

Modeling long-term fluctuations in the distribution and abundance of *Engraulis anchoita* eggs and larvae in the southeastern Brazilian bight

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ABSTRACT: Most data sets of ichthyoplankton contain a high frequency of zeros, and, not considering the possible inflation of zero counts, as in most studies, may result in incorrect model predictions. Thus, we modeled abundance of *Engraulis anchoita* eggs and larvae sampled during 18 oceanographic cruises conducted between 1974 and 2010 using zero-inflated (ZI) models. ZI models are mixture models with 2 components: (1) containing false zeros (due to design, survey or observer errors) modeled using a binomial generalized linear model (GLM); (2) containing abundance data that may produce zeros (true zeros), and modeled with a negative binomial GLM (ZINB). Although ZINB has been used in other areas of research, we are not aware of its previous use for ichthyoplankton. Common to larvae and eggs, the probability of false zeros was lowest in the southern area of the southeastern Brazilian Bight and higher at deeper station depths. The probability of false zeros was higher in 0.505 mm mesh-size samples than in 0.333 mm mesh only for eggs. Egg and larval abundance was negatively related to temperature in the count portion of the model; only larval abundance was negatively related to salinity. Egg abundance was higher in years sampled with 0.333 mm mesh under conditions of moderate/strong El Niño. The high inter-annual variability in the abundance and distribution of eggs emphasizes the importance of long-term studies to better understand patterns of fluctuations in the occurrence of ichthyoplankton that are related to environmental conditions.

KEY WORDS: Zero-inflated models · Engraulidae · Ichthyoplankton · Brazil

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INTRODUCTION

The small pelagic fish *Engraulis anchoita* Hubbs & Marini, 1935 (Clupeiformes: Engraulidae) exhibits a wide distribution in the western South Atlantic, from Gulf San Jorge (Argentina, 48° S) to Cape São Tomé (Brazil, 20° S) (Bakun & Parrish 1991). Within this wide distribution, 3 stocks with biological differences are identified: the *patagonic* (48–41° S, Argentina), the *bonaerense* (41–28° S, northern Argentina, Uruguay and southern Brazil) and the southeastern Brazilian Bight (SBB) stocks (28–20° S, Brazil) (Car-

valho & Castello 2013). All 3 stocks are ecologically important, transferring energy and nutrients from the bottom of the food chain to higher predators, such as other fish, marine mammals and seabirds (Frederiksen et al. 2006, Castello 2007). Regarding the fisheries, *E. anchoita* is an important resource in Argentina and Uruguay where the catch was about 21 164 t in 2011 (FAO 2013). In southern Brazil, the exploitation of the *bonaerense* stock has only recently begun, and stocks in the SBB are in almost pristine condition, but could be exploited in the near future (Madureira et al. 2009, Carvalho & Castello 2013).

Probably due to the fisheries differences between stocks, most studies have focused on *E. anchoita* from Argentina and Uruguay, with fewer studies from southern Brazil, and even fewer from the SBB. The SBB is oceanographically different from the areas where the *bonaerense* and the *patagonic* stocks occur. Some coastal areas in the SBB are under the influence of waters outflowing from large embayments such as Paranaguá Bay (around 25.5° S) and the Cananéia-Iguape Coastal System (around 25° S), but with no major freshwater input such as the discharges from the Plata River (Plata Plume Water) located between Argentina and Uruguay and the Patos Lagoon, located in southern Brazil (Piola et al. 2005). *E. anchoita* eggs and larvae are associated with freshwater discharges in southern Brazil, Argentina and Uruguay (Bakun & Parrish 1991, Matsuura & Kitahara 1995, Macedo-Soares et al. 2014), where baroclinic circulation caused by the Plata River and by the Patos Lagoon runoff is a mechanism for *E. anchoita* larval retention (Vaz et al. 2007).

Another difference between the areas of *E. anchoita* occurrence is that in the SBB, nutrient enrichment of the euphotic zone is mainly dependent on mesoscale physical processes that are regulated by the seasonal pattern of the wind and the flow dynamics of the Brazil Current (BC): during the late spring and summer, northeast winds cause Ekman transport of the surface waters offshore, causing onshore bottom intrusions of South Atlantic Central Water (SACW) (Castro & Miranda 1998, Campos et al. 2000). Three major coastal upwelling centers are identified in the SBB: Cape São Tomé (22° S), Cape Frio (23° S) and Cape Santa Marta Grande (28° S), with intrusion events at Cape Frio usually being the most intense (Ciotti et al. 2014). This upwelling brings new nutrients shoreward, increasing their concentrations in the lower euphotic zone and leading to an increase in net phytoplankton production (Gaeta & Brandini 2006, Lopes et al. 2006). The subsequent increase in zooplankton biomass (Lopes et al. 2006) influences ichthyoplankton survival and distribution (Katsuragawa & Matsuura 1992, Matsuura 1996, Katsuragawa et al. 2006).

In southeastern and southern Brazil, ichthyoplankton has been studied since the 1960s. However, after the 1980s a change in the research focus occurred, from studies mostly related to the identification, description of developmental stages, assessment of fish stocks and spawning biomass, and distribution and abundance of eggs and larvae in a certain area, to studies with efforts to understand the control exerted by environmental factors on the early life history of

fish (Katsuragawa et al. 2006). Most of these studies examined environmental influences on ichthyoplankton over short/medium temporal scales, especially seasonal ones (e.g. Garbini et al. 2014, Katsuragawa et al. 2014, Porcaro et al. 2014). At present, studies are seeking to understand the influence of large-scale environmental factors, such as El Niño/La Niña, on fish larvae and eggs worldwide (e.g. Flores-Coto et al. 2008, Funes-Rodríguez et al. 2011, Busby et al. 2014, Mujica et al. 2016). Along the Oregon coast (USA), for example, large-scale climate variations, such as the Pacific Decadal Oscillation and El Niño, explained more variation in the concentration and diversity of fish larvae than small-scale factors such as upwelling and Ekman transport (Auth et al. 2011)

Despite the importance of studies analyzing long-temporal-scale influences on fish, in the SBB no study has related long-term environmental factors to the distribution and abundance of the ichthyoplankton. Thus, the main objective of the present study was to evaluate long-term fluctuations in the distribution and abundance of *E. anchoita* eggs and larvae in the SBB from 1974 to 2010, and relate those fluctuations to oceanographic factors. The zero-inflated model, a new modeling approach, was used and is discussed.

MATERIALS AND METHODS

Data collection and preparation

All samples used in the present study were collected in historical oceanographic surveys and stored in the Biological Collection 'Prof. E. F. Nonato' (ColBIO) of the Oceanographic Institute, University of São Paulo. The ColBIO was inaugurated in 2012 with the objective of promoting the permanent maintenance of biological samples collected during various cruises conducted along the Brazilian and Antarctic coasts in the last 50 yr, making all samples accessible and available to the scientific community.

