Anais da Academia Brasileira de Ciências (2019) 91(1): e20170567
(Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690
http://dx.doi.org/10.1590/0001-3765201820170567
www.scielo.br/aabc | www.fb.com/aabcjournal

Large-Scale Spatial and Temporal Variability of Larval Fish Assemblages in the Tropical Atlantic Ocean

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Manuscript received on July 28, 2017; accepted for publication on April 30, 2018

How to cite: SOUZA CS AND JUNIOR POM. 2019. Large-Scale Spatial and Temporal Variability of Larval Fish Assemblages in the Tropical Atlantic Ocean. An Acad Bras Cienc 91: e20170567. DOI 10.1590/0001-3765201820170567.

Abstract: This study investigated the large-scale spatial and temporal variability of larval fish assemblages in the west tropical Atlantic Ocean. The sampling was performed during four expeditions. Identification resulted in 100 taxa (64 families, 19 orders and 17 suborders). During the four periods, 80% of the total larvae taken represented eight characteristics families (Scombridae, Carangidae, Paralepididae, Bothidae, Gonostomatidae, Scaridae, Gobiidae and Myctophidae). Fish larvae showed a rather heterogeneous distribution with density at each station ranging from 0.5 to 2000 larvae per 100m3. A general trend was observed, lower densities at oceanic area and higher densities in the seamounts and islands. A gradient in temperature, salinity, phytoplankton biomass, zooplankton biomass and station depth was strongly correlated with changes in ichthyoplankton structure. Myctophidae, and Paralepididae presented increased abundance at high salinities and temperatures. Bothidae and Gobiidae were more abundant at higher phytoplankton biomass and zooplankton biomass. Scaridae, Scombridae and Gonostomatidae had higher abundances at deep offshore stations. Different events might be responsible for the formation, maintenance and breakdown of fish larvae assemblage in the tropical oceanic area of Brazil. The results suggested that the oceanographic variables (temperature, salinity, phytoplankton biomass, zooplankton biomass and station depth) played an important role on the distribution patterns of ichthyoplankton.

Key words: Abiotic and biotic interactions, abundance, distribution, ichthyoplankton.

INTRODUCTION

Ichthyoplankton studies play a key role in the understanding of the ecology and evolution of fish fauna and their constituent populations (Moser and Smith 1993). Demand for knowledge on the distribution and abundance of ichthyoplankton has increased in fishery research to complement independent stock assessments and help predict fisheries yields (Lessa et al. 1999).

It is known that larval fish assemblages result from adult spawning strategies and environmental influences (Franco-Gordo et al. 2002). An understanding of the recruitment process requires knowledge of their small, medium and large-scale distributions in relation to abiotic and biotic parameters (Röpke 1993).

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Variations in oceanographic conditions may result in changes in fish community structure due to the effect that this change would have on the abundance and species composition associated with it (Whitfield and Paterson 2003).

The area covered in the present study consists of continental shelf, slope and deep seamounts and islands, which represent the main regional sites for commercial and artisanal fisheries, yielding almost all the fish caught in the open oceanic area of North-Eastern Brazil (Travasso et al. 1999). It could be expected that each of these different systems would have an impact on productivity and fish communities in the oceanic waters.

In the continental shelf and slope, continental runoff and coastal wind-induced upwelling play an important role in ichthyoplankton species composition (Lopes et al. 2006, Muhling et al. 2008). The role of seamounts and oceanic islands in fishery production is well known to fishermen, since they cause remarkable concentrations of commercially valuable species, as a result of the enhancement process (Fonteneau 1991).

Knowledge of abiotic and biotic interactions in these environments are important for a greater understanding of functioning and conservation of the spawning area as well as the recruitment processes and the overall dynamics of fish populations.

In our study, temporal and spatial changes in the fish larvae assemblages were examined to test the hypothesis that the large-scale distribution of ichthyoplankton in the west tropical Atlantic Ocean is associated with oceanographic conditions (temperature, salinity, phytoplankton biomass, zooplankton biomass and station depth).

MATERIALS AND METHODS

The samples for this study were collected during the Revizee Projects aboard the ANTARES oceanographical ship. A total of 562 samples were collected during four expeditions. The study area comprised the tropical oceanic region between 0 and 14° S and 28 and 42° W (Figure 1). The expeditions were made on August – October of 1995 (Period 1), January – April of 1997 (Period 2), April – July of 1998 (Period 3) and September – December of 2000 (Period 4). Ichthyoplankton samples were collected by Bongo nets with 50 cm – diameter mouth, 500 and 300 μm meshes, but only the ichthyoplankton collected with 500 μm net were considered in this study. The nets were equipped with two independent flowmeters. Flowmeters were fitted in the mouth of each net to determine the amount of water filtered per tow.

