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Benefits of frontal waters for the growth of *Engraulis anchoita* larvae: The influence of food availability

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ABSTRACT

We studied the abundance, size and growth rates of *Engraulis anchoita* larvae during the end of the species' spawning season in relation to environmental variables. Two sampling transects, one in Península Valdés (northern transect: NT) and the other in Isla Escondida (southern transect: ST), with four stations each, were established in late summer. Both locations are characterized by high concentrations of *E. anchoita* larvae in spring, strongly associated with the presence of frontal waters, at the beginning of the species' spawning season. Zooplankton and ichthyoplankton were sampled, and temperature profiles and chlorophyll-*a* satellite images were analyzed for each sampling station. Zooplankton samples were divided in size fractions, and composition and abundances were estimated. Standard length (SL), ontogenetic stages, and abundance (including eggs) were estimated. Additionally, age and growth rates were determined by otolith analysis. Two different scenarios were observed in both transects. In the NT, a frontal structure was found, while at the ST, the water column was completely homogeneous. Total zooplankton abundance was maximum at frontal waters, with 22,195 ind. m⁻³, being the small size fraction (< 200 μm) the most abundant, mainly composed of nauplii (9000 ind. m⁻³) and cyclopoid copepodites (4000 ind. m⁻³). The NT showed higher abundance (mean of 126.5 ind. m⁻² per station in NT; 29.75 ind. m⁻² in ST), faster growth rates of *E. anchoita* larvae (NT: 0.45 ± 0.04 mm day⁻¹; ST: 0.34 ± 0.09 mm day⁻¹; n = 90), and higher mean SL at frontal waters (7.57 ± 1.52 mm SL) than the ST. In the NT, *E. anchoita* growth rates were constant in time, whereas in the ST, they decreased with age. Our results support the classical theory, which states that frontal waters provide advantageous environmental conditions for fish larvae feeding, growth and, thus, survival.

1. Introduction

Frontal waters are characterized by circulations that are a consequence of differential densities between two water masses, which generate a convergence at the surface or bottom boundary (Largier, 1993; Mann and Lazier, 1996). Oceanographic characteristics of seasonal fronts such as nutrition enrichment and water stratification generate favorable conditions for the development of phytoplankton, zooplankton, ichthyoplankton and top predators (Bakun et al., 2010; Mann and Lazier, 1996). According to the hypothesis of Bakun (1996), the "Bakun's Fundamental Triad", frontal areas have three essential

characteristics that enhance survival and recruitment of pelagic fish during their early stages: i) the enrichment of surface water layers caused by the rise of deeper water rich in nutrients; ii) the concentration of planktonic organisms that constitute food items for fish larvae and iii) the retention of fish eggs and larvae in favorable areas.

A conspicuous feature in the Patagonian coastal area is the development of the tidal thermal front of Península Valdés during spring and summer (Fig. 1). When the frontal system is fully formed, it extends between 41° and 45°S, following the 75–80 m isobath (Sabatini et al., 2004). High tidal dissipation rates generate strong vertical mixing in near shore waters, which homogenizes the entire water column. Wind

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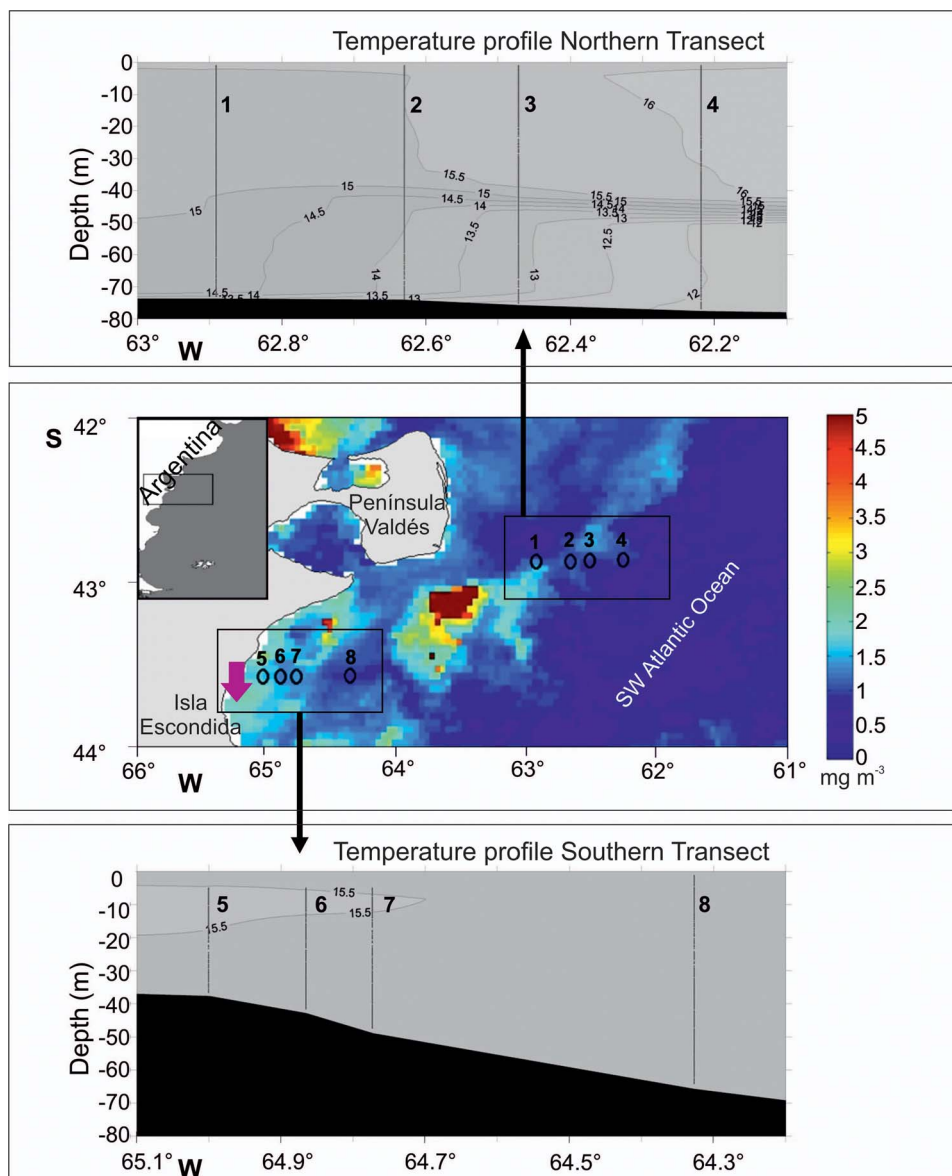


