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Seasonal patterns of Patagonian sprat *Sprattus fuegensis* early life stages in an open sea Sub-Antarctic Marine Protected Area

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Abstract
The Patagonian sprat *Sprattus fuegensis* is a species of ecological importance in the Southwest Atlantic Ocean. However, information regarding *S. fuegensis* in the Namuncurá Marine Protected Area–Burdwood Bank (NMPA–BB), an open sea Sub-Antarctic Marine Protected Area located in the Argentinian shelf, is outdated and fragmented. Understanding the dynamics of species inhabiting the NMPA–BB is relevant to establish future adequate management strategies. We assessed the abundance, size, and development of *S. fuegensis* early life stages during spring, summer, and autumn in order to evaluate their seasonal patterns. Compared to neighboring areas, *S. fuegensis* was particularly abundant in the NMPA–BB, which can be considered a major spawning and nursery ground. Within the NMPA–BB, abundances tend to be higher at the center, probably as a result of the marine currents. Eggs were only recorded in spring, while larvae were recorded in all seasons sampled, with maximum abundances occurring during spring. Larger larval sizes and more developed stages occurred in summer and autumn. Analysis of otolith microstructure showed that spawning periods take place between October and March, peaking in November. Slow growth rates (maximum of 0.30 mm day^{-1}) and prolonged larval phase would respond to the low temperatures recorded in the NMPA–BB. Additionally, marked monthly differences in otolith growth would suggest a seasonal effect on the developmental patterns of *S. fuegensis* larvae. Future studies will be necessary to completely understand *S. fuegensis* development and determine its trophic role in the NMPA–BB.

Introduction

The Argentinian shelf along with the shelf-break front is known to be a highly productive environment, exhibiting high chlorophyll concentrations (Rivas et al. 2006; Romero et al. 2006; Carreto et al. 2007) and offering feeding and reproductive habitats for several organisms such as fishes, squids, and mammals (Acha et al. 2004 and references therein). In particular, the Burdwood Bank (BB) is considered an ecologically important area. This submarine plateau located at 150 km eastward of Isla de los Estados (Staten Island) shelters various top predators and represents a reproduction site for harvested fishes, such as the southern blue whiting and the Patagonian toothfish (Perrotta 1982; Laptikhovsky et al. 2006). Accompanying the ongoing exponential increase in the creation of Marine Protected Areas worldwide (Worm 2017), the area encompassed by the 200 m isobath of the BB was declared the first Argentinian open-sea Marine Protected Area in 2013 based on high benthic

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species richness and the presence of vulnerable benthic sessile fauna such as cold-water corals, among others (Falabella et al. 2013; Schejter et al. 2016). Three areas with different levels of protection were established, defined as *transition*, *buffer*, and *core* areas (Fig. 1), the latter being a permanently prohibited fishing zone since 2008 (Federal Fishing Council by Acta 18/2008, Argentina).

The Namuncurá Marine Protected Area-BB (NMPA–BB) is governed by a particularly complex physical setting, resulting from the marine currents influencing the area and the abrupt bathymetric changes within its margins. The NMPA–BB exhibits a minimum depth of 40–50 m, a wide plateau with an average depth of about 100 m and steep flanks leading to much deeper areas, particularly on the southern border which faces the Yaghan Basin. The study area is subject to the eastward flow of the Antarctic Circumpolar Current which, upon approaching South America, meets a relative constrainment between Tierra del Fuego and the Antarctic Peninsula. This current is then deflected towards the north-east, encountering a barrier in the North Scotia Ridge, a sequence of islands and shoals to which the BB belongs (Dalziel and Elliot 1973). In this region, two main currents can be recognized: the Cape Horn Current flowing around the tip of South America and transporting relatively freshened waters, and the Malvinas Current, which contours the bank from passages at its eastern and western limits to join further and flow northward along the shelf-break (Piola and Gordon 1989; Smith et al. 2010; Reta et al. 2014).

The Patagonian sprat *Sprattus fuegensis* is widely distributed in the NMPA–BB (Sánchez and Ciechomski 1995), representing one of the main pelagic resources of the Austral Patagonian Sea due to its high biomass shoals (Bellisio et al.

1979). Although in Argentina catches of this species are still incidental, sprats are common target species for fisheries worldwide. *Sprattus sprattus* is one of the most commercially exploited species in the North Sea (ICES 2016), as *S. fuegensis* is in the inland sea of the Chiloe Island, southern Pacific Ocean (Cerna et al. 2014). The Patagonian sprat also plays an important role in the food web as an intermediate link, feeding on zooplankton and representing a common prey in the diet of various fish such as hakes (Bezzi 1984; Belleggia et al. 2014), as well as sea birds and cetaceans (Schiavini et al. 1997; Ciancio et al. 2008; Scioscia et al. 2014). Furthermore, it is known that small pelagic zooplanktivorous fishes like sprats can operate at the "wasp-waist" level in up-welling ecosystems, imposing either top-down or bottom-up control over the other trophic levels, affecting the energy flux of the entire food web (Bakun 2006; Fauchald et al. 2011). Understanding the ecology of *S. fuegensis* is therefore of crucial importance as changes in their distribution and abundances can have major ecological implications.

On the basis of adult morphometric characters, growth parameters and shoals attributes, two sprat populations have been previously identified in the South-west Atlantic Ocean (Cousseau 1982; Gru and Cousseau 1982; Casarsa 2005). One population inhabits the Coasts of Santa Cruz and Tierra del Fuego, while the other inhabits the Malvinas (Falkland) Islands. Most studies have focused on the former, with emphasis in the abundance and distribution of early life stages (Ciechomski and Weiss 1974; Ciechomski et al. 1975; Sánchez and Ciechomski 1995; Sánchez et al. 1995, 1997; Bruno et al. 2018). Growth studies have also been performed in larval, juvenile, and adult specimens from this population (Gru and Cousseau 1982; Brown and Sánchez 2010). In contrast, the Malvinas Island population has been investigated

