 (March/April and April/May, respectively). Temperature and salinity were measured with a Sea-Bird 19 CTD at each sampling station. Sprat larvae were sampled using a 300- μ m mesh, 60-cm diameter Bongo net in all surveys. Metamorphosing and juvenile sprat were caught with an Isaacs-Kidd Midwater Trawl (IKMT) employed only in 2017 at the same sampling stations surveyed with the Bongo net. The nets were towed obliquely for 5 min at 2–3 knots from 180 m to the surface or less, reaching the proximity of the bottom when possible. A total of 273 Fuegian sprat were sorted on board and placed in labeled sterile cryovials which were frozen and stored in liquid nitrogen in the spring survey (2014) or in a cold room at -20°C in the autumn surveys (2016 and 2017). Once in the laboratory cryovials were stored at -86°C in an ultra-freezer.

Frozen sprat were posteriorly thawed and developmental stages were determined. Larval stages were assigned based on the flexion degree of the notochord, distinguishing preflexion, flexion and postflexion larvae (Kendall et al., 1984). Average standard length (SL) of flexion larvae in TDF waters was estimated as 12.14 mm (no flexion larvae from the MPAN/BB were analyzed in this study). Individuals of later developmental stages were classified as metamorphosing (transitional larvae) or juvenile, with the former showing

| Habitat | | df | Sum. sq | Mean sq | F value | p-value |
|---------|-----------|-----|---------|---------|---------|---------|
| TDF | SL | 1 | 64.079 | 64.079 | 39.884 | <.0001 |
| | Residuals | 159 | 255.457 | 1.607 | | |
| MPAN/BB | SL | 1 | 26.557 | 26.557 | 17.698 | .0001 |
| | Residuals | 48 | 72.025 | 1.501 | | |

Abbreviations: MPAN/BB, Marine Protected Area Namuncurá/Burdwood Bank; SL, standard length; TDF, Tierra del Fuego.

scales primarily in the ventral keel but with remaining body parts transparent and the latter totally covered with scales (Lebour, 1921). SL was measured from the tip of the snout to the end of the notochord without applying any shrinkage correction (Petereit et al., 2008). Larval SL was measured to the nearest micrometer using a Carl Zeiss stereoscope equipped with Axio Vision software while SL of metamorphosing and juvenile sprat was measured to the nearest millimeter with a scale. Due to tissue effects on RNA and DNA concentration (Olivar et al., 2009), guts and heads were separated from the rest of the body and the reported RNA/DNA ratios correspond with muscle tissue. Conversion factors provided by Olivar et al., (2009) might be applied to sRD ratios estimated here for comparisons with other studies employing whole-bodied individuals. The removal of heads and guts was performed on ice to avoid nucleic acid degradation. Larval bodies and an equivalent portion in weight of metamorphosing and juvenile sprat (1 x 2 cm² of lateral muscle approximately) were lyophilized for 24 h, and their dry weight (DW) was determined using a Sartorius microbalance. This material was maintained at -86°C until nucleic acid analyses were carried out.

2.3 | Determination of nutritional condition

Nucleic acid concentrations were quantified following the protocol described by Caldarone et al. (2001) and modifications proposed by Diaz and Pájaro (2012). The main modification involved use of 1 or 2 ml of assay samples instead of a microplate. Cells were broken apart by adding 500 µl of Sarkosyl Tris EDTA (STE) 1% to Eppendorf vials containing dried larval muscle tissue. Vials were posteriorly placed on a shaker with ice for an hour and afterward micro-centrifuged for 15 min at 13,400 rpm (15,314 g) at 2°C. A subsample of 100 µl of the supernatant was combined with 850 µl of Tris Edta Buffer (TE) and 50 µl of ethidium bromide (EB, 0.1 mg/ml), reaching a 0.05% concentration of TES when measuring fluorescence. The same protocol was applied to metamorphosing and juvenile sprat; however, 2% STE and 1850 µl of TE were employed to guarantee the complete immersion of the processed material. Fluorescence measurements were carried out using a Perkin Elmer spectrofluorometer (excitation: 360 nm, emission: 590 nm). The first reading corresponded to total nucleic acid fluorescence (TNA). Samples were then incubated for 30 min at 37°C with 50 µl of ribonuclease (Sigma R 6513) at a concentration of 20 U/ml and a second reading, corresponding to DNA fluorescence, was carried out. RNA fluorescence was calculated as the difference between TNA and DNA fluorescences. Nucleic acid concentrations

TABLE 1 Analysis of variance of fitted linear models assessing the relationship between standardized RNA/DNA ratios and standard length of *Sprattus fuegensis* larvae according to the habitat

(µg per milligram of DW) were determined by running calibration curves using ultrapure solutions of DNA (lambda DNA, digested with Hind III, Roche 10236250001) and RNA (16S-23S RNA from *Escherichia coli*, Roche 10206938001) in an appropriate range of concentrations with EB. The average ratio of the slopes of DNA and RNA standard curves was 1.87 ± 0.33.

RNA/DNA ratios (RD) were calculated for each sprat and their values were standardized (sRD) according to Caldarone et al., (2006). Reliable sRD values were only considered from a minimum mass of 33 µg mgDW⁻¹. Larval sRD threshold level for growth (i.e., the turning point from positive to negative growth) was calculated by considering a null growth (G = 0) in the multi-species growth model performed by Buckley et al. (2008):

$$G = 0.0145 * sRD + 0.0044 * sRD * T - 0.0780 \quad (1)$$

where G is the instantaneous growth rate and T (°C) is the temperature measured in situ at 10 m depth, where Fuegian sprat larvae are mainly found (Contreras et al., 2014; Landaeta et al., 2013). Larval growth performance (GPF) was estimated as the quotient between the observed growth rate (G) and a theoretical growth rate achieved under optimal feeding and environmental conditions (Gmax). This value represents an objective measure of larval condition in which quotients equal or bigger than 1 would indicate favorable nutritional conditions (Buckley et al., 2008). Due to the lack of a Gmax model for *S. fuegensis*, G values were compared with a reference growth rate (Gref; Houde & Zastrow, 1993):

$$G_{ref} = 0.0106 * T - 0.0203 \quad (2)$$

2.4 | Data analysis

Temperature and salinity signatures at 10 m depth were evaluated in each habitat and survey, with variability being qualitatively assessed due to insufficient independent observations. Mean values and their standard deviations were estimated for SL, DNA, and RNA concentrations and sRD of larval, metamorphosing, and juvenile sprat according to habitat and developmental stage. Substantial overlap was observed among sRD values of equal stages from different surveys, so they were pooled according to habitat and stage in posterior analyses. Only larval data were statistically compared due to the absence of metamorphosing and juvenile sprat in the MPAN/BB. sRD and GPF (dependent variables) of equivalent developmental stages were compared across habitats (independent variable) with

a Mann-Whitney U test. Generalized linear models (GLMs) with a Gaussian error distribution were employed for the analysis of larval nutritional condition in relation to environmental variables (temperature, salinity, and depth). Since preliminary analysis revealed a strong correlation between sRD and SL (p values $<.05$ for both habitats; Table 1), a residual approach was used to remove the allometric effect (Teodósio et al., 2017). Residuals of an overall simple regression of $\ln(\text{sRD})$ on $\ln(\text{SL})$ were estimated (sRD_{res}) and an automated model selection was performed starting from the model considering all possible explanatory variables. The best model was selected based on Akaike information criterion (AIC).

Statistical analyses were performed in the R environment (R Core Team, 2019) with the “stats” (R Core Team, 2019), “dplyr” (Wickham et al., 2019), “MuMin” (Barton, 2019), “nlme” (Pinheiro et al., 2018), and “car” (Fox & Weisberg, 2011) packages. When detected, variance heterogeneity was modeled and outliers were removed. The level of statistical significance used was 0.05.

3 | RESULTS

Three groups of stations can be distinguished by salinity and temperature: the MPAN/BB and, in the TDF habitat, the BC and the CS regions (Figure 2). Higher salinities were measured in the MPAN/BB, with values ranging around 34.00. Salinities in the CS were very similar across the two years of autumn surveys (32.85 ± 0.12). Fresher water was present in the BC in the spring of 2016 (mean of 31.82 ± 0.28). Colder temperatures were observed in the MPAN/BB, where the coldest value occurred in spring, 2014 (5.34°C), compared with autumn of 2016 ($6.61 \pm 0.15^\circ\text{C}$) and 2017 ($7.03 \pm 0.15^\circ\text{C}$). The temperature during spring in the BC was also colder ($7.06 \pm 0.21^\circ\text{C}$) than during the autumn of 2016 and 2017 in the CS (8.50°C and $9.48 \pm 0.23^\circ\text{C}$, respectively).

