PANAMJAS
Pan-American Journal of Aquatic Sciences

Horizontal and vertical distribution of larvae of *Engraulis anchoita* (Hubbs & Marini 1935) off Albardão, Southern Brazil

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Abstract. This study aimed to understand the role of physical and biological features on the vertical distribution of *Engraulis anchoita* larvae. Samples were obtained during winter 2005 and summer 2007 off Albardão (33°S) during day and night with a Multinet equipped with two 200 µm and three 330 µm mesh-nets. Vertical profiles of salinity, temperature and larval abundance were made to evaluate spatial distribution patterns. Temperature-Salinity-Icthyoplankton (TSI) diagrams were used to infer anchovy larvae distribution with respect to water mass composition. Diel variation in the vertical distribution was analyzed by estimating the depth of the center of mass (ZMC). Results showed seasonal differences in the number of anchovy larvae with much more larvae recorded during winter than in summer. In winter, anchovy larvae were located mainly in cold, low salinity and non-stratified waters from Río de la Plata Plume Water. Diel vertical movements indicated reverse and small scale migration through the water column. During summer, all larvae were recorded above twenty-three meters depth and in stations which presented warm water. There was also evidence that larvae performed small and reverse vertical movements. Our data suggest that the seasonal abundance and distribution of larvae of *E. anchoita* seem to be synergistically influenced by adult reproductive behavior and environmental factors.

Keywords: Anchovy, Subtropical Shelf Front, Río de la Plata, Ichthyoplankton, Southwest Atlantic Ocean.

Resumo. **Distribuição horizontal e vertical de larvas de *Engraulis anchoita* (Hubbs & Marini 1935) off Albardão, Sul de Brasil.** Este estudo buscou compreender a influência dos fatores físicos e biológicos sobre a distribuição vertical de larvas de *Engraulis anchoita*. As amostras foram obtidas durante o inverno de 2005 e verão de 2007 em Albardão (33°S) durante noite e dia com uma rede Multinet equipada com malhas de 200 µm e de 330 µm. Foram realizados perfis verticais de salinidade, temperatura e abundância de larvas para avaliar os padrões de distribuição espacial. Diagramas TSI foram usados para inferir a distribuição de larvas de anchoita com relação à composição das massas de água. Variação diária na distribuição vertical foi analisada pela posição média do centro de massa (ZMC). No inverno, as larvas de anchoita foram localizadas principalmente em águas frias, de baixa salinidade e não-estratificadas da Pluma do Rio da Prata. Movimentos verticais indicaram migração inversa e de pequena escala. Durante o verão, todas as larvas foram registradas acima de 23 metros de profundidade, principalmente em águas com temperaturas maiores que 20°C e que apresentaram estratificação vertical. O resultado mostrado pelo ZCM indicou que as larvas realizaram movimentos reversos e de pequena escala. Nossos dados sugerem que a abundância e distribuição sazonal das larvas de *E. anchoita* parecem estar sinergicamente influenciado pelo comportamento reprodutivo de adultos e fatores ambientais.

Palavras-chave: Anchoita, Frente Subtropical de Plataforma, Rio da Prata, Ictioplâncton, Oceano Atlântico Sudoeste.

Introduction

A front is a vertically inclined interface between water masses with different properties. Its physical structures are usually associated with spatial heterogeneities in the distribution of biological characteristics. Fronts also function as nurseries and therefore have significant influence on recruitment and distribution of pelagic fishes (Largier 1993, Sournia 1994). Despite the existence of abundant frontal systems in coastal waters surrounding South America, biological process are seldom studied in the context of physical oceanographic processes (Acha *et al.* 2004).

The Subtropical Shelf Front (STSF), as defined by Piola *et al.* (2000), is the outcome of the encounter of two water masses, the Subtropical Shelf Water (STSW) and the Subantartic Shelf Water (SASW). The STSF occurs to the north of the mouth of the Río de la Plata which discharges around 23,000 $m^3.s^{-1}$ of freshwater into the western South Atlantic shelf. Historical hydrographic data suggest that the capacity of the river plume penetration is strongly influenced by seasonal changes in wind stress and continental rainfall (Piola *et al.* 2005). The plume may reach beyond 27°S in winter and 32°S during summer (Piola *et al.* 2008a). This continental runoff discharge of freshwater, sediments, organic material and dissolved substances produces a significant impact on the near-shore marine ecosystem (Piola *et al.* 2008b).

The region off Albardão (between 33°S and 34°S) is located on the South Brazilian coast and is under influence of Río de la Plata Plume Waters (PPW) and STSF (Fig. 1) which contributes to space-time variability of the water column properties, and makes the region relevant to biological processes (Muelbert *et al.* 2008).

Due to these characteristics, off Albardão is recognized as an important nursery area where a wide range of fish species eggs and larvae can be found among them *Engraulis anchoita* (anchovy) is the most abundant and the only species common during both winter and summer (Lima & Castello 1995, Muelbert *el al.* 2008). This species plays a significant role in the ecosystem energy flow. *E. anchoita* is most commonly second order consumers and occasionally first order consumer (Schwingel & Castello 1994). Moreover, it is an important food source for many other groups such as cephalopods (Ivanovic & Brunetti 1994), seabirds (Frere *et al.* 1996), mammals (Naya 2002) and other fishes.

The coupling between environmental process and fish reproductive strategy is a key in understanding how fish larvae are distributed and how fish stocks persist in time. Most pelagic organisms, including fish larvae, are strongly influenced by hydrographic features and are therefore heterogeneously distributed along the water column (Santos *et al.* 2006). Many studies have reported high concentration of anchovy larvae associated with fronts and low salinity outflow from continental water discharge, indicating that these locations may be important spawning areas for anchovy species (e.g. Palomera 1992, Olivar & Sabatés 1997, Espinosa-Fuentes & Flores-Coto 2004, Lloret *et al.* 2004, Palomera *et al.* 2007, Sabatés *et al.* 2007).

The purpose of this study is to describe patterns of distribution of *Engraulis anchoita* larvae across the STSF under prevailing oceanographic conditions, and to compare current findings with previous results obtained for the same species along the Southwestern Atlantic, and with results reported for other *Engraulis* species around the world. The working hypothesis behind this study is that distribution of *E. anchoita* larvae is influenced by freshwater discharge from the Río de la Plata and by the STSF.

Methods

Physical and biological data were obtained during two interdisciplinary research cruises carried out in winter 2005 and summer 2007 off Albardão. The surveys were composed of three transects extending from the coast to the shelf-break and each one was comprised of six stations spaced 17 miles apart, that yielded 18 stations sampled during each cruise (Fig.1).

Larvae of *E. anchoita* were collected continuously during day and night with a 0.25 m^2 MultiNet, towed at a speed of 2 knots and equipped with two 200 µm (nets 2 and 4) and three 330 µm (nets 1, 3, and 5) mesh-nets. An internal and an external flow-meter were coupled to the net frame to control filtration efficiency and determine volume of water filtered. The volume filtered was determined by the internal flow-meter. The MultiNet was deployed with the first net opened and lowered to the maximum sampling depth as one oblique haul. Then, the MultiNet was hauled back performing a stratified sampling with four horizontal hauls at different depth intervals. Depth intervals varied between stations depending on the thermal and acoustic profiles at each sampling station.