Fig. 1 Location of the Namuncurá Marine Protected Area–Burdwood Bank (NMPA–BB) with the present zonation, an anticyclonic current surrounding the bank (AC) and main currents influencing the area: Malvinas Current and Cape Horn Current (CHC) Modified from Piola and Rivas (1997)
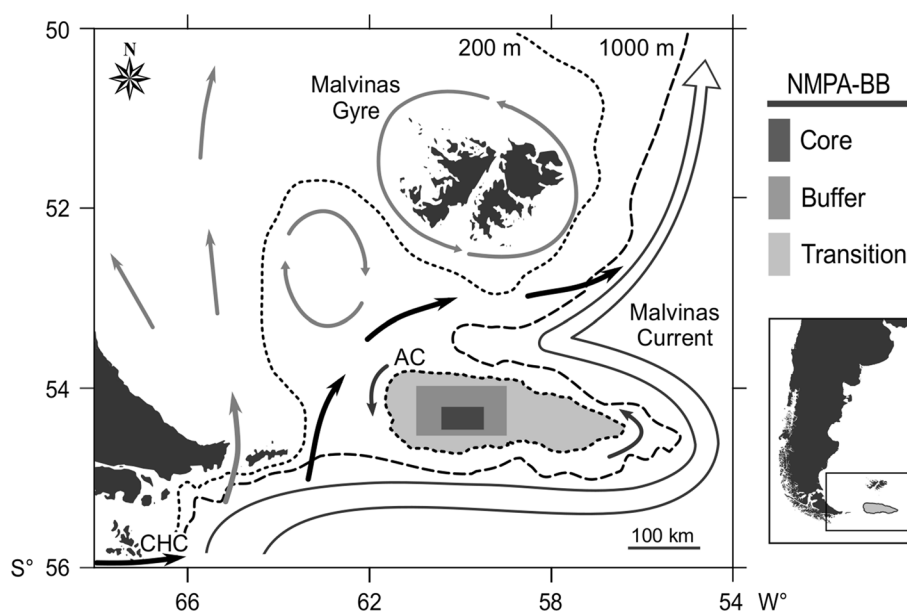
by a few, relatively old studies (Ciechomski 1971; Ciechom-ski et al. 1975; Shirokova 1978; Sánchez and Ciechomski 1995; Sánchez et al. 1997).

Although *S. fuegensis* eggs and larvae have been identified in NMPA–BB during several oceanographic cruises (Ciechomski and Weiss 1974; Ciechomski et al. 1975; Sánchez and Ciechomski 1995), it is still unknown which of the two sprat populations chooses the NMPA–BB as a spawning ground or if a third population is yet to be recognized. Harsh climatic conditions prevented to gather information regarding seasonal patterns of early life stages distribution and abundance, which can be major determinants of recruitment success and, consequently, of adult population size (Sinclair and Iles 1988; Boehlert and Mundy 1993; Govoni 2005; Moser and Watson 2006). Among some of the key factors determining these patterns there are wind-induced and/or tidal mixing of the surface layer and up-welling, processes commonly found in submarine banks and seamounts. They act as mechanisms of retention and concentration of fish larvae in recruiting areas and create favorable marine conditions for their growth and survival (Alemany et al. 2006; Falcini et al. 2015).

As the NMPA–BB is included in the Argentinian Pampa Azul Marine National Science Project, several oceano-graphic cruises have now been carried out in this area aiming to investigate biodiversity, seasonal dynamics, and trophic relationships of the local fauna. The results of these studies are crucial to generate appropriate management policies conservation strategies in the NMPA–BB, which have been exclusively based on benthic fauna (Falabella et al. 2013). The aims of the present study were to evaluate the seasonal abundance and spatial distribution of *S. fuegensis* early life stages at the NMPA–BB in relation to oceanographic parameters, and to estimate spawning periods and growth parameters of larvae.

Materials and methods

Sampling

Fish samples were obtained during four oceanographic cruises in the NMPA–BB and its proximities in spring (4–7 November 2014 and 1–17 December 2015), summer (17–23 February 2015), and autumn (26 March–26 April 2016). In all cruises, sampling stations were selected in an attempt to cover the longitudinal extension of the NMPA–BB, comprising the three areas legally recognized. The November 2014 (Nov-2014) and April 2016 (Apr-2016) cruises were performed by the ARA Puerto Deseado oceanographic vessel, while the February 2015 (Feb-2015) and the December 2015 (Dec-2015) cruises were performed by the SB-15 "Tango" and GC-189 "Prefecto García" respectively (PNA, Argentine

Coastguards). Hydrographic seasonal variations were evaluated for spring (Nov-2014) and autumn (Apr-2016) cruises where water temperature and salinity were obtained with a Sea Bird 19 CTD. Measures were calibrated with water samples collected with Niskin bottles.

A total of twenty seven ichthyoplankton samples were collected in the NMPA–BB (5 in Nov-2014, 5 in Feb-2015, 4 in Dec-2015 and 13 in Apr-2016) through oblique tows performed from 180 m to the surface or less, reaching bottom proximities when possible. A 60-cm diameter Bongo net with 300-µm mesh size was used in Nov-2014 and Apr-2016. In these cruises, at least 50 larvae representative of the size range were fixed in 80% alcohol, while the rest of the sample was fixed in 4% formaldehyde. During the other two cruises a MiniBongo net of 30-cm diameter and 200-µm mesh size was used as Argentine Coastguards are not enabled to use large gears. These samples were fixed in 4% formaldehyde. During all trawls, a mechanical flow meter was added to the net mouth to calculate the volume of filtered water.

Laboratory procedures

Fish eggs and larvae from fixed samples were separated and identified using a Leica S6 D Greenough stereo microscope. They were counted and their abundances per station were standardized as density values (eggs or larvae m^{-2}). Standard length of Patagonian sprat larvae was measured to the nearest 0.25 mm, applying shrinkage corrections to specimens fixed in 80% alcohol and 4% formaldehyde following Fey (1999) and Petereit et al. (2008) for *S. sprattus* larvae. When more than 100 larvae per station were counted, a subsample of 50 larvae was measured. Larval developmental stage was assigned by recognizing four stages based on the presence/absence of a yolk-sac and the flexion degree of the notochord: yolk-sac, preflexion, flexion, and postflexion (Kendall et al. 1984).

Sagittal otoliths from alcohol fixed larvae were extracted using fine dissection needles and placed onto glass slides covered with Protexx (transparent mounting medium). Daily increments were observed under a binocular optical microscope (×400 or ×1000) with transmitted light connected to a computer provided with software for image analysis (Kontron software). The daily deposition pattern was established following the recommendations of Campana (1992). Otolith increment widths were measured to the nearest 0.01 µm.