Fig. 1. Position of transects and distribution of stations with mean surface chlorophyll-*a* values (mg C m^{-3}) calculated as an average of eight days centered on April 3rd, 2013 (center). Detail of temperature profiles ($^{\circ}\text{C}$) of the northern and southern transects (above and below, respectively). The purple arrow indicates the location of Isla Escondida.

pressure on the surface layer also contributes to forming and maintaining the homogeneity near the shore. On the other hand, seasonal surface warming induces a strong stratification of the shelf waters. As a consequence, a clear separation can be observed between highly mixed coastal and stratified offshore waters (Tonini et al., 2013). Between the homogeneous and stratified waters, there is a transitional zone, with a weaker thermocline, which constitutes the frontal area (Carreto et al., 1986; Glorioso, 1987). This structure is maintained until autumn, when the stratification is weakened due to the wind effect and decreasing solar heating (Acha et al., 2004).

The Península Valdés tidal front is important to several fish resources that are subject to commercial fishery, e.g. the hake, the southern blue whiting, the Argentine shortfin squid, the mackerel and the patagonic Argentine anchovy (Alemany et al., 2014; Brunetti et al., 1998). The latter, *Engraulis anchoita* (Hubbs and Marini, 1935), is a small pelagic fish, important in the food web of the Argentine Sea, being in the dietary base of several commercially exploited species. *Engraulis anchoita* represents one of the most important fish resources in terms of biomass in the Southwest Atlantic Ocean (Hansen and Madirolas, 1996; Madureira et al., 2009; Pájaro et al., 2009). The

patagonic stock of *E. anchoita* spawns between 41° and 47°S from austral spring to autumn, with a maximum spawning peak in December, from the coast to 150 km offshore. Each female lays eggs multiple times during the entire spawning season, forming areas with large concentrations of larvae. Two main areas of larval concentration have been previously detected: one near Península Valdés and the other a few kilometers south, in the area of Isla Escondida (Sánchez, 1995; Sánchez and Ciechowski, 1995). *Engraulis anchoita* is a zooplanktivorous species throughout its life cycle, being a key component of the dynamics of pelagic ecosystems, performing a “wasp-waist” type control (Bakun, 2006; Cury et al., 2000; Hunt and McKinnell, 2006). Thus, variations in the adult biomass of *E. anchoita* could generate drastic changes at both higher and lower trophic levels.

Ciechowski (1966) and Ciechowski and Weiss (1974) reported that larval stages up to around 38 mm of standard length feed mainly on small organisms, mostly copepod eggs, nauplii and small copepodites (Sabatini, 2004; Sánchez and Manazza, 1994; Sato et al., 2011; Viñas and Ramírez, 1996). Copepod ontogenetic stages have been related to the degree of water stratification. Previous studies in the frontal system of Península Valdés have reported the highest abundance value of

nauplii in the transitional area, in coincidence with the maximum trophic incidence of *E. anchoita* larvae (Derisio et al., 2014; Viñas and Ramírez, 1996). The prey of *E. anchoita* larvae is generally smaller than 500 µm, most commonly smaller than 300 µm (Sato et al., 2011; Spinelli et al., 2012; Viñas and Ramírez, 1996).