The samples were preserved in 4% borax buffered formaldehyde. Anchovy larvae were sorted,

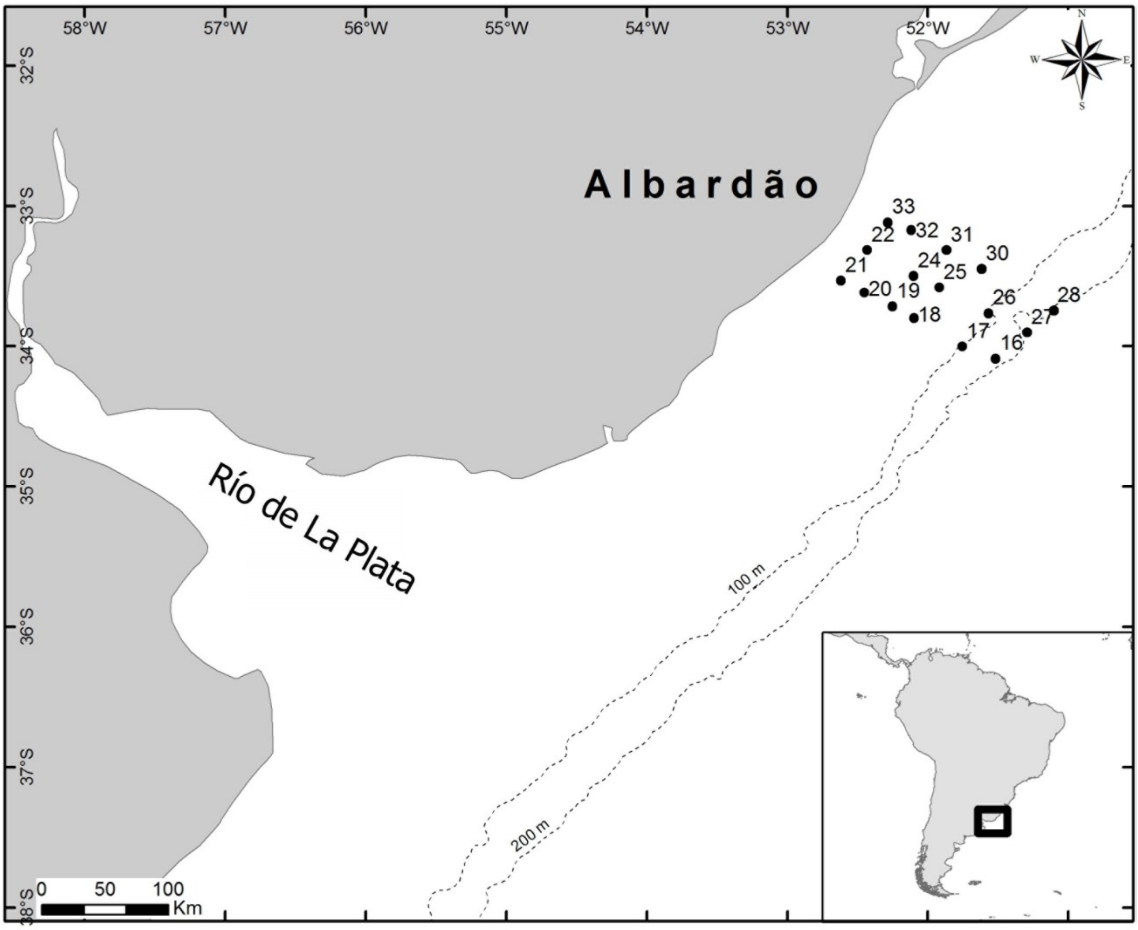

Figure 1. Distribution of stations sampled in three transects during winter 2005 and summer 2007 off Albardão, in Southern Brazil.

counted and measured; their abundance was standardized to 100 m³.

The developmental stages of the larvae were categorized based on Sabatini (2004) and Alheit *et al.* (1991) who determined that the size of first feeding occurs when larvae are around 4 mm, and flexion of larvae occurs between 8 – 12.9 mm SL. Three size categories were created: larvae less than 4 mm, larvae between 4 – 10 mm (pre- and in-flexion) and larvae larger than 10 mm (post-flexion), only the latter two categories were used in the center of mass analysis, since larvae less than 4 mm do not have swimming capacity.

In order to evaluate the effects of biological processes on anchovy distribution all development stages were related to prey and predator vertical distribution. Copepod biomass (prey) was measured as ash-free dry mass from a 10% subsample (for details see: Muxagata & William 2011). This method was chosen to avoid over-estimation of zooplankton biomass caused by contamination of inorganic materials such as phytoplankton-originated detritus and re-suspended. These problems are more severe in studies on coastal water susceptible to river runoff and sediment re- suspension (Nagao et al. 2001). The abundance of chaetognatha (predator) was also estimated from a 10% subsample, and individuals were manually counted and their abundance standardized to 1 m³. Coelenterates were not considered as potential predator since the material was not preserved adequately for these organisms.

Vertical profiles of temperature and salinity were obtained at each station with a CTD Seabird 19E. As a measure of stratification we used the potential energy relative to the mixed state proposed by (Simpson *et al*. 1978) and defined by:

$$\varphi = \frac{1}{h}\left(\rho - \acute{\rho}\right) gzdz \; with \; \acute{\rho} = \frac{1}{h}\int_{-h}^{0} \rho\left(z\right) dz$$

Where g is the acceleration of gravity (9.82 m.s^{-2}), ρ is the water density (kg.m^{-3}), h is the maximum depth of integration and z is the depth interval (m). The stratification parameter φ represents the amount of work per cubic meter (J.m^{-3}) needed to mix the water column, thus greater φ values represent stronger vertical stratification. A critical value of 40 Jm^{-3} was used to separate mixed and stratified waters (Martos & Sánchez 1997). We made the integration until 100 m depth. Results on stratification index values are presented only for stations corresponding to the middle transect.

Variation in depth distribution of larval *E. anchoita* was represented by the index of vertical displacement of the mean center of mass (ZCM) (as in Fortier & Leggett 1983, Stephenson & Power 1988):

$$ZCM = \sum_{i=1}^{x} p_i z_i$$

Where, p_i is the proportion of larvae occurring at depth *i,* and z_i is the average depth of the *i*th stratum; for example, a value of 7.5 m was used for anchovy larvae that were sampled in the stratum from 5 to 10. Similarly, a value of 35 was used for larvae located in the stratum from 30 to 40.

Finally, salinity, temperature and fish larvae abundance profiles, and TSI (Temperature, Salinity and Ichthyoplankton) diagrams were made with the Ocean Data View 3.4.1 program (Schlitzer 2008) in order to evaluate spatial distributional patterns based on oceanographic conditions. Data from horizontal tows were used to make vertical profiles while horizontal profiles also included data from vertical tows. The thermohaline intervals for each water mass were defined according to Möller *et al.* (2008). Based on this information we could infer the water mass in which the larvae were collected.

