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Ichthyoplankton community structure on the shelf break off northeastern Brazil

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Abstract: Oceanographic features influence the early stages of fish to a high degree. We investigated the influence of continental shelf-slope gradient on the ichthyoplankton composition and distribution off Northeastern Brazil. Two oceanographic campaigns were performed during July-August 2010 and 2012. The samplings were performed along three transects composed by three stations, covering the continental shelf and slope areas. Abiotic data were obtained by an ADCP and a CTD. The ichthyoplankton was sampled through diurnal and nocturnal hauls using a 500-µm bongo net from 200 m to the surface. A total of 1634 larvae and 4023 eggs, representing 91 genera and 76 species, were collected. Higher concentrations of fish eggs were found on the continental shelf, probably because of the North Brazil Undercurrent flux. Higher concentrations of larvae were found at night and could be associated with net avoidance or natural variation. Neritic, oceanic and transition groups of species association were determined. Larvae of neritic, demersal and pelagic fishes prevailed on the continental shelf, while larvae of oceanic, mesopelagic and bathypelagic fishes on the continental slope. Melanostomiidae, *Scorpaena* sp., *Lestidium atlanticum*, *Lampadena* sp. and *Diaphus* sp. were identified as indicators of the continental slope.

Key words: continental shelf-slope gradient, early life stages of fishes, indicator species, spatial distribution.

INTRODUCTION

The ichthyoplankton is composed by fish eggs and larvae and constitutes a major component of the meroplanktonic communities (Ciechomski 1981). The spatial distribution of the ichthyoplanktonic assemblage is highly influenced by mesoscale physical processes commonly occurring over continental shelf break areas, such as eddies or density fronts (Grimes & Finucane 1991, Sabatés & Olivar 1996). Temperature and salinity may also play important roles in the structure of the ichthyoplanktonic assemblages (Osorio-Zúñiga et al. 2018).

Studies related to the influence of mesoscale physical processes over biological communities are still inceptive in the South Atlantic waters and concentrate at the southern portion of the Atlantic basin (e.g. Franco et al. 2006, Acha et al. 2004). In the Brazilian waters, such studies were mainly performed over continental shelf break areas of the Southern region (e.g. Muelbert & Sinque 1996, Macedo-Soares et al. 2014). The relationships among mesoscale physical processes and biological communities remain poorly understood at the western tropical Atlantic waters off Northeast Brazil.

The shelf break and continental slope regions in northeastern Brazil are dominated by oligotrophic warm waters (Peterson & Stramma 1991), which leads to low biological productivity (e.g. Lessa et al. 2009, Knoppers et al. 2002, Souza et al. 2013) yielding ~ 75 g C m^{-2} y^{-1} (Longhurst et al. 1995).

Commonly, coastal areas receive nutrients through the influx of rivers in association with mangrove ecosystems (Ekau et al. 1999), while oceanic areas are richer in nutrients in places where upwelling occurs, e.g. around islands and seamounts (Ekau et al. 1999, Knoppers et al. 2002), since this process weakens the stratification of the water column, allowing nutrients in deeper layers to reach surface waters. This enrichment may also occur at the region of the shelf break owing to the dynamics of physical processes, which may interfere in the ichthyoplanktonic biomass (e.g. González-Quirós et al. 2003, Franco et al. 2006, Katsuragawa et al. 2014). Nevertheless, physical processes such as meanders and vortices may transport fish larvae from one area to another, as from the continental shelf to oceanic waters, influencing the abundance and composition of fish larvae assemblages of different areas (Franco et al. 2006).

The intense fishery accentuates the necessity of investigations on early stages of fishes, as well as on their relationship with physical and biological processes, to achieve a better comprehension of the variability in the recruitment of fishery resources (Hunter & Alheit 1997). Physical and biological processes that occur in the shelf break are primordial to the recruitment of some fish species, granting the regulation of some of its populations (González-Quirós et al. 2003). Although the number of studies related to the ichthyoplankton at shelf break areas at the Southern region of Brazil is increasing (e.g. Franco & Muelbert 2003, Franco et al. 2006, Katsuragawa et al. 2014), at the Northeastern region it is only inceptive.

The Northeastern Brazilian continental shelf concentrates many commercially and ecologically important species, such as the catfish, needlefish, tuna fish and others (Nóbrega & Lessa 2007). In the Northeast, although the fishery is intense, especially in the continental shelf (Nóbrega & Lessa 2007), there is scarcity of works focusing on the relationship among the ichthyoplankton distribution and physical-biological processes occurring in the region.

Based on this, the present work aims to investigate a potential gradient in the distribution and structure of the ichthyoplanktonic assemblage among the outer continental shelf and the deep continental slope, as well as the influence of the environmental variables over the ichthyoplankton at such domains.

MATERIALS AND METHODS

Study area

The neritic (shelf) and oceanic (slope) areas off the States of Pernambuco (PE), Paraíba (PB) and Rio Grande do Norte (RN) are located at the northwest South Atlantic. The continental shelf in the northeastern region of Brazil is on average 40 – 50 km wide and its depth is under 40 meters in most of its extension. The continental slope is on average 85 – 105 km wide, with a maximum width of 140 km in the adjacencies of the Pernambuco plateau. The continental rise is located between 4800 – 5200 meters' depth (Coutinho 2009).

The relief of the continental shelf is flat and alternated with a wavy bottom, fields of sandwaves and irregular features of calcareous algae (Coutinho 2009). These areas are under the influence of warm waters belonging to the North Brazil Undercurrent (NBUC). The NBUC is the northern limb of the bifurcation of the south branch of the South Equatorial Current (sSEC), while the south limb becomes the Brazil Current (BC) (Veleda et al. 2012, Stramma et al. 2005).

The NBUC flows below 50 m and may reach 900 m (Veleda et al. 2012). It presents a maximum flow in July and a minimum during the period of October to November, when its mean flow structure is well developed in the latitude of 11°S (Schott et al. 2005). In the proximities of the Equator, the east branch of the South Equatorial Current (eSEC) overlaps the nuclei of subsurface of the NBUC and forms the North Brazil Current (NBC), intensified at the surface (Stramma & England 1999).