A total of 273 Fuegian sprat were assessed (50 from the MPAN/BB and 223 from TDF waters) comprising different developmental stages and SL depending on the survey (Table 2). Early larvae (pre-flexion/flexion) were only sampled during the spring survey of 2014 while postflexion larvae were assessed in the autumn of both years in the two habitats. Only one preflexion larva was sampled, in the MPAN/BB during the autumn of 2016. Metamorphosing and juvenile sprat sampled in 2017 were only captured in TDF. Overall, SL varied between 5.66 and 83 mm, with mean sizes increasing with developmental stage. Similar sizes were observed among specimens of equal developmental stages across habitats. The mean SL of postflexion larvae was higher in 2017 than in 2016 in both habitats.

Nucleic acid concentrations per milligram of DW varied according to SL and ontogenetic stage in both habitats, with a general tendency to decrease with increasing size and more advanced developmental stages (Figure 3). DNA values ranged overall between 0.13 and $33.43 \mu\text{g}/\text{mg}$, with similar minimum and maximum values in both habitats. Preflexion larvae had the widest range of DNA values among stages in both habitats and also the highest mean values in both TDF waters ($13.50 \pm 4.57 \mu\text{g}/\text{mg}$) and the MPAN/

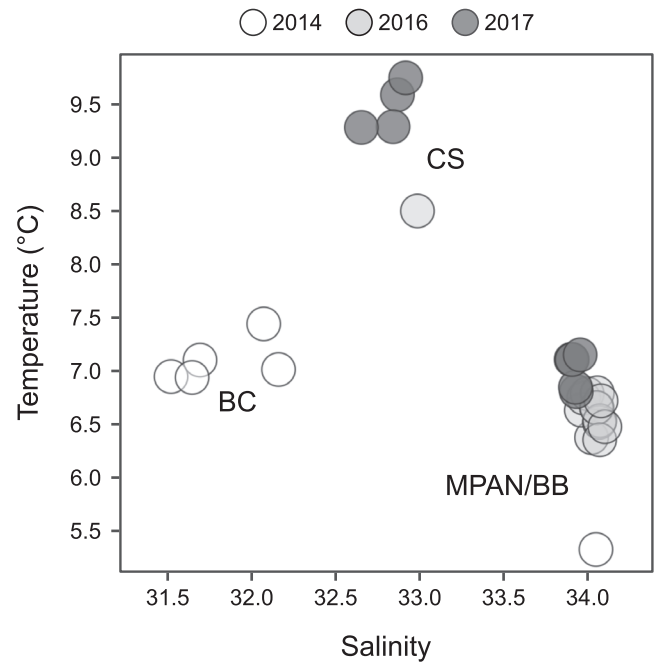


FIGURE 2 Salinity and temperature ($^\circ\text{C}$) at 10 m depth of stations at which *Sprattus fuegensis* early stages were analyzed according to the survey (colors). BC, Beagle Channel; CS, continental shelf; MPAN/BB, Marine Protected Area Namuncurá/Burdwood Bank

BB ($17.16 \pm 6.56 \mu\text{g}/\text{mg}$). DNA concentrations of postflexion larvae were at least an order of magnitude lower than for preflexion larvae, with mean values of $0.66 \pm 0.69 \mu\text{g}/\text{mg}$ in TDF waters and of $1.89 \pm 1.64 \mu\text{g}/\text{mg}$ in the MPAN/BB. DNA values of metamorphosing and juvenile sprat sampled in TDF waters were below $1.00 \mu\text{g}/\text{mg}$, with the lower mean of $0.40 \pm 0.16 \mu\text{g}/\text{mg}$ estimated for juveniles. A similar decreasing pattern was observed for RNA concentrations. Higher RNA than DNA concentrations were estimated for preflexion larvae in TDF waters (mean of $29.59 \pm 10.33 \mu\text{g}/\text{mg}$), while they were lower for sprat in this developmental stage in the MPAN/BB (mean of $14.27 \pm 6.03 \mu\text{g}/\text{mg}$). It was also observed that RNA values measured in preflexion larvae of the MPAN/BB strongly overlapped with values for postflexion larvae. Once again, the lower mean was estimated for juveniles captured in TDF waters ($0.24 \pm 0.11 \mu\text{g}/\text{mg}$).

After standardizing the quotient among these nucleic acid concentrations, sRD values ranged between 0.24 and 8.53 overall. As seen for DNA and RNA, a common pattern was observed among larval stages for both habitats, although in this case, sRD values increased from early larvae (preflexion/flexion) toward postflexion. Great variability in sRD ratios was found among specimens of similar sizes within each stage. Mean values ranged between 2.93 ± 1.08 and 1.52 ± 0.92 for preflexion larvae and 4.55 ± 1.81 and 3.91 ± 1.22 for postflexion larvae in TDF waters and the MPAN/BB respectively. Flexion larvae found only in TDF had a mean sRD of 4.15 ± 1.40 , while metamorphosing and juvenile sprat had the lowest sRD values despite increasing size or developmental stage, with mean values of 1.09 ± 0.45 for metamorphosing sprat and 0.95 ± 0.40 for juveniles.

| Habitat | Survey | Stage | N | Mean SL (mm) | Range (mm) |
|---------|--------|---------------|-----|--------------|---------------|
| TDF | BC | Preflexion | 126 | 8.51 ± 0.14 | 5.66 – 13.90 |
| | | Flexion | 3 | 12.14 ± 1.00 | 10.31 – 13.77 |
| | CS | Postflexion | 3 | 22.67 ± 1.10 | 20.48 – 23.97 |
| | | Postflexion | 29 | 26.92 ± 0.26 | 23.47 – 29.77 |
| | | Metamorphosis | 52 | 39.99 ± 0.59 | 32 – 51 |
| MPAN/BB | 2014 | Juvenile | 10 | 71.50 ± 3.08 | 53 – 86 |
| | | Preflexion | 5 | 8.22 ± 0.54 | 6.39 – 9.69 |
| | 2016 | Preflexion | 1 | 8.50 | - |
| | | Postflexion | 17 | 22.35 ± 0.65 | 17.75 – 25.75 |
| | 2017 | Postflexion | 27 | 24.99 ± 0.38 | 20.07 – 30.30 |

TABLE 2 Number and standard length of *Sprattus fuegensis* early stages assessed according to the habitat, survey and developmental stage

Note: Variability around the mean standard length is displayed as the standard error.

Abbreviations: BC, Beagle Channel; CS, Continental Shelf; MPAN/BB, marine Protected Area Namuncurá/Burdwood Bank; N, number of sprat; SL, standard length; TDF, Tierra del Fuego.

Values of sRD were significantly different between preflexion larvae from TDF waters and from the MPAN/BB (Mann-Whitney *U* test, *p* value <.01), whereas no differences were found in postflexion larvae (Figure 4). The sRD threshold for growth was estimated at 1.56 for TDF and 1.80 for the MPAN/BB, with more than 65% of preflexion larvae under this value in the MPAN/BB but only 10% in TDF. In contrast, there were no postflexion larvae under the threshold in the MPAN/BB while just 3% were below the threshold in TDF waters. An equivalent pattern was observed for larval growth performance (GPF): values of preflexion larvae differed significantly across habitats (Mann-Whitney *U* test, *p* value <.01), whereas growth performance of postflexion larvae did not, and the percentage of larvae below optimal nutritional conditions (values smaller than 1) were higher for preflexion than postflexion larvae, reaching up to 100% for the MPAN/BB.

The correlation of environmental variables (salinity, temperature, and station depth) with nutritional condition was assessed using sRD_{res}, removing the allometric effect over sRD. Based on the AICc, the best model explaining sRD_{res} only involved the effect of station depth (Table 3). This variable had a significant effect (chi-square test: $\chi^2 = 30.18$, *df* = 1, *p* value <.001) and the general resulting model was

$$\text{sRD}_{\text{res}} = 0.35833 - 0.00289 * \text{depth} \quad (3)$$

where station depth has a negative effect on sRD_{res}.