The sampling method used was described by Smith and Richardson (1977). Sampling was done through oblique hauls with duration of 10 minutes. Sampling depth of the tows ranged from 5 m above the bottom at shallow stations, to 200 m at offshore stations. The samples obtained were preserved in 4% buffered formalin – seawater. In the laboratory, all larvae were removed from each sample and stored in 70% alcohol. The larvae were identified according to the morphological characters of each group and classified in relation to habitat of adult fish groups by Moyle and Cech Jr (1982) and Nelson (1994). Standard densities of individual taxa were expressed as the number per 100 m^3 of filtered water for each collection.

Temperature and salinity were recorded by CTD. Seawater samples for the analysis of phytoplanktonic biomass (chlorophyll *a*) were collected using Nisken Bottles. Chlorophyll *a* analysis was carried out spectrophotometrically using methods developed from Strickland and Parsons (1972). The determination of the zooplanktonic biomass (dry weight) was carried through according to the methodology of Omori and Ikeda (1984).

DATA ANALYSIS

Maps of the horizontal distribution were made using SURFER for Windows package of Golden

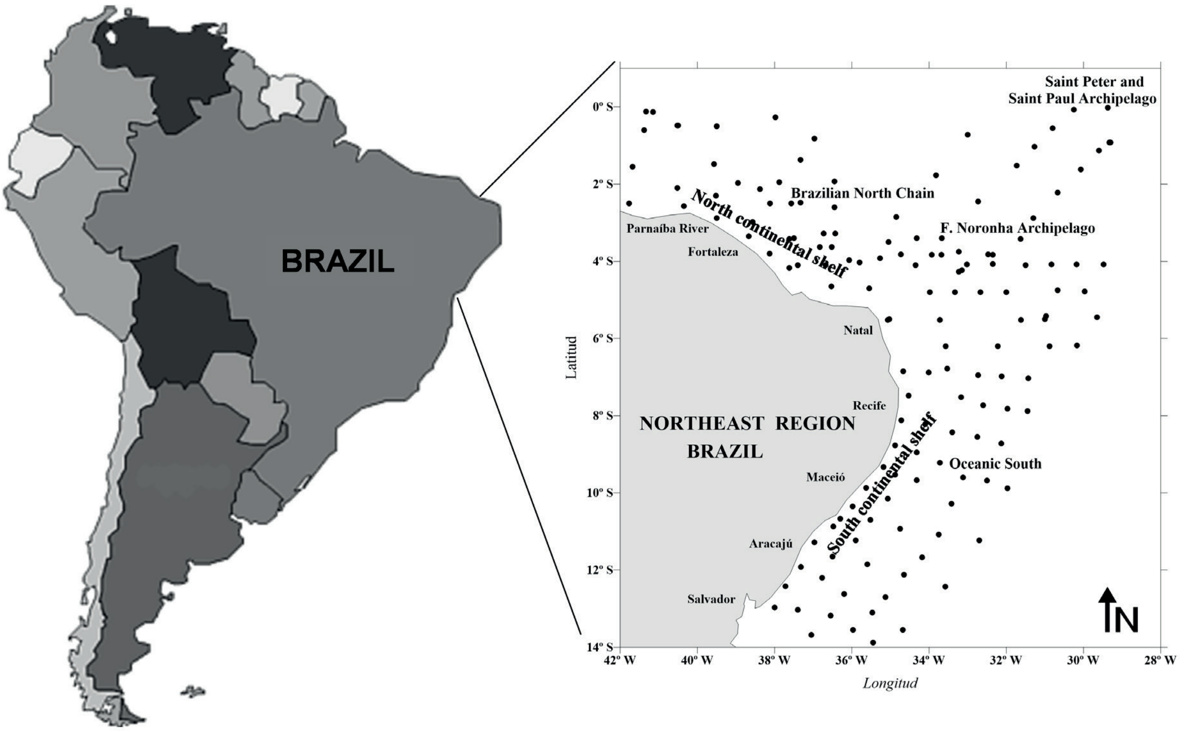

Figure 1 - Study area, showing the sampling stations in the west tropical Atlantic Ocean.