Collecting methods

The samplings were performed during the period of July and August of 2010 and 2012 aboard of the Brazilian Navy's NHo Cruzeiro do Sul vessel, during the execution of the Camadas Finas I and II projects. Three transects of profiles perpendicular to the coastline were designed. The transect 1 (south) was located off the borders of the States of Pernambuco and Paraíba; the transect 2 (central) was located off the Paraíba State; and the transect 3 (north) was located off the borders of the States of Paraíba and Rio Grande do Norte. Each transect consisted of three stations positioned over different isobaths (Figure 1). One station was considered neritic and was located on the outer continental shelf (A), with depths varying between 40 – 70 m. The other stations were considered oceanic and were located on the upper continental slope (B), with depths varying between 200 – 500 m, and on the deep continental slope (C), with depths varying between 600 – 900 m. The samplings were performed at each station during the diurnal and nocturnal periods.

A Seabird 9 Plus CTD was used to obtain temperature, salinity, dissolved oxygen, fluorescence and water density profiles. Measurements of current flow speed and direction were obtained throughout the whole area among the transects by means of an Ocean Surveyor Broadband/Narrowband ADCP (Acoustic Douppler Current Profiler).

The ichthyoplankton was sampled through diurnal and nocturnal double oblique tows from surface to 200 m on the continental slope or to a depth at 10 m from the bottom on the continental shelf to prevent the equipment from damage. The depth of the Bongo was controlled by calculating the amount of necessary towing cable to be lowered on the water by correcting for the inclination angle using an inclinometer. On the continental slope, the Bongo was lowered once and on the continental shelf the Bongo was lowered twice to increase the volume

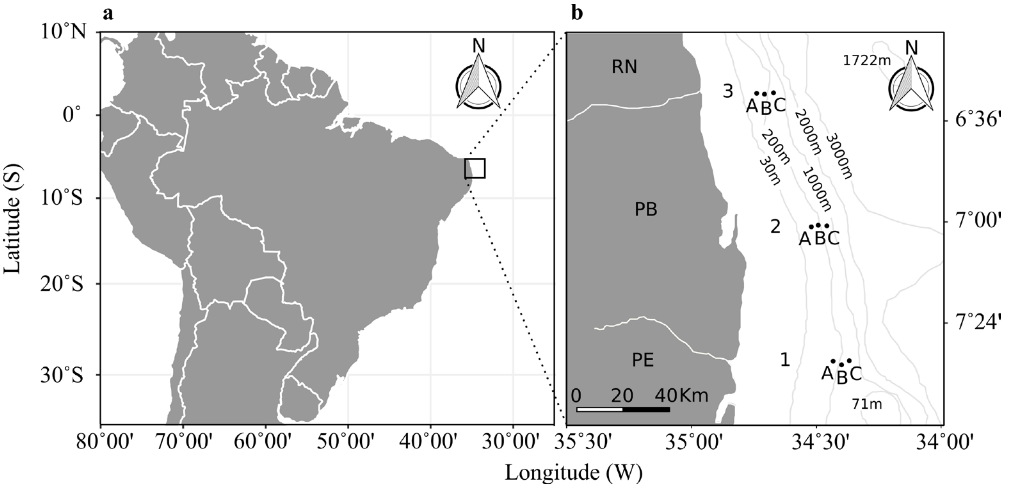

Figure 1. (a) Location of the study area in the South America and (b) positioning of the oceanographic stations in the regions of the outer continental shelf (A) and continental slope (B and C) in the western Tropical Atlantic, Brazil.

of water filtered. The Bongo was equipped with nets of 500 µm and 300 µm mesh size and had an opening diameter of 60 cm. A flowmeter was attached to the mouth of the bongo net to assess the total volume filtered by the tow. The samples were fixed in borax-neutralized formaldehyde in a final concentration of 4%. Only the samples collected with the 500 µm net were considered, yielding a total of 36 analyzed unity samples.

All larvae were sorted under the stereomicroscope and identified to the lowest possible taxonomic level with basis on the specialized literature (e.g. Neira et al. 1998, Leis & Carson-Ewart 2002, Richards 2006). All larvae were deposited in the Ichthyoplankton Collection (COLICT) of the Museu de Oceanografia Petrônio Alves Coelho (MOUFPE) of the Universidade Federal de Pernambuco (UFPE). For all the individuals, a morphometric, meristic and morphologic characterization was performed, and linear dimensions were measured using a micrometric ocular, aiming to help in the identification process. The individuals were sorted in relation to the degree of the notochord flexion (pre-flexion, flexion and post-flexion stages), according to Miller & Kendall Jr. (2009).

Data analysis

The species richness was calculated using the Margalef index (Margalef 1957) (D_{Mg}), the specific diversity index (H') according to Shannon (1948) and the equitability (J') according to Pielou (1984).

The comparisons of the total density of fish eggs and larvae, as well as of the D_{Mg}, H' and J' between isobaths, years and day period were carried out by means of the Fisher-Pitman permutation test. A total of 4999 permutations were performed using the Monte-Carlo resampling procedure. The Fisher-Pitman permutation test has the advantage of being free of the assumptions underlying the parametric correspondent F test.

The method of the non-parametric permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001) was used to investigate the existence of differences in the structure of the fish larvae assemblage in relation to the sampled distances (outer continental shelf and continental slope), day period (diurnal and nocturnal periods) and transects (1, 2 and 3). The PERMANOVA was performed with basis on a Hellinger distance matrix, which is the Euclidian distance calculated on the biological matrix transformed by Hellinger, as described in Legendre & Gallagher (2001). This distance was adopted since its use has been recommended for community composition data. A total of 999 permutations were performed. Prior to the PERMANOVA, an analysis of multivariate homogeneity of groups dispersions (Anderson 2006) was performed to test if the assumption of homogenous groups dispersions was fulfilled. As the PERMANOVA is sensitive to differences in the dispersion of the observations (Anderson 2001), the analysis was performed only in those cases in which the groups dispersions were homogenous.

Aiming to investigate the existence of species associated to individual or combinations of isobaths an Indicator Value analysis (IndVal) (Dufrêne & Legendre 1997) extended for combination of groups (de Cáceres et al. 2010) was performed. The significance of the associations of the species and isobaths was tested by means of permutation tests based on 999 permutations.

To investigate the existence of groups of species association, a non-hierarchical cluster analysis was performed in R mode using species that occurred at least twice on the samples. The method of the k means partitioning was adopted and different numbers of groups were considered in the analysis. For each number of groups tested, 100 initial random configurations were used. The Calinski-Harabasz criterion was adopted to define the best number of groups of species association and the Kendall coefficient of concordance W was calculated for each group and tested for significance by means of a permutation test (Legendre 2005).