Data analysis

Surface currents in the NMPA–BB and adjacent waters were obtained for spring (Nov-2014) and autumn (Apr-2016) from the data set "OSCAR third degree resolution ocean surface currents", which is available at the Physical Oceanography

Distributed Active Archive Center (https://podaac.jpl.nasa.gov). Some oceanographic stations representing the extension of the NMPA–BB from these cruises were selected to investigate temperature and salinity vertical profiles with the Data-Interpolating Variational Analysis gridding software integrated to the Ocean Data View software package (Schlitzer 2017).

Seasonal larval abundances were statistically analyzed for spring (Nov-2014) and autumn (Apr-2016) cruises in which sampling was carried out with a Bongo net. A generalized linear model (GLM) with Poisson distribution was fitted. However, since strong over dispersion was detected in the analysis, a negative binomial GLM was used instead.

Larval age and growth rates were determined by counting and measuring daily increments in *sagitta* otoliths. When both otoliths of the same individual were read, 90% of coincidence in the number of increments between them was assured, and one of them was randomly selected. When only one otolith was available, its number of increments was considered. To determine the larval age, 6 days were added to the number of increments to compensate the yolk-sac stage when larvae do not feed exogenously nor deposit daily increments (Alshuth 1988). Growth was modeled by fitting a Laird–Gompertz (LG) curve to the length-at-age data. The general LG equation is:

$$L_{(t)} = L_0 \cdot \exp(G \cdot (1 - \exp(-\alpha \cdot t))),$$

where t is larval age (number of daily increments plus 6 days), $L_{(t)}$ is standard length-at-age t, L_0 is standard length at first increment deposition established at 7.10 mm (Brown and Sánchez 2010), G is specific rate of exponential growth, α is rate of exponential decay.

The derivate of the LG equation corresponded to the instantaneous growth rate (IGR) as a function of size (Sánchez et al. 1999):

$$IGR_L = \alpha \cdot L_{(t)} \cdot \left(\ln \left(L_{(t)} L_0 \right) - G \right).$$

Hatching dates from all sampled larvae were estimated by converting size data into ages with the LG model, and 7 days (i.e., egg incubation time) were posteriorly added to calculate spawning dates as seen for sprats in the North Sea for water temperature between 5 and 6 °C (Milligan 1986). Once hatching periods were determined, otolith increments widths mean values, mean monthly values, and their standard deviations were estimated. The increment widths of the otoliths at four different ages (10, 30, 50, and 70 days) were statistically compared among larvae hatched in different months by means of a repeated measures analysis. Only larvae collected in the autumn cruise (Apr-2016) which hatched in Dec-2015 and Jan-2016 were evaluated, to comply with the requirement of identical record lengths for all individuals. Several models of covariance were tested and the most parsimonious model was retained based on minimal

Akaike's information criterion (AIC; Sakamoto et al. 1986) score. Such model contemplated a first order autoregressive correlation between observations from each larvae and modeled variance heterogeneity for each number of increment. A significant interaction between the hatching month and the number of increment was observed, so a post-hoc pair-wise comparison for such interaction was carried on using least squares method and adjusting p-values with a Bonferroni correction.

Statistical analyses were performed in the R environment (R Core Team 2017) with the packages stats (R Core Team 2017), nlme (Pinheiro et al. 2017), multcomp (Hothorn et al. 2008), car (Fox and Weisberg 2011), lsmeans (Lenth 2016), and MASS (Venables and Ripley 2002).

Results

Oceanographic setting

Major circulation patterns were found in the surface current analysis (Fig. 2a, d) for both seasons considered (spring and autumn). A strong eastward water flow bordering the southern edge of the bank and forming a meander, which is characteristic of the Malvinas Current, was evidenced, as well as two branches detaching from this current with a northward direction, along the passages east and west of the bank. In spite of strong tidal currents taking place on the bank, the residual currents appeared fairly low over it, which contrasts with the strong flow in its surroundings, particularly south and east of the bank.

Vertical stratification of the water column was weak to absent along the three delimited areas of the NMPA–BB for both seasons, with seawater temperature being 1 °C colder in autumn than in spring (around 5.5 and 6.5 °C, respectively) (Fig. 2b, e). On the other hand, water salinity showed a remarkably narrow range of seasonal variation, with a mean salinity of 34.05 for spring and 34.025 for autumn (Fig. 2c, f).

Overall, the oceanographic pattern at the NMPA–BB was that of a fairly homogeneous water column stirred by strong tidal mixing, but where advection is nonetheless weak, implying a certain retention of water over the bank. Vertical homogeneity is more pronounced on the western half of the bank.