In clupeiform fishes as anchovy, environmental variability has a strong influence on early developmental stages (Sánchez, 1995), and larvae are subject to high mortality rates that could impact on the recruitment of adults. In particular, pelagic fish populations have demonstrated to be variable and sensitive to various internal factors, such as the growth rate, natural mortality, predation mortality and nutritional condition; and external factors, such as the stability of the water column, temperature, upwelling periods and food availability. In addition, each internal factor depends on the environmental conditions (Houde, 2008). Particularly, in several species of marine fish, larval growth influences the recruitment of adult stocks (Campana, 1996; García et al., 2003; Takasuka et al., 2007). Larval growth is commonly studied by the analysis of the otolith microstructure, a methodology that allows determining the age, growth rates and hatching date, by counting and measuring the otolith daily increments (Baumann et al., 2003; Brown et al., 2004). This methodology has been successfully applied to *E. anchoita* larvae and juveniles (Brown and Sánchez, 2010; Brown et al., 2013; Castello and Castello, 2003; Leonarduzzi et al., 2010).

The aim of this study was to study the growth of *E. anchoita* larvae through the analysis of the otolith microstructure in two different oceanographic scenarios at the end of the spawning season. Frontal waters are expected to favor higher chlorophyll-*a* concentration and zooplanktonic prey availability, resulting in faster growth rates. Thus, our work intends to reassert the importance of frontal systems as nursery areas.

2. Materials and methods

2.1. Study area and sample collection

Zooplankton samples were taken on board the oceanographic ship ARA Puerto Deseado, along two transects, a northern (NT) and a southern one (ST), with four stations each (stations 1–4 and 5–8 respectively), during March 2013 (29 and 30th). Both transects were planned considering two known major larval concentration areas: the area of Península Valdés and the proximities of Isla Escondida (Fig. 1).

At each station, zooplankton samples were collected with a MiniBongo net of 67 µm mesh size and 20 cm in mouth diameter, performing oblique hauls, from near the bottom to the surface, and then fixed in 5% formaldehyde. Ichthyoplankton samples were collected with a Bongo net of 300 µm mesh size and 60 cm in mouth diameter, also by oblique hauls. The ship moved at 2 knots during the trawls and a mechanical flowmeter was used in the mouth of each net to measure the volume of filtered water. A subsample of larvae ($n = 90$) was taken from each station and the individuals were frozen on board in liquid nitrogen at -196°C ; the rest of the samples were fixed in 5% formaldehyde. Hydrographic conditions were determined by measuring temperature and conductivity at each station with a CTD Seabird 911. Satellite images of surface chlorophyll-*a* were obtained from MODIS Composite Software Giovanni System – Interactive Visualization and Analysis, with the mean values of eight days focused on April 3rd, 2013. Due to cloudiness, we chose the closer date to the sampling period showing a suitable image resolution.

2.2. Sample processing

The zooplankton obtained by using the MiniBongo net was divided into three size fractions through filters with appropriate mesh openings: larger than 500 µm (large fraction), between 200 and 500 µm (intermediate fraction), and smaller than 200 µm (small fraction). The large

fraction, although underrepresented by the MiniBongo net capture capacity, was considered as a proxy of the abundance of larger zooplankton organisms. Each size fraction was filtered and resuspended in seawater (between 300 and 800 mL of total volume) and taxonomic groups (appendicularians, chaetognaths, copepods and their naupliar stages) were identified under a dissecting microscope. A variable number of 5-mL aliquots were taken from each size fraction, depending on the total abundance and composition of organisms found. In all cases, it was assured that the number of aliquots reached a stable proportion of zooplankton organisms. The total number of individuals counted was 11,261 in the NT and 10,731 in the ST. The abundance of specimens was calculated by analyzing fractions of the material in seawater (distilled water with 35 NaCl g L^{-1}). Copepods in the intermediate and large size fractions were identified to species level (Bradford-Grieve et al., 1999), whereas those in the small fraction were identified only to Order level (Cyclopoida, Calanoida and Harpacticoida).

Egg and larvae of *E. anchoita* collected with the Bongo net were separated from the rest of the sample, and their abundances (ind. m^{-2}) were estimated. The standard length (SL) of each larva was measured under a binocular microscope equipped with a video camera. When larvae were curved due to fixation effects, SL was measured considering several straight sections. When there were less than 100 individuals per sample, all the individuals were measured, whereas when there were more than 100 individuals per sample, subsamples of about 100 anchovy larvae were randomly selected. Larvae were classified according to the ontogenetic stages described by Alheit et al. (1991) as: preflexion (SL < 8.00 mm), flexion (8.00–12.90 mm SL) and postflexion (12.90–50.00 mm SL). As normality and homoscedasticity assumptions were not met, a Kruskal Wallis test was used to compare SL mean values among stations.

Heads of the frozen larvae were cut and preserved in 96% alcohol; head soft tissues were dissolved with sodium hypochlorite and cleaned with distilled water. Sagittal otoliths were removed under a binocular stereoscope. Otolith pairs were mounted on transparent medium (Protex-xylene) and dried for 48 h. The microstructure was analyzed with a Zeiss Axioscop binocular microscope at maximum magnification ($\times 1000$). Images were enhanced and analyzed using Kontron software (KS-300). The sagittal otolith radius (OR) and the number and width of daily increments were measured using a digital image processing software, considering the major axis of the otolith. Increments were counted in both otoliths of the pair and when there was at least 90% of coincidence between them (e.g. 10 and 11 increments), the number of increments of the otolith of the clearest image was assumed as the larval age in days. When only one otolith from the pair was available due to the loss of the other during the extraction, such information was considered (Brown et al., 2013).