All the univariate and multivariate statistical analyses were performed using the R (R Core Team 2016) and RStudio Softwares implemented with the packages “coin” (Hothorn et al. 2008), “indicspecies” (de Cáceres & Legendre 2009) and “vegan” (Oksanen et al. 2016).

RESULTS

Hydrography

There was little variation in temperature and salinity among the different transects, which characterizes a general pattern of warm surface waters with a thermocline beginning at 75 – 100 m at the continental slope areas. On the continental shelf, no thermocline was found.

The amplitude variation of the fluorescence values was narrower at the outer continental slope area (with minimum values varying between 0.07 and 0.31 µg L^{-1} and maximum values varying between 0.11 and 0.95 µg L^{-1}). At the continental slope areas, minimum values of fluorescence between 0.00 and 0.12 µg L^{-1} and maximum values of fluorescence between 0.40 and 1.05 µg L^{-1} were detected. At most of the stations over the continental slope areas, the fluorescence peaks coincided with the depth of onset of the thermocline (75 – 100 m). In a few cases, the fluorescence peak was slightly above or under the depth of onset of the thermocline. At the continental shelf area, the fluorescence maximum was always close to the bottom (45 – 58 m).

Two water masses were found throughout the sampled isobaths, the Tropical Surface Water (TSW), which presents temperature values higher than 20˚C and salinity higher than 36, and the South Atlantic Central Water (SACW), which presents temperature values between 6 and 20˚C and salinity between 34.5 and 36. On the continental shelf stations, only the TSW was found and it extended from the surface to the bottom. At the continental slope stations, the TSW and SACW were present. The TSW extended from the surface to a depth of 115 – 177 m and the SACW occurred from a depth ranging between 123 and 179 m and extended to the deepest sampled depths (200 m).

The surface circulation pattern has not varied throughout the transects and isobaths. Comparing the years, however, there was a slight variation on the intensity and direction of the current. In 2010, the surface current flowed northward-northwestward with a small inclination angle in relation to the magnetic north (i.e., alongshore) and slightly stronger flux, with speeds of approximately 0.5 m s^{-1} (Figure 2). In 2012, the surface current flowed basically westward towards the coastline (i.e., onshore), throughout the whole study area, with a mean current speed of 0.3 m s^{-1}.

Ichthyoplanktonic assemblage and spatial distribution

A total of 4023 fish eggs and 1634 fish larvae were collected and these represented 59 families, 91 genus and 76 species (Table I). Regarding the stage of notochord flexion, most of the larvae were in the flexion stage (62.4%), followed by the pre-flexion stage (33.3%) and post-flexion stage (1.3%). A portion of 3% of the larvae were damaged and could not be classified according to the stage of notochord flexion. Most of the larvae in the flexion stage were found on the deep continental slope (45.5%), and on the upper

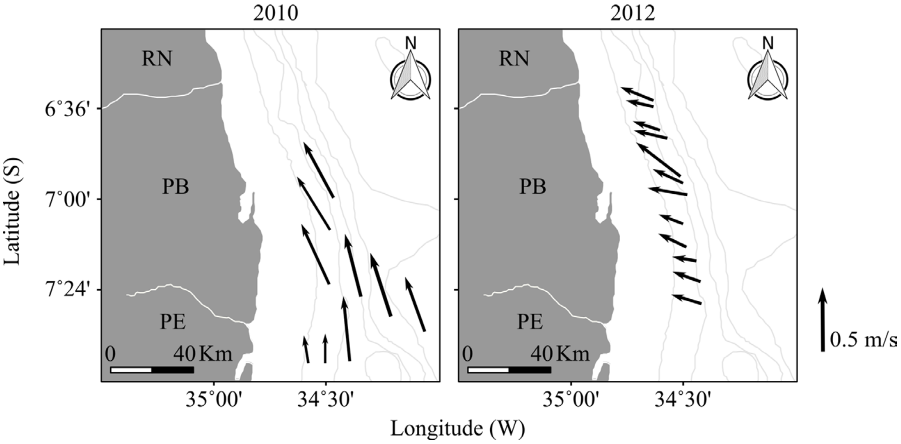

Figure 2. Surface circulation pattern (30 m) in the area between the transects during the sampling periods of 2010 and 2012.

continental slope (40.3%), with the remaining 12.2% on the outer continental shelf. In the preflexion stage, the pattern was the same with 45.5% on the deep continental slope, and 35.4% on the upper continental slope and 19.1% on the outer continental shelf. In relation to the postflexion stage, most of the larvae concentrated on the deep continental slope (55%), followed by the outer continental shelf (25%) and upper continental slope (20%).

The most frequent species were *Diaphus* sp. 1 (82.4%), *Diaphus* sp. 2 (67.7%), *Decapterus punctatus* (41.2%), *Lampadena* sp. 2 and *Sparisoma* sp. (35.3%). The species *Diaphus* sp. 1 was the most abundant in the transects 1 (31%) and 2 (30%), while the family Sciaenidae was the most abundant in the transect 3 (18.7%).

At the outer continental shelf, the taxonomic groups that prevailed were mainly demersal and pelagic fishes belonging to families such as Sciaenidae (max. of 28.8 larvae 100 m^{-3}), Serranidae (average 0.9 larvae 100 m^{-3}; max. of 6.3 larvae 100 m^{-3}), Mullidae (max. of 6.3 larvae 100 m^{-3}), among other families associated to coral reefs (Holocentridae, Sygnathidae, Apogonidae) and species associated to estuaries such as *Opisthonema oglinum* and *Dormitator maculatus*. However, oceanic and bathypelagic species belonging to the genera *Diaphus* and *Lampadena* (Myctophidae) also occurred.

The areas of the continental slope, on the other hand, were more characterized by the presence of oceanic mesopelagic and bathypelagic taxonomic groups. The species *Diaphus* sp. 1 (max. of 26.7 larvae 100 m^{-3}) and *Lampadena* spp. (max. of 1.5 larvae 100 m^{-3}), in addition to non-identified myctophids (max. of 24.2 larvae 100 m^{-3}), presented an increase in density towards the oceanic areas. Furthermore, several oceanic species occurred exclusively in the continental slope areas, such as *Lestidium atlanticum*, *Cyclothone braueri*, *Hygophum reinhardtii*, *Myctophum asperum*, *Chiasmodon niger*, *Katsuwonus pelamis*, *Ranzania laevis*, among other. The number of taxonomic groups occurring in the continental slope was considerably higher than the number occurring in the outer continental shelf and this trend was statistically confirmed.