Seasonal dynamics of *Sprattus fuegensis* eggs and larvae

During the four oceanographic cruises in the NMPA–BB, *S. fuegensis* was the dominant species in most stations, with 2179 larvae and 7724 eggs caught overall. Only few eggs of an undetermined species and larvae corresponding to the
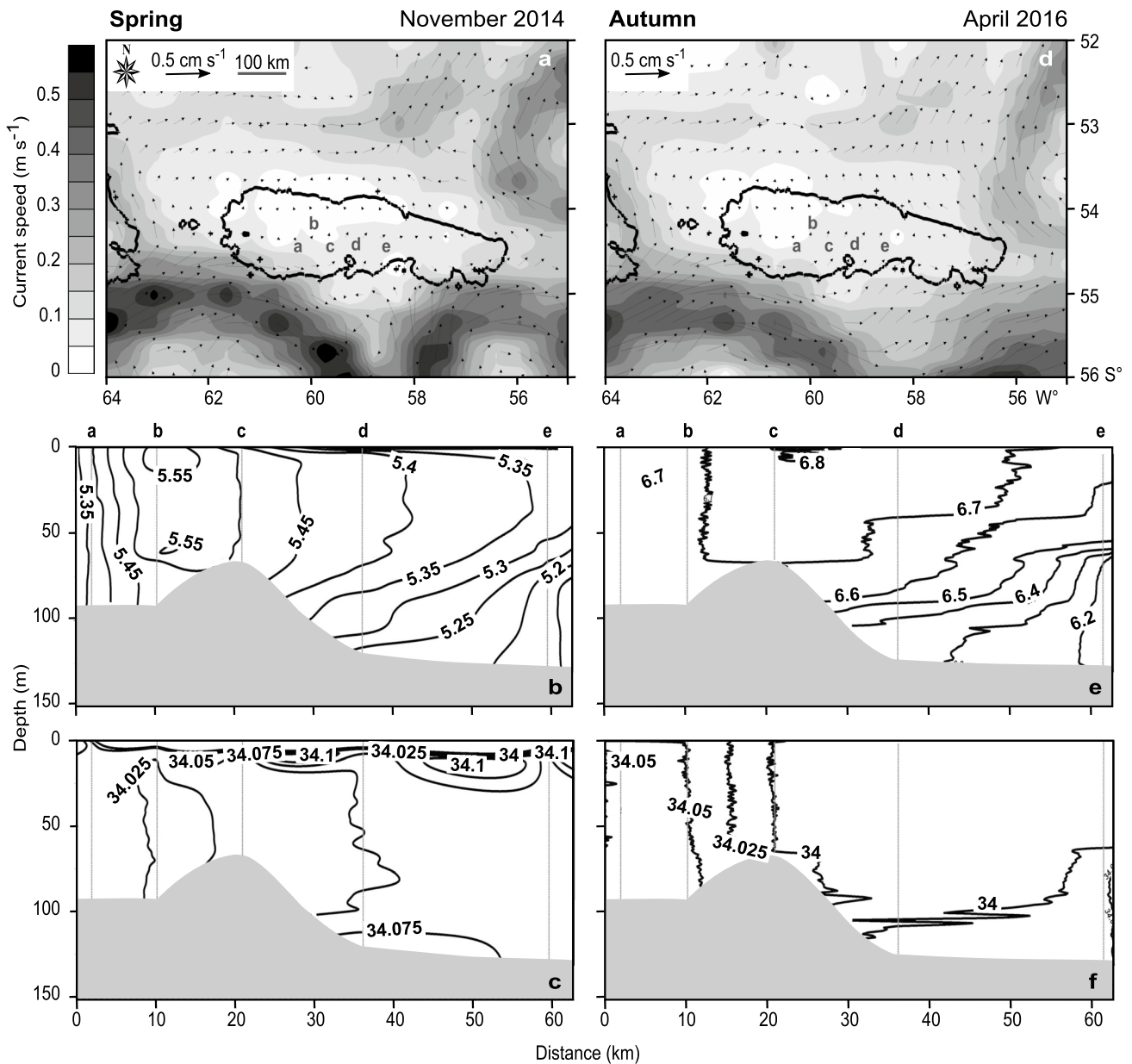
Fig. 2 Seasonal oceanographic setting of the study area and its vicinities: surface currents (**a** and **d**), temperature (**b** and **e**) and salinity vertical profiles (**c** and **f**) in spring (Nov-2014) and autumn (Apr-2016). Sampling stations *a* and *d* corresponded to the *buffer* area, *b* and *c* to the *core* area and *e* to the *transition* area of the Namuncurá Marine Protected Area–Burdwood Bank

Myctophidae and Nototheniidae families were identified (data not shown). Early life stages of *S. fuegensis* evidenced seasonal and spatial variation, with eggs only present in spring, displaying peaks of 2500 eggs m^{-2} in Nov-2014 and 800 eggs m^{-2} in Dec-2015 (Fig. 3). On the contrary, Patagonian sprat larvae appeared in all sampled seasons (spring, summer, and autumn), although the maximum abundance (900 larvae m^{-2}) was found in spring. When considering the overall spatial distribution, both eggs and larvae highest abundances were recorded in the center of the NMPA–BB (*buffer* area, see Fig. 1) with the exception of larvae in

Dec-2015 which displayed major abundances east and west of the center of the bank (*buffer* and *transition* area, respectively). Significant seasonal differences were found for larval abundances (χ^2 test, LR = 30.542, $p < 0.0001$), with mean larval abundance higher in spring (228 ± 171.85 larvae m^{-2}, $n = 5$) than in autumn (3.84 ± 2.15 larvae m^{-2}, $n = 13$).

Size of *S. fuegensis* larvae also evidenced seasonal variability, consistent with changes in their developmental stages. Smaller larvae at younger developmental stages were collected in spring, while larger individuals at more advanced stages were collected in summer and autumn
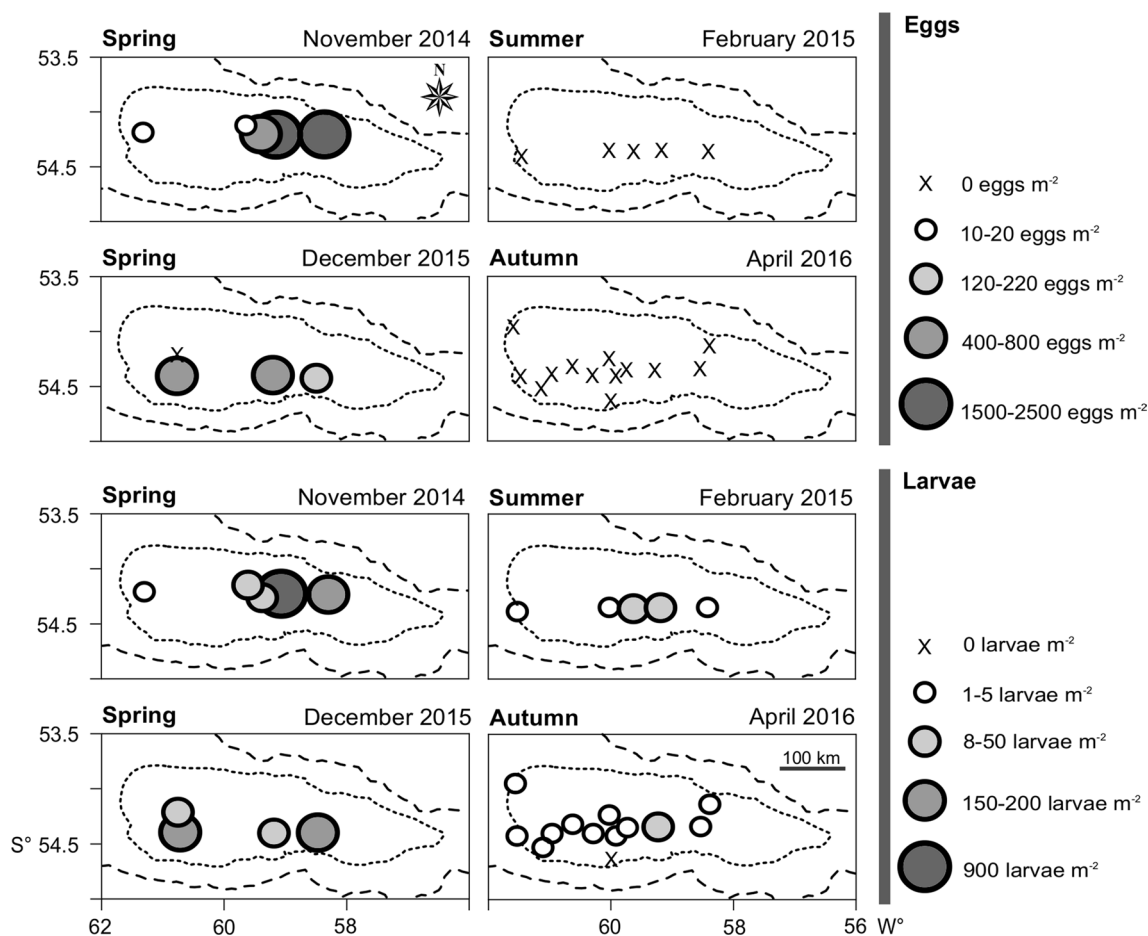
Fig. 3 Seasonal distribution of *Sprattus fuegensis* eggs and larvae abundances in the Namuncurá Marine Protected Area–Burdwood Bank