Oceanographic cruises were selected from the austral late spring and beginning of summer from 1974 to 2010, with the exception of 2 years (1982, 2001) when sampling occurred in March and May (Table 1). Late spring and beginning of summer corresponds to the *Engraulis anchoita* peak spawning period (Matsuura et al. 1992, Favero et al. 2017a). Fig. 1 shows the SBB (roughly between 22 and 29° S) and the area covered by each cruise per decade. Areas were defined based on *E. anchoita* stock identification (Carvalho & Castello 2013) (Area 3) and on

Table 1. Project name and oceanographic cruise number, month and year of the cruise, number of plankton samples obtained (N), bongo net mesh size used in the present study, and El Niño and La Niña intensity of each year (based on information obtained at: <http://enos.cptec.inpe.br>). Surveys that lack El Niño/La Niña condition are neutral years

Project	Month	Year	N	Mesh size (mm)	El Niño	La Niña
ICTIO-1	Nov/Dec	1974	139	0.505		Strong
FINEP-1	Nov/Dec	1975	140	0.505		Strong
FINEP-5	Dec	1976	140	0.505	Weak	
FINEP-7	Jan	1978	134	0.505	Weak	
FINEP-10	Jan/Feb	1979	83	0.505		
FINEP-11	Jan	1980	42	0.505	Weak	
FINEP-12	Jan	1981	43	0.505		
FINEP-14	Mar	1982	32	0.505		
EPM-Sardinha	Jan	1988	78	0.333	Moderate	
V. Hensen/JOPS	Dec	1990	89	0.333	Strong	
Sardinha 1	Dec	1991	110	0.333	Strong	
Sardinha 2	Jan	1993	108	0.333	Strong	
PADCT-1	Nov/Dec	1997	47	0.333		
PADCT-2	May	2001	46	0.333		
DEPROAS-3	Jan	2002	72	0.333		
ECOSAR-4	Jan/Feb	2008	46	0.505		Strong
ECOSAR-5	Nov	2008	60	0.505		
ECOSAR-7	Mar	2010	55	0.505	Weak	

the oceanographic conditions described by Miranda & Katsuragawa (1991) and Mahiques et al. (2004) (Areas 1 and 2).

Plankton samples were collected, following Smith & Richardson (1977), with a bongo net with a 0.61 m diameter mouth opening, equipped with paired cylindrical-conical 0.333 mm and/or 0.505 mm mesh-size nets towed obliquely from the surface to the maximum depth possible, not exceeding 200 m. A flowmeter was attached at the center of each mouth opening to measure the filtered water volume. Samples from only 1 cylindrical-conical net were analyzed, from which samples were preserved in 4% buffered formalin/seawater solutions (Table 1).

Temperature and salinity data were obtained from Nansen bottles and reversing thermometers until 1988. After this date, a conductivity-temperature-depth profiler (CTD) was used. Table 1 presents further details about each oceanographic cruise.

Under a stereomicroscope with a digital camera attached, Engraulidae eggs were sorted based on their ellipsoid shape, segmented yolk and, usually, absence of oil droplets (Ciechomski 1965, Phonlor 1984a), and then imaged. Major and minor axes of the photographed eggs were measured using the program ImageJ (IJ 1.46r). All Engraulidae eggs were measured, except when the number of individuals for a given oceanographic cruise exceeded 100. In these instances, about 100 eggs were randomly selected for measurement. *E. anchoita* eggs were

identified by discriminant analysis as described by Favero et al. (2015a).

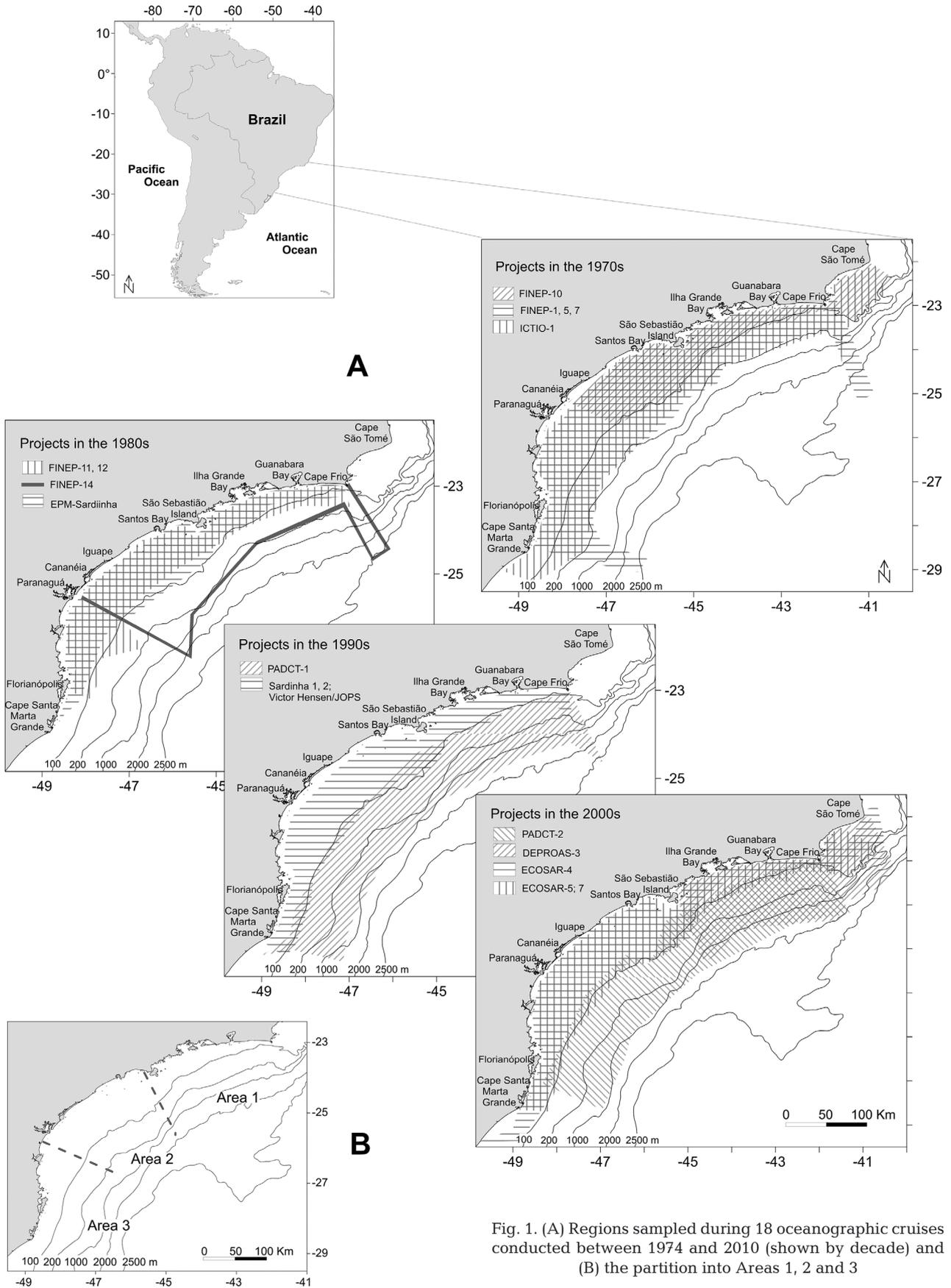
Fish larvae available at ColBIO were previously sorted as Engraulidae. *E. anchoita* larvae were identified following Ciechomski (1965), Phonlor (1984b) and Bonecker et al. (2014). The classification of larvae according to their developmental stage was based on the degree of flexion of the terminal section of the notochord during caudal fin development (Richards 2006).