The species richness (D_{Mg}) was significantly higher at the continental slope areas (Fisher-Pitman permutation test, $p < 0.05$). At these areas, the D_{Mg} values varied between 0.75 and 13.7 with averages of 5.7 and 6.6 at the upper and deep continental slope, respectively. At the outer continental shelf, it varied between 0 and 7.7, with an average of 3.1. The period of day and the year of sampling had no effect on the species richness. No difference in the values of species diversity (*H'*) and equitability (*J'*) was found among the outer continental shelf and the upper and deep continental slope areas. The day period, as well as the year of sampling had also no effect on *H'* and *J'*.

The spatial distribution of the fish eggs was not homogenous throughout the outer continental shelf and continental slope areas and considerably higher values were found on the outer continental shelf (Fisher-Pitman permutation test, $p < 0.05$; Figure 3). An average of 182.5 eggs 100 m^{-3} (median of 167 eggs 100 m^{-3}) was found on the outer continental shelf, with minimum and maximum values of 9.7 and 428 eggs 100 m^{-3}, respectively. On the upper continental slope, an average of 47.2 eggs 100 m^{-3} (median of 20.4 eggs 100 m^{-3}), with minimum of 0.3 and maximum of 249.4 eggs 100 m^{-3} was found. On the deep continental slope, an average of 7.7 eggs 100 m^{-3} (median of 5 eggs 100 m^{-3}), with minimum of 0 and maximum of 25.7 eggs 100 m^{-3} was found.

This pattern of decrease in density values from the outer continental shelf towards the continental slope was not observed for the fish larvae (Fisher-Pitman permutation test, $p > 0.05$; Figure 3). Nevertheless, higher values of total density of fish larvae were observed during the nocturnal period (Fisher-Pitman permutation test, $p < 0.05$), as well as different community structures during the diurnal and nocturnal periods (PERMANOVA, $p < 0.05$). An average of 12.8 larvae 100 m^{-3} (median of 11.2 larvae 100 m^{-3}) was found during the diurnal period, with a minimum of 1.5 and maximum of 37.2 larvae 100 m^{-3}. During the nocturnal period, an average of 23.2 larvae 100 m^{-3} (median of 15 larvae 100 m^{-3}), with a minimum of 1.5 and maximum of 76.8 larvae 100 m^{-3} was found.

Table I. List of taxonomic groups, frequency of occurrence (%) and mean density in the isobaths A (outer continental shelf), B (upper continental slope) and C (deep continental slope). FO – frequency of occurrence; – average density (ind. 100 m^{-3}); MD – maximum density (ind. 100 m^{-3}); n.i. – non-identified at the species level.

	Taxonomic groups	Isobath A (40 – 70 m)			Isobath B (200 – 500 m)			Isobath C (600 – 900 m)		
		FO		MD	FO		MD	FO		MD
Albulidae	n.i.	0	0	0	0	0	0	9.1	0	0.2
Anguilliformes	n.i.	16.7	0.2	1.2	27.3	0.1	0.6	9.1	0	0.2
Nettastomatidae	*Saurenchelys* sp.	0	0	0	9.1	0	0.4	9.1	0	0.3
Engraulidae	*Anchoa* sp.	8.3	0.1	1.2	18.2	0.2	1.1	36.4	0.2	1.2
	n.i.	0	0	0	9.1	0	0.5	27.3	0.1	0.3
Clupeidae	*Opisthonema oglinum*	8.3	0.1	1.2	0	0	0	9.1	0	0.2
	n.i.	0	0	0	36.4	0.2	1.5	27.3	0.1	0.5
Gonostomatidae	*Cyclothone braueri*	0	0	0	18.2	0.1	0.4	18.2	0	0.2
	Cyclothone pseudopallida	0	0	0	9.1	0	0.4	0	0	0
	Cyclothone sp.	0	0	0	0	0	0	9.1	0	0.2
	Manducus maderensis	0	0	0	0	0	0	18.2	0	0.3
	n.i.	0	0	0	9.1	0	0.4	9.1	0	0.3

Table I. (Continuation)

Sternoptychidae	*Sternoptyx* sp.	0	0	0	0	0	0	9.1	0	0.5
Phosichthyidae	n.i.	0	0	0	9.1	0	0.3	0	0	0
Stomiidae	Melanostomiinae	0	0	0	36.4	0.4	2.6	0	0	0
	Astronesthinae	8.3	0	0.4	0	0	0	0	0	0
	n.i.	8.3	0.1	0.7	18.2	0.1	0.5	9.1	0.1	1.1
Scopelarchidae	*Benthalbella infans*	0	0	0	0	0	0	9.1	0	0.3
	Scopelarchus guentheri	0	0	0	9.1	0	0.2	0	0	0
	n.i.	0	0	0	0	0	0	9.1	0	0.3
Paralepididae	*Arctozenus risso*	8.3	0	0.4	0	0	0	9.1	0	0.2
	Lestidiops jayakari	0	0	0	0	0	0	9.1	0	0.2
	Lestidiops mirabilis	0	0	0	0	0	0	18.2	0	0.2
	Lestidium atlanticum	0	0	0	18.2	0.1	0.4	45.5	0.3	1
	Lestrolepis intermedia	0	0	0	0	0	0	9.1	0.1	0.6
	Lestrolepis sp.	0	0	0	0	0	0	9.1	0	0.2
	Uncisudis advena	0	0	0	0	0	0	9.1	0	0.5
Myctophidae	*Benthosema suborbitale*	0	0	0	0	0	0	9.1	0	0.2
	Bolinichthys distofax	0	0	0	0	0	0	9.1	0	0.2
	Ceratoscopelus maderensis	0	0	0	0	0	0	9.1	0	0.5
	Ceratoscopelus warmingii	16.7	0.2	1.3	9.1	0	0.3	0	0	0
	Diaphus garmani	0	0	0	0	0	0	9.1	0	0.3
	Diaphus mollis	0	0	0	9.1	0	0.3	9.1	0	0.4
	Diaphus sp. 1	50	2.3	12.7	100	7.5	26.7	100	4.8	13.9
	Diaphus sp. 2	50	2.4	9.3	81.8	0.6	1.8	54.5	1.3	4.4
	Diaphus sp. 3	8.3	0.1	1.3	9.1	0.7	7.3	27.3	0.7	6.5
	Diaphus sp. 4	25	0.5	3.6	18.2	0.1	0.6	0	0	0
	Electrona risso	0	0	0	18.2	0	0.4	9.1	0	0.2
	Hygophum reinhardtii	0	0	0	18.2	0.1	0.3	0	0	0
	Hygophum sp.	0	0	0	0	0	0	9.1	0	0.2
	Lampadena luminosa	0	0	0	0	0	0	9.1	0	0.4
	Lampadena sp. 1	0	0	0	9.1	0	0.4	36.4	0.3	1.6
	Lampadena sp. 2	16.7	0.3	2.2	54.5	0.3	1	36.4	0.2	1.2
	Lampadena sp. 3	16.7	0.3	2.2	54.5	0.5	1.5	27.3	0.1	0.6
	Lampanyctus tenuiformis	0	0	0	0	0	0	9.1	0	0.4