2.3. Data analysis

Hatching dates were determined by subtracting the number of daily increments from the dates of capture. Power relationships between OR and SL and between OR and age (number of daily increments) were regressed. Larval growth was analyzed by back-calculation of past sizes at previous ages (growth trajectories). To obtain past size values, we used the methodology described by Watanabe and Kuroki (1997) and Watanabe and Nakamura (1998). After fitting SL and OR to a power relationship, the relationship of the *i*th otolith radius (OR_i) and SL on the day of the *i*th increment (SL_i) was considered to be expressed by this formula for each larva:

$$SL_i = aOR_i^b \quad (1)$$

a
b

$$SL_1 = aOR_1^b \quad (2)$$

$$SL_{\text{captured}}^b = aOR_{\text{captured}}^b \quad (3)$$

where

SL_1 = standard length at first-increment deposition (4 mm; Leonarduzzi et al., 2010);

OR_1 = measured otolith radius of the first daily increment (μm);

SL_{captured} = measured standard length at capture (mm);

OR_{captured} = otolith radius (μm) at capture.

For the statistical analysis, we transformed the power relationships (OR – age and SL – OR) applying natural logarithm (Ln). Then, we tested differences between the slopes of the linearized relationships obtained for larvae from the NT and the ST (Zar, 1996). Somatic growth rates of larvae were calculated as mean values of differences between two consecutive back-calculated sizes of the individuals: $SL_j(i+1)$, $SL_j(i)$ (Leonarduzzi et al., 2010):

$$\sum_{j=1}^n \frac{(SL_j(i+1) - SL_j(i))}{n} \quad (4)$$

where

n = number of individuals at age i ;

$SL_j(i)$ = standard length back-calculated for an individual j at age i ;

$SL_j(i+1)$ = standard length back-calculated for an individual j at age $i+1$

To analyze the influence of spatial differences on larval growth, growth rates per age from both transects were compared. After verifying statistical assumptions (see Supplementary material 1 for details), a General Linear Mixed Model was applied to analyze the differences between both transects, ages and individuals. The age-transect interaction was also tested and the model was expressed as:

$$\text{Growth rate} \sim \text{Transect} + \text{Age} + \text{Transect} \times \text{Age} + \text{Individual}(\text{Transect}) \quad (5)$$

Growth rate = continuous numerical variable that represents the daily growth rate. Previous to the analysis, this variable was transformed by Box-Cox to achieve better normality and homoscedasticity of the data.

Transect = fixed factor that represents the transect analyzed;

Age = fixed factor that represents the larval age in days;

Transect \times *Age* = interaction between both factors;

Individual (Transect) = random factor representing each individual, nested within each transect.

3. Results

The persistence of the tidal front was detected only in the NT, and stratified waters were observed in the offshore area (stations 3 and 4), as shown in the temperature profiles (Fig. 1). Transitional waters were detected in station 2. In station 4, which showed the greatest stratification degree, the thermocline was located between 40 and 50 m deep. Station 1 of the NT and all stations of the ST presented homogeneous waters. No strong halocline was detected in the NT or ST (see Supplementary material 2 for details). The values of chlorophyll-*a* concentration were slightly higher in the ST than in the NT, and a patch of high chlorophyll-*a* concentration was observed at the coastal area around 43°S (Fig. 1).

Zooplankton abundance was markedly higher in the NT than in the ST (Fig. 2), with the maximum values located in transitional (13,327 ind. m^{-3} in station 2) and stratified waters (22,195 ind. m^{-3} in station 3). The maximum zooplankton abundance value in the ST was observed in station 5, with 4617 ind. m^{-3} . Intermediate and small size fractions were the predominant ones in the entire area, with a maximum abundance value of the small size fraction in station 3, mainly composed of nauplii (9000 ind. m^{-3}) and cyclopoids (4000 ind. m^{-3}). Appendicularians and cyclopoids occurred in the most offshore stations of the NT (stations 3 and 4), while calanoids were especially abundant

in transitional (station 2) and homogeneous waters (station 1). Additionally, a high abundance of the dinoflagellate *Noctiluca scintillans* was observed in the samples from transitional and frontal stations 2 and 3 (see Supplementary material 3 for details). The intermediate size fraction had a maximum abundance value in transitional waters (station 2) and was mainly composed of calanoids, both adults and copepodites (Fig. 2). As expected due to the mesh size of the MiniBongo net, the large size fraction abundance was low, being mainly composed of calanoid adults. In the ST, unlike that recorded in the NT, the intermediate size fraction was the most abundant, followed by the large size fraction and finally by the small size fraction. This transect was mainly composed of large and intermediate sizes of calanoids, followed by small and intermediate sizes of cyclopoids. The calanoids *Acartia tonsa* and *Paracalanus parvus* and the cyclopoids *Oithona similis* and *O. nana* were the copepod species that dominated both transects. Furthermore, the calanoid *Calanus australis* was found in stratified (stations 3 and 4) and transitional waters (station 2) and only one harpacticoid, *Euterpina acutifrons*, occurred in the ST (see Supplementary material 4 and 5 for details). In all stations, the presence of other large zooplankton organisms was recorded (see Supplementary material 3 for details).