Data analysis

Abundance data and frequency of occurrence

Egg and larval abundance were calculated as $N = xdV^{-1}$ (Tanaka, 1973), where N is the egg/larval abundance (number of eggs or larvae m^{-2} —per unit area water column—at each sampling station), x is the number of eggs/larvae sampled, d is the maximum depth sampled in meters, and V is the volume of water filtered in cubic meters. The mean abundance of each cruise was calculated for all the sampling stations.

The calculation of the frequency of occurrence (FO) of eggs/larvae was based on Guille (1970): $FO = (pi/p) \times 100$, where pi is the number of stations where eggs or larvae were present, and p is the total number of stations.



Modeling *E. anchoita* egg and larval abundance

For the modeling, we standardized the data using only oceanographic stations shallower than 200 m depth, from Cape Frio to Cape Santa Marta Grande, and excluding the years when the entire SBB was not sampled (1979, 2002), when the only sampled stations were further away from the coast (1982, 1997, 2001), and when stations were sampled during different months than the other years (beginning of November 2008 and March 2010).

Many null samples were obtained, indicating that *E. anchoita* egg- and larvae-count data might be zero-inflated (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m587p159_supp.pdf), which may cause overdispersion and bias in the variance estimates and in the inferences (Welsh et al. 1996, Zuur et al. 2009). Thus, we used zero-inflated (ZI) models to deal with the excessive zeros (Zuur et al. 2009, Otero et al. 2016). ZI models are mixture models with 2 components: the first contains false zeros and the second contains the count data that may produce zeros (true zeros) and values greater than zeros. False zeros were modeled using a binomial generalized linear model (GLM), and the count data were modeled with a Poisson (ZIP) or a negative binomial GLM (ZINB) (Martin et al. 2005, Zuur et al. 2009).

Before model fitting, we estimated successive variance inflation factors (VIF) and dropped collinear covariates one at a time until all VIF values were around 3, comparing all covariates to exclude those that presented collinearity (Tables S1 & S2 in the Supplement) (Zuur et al. 2010).

From previous knowledge, we hypothesized that the false zeros were caused by the mesh size used, the area sampled, the distance from the coast and the local depth of each oceanographic station. The count process was then modeled as a function of surface temperature, surface salinity, plankton abundance, distance from the coast, local depth, latitude, areas and years sampled. Following Otero et al. (2016), we used the volume of water filtered (in m³ and ln-transformed) as an offset in the count part of the ZI models. Model selection was performed excluding non-significant covariates in both parts of the model and models with and without the non-significant covariate were compared using Akaike's information criterion (AIC); the model with the lowest AIC value was considered the 'best' model. We also contrasted the optimal ZI models using Poisson and negative binomial distributions. In the end, we used the residuals of the optimal models for validation.

The data treatment and analyses were performed using R (R Core Team 2015), and the 'MASS 7.3-26' (Venables & Ripley 2002) and 'pscl 1.04.4' (Zeileis et al. 2008) packages.

RESULTS

Environmental data

Surface temperature obtained during the sampling period of each year varied from 14.9 to 29.1°C (mean \pm SD, 24.6 \pm 1.9°C); at 10 m depth, the temperature range was from 12.7 to 28.8°C (23.6 \pm 2.5°C). In most of the years sampled, it is possible to observe a colder water (less than 20°C) patch in the Cape Frio area (23° S), probably representing the SACW intrusion. In some years, the SACW intrusion can also be observed in the area around Cape São Tomé (22° S) (Fig. 2, and see Fig. S2 in the Supplement)

Surface salinity varied from 28.1 to 38.5 (mean \pm SD, 35.4 \pm 1.1); at 10 m depth, the range was from 32.7 to 38.5 (35.6 \pm 0.9). Lower salinity values are observed closer to the coast, especially off Cananéia-Iguape Coastal System (around 25° S) (Fig. 3 and Fig. S3).

Engraulis anchoita data

A total of 102 274 Engraulidae eggs were sampled. *E. anchoita* represented 83.1% of all engraulid eggs sampled (n = 85 024). Of 1464 sampling stations, Engraulidae eggs occurred at 29.0% and *E. anchoita* eggs at 24.7% of stations.

E. anchoita larvae totaled 64 403 individuals. Pre-flexion larvae were the most abundant (n = 39 962), followed by flexion (n = 12 551) and postflexion (n = 11 406). No yolk-sac larvae were obtained, and 484 larvae could not be classified by stage of development because they were damaged. Engraulidae larvae occurred at 74.9% of all sampling stations, with *E. anchoita* comprising 69.6% of the engraulid larvae.

Years that had low *E. anchoita* egg abundance were those sampled in months outside of the main sampling period, such as November 2008, at stations further away from the coast, such as November/December 1997, or for a combination of reasons (outside of the main sampling period and far away from the coast), as in March 1982 and May 2001 (Table 2, Fig. 4). FO was higher for larvae than for eggs (Table 2). Mean abundance varied considerably, and

