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Seasonal and regional variation in egg size of the Argentine anchoita (*Engraulis anchoita*) in the southeastern Brazilian Bight

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Abstract—Eggs of the Argentine anchoita (*Engraulis anchoita*) are very abundant and frequently collected in research ichthyoplankton tows along the southern–southeastern Brazilian coast. The commercial exploitation of Argentine anchoita has also recently begun in southern Brazil. Therefore, there is a need for a better understanding of the population structure and dynamics of this species in order to manage the fishery for this species. Our objective was to determine seasonal and regional variability in the size of eggs of Argentine anchoita in the southeastern Brazilian Bight (SBB). Because there are no physical barriers in the ocean, defining stock limits for fish populations is difficult, particularly for a semimigratory species such as the Argentine anchoita. Eggs from the south of the SBB were larger than those from the north, indicating that eggs from the northern Santa Marta Cape region probably belong to the *bonaerense* stock. Also, eggs collected during the winter were larger than those collected during the summer. This difference in egg size may be due to either 1) larger adults coming from the south and spawning in or closer to the area sampled during winter, or 2) an adaptive response of spawning females to the changes in the abiotic conditions or 3) a combination of these 2 features.

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Most marine fish eggs are identified by their size, shape and pigment characters, but many newly fertilized eggs are unpigmented and therefore egg diameter is the most distinguishing feature (Bagenal, 1971). Automated identification of fish eggs, based on their size and shape (Favero et al., 2015) is possible; however, egg size varies among species, among populations, and within populations of the same species owing to temporal, spatial, biological, and environmental factors (e.g., Phonlor, 1984; Wootton, 1990; Chambers and Waiwood, 1996; Llanos-Rivera and Castro, 2004). In addition to identification of fish eggs, it is important to understand variation in egg sizes because larger eggs typically hatch into larger larvae with the possibility of conferring a higher survival potential on the resulting offspring (e.g., Blaxter and Hempel, 1963; Blaxter and Hunter, 1982; Marteinsdottir and Able, 1992).

The Argentine anchoita (*Engraulis anchoita*) (Engraulidae: Clupeiformes) is a small pelagic fish, which is important as a secondary consumer near the bottom of the food chain, and is an essential prey for other fish species, marine mammals, and seabirds (Castello, 2007). It is economically important to the Argentine and Uruguayan fishery fleets (FAO, 2014), and exploitation of Argentine anchoita has recently begun in southern Brazil (Carvalho and Castello, 2013). This species is widely distributed over the continental shelf of the southwest Atlantic, from Vitoria, Brazil (20°S) to Gulf San Jorge, Argentina (48°S) (Castello, 2007). There are 3 distinct stocks: the *patagonic* (48–41°S), the *bonaerense*

(41–27°S) and a third, ranging from 27°S and 20°S, is known as the "Brazilian Southeastern Bight stock" (Carvalho and Castello, 2013). Different methods have been used to identify the 3 stocks: to distinguish the *patagonic* from the *bonaerense*, Hansen (1994) used growth rates, size–weight relationships and length at first maturation; Castello and Castello (2003) compared larval growth and length at first feeding from southeastern and southern Brazil; and Carvalho and Castello (2013) analyzed size and age composition and length-at-age data and concluded that anchovies from the Santa Marta Region (30–27°S) should be considered as a part of the *bonaerense* stock. Although the parameters used cannot reveal the genetic discreteness of these stocks, they are still powerful tools for stock identification purposes (Begg, 2005).

No study dedicated specifically to variation in egg size of the Argentine anchoita has been conducted in the southeastern Brazilian Bight (SBB; roughly between 22°S and 28°S). A few studies have focused off the southern coast of Brazil, and the coasts of Uruguay and Argentina (Ciechomski, 1973; Phonlor, 1984), but they cover only the *bonaerense* stock. Therefore, our objective was to evaluate seasonal and regional variability in the size of eggs of Argentine anchoita in the SBB, and to consider factors that may cause such variation.

Materials and methods

Study area

The Brazil Current flows southward along the continental slope of the SBB (Silveira et al., 2000) transporting warm and saline Tropical Water in the upper mixed layer and cold South Atlantic Central Water (SACW) at the pycnocline. An additional water mass exists in the neritic zone, the warm Coastal Water, with lower salinity than the Tropical Water (Castro Filho and Miranda, 1998). Except for some coastal areas that are under the influence of waters flowing from large embayments, such as Guanabara Bay in the state of Rio de Janeiro, oligotrophic conditions prevail in the study area owing to the dominance of Tropical Water in the upper layers, and oceanic nutrients trapped within the SACW (Lopes et al, 2006).

The intermittent coastal upwelling off Cape Frio is an important process that brings the nutrient-rich SACW into the euphotic zone (Valentin et al., 1987). These SACW intrusions vary seasonally, advancing toward the coast during spring and summer and retreating toward the shelf break in the autumn and winter (Cerda and Castro, 2014). Another physical process that fertilizes the euphotic zone occurs during the winter, when subantarctic and the Plata River Plume waters are driven northward by southerly winds from the continental shelf of Argentina and Uruguay into most of the inner shelf in the south of Brazil and even the SBB (Brandini 1990; Stevenson et al., 1998; Piola et al., 2000; Gaeta and Brandini, 2006; Piola et al., 2008a; Piola et al., 2008b).

To address the possible role of spatial (regional) and temporal (seasonal) variation in egg size of Argentine anchoita, we used data collected from 2 different sets of research cruises: for the regional variation, the study area comprised most of the SBB, between Cape Frio, in the state of Rio de Janeiro, and Cape Santa Marta Grande, in the state of Santa Catarina (roughly between 23°S and 28°S). For the seasonal variation, the study was carried in the northern part of the SBB, from off Cape São Tomé (22ºS) to São Sebastião Island (24ºS), in the state of São Paulo during the summer and winter of 2001 and 2002 (Fig. 1).

In situ data

To assess the seasonal variation in egg size of Argentine anchoita, we took advantage of biotic and abiotic data obtained from a set of 4 oceanographic cruises carried out during the summer and winter of 2001 and 2002. During both seasons of 2001, only one transect was performed in the Cape Frio region, but some sampling stations were sampled twice. Summer of 2002 covered 14 transects and winter of 2002 included 13 transects (Table 1, Fig. 1).

In order to address patterns in the spatial variation in egg size of Argentine anchoita, data were obtained from another set of cruises conducted during the summers over 5 years (1975, 1988, 1990, 1991, and 1993; Table 1) and the SBB was divided into 3 areas: area 1 from Cape São Tomé to São Sebastião Island; area 2 from São Sebastião Island to Paranaguá Bay; and area 3 from Paranaguá Bay to Cape Santa Marta Grande (Fig. 1). These areas were defined on the following bases: 1) Argentine anchoita stock identification as defined by Carvalho and Castello (2013) (area 3); 2) oceanographic conditions described by Miranda and Katsuragawa (1991) and Mahiques et al. (2004) (area 1 and area 2); 3) a spawning map obtained by Favero et al. (2017), so that the divisions would not separate any important spawning area.

Temperature and salinity data were obtained from Nansen bottles and reversing thermometers in 1975 and 1988. In the other 3 years, a conductivity, temperature, and depth (CTD) profiler, an SBE 917*plus*[1] (Sea-Bird Scientific, Bellevue, WA), was used to collect this information.