Software Inc. (Keekler 1995). All surface salinity, temperature and phytoplanktonic biomass maps refer to data collected at 10 m depth.

Canonical correspondence analysis (CCA), which incorporates environmental variables by aligning species and station data along environmental gradients, was used to explore the relationship between fish larvae and oceanographic variables (temperature, salinity, phytoplankton biomass, zooplankton biomass and station depth).

Thirty-six of the 562 original collections were excluded based on the absence of fish larvae, leaving 526 collections for the CCA. Only eight dominant taxa were retained in the CCA. The large number of collections ensured a robust result.

For the CCA, 1946 cases of species abundances were entered as log transformed densities, i.e ln(no. x100 m^{-3}), representing all occurrences of the 8 taxa from the 526 samples. The 5 environmental variables were all entered into the CCA in their standardized form (i.e. adjusted for a mean of 0 and SD of 1). Monte Carlo test was employed to determine the statistical significance for the first CCA axes and all CCA axes.

The species-environment correlation is a measure of the strength of the relation between the species data and the environmental data for each CCA dimension (ter Braak and Smilauer 2002). Canonical correspondence analysis (CCA), a unimodal for non-linear multivariate gradient analysis, was employed for this study using the CANOCO program.

RESULTS

OCEANOGRAPHIC CONDITIONS

The T/S-values of the areas are similar, indicating the same water mass composition; therefore, the data in Figure 2 are treated together for the whole area. A T/S-diagram is given for the upper 200 m water layer, which corresponds to the maximum depth of the plankton hauls. It shows warm, saline Tropical Water (TW) down to 100 m and below this, a zone influenced by this South Atlantic Central Water (SACW). The TW is characterized by temperatures > 20 °C and salinities > 36. The SACW is characterized by temperatures between 5 and 20 °C and salinities between 34.5 and 36 (Figure 2).

Higher temperatures were found in the continental shelf between Natal and Maceio during Period 2 (T>29 °C) and in the North continental shelf during Period 3 (T>28 °C). A portion of the South continental shelf between Recife and Salvador is occupied by a pool of almost isothermal and relatively cooler water (25<T<26 °C) during Period 3. In the Saint Peter and Saint Paul Archipelago, a relatively cold water core (26 °C<T< 26.6 °C) was observed on the upper layers between 10 and 25 m depth during Period 2.

A significant correlation is observed between the horizontal distribution of salinity and temperature, during Periods 1, 3 and 4. In general, the local temperature minima (T<26 °C) over the South continental shelf were associated with salinity water varying between 36.6 and 37.2. The surface salinity did not show any significant variation down to 25 m depth.

PHYTOPLANKTON BIOMASS

Phytoplankton biomass as chlorophyll *a* showed a gradient decreasing gradually from North area to the South area. Higher chlorophyll *a* values were observed near the Saint Peter and Saint Paul Archipelago (3.8µ/L) during Period 2, (5.41µ/L) during Period 4 and in the continental shelf area between Recife and Parnaiba river (4.9µ/L) during Period 3 (Figure 3).

ZOOPLANKTON BIOMASS

Differences between the North area (seamounts and islands) and the South area (oceanic) became clearly evident in zooplankton biomass (Figure 4). The total biomass of the 500 µm catches varied between 0.1 and 10.5 $g.100m^{-3}$, with an average of 0.97 $g.100m^{-3}$. Higher biomass values were found in the Saint Peter and Saint Paul Archipelago, during Periods 2 and 3 and in the Brazilian North Chain, Fernando de Noronha Archipelago and South continental shelf, during Period 4. Biomass maxima corresponded to the Brazilian North Chain during Period 2 (Figure 4).

LARVAL FISH COMPOSITION AND ABUNDANCE

From the 19,425 larvae collected during Period 1 (2,969 larvae), Period 2 (5,941 larvae), Period 3 (4,697 larvae) and Period 4 (5,818 larvae), 100 taxa (64 families, 19 orders and 17 suborders) were identified.