Results

A total of 139 anchovy larvae belonging to all development stages were collected during both cruises. The mean abundance of larvae was much higher during winter than during summer (*t*-test, $p < 0.001$) (Table 1). In both seasons larvae were present in all transects, although they were always more abundant in the southward transect (Fig. 2, 3 and 4). The size of anchovy larvae collected ranged from 2.0 to 32.0 mm SL.

Winter

Anchovy larvae were recorded mainly in coastal waters in less than 30 meters depth. In offshore and deeper stations, larvae were located only in layers above 22 meters depth. Only larvae in advanced development stage were found in offshore stations. Coastal stations did not present vertical stratification (φ < 40 $J.m^{-3}$), while waters further offshore were stratified. With the exception of the third station, where waters were weakly stratified, anchovy larvae were found only in well-mixed waters (Fig. 2 and 4). Stations closer to the coast were influenced by cold and low salinity waters from PPW and STSW (Fig. 5). Larvae in pre-flexion stage were present exclusively in PPW at salinity and temperature ranges of 28.58 to 33.90 and 12.03 to 16.03°C, respectively. Post-flexion larvae were also sampled in STSW, which is warmer and saltier, and at the interface between STSW and South Atlantic Central Water (SACW). These individuals were present in waters with temperature that varied from 12.41°C to 17.65°C and salinity that ranged from 28.56 to 35.29.

Results regarding diel vertical movements of anchovy (assessed by ZCM) showed that both larvae larger and smaller than 10 mm migrated throughout the water column. For small larvae, ZCM changed from 7.5 m during daytime to 11.3 m at night, large larvae exhibited the same trend but they migrated from 9.6 m during the day to 15.9 m at night (Table 2). This variation indicated a reverse and small scale vertical migration pattern, with the center of mass located closer to the surface during the day; however depth difference between day and night was relatively small. Larvae larger than 10 mm were recorded until 50 m deep, close to the thermocline, while those smaller did not reach layers deeper than 30 m, above the thermocline (Fig. 6).

Summer

During summer all larvae were recorded above twenty-three meters depth and were concentrated in the inner continental shelf. Larvae were registered in stations which presented vertical stratification (φ > 40 $J.m^{-3}$) (Fig. 3 and 4). Closer to the shore, PPW was the predominant water mass. Offshore, PPW was replaced by STSW, and SACW near the bottom. Anchovy larvae were mostly distributed in the STSW. Tropical Water (TW) was present towards the edge of the shelf, but no anchovy larvae were collected in this water mass (Fig. 5). Larvae in pre-flexion stage were present in water with salinity that varied from 33.47 to 36.72 and temperature that ranged from 16.11°C to 23.91°C while larvae in-flexion and post-flexion were sampled in water with salinity from 33 to 34.38 and temperature that ranged from 19.12°C to 23.75°C.

Table 1. Absolute abundance of *Engraulis anchoita* caught per station sampled and development stage.

Station	Nº Indivuduals		Pre-Flexion		In-Flexion		Post-Flexion		Nº of ind/100m³	
	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer	Winter	Summer
16	0	0	0	0	0	0	0	0	0.0	0.0
17	0	0	0	0	0	0	0	0	0.0	0.0
18	3	0	0	0	0	0	2	0	2.0	0.0
19	6	1	0	0	1	0	1	1	3.8	2.5
20	8	1	0	0	1	0	5	1	7.7	2.5
21	18	0	1	0	13	0	0	0	28.4	0.0
22	5	0	0	0	1	0	2	0	5.2	0.0
23	4	4	2	0	0	2	0	1	3.5	8.3
24	0	2	0	0	0	2	0	0	0.0	3.0
25	0	0	0	0	0	0	0	0	0.0	0.0
26	0	0	0	0	0	0	0	0	0.0	0.0
27	0	0	0	0	0	0	0	0	0.0	0.0
28	0	0	0	0	0	0	0	0	0.0	0.0
29	0	0	0	0	0	0	0	0	0.0	0.0
30	1	3	0	0	0	2	1	0	0.7	5.0
31	2	4	0	2	0	1	1	0	1.0	6.5
32	73	4	1	2	7	2	48	0	45.7	7.0
33	0	0	0	0	0	0	0	0	0.0	0.0

Small and large larvae performed small and reverse movements along the water column. ZCM values for small larvae changed from 17.2 m during the day to 23.2 m during nighttime. Larger larvae migrated from 16.3 to 22 m (Table 2). The thermocline was shallower than during wintertime, and both small and large larvae were positioned in and above it (Fig. 6).

Discussion

Results presented in this work suggest that anchovy larvae are adapted to a wide range of physical conditions since they were recorded in temperatures from 12.30°C, in PPW during winter, to 24.55°C, in STSW during summer, and in salinity ranging from 16.11 to 33.90. This supports previous studies that have also found anchovies to be tolerant of a wide range of temperatures (Ciechomski 1967, Brewer 1976, Matsuura & Kitahara 1995). This thermal tolerance enables larvae to exploit different habitats (Matsuura *et al.* 1992) and seasons.

Despite their wide thermal range our results also showed significant seasonal differences in the number of anchovy larvae which suggests temporal changes in spawning activity of the adult stock. These changes are likely results of the biology of the species and regional oceanographic variability. This theory is supported by the spatial and seasonal distribution of larvae. These differences should be linked to hydrographic conditions. Historical data show that the extension of PPW over the continental shelf undergoes large amplitude fluctuations, causing an impact on physical, chemical and consequently biological properties (Piola *et al.* 2008b) which are reflected on the local larval fish assemblage composition (Muelbert *et al.* 2008).

Oceanographic events occurring during the winter seem to produce an optimal environmental window for anchovy larvae, leading adults to spawn intensively across the region (Muelbert *et al.* 2008). As many other studies around the world (Olivar & Sabatés 1997, Lloret *et al.* 2004, Kim *et al.* 2005, Muelbert *et al.* 2008), high abundance of anchovy larvae have been reported in low salinity waters from river runoff where this taxa should find favorable conditions for larval development (Sabatés *et al.* 2007). In wintertime, PPW extends northward as a result of prevailing southwestern winds, producing a well-mixed and biological rich environment (Lima & Castello 1995, Muelbert *et al.* 2008). These conditions provide resources to support many small larvae that were abundant in this water