(Fig. 4). In spring, larval size varied between 2 and 13 mm, being 4–5 mm the most frequent sizes. In Nov-2014 more than 63% of larvae were in preflexion, while less number of individuals presented a yolk-sac and very few were already in flexion. In Dec-2015 most larvae exhibited a yolk-sac (65.71%) and the other were in preflexion. In this season, the length frequency distributions of each developmental stage exhibited a single peak. Larger larvae were found in summer (Feb-2015) and autumn (Apr-2016), exhibiting sizes between 5–30 and 11–33 mm, respectively; most of them were in postflexion (75.30% in summer and 91.87% in autumn), displaying multimodal length frequency distributions.

Otolith microstructure analysis

After otolith reading, the LG model was fitted to the length-at-age data of 109 individuals. According to this model, the inflection point occurs at 18 days and 12.37 mm larval size, with the asymptotic length (SL∞) attained at 33.63 mm (Fig. 5a). The derivative equation of the LG model

represents the IGRs values (Fig. 5b). The IGR corresponding to larvae from 0 to 18 days (sizes 7.10–12.37 mm) increased from 0.28 to 0.30 mm day^{-1}, presenting the maximum value at the inflection point of the LG model. IGR decreased from the inflection point to 0.06 mm day^{-1} for the older larvae (123 days, 33 mm larval size). Spawning dates were calculated by applying the LG model to the length-at-age data of larvae from all cruises, allowing the detection of two spawning periods: (1) from Oct-2014 to Feb-2015 and (2) from Oct-2015 to Mar-2016. In both cases spawning began in spring (October), exhibiting a peak in November, but ended in summer (February) and autumn (March), respectively, thus presenting spawning periods of 5–6 months (Fig. 5c).

When considering the increment widths of all larvae captured in the autumn cruise (Apr-2016), it could be observed that mean increment widths increased during the first 50 days, reaching a plateau extending approximately 95 days and then decreased (Fig. 6a). However, when the increment widths were differentiated according to different larval hatching months, different patterns arose (Fig. 6b). First born larvae (December) followed closely
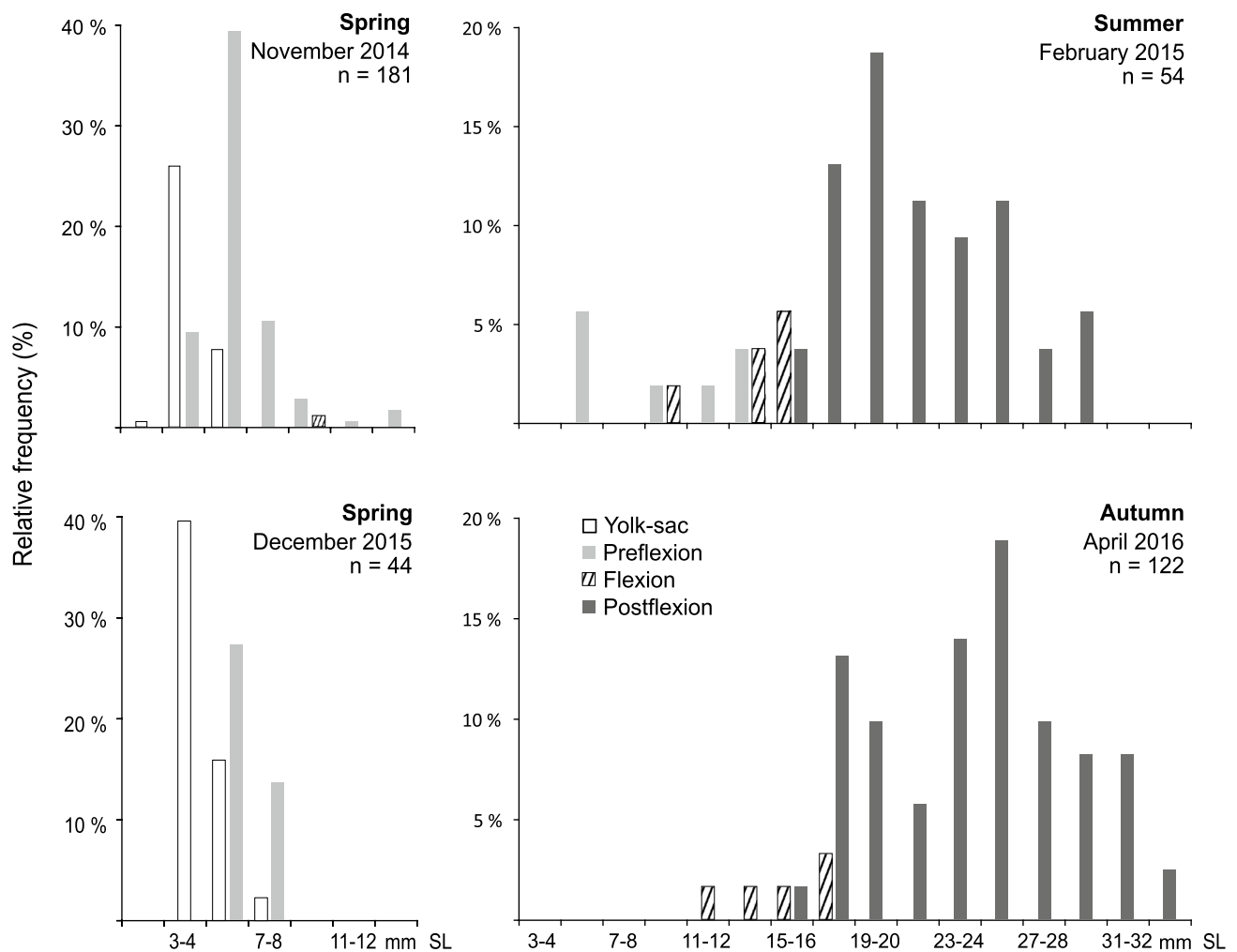
Fig. 4 *Sprattus fuegensis* seasonal standard lengths (SL) and developmental stages (yolk-sac, preflexion, flexion, postflexion) in the Namuncurá Marine Protected Area–Burdwood Bank. The number of measured individuals are specified (*n*)