4 | DISCUSSION

To our knowledge, this study represents the first investigation of the physiological status of Fuegian sprat in the Southwest Atlantic Ocean. The marked ontogenetic variability in nucleic acid concentrations and nutritional condition of *S. fuegensis* early life stages is notable. Both RNA and DNA content per milligram of DW showed a tendency to decrease with increasing SL and ontogenetic stage in both habitats. The negative relationship between nucleic acid

concentration and size has been explained by the change from a higher proportion of hyperplasia (more cells per milligram of DW) at the beginning of the ontogeny toward a greater proportion of hypertrophy (predominantly an increase in cell size instead of an increase in the number of cells) for more advanced stages (Chícharo & Chícharo, 2008). The sRD index was also ontogenetically determined, although values did not vary in a single direction with respect to developmental stages or SL as nucleic acid concentrations did.

During the larval phase, the sRD index increased from preflexion toward postflexion. This pattern has also been documented for *Engraulis anchoita*, a small pelagic clupeid that resides north of *S. fuegensis*' distribution in the Argentine shelf (Do Souto et al., 2019), and for *Sprattus sprattus* in the North and Baltic Seas (Kanstinger & Peck, 2009; Voss et al., 2006). Such ontogenetic variability could be a consequence of the allometric relationship between SL and sprat mouth gape. As larvae grow, they may prey upon a wider range of zooplankters which could account for the increase in their sRD (Dickmann et al., 2007). Increasing swimming activity and sensory acuity (e.g., orientation behavior) have also been reported to occur from preflexion to postflexion in other fishes including clupeids such as *Sardina pilchardus*, leading to improved foraging activities for larger larvae which in turn allow them to achieve high growth rates and better nutritional condition (Faillettaz et al., 2020; Grorud-Colvert & Sponaugle, 2006; Silva et al., 2014; Teodósio et al., 2016). Also, density-dependent mechanisms such as food limitation are key determinants for growth at high latitudes (Houde, 1989) and are known to affect other sprat nutritional condition (Baumann et al., 2007). This regulation may play a lesser role during postflexion given that maximum Fuegian sprat abundances occur during the early larval phase and not during the latter (García Alonso et al., 2018).

In metamorphosing and juvenile sprat, sRD values remained low and almost invariant throughout the shift between developmental stages and despite increasing SL. Their sRD were the lowest overall, although this does not necessarily imply that they were in bad condition. The relationship between sRD and growth can vary depending on the life stage assessed (Teodósio et al., 2017). Low sRD

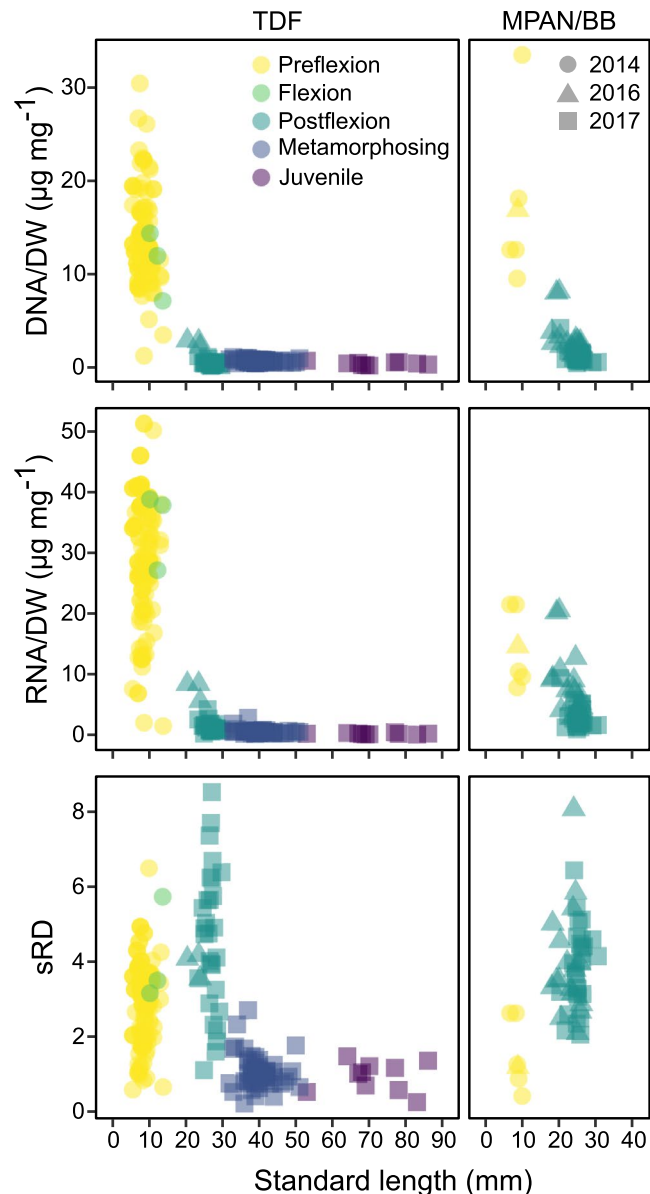


FIGURE 3 Nucleic acid concentrations (μg of DNA and RNA) per milligram of dry weight (DW) and standardized RNA/DNA ratios (sRD) of *Sprattus fuegensis* early stages in relation to standard length. Colors and shapes represent their developmental stage and survey. MPAN/BB, Marine Protected Area Namuncurá/Burdwood Bank; TDF, Tierra del Fuego

measured could be the result of slower growth, characteristic of metamorphosing and juvenile sprat (Günther et al., 2012). A shift in energy allocation from somatic growth toward enzyme and cell turnover could account for the low values measured in muscle tissue (Chícharo and Chícharo, 2008). Also, a rapid decrease in protein synthesis can be a direct consequence of the relatively few energy reserves left after the high metabolic costs of rapid growth and final metamorphosis (Peck et al., 2015). It is still unclear which process or if a combination of them is responsible for the lower values of sRD measured in metamorphosing and juvenile *S. fuegensis* in TDF and if the same tendency is repeated in other habitats. However, given the

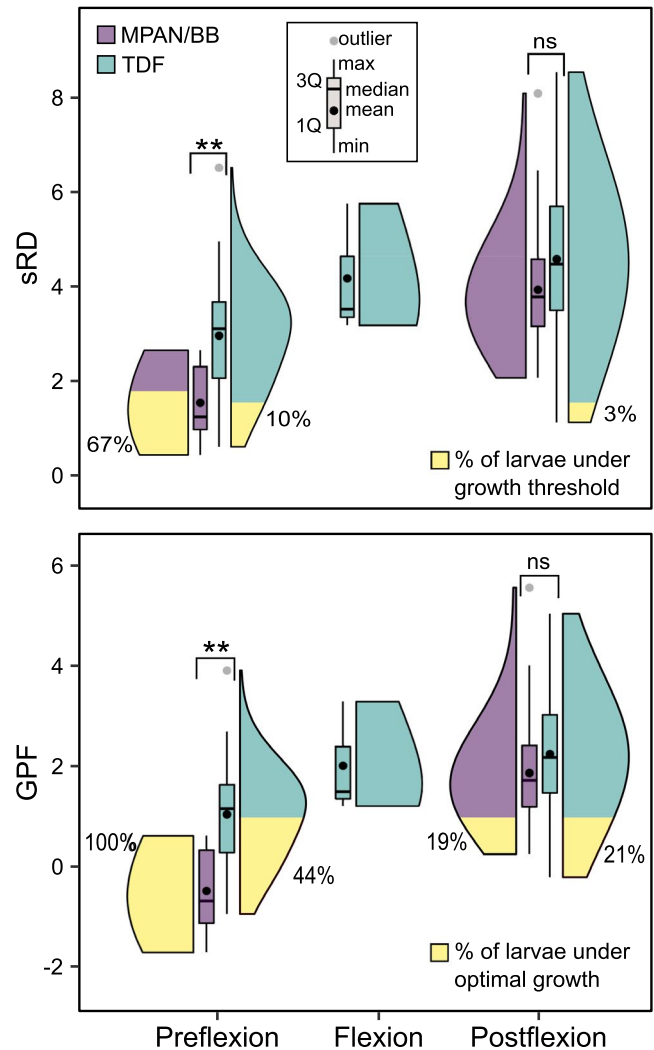


FIGURE 4 Standardized RNA/DNA ratios (sRD) and growth performance factor (GPF) of larval *Sprattus fuegensis* in Tierra del Fuego (TDF) and the Marine Protected Area Namuncurá/Burdwood Bank (MPAN/BB). Data are differentiated according to developmental stage. Results of the Mann-Whitney U test across habitats are shown (**= p value < 0.01; ns = p value > 0.05). Areas in yellow represent the percentage of larvae under sRD thresholds for positive growth (1.56 in TDF and 1.80 in the MPAN/BB) and below optimal nutritional condition (GPF < 1; a GPF = 1 is expected under optimal conditions)

similarities encountered during the larval phase, a similar pattern is expected to occur for metamorphosing and juvenile Fuegian sprat from the MPAN/BB.