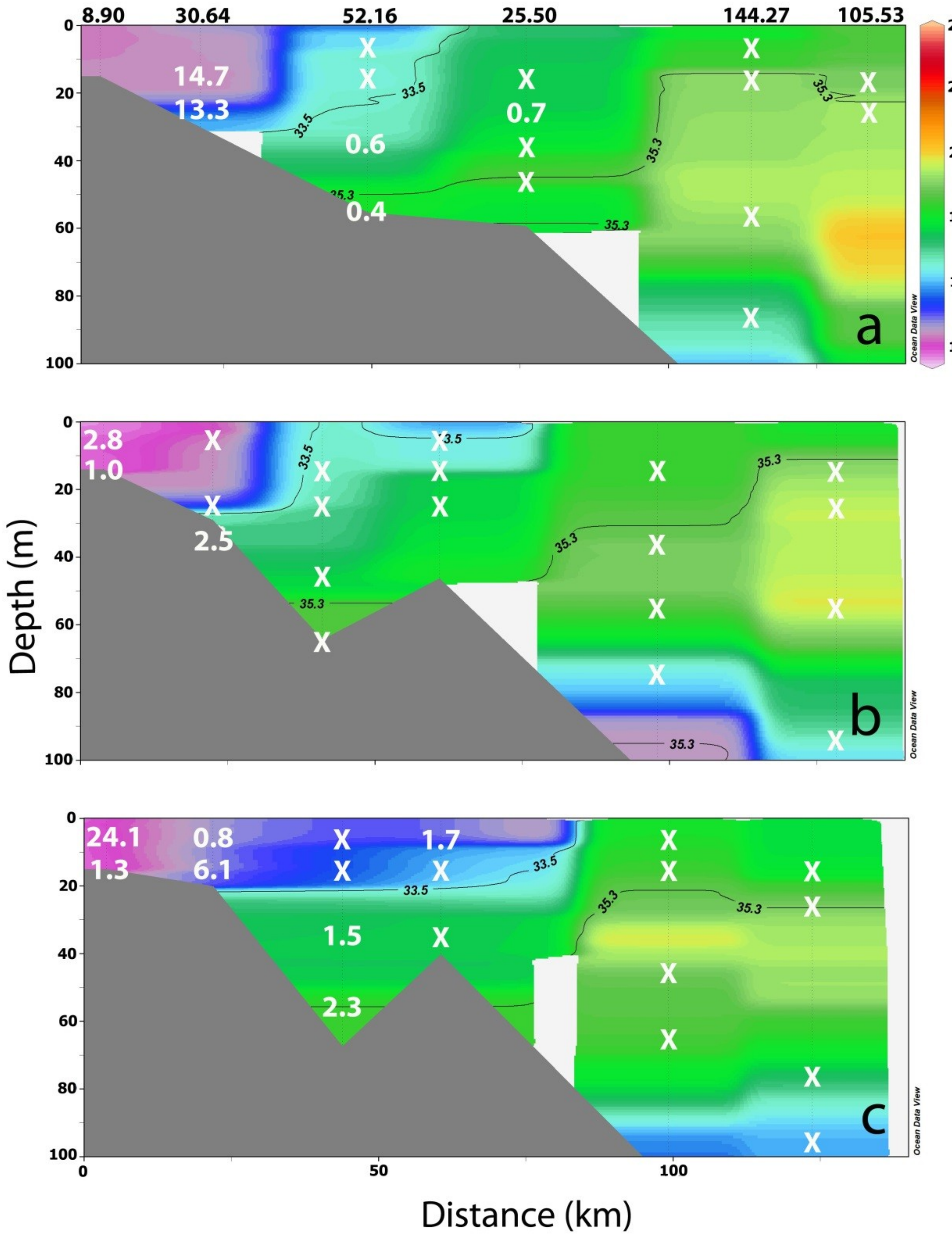

Figure 2. Vertical distribution patterns observed off Albardão of *E. anchoita* larvae (ind. 100 m^{-3}) in wintertime collected with a MultiNet system along three transects north (a), middle (b) and south (c). Temperature is represented by colors according to the vertical palette while salinity is represented by solid lines. Vertical stratification indexes are represented by values on the top of profiles. The X represents depths where samples were taken but did not have anchovy larvae.

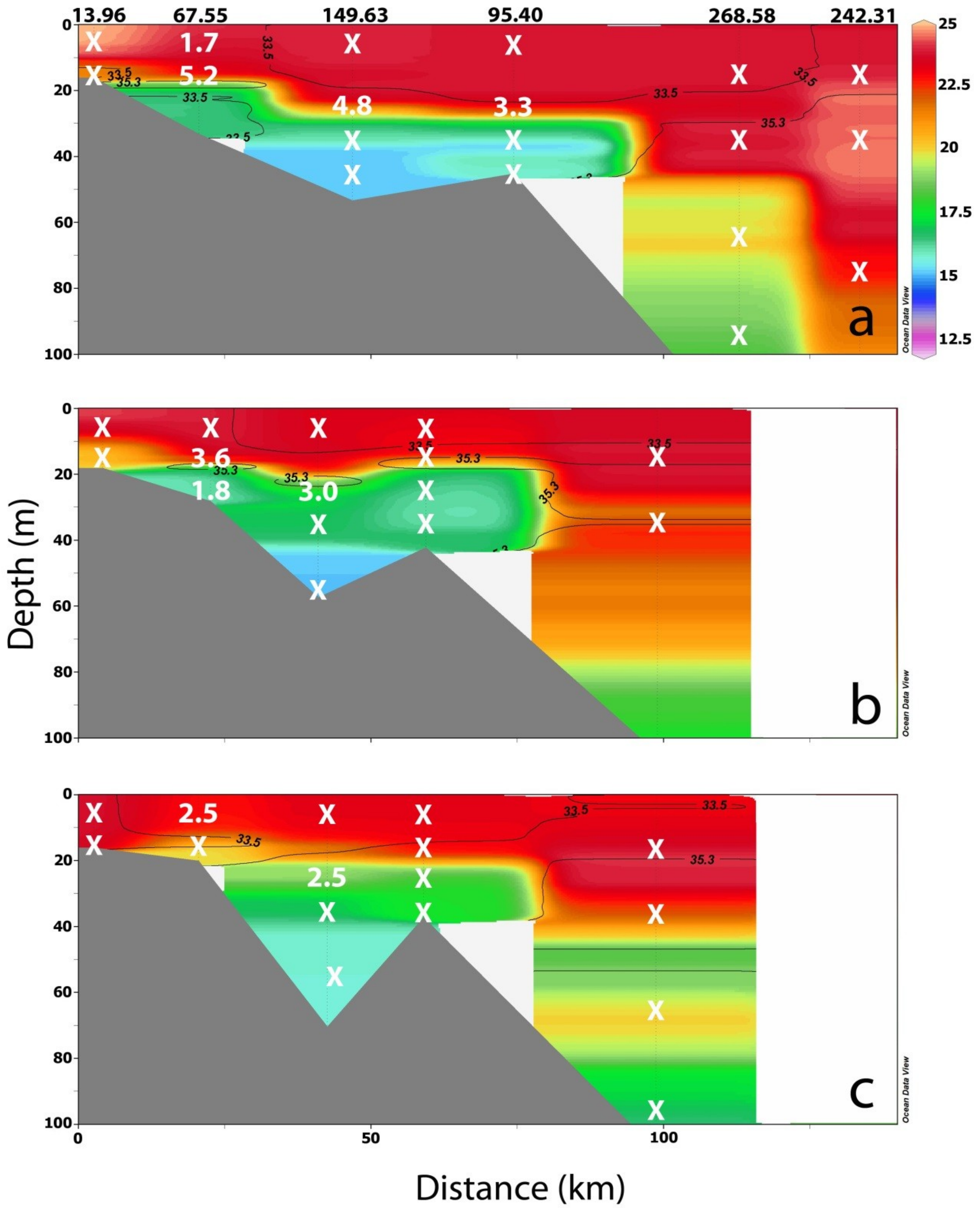

Figure 3. Vertical distribution patterns observed off Albardão of *E. anchoita* larvae (ind. 100 m^{-3}) in summertime collected with a MultiNet system along three transects north (a), middle (b) and south (c). Temperature is represented by colors according to the vertical palette while salinity is represented by solid lines. Vertical stratification indexes are represented by values on the top of profiles. The X represents depths where samples were taken but did not have anchovy larvae.