As described by Smith and Richardson (1977), a bongo net with a 0.61-m diameter mouth opening was used to sample ichthyoplankton. It was equipped with paired cylindrical-conical 0.333-mm and 0.505-mm mesh-size nets and with a flowmeter attached at the center of the mouth opening of each net in order to measure the volume of filtered water. The net was towed obliquely from the surface to the maxi-

[1] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

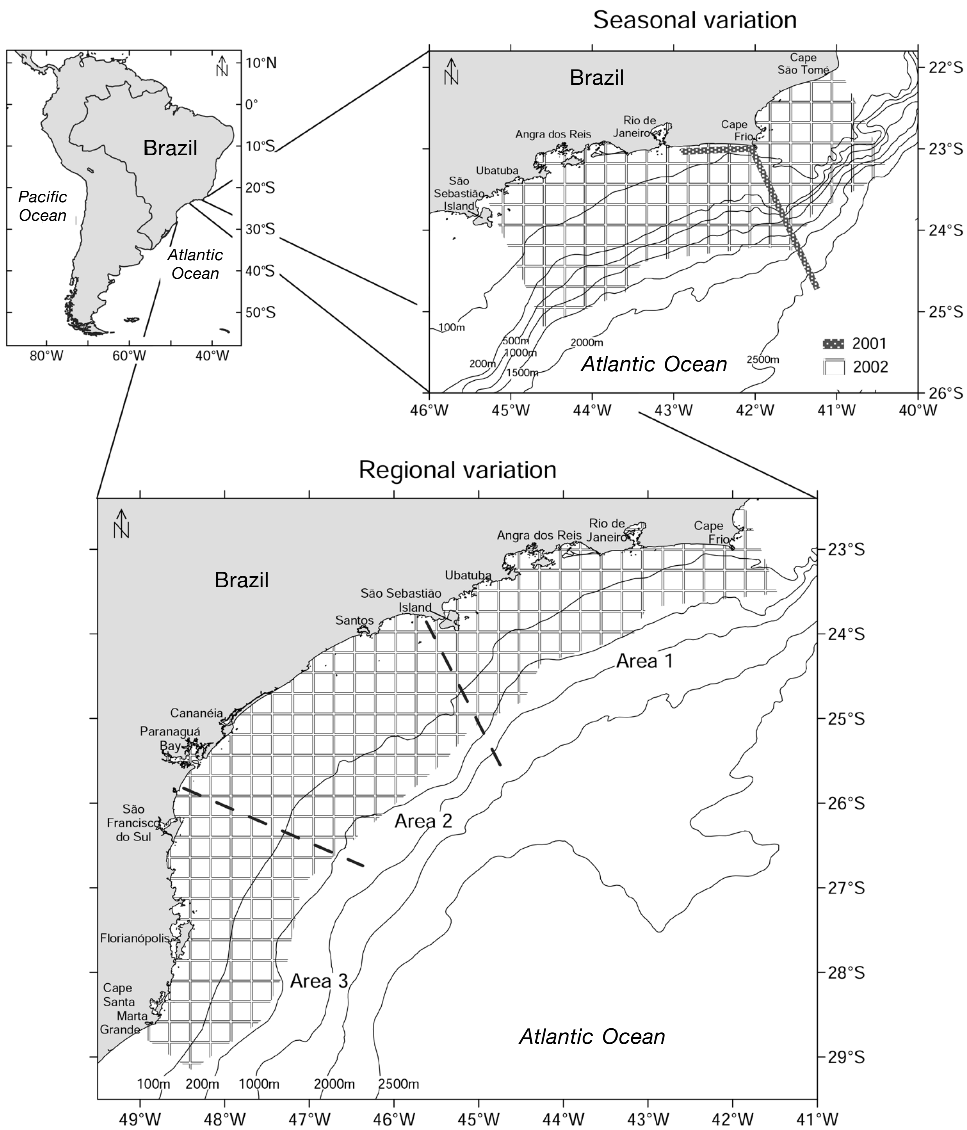

Figure 1

Maps of the study areas for our investigation of variation in egg size of Argentine anchoita (*Engraulis anchoita*): (upper right) area of the northern part of the southeastern Brazilian Bight sampled in 2001 and 2002 was used for the seasonal variation analyses, and (bottom) area of the nearly entire Southeastern Brazilian Bight sampled and divided into 3 areas, in 1975, 1988, 1990, 1991, and 1993, was used for the regional variation analyses. The 3 areas were those of Cape Frio to São Sebastião Island (area 1), São Sebastião Island to Paranaguá Bay (area 2), and Paranaguá Bay to Cape Santa Marta Grande (area 3).

mum depth possible, which did not exceed 200 m. If a sampling station was shallower than 60 m, the bongo net was lowered twice close to the bottom, increasing the volume of water filtered. Towing speed was about 2.8–3.7 km/h. We analyzed only the samples from the 0.333-mm mesh size net and that had been preserved at sea in 4% buffered formalin in seawater. All samples were archived in the Biological Collection "Prof. E. F. Nonato" (ColBIO) of the Oceanographic Institute, University of São Paulo, Brazil.

Eggs of Engraulidae were sorted on the basis of their ellipsoid shape, segmented yolk, and usually, absence of oil droplets (Ciechomski, 1965; Phonlor, 1984) and then imaged by using a digital camera attached to a stereomicroscope. Their major and minor axes were measured from the photographs by using the image-analysis program ImageJ2 (Schindelin et al., 2015) and egg volume was calculated by following the method of Vanzolini (1977). Finally, eggs of Argentine anchoita were identified by their morphometric characteristics

Table 1

Start and end dates for oceanographic cruises and number of sampling stations (N) used as data sources for analyses of seasonal and regional variation in egg sizes of Argentine anchoita (*Engraulis anchoita*) in the southeastern Brazilian Bight.

Oceanographic cruise	Date Start	End	N
Seasonal			
Deproas I	2/7/01	2/13/01	19
Deproas II	7/12/01	7/19/01	17
Deproas III	1/5/02	1/24/02	72
Deproas IV	8/3/02	8/21/02	66
Regional			
FINEP I	11/29/75	12/18/75	140
EPM Sardinha	1/10/88	1/30/88	78
V. Hensen/JOPS	12/28/90	1/11/91	89
Sardinha I	12/8/91	12/18/91	110
Sardinha II	1/9/93	1/18/93	108

by using discriminant analysis, as described by Favero et al. (2015). Only a subsample of about 100 eggs per sampling station was measured.