Species list

Phylum Chordata
Other Elopiformes

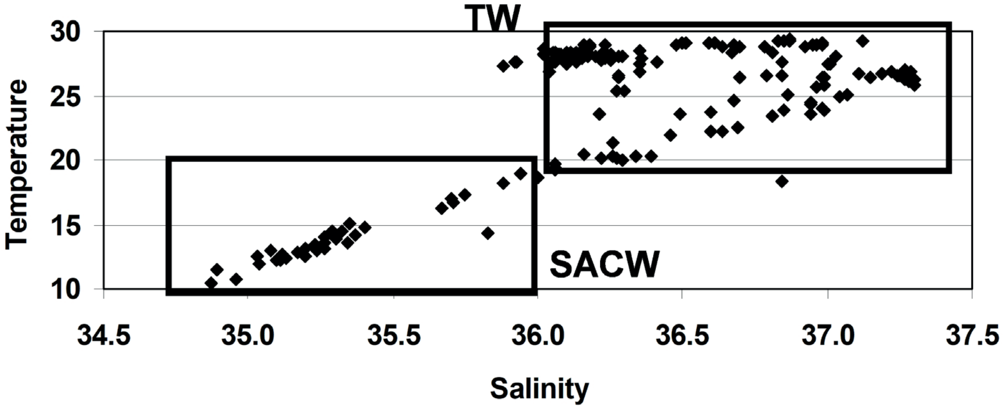

Figure 2 - Temperature-salinity diagrams.