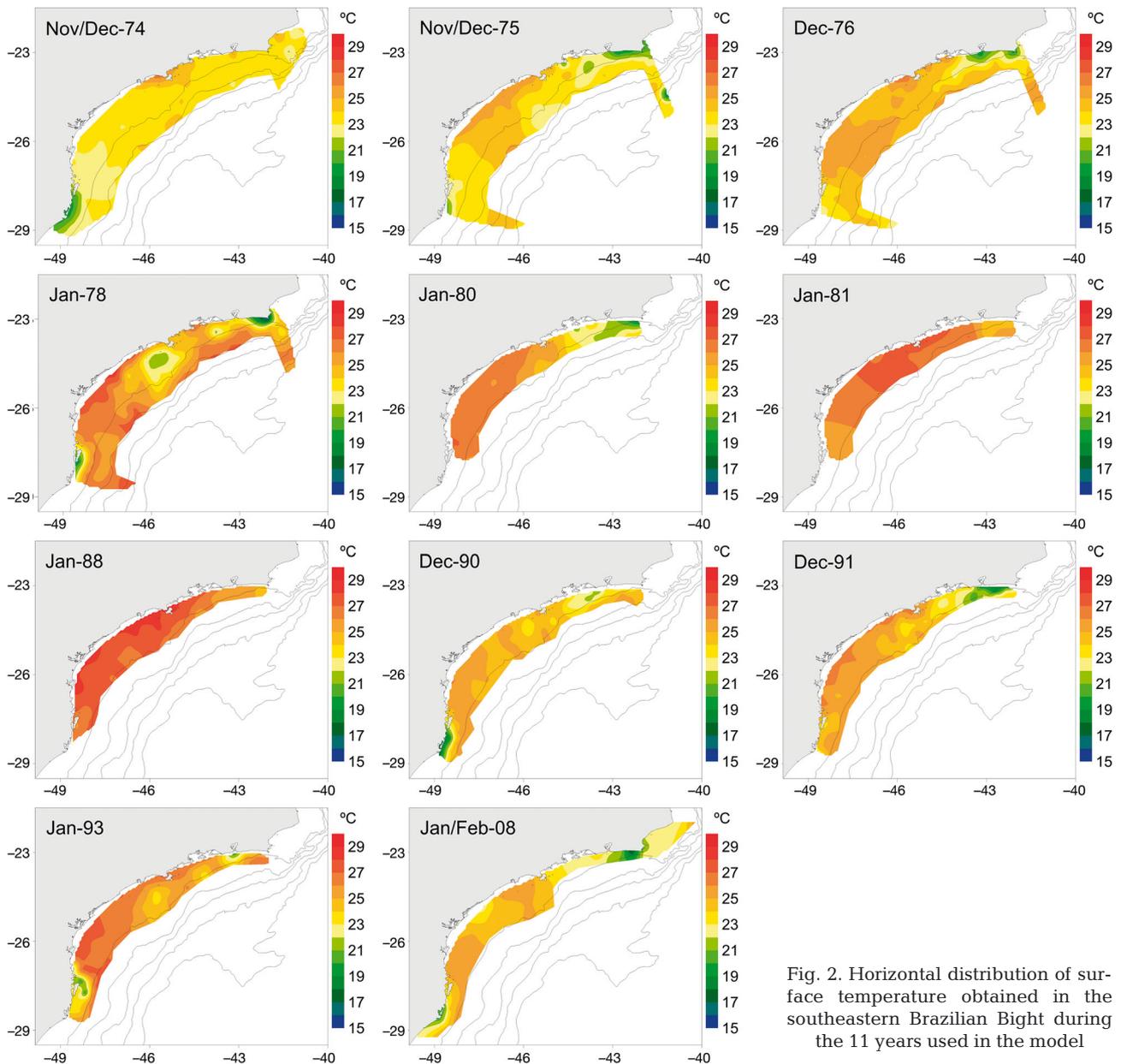


Fig. 2. Horizontal distribution of surface temperature obtained in the southeastern Brazilian Bight during the 11 years used in the model

in some years was higher for larvae but in others for eggs (Table 2). However, the eggs had the highest amplitude of abundance variation and the highest maximum values when compared with those of the larvae (Table 2).

The spatial distribution of eggs and larvae was slightly different: eggs were usually more aggregated than larvae (fewer stations with higher abundance), while larvae were sampled throughout the studied area, even at stations far away from where eggs were sampled, as in the years 1976 and 1980 (Figs. 4 & 5), and further away from the coast, as in the years 1997 and 2001 (Figs. S4 & S5).

Models relating abiotic and biological data

The final egg model with a ZIP distribution was not more optimal than the ZINB (AIC ZIP = 251 588.97). The results of the final ZINB model fitted to *E. anchoita* egg abundance are presented in Table 3 and the model selection process in Table S3. The expected counts of *E. anchoita* eggs decreased as surface temperature and local depth increased (Table 3). In the years that had significant influence on *E. anchoita* egg counts, this influence was positive (Table 3). In those years, a 0.333 mm mesh-size net was used, and moderate or strong El Niño conditions