Satellite data

Sea-surface temperature (SST) corresponds with level-3 gridded images obtained from the advanced very high resolution radiometer (AVHRR) on board NOAA satellites and processed by the Pathfinder Project. The Pathfinder data set is the result of a collaboration between the NOAA National Oceanographic Data Center and the University of Miami Rosenstiel School of Marine and Atmospheric Science, and is distributed at NASA's Physical Oceanography Distributed Active Archive Center (AVHRR Pathfinder Level 3 Daily SST, vers. 5: daytime, PODAAC-PATHF-DYD50, website, and nighttime, PODAAC-PATHF-DYN50, website, accessed December 2015) on a global scale, with a linear gridded projection, and within a spatiotemporal resolution of 4 km×4 km×1 month. Day and night-time data were used to compute SST monthly means. Surface chlorophyll-*a* concentration (CHL) was acquired by level-3 mapped images obtained from the Sea-viewing Wide Field-of-view Sensor on board the SeaStar satellite. These data were processed by the NASA Goddard Space Flight Center by using the Ocean Chlorophyll 4 algorithm, vers. 4 (O'Reilly et al., 2000), and distributed at NASA's Ocean Color Web (chlor_a, website, accessed December 2015) on a global scale, with cylindrical equidistant projection, and a spatiotemporal resolution of 9 km×9 km×1 month. Because the CHL is logarithmically distributed within the oceans, we chose to work with the log10-transformed CHL. We used monthly means of SST and surface CHL to characterize the typical summer and winter scenarios of 2001 and 2002, to correspond with the periods when the cruises were undertaken (Table 1). Monthly means were chosen to represent our study area for 2 reasons: 1) monthly means serve as a low-pass filter that removes high-frequency external processes that could be involved in the variability of SST and surface CHL (e.g., processes driven by the atmosphere), and 2) unlike the averages for the specific days of the cruises, monthly means include processes with a lag between their cause and effect (e.g., the time lag between the supply of nutrients to the upper ocean and the growth of primary production for a given area).

Data analyses

Egg abundance was calculated as

$$N=(x \times d)/V \text{ (Tanaka, 1973)},$$

where N = egg abundance (number of eggs per square meter at each sampling station);
x = the number of eggs sampled;
d = the maximum depth sampled in meters; and
V = the volume of water filtered in cubic meters.

The mean abundance was calculated for all the sampling stations, not just for those where eggs were collected. The calculation of the frequency of egg occurrence was based on Guille (1970).

One-way analysis of variance was used to test the differences in the egg major and minor axes, egg volumes, temperature, and salinity (at 10-m depth), when compared by season (winter and summer) and by area (areas 1, 2 and 3) within each year. A posteriori Tukey's honest significant difference test was performed in order to find means that were significantly different from each other. Temperature–salinity diagrams in relation to egg volume from ichthyoplankton tows were plotted to infer the distribution of egg sizes for Argentine anchoita with respect to water mass for each year, area, and season. We used the 10-m measurement for the abiotic data because the eggs of anchovies mainly occur close to the surface, in the upper 20 m (Tanaka, 1992; Sabatés et al., 2008). R software, vers. 3.2.1(R Core Team, 2015) was used for these analyses.

Results

Seasonal variation

Oceanographic conditions Mean seawater temperature measured at a depth of 10 m varied significantly within each period analyzed (F=8.732, df=3, P<0.01). Mean summer temperatures were higher than those of winter for both years, but the lowest individual temperature values were measured during summer (Table 2), owing to the SACW intrusion that occurred in both years surveyed, 2001 and 2002 (Goçalo et al., 2011; Araújo, 2013). The standard deviation (SD) in temperature pro-

Table 2

Mean, with standard deviation (SD), and the range of temperature (°C; Temp.) and salinity (Sal.) values measured at a 10-m depth during summer and winter of 2001 and 2002 in the northern area of the southeastern Brazilian Bight. Results are given from analysis of variance (ANOVA) and a posteriori Tukey's honestly significant difference (HSD) test that compared means between the summer and winter of 2001 and 2002. S01=summer 2001; W01=winter 2001; S02=summer 2002; W02=winter 2002.

		Period				ANOVA		Tukey's HSD (P)	
		Summer 2001	Winter 2001	Summer 2002	Winter 2002	F	P	S01 vs. W01	S02 vs. W02
Temp.	Mean (SD)	24.65 (3.18)	22.77 (0.62)	23.79 (2.86)	22.32 (1.21)	8.732	<0.01	0.009	0.001
	Range	14.70–27.65	22.17–24.72	14.88–27.08	16.50–24.44				
Sal.	Mean (SD)	36.83 (0.42)	36.04 (0.53)	36.08 (0.69)	35.58 (1.04)	15.13	<0.01	0.002	0.003
	Range	35.73–37.48	35.14–37.14	34.67–37.01	33.16–37.37				

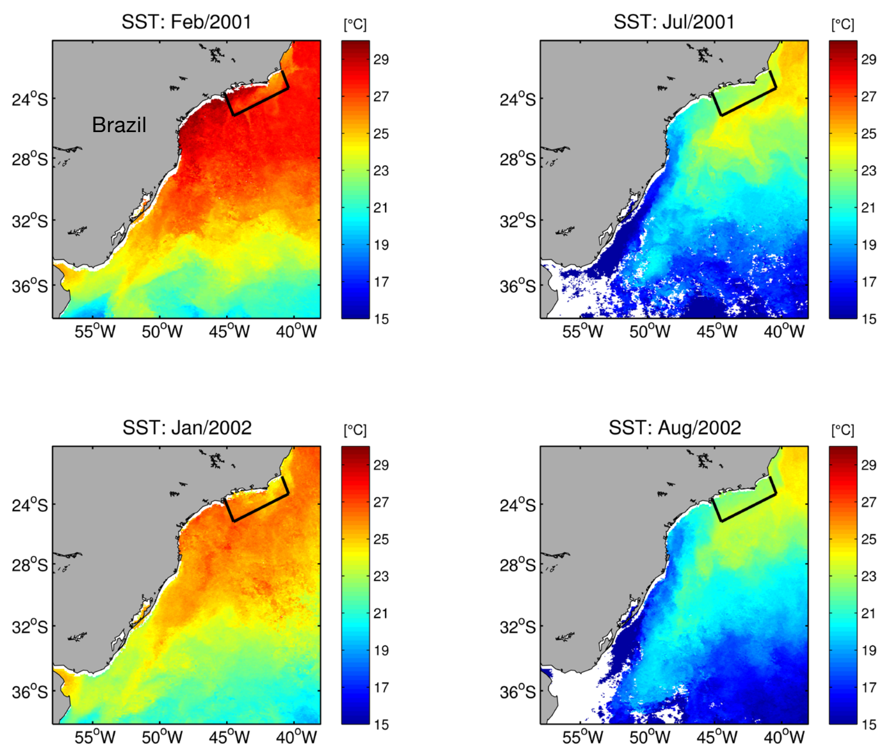

Figure 2

Horizontal distribution of sea-surface temperature (SST, °C), based on satellite data, during the winter (February or January) and summer (July or August) of 2001 and 2002 in the southwestern Atlantic Ocean off Brazil. The black line highlights the northern part of the southeastern Brazilian Bight that was the study area in 2002.

vided another indicator of SACW intrusion, which was greatest in summer for both years. Mean salinity at a depth of 10 m also varied significantly within the periods analyzed (F=15.13, df=3, P<0.01), with summer values higher than winter values in both years (Table 2).

The SST fields of the southwestern Atlantic showed strong thermal gradients in summer as a consequence of the mixing of relatively warmer waters from the Brazil Current and colder waters transported by the Malvinas Current from the south. Strong thermal gradients were also observed during winter but those were restricted to the Brazilian coast because of a northward advection of colder coastal waters coming from higher latitudes over the continental shelf and the weakening of the Brazil Current. No colder coastal waters coming from the south were observed in summer close to the study area (Fig. 2).