Following the same trend as zooplankton prey, *E. anchoita* larvae were more abundant in the NT than in the ST, with a maximum value of 220 ind. m^{-2} in station 3. In the ST, a maximum abundance of 85 ind. m^{-2} was detected in station 8. Anchovy eggs mainly occurred in the most offshore station of the NT (175 eggs m^{-2} in station 4) and, when present in the remaining stations, did not exceed 1 egg m^{-2} (Fig. 3). Anchovy larvae from the NT hatched from February 26 to March 27, whereas those from the ST hatched from February 16 to March 27. In both transects, larvae hatching occurred mostly from March 18 to March 22. Older larvae were located in the most coastal stations, while younger ones were in a more offshore position. Pre-flexion larvae were the most abundant in all stations. Postflexion larvae occurred in low quantities and did not exceed 15.5 mm SL. The maximum density of flexion larvae was observed in the NT, particularly in frontal waters (station 3). In this location, the mean SL value (mean SL: 7.57 ± 1.52 mm) was the highest of the whole transect ($p < 0.05$).

When OR/age values (Fig. 4A) were compared between transects (considering the same age range of 4–27 days), the slope of the linearized relationship was significantly higher for the larvae from the NT ($p < 0.001$). The same occurred with the linearized relationships between OR and SL (Fig. 4B), where a higher slope value was found for the larvae from the NT ($p < 0.001$). Therefore, when comparing larvae of the same age or SL, a faster otolith growth rate was detected in larvae from the NT.

The results of the General Linear Mixed Model showed significant differences between transects in larval growth per age (Table 1). Statistical differences between individuals from each transect were also detected, demonstrating the existence of high variability between larval growth trajectories. Total mean growth rates (considering average values per age) were 0.45 ± 0.04 mm day^{-1} for the NT and 0.34 ± 0.09 mm day^{-1} for the ST. When larval growth rates were plotted for each age and compared between transects, values of larvae of the NT were higher than the ones of the ST; the difference was more noticeable in older larvae (Fig. 5).

4. Discussion

4.1. Oceanography, zooplankton abundance and size composition

In the present study, we found two different oceanographic scenarios across two known spawning and nursery grounds of *E. anchoita* larvae, with chlorophyll-*a* values at the coastal area in coincidence with the autumn pattern described by Paparazzo et al. (2010) and Rivas et al. (2006). Nevertheless, the maximum zooplankton abundance value was found at a low-concentration chlorophyll-*a* patch. This could have been caused by a large grazing effect, consequence of an active feeding of the