Table I. (Continuation)

	Lepidophanes guentheri	0	0	0	9.1	0	0.2	0	0	0
	Lobianchia gemellarii	0	0	0	0	0	0	9.1	0	0.2
	Myctophum affine	0	0	0	0	0	0	9.1	0	0.3
	Myctophum asperum	8.3	0.1	0.7	18.2	0.1	0.5	18.2	0	0.3
	Myctophum nitidulum	0	0	0	0	0	0	9.1	0	0.2
	Myctophum obtusirostre	0	0	0	0	0	0	18.2	0.1	0.7
	Myctophum selenops	0	0	0	9.1	0	0.2	0	0	0
	Myctophum sp.	0	0	0	27.3	0.3	1.9	0	0	0
	Notoscopelus caudispinosus	0	0	0	9.1	0	0.3	0	0	0
	n.i.	25	0.5	3.1	45.5	2.9	24.2	63.6	1.4	7.7
Bregmacerotidae	*Bregmaceros atlanticus*	0	0	0	18.2	0.1	0.4	18.2	0.1	0.7
Moridae	n.i.	0	0	0	0	0	0	9.1	0	0.2
Ophidiidae	*Lepophidium* sp.	0	0	0	0	0	0	9.1	0	0.2
	Ophidion selenops	8.3	0	0.4	0	0	0	9.1	0	0.2
	n.i	0	0	0	9.1	0	0.3	9.1	0	0.2
Lophiidae	*Lophius gastrophysus*	8.3	0.1	1.3	0	0	0	0	0	0
Gigantactinidae	*Gigantactis* sp.	8.3	0.1	1.3	0	0	0	0	0	0
Mugilidae	*Mugil cephalus*	0	0	0	9.1	0	0.3	0	0	0
	Mugil sp.	8.3	0.1	0.8	27.3	0.2	1.9	18.2	0	0.2
	n.i.	8.3	0.1	1.3	9.1	0	0.3	18.2	0.1	0.7
Exocoetidae	*Parexocoetus brachypterus*	0	0	0	9.1	0	0.2	0	0	0
Anoplogastridae	*Anoplogaster cornuta*	0	0	0	9.1	0	0.2	0	0	0
Holocentridae	*Myripristis jacobus*	8.3	0.1	1.1	9.1	0	0.5	9.1	0	0.2
	Sargocentron bullisi	0	0	0	9.1	0.1	1.1	27.3	0.2	1.4
	n.i.	16.7	0.1	0.7	0	0	0	18.2	0	0.3
Syngnathidae	n.i.	8.3	0.1	1.2	9.1	0	0.4	9.1	0	0.2
Scorpaenidae	*Pontinus rathbuni*	0	0	0	9.1	0	0.4	0	0	0
	Pontinus sp.	16.7	0.3	2.5	0	0	0	9.1	0	0.2
	Scorpaena sp.	0	0	0	36.4	0.2	0.6	9.1	0	0.3
	n.i.	0	0	0	9.1	0	0.4	0	0	0
Serranidae	*Anthias nicholsi*	8.3	0	0.4	9.1	0	0.4	27.3	0.2	1
	Anthias sp.	0	0	0	9.1	0.1	0.6	9.1	0	0.2
	n.i.	33.3	0.9	6.3	36.4	0.3	1.1	54.5	0.6	3.6
Opistognathidae	*Opistognathus* sp.	0	0	0	9.1	0	0.3	0	0	0

Table I. (Continuation)

Priacanthidae	n.i.	33.3	0.4	1.6	27.3	0.1	0.4	45.5	0.2	0.7
Apogonidae	*Apogon* sp.	8.3	0.1	1.1	9.1	0	0.3	9.1	0	0.2
Coryphaenidae	*Coryphaena equiselis*	8.3	0	0.4	0	0	0	9.1	0	0.5
	Coryphaena sp.	8.3	0.1	1.1	0	0	0	0	0	0
Carangidae	*Carangoides bartholomaei*	8.3	0	0.4	0	0	0	18.2	0	0.2
	Caranx crysos	0	0	0	9.1	0	0.2	9.1	0	0.2
	Caranx latus	0	0	0	0	0	0	9.1	0.1	0.7
	Caranx sp.	0	0	0	9.1	0	0.2	9.1	0	0.2
	Decapterus punctatus	25	0.6	3.9	45.5	0.2	0.6	54.5	0.3	1.4
	Decapterus sp.	8.3	0.1	0.8	0	0	0	0	0	0
	Selar crumenophthalmus	16.7	0.2	1.3	9.1	0.1	0.6	27.3	0.1	0.7
	Trachurus lathami	16.7	0.1	1.3	0	0	0	0	0	0
	n.i.	33.3	0.6	3.2	54.5	0.2	0.4	36.4	0.5	4.1
Lutjanidae	*Lutjanus analis*	0	0	0	9.1	0	0.2	9.1	0	0.4
	Lutjanus sp.	16.7	0.1	1.1	0	0	0	36.4	0.2	0.8
	Pristipomoides sp.	8.3	0	0.4	0	0	0	0	0	0
	n.i.	8.3	0.1	1.2	0	0	0	0	0	0
Gerreidae	*Eucinostomus* sp.	0	0	0	0	0	0	9.1	0	0.4
Haemulidae	*Haemulon aurolineatum*	0	0	0	0	0	0	9.1	0.1	0.7
	Haemulon sp.	0	0	0	0	0	0.3	9.1	0.5	0
Sparidae	*Calamus* sp.	16.7	0.1	1	0	0	0	0	0	0
	Lagodon sp.	0	0	0	0	0	0	9.1	0	0.2
	n.i.	0	0	0	0	0	0	9.1	0.1	1.2
Sciaenidae	*Cynoscion* sp.	8.3	0.1	1.6	9.1	0	0.4	9.1	0	0.3
	Menticirrhus americanus	0	0	0	9.1	0	0.5	0	0	0
	n.i.	25	2.6	28.8	0	0	0	18.2	0.5	5.4
Mullidae	*Mulloidichthys* sp.	0	0	0	9.1	0.1	0.6	18.2	0.1	0.8
	n.i.	33.3	0.8	6.3	9.1	0	0.2	9.1	0.1	0.6
Pomacentridae	*Stegastes* sp.	0	0	0	9.1	0	0.2	9.1	0.1	0.7
Labridae	*Decodon puellaris*	0	0	1.6	9.1	0	0.4	0	0	0.3
	Doratonotus megalepis	0	0	0	9.1	0	0.2	0	0	0
	Halichoeres sp.	0	0	0	9.1	0	0.3	0	0	0
	n.i.	8.3	0.1	0.7	9.1	0	0.3	9.1	0.1	0.7
Scaridae	*Scarus* sp.	8.3	0.1	0.7	9.1	0	0.3	0	0	0