Table 3

Number of eggs of Argentine anchoita (*Engraulis anchoita*) sampled (*N*), frequency of occurrence (FO), and mean and standard deviation (SD) values of abundance, egg volume, egg major axis, and egg minor axis, obtained during summer and winter of 2001 and 2002 in the northern area of the Southeastern Brazilian Bight. Results are given from analysis of variance (ANOVA) and a posteriori Tukey's honestly significant difference (HSD) test which compared egg-size values from the summer and winter of 2001 and 2002. S01=summer 2001; W01=winter 2001; S02=summer 2002; W02=winter 2002.

	Period				ANOVA		Tukey's HSD (*P*)	
	Summer 2001	Winter 2001	Summer 2002	Winter 2002	*F*	*P*	S01 vs. W01	S02 vs. W02
N	99	56	9904	430				
FO (%)	4.27	26.96	27.78	18.18				
Abundance (eggs/m²)	1.9 (9.3)	0.7 (1.5)	32.8 (148.8)	1.4 (5.5)				
Volume (mm³)	0.142 (0.015)	0.206 (0.018)	0.177 (0.020)	0.206 (0.021)	415.4	<0.01	0.000	0.000
Major axis (mm)	1.031 (0.047)	1.138 (0.047)	1.106 (0.053)	1.140 (0.052)	133.2	<0.01	0.000	0.000
Minor axis (mm)	0.512 (0.026)	0.587 (0.022)	0.552 (0.023)	0.587 (0.025)	429.8	<0.01	0.000	0.000

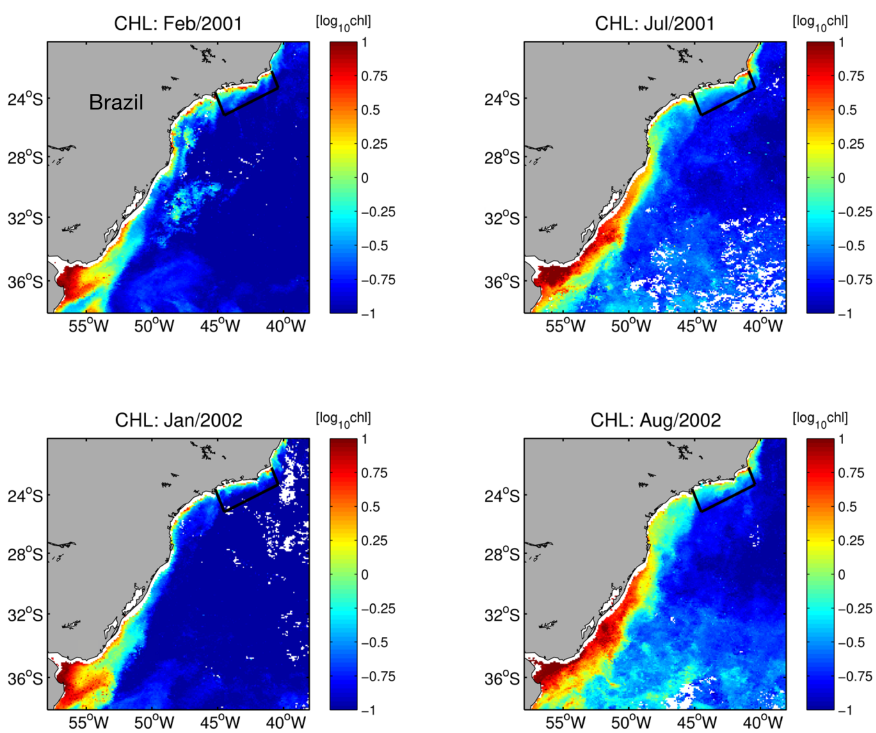

Figure 3

Horizontal distribution of the log10-transformed surface chlorophyll-*a* concentration (CHL, mg/m³), determined from satellite data, during the winter (February or January) and summer (July or August) of 2001 and 2002 in the southwestern Atlantic Ocean off Brazil. The black line highlights the northern part of the southeastern Brazilian Bight that was the study area in 2002.

The highest values of the surface CHL were observed close to the estuary of the Plata River (around 36°S) in summer. During the winter of both years the high CHL spread from the Plata River to the southernmost region of the SBB, reaching latitudes of about 28°S (Fig. 3).

Further information about water column stratification, water mass intrusions, and horizontal distribution of the SST for the same area and period studied was described by Goçalo et al. (2011) and Namiki et al. (2017).

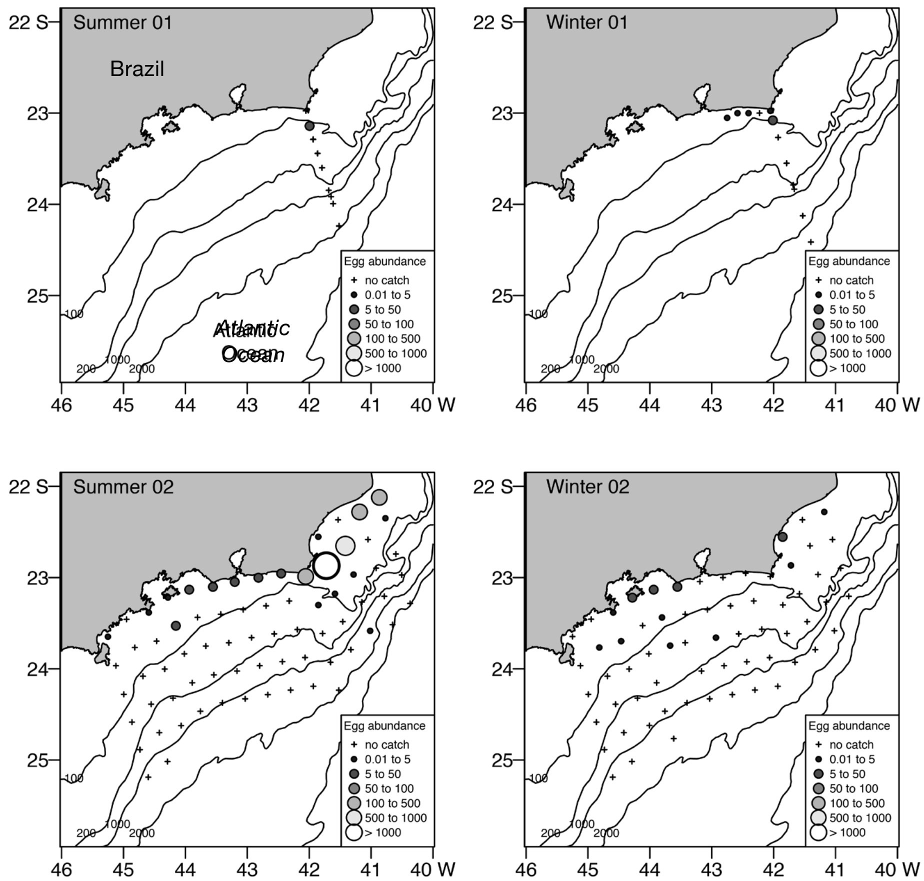

Figure 4

Spatial distribution of abundance of eggs (eggs/m^2) of Argentine anchoita (*Engraulis anchoita*) sampled in the northern part of the southeastern Brazilian Bight with ichthyoplankton tows during summer and winter of 2001 and 2002.