Overall, sRD values measured in *S. fuegensis* larvae (0.44–8.53) were similar to those obtained for *E. anchoita* by Diaz et al. (2011) and Do Souto et al. (2019), which employed the same methodological approach used in this study. Preflexion larvae of both clupeid species were more vulnerable and in poorer condition than further developed larvae. This was reflected by, not only their lower sRD values, but also the greater percentages of specimens under the corresponding thresholds for growth and optimal condition (see Figure 4), possibly representing an intrinsic characteristic of clupeids in the

| Station depth | Salinity | Temperature | df | logLik | AICc | Delta |
|---------------|----------|-------------|----|---------|--------|-------|
| x | | | 3 | -293.90 | 593.92 | 0.00 |
| x | x | | 4 | -293.67 | 595.54 | 1.63 |
| x | | x | 4 | -293.71 | 595.62 | 1.70 |
| | x | | 3 | -295.25 | 596.62 | 2.70 |
| | x | x | 4 | -294.40 | 597.00 | 3.08 |
| x | x | x | 5 | -293.40 | 597.09 | 3.17 |
| | | | 2 | -297.96 | 599.98 | 6.06 |
| | | x | 3 | -296.94 | 599.99 | 6.08 |

Note: The nutritional condition was assessed upon the residuals of a linear regression of standard length on standardized RNA/DNA ratios. Variables considered in each model are marked by a cross (x). Salinity and temperature were assessed at 10 m depth. Models are ranked by AICc.

TABLE 3 Automated model selection assessing environmental forcing over allometric deprived nutritional condition of *Sprattus fuegensis* larvae

Argentine shelf. The high percentages of sRD values below these thresholds are in accordance with high rates of natural mortality in young larvae (e.g., Bailey & Houde, 1989; Govoni, 2005; Hjort, 1914). Due to the absence of experimental confirmation on the relation between nucleic acid concentrations and growth for these species, a multi-species growth model and a reference growth rates were employed to assess nutritional condition in *S. fuegensis* and *E. anchoita*. This implies that the estimated percentages may change if parameters are further calibrated. Acquiring more precise estimates of these parameters is, therefore, one of the main issues that should be tackled in forthcoming studies for species in the Southwest Atlantic Ocean since even small changes in this percentages could ultimately contribute to large differences in adult abundance (Houde, 1987).

Besides varying ontogenetically, we initially hypothesized that nutritional condition would also differ across habitats in response to environmental forcing. Water temperature was expected to be the most important variable in the modulation of nutritional condition given its direct effect over metabolic activity (Buckley et al., 2008) and higher sRD were expected to occur in TDF waters as a consequence. The increase in sRD from preflexion to postflexion matched with the increase in water temperature from spring to autumn, and the lowest sRD values did occur at the MPAN/BB where temperature is colder (Guerrero et al., 1999). Following this assumption, we also expected an inter-annual variation in the sRD of postflexion larvae, which in 2017 had larger SL than in 2016, associated with higher temperatures registered in that year (see Figure 2), although this difference could also be a direct consequence of the gear employed in 2017 (including an IKMT net besides the Bongo net) allowing to capture larger individuals. However, when statistically assessed, we only found differences for preflexion larvae, and only depth (neither temperature nor salinity) had a significant effect over the allometric deprived nutritional condition of sprat larvae (see Table 3). Therefore, sRD values of postflexion larvae strongly overlapped among years and habitats. This spatio-temporal similarity in nutritional condition contrasts with recent results based on otolith microstructure analyses of Fuegian sprat captured in the same surveys (García Alonso et al., 2020). Both spatial and temporal variability in *S. fuegensis* increment widths and growth rates were found and an

overall resemblance between growth trajectories and sea surface temperature was also identified. Thus, results addressing these two life traits reinforce a prevailing ontogenetic constraint of nutritional condition over environmental forcing during postflexion and also reveals a discrepancy in the effect of temperature over early development of *S. fuegensis* in the Southwest Atlantic Ocean, highlighting the importance of integrating different proxies of growth and condition and applying a multidisciplinary approach in the pursuit to correctly assess survival and recruitment success (Rogers et al., 2020; Voss et al., 2012).

Significant differences in sRD were found across habitats for preflexion larvae, with lower values occurring at the MPAN/BB. It is important to consider that the small sample size analyzed for this stage in the MPAN/BB may not represent the entire larval population. High individual variability has been previously reported for nucleic acid-based techniques in other larval sprat such as *S. sprattus* (Peck et al., 2007). However, preflexion larvae of *S. fuegensis* appear to present less variability in sRD values compared with other larval stages implying that the observed trend should not be overlooked. There is abundant evidence supporting the effect of food availability both in terms of quantity and quality over the nutritional condition of fish larvae (Diaz et al., 2016; Voss et al., 2006), being a predominant factor conditioning growth when the temperature range is narrow (Buckley, 1984). Nauplii, copepods, and cladocerans are main prey items for sprat early life stages, with an increasing selectivity for larger copepods with increasing length and with microplankton (i.e., diatoms, ciliates and other unicellular organisms) as predominant prey during the beginning of the spawning season (Arrhenius, 1996; Dickmann et al., 2007; Voss et al., 2003). Abundant suitable zooplanktonic prey was registered in the MPAN/BB during the spring survey of 2014 in which preflexion larvae were sampled, with nauplii and copepods comprising 77.8% and 18%, respectively, of the total abundance (Spinelli et al., 2020). A pronounced algal bloom, characterized by high abundances of the diatom *Rhizosolenia crassa*, was also reported in the MPAN/BB in that same survey (Bértola et al., 2018). This diatom possesses large frustules and forms dense macro-aggregates, which may have hindered consumption and the encounter of sprat with other prey items, or even harm or clog their

gills (Hallegraeff, 1993). It is still unclear whether these blooms periodically occur at the MPAN/BB, and also whether there is any effect of summer blooms in TDF (Guinder et al., 2020). It is necessary to acquire more samples of preflexion larvae along with phytoplankton samples in order to assess this potential bottom-up control and its effect on the nutritional condition of Fuegian sprats' early stages.

Food availability not only depends on prey quantity and quality, but also on prevailing oceanographic features enabling prey-predator encounter as mentioned above. Our results do identify a negative effect of the station depth over larval sRD of Fuegian sprat. We assume this variable is indirectly related to other environmental characteristics. A similar negative relation between depth and sRD was also observed for anchovy larvae in the Cadiz Gulf (Teodósio et al., 2017) and for other short-latency proxies of nutritional condition such as the protein:SL and DNA:DW ratios of *S. sprattus* from the Bornholm Basin (Dänhardt et al., 2007). Shallower depths, higher temperatures, and lower salinities in TDF waters induce stratification in the water column, a well-defined feature along the BC in spring/summer (Balestrini et al., 1998) but less pronounced in the CS as a result of strong tidal mixing (Piola et al., 2018). Despite differences in the intensity, water stratification can concentrate prey and sprat near the thermo-haloclines and, thus, favor a higher predation rate of larvae on zooplankters. This scenario has been registered in the North Patagonian shelf, where higher sRD values of *E. anchoita* larvae were measured in a coastal frontal area (42–44°S) with strong water stratification compared with a less stratified one (Diaz et al., 2016). On the contrary, intense upwelling and mixing occur over the MPAN/BB, resulting in weak water stratification (Guerrero et al., 1999; Matano et al., 2019). The strong currents occurring within the MPAN/BB may further reduce the possibility of preflexion larvae with poor swimming capacity to encounter their prey and could, therefore, explain their lower nutritional condition.