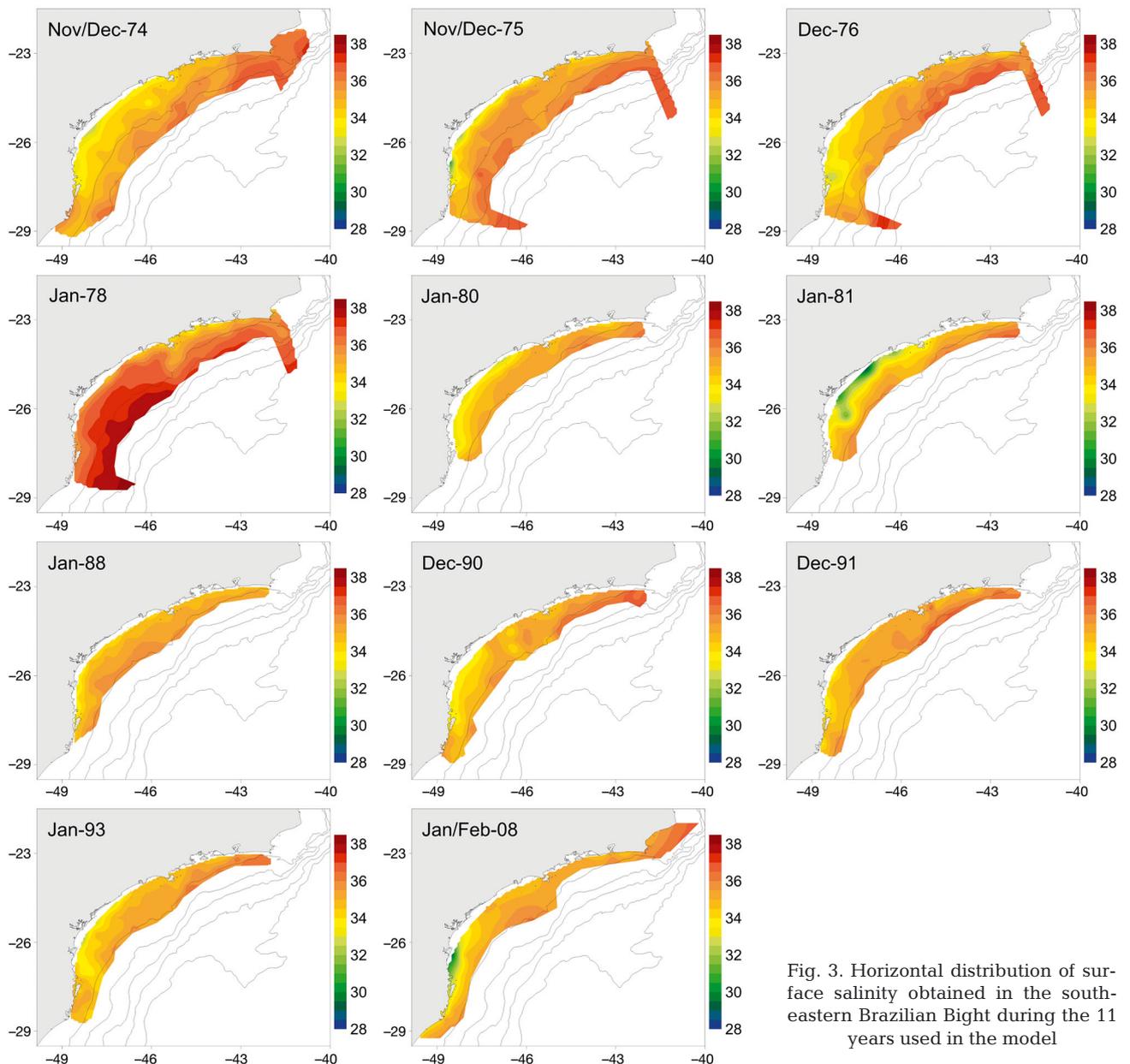


Fig. 3. Horizontal distribution of surface salinity obtained in the southeastern Brazilian Bight during the 11 years used in the model

occurred (Table 1). Note that the AIC of Model 8 increased when the non-significant parameter local depth was dropped from the final model (Model 7) (Table S3). In addition, the probability of false zeros was the lowest in Area 3 and higher in Area 2 than Area 1 for both mesh sizes (Fig. 6). Sampling with the 0.505 mm mesh size increased the probability of false zeros for all areas, and this mesh was less likely to catch *E. anchoita* eggs as the local depth increased (Fig. 6). We could not detect any pattern in the model residuals (Fig. S6).

The final larvae model with a ZIP distribution was not more optimal than the ZINB (AIC ZIP =

86 379.205). The results of the final ZINB model fitted to *E. anchoita* larval abundance are presented in Table 4 and the model selection process in Table S4. Covariates that explained the larval abundance and the probability of false zeros were slightly different from the ones observed for eggs. The expected counts of *E. anchoita* larvae decreased as surface temperature, salinity and distance from the coast increased. Note that dropping latitude (non-significant) from the final Model 4 slightly increased the AIC value (Model 5), but after that, dropping non-significant covariates caused a decrease in the AIC value (Table S4). With the exception of the year 1980,

Table 2. Number of sampled stations (N), frequency of occurrence (FO), mean \pm SD and maximum (Max) abundance of eggs and larvae in each period analyzed

Month-year	N	Eggs			Larvae		
		FO (%)	Mean \pm SD (m ⁻²)	Max (m ⁻²)	FO (%)	Mean \pm SD (m ⁻²)	Max (m ⁻²)
Nov/Dec-74	139	21.6	4.5 \pm 28.0	307.9	70.5	4.4 \pm 9.3	64.5
Nov/Dec-75	140	22.1	22.1 \pm 217.5	2551.0	82.1	18.7 \pm 35.2	220.1
Dec-76	140	14.3	1.6 \pm 8.6	85.0	68.6	8.4 \pm 13.8	99.3
Jan-78	134	13.4	2.3 \pm 17.9	183.4	64.2	18.1 \pm 45.2	308.2
Jan/Feb-79	83	22.9	10.3 \pm 62.8	411.4	69.9	7.8 \pm 35.5	318.4
Jan-80	42	21.4	21.4 \pm 125.1	809.8	83.3	5.9 \pm 9.0	42.5
Jan-81	43	34.9	3.0 \pm 10.9	51.7	81.4	14.3 \pm 24.3	112.3
Mar-82	32	6.3	0.3 \pm 1.8	10.3	56.3	8.3 \pm 15.7	71.3
Jan-88	78	38.5	19.7 \pm 73.5	506.5	82.1	24.9 \pm 68.9	468.7
Dec-90	89	42.9	16.1 \pm 52.3	427.2	65.2	4.3 \pm 8.9	53.6
Dec-91	110	47.4	20.6 \pm 68.6	493.6	74.6	38.1 \pm 65.0	388.6
Jan-93	108	44.4	40.1 \pm 235.3	2399.7	81.5	13.7 \pm 24.9	127.6
Nov/Dec-97	47	0	0	0	38.3	9.1 \pm 28.5	181.2
May-01	46	2.2	0.2 \pm 1.5	10.1	26.1	1.6 \pm 5.9	36.8
Jan-02	72	27.8	32.9 \pm 148.8	1083.5	47.2	21.7 \pm 96.7	774.3
Jan/Feb-08	46	28.3	7.2 \pm 36.7	247.3	84.8	14.7 \pm 31.3	181.0
Nov-08	60	15	0.1 \pm 0.5	3.3	76.7	12.7 \pm 25.8	124.6
Mar-10	55	5.5	2.3 \pm 11.8	64.2	67.3	7.1 \pm 15.5	86.1

all other years had significant positive influences on *E. anchoita* larvae counts (Table 4). The probability of false zeros was highest in Area 1, followed by Areas 2 and 3. After a certain local depth, the probability of false zeros increased as the depth of the sample station increased, irrespective of the area (Fig. 7). We could not detect any pattern in the model residuals (Fig. S7).

DISCUSSION

ZI modeling

Many null samples in a data set are common in research on fish eggs and larvae (e.g. Pennington 1983, Borchers et al. 1997, Fox et al. 2000, Ciannelli et al. 2007, Knutsen et al. 2007). To deal with a high number of null samples, ichthyoplankton are usually modeled considering only the non-zero counts (e.g. Ciannelli et al. 2007, Knutsen et al. 2007) or using a 2-step approach (e.g. Welsh et al. 1996, Borchers et al. 1997, Fox et al. 2000). Models that consider only the positive stations exclude any information carried by the zero counts. Meanwhile, the 2-step approach considers the null-sample information, but to make any inference is complicated as there are 2 sets of environmental influences to deal with, one from the binary and one from the abundance model, usually with different results (Barry & Welsh 2002). More appropriate than the approaches cited above is the

use of ZI models, as used in the present study, which assume that the abundance data may include zero and non-zero values and also deal with the different types of zeros, true or false (Martin et al. 2005, Minami et al. 2007). ZI models have been used in many areas of research (e.g. Hall 2000, Agarwal et al. 2002, Maunder & Punt 2004, Minami et al. 2007, Otero et al. 2016), but to our knowledge, they have not been used in any ichthyoplankton study to date.