Seasonal variation in eggs A total of 10,710 eggs of Engraulidae were sampled. Eggs of Argentine anchoita represented 98.6% of all eggs sampled (n=10,489) and they were more abundant during the summers of both years (Table 3).

During the summer of 2001, on the only transect sampled, eggs occurred at only one sampling station close to the coast. During the winter of 2001 eggs were collected at 7 stations, all close to the coast (Fig. 4). During the summer of 2002, eggs of Argentine anchoita were more abundant at Cape Frio and Cape São Tomé, in the north of the area sampled. Conversely, during the winter, these eggs were much less abundant, and were frequently found in the southern part of the area sampled (Fig. 4).

Eggs of Argentine anchoita experienced large variations in temperature and salinity and were collected within the entire range of temperature and salinity values that characterized the 3 water masses occurring in the study areas. Low numbers of eggs were found in waters with a salinity higher than 36.5 (Fig. 5). Stations with higher mean egg volume occurred during the winter and when temperatures were lower (Fig. 5).

Of the total number of eggs of Argentine anchoita that were collected, 2794 were measured. Volume, major axis and minor axis mean values were significantly different in comparisons of eggs from summer and winter of 2001 and 2002 (Table 3). Eggs were larger in winter than in summer for both years. A posteriori Tukey's tests showed that when only comparing both winters, the egg-size mean values were not significantly different (volume: P=0.994; major axis: P=0.991; minor axis: P=0.999) (Table 3).

Regional variation

Oceanographic conditions Temperature and salinity varied among the 3 areas analyzed during each year, except in January 1988, when no significant difference in salinity was found (Table 4). During January of 1988 there was a weak SACW intrusion at Cape Frio (located in area 1) (Fig. 6), represented by the lowest SD in temperature calculated for this area. Area 1 was usually the coldest and saltiest area, owing to the stronger SACW intrusions in this area. Temperature and salinity values were not significantly different between areas 2 and 3 (Table 4).

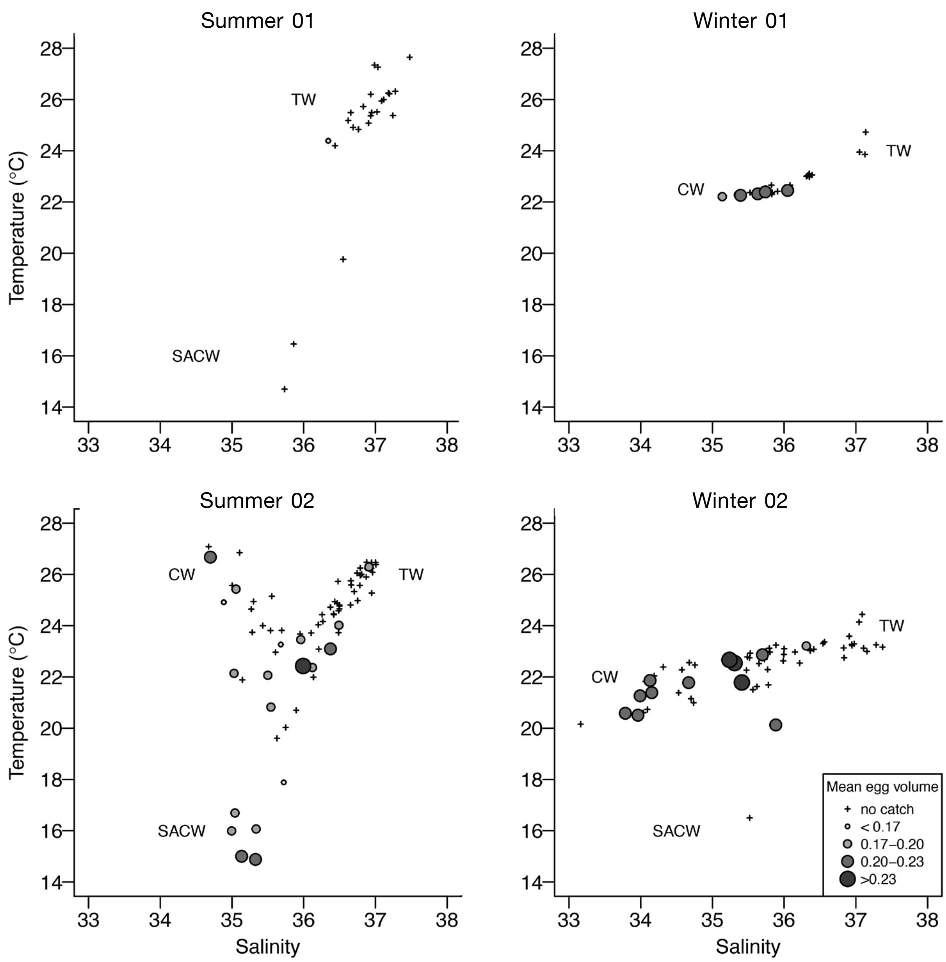

Figure 5

Temperature–salinity diagrams with mean volume of eggs (mm^3) of Argentine anchoita (*Engraulis anchoita*) per station in the southeastern Brazilian Bight sampled with ichthyoplankton tows during summer and winter of 2001 and 2002. Temperature and salinity were measured in situ at 10-m depth; TW=Tropical Water; SACW=South Atlantic Coastal Water; CW=Coastal Water.

Regional variation in eggs A total of 73,104 eggs of Engraulidae were collected. Argentine anchoita eggs represented 80.5% of all engraulid eggs sampled (n=58,826). They were sampled throughout the SBB, and their spatial horizontal distribution varied from one year to another (Fig. 7). Eggs of Argentine anchoita were collected over a wide range of temperatures and salinities in each area (Fig. 8).

A total of 8809 eggs of Argentine anchoita that were collected during the summer over 5 years and in all 3 areas were measured (Table 5). In a comparison of only areas 1 and 3, it was observed that, in general, eggs in area 3 were larger than eggs in area 1, with the exception of January 1988 when the opposite was found to be true. No size pattern was observed for eggs collected in area 2; egg sizes from this area were usually in between those of areas 1 and 3 and showed no significant differences in size when compared with eggs from other areas. During December of 1991 and January of 1993, eggs from area 2 were the largest sizes throughout the time period (Table 5, Fig. 8).

Discussion

Egg size varies among species and among populations because of temporal, biological, spatial, or environmental factors (or a combination of these factors). Within a species, planktonic egg size decreases as the spawning season progresses (Bagenal, 1971; Chambers and Waiwood, 1996). For species of Clupeiformes, this decrease in the egg size may be due to a reduction in maternal energy reserves over the spawning season, a switch in the stored energy from reproduction to

Table 4

Mean and standard deviation values of temperature (Temp. °C) and salinity (Sal.) and results from analysis of variance (ANOVA) and a posteriori paired Tukey's honestly significant difference (HSD) test that compared data from the 3 areas sampled (areas 1, 2, and 3) in the southeastern Brazilian Bight during the 5 years studied (December 1975, January 1988, December 1990, December 1991, and January 1993). *N* is the number of sampling stations considered. The 3 areas were from Cape Frio to São Sebastião Island (area 1), from São Sebastião Island to Paranaguá Bay (area 2), and from Paranaguá Bay to Cape Santa Marta Grande (area 3).