The plasticity in growth, survival, and other life traits of small pelagic fishes like sprat make them suitable targets for testing the impact of climate variability on marine ecosystems and fish populations (Alheit & Hagen, 2001). Despite environmental differences across habitats, both TDF and the MPAN/BB emerged as suitable nursery grounds in which Fuegian sprat late larvae can attain a good physiological status in the Southwest Atlantic Ocean. It would appear that achieving high sRD values may be a necessary step to face posterior metamorphosis, acquiring adequate swimming capacity and sensory acuity that enables them to migrate to suitable habitats (Baptista et al., 2019; Teodósio et al., 2016) and possibly increasing survival success. Nonetheless, future monitoring of the effect of environmental variability in early life traits of *S. fuegensis* is strongly suggested. There is strong evidence supporting the existence of physical and chemical changes in oceans around the world as a consequence of climate change and/or ocean acidification (Hoegh-Guldberg et al., 2014), with increasing sea surface temperature and decreasing pH among the most important outcomes affecting fishes (Nilsson & Lefevre, 2016). High values of carbon dioxide (CO₂) have been associated with reduced metabolism and increased larval malformations

for clupeids like *Clupea harengus* L. (Leo et al., 2018). Moreover, phylogenetic evidence supports that higher temperatures may result in smaller fishes, diminishing their ability to move (Avaria-Llautureo et al., 2020), which is key for guaranteeing successful migration of sprat to foraging areas (Beyst et al., 1999).

In conclusion, a strong ontogenetic constraint was observed on nutritional condition of *S. fuegensis* early stages, highlighting the importance of making stage-specific comparisons when addressing growth and condition analyses. Moreover, environmental forcing of depth over the RNA/DNA index was also found. Additional analyses are still needed to further comprehend Fuegian sprat development and its implications for recruitment success. Given the current climate change scenario, gaining such knowledge is a fundamental step in the pursuit to generate adequate management strategies. Understanding recruitment success in the MPAN/BB has implications for future conservation of this region's pelagic ecosystem services. Besides sheltering a high biodiversity including vulnerable benthic fauna as cold-water corals, this submarine seamount also sustains a main spawning ground for various fishes and represents an important foraging site for numerous top predators (Falabella et al., 2009; Sánchez and Ciechowski, 1995; Schejter et al., 2020). To successfully preserve this rich habitat, in which Fuegian sprat play a key trophic role (Ricciardelli et al., 2020), it is indispensable to understand the governing dynamics and generate appropriate ecosystem-based management strategies (Ruckelshaus et al., 2008; Sponaugle, 2010). Furthermore, this information would also be crucial to address ecosystem-based fisheries management whether *S. fuegensis* begins to be commercially exploited in the Southwest Atlantic Ocean, establishing extractive practices which optimize economic profits, while maintaining the ecosystems in a healthy, productive, and resilient condition (Brodziak & Link, 2002; Ruckelshaus et al., 2008; Voss et al., 2014). Results obtained here represent a baseline from which future assessments can evaluate the health of these habitats and their resilience to climate variability.

ACKNOWLEDGMENTS

This study was supported by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina (PIP 11220150100109CO 2015-2017), the Universidad de Buenos Aires, Argentina (UBACYT 20020160100045BA 2017-2020) and the Pampa Azul Interministerial Initiative implemented by the Argentinian Ministry for Science, Technology and Productive Innovation. The authors would like to thank the anonymous reviewers and the editor for their thorough corrections and suggestions which greatly improved the manuscript. The authors would also like to thank Luciano Padovani, Alejandro Martinez, and everyone who participated in the oceanographic surveys for their collaboration during sample collection and preparation, Marina Do Souto for her help during material processing and Pablo S. Milla Carmona for his statistical advice. This is INIDEP contribution N° 2243 and Marine Protected Area Namuncurá-Burdwood Bank (Law 26,875) contribution N° 48.

CONFLICT OF INTERESTS

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTIONS

VA García Alonso, MV Díaz, and FL Capitanio conceived and designed the study. VA García Alonso conducted the fieldwork. M Pájaro and FL Capitanio provided the necessary sampling gear and materials. MV Díaz and VA García Alonso carried out the nutritional condition assessments. VA García Alonso organized the database, performed the data analyses, and wrote the manuscript. All the authors participated in the edition and discussion of the manuscript making valuable contributions.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

ORCID

Virginia Andrea García Alonso  <https://orcid.org/0000-0003-2224-8376>

[org/0000-0003-2224-8376](https://orcid.org/0000-0003-2224-8376)

Marina Vera Díaz  <https://orcid.org/0000-0002-2912-5232>

REFERENCES

- Acha, E. M., Pájaro, M., & Sánchez, R. P. (1999). *The reproductive response of clupeoid fishes to different physical scenarios. Three study cases in the Southwest Atlantic*. ICES Annual Science Conference. <https://www.ices.dk/sites/pub/CM%20Documents/1999/K/K1299.pdf>
- Alheit, J., & Hagen, E. (2001). The effect of climatic variation on pelagic fish and fisheries. In P. D. Jones, A. E. J. Ogilvie, T. D. Davies, & K. R. Briffa (Eds.), *History and Climate* (pp. 247–265). Springer.
- Amante, C., & Eakins, B. W. (2009). *ETOPO1 1 Arc-Minute Global Relief Model: Procedures, Data Sources and Analysis*. NOAA Technical Memorandum NESDIS NGDC-24. Boulder, CO: National Geophysical Data Center, NOAA.
- Antezana, T. (1999). Hydrographic features of Magellan and Fuegian inland passages and adjacent Subantarctic waters. *Scientia Marina*, 63, 23–34. <https://doi.org/10.3989/scimar.1999.63s123>
- Aranis, A., Meléndez, R., Pequeño, G., & Cerna, F. (2007). *Sprattus fuegensis* en aguas interiores de Chiloé, Chile (Osteichthyes: Clupeiformes: Clupeidae). *Gayana (Concepción)*, 71, 102–113. <https://doi.org/10.4067/S0717-65382007000100011>
- Arrhenius, F. (1996). Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea. *ICES Journal of Marine Science*, 53, 701–712. <https://doi.org/10.1006/jmsc.1996.0089>
- Avaria-Llatureo, J., Venditti, C., Rivadeneira, M. M., Inonostroza-Michael, O., Rivera, R. J., Hernandez, C. E., & Canales-Aguirre, C. B. (2020). Shrinking of fish under warmer temperatures decrease dispersal abilities and speciation rates. *bioRxiv*. <https://doi.org/10.1101/2020.10.27.357236>
- Bailey, K. M., & Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology*, 25, 1–83. [https://doi.org/10.1016/S0065-2881\(08\)60187-X](https://doi.org/10.1016/S0065-2881(08)60187-X)
- Balestrini, C., Manzella, G., & Lovrich, G. A. (1998). Simulación de corrientes en el Canal Beagle y Bahía Ushuaia, mediante un modelo bidimensional. *Servicio De Hidrografía Naval*, 98, 1–58. <https://doi.org/10.13140/RG.2.1.1196.272>
- Baptista, V., Morais, P., Cruz, J., Castanho, S., Ribeiro, G., Pousão-Ferreira, P., Leitão, F., Wolanski, E., & Teodósio, M. A. (2019). Swimming abilities of temperate pelagic fish larvae prove that they may control their dispersion in coastal areas. *Diversity*, 11, 185. <https://doi.org/10.3390/d11100185>
- Barton, K. (2019). *MuMIn: Multi-Model Inference. R package version 1.43.15*. <https://CRAN.R-project.org/package=MuMIn>
- Baumann, H., Peck, M. A., Götze, H. E., & Temming, A. (2007). Starving early juvenile sprat *Sprattus sprattus* (L.) in western Baltic coastal waters: evidence from combined field and laboratory observations in August and September 2003. *Journal of Fish Biology*, 70, 853–866. <https://doi.org/10.1111/j.1095-8649.2007.01346.x>
- Belleggia, M., Figueroa, D. E., Irusta, G., & Bremec, C. (2014). Spatio-temporal and ontogenetic changes in the diet of the Argentine hake *Merluccius hubbsi*. *Journal of the Marine Biological Association of the United Kingdom*, 94, 1701–1710. <https://doi.org/10.1017/S0025315414000629>
- Bellisio, N., López, R. B., & Torno, A. (1979). *Peces marinos patagónicos*. Secretaría de Estado de Intereses Marítimos, Subsecretaría de Pesca.
- Bértola, G., Olguín Salinas, H., & Alder, V. A. (2018). Distribución espacial de *Rhizosolenia crassa*, ¿especie clave del banco Burdwood? In A. Menoret, M. Güller, V. Alder, M. Saraceno, & F. Capitanio (Eds.), *Libro de resúmenes X Jornadas Nacionales de Ciencias del Mar 2018* (p. 74). Buenos Aires.
- Beyst, B., Mees, J., & Cattrijsse, A. (1999). Early postlarval fish in the hyperbenthos of the Dutch Delta (south-west Netherlands). *JMBA-Journal of the Marine Biological Association of the United Kingdom*, 79, 709–724. <https://doi.org/10.1017/S0025315498000861>
- Brodziak, J., & Link, J. (2002). Ecosystem-based fishery management: what is it and how can we do it? *Bulletin of Marine Science*, 70, 589–611.
- Brown, D. R., & Sánchez, R. P. (2010). Larval and juvenile growth of two Patagonian small pelagic fishes: *Engraulis anchoita* and *Sprattus fuegensis*. *Revista De Investigación Y Desarrollo Pesquero INIDEP*, 20, 35–50.
- Buckley, L. J. (1984). RNA-DNA ratio: an index of larval fish growth in the sea. *Marine Biology*, 80, 291–298. <https://doi.org/10.1007/BF00392824>
- Buckley, L. J., Caldarone, E. M., & Clemmesen, C. (2008). Multi-species larval fish growth model based on temperature and fluorometrically derived RNA/DNA ratios: results from a meta-analysis. *Marine Ecology Progress Series*, 371, 221–232. <https://doi.org/10.3354/meps07648>
- Bulow, F. J. (1970). RNA-DNA ratios as indicators of recent growth rates of a fish. *Journal of the Fisheries Research Board of Canada*, 27, 2343–2349. <https://doi.org/10.1139/f70-262>
- Caldarone, E. M., Clemmesen, C. M., Berdalet, E., Miller, T. J., Folkvord, A., Holt, G. J., Olivar, M. P., & Suthers, I. M. (2006). Intercalibration of four spectrofluorometric protocols for measuring RNA/DNA ratios in larval and juvenile fish. *Limnology and Oceanography: Methods*, 4, 153–163. <https://doi.org/10.4319/lom.2006.4.153>
- Caldarone, E., Wagner, M., St Onge-Burns, J., & Buckley, L. J. (2001). *Protocol and guide for estimating nucleic acids in larval fish using a fluorescence microplate reader*. Northeast Fisheries Science Center Reference Documents, 01-11, 22pp. National Marine Fisheries Service. <https://repository.library.noaa.gov/view/noaa/5145>
- Casarsa, L., Diez, M. J., Madirolas, A., Cabreira, A. G., & Buratti, C. C. (2019). Morphometric description of schools from two different stocks of the southernmost sprat *Sprattus fuegensis*. *Fisheries Research*, 212, 29–34. <https://doi.org/10.1016/j.fishres.2018.12.004>