Table I. (Continuation)

	Cryptotomus roseus	0	0	0	9.1	0	0.3	9.1	0	0.2
	Sparisoma sp.	25	0.4	2.4	54.5	0.8	3.6	27.3	0.1	0.4
	n.i.	0	0	0	0	0	0	9.1	0	0.2
Chiasmodontidae	*Chiasmodon niger*	0	0	0	9.1	0.1	0.6	18.2	0.1	0.4
Callionymidae	*Callionymus bairdi*	16.7	0.2	1.1	9.1	0	0.5	9.1	0	0.3
Eleotridae	*Dormitator maculatus*	8.3	0.1	1.1	0	0	0	9.1	0	0.2
Gobiidae	*Ctenogobius boleosoma*	8.3	0.1	1.1	18.2	0	0.3	0	0	0
	Ctenogobius sp.	0	0	0	9.1	0.1	0.6	0	0	0
	Gobionellus oceanicus	0	0	0	9.1	0.1	0.6	9.1	0	0.3
	Gobiosoma sp.	0	0	0	9.1	0	0.4	0	0	0
	n.i.	0	0	0	9.1	0.1	0.6	9.1	0	0.3
Microdesmidae	*Ptereleotris randalli*	0	0	0	18.2	0.1	0.6	27.3	0.3	1.9
Acanthuridae	*Acanthurus* sp.	0	0	0	18.2	0.1	0.4	0	0	0
Scombrolabracidae	*Scombrolabrax heterolepis*	8.3	0	0.4	0	0	0	0	0	0
	n.i.	0	0	0	0	0	0	9.1	0	0.2
Sphyraenidae	*Sphyraena* sp.	8.3	0.2	0	0	0	0	0	0	0.2
Gempylidae	*Diplospinus multistriatus*	0	0	0	9.1	0	0.4	0	0	0
	Gempylus serpens	8.3	0.1	0.7	0	0	0	0	0	0
	Neoepinnula americana	0	0	0	0	0	0	18.2	0.1	0.4
	Nesiarchus nasutus	8.3	0.1	0.7	0	0	0	0	0	0
	Promethichthys prometheus	0	0	0	0	0	0	9.1	0	0.3
	Ruvettus pretiosus	0	0	0	18.2	0.1	0.4	0	0	0
Trichiuridae	*Benthodesmus tenuis*	0	0	0	0	0	0	9.1	0	0.3
Scombridae	*Katsuwonus pelamis*	8.3	0.2	2.4	0	0	0	18.2	0.1	0.5
	Thunnus atlanticus	0	0	0	9.1	0	0.2	0	0	0
	n.i.	8.3	0	0.4	0	0	0	0	0	0
Paralichthyidae	*Etropus* sp.	0	0	0	9.1	0	0.2	0	0	0
	Syacium papillosum	33.3	0.5	3.5	0	0	0	36.4	0.1	0.7
Bothidae	*Bothus ocellatus*	0	0	0	0	0	0	9.1	0.1	0.7
Cynoglossidae	*Symphurus* sp.	0	0	0	9.1	0	0.4	0	0	0
Balistidae	*Xanthichthys ringens*	0	0	0	0	0	0	9.1	0.1	1.4
	n.i.	0	0	0	0	0	0	9.1	0	0.4
Monacanthidae	*Monacanthus ciliatus*	0	0	0	0	0	0	9.1	0	0.5

Table I. (Continuation)

	Monacanthus spp.	0	0	0	0	0	0	9.1	0	0.2
	n.i.	0	0	0	0	0	0	18.2	0	0.2
Tetraodontidae	*Lagocephalus lagocephalus*	8.3	0.1	1.4	0	0	0	0	0	0
	Sphoeroides sp.	0	0	2.1	0	0	0	9.1	0	0
	n.i.	0	0	0	27.3	0.1	0.4	0	0	0
Diodontidae	*Diodon holocanthus*	0	0	0	0	0	0	9.1	0	0.5
	Diodon sp.	8.3	0.1	1	18.2	0.1	0.4	9.1	0	0.2
	n.i.	0	0	0	0	0	0	9.1	0	0.2
Molidae	*Ranzania laevis*	16.7	0.1	1.1	0	0	0	27.3	0.1	0.5
Damaged	Damaged	66.7	1	2.5	63.6	0.7	2.5	81.8	0.9	2.7
Non-identified	Non-identified	25	0.3	1.3	27.3	0.1	0.8	45.5	0.4	1.4