Biological and oceanographic factors

Aggregation or patchiness index curves in pelagic fish species usually exhibit a 'U' shape: high initial patchiness of eggs reflecting the adult aggregation behavior followed by a rapid decline as the larvae disperse due to hydrographic factors, followed by an increase in patchiness as the developing fish begin to aggregate in schools (e.g. Hewitt 1981, Houde & Lovdal 1985, Matsuura & Hewitt 1995). Although we did not calculate these indexes, it is possible to infer that *E. anchoita* eggs are more aggregated than larvae, since the FO of larvae was higher in all periods analyzed, larvae were sampled even at stations far away from where eggs were obtained, and maximum egg abundance was commonly the highest. As a consequence, different environmental conditions could influence egg and larvae distributions and abundance, so we modeled them separately. This distribution pattern was also observed in *E. anchoita* eggs

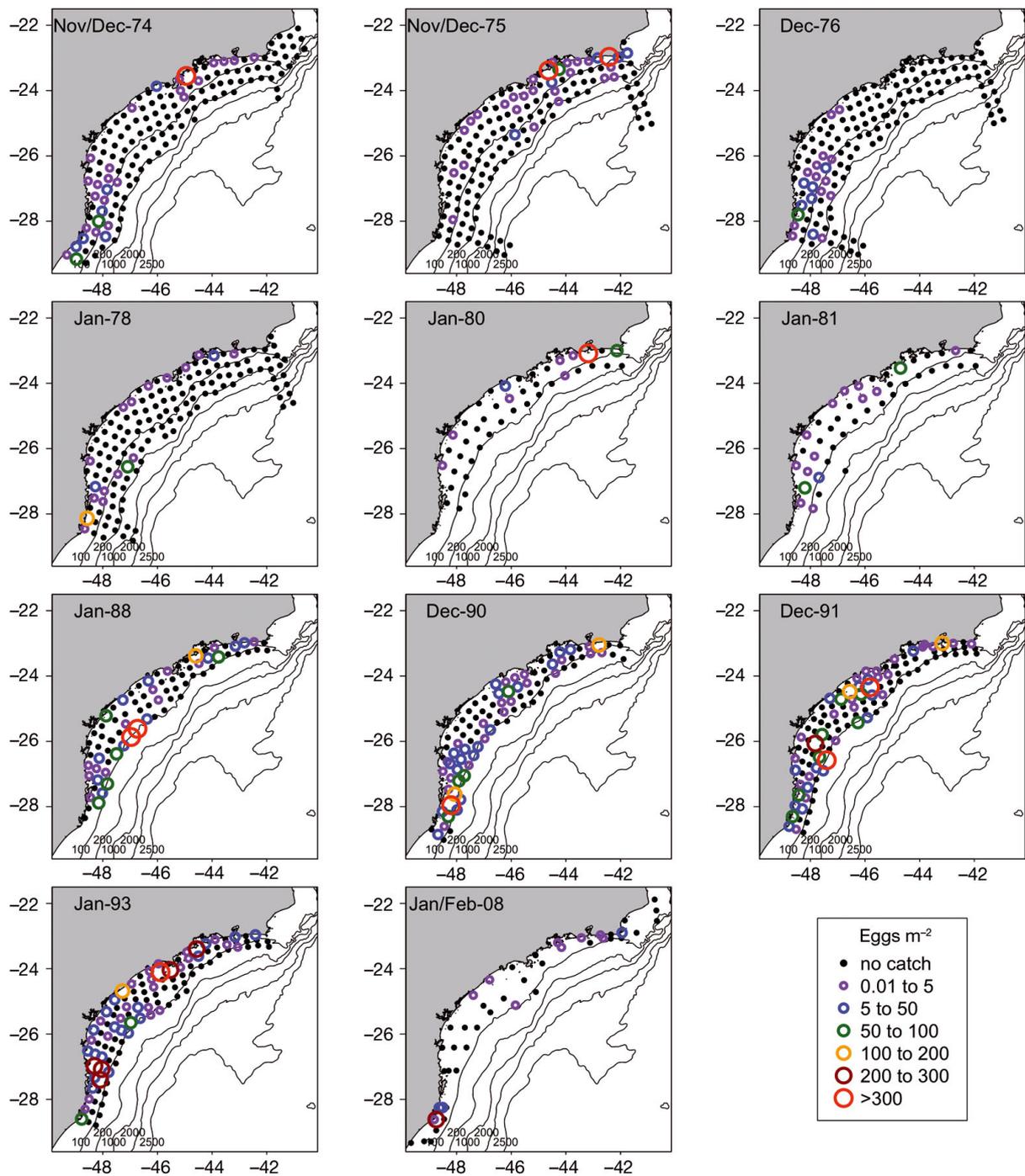


Fig. 4. Spatial distribution of *Engraulis anchoita* egg abundance sampled in the southeastern Brazilian Bight during the 11 years used in the model

and larvae for the Uruguayan and Argentinian coasts, where the larvae were more widespread (Marrari et al. 2013).

E. anchoita egg and larval abundance sharply decreased toward deeper sites. Katsuragawa et al. (2014) also related greater abundance of *E. anchoita*

larvae to shallower stations. The probability of false zeros increased as the sampling sites became deeper and it was lower in Area 3 than in the other 2 areas, for both eggs and larvae. Area 3 includes the area with the highest probability of *E. anchoita* eggs, around 27° S (Favero et al. 2017b).