- Catalán, I. A., Olivar, M. P., Palomera, I., & Berdalet, E. (2006). Link between environmental anomalies, growth and condition of pilchard *Sardina pilchardus* larvae in the northwestern Mediterranean. *Marine Ecology Progress Series*, 307, 219–231. <https://doi.org/10.3354/meps307219>
- Cepeda, G. D., Temperoni, B., Sabatini, M. E., Viñas, M. D., Derisio, C. M., Santos, B. A., & Padovani, L. N. (2018). Zooplankton communities of the Argentine Continental Shelf (SW Atlantic, ca. 34°–55° S), an overview. In M. Hoffmeyer, M. Sabatini, F. Brandini, D. Calliari, & N. Santinelli (Eds.), *Plankton ecology of the Southwestern Atlantic* (pp. 171–199). Springer International Publishing AG. https://doi.org/10.1007/978-3-319-77869-3_9
- Checkley, D. M. Jr, Alheit, J., Oozeki, Y., & Roy, C. (Eds.) (2009). *Climate change and small pelagic fish*. Cambridge University of Press.
- Chícharo, M. A., & Chícharo, L. (2008). RNA: DNA ratio and other nucleic acid derived indices in marine ecology. *International Journal of Molecular Sciences*, 9, 1453–1471. <https://doi.org/10.3390/ijms9081453>
- Chícharo, M. A., Esteves, E., Santos, A. M. P., dos Santos, A., Peliz, Á., & Ré, P. (2003). Are sardine larvae caught off northern Portugal in winter starving? An approach examining nutritional conditions. *Marine Ecology Progress Series*, 257, 303–309. <https://doi.org/10.3354/meps257303>
- Contreras, T., Castro, L. R., Montecinos, S., Gonzalez, H. E., Soto, S., Muñoz, M. I., & Palma, S. (2014). Environmental conditions, early life stages distributions and larval feeding of patagonian sprat *Sprattus fuegensis* and common sardine *Strangomera bentincki* in fjords and channels of the northern Chilean patagonia. *Progress in Oceanography*, 129, 136–148. <https://doi.org/10.1016/j.pcean.2014.10.005>
- Cousseau, M. B. (1982). Revisión taxonómica y análisis de los caracteres morfológicos y merísticos de la sardina fueguina, *Sprattus fuegensis* (Jenyns, 1842) (Pisces, Clupeidae). *Revista De Investigación Y Desarrollo Pesquero INIDEP*, 3, 77–94.
- Cury, P., Bakun, A., Crawford, R. J., Jarre, A., Quinones, R. A., Shannon, L. J., & Verheye, H. M. (2000). Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES Journal of Marine Science*, 57, 603–618. <https://doi.org/10.1006/jmsc.2000.0712>
- Cury, P., & Roy, C. (1989). Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46, 670–680. <https://doi.org/10.1139/f89-086>
- Dänhardt, A., Peck, M. A., Clemmesen, C., & Temming, A. (2007). Depth-dependent nutritional condition of sprat *Sprattus sprattus* larvae in the central Bornholm Basin, Baltic Sea. *Marine Ecology Progress Series*, 341, 217–228. <https://doi.org/10.3354/meps341217>
- Díaz, M., Do Souto, M., Peralta, M., Pájaro, M., Spinelli, M., Saraceno, M., Balestrini, C., & Capitanio, F. (2016). Comer o ser comido: factores que determinan la condición nutricional de larvas de *Engraulis anchoita* de la población patagónica de la especie. *Ecología Austral*, 26, 120–133.
- Díaz, M. V., & Pájaro, M. (2012). Protocolo para la determinación de ácidos nucleicos en larvas de peces. *Informe De Investigación INIDEP*, 20, 1–9.
- Díaz, M. V., Pájaro, M., Olivar, M. P., Martos, P., & Macchi, G. J. (2011). Nutritional condition of Argentine anchovy *Engraulis anchoita* larvae in connection with nursery ground properties. *Fisheries Research*, 109, 330–341. <https://doi.org/10.1016/j.fishres.2011.02.020>
- Dickmann, M., Möllmann, C., & Voss, R. (2007). Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival. *Marine Ecology Progress Series*, 342, 277–289. <https://doi.org/10.3354/meps342277>
- Do Souto, M., Brown, D. R., Leonarduzzi, E., Capitanio, F. L., & Díaz, M. V. (2019). Nutritional condition and otolith growth of *Engraulis anchoita* larvae: The comparison of two life traits indexes. *Journal of Marine Systems*, 193, 94–102. <https://doi.org/10.1016/j.jmarsys.2019.01.008>
- Faillietaz, R., Johnson, E., Dahlmann, P., Syunkova, A., Stieglitz, J., Benetti, D., Grosell, M., & Paris, C. B. (2020). Ontogeny of orientation during the early life history of the Pelagic Teleost Mahi-Mahi, *Coryphaena hippurus* Linnaeus, 1758. *Oceans*, 2020(1), 237–250. <https://doi.org/10.3390/oceans1040017>
- Falabella, V., Campagna, C., & Croxall, J. (2009). *Atlas of the Patagonian Sea, species and spaces*. Wildlife Conservation Society and Bird Life International. <http://www.atlas-marpatagonico.org>
- FAO (2019). *FAO yearbook. Fishery and Aquaculture Statistics 2017*. FAO.
- Ferron, A., & Leggett, W. C. (1994). An appraisal of condition measures for marine fish larvae. *Advances in Marine Biology*, 30, 217–303. [https://doi.org/10.1016/S0065-2881\(08\)60064-4](https://doi.org/10.1016/S0065-2881(08)60064-4)
- Fox, J., & Weisberg, S. (2011). *An R companion to applied regression*, 2nd ed. Sage. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>
- García Alonso, V. A., Brown, D., Martín, J., Pájaro, M., & Capitanio, F. L. (2018). Seasonal patterns of Patagonian sprat *Sprattus fuegensis* early life stages in an open sea Sub-Antarctic Marine Protected Area. *Polar Biology*, 41, 2167–2179. <https://doi.org/10.1007/s00300-0-018-2352-z>
- García Alonso, V. A., Brown, D. R., Pájaro, M., & Capitanio, F. L. (2020). Growing up down south: spatial and temporal variability in early growth of Fuegian sprat *Sprattus fuegensis* from the Southwest Atlantic Ocean. *Frontiers in Marine Science*, 7, 322. <https://doi.org/10.3389/fmars.2020.00322>
- Govoni, J. J. (2005). Fisheries oceanography and the ecology of early life histories of fishes: a perspective over fifty years. *Scientia Marina*, 69, 125–137. <https://doi.org/10.3989/scimar.2005.69s1125>
- Grorud-Colvert, K., & Sponaugle, S. (2006). Influence of condition on behavior and survival potential of a newly settled coral reef fish, the bluehead wrasse *Thalassoma bifasciatum*. *Marine Ecology Progress Series*, 327, 279–288. <https://doi.org/10.3354/meps327279>
- Guerrero, R. A., Baldoni, A. G., & Benavides, H. R. (1999). Oceanographic conditions at the southern end of the Argentine continental slope. *Documento Científico INIDEP*, 5, 7–22.
- Guinder, V. A., Malits, A., Ferronato, C., Krock, B., Garzón-Cardona, J., & Martínez, A. (2020). Microbial plankton configuration in the epipelagic realm from the Beagle Channel to the Burdwood Bank, a Marine Protected Area in Sub-Antarctic waters. *PLoS One*, 15, e0233156. <https://doi.org/10.1371/journal.pone.0233156>
- Günther, C. C., Temming, A., Baumann, H., Huwer, B., Möllmann, C., Clemmesen, C., & Herrmann, J. P. (2012). A novel length back-calculation approach accounting for ontogenetic changes in the fish length-otolith size relationship during the early life of sprat (*Sprattus sprattus*). *Canadian Journal of Fisheries and Aquatic Sciences*, 69, 1214–1229. <https://doi.org/10.1139/f2012-054>
- Hallegraeff, G. M. (1993). A review of harmful algal blooms and their apparent global increase. *Phycologia*, 32, 79–99. <https://doi.org/10.2216/i0031-8884-32-2-79.1>
- Hjort, J. (1914). Fluctuations in the great fisheries of Northern Europe. *ICES Rapports Et Procès-Verbaux Des Réunions*, 20, 1–228.
- Hoegh-Guldberg, O., Cai, R., Poloczanska, E. S., Brewer, P. G., Sundby, S., Hilmi, K., Fabry, V. J., & Jung, S. (2014). The Ocean. In V. R. Barros, C. B. Field, D. J. Dokken, M. D. Mastrandrea, K. J. Mach, T. E. Bilir, M. Chatterjee, K. L. Ebi, Y. O. Estrada, R. C. Genova, B. Girma, E. S. Kissel, A. N. Levy, S. MacCracken, P. R. Mastrandrea, & L. L. White (Eds.), *Climate change 2014: Impacts, adaptation, and vulnerability. Part A: Global and sectoral aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 1655–1731). Cambridge University Press.
- Houde, E. D. (1987). Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium*, 2, 17–29.