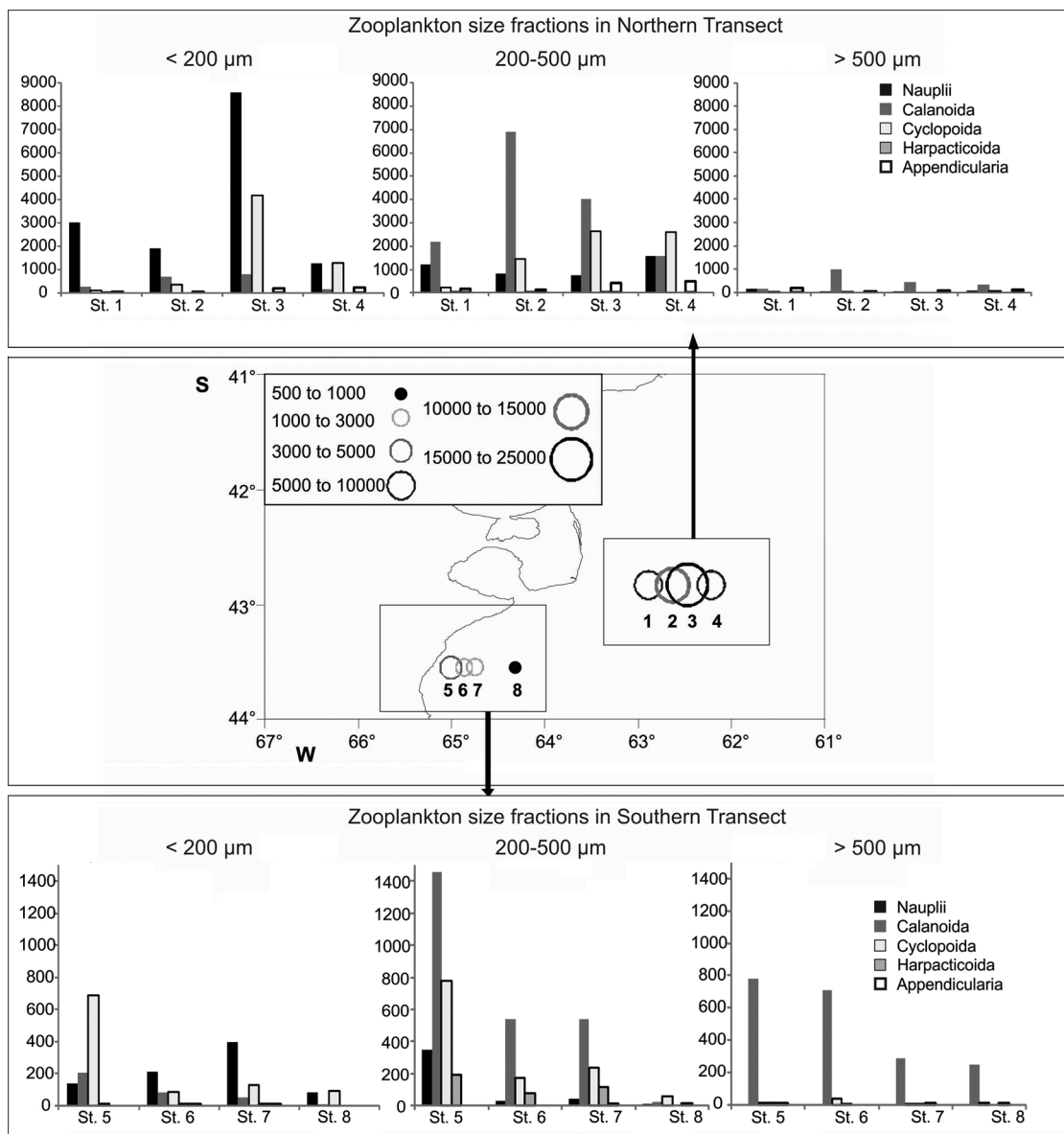


Fig. 2. Total zooplankton abundance (ind. m⁻³) in each station (center). Composition of zooplankton size fractions (small (< 200 μm), intermediate (200–500 μm) and large (> 500 μm)) of nauplii, calanoids, cyclopoids, harpacticoids and appendicularians from the northern and southern transects (above and below, respectively). Note the difference in the scale between both transects.

abundant zooplankton organisms located there. We found that zooplanktonic groups showed a differential spatial distribution in relation to water stratification, in agreement with that found by Sabatini and Martos (2002) in the same area during spring. These authors observed distinct physical environments characterizing the northern and southern boundaries of the tidal front (Península Valdés and Isla Escondida respectively), mainly due to differential wind/tidal relative forcing, which led to the occurrence of different plankton assemblages. They also found that cyclopoids and appendicularians were conspicuous toward the north (Península Valdés), and suggested that the microbial food web played an important role in the area, while in further south (Isla Escondida), where calanoid copepods were dominant, a classic herbivorous food web was probably the case. In our study, zooplankton groups in the northern and southern transects were distributed in a similar way to that described by these authors during spring. Total zooplankton abundances recorded in the NT were higher than or quite similar to the ones described during November/December (austral spring) blooms at the beginning of the anchovy spawning season (Sabatini et al., 2004; Spinelli et al., 2012). The great abundance

of the dinoflagellate *N. scintillans* found in our study suggests that transitional waters were enriched, supported by the high abundance of the small size zooplankton fraction (< 200 μm), mainly composed of copepod nauplii and small cyclopoids. The same happened with the intermediate zooplankton size fraction (200–500 μm) in the frontal position next to transitional waters, where both small and intermediate size fractions represented suitable prey for the *E. anchoita* larvae that were growing in the NT.

4.2. *Engraulis anchoita* eggs and larval distribution

Low abundance of anchovy eggs was expected, as the sampling took place at the end of the reproductive season, which has been established around April, in coincidence with the start of the austral autumn (Sánchez, 1995). Since eggs and newly hatched larvae were detected in the offshore station, and older larvae in postflexion stage were present in the coastal stations, a displacement of the spawning towards offshore waters could be occurring, a phenomenon previously observed by Brown et al. (2013) and Sánchez (1995). These authors described the