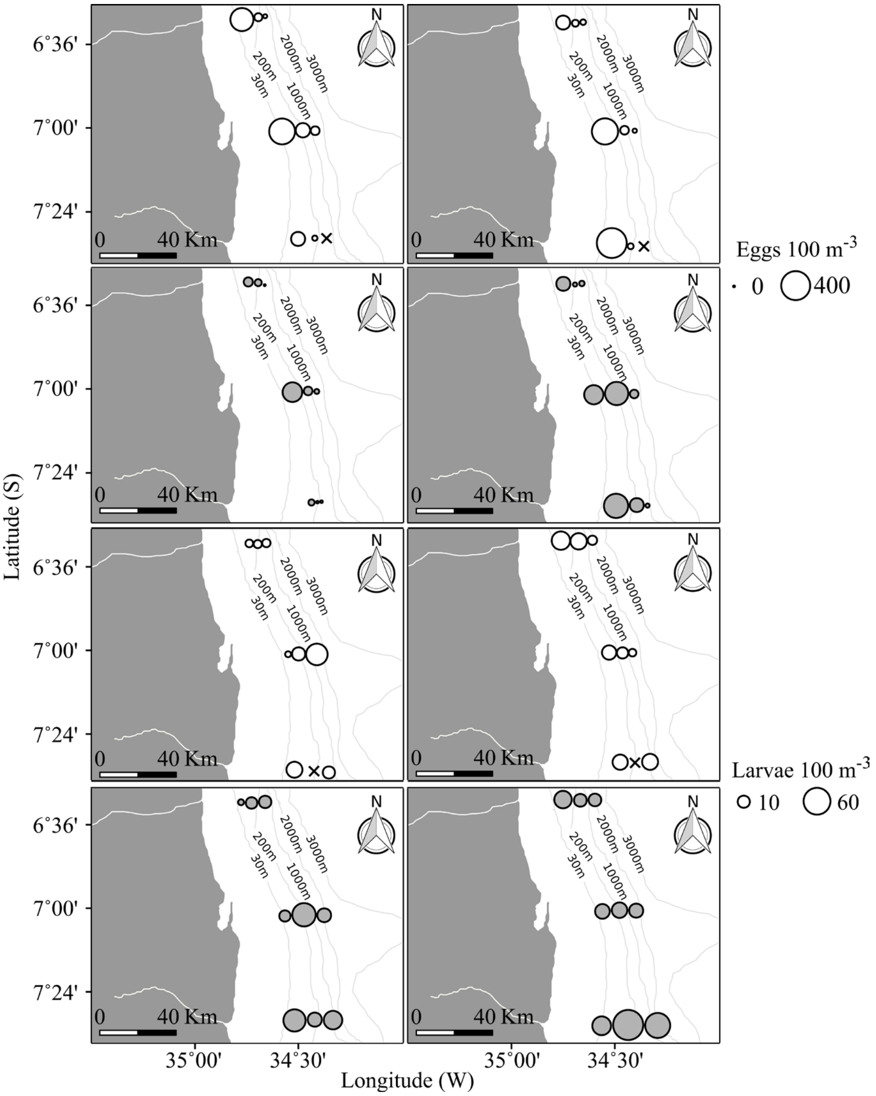

Figure 3. Spatial distribution of fish eggs and larvae (100 m^{-3}) across the outer continental shelf – deep continental slope areas during 2010 (left) and 2012 (right). The empty circles represent the diurnal period and the gray-filled circles represent the nocturnal period. The area of the circles is proportional to the density values. The x represents missing data (damaged net).

Species association and indicator value

Three groups of species association were found and could be described as a neritic, an oceanic and a transition group (Table II). The transition group was composed by neritic and oceanic species. All the groups were significant (permutation test, $p < 0.01$), which means that within all groups there were species positively correlated among each other.

The indicator value analysis (IndVal) revealed the existence of five ecological indicators for the upper and deep continental slope areas (Table III). Melanostomiidae and *Scorpaena* sp. were specifically related to the upper continental slope (isobath B), while *Lestidium atlanticum* and *Lampadena* sp. were specifically related to the deep continental slope (isobath C). The species *Diaphus* sp. 1 was related to both continental slope areas (isobaths B + C).

Table II. Groups of species association found with the k means partitioning.

Groups of species association		
Neritic	**Oceanic**	**Transition (Neritic + Oceanic)**
Acanthurus sp.	*Ctenogobius boleosoma*	*Chiasmodon niger*
Caranx crysus	*Cyclothone braueri*	*Cryptotomus roseus*
Caranx sp.	*Electrona risso*	*Decapterus punctatus*
Myripristis jacobus	*Lampadena* sp. 3	*Diaphus mollis*
	Melanostomiidae	*Diaphus* sp. 1
	Myctophum asperum	*Gobionellus oceanicus*
	Myctophum sp.	*Lestidiops mirabilis*
	Sparisoma sp.	*Lestidium atlanticum*
		Manducus maderensis
		Pontinus sp.
		Sargocentron bullisi
$p < 0.01$	$p < 0.01$	$p < 0.01$

Table III. Ecological indicators of the continental slope area. IndVal – statistic value of the test; *p* – permutation *p* value.

Taxa	Isobath	IndVal	*p*
Melanostomiidae	B	0.60	<0.05
Scorpaena sp.	B	0.56	<0.05
Lestidium atlanticum	C	0.62	<0.01
Lampadena sp.	C	0.57	<0.05
Diaphus sp.1	B+C	0.92	<0.01

DISCUSSION

This study investigated the ichthyoplankton community structure in western Tropical Atlantic areas close to the shelf break (outer continental shelf and continental slope), as well as its relationship with the abiotic variables. It was possible to observe that there was a higher concentration of fish eggs and a predominance of larvae at pre-flexion and flexion stages of notochord development at the outer continental shelf, which indicates a possible spawning process in this area. The NBUC flowed towards the coast, which may have contributed to the movement of these organisms towards the outer continental shelf.

Ichthyoplankton distribution

In general, the waters in tropical regions were characterized by the presence of a permanent thermocline (Travassos et al. 1999) caused by the high solar incidence throughout the year, making these waters warm and oligotrophic (Ekau et al. 1999).

The study area is characterized by presenting low values of biological productivity, as indicated by the low chlorophyll-a concentrations (ranging from 0.46 to 1.65 μg L^{-1}) previously observed (Souza et al. 2013). Unfortunately, the western South Atlantic remain poorly known and no estimate of primary production for the study area using ^{14}C technique is available. According to Longhurst et al. (1995), the study area is characterized by a low value of 75 g C m^{-2} y^{-1}. However, in areas of continental shelf break, the development of mesoscale physical mechanisms – such as meanders and eddies – is possible and may allow a higher retention of the plankton leading to a higher concentration of planktonic density and biomass (e.g. Franco et al. 2006, Okazaki & Nakata 2007, Katsuragawa et al. 2014). In addition, processes such as the formation of eddies, as an example, may retain fish larvae at its surrounding and transport the larvae to other areas influencing the assemblage abundance and composition (Franco et al. 2006).