- Houde, E. D. (1989). Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *Fishery Bulletin*, 87(3), 471–495.
- Houde, E. D., & Zastrow, C. E. (1993). Ecosystem -and taxon- specific dynamic and energetics properties of larval fish assemblages. *Bulletin of Marine Science*, 53, 290–335.
- Kanstinger, P., & Peck, M. A. (2009). Co-occurrence of European sardine (*Sardina pilchardus*), anchovy (*Engraulis encrasicolus*) and sprat (*Sprattus sprattus*) larvae in southern North Sea habitats: abundance, distribution and biochemical-based condition. *Scientia Marina*, 73, 141–152. <https://doi.org/10.3989/scimar.2009.73s1141>
- Kendall, A. W., Ahlstrom, E. H., & Moser, H. G. (1984). Early life history stages of fishes and their characters. In H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, & S. L. Richardson (Eds.), *Ontogeny and systematics of fishes* (pp. 11–22). Allen Press Inc.
- Landaeta, M. F., Martínez, R. A., Bustos, C. A., & Castro, L. R. (2013). Distribution of microplankton and fish larvae related to sharp clines in a Patagonian fjord. *Revista De Biología Marina Y Oceanografía*, 48, 401–407. <https://doi.org/10.4067/S0718-19572013000200020>
- Leal, E., Muñoz, C., Moyano, G., Bernal, C., & Aranís, A. (2017). A first experience of Patagonian sprat *Sprattus fuegensis* spawning in captivity: Adult acclimation, egg and larval measurements. *Revista De Biología Marina Y Oceanografía*, 52, 641–645. <https://doi.org/10.4067/S0718-19572017000300021>
- Lebour, M. V. (1921). The larval and post-larval stages of the pilchard, sprat and herring from Plymouth district. *Journal of the Marine Biological Association of the United Kingdom*, 12, 427–457. <https://doi.org/10.1017/S0025315400006299>
- Leggett, W. C., & Deblois, E. (1994). Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? *Netherlands Journal of Sea Research*, 32, 119–134. [https://doi.org/10.1016/0077-7579\(94\)90036-1](https://doi.org/10.1016/0077-7579(94)90036-1)
- Leo, E., Dahlke, F. T., Storch, D., Pörtner, H. O., & Mark, F. C. (2018). Impact of Ocean Acidification and Warming on the bioenergetics of developing eggs of Atlantic herring *Clupea harengus*. *Conservation Physiology*, 6, coy050. <https://doi.org/10.1093/conphys/coy050>
- Martinetto, P., Alemany, D., Botto, F., Mastrángelo, M., Falabella, V., Acha, E. M., Antón, G., Bianchi, A., Campagna, C., Cañete, G., Filippo, P., Iribarne, O., Latorra, P., Martínez, P., Negri, R., Piola, A. R., Romero, S. I., Santos, D., & Saraceno, M. (2020). Linking the scientific knowledge on marine frontal systems with ecosystem services. *Ambio*, 49, 541–556. <https://doi.org/10.1007/s13280-019-01222-w>
- Matano, R. P., Palma, E. D., & Combes, V. (2019). The Burdwood Bank circulation. *Journal of Geophysical Research: Oceans*, 124, 6904–6926. <https://doi.org/10.1029/2019JC015001>
- Nilsson, G. E., & Lefevre, S. (2016). Physiological challenges to fishes in a warmer and acidified future. *Physiology*, 31(6), 409–417. <https://doi.org/10.1152/physiol.00055.2015>
- Olivar, M. P., Diaz, M. V., & Chicharo, M. A. (2009). Tissue effect on RNA: DNA ratios of marine fish larvae. *Scientia Marina*, 73, 171–182. <https://doi.org/10.3989/scimar.2009.73s1171>
- Peck, M. A., Baumann, H., Clemmesen, C., Herrmann, J. P., Moyano, M., & Temming, A. (2015). Calibrating and comparing somatic, nucleic acid-, and otolith-based indicators of growth and condition in young juvenile European sprat (*Sprattus sprattus*). *Journal of Experimental Marine Biology and Ecology*, 471, 217–225. <https://doi.org/10.1016/j.jembe.2015.06.011>
- Peck, M. A., Kühn, W., Clemmesen, C., Hinrichsen, H. H., Holtappels, M., Huwer, B., & Pohlmann, T. (2007). Variability in growth rates of larval fish at frontal stations in the southern North Sea: is the “mean” all that matters? *GLOBEC International Newsletter*, 13(2), 70–71.
- Peck, M. A., Reglero, P., Takahashi, M., & Catalán, I. A. (2013). Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Progress in Oceanography*, 116, 220–245. <https://doi.org/10.1016/j.pocean.2013.05.012>
- Petereit, C., Haslob, H., Kraus, G., & Clemmesen, C. (2008). The influence of temperature on the development of Baltic Sea sprat (*Sprattus sprattus*) eggs and yolk sac larvae. *Marine Biology*, 154, 295–306. <https://doi.org/10.1007/s00227-008-0923-1>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team (2018). *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-137*. <https://CRAN.R-project.org/package=nlme>
- Piola, A. R., Palma, E. D., Bianchi, A. A., Castro, B. M., Dottori, M., Guerrero, R. A., & Saraceno, M. (2018). Physical oceanography of the SW Atlantic shelf: A review. In M. Hoffmeyer, M. Sabatini, F. Brandini, D. Calliari, & N. Santinelli (Eds.), *Plankton ecology of the Southwestern Atlantic* (pp. 37–56). Springer International Publishing AG. https://doi.org/10.1007/978-3-319-77869-3_2
- Piola, A. R., & Rivas, A. L. (1997). Corrientes en la plataforma continental. In E. E. Boschi (Ed.), *El Mar Argentino y sus recursos pesqueros. Tomo 1. Antecedentes históricos de las exploraciones en el Mar Argentino y las características ambientales* (pp. 119–132). Instituto Nacional de Investigación y Desarrollo Pesquero.
- R Core Team (2019). *R: A language and environment for statistical computing*. The R Foundation for Statistical Computing. <http://www.R-project.org/>
- Riccialdelli, L., Becker, Y. A., Fioramonti, N. E., Torres, M., Bruno, D. O., Rey, A. R., & Fernández, D. A. (2020). Trophic structure of southern marine ecosystems: a comparative isotopic analysis from the Beagle Channel to the oceanic Burdwood Bank area under a wasp-waist assumption. *Marine Ecology Progress Series*, 655, 1–27. <https://doi.org/10.3354/meps13524>
- Rogers, L. A., Wilson, M. T., Duffy-Anderson, J. T., Kimmel, D. G., & Lamb, J. F. (2020). Pollock and ‘the Blob’: Impacts of a marine heatwave on walleye pollock early life stages. *Fisheries Oceanography*, <https://doi.org/10.1111/fog.12508>
- Ruckelshaus, M., Klinger, T., Knowlton, N., & DeMaster, D. P. (2008). Marine ecosystem-based management in practice: scientific and governance challenges. *BioScience*, 58, 53–63. <https://doi.org/10.1641/B580110>
- Sabatés, A., Salat, J., & Olivar, M. P. (2001). Advection of continental water as an export mechanism for anchovy, *Engraulis encrasicolus*, larvae. *Scientia Marina*, 65(S1), 77–88. <https://doi.org/10.3989/scimar.2001.65s177>
- Sánchez, R. P., & Ciechowski, J. D. (1995). Spawning and nursery grounds of pelagic fish species in the sea-shelf off Argentina and adjacent areas. *Scientia Marina*, 59, 455–478.
- Sánchez, R. P., Remeslo, A., Madirolas, A., & De Ciechowski, J. D. (1995). Distribution and abundance of post-larvae and juveniles of the Patagonian sprat, *Sprattus fuegensis* and related hydrographic conditions. *Fisheries Research*, 23, 47–81. [https://doi.org/10.1016/0165-7836\(94\)00339-X](https://doi.org/10.1016/0165-7836(94)00339-X)
- Schejter, L., Genzano, G., Gaitán, E., Perez, C. D., & Bremec, C. S. (2020). Benthic communities in the Southwest Atlantic Ocean: Conservation value of animal forests at the Burdwood Bank slope. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 30(3), 426–439. <https://doi.org/10.1002/aqc.3265>
- Scioscia, G., Raya Rey, A., Saenz Samaniego, R. A., Florentín, O., & Schiavini, A. (2014). Intra- and interannual variation in the diet of the Magellanic penguin (*Spheniscus magellanicus*) at Martillo Island, Beagle Channel. *Polar Biology*, 37, 1421–1433. <https://doi.org/10.1007/s00300-014-1532-8>
- Silva, L., Faria, A. M., Teodósio, M. A., & Garrido, S. (2014). Ontogeny of swimming behaviour in sardine *Sardina pilchardus* larvae and effect of larval nutritional condition on critical speed. *Marine Ecology Progress Series*, 504, 287–300. <https://doi.org/10.3354/meps10758>
- Spinelli, M., Malits, A., García Alonso, V. A., Martín, J., & Capitano, F. (2020). Zooplankton diversity and spring assemblages at a sub-antarctic open ocean Marine Protected Area: contributions to the base line and management of the Namuncurá/Burdwood Bank, SW