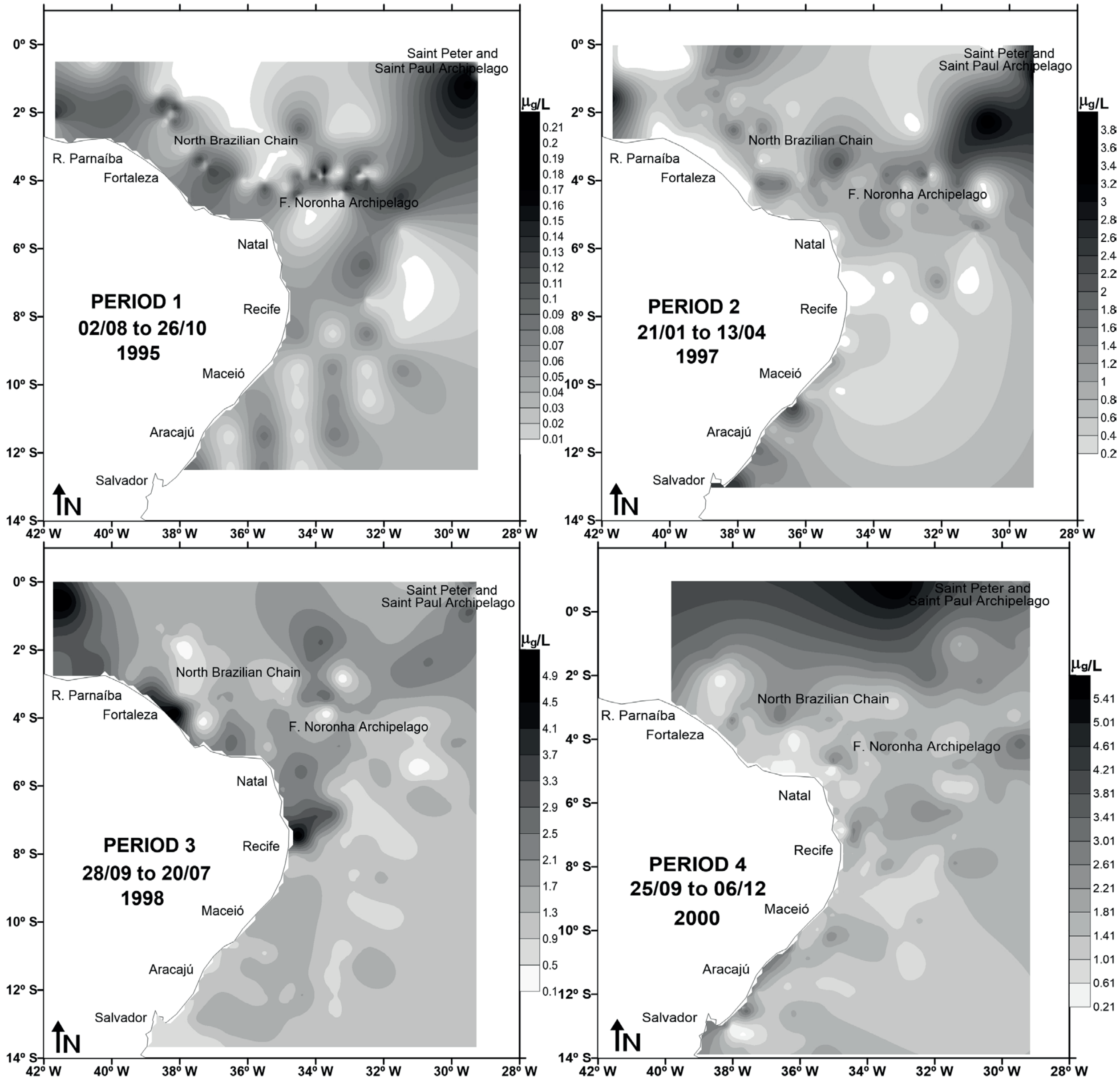

Figure 3 - Horizontal distribution of Chlorophyll *a* (mg L-1) at the 1% in the west tropical Atlantic Ocean.

- Family Elopidae
  - *Elops* sp.
- Other Albuliformes
  - Family Albulidae
    - *Albula* **sp.**
- Other Anguilliformes
  - Family Ophichthidae
    - *Myrichthys* **sp.**
    - *Ophichthus* **sp.**
- Other Clupeiformes
  - Family Engraulididae
    - *Lycengraulis grossidens* (Spix & Agassiz, 1829)
  - Family Clupeidae
- Other Osmeriformes
  - Family Osmeridae
- Other Stomiiformes
  - Family Gonostomatidae