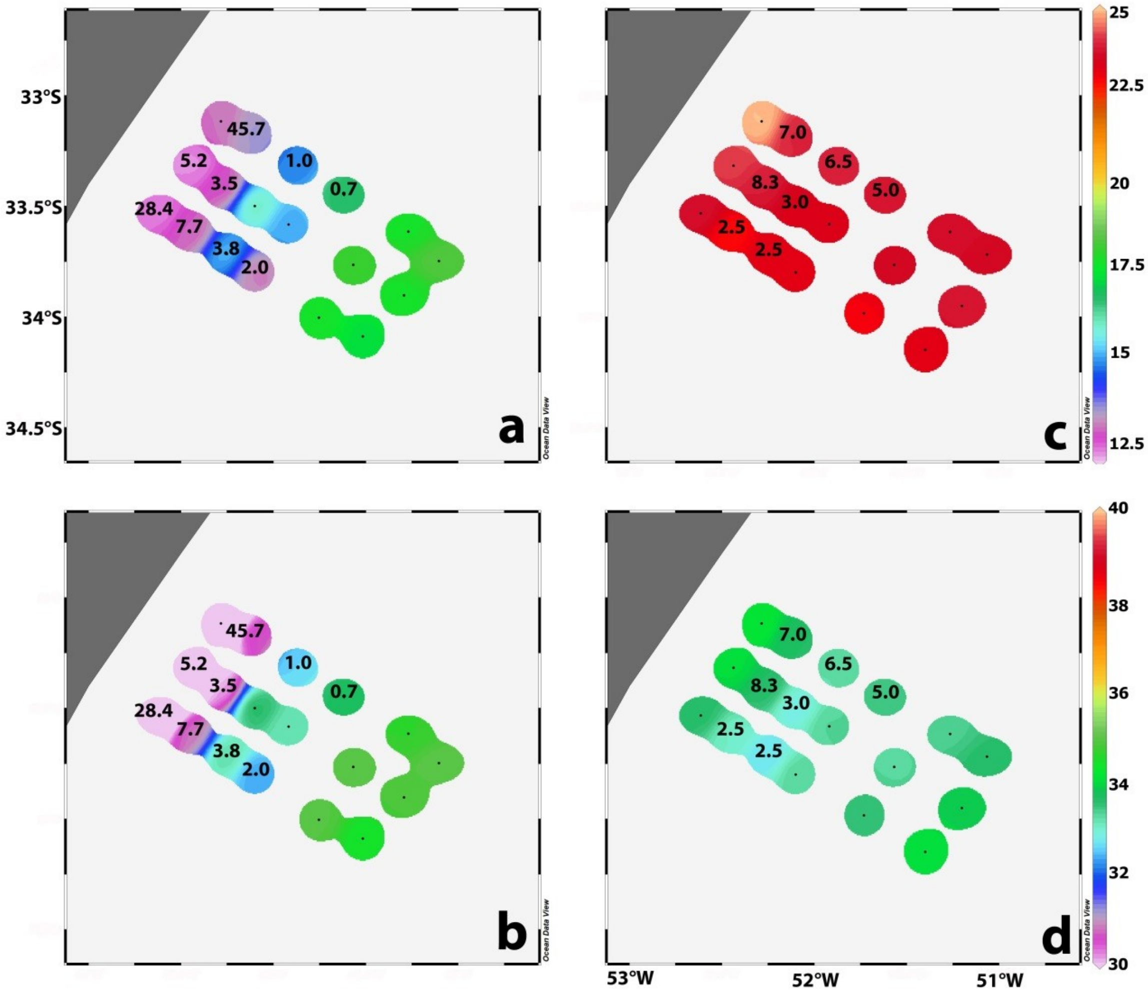

Figure 4. Horizontal distributional patterns of *E. anchoita* abundance (ind.100 m^{-3}) observed off Albardão during winter 2005 (a, b) and summer 2007 (c, d). Surface temperature (a,c) and salinity (b,d) are represented by colors according to the vertical palette.

mass. During summer the wind veers from the northeast, and the tongue of low salinity and temperature retracts southward (Campos *et al.* 2013). Although PPW was still present at Albardão both small and large larvae were present principally in STSW and SASW or in the vicinity of the transition between these two water masses.

The Subtropical Shelf Front is described as an important spawning area for pelagic fish species (Muelbert *et al,* 2008). This area presents different water masses that may vary along interannual time scales. However, the larvae of *E. anchoita* were found in wintertime, mainly only in two of them, STSW and PPW. Other water masses did not present larvae, i.e., SASW in winter and TW in summer, these water masses were located too deep and far away from the coast, respectively. In seasons and regions where cool waters reach the surface close to shore *E. anchoita* is significantly abundant in SACW (Matsuura *et al.* 1992, Matsuura & Kitahara 1995).

Usually, STSW and PPW are restricted to the neritic zones and shallow depths where anchovy spawn (Lima & Castello 1995) and where larvae remain until they become able to swim downward and cross the thermocline (Lloret *et al.* 2004). This relatively near-surface distribution observed for *E. anchoita* larvae seems typical of Clupeiforms (Stephenson & Power 1988, Matsuura *et al.* 1992, Matsuura & Kitahara 1995, Castro *et al.* 2000, Spinelli *et al.* 2013). At Albardão larval distribution pattern is coupled with nutrient and copepod distribution, as well as salinity and temperature gradients. Nutrient and copepod concentration decrease from onshore to offshore and above the thermocline (Muelbert *et al*. 2008) while salinity and temperature increase toward offshore.

Table 2. Mean center of mass (ZCM) of *Engraulis anchoita* in the water column during winter and summer. Rows represent fraction of larvae occurring at each depth interval.