- Atlantic Ocean. *Journal of Marine Systems*, 210, 103398. <https://doi.org/10.1016/j.jmarsys.2020.103398>
- Sponaugle, S. (2010). Otolith microstructure reveals ecological and oceanographic processes important to ecosystem-based management. *Environmental Biology of Fishes*, 89(3–4), 221–238. <https://doi.org/10.1007/s10641-010-9676-z>
- Stephenson, R. L., & Smedbol, R. K. (2001). Small pelagic species fisheries. In J. H. Steel, S. Thorpe, & K. Turekian (Eds.), *Encyclopedia of Ocean Sciences* (2nd ed., pp. 268–473). Academic Press. <https://doi.org/10.1016/B978-012374473-9.00447-1>
- Teodósio, M. A., Garrido, S., Peters, J., Leitão, F., Ré, P., Peliz, A., & Santos, A. M. P. (2017). Assessing the impact of environmental forcing on the condition of anchovy larvae in the Cadiz Gulf using nucleic acid and fatty acid-derived indices. *Estuarine, Coastal and Shelf Science*, 185, 94–106. <https://doi.org/10.1016/j.ecss.2016.10.023>
- Teodósio, M. A., Paris, C. B., Wolanski, E., & Morais, P. (2016). Biophysical processes leading to the ingress of temperate fish larvae into estuarine nursery areas: A review. *Estuarine, Coastal and Shelf Science*, 183, 187–202. <https://doi.org/10.1016/j.ecss.2016.10.022>
- Voss, R., Clemmesen, C., Baumann, H., & Hinrichsen, H. H. (2006). Baltic sprat larvae: coupling food availability, larval condition and survival. *Marine Ecology Progress Series*, 308, 243–254. <https://doi.org/10.3354/meps308243>
- Voss, R., Köster, F. W., & Dickmann, M. (2003). Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. *Fisheries Research*, 63, 97–111. [https://doi.org/10.1016/S0165-7836\(02\)00282-5](https://doi.org/10.1016/S0165-7836(02)00282-5)
- Voss, R., Peck, M. A., Hinrichsen, H.-H., Clemmesen, C., Baumann, H., Stepputtis, D., Bernreuther, M., Schmidt, J. O., Temming, A., & Köster, F. W. (2012). Recruitment processes in Baltic sprat—A re-evaluation of GLOBEC Germany hypotheses. *Progress in Oceanography*, 107, 61–79. <https://doi.org/10.1016/j.pocean.2012.05.003>
- Voss, R., Quaas, M. F., Schmidt, J. O., Tahvonen, O., Lindegren, M., & Möllmann, C. (2014). Assessing social-ecological trade-offs to advance ecosystem-based fisheries management. *PLoS One*, 9, e107811. <https://doi.org/10.1371/journal.pone.0107811>
- Wickham, H., François, R., Henry, L., & Müller, K. (2019). *dplyr: A Grammar of Data Manipulation. R package version 0.8.0.1*. <https://CRAN.R-project.org/package=dplyr>

How to cite this article: García Alonso VA, Díaz MV, Pájaro M, Capitanio FL. Ontogeny versus environmental forcing off the Southwest Atlantic Ocean: Nutritional condition of Fuegian sprat (*Sprattus fuegensis*) early stages. *Fish Oceanogr.* 2021;00:1–13. <https://doi.org/10.1111/fog.12543>