the general pattern previously described, exhibiting the highest increment widths at 50 days of age. Individuals born in January did not attain such high increment widths, but slowly increased at a relatively constant rate reaching values similar to those shown by larvae born in December after approximately 70 days. Finally, larvae born in February and March presented initial increment widths similar to larvae born in December and January, but later on exhibited a more dispersed pattern with a decreasing tendency. The repeated measures analysis of the otolith increment widths at four different ages (10, 30, 50, and 70 days) among larvae hatched in Dec-2016 and Jan-2017 confirmed a significant interaction between hatching month and number of increment. A mean separation test of the pair-wise interactions showed significant differences for the increments widths at an age of 50 days among larvae hatched in different months (Table 1).

Discussion

Patagonian sprat eggs and larvae have been encountered in the NMPA–BB since 1973 (Ciechomski and Weiss 1974; Sánchez et al. 1995). Nevertheless, the present study represents the first thorough analysis of the Patagonian sprat *S. fuegensis* early life stages patterns in the NMPA–BB. The seasonal surveys analyzed have accounted for their ongoing presence, supporting the species long-time occurrence for more than 40 years in the area. Maximum seasonal abundances of eggs and larvae of the Patagonian sprat reported from the Argentinian coast, the Malvinas (Falkland) Islands, and the NMPA–BB are summarized in Table 2. Although different sampling gears have been previously employed, maximum abundance found in our study during spring was among the highest values reported
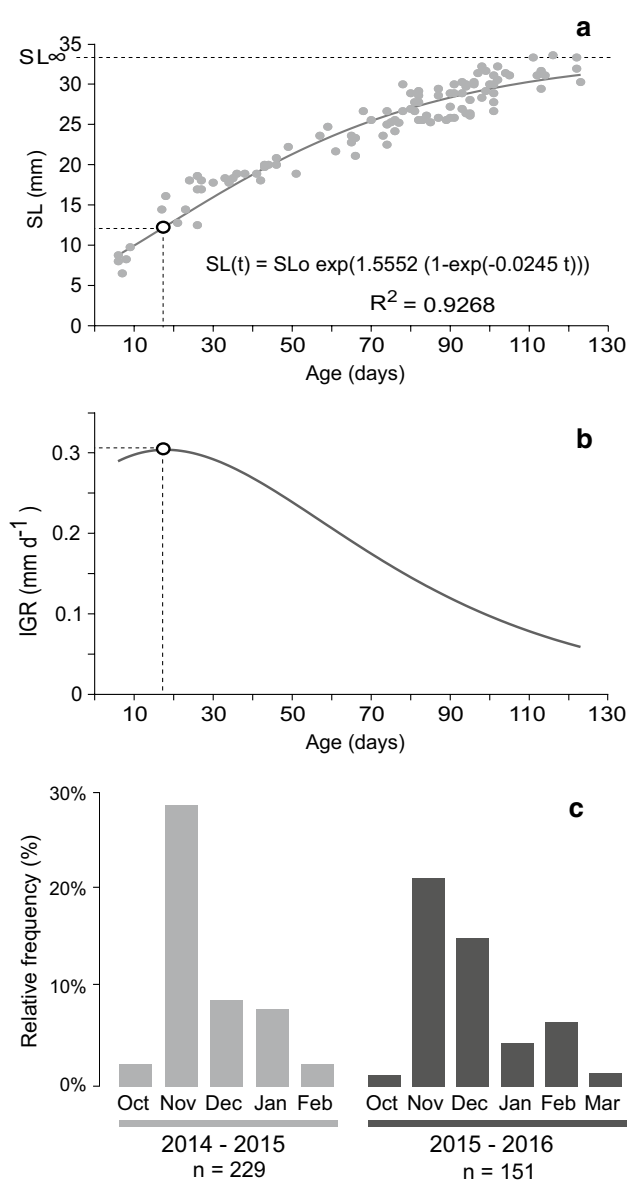
Fig. 5 Laird–Gompertz (LG) model fitted to the length-at-age data (**a**), instantaneous growth rates (IGR) obtained from the derivative expression (**b**) and relative frequency (%) of back calculated spawning dates of *Sprattus fuegensis* larvae for the two sampled periods (**c**). The inflection point (**O**) and the asymptotic length (SL∞) calculated by the LG model are indicated

up to date, acknowledging the NMPA–BB as an important spawning and nursery ground for *S. fuegensis*.

Patagonian sprat early life stages exhibited a distinctive spatial pattern at the NMPA–BB. Although abundances recorded with the MiniBongo net were probably underestimated, maximum eggs and larvae abundances in all seasons sampled were generally observed in the middle of the NMPA–BB (*buffer* area). Such spatial pattern was likely determined by the combination of weak advection in the NMPA–BB in contrast to the strong currents around it,

resulting in a relative confinement. The anticyclonic current surrounding the NMPA–BB (Reta et al. 2014) would not only operate as a retentive structure, but would also be responsible for generating currents converging from the border of the bank to the center, gathering and retaining fish eggs and larvae.