	Winter				**Summer**			
Depth	Shorter than 10mm		Larger than 10mm		Shorter than 10mm		Larger than 10mm	
	Day	Night	Day	Night	Day	Night	Day	Night
0 - 5	0	0	0.37	0	0.15	0	0.25	0
5 - 10	1	0.72	0.29	0.12	0	0	0	0
10 - 20	0	0.13	0.2	0.78	0.44	0.18	0.31	0.3
20 - 30	0	0.13	0.14	0.06	0.41	0.82	0.44	0.7
30 - 40	0	0.02	0	0.02	0	0	0	0
40 - 50	0	0	0	0	0	0	0	0
50 - 60	0	0	0	0.02	0	0	0	0
60 - 70	0	0	0	0	0	0	0	0
70 - 80	0	0	0	0	0	0	0	0
80 - 90	0	0	0	0	0	0	0	0
90 - 100	0	0	0	0	0	0	0	0
ZCM	**7.5**	**11.3**	**9.6**	**15.9**	**17.23**	**23. 2**	**16.28**	**22**

Winter: Nday = 10 Stations (13 larvae) Nnight = 8 Stations (107 larvae)
Summer: Nday = 13 Stations (13 larvae) Nnight = 5 Stations (9 larvae)

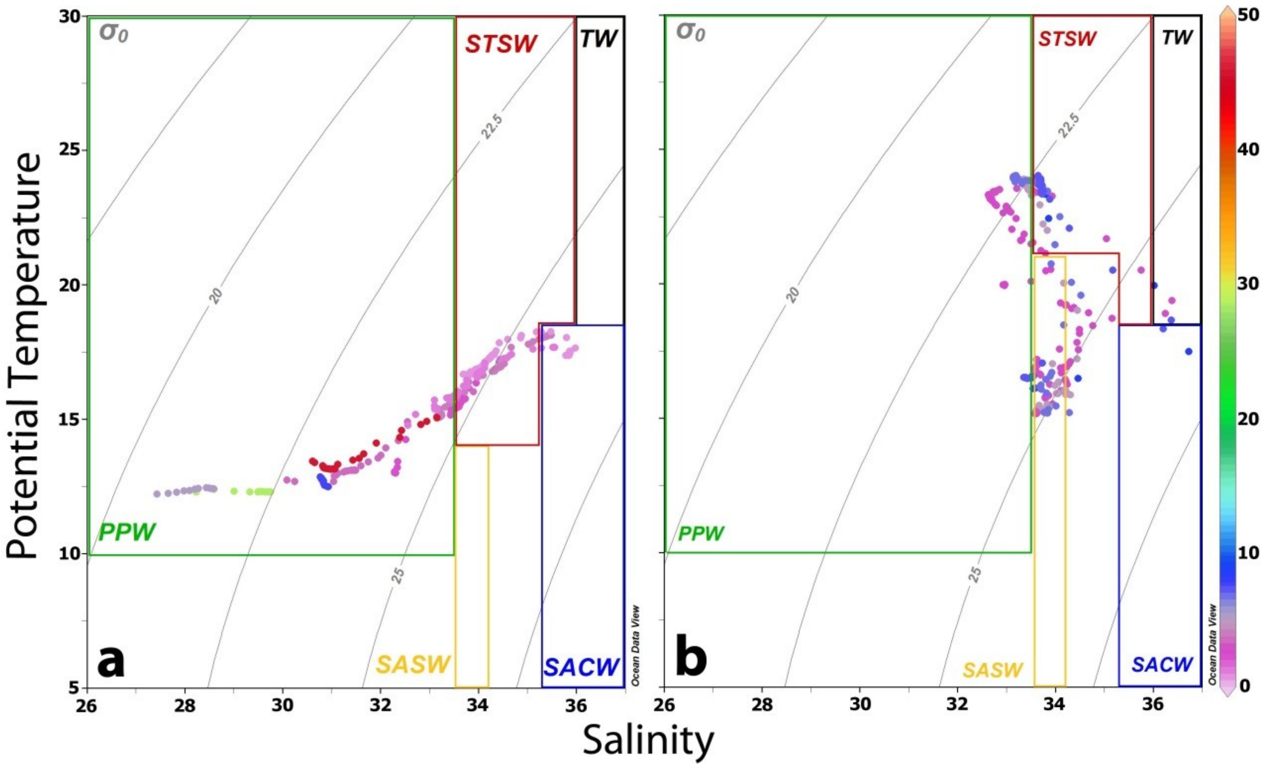

Figure 5. TSI diagrams with *E. anchoita* larvae abundance across different water masses during winter 2005 (a) and summer 2007 (b). Color bar represents *E. anchoita* abundance (ind.100m^{-3}). STSW – Subtropical Shelf Water, TW – Tropical Water, PPW – Río de La Plata Plume Water, SASW – Subantartic Shelf Water, SACW – South Atlantic Central Water.