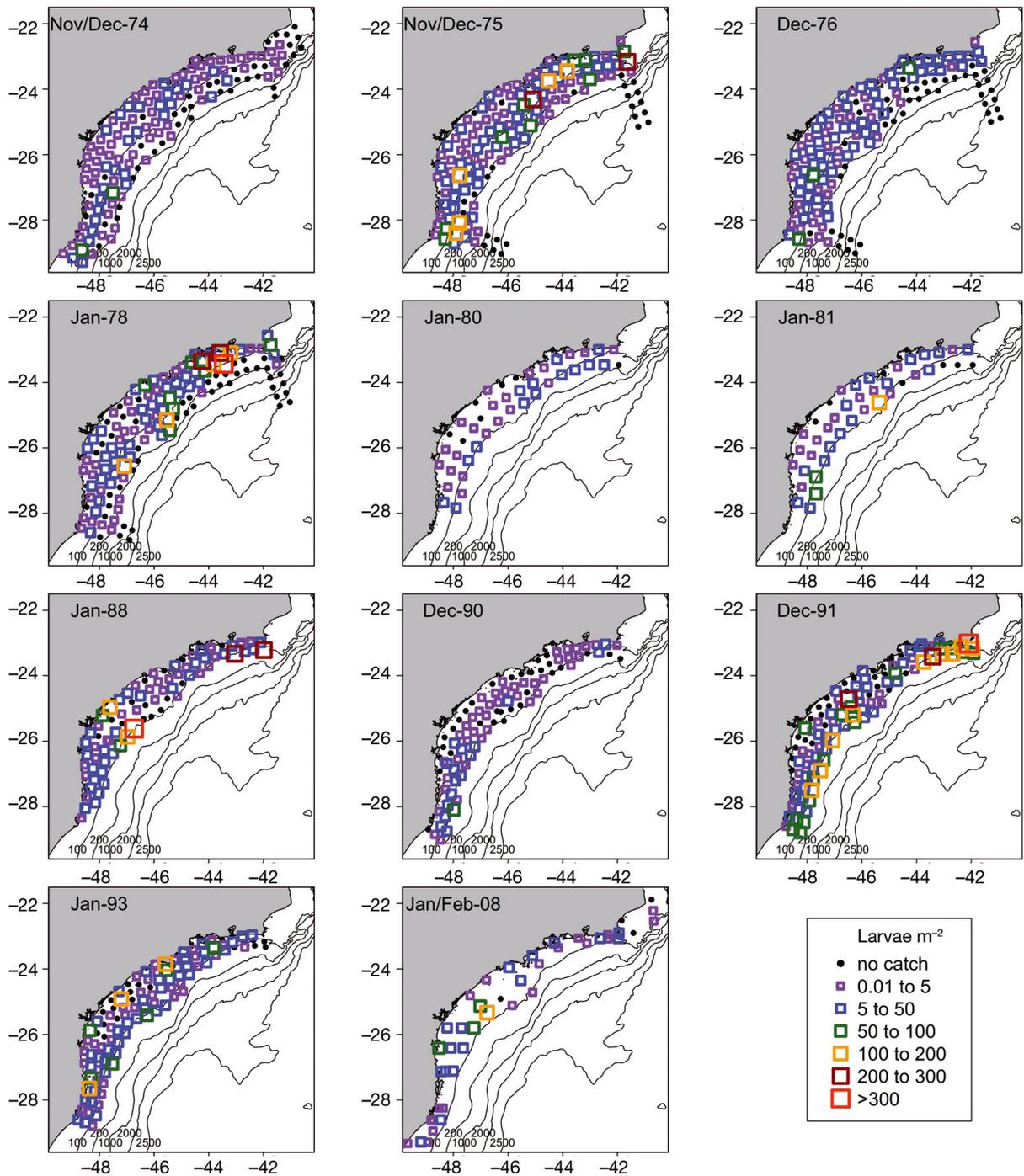


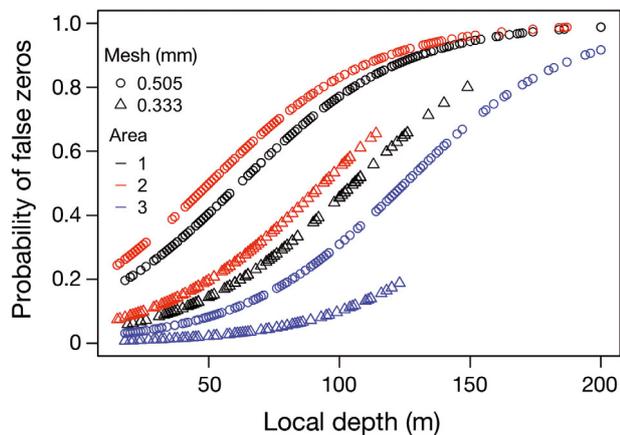
Fig. 5. Spatial distribution of *Engraulis anchoita* larval abundance sampled in the southeastern Brazilian Bight during the 11 years used in the model

The difference in the mesh-size probability of false zeros was only significant in the egg binomial part of the ZI model, being higher for the 0.505 mm mesh size in all areas. This result agrees with Favero et al. (2015b), who showed that the FO of *E. anchoita* eggs was higher in the 0.333 mm than the 0.505 mm mesh-

size net. It is also important to note in Fig. 6 that until around 50 m local depth, the difference in the probability of false zeros between both mesh sizes was smaller in Area 3 than in the other 2 areas analyzed. This difference may be caused by regional variation in egg size: according to Matsuura & Nakatani

Table 3. Summary of the optimal zero-inflated negative binomial model fitted to *Engraulis anchoita* egg abundance

Parameter	Estimate	SE	z	p
Count model coefficients				
Intercept	8.21103	2.74180	2.995	0.00275
Surface temp. (°C)	-0.36854	0.11162	-3.302	0.00096
Local depth (m)	-0.01166	0.00605	-1.926	0.05404
Year 1975	0.30406	0.71403	0.426	0.67022
Year 1976	-0.89560	0.61079	-1.466	0.14256
Year 1978	-0.53036	0.73281	-0.724	0.46922
Year 1980	0.41332	0.81136	0.509	0.61046
Year 1981	0.01566	0.79003	0.020	0.98418
Year 1988	1.83312	0.66664	2.750	0.00596
Year 1990	0.56908	0.56987	0.999	0.31798
Year 1991	1.05925	0.54914	1.929	0.05374
Year 1993	2.40851	0.57721	4.173	3.01×10^{-5}
Year 2008	-0.92538	0.83450	-1.109	0.26748
Logistic model coefficients				
Intercept	-3.381958	0.644259	-5.249	1.53×10^{-7}
Local depth (m)	0.032024	0.005132	6.240	4.38×10^{-10}
Mesh size 0.505 cm	1.396904	0.375810	3.717	0.000202
Area 2	0.375719	0.355080	1.058	0.289998
Area 3	-2.020532	0.524025	-3.856	0.000115

Fig. 6. Predicted probabilities of false zeros for *Engraulis anchoita* eggs for the different mesh sizes used and areas sampled as a function of the local depth based on the binomial part of the zero-inflated negative binomial model

(1980), the 0.333 mm mesh net collected more *E. anchoita* eggs than the 0.505 mm mesh net in the Santos area, in the central part of the SBB; on the other hand, Sanchez & Ciechomski (1984) did not observe any difference in *E. anchoita* egg abundance between both mesh sizes in Uruguay and Argentina. The locale where the samples came from caused this difference, as the minor and major axes of the *E. anchoita* eggs sampled on the Uruguayan and

Argentinian coasts were larger than the ones sampled in the Santos area (Sanchez & Ciechomski 1984).

The non-significant difference in mesh size probability of false zeros in the larvae binomial part of the ZI model may be related to the fact that we did not obtain any yolk-sac larvae, the initial larval stage that is more prone to extrusion by larger mesh sizes (Houde & Lovdal 1984, Leslie & Timmins 1989, Johnson & Morse 1994, Somarakis et al. 1998). Matsuura & Nakatani (1980) compared the catches of *E. anchoita* larvae in bongo nets fitted with 0.333 and 0.505 mm mesh sizes, and found that larvae were obtained with both nets in all oceanographic stations, but the finer mesh retained more larvae than the coarse one. However, the authors showed that this difference was only significant when analyzing larvae up to 7 mm standard length.

E. anchoita is widely distributed and is tolerant of a broad range of temperatures and salinities (Ciechomski 1966, Matsuura & Kitahara 1995, Torquato & Muelbert 2014). In controlled laboratory experiments, Brewer (1976) found that *E. mordax* eggs hatch at temperatures between 8.5 and 28.5°C and larvae tolerated from 7 to 30°C. However, the same author showed that the number of larvae developing in a normal manner decreased when temperatures were outside of the range of 11.5 to 27°C, highlighting the importance of temperature in the early life stages. In fact, the present study showed that temperature was a significant covariate in the count part of the model for both eggs and larvae. These abundances exhibited negative relationships with temperature, in agreement with the results from Macedo-Soares et al. (2014) and Katsuragawa et al. (2014). On the other hand, salinity was a significant covariate only in the larvae count part of the model, also exhibiting a negative relationship, in agreement with Katsuragawa et al. (2014).