It has been claimed that both topographic up-welling and winter convection take place on BB (Peterson and Whitworth 1989), making it a very dynamic environment that could sustain high levels of primary productivity. In this study, no significant vertical stratification in terms of temperature or salinity was found during spring and autumn. Mixing of the water column is likely to be caused by strong tidal currents, which are predicted by numerical models (Glorioso and Flather 1995) and inferred from in situ data collected recently by means of a Eulerian current meter (unpublished data). Other sprat populations exhibited high larval abundances forming nuclei of distribution in well mixed waters, such as *S. sprattus* in the North Sea (Munk 1993; Valenzuela and Vargas 2002).

Fish with pelagic eggs like clupeids often reproduces in productive environments such as gyres and fronts to assure food availability for larvae and recruits (Loeb 1980; Frank and Leggett 1983). Seamounts and submerged banks are among these sites, thus becoming some of the richest fishing grounds worldwide, with current gyres over them serving as partial mechanisms retaining spawning products and maintaining stock integrity (Lough and Bolz 1989 and references therein). This scenario has been proposed for *S. fuegensis* in the Malvinas (Falkland) Islands, with the Malvinas gyre operating as a true retention area where spawning and nursery grounds overlap and the life cycle is fully accomplished (Acha et al. 1999). On the other hand, the Argentinian coastal sprat population exhibits a gyre-associated spawning and nursery strategies, but these areas are spatially separated according to an anti-clockwise wind-driven circulation cell (Sánchez et al. 1995; Acha et al. 1999).

Present results strongly suggest that the NMPA–BB is both spawning and nursery grounds for Patagonian sprat early life stages, similarly to the Malvinas Island sprat population. However, the strength of the retentive current in the northern boundary of the bank is weak, possibly being crossed by juveniles and adults. Further sampling is needed to address whether the whole life cycle occurs entirely at the NMPA–BB thus recognizing a third sprat population or, alternatively, juveniles and adults would migrate to the Argentinian coast, the Malvinas Island or other territories.

Based on otolith microstructure analyses, spawning of *S. fuegensis* in the NMPA–BB occurred from October to March, peaking in November. A similar spawning period was reported for *S. fuegensis* in the Argentinian coast (October–January; Sánchez et al. 1995), while spawning in Chile and the Malvinas Islands began a little earlier, as eggs were

Fig. 6 Otolith increments widths of *Sprattus fuegensis* larvae in relation to age: mean values (**a**) and mean monthly values based on their respective hatching periods (**b**). Standard deviations are showed. The grey plane indicates an identified plateau
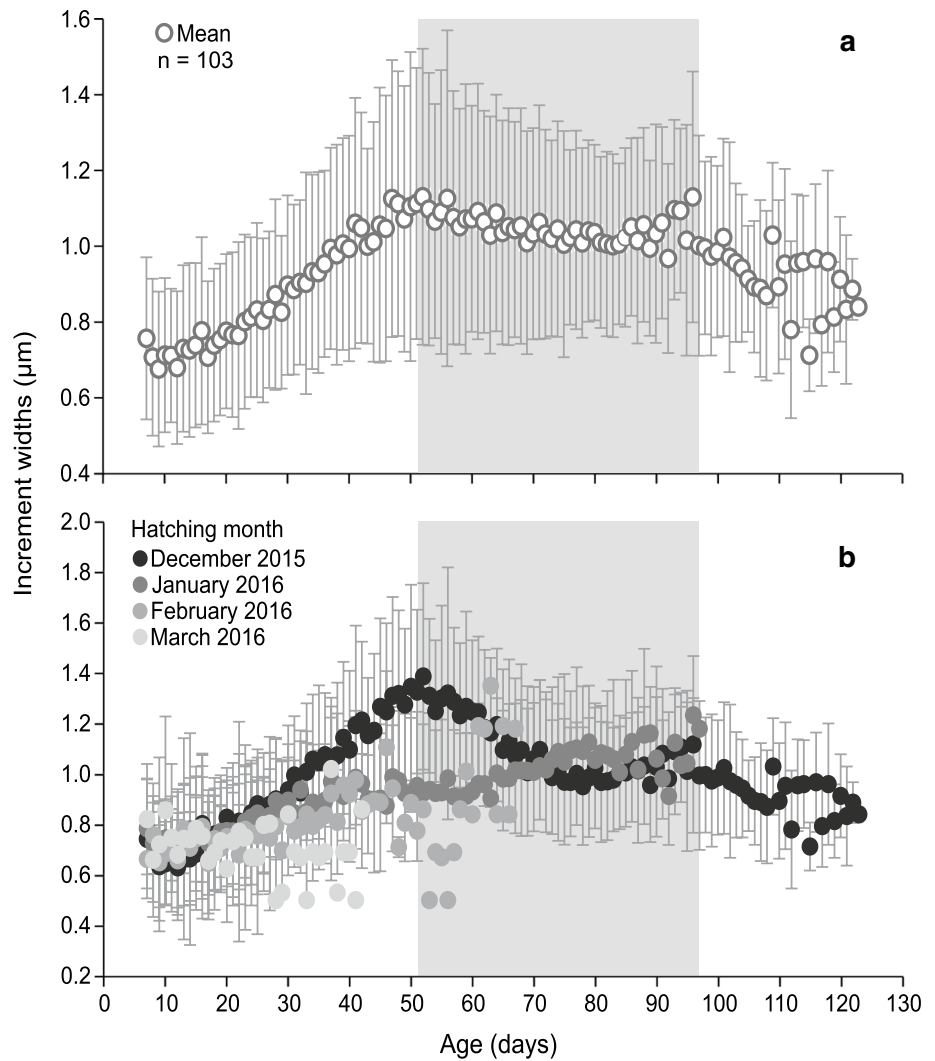
Table 1 *Post-hoc* pair-wise comparison between hatching month and age for otolith increment width of *Sprattus fuegensis* larvae captured in the autumn cruise (Apr-16) using least square method