	Area			ANOVA		Tukey's HSD		
	1	2	3	*F*	*P*	2 vs. 1	3 vs. 1	3 vs. 2
Dec 75								
N	53	44	43					
Temp.	22.06 (2.17)	23.76 (0.97)	23.47 (0.87)	17.72	<0.01	0	0	0.65
Sal.	35.99 (0.67)	35.30 (0.76)	35.49 (0.94)	9.76	0	0	0	0.51
Jan 88								
N	24	35	19					
Temp.	24.16 (1.37)	26.40 (1.34)	25.40 (2.93)	10.41	0	0	0.08	0.15
Sal.	35.41 (0.33)	35.22 (0.60)	35.14 (0.73)	1.27	0.29			
Dec 90								
N	25	40	24					
Temp.	22.71 (1.92)	24.81 (0.56)	24.12 (2.78)	10.44	<0.01	0	0.02	0.31
Sal.	35.95 (0.63)	34.84 (0.63)	34.74 (0.86)	24.37	<0.01	0	0	0.86
Dec 91								
N	33	48	29					
Temp.	20.34 (2.94)	24.47 (1.91)	24.15 (1.86)	36.11	<0.01	0	0	0.81
Sal.	36.25 (0.70)	35.49 (0.68)	35.54 (0.52)	24.11	<0.01	0	0	0.06
Jan 93								
N	32	47	29					
Temp.	21.33 (3.33)	25.13 (1.79)	24.55 (2.82)	21.11	<0.01	0	0	0.62
Sal.	36.01 (0.55)	35.12 (0.59)	34.91 (0.47)	36	<0.01	0	0	0.25

growth, seasonal changes in the age structure of the spawning populations, changes during oogenesis that are correlated with some environmental conditions (e.g., temperature, photoperiod, and food supply) (Blaxter and Hunter, 1982; Chambers, 1997) or a co-occurrence of these factors, as suggested by Llanos-Rivera and Castro (2004) for eggs of anchoveta (*Engraulis ringens*) off the Chilean coast. Ciechomski (1973), who reported that the volume of eggs of Argentine anchoita off the Argentinian and Uruguayan coast decreased 23% throughout the spawning season, probably owing to multiple spawning or length composition of the spawners (or both) correlated with the differences in growth rate in relation to temperature.

Egg size increases with latitude, as shown by Llanos-Rivera and Castro (2004) who studied anchoveta from Chile and by Ciechomski (1973), who showed that egg size of Argentine anchoita increased from the north (35–36°S) to the south (40–41°S) and that this increase was not correlated with temperature or salinity because both parameters were similar throughout the area sampled. Egg size typically varies inversely with temperature and salinity, as has been shown for European anchovy (*Engraulis encrasicolus*) by Demir (1974) and for Argentine anchoita by Phonlor (1984). In our results, area 1, which usually exhibited the lowest temperature and highest salinity values, was the area that had the smallest eggs in 4 out of 5 years sampled. The exception occurred in January 1988, when the largest eggs were collected in that area. January 1988 was also a period of a weak SACW intrusion at Cape Frio (Fig. 6), which is reflected by greater temperature variability (SD, Table 4). Temperatures and salinities were similar throughout the 3 areas during this period in 1988. Conversely, in area 3 the highest temperature and lowest salinity values were found, and this area usually had the largest eggs. It is important to highlight that area 3 encompasses most of the *bonaerense* stock, whereas area 1 contains only the Brazilian Southeastern Bight stock. According to Carvalho and Castello (2013), who analyzed fewer samples than we did, the boundary between the Brazilian Southeastern Bight stock and the *bonaerense* stock (~27°S) is not well defined. Because the geographic limits of each stock are not clear, and the eggs from area 2 exhibited no consistent pattern, with the largest eggs in some samples, or with egg sizes exhibiting no significant differences between area 1 or area 3, area 2 was considered a transition zone, and will not be considered further in this discussion.

Individual Argentine anchoita from southeastern Brazil (22–27°S) were shorter at comparable ages than

Table 5

Mean and standard deviation values of the major axis (mm), minor axis (mm), and volume (mm^3) of eggs of Argentine anchoita (*Engraulis anchoita*) obtained in the southeastern Brazilian Bight in December 1975, January 1988, December 1990, December 1991 and January 1993 and results from analysis of variance (ANOVA) and a posteriori paired Tukey's honestly significant difference (HSD) test that compared data from the 3 areas sampled (areas 1, 2, and 3) during the 5 years studied. The 3 areas were from Cape Frio to São Sebastião Island (area 1), from São Sebastião Island to Paranaguá Bay (area 2), and from Paranaguá Bay to Cape Santa Marta Grande (area 3). *N* is the number of eggs measured.

	Area			ANOVA		Tukey's HSD		
	1	2	3	*F*	*P*	2 vs. 1	3 vs. 1	3 vs. 2
Dec 75								
N	437	139	322					
Major axis	1.022 (0.06)	1.021 (0.06	1.037 (0.05)	7.58	<0.01	0.99	0	0.01
Minor axis	0.523 (0.03)	0.515 (0.02)	0.533 (0.03)	26.36	<0.01	0.01	0	0
Volume	0.147 (0.02)	0.142 (0.02)	0.155 (0.02)	22.62	<0.01	0.06	0	0
Jan 88								
N	532	1123	398					
Major axis	1.111 (0.06)	1.066 (0.05)	1.077 (0.05)	124.1	<0.01	0	0	0
Minor axis	0.548 (0.03)	0.551 (0.03)	0.536 (0.03)	32.57	<0.01	0.19	0	0
Volume	0.176 (0.02)	0.171 (0.03)	0.163 (0.03)	33.41	<0.01	0	0	0
Dec 90								
N	249	400	651					
Major axis	1.096 (0.06)	1.114 (0.05)	1.121 (0.05)	18.33	<0.01	0	0	0.09
Minor axis	0.553 (0.03)	0.560 (0.03)	0.566 (0.03)	19.13	<0.01	0.01	0	0
Volume	0.177 (0.03)	0.184 (0.03)	0.189 (0.02)	22.97	<0.01	0	0	0
Dec 91								
N	132	544	557					
Major axis	1.052 (0.05)	1.044 (0.06)	1.043 (0.06)	1.33	**0.26**			
Minor axis	0.511 (0.03)	0.534 (0.03)	0.526 (0.03)	30.68	<0.01	0	0	0
Volume	0.145 (0.02)	0.157 (0.03)	0.152 (0.02)	16.77	<0.01	0	0	0
Jan 93								
N	391	1583	1351					
Major axis	1.066 (0.06)	1.077 (0.05)	1.053 (0.05)	74.40	<0.01	0	0	0
Minor axis	0.533 (0.03)	0.564 (0.04)	0.545 (0.03)	223.30	<0.01	0	0	0
Volume	0.160 (0.02)	0.184 (0.02)	0.164 (0.02)	219.30	<0.01	0	0	0

those from southern Brazil (30–35°S) (Carvalho and Castello, 2013). The southern region also exhibited a more diverse age composition, with older individuals ranging up to age 4, whereas the southeastern region had a predominance of 1-year-old anchovies (Carvalho and Castello, 2013). In relating sizes of females to eggs, 2 possibilities can occur: 1) larger females produce larger eggs (e.g., Ciechomski, 1966) or, 2) relative fecundity is higher in larger females (e.g., Pájaro et al., 1997). Knowing that the individuals from the *bonaerense* stock are larger than those making up the southeastern stock, it is possible to infer that eggs from area 3 would be larger than those from area 1 as a result of the differences in the composition of the respective maternal stocks.