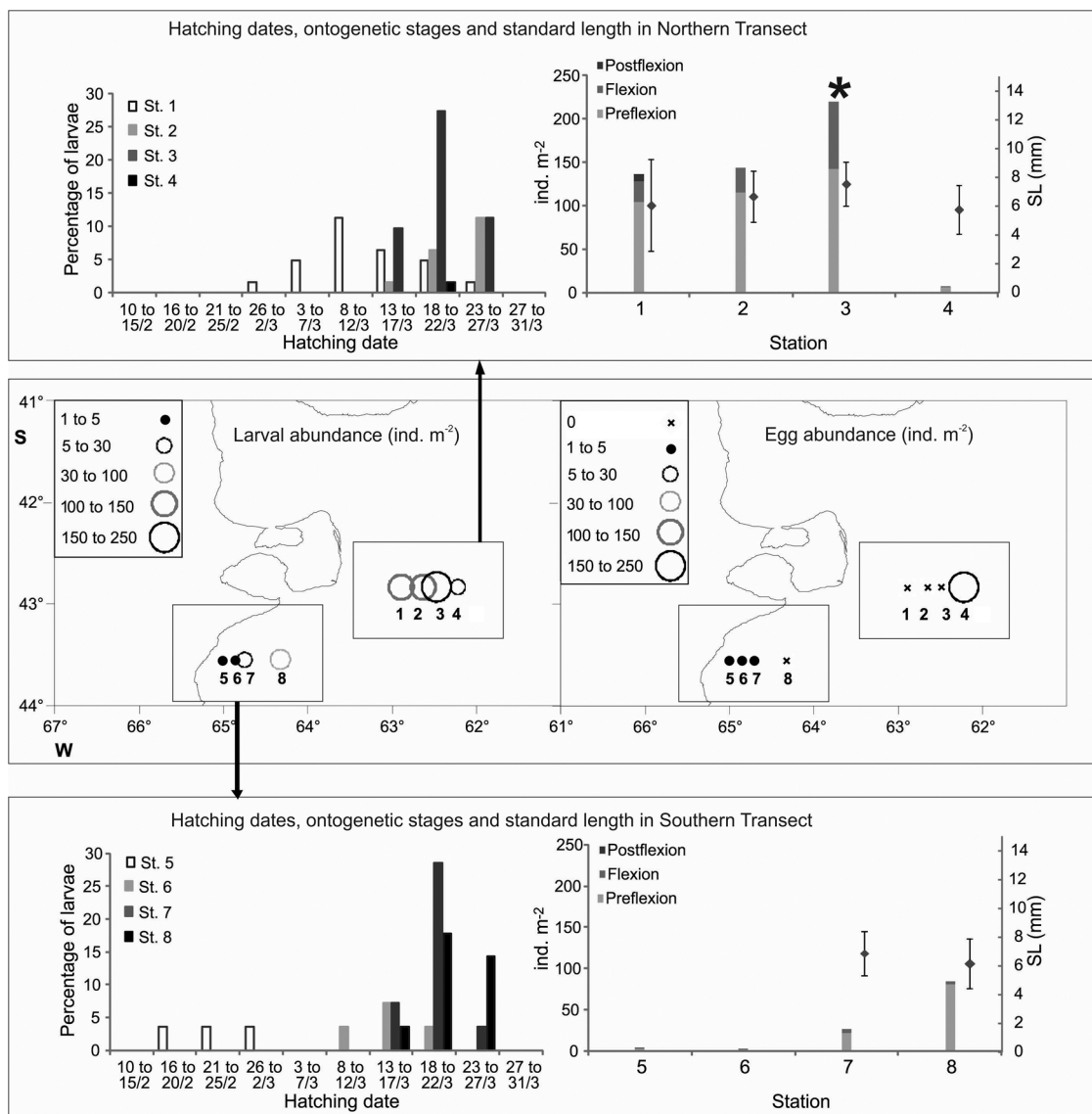


Fig. 3. Abundance (ind. m⁻²) of *Engraulis anchoita* larvae and eggs in each station (center). Hatching dates, ontogenetic stages (preflexion, flexion and postflexion) and mean standard length (SL) values of *E. anchoita* larvae from the northern and southern transects (above and below, respectively). * indicates a significant difference ($p < 0.05$) in mean SL values.

displacement of the spawning area from coastal waters to outer waters as the reproductive season progresses. Hansen et al. (2001) detected that changes in the tidal front position were followed by similar changes in the location of the *E. anchoita* spawning adults. Such location of adults would determine the position of eggs and larvae, coinciding with stratified water masses.

4.3. Growth rates of *E. anchoita* larvae at the end of the spawning season

The growth rates of *E. anchoita* larvae (0.34–0.45 mm day⁻¹) obtained in this work coincide with those reported for this species during spring time. Brown and Sánchez (2010) and Brown et al. (2013) recorded values between 0.35 and 0.51 mm day⁻¹. In another frontal area of the Southwestern Atlantic Ocean (near the Buenos Aires province), Leonarduzzi et al. (2010) detected larval growth rates between 0.41 and 0.51 mm day⁻¹. Spatial differences in *E. anchoita* larval growth related to the presence of a frontal system were detected in this study for the first time. These growth differences were mainly observed for the older larvae, while younger individuals had similar growth rates in both areas. Probably, environmental conditions turn out to be more influential when larval feeding becomes active. Thus, the advantageous

environmental conditions of the NT would have influenced positively on older anchovy larvae.

The main external factors that affect fish larvae growth are temperature and food availability (Heath, 1992; Stevenson and Campana, 1992). Castello and Castello (2003) analyzed *E. anchoita* larval growth in Brazilian waters in winter and spring, and found growth rates from 0.40 to 0.50 mm day⁻¹ in a thermal range of 17–25 °C. In another study performed in southern Brazil, where temperature values varied between 20 and 22 °C, Ekau (1998) obtained a growth rate range of anchovy larvae from 0.7 to 1 mm day⁻¹. All these growth rate values were higher than those herein reported. Nevertheless, our temperature range was 12–16 °C, thus, the slower growth rates reported here could be the result of the lower mean temperature due to latitudinal effects.