Hatching months	Age	Mean width	Lower CL	Upper CL	Group
December 2016	10	0.646	0.569	0.722	a
January 2017	10	0.743	0.667	0.820	ab
December 2016	30	0.936	0.822	1.051	c
January 2017	30	0.902	0.787	1.106	c
December 2016	50	1.346	1.172	1.520	d
January 2017	50	0.934	0.60	1.108	bc
December 2016	70	1.059	0.925	1.192	c
January 2017	70	1.009	0.875	1.142	c

Otolith width means (μm) and the limits of their 95% confidence intervals (CL) are shown. For each increment (age), different letters indicate significant differences between hatching months ($p < 0.05$)

found from September to December (Ciechomski 1971; Shirokova 1978; Leal et al. 2011; Cerna et al. 2014). It is known that Patagonian sprats are multiple spawners, with spawning occurring primarily during spring–summer (Hansen 1999; Leal et al. 2011). In the NMPA–BB, they showed a more protracted period which extends until early autumn. Cushing (1990) suggested that long spawning periods could represent an adaptation of species living at the limit of their geographical distribution to cope with the wider range of interannual variability observed in such environments. Moreover, coastal species could present protracted spawning periods, along with increasing fecundities and multiple spawning sites, as a way to increase their recruitment in response to the high mortalities associated with unstable environments. In this regard, Agnew (2002) observed that adults of the Malvinas Island sprat population were generally captured in July and August close to the shore west and south of the Islands, while in September and October they moved to the south of the islands including offshore waters. This suggests that the

Table 2 Maximum abundances of *Sprattus fuegensis* eggs and larvae in the Southwest Atlantic Ocean

	Area	Sampling dates	Sampling gear	Maximum abundances	Source of information
Eggs	Argentinian coast	Spring	Nackthai 400 μm	53 eggs m^{-2}	Sánchez et al. (1997)
	Malvinas Islands NMPA–BB	Winter/spring	Hensen 420 μm	760 eggs m^{-2}	Ciechomski (1971)
		Winter	Nackthai 400 μm	1000 eggs m^{-2}	Sánchez et al. (1997)
		Spring	Bongo 300 μm	2500 eggs m^{-2}	This study
Larvae	Argentinian coast	Spring	Bongo 300 μm	90 larvae 100 m^{-3}	Ciechomski et al. (1975)
		Autumn	IKMT 2000 μm	10 larvae 100 m^{-3}	Sánchez et al. (1995)
		Autumn	Nackthai 400 μm	1000 larvae m^{-2}	Sánchez et al. (1997)
		Spring	Nackthai 400 μm	136 larvae m^{-2}	Sánchez et al. (1997)
		Autumn	Conical net 200 μm	4.55 larvae 100 m^{-3}	Bruno et al. (2018)
	Malvinas Islands NMPA–BB	Spring	Bongo 300 μm	2 larvae 100 m^{-3}	Ciechomski et al. (1975)
		Spring	Bongo 300 μm	1 larvae 100 m^{-3}	Ciechomski et al. (1975)
		Summer	MiniBongo 200 μm	8 larvae m^{-2}	This study
		Spring	Bongo 300 μm	900 larvae m^{-2} (= 112 larvae 100 m^{-3})	This study
		Autumn	Bongo 300 μm	166 larvae m^{-2}	This study

Sampling dates (seasons) and gears employed are specified

Malvinas sprat population possibly migrate south towards the NMPA–BB to spawn, expanding their distribution to this site where physical processes sustain favorable biological conditions for growth and survival.

Metamorphosis and associated growth rates are important survival determinants for larval and juvenile stages (Houde 1989a), being also powerful tools to differentiate fish populations (Brophy 2013). In sprat species, metamorphosis was characterized by a "decoupling" in length and otolith growth, with reduced length growth (Günther et al. 2012) and maximal daily accretion on the otolith (Baumann et al. 2005; Günther et al. 2012). During this developmental stage, sprats shift from an elongate, slender larva to a spindle-shaped juvenile. An accelerated growth in body height would be responsible for this "decoupling" in smaller sprat and, therefore, otoliths would record somatic growth rather than growth in length (Günther et al. 2012). According to our results, *S. fuegensis* also evidenced "decoupling" between otolith and length growth. Larvae between 50 and 95 days of age (21–29 mm of SL) exhibited low growth rates in length and the highest otolith increment widths. It was also acknowledged that those high values of otolith increments widths in relation to age conformed a plateau instead of a parabola (e.g., Günther et al. 2012). This feature would indicate that *S. fuegensis* undergoes a prolonged larval phase, an expected scenario for species developing in low temperatures which evidence low growth rates (Houde 1989b; Pepin 1991; Günther et al. 2012; Nikolioudakis et al. 2014).

The maximum growth rate in length (IGR) calculated in our study for *S. fuegensis* larvae at the NMPA–BB (0.30 mm day^{-1}) was lower than those calculated for the Argentinian coastal population (0.32 and 0.37 mm day^{-1}) (Sánchez et al. 1997; Brown and Sánchez 2010) and for the Chilean population (0.45 mm day^{-1}) (Landaeta et al. 2012). Beside temperature, reduction on larval growth rates could be a consequence of high larval abundance and severe food deprivation as seen by Baumann et al. (2007) for European sprat. It was also noticed that some otolith increment widths were significantly different according to larvae's hatching months (see Fig. 6b). Seasonal influence in the increment widths has been reported for other clupeids as *S. sprattus* and the sardine *Sardina pilchardus* (Baumann et al. 2006; Schismenou et al. 2016). Particularly, Patagonian sprat larvae born in December (close to the spawning peak) exhibited higher values in contrast to later born larvae. We hypothesize that *S. fuegensis* in the NMPA–BB overlaps the spawning peak (spring) and the most favorable conditions (e.g., temperature, food availability, photoperiod) to guarantee larval survival (e.g., Cushing 1990; Buckley et al. 2006).

Further research addressing growth in relation to environmental characteristics such as food availability is needed to fully comprehend the development of Patagonian sprats in the NMPA–BB. Combining this information with data from older stages (juvenile and adults) will probably allow to elucidate the spawning pattern and the role of *S. fuegensis* in the NMPA–BB food web. If sprats control the energy flux of the NMPA–BB at the ''wasp-waist' level, future management policies should include the possibility to enlarge the *core* area, in order to secure a major spawning and nursery ground of *S. fuegensis*.

Compliance with ethical standards

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