In the SBB, the Argentine anchoita spawns year-round and peak spawning occurs during late spring and early summer (Matsuura et al., 1992). The Argentine anchoita is a semimigratory species that carries out trophic and reproductive migrations (Ciechomski, 1973) and no physical barriers exist that would prevent individual fish from moving between areas. During the austral winter, adults of Argentine anchoita migrate from Uruguayan and Argentinean waters off the Plata River (35–34°S) to Brazilian waters (34–29°S) where favorable spawning and feeding conditions prevail. They return southward in late spring (Lima and Castello, 1995). Even though our study area was north of the one described by Lima and Castello (1995), there is an equatorward flow of the colder and fresher Plata plume water in the inner shelf (Piola et al., 2008a; Piola et al., 2008b). This flow can transport biota of benthic and planktonic origin, such as species of Foraminifera, ostracods, and microbivalves, from cold and temperate waters to a tropical bay located at around 23°S (Stevenson et al., 1998). In addition, the Plata River estuarine front is well documented as an important area for feeding for Argentine anchoita because

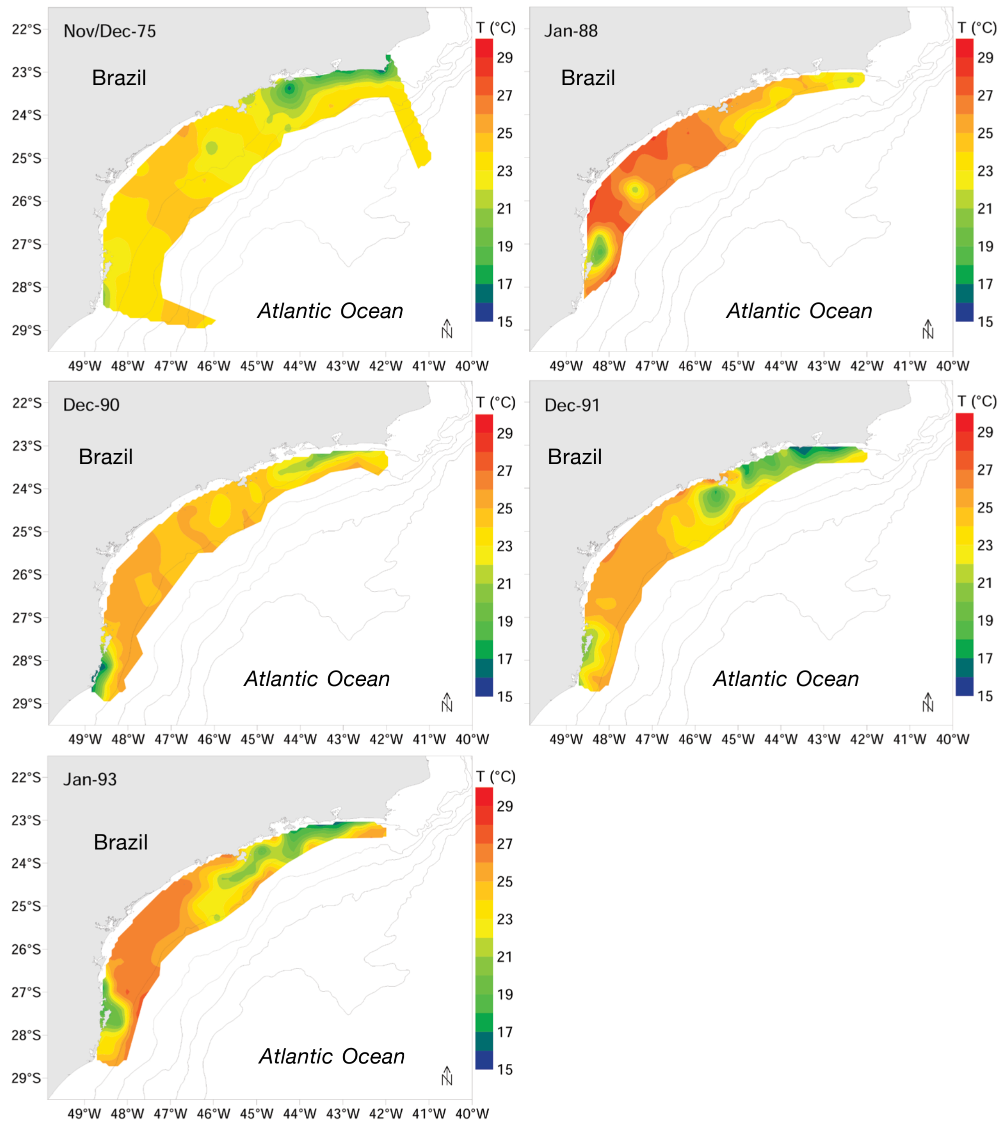

Figure 6

Horizontal distribution of temperature (°C) at a 10-m depth from in situ measurements taken during cruises conducted in the southeastern Brazilian Bight in 1975, 1988, 1990, 1991, and 1993.

the highest stomach fullness values were found at stations close to the surface salinity front (Padovani et al., 2011).

The satellite images in Figures 2 and 3 probably indicate the flow of Plata plume water carrying chlorophyll from the south to the north during the winter on the inner shelf. This flow could be guiding the migration of the Argentine anchoita northward, which also happens during the winter. Because the eggs collected during the winter are larger than those from the summer, one possibility for this difference is that larger adults coming from the south would be spawning in or closer to the study area in winter, but no conclusion can be made with the data from this study because there have been no studies in which the length and age structure of Argentine anchoita have been compared during different seasons in the SBB, nor have there been any genetic studies to differentiate the stocks of this species.

Seasonal variation in egg size may also be an adaptive response to the changes in the abiotic conditions that the eggs will encounter. An increase in temperature decreases the incubation period (time from fertilization to hatching), and a decrease in egg size decreases the incubation period (Wootton, 1990). In our results, temperature and salinity were higher during the summer than during winter for both years and, as expected, the eggs were smaller. Smallest eggs in populations spawning during the summer were also observed in the Atlantic herring (*Clupea*