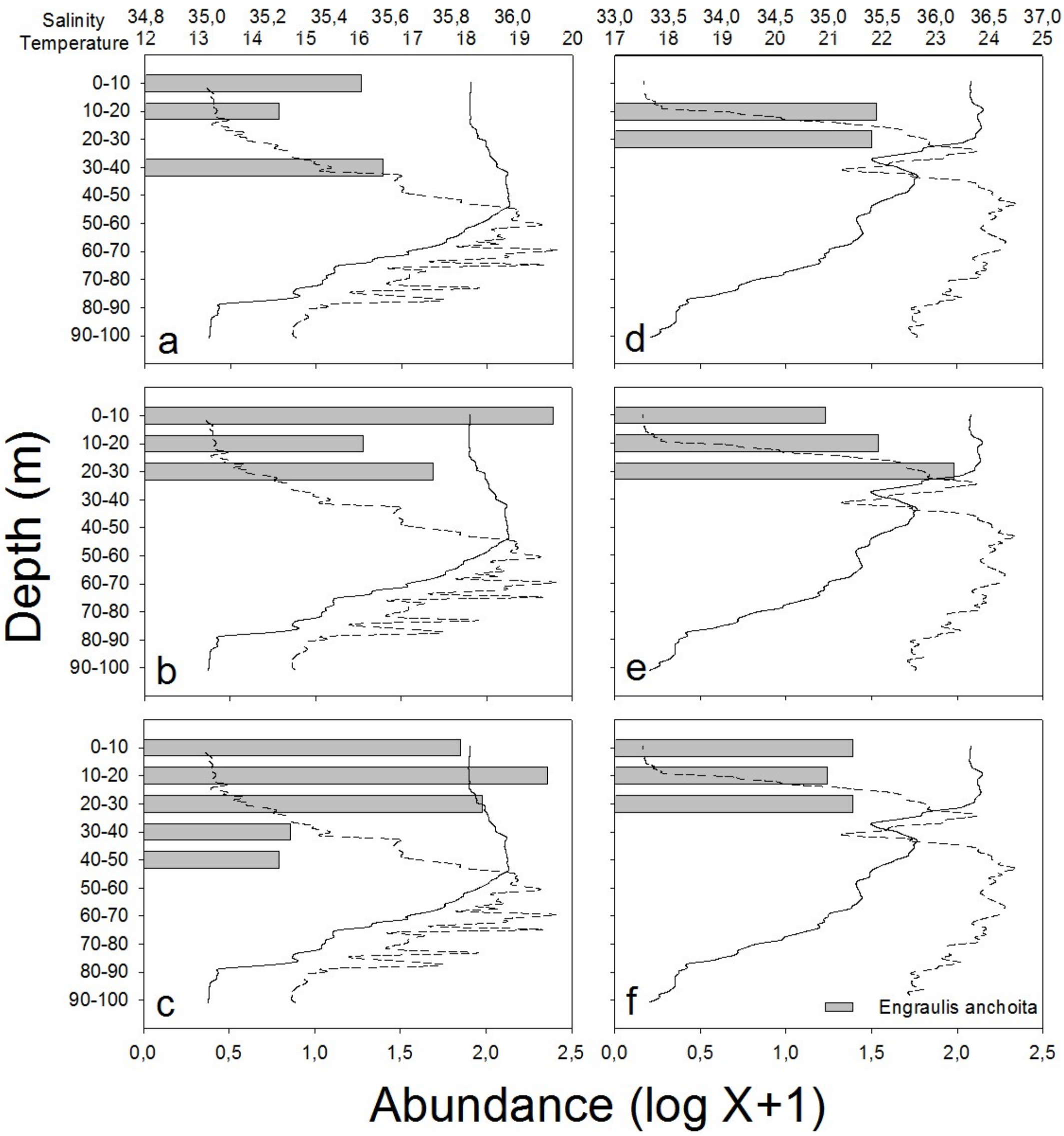

Figure 6. Bar graphics indicating anchovy larvae abundance (ind.100m^{-3}): shorter than 4mm (a, d), between 4-10mm (b, e) and larger than 10mm (c, f) in winter (a, b, c) and summer (d, e, f). Solid line represents temperature (°C) profile and dotted line represents salinity profile.

Water column stability is a key factor for anchovies spawning (Lasker 1975, 1978). Our vertical profiles and model of stratification and mixing indicate that in wintertime Río de la Plata runoff promotes vertical mixing across the coastal zone, this occurred close to the coast where the most larvae were recorded. The retention of larvae at non-stratified stations contradicts the hypothesis proposed by Lasker (1975) who states water column stability as an essential condition for successful recruitment. Our suggestion is that in some cases, i.e., in shallow areas less than 30 meters depth under influence of a river plume, the water column stability is not a significant factor for recruitment.

Our results did not reveal large diel vertical distances covered by anchovy larvae. Few meters should not be significant for hypotheses related to prey-predator interaction which support that reverse migration appears to be simply a response to finding optimum light levels for detection of suitable food (Hunter 1977, Tudela *et al*. 2002), however, sometimes a few meters can separate two water masses, thus small vertical movement may lead larvae from one water mass to another with different physical properties, thus this behavior should be considered important on larval fish recruitment. (Santos *et al.* 2006).

As proposed by Matsuura & Kitahara (1995) and revealed here, postflexion larvae may swim downward and participate in vertical migration along their life cycle. Migration of younger larvae was also found, but it was less pronounced than in the later larval stage. Amplitude of movement depends on the ontogenetic development as shown in Figure 6. The swim bladder formation in anchovy occurs at a total length of 7 mm and diel rhythms of swim-bladder inflation at 10 mm. Moreover at 11 mm length dorsal and anal fin rays are well developed and thus larger larvae are able to accomplish more extensive migrations (Ré 1986).

As well as other anchovies around the world that tend to utilize different oceanography events as spawning and nursery areas (Castro *et al.* 2000), larvae of *E. anchoita* are very well adapted to the environmental variability caused by local oceanographic events through the year. Furthermore, the variability in the spatial and temporal abundance and distribution seem to be synergistically influenced by adult reproductive behavior and environmental factors.

Acknowledgements
We would like to thank the Brazilian National Research Council (CNPq) for financial support and the Laboratório do Zooplâncton Marinho - FURG for providing a logistic support. We are grateful to Miguel Lavin of the CICESE (Mexico). We also thank Paul Kinas, Erik Muxagata, Jorge Castello, Marcelo Acha, Anne Benolkin and two anonymous reviewers for their helpful comments. JHM was supported by a CNPq grant (Proc. 310931/2012-8).

References

Acha, E.M., Mianzan, H.W., Guerrero, R.A., Favero, M. & Bava, J. 2004. Marine fronts at the continental shelves of austral South America Physical and ecological processes. **Journal of Marine Systems**, 44: 83 – 105.

Alheit, J., Ciechomski, J.D. de, Djurfeldt, L., Ebel, C., Ehrlich, M.D., Elgue, J.C., Mantero, G., Matsuura, Y.,Mianzan, H.W., Nellen, W., Oderbrecht, C., Ramirez, F.C., Sánchez, R.P., Shaffer, G. & Viñas, M.D. 1991. SARP Studies on Southwest Atlantic anchovy, *Engraulis anchoita*, off Argentina, Uruguay and Brasil. **ICES Biological Oceanography Committee**.

Brewer, G.D. 1976. Thermal tolerance and resistence of the northern anchovy *Engraulis mordax*. **Fishery Bulletin National Marine Fish Service U.S.**, 74: 1-8.

Campos, P.C., Möller-Jr, O.O., Piola, A.R. & Palma, E.D., 2013. Seasonal variability and coastal upwelling near Cape Santa Marta (Brazil). **Journal of Geophysical Research**, 118: 1 – 14.

Castro, L.R., Salinas, G.R. & Hernández, E.H., 2000. Environmental influences on winter spawning of the anchoveta *Engraulis ringens* off Central Chile. **Marine Ecology Progress Series**, 197: 247 – 258.

Ciechomski, J.D., 1967. Influence of some environmental factors upon the embryonic development of the Argentine anchovy *Engraulis anchoita*. **California Cooperative Oceanic Fisheries Investigation Reports**, 11: 67 - 71.

Espinosa-Fuentes, M.L. & Flores-Coto, C., 2004. Cross-shelf and vertical structure of ichthyoplankton assemblages in continental shelf waters of the Southern Gulf of Mexico. **Estuarine, Coastal and Shelf Science**, 59: 333 – 352.

Fortier, L. & Leggett, W.C., 1983. Vertical migration and transport of larval fish in a partially mixed estuary. **Canadian Journal of Fisheries and Aquatic Science**, 40: 1543 – 1555.

Frere, E., Gandini, P. & Lichtschein, V., 1996. Variacion latitudinal en la dieta del pinguino de magallanes (Spheniscus magallanicus) en la costa patagonica, Argentina. **Ornitologia Neotropical**, 7: 35 – 41.

Hunter, J.R., 1977. Behavior and survival of northern anchovy *Engraulis mordax* larvae. California Cooperative Oceanic **Fisheries Investigations**, 19: 138 – 146.

Ivanovic, M.L. & Brunetti, N.E., 1994. Food and feeding of *Illex argentinus*. **Antartic Science**, 6: 185 – 193.

Kim, J., Kang, Y., Oh, H., Suh, Y. & Hwang, J., 2005. Spatial distribution of early life stages of anchovy (*Engraulis japonicas*) and hairtail (*Trichiurus lepturus*) and their relationship with oceanographic features of the East China Sea during the 1997-1998 El Niño event. **Estuarine, Coastal and Shelf Science**, 63: 13 – 21.

Largier, J.L. 1993. Estuarine Fronts: How important are they? **Estuaries**, 16: 1 – 11.

Lasker, R., 1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. **Fisheries Bulletin**: 73, 453 – 462.