Even so, in the present study, temperature differences between sampling stations did not exceed 1 °C, and such thermal variation could not lead to growth rate differences in a species that inhabits a broad latitudinal range. In contrast, food availability seems to have played a key role, while growth rates are driven mainly by early life trophic dynamics according to the results presented by Catalán et al. (2010) for *E. encrasicolus* in the Aegean Sea. Accordingly, while analyzing the influence of seasonality on larval growth, Leonarduzzi et al. (2010) did

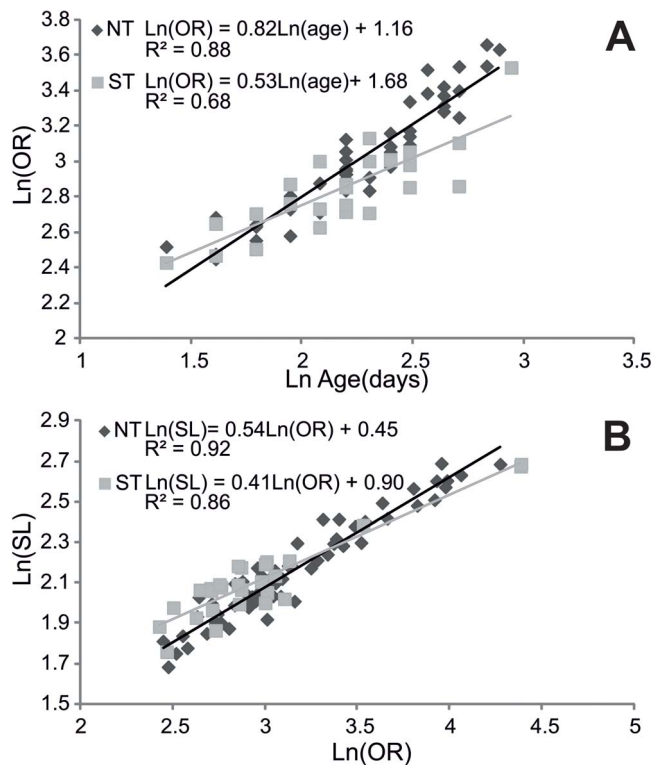


Fig. 4. Linearized logarithm (Ln) relationships between otolith radius (OR) and age (A) and between standard length (SL) and OR, (B) of *Engraulis anchoita* larvae from the northern and southern transects. Larvae from 0 to 27 days old were considered for statistical comparison.

Table 1
GLM-ANOVA Univariate Tests of Significance for the growth rate (dependent variable) of *Engraulis anchoita* larvae, and potentially explanatory factors of Transect, Age, Individual and interactions.

Factor	Degree of Freedom	Sum of Squares	Mean Squares	F statistic	p value
Transect	1	0.0360	0.0360	6.803	0.0097
Age	26	0.1507	0.0060	2.182	0.0006
Transect × Age	26	0.1637	0.0063	2.370	0.0002
Individual (Transect)	87	1.4684	0.0169	6.353	0.0000
Error	834	2.2157	0.0027		

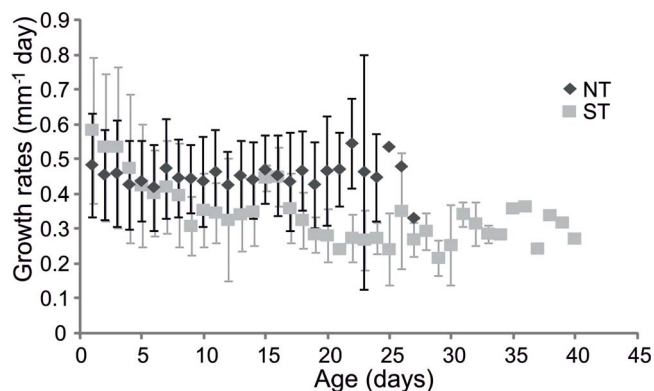


Fig. 5. Average growth rates (mm day^{-1}) by age of *Engraulis anchoita* larvae from the northern (NT) and southern transects (ST) at the Península Valdés Frontal System.

not attribute differences in growth rate to temperature, but proposed that growth differences could be related to food availability. Taking into account the concept of Hjort’s critical period (Hjort, 1926), Houde

(2008) supported the existence of a positive relationship between prey availability and larval survival and stated that well-fed individuals would acquire a larger size in a shorter time, which would reduce the chances of mortality due to predation. Clemmesen (1994) stated that when prey availability is not a limiting factor for fish larvae in terms of quality or quantity, larval growth rates will increase and a better nutritional condition will be obtained. Moreover, Diaz et al. (2016) analyzed the nutritional condition of anchovy larvae by means of the RNA/DNA index, with specimens collected in the same oceanographic ship as the anchovy larvae analyzed in this study, and found that anchovy larvae from Península Valdés had a better condition than the ones from Isla Escondida area. These authors proposed that larvae in better nutritional condition are expected to have advantages in food competition and predator evasion.

An important issue studied in fisheries research is the mechanisms of population control. However, assessing which factors determine larval abundance is complex since many factors act simultaneously. Although the developmental stage at which recruitment is determined is under discussion, larval success is very important in this concern (Bailey and Houde, 1989). In our study, frontal waters with their enrichment and development of planktonic organisms fulfilled what was expected by Bakun’s theory. This fact could imply an impact on the survival and recruitment of *E. anchoita* larvae (García et al., 2003). The consequences of the variations in larval abundance, growth and condition herein reported on *E. anchoita* recruitment are yet to be understood.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fishres.2018.02.019>.

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