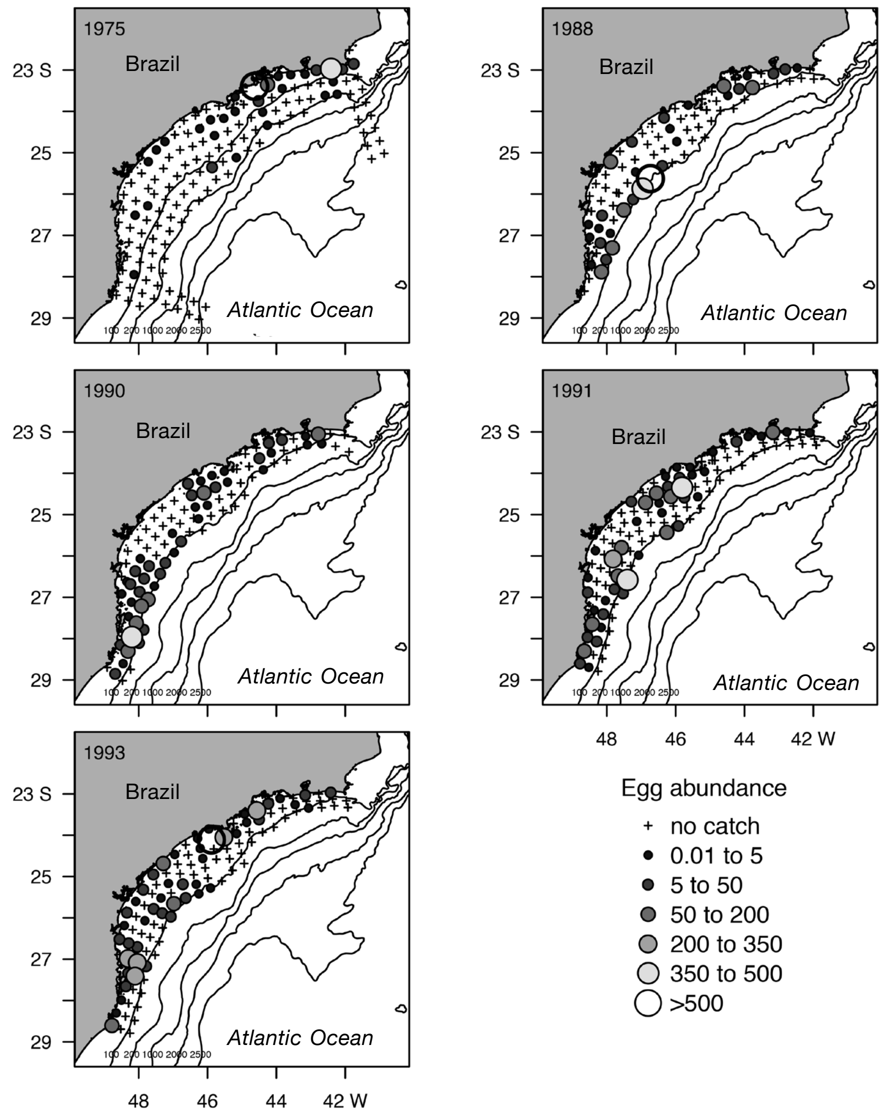

Figure 7

Spatial distribution of abundance of eggs (eggs/m²) of Argentine anchoita (*Engraulis anchoita*) sampled in the southeastern Brazilian Bight with ichthyoplankton tows during 1975, 1988, 1990, 1991, and 1993.

harengus) in the North Atlantic (Blaxter and Hempel, 1963).

The regional variations in the egg size of Argentine anchoita were probably a result of the differences in the stocks analyzed, whereas the reasons behind these seasonal variations remain unknown. At least 2 possibilities exist that would explain the observed seasonal variation in egg size of Argentine anchoita: differences in the maternal stock (e.g., migration northward of larger adults during the winter) and abiotic variability (e.g., temperature variability). As noted above, further studies are necessary to confirm our hypotheses, including comparisons between the size composition of the adults of the different seasons and the different areas, as well as genetic studies. The information that the regional variability in egg size may be caused due to different aspects of the stocks analyzed may be useful for management purposes.

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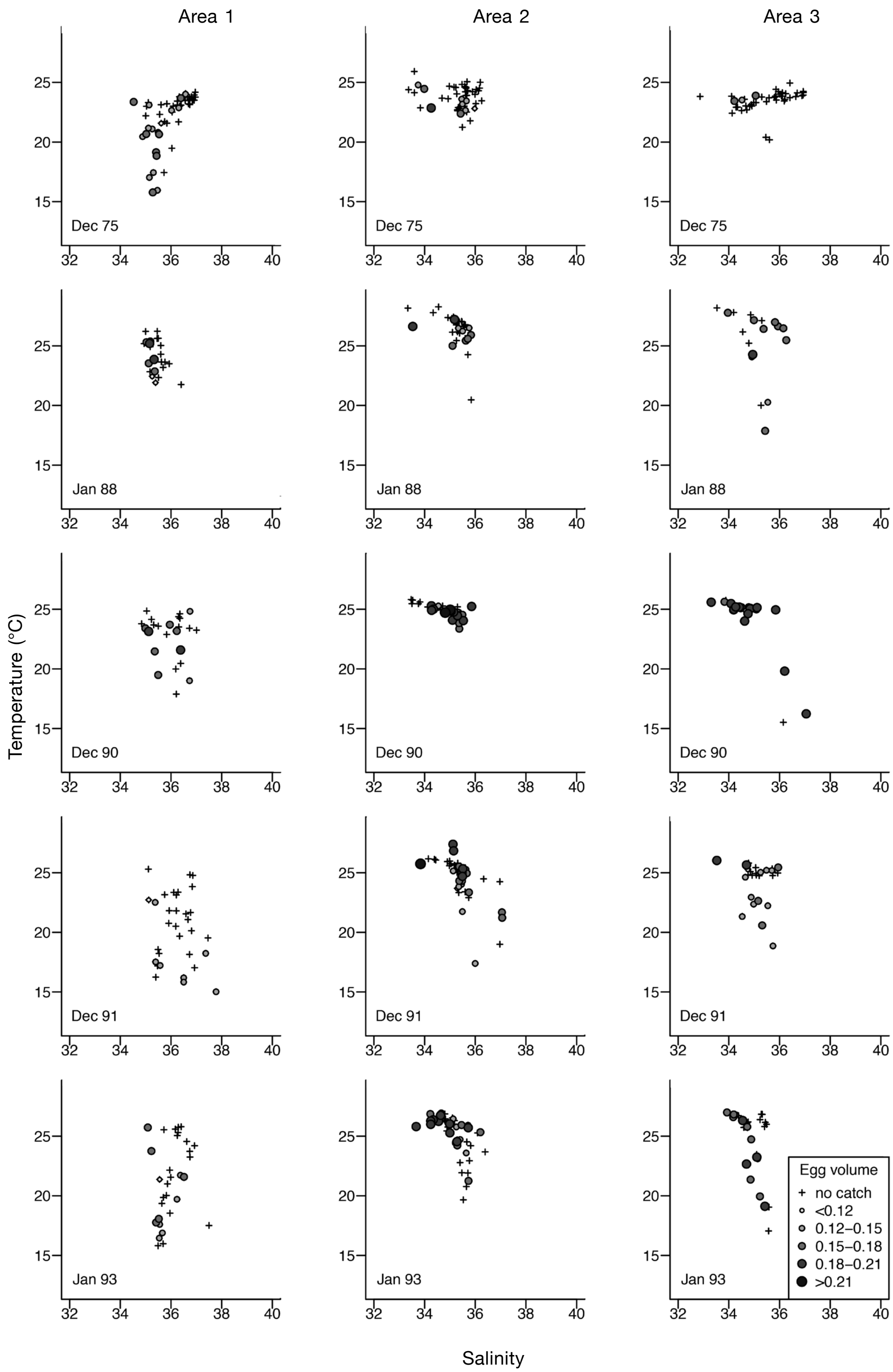

Figure 8

Temperature–salinity diagrams with mean volume of eggs (mm^3) of Argentine anchoita (*Engraulis anchoita*) per sampling station for the 3 areas sampled in the southeastern Brazilian Bight with ichthyoplankton tows in 1975, 1988, 1990, 1991, and 1993.

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