Environmental parameters that were not measured in the present study may influence ichthyoplankton abundance and distribution. For example, *E. anchoita* larvae abundance was negatively associated with strong currents near a shelf front (Auaud & Martos 2012) and positively correlated with oxygen stratification, silicate and phosphate concentration (Macedo-Soares et al. 2014). Eggs were positively

Table 4. Summary of the optimal zero-inflated negative binomial model fitted to the *Engraulis anchoita* larval abundance. Distance: distance from the coast

Parameter	Estimate	SE	z	p
Count model coefficients				
Intercept	14.807366	3.387892	4.371	1.24×10^{-5}
Surface temp. (°C)	-0.119898	0.043406	-2.762	0.00574
Surface salinity	-0.413385	0.083148	-4.972	6.64×10^{-7}
Distance (km)	-0.002233	0.001396	-1.600	0.10963
Year 1975	1.564267	0.227420	6.878	6.06×10^{-12}
Year 1976	1.157931	0.238681	4.851	1.23×10^{-6}
Year 1978	2.204941	0.277133	7.956	1.77×10^{-15}
Year 1980	0.340486	0.310544	1.096	0.27290
Year 1981	1.411186	0.336050	4.199	2.68×10^{-5}
Year 1988	2.276268	0.307200	7.410	1.27×10^{-13}
Year 1990	0.326371	0.257514	1.267	0.20502
Year 1991	2.437804	0.243977	9.992	$<2 \times 10^{-16}$
Year 1993	1.807330	0.260818	6.929	4.22×10^{-12}
Year 2008	1.801693	0.317480	5.675	1.39×10^{-8}
Logistic model coefficients				
Intercept	-7.37752	1.17379	-6.285	3.27×10^{-10}
Local depth (m)	0.05216	0.00905	5.764	8.22×10^{-9}
Area 2	-1.91290	0.76374	-2.505	0.012257
Area 3	-2.77628	0.80957	-3.429	0.000605

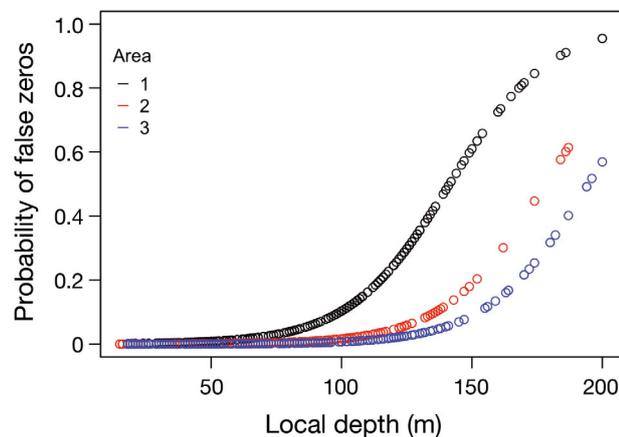


Fig. 7. Predicted probabilities of false zeros for *Engraulis anchoita* larvae in the areas sampled as a function of the local depth based on the binomial part of the zero-inflated negative binomial model

correlated with abundance of small species of copepods (Viñas et al. 2002). Bakun & Parrish (1991) reiterated the importance of a balance between different physical processes that affect water column stability, retention in a favorable habitat and nutrient enrichment that provides appropriate larval food particles in the selection of the spawning habitat. Some of these environmental conditions may be masked in the high interannual variation observed in the abun-

dance and distribution of *E. anchoita* eggs and larvae, reinforced with the fact that the different years sampled were a significant covariate for both stages in the count part of the model. *E. anchoita* has a relatively low trophic position in the marine food web (Capitanio et al. 2005) and lives only a short period of time (1–4 yr) (Carvalho & Castello 2013). Those factors make this species highly susceptible to environmental variability (Bakun 1996), resulting in the large interannual fluctuations observed. Those fluctuations in small pelagic fish populations are common in different species worldwide (see Lluch-Belda et al. 1992, Schwartzlose et al. 1999, Oozeki et al. 2007, Checkley et al. 2009, Asch & Checkley 2013).

One oceanic–atmospheric phenomenon that scientists have tried to relate to such small pelagic fish fluctuations is El Niño (e.g. Fiedler 1983, Kim et al. 2005, Asch 2015). In the western South Atlantic, El Niño induces an increase of Plata River outflow and a decrease of Malvinas current sea surface temperature (Severov et al. 2004), negatively influencing the *E. anchoita* stock from southern Brazil (Macedo-Soares 2015): higher Plata River outflow increases offshore transport of *E. anchoita* eggs and larvae far from a suitable area for their development (Sanchez & Ciechowski 1995), and a decrease in the water temperature reduces the larvae survival rates, as it slows larval development (Pepin 1991). In the studied area, the occurrence of strong El Niño tends to favor the offshore transport of water and the upwelling of the SACW (Paes & Moraes 2007). Primary production is therefore expected to increase, in turn increasing the *Sardinella brasiliensis* catches 1 or 2 yr after an intense event. On the other hand, after a ‘moderate’ or ‘weak’ El Niño, or a strong La Niña, the pelagic fishery production would decrease (Paes & Moraes 2007). Our results showed that in years when moderate or strong El Niño occurred, *E. anchoita* egg abundance was positively influenced, but further analyses are necessary to better understand this relationship. It is important to be cautious when relating egg and larvae distributions and abundances to SACW intrusion: in years when the SACW intrusion is weak, there may be an increase in larval mortality due to a decrease in the zooplankton biomass (Katsuragawa et al. 2006); and in years with a strong upwelling, lar-

val mortality rates would also increase, as the wind-induced upwelling at Cape Frio tends to transport individuals to unsuitable areas (Dias et al. 2014).

Long-temporal-scale studies, such as the one presented here, are relevant to better understand fluctuations in the occurrence of ichthyoplankton that are related to environmental conditions. We are aware of the imperfection of our data set: samples were not collected every year during the 40 yr period, the spatial location of the oceanographic stations varied, and 2 different mesh sizes were used. Beyond that, a wide range of environmental conditions could be considered, as discussed above. Remotely-sensed data could be obtained and used, but such data do not cover some earlier years. Nonetheless, we believe that the best long-term *E. anchoita* egg and larvae data from the SBB were analyzed in the present study, using one of the best statistical approaches available and *in situ* abiotic measurements. Our results provide new information about the early life history of an important pelagic species that, although not yet commercially fished in the studied area, can assist in the management of this species in southern of Brazil, Argentina and Uruguay.

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