There was a significantly higher concentration of fish eggs at the outer continental shelf and this may be associated with the predominant current – NBUC – which was flowing towards the coast and could have contributed to the transport of these eggs towards the continental shelf. The swimming capability of the yolk-sac larvae is low and absent for eggs (Purcell & Arai 2001), leaving the latter completely dependent upon the movement of the current. Although no spatial distribution pattern for the larvae could be statistically determined, most of these might also have been under influence of the current, since most of the larvae were in the first stages of flexion of the notochord and deprived of much swimming capability, which increases with age (Fisher 2005, Fisher et al. 2000). Alternatively, the mixture of larval fish taxa may have obscured the spatial pattern of fish larvae when seen as a whole.

A higher concentration of eggs in the region of the outer continental shelf may also be related to a spawning strategy in response to favorable environmental conditions (Franco & Muelbert 2003, Okazaki & Nakata 2007), such as an increase in the phytoplanktonic production (González-Quirós et al. 2003) and a higher availability of prey for the future larvae (Boehlert & Mundy 1994). Indeed, fluorescence measures indicated that the lowest availability of phytoplanktonic cells at the outer continental shelf was higher than its lowest availability at the continental slope areas. Furthermore, stomach content analyses are also revealing that these larvae are feeding on microplanktonic organisms such as centric and pennate diatoms, as well as tintinnid ciliates (JR Santana, unpublished data). Another possibility is that spawning in the shelf break during a given time may aid to transport eggs and larvae to a nursery ground found in another place, as has been observed in other areas (e.g. Landaeta & Castro 2002).

The ability of fish larvae and other zooplanktonic organisms – such as copepods and decapods – to avoid net sampling is a long-known phenomenon (e.g. Ahlstrom 1954, Bridger 1956). During the night, the catches were significantly higher than during the day, e.g. night/day ratios of 1.62:1 (Morse 1989) and 15.2:1 (Bridger 1956). The higher total density values observed during the nocturnal period are in agreement with these estimates, since an average night/day ratio of 1.53:1 was estimated for the study area.

Taxonomic composition

The high abundance of the family Myctophidae at oceanic regions of the western South Atlantic was previously observed (e.g. Franco & Muelbert 2003, Franco et al. 2006, Katsuragawa et al. 2014). Myctophidae is a characteristically oceanic and mesopelagic family (Franco & Muelbert 2003, Katsuragawa et al. 2014), associated with the Tropical Water (TW) and very abundant at the continental shelf break, as well as at oceanic areas (Franco & Muelbert 2003).

A non-identified species of the genus *Diaphus* was the most abundant species at the studied area, occurring in all the stations and being classified as an indicator species of the continental slope areas (isobaths B and C). *Diaphus* is an oceanic genus, which belongs to the family Myctophidae and is also associated to the TW (Franco & Muelbert 2003), since it is common in waters with higher temperature values (Okazaki & Nakata 2007). Although the genus is oceanic, its larvae and adult forms also occur over the inner and outer continental shelf, with a vertical distribution relatively superficial (Okazaki & Nakata 2007). *Diaphus* may be found between 20 and 30 m (Sassa et al. 2002), what explains the fact that it was so well distributed across the studied area.

Several taxonomic groups occurred exclusively at the continental slope areas and formed a group of associated species common to the continental slope, as *Lestidium atlanticum* (Paralepididae) and *Cyclothone braueri* (Gonostomatidae). *Lestidium atlanticum* was one of the deep continental slope indicator species. This result agrees with Okazaki & Nakata (2007), which state that species belonging to the family Paralepididae and of the genus *Cyclothone* would probably not be affected by fronts and eddies, since according to Sassa et al. (2002), both taxa are related with a deep vertical distribution.

The neritic taxonomic groups of the present study are also associated by its ecology and most of them were concentrated at the outer continental shelf. The main families were Carangidae, Sciaenidae, Mullidae, Serranidae, Syngnathidae, Clupeidae, Lutjanidae, among other. Adult individuals of the families Sciaenidae, Carangidae, Serranidae, Clupeidae and Bothidae are abundant at Brazilian's continental shelf areas (Haimovici et al. 1996). Thus, both larvae and adult individuals are well distributed over the continental shelf. Many of these groups were represented by species known to be associated with reef environments, such as *Acanthurus* sp., *Caranx crysus*, *Caranx* sp. and *Myripristes jacobus*, as well as species known to be associated to estuaries, e.g. *Opisthonema oglinum* (Lessa & Nóbrega 2000).

Among the neritic families, Carangidae was one of the most abundant and the species *Decapterus punctatus* was the one with the broadest distribution. The distribution of this species extends from the coast at approximately 16 m to the continental shelf break and may even reach the oceanic zone (Katsuragawa &

Matsuura 1992, Souza & Mafalda Jr 2008). This species was pointed out as the most abundant in the neritic zone of the northeastern region of Brazil (Souza & Mafalda Jr 2008).

A continental shelf-slope gradient in the composition of the fish larvae assemblage was clear because of the formation of a neritic, an oceanic and a transition species association group, the last with neritic and oceanic species. This pattern was registered by other authors (Ekau et al. 1999, Franco & Muelbert 2003, Katsuragawa et al. 2014).

Species richness increased towards oceanic waters. According to Franco & Muelbert (2003), when there is a predominance of the TSW and SACW water masses over the Brazilian south continental shelf, there is an increase in the number of fish families. This may explain the increase in species richness towards the oceanic waters, since at the upper and deep continental slope areas (isobaths B and C), both the TSW and the SACW are present. In addition to water masses, physical processes such as eddies also interfere in the composition of fish larvae assemblage (Katsuragawa et al. 2014). Anticyclonic eddies that are present in the Brazilian south continental shelf, as an example, transport Engraulidae, Bregmacerotidae and Carangidae larvae from one place to other (Franco & Muelbert 2003, Franco et al. 2006).

The present study indicated that in the northeast region of Brazil, the outer continental shelf is an important area of concentration of fish eggs and larvae at early stages, which indicates a spawning area. The North Brazil Undercurrent may aid in the transport of these organisms towards the continental shelf, once they have low or no swimming capability. The distribution and composition of the fish larvae were influenced by the spatial-temporal variables leading to the formation of three species association groups. A neritic group representing the outer continental shelf, an oceanic group representing the continental slope, and a transition group formed by neritic and oceanic species.

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