Lasker, R. 1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. **Réunion du Conseil international pour l´Exploration de la Mer**, 173: 212 – 230.

Lima, I.D. & Castello, J.P.C. 1995. Distribution and abundance of South-west Atlantic anchovy spawners (*Engraulis anchoita*) in relation to oceanographic processes in the southern Brazilian shelf. **Fisheries Oceanography**, 4(1): 1 – 16.

Lloret, J., Palomera, I., Salat, J. & Sole, I., 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). **Fisheries Oceanography**, 13(2): 102 – 110.

Martos, P. & Sánchez, R.P. 1997. Caracterización oceanográfica de regiones frontales en la plataforma Patagónica en relación con áreas de desove y cría de la anchoita (*Engraulis anchoita*). **Coloquio Argentino de Oceanografía, IAPSO-IADO (Conicet)**.

Matsuura, Y., Spach, H.L. & Katsuragawa, M. 1992. Comparsion of spawning patterns of the Brazilian sardine (*Sardinella brasiliensis*) and anchoita (*Engraulis anchoita*) in Ubatuba region, southern Brazil during 1985 through 1988. **Boletim Instituto Oceanografia USP**, 40: 101 – 115.

Matsuura, Y. & Kitahara, E.M. 1995. Horizontal and vertical distribution of anchovy *Engraulis anchoita* eggs and larvae off Cape Santa Marta Grande in southern Brazil. **Archive of Fishery and Marine Research**, 42: 239 – 250.

Möller-Jr, O.O., Piola, A.R., Freitas, A.N., and Campos, E.J.D., 2008. The effects of river discharge and seasonal winds on the shelf off southeastern South America. **Continental Shelf Research**, 28: 1607 – 1624.

Muelbert, J.H., Acha, M., Mianzan, H., Guerrero, R., Reta, R., Braga, E.S., Garcia, V.M.T., Berasategui, A., Gomez-Erache, M., and Ramírez, F., 2008. Biological, physical and chemical properties at the Subtropical Shelf Front Zone in the SW Atlantic Continental Shelf. **Continental Shelf Research**, 28: 1662 – 1673.

Muxagata, E. & Williams, J.A. 2011. Larval body size-mass relationship of arnacles common to the English channel coast of the UK. **Journal of the Marine Biological Association of the United Kingdom,** 91(1): 181 – 189.

Nagao, N., Toda, T., Takahashi, K., Hamasaki, K., Kikuchi, T. & Taguchi, S. 2001. High ash content in net-plankton samples from shallow coastal waters: Possible source of error in dry weight measurement of zooplankton biomass. **Journal of Oceanography,** 55: 105 – 107.

Naya, D.E., 2002. Diet of south american fur seals (Arctocephalus australis) in isla de Lobos, Uruguay. **Marine Mammal Science**, 18(3): 734 – 745.

Olivar, M.P. & Sabatés, A. 1997. Vertical distribution of fish larvae in the north-west Mediterranean Sea in spring. **Marine Biology**, 129: 289 – 300.

Palomera, I. 1992. Spawing of anchovy *Engraulis encrasicolus*, in the North-Western Mediterranean relative to hydrographic features in the region. **Marine Ecology Progress Series**, 79: 215 – 223.

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A. & Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. **Progress in Oceanography**, 74: 377 – 396.

Piola, A.R., Campos, E.J.D., Möller-Jr, O.O., Charo, M. & Martinez, C. 2000. Subtropical Shelf Front. **Journal of Geophysical Research**, 105: 6565 – 6578.

Piola, A.R., Matano, R.P., Palma, E.D., Möller-Jr, O.O. & Campos, E.J.D. 2005. The influence of the Plata River discharge on the western South Atlantic shelf. **Geophysical Research Letters**, 32: L01603.

Piola, A.R., Möller-Jr, O.O., Guerrero, R.A. & Campos, E.J.D. 2008a. Variability of the subtropical shelf front off eastern South America: Winter 2003 and summer 2004. **Continental Shelf Research**, 28: 1639 – 1648.

Piola, A.P., Romero, S.I. & Zajaczkovski, U. 2008b. Space-time variability of the La Plata plume inferred from ocean color. **Continental Shelf Research**, 28: 1556 – 1567.

Ré, P. 1986. Sobre a identificação dos primeiros estados larvares planctónicos de *Sardina pilchardus* (Walbaum, 1792) e de *Engraulis encrasicolus* (Linnaeus, 1758). Ciência Biológica. **Ecology Systematics**, 6: 135 - 140.

Sabatés, A., Olivar, M.P., Salat, J., Palomera, I. & Alemany, F. 2007. Physical and biological process controlling the distribution of fish larvae in the NW Mediterranean. **Progress in Oceanography**, 74: 355 – 376.

Sabatini, M.E. 2004. Características ambientales, reproducción y alimentación de la merluza (Merluccius hubbsi) y la anchoita (Engraulis anchoita) em su hábitat reproductivo patagónico. Síntesis y perspectivas. **Revista Invest Desarrolo Pesquero**,16: 5 – 25.

Santos, A.M.P., Ré, P., Santos, A. & Péliz, A. 2006. Vertical distribution of the European sardine (*Sardina pilchardus*) larvae and its implications for their survival. **Journal of Plankton Research**, 28: 523 – 532.

Schlitzer, R. 2008. **Ocean Data View,** accessible at http://odv.awi.de (Accessed 25/11/2012)

Schwingel, P.R. & Castello, J.P. 1994. La Alimentacion de Anchoita (Engraulis Anchoita) En El Sur de Brasil. **Frente Marítimo**, 15: 67 – 86.

Simpson, J.H., Allen, C.M. & Morris, N.C.G. 1978. Fronts on the continental shelf. **Journal of Geophysical Research**, 83: 4607 – 4614.

Simpson, J.H., & Hunter, J.R. 1974. Fronts in the Irish Sea. **Nature**, 250: 404 – 406.

Sournia, A. 1994. Pelagic biogeography and fronts. **Progress in Oceanography**, 34: 109 – 120.

Spinelli, M.L., Guerrero, R., Pajaro, M. & Capitanio, F.L. 2013. Distribution of *Oikopleura dioica* (Tunicata, Appendicularia) associated with a coastal frontal system (39°- 41°S) of the SW Atlantic Ocean in the spawning area of *Engraulis anchoita* anchovy. **Brazilian Journal of Oceanography,** 61(2): 141 - 148.

Stenevik, E.K., Sundby, S. & Cloete, R. 2007. Diel vertical migration of anchovy *Engraulis encrasicolus* larvae in the northern Benguela. **African Journal of Marine Science**, 2007: 127 – 136.

Stephenson, R.L. & Power, M.J. 1988. Semidiel vertical movements in the Atlantic herring *Clupea harengus* larvae: a mechanism for larval retention? **Marine Ecology Progress Series**, 50: 3 – 11.

Tudela, S., Palomera, I. & Quílez, G. 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. **Journal of Marine Biological Association of United Kingdom**, 82: 349 – 350.

Received May 2014
Accepted October 2014
Published online November 2014