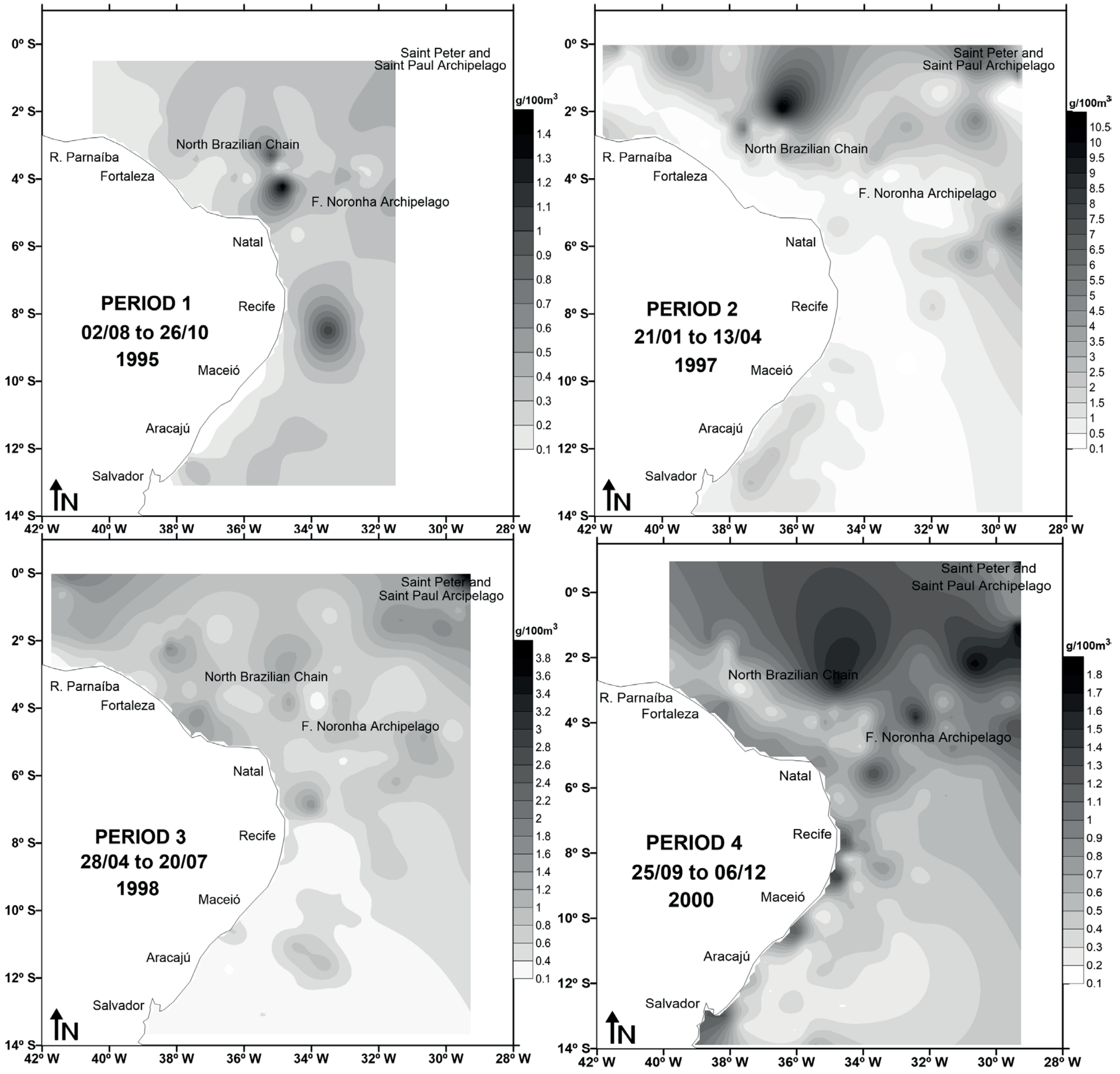

Figure 4 - Zooplankton biomass (g/100m^3) in the west tropical Atlantic Ocean.

    - *Cyclothone* **sp.**
  - Family Phosichthyidae
    - *Vinciguerria* **sp.**
  - Family Stomiidae
    - *Stomias* **sp.**
  - Family Melanostomiidae
  - Family Idiacanthidae
    - *Idiacanthus* **sp**
- Other Aulopiformes
  - Family Scopelarchidae
  - Family Paralepididae
    - *Lestidium* **sp.**
  - Family Evermannellidae
    - *Evermannela* **sp.**
- Other Myctophiformes
  - Family Neoscopelidae
  - Family Myctophidae
    - *Diogenichthys atlanticus* (Tåning, 1928)
    - *Hygophum* **spp.**
    - *Myctophum* **spp.**

- *Diaphus* ***spp.***
- *Lampadena* ***sp.***
- *Notoscopelus* ***sp***
- Other Ophidiiformes
  - Family Ophidiidae
  - Family Carapidae
- Other Gadiiformes
  - Family Macrouridae
  - Family Bregmacerotidae
    - *Bregmaceros cantori* Milliken & Houde, 1984
  - Family Gadidae
- Other Lophiformes
  - Family Ceratiidae
- Other Mugiliformes
  - Family Mugilidae
    - *Mugil* ***sp***
- Other Beloniformes
  - Family Exocoetidae
    - *Cypselurus cyanopterus (Valenciennes, 1846)*
    - *Hirundichthys affinis (Gunther, 1866)*
  - Family Hemiramphidae
    - *Hemiramphus brasiliensis* (Linnaeus, 1758)
    - *Hyporhamphus unifasciatus* (Ranzani, 1841)
- Other Beryciformes
  - Family Holocentridae
    - *Holocentrus* ***sp.***
- Other Gasterosteiformes
  - Family Syngnathidae
    - *Hippocampus reidi Ginsburg, 1933*
  - Family Fistularidae
    - *Fistularia petimba* Lacepède, 1803
- Other Scorpaeniformes
  - Family Dactylopteridae
    - *Dactylopterus volitans (Linnaeus, 1758)*
  - Family Scorpaenidae
  - Family Triglidae
  - Family Cottidae
- Other Perciformes
  - Family Serranidae
    - *Epinephelus* ***sp.***
  - Family Priacanthidae
    - *Priacanthus* ***sp.***
  - Family Apogonidae
  - Family Echeneidae
  - Family Carangidae
    - *Carangoides spp.*
    - *Caranx spp.*
    - *Chloroscombrus chrysurus (Linnaeus, 1766)*
    - *Decapterus punctatus (Cuvier, 1829)*
    - *Elagatis bipinnulatus (Quoi & Gaimard, 1824)*
    - *Selene setapinnis (Mitchill, 1815)*
    - *Selene vomer (Linnaeus, 1758)*
    - *Trachurus lathami Nichols, 1920*
  - Family Bramidae
  - Family Lutjanidae
    - *Lutjanus* ***sp.***
  - Family Gerreidae
  - Family Haemulidae
  - Family Sparidae
  - Family Pomacanthidae
  - Family Pomacentridae
  - Family Labridae
  - Family Scaridae
    - *Cryptotomus roseus* Cope, 1871
    - *Sparisoma sp.*
  - Family Blenniidae
  - Family Callionymidae
  - Family Gobiidae
  - Family Acanthuridae
    - *Acanthurus* ***spp.***
  - Family Scombrolabracidae
    - *Scombrolabrax heterolepis* Roule, 1921
  - Family Sphyraenidae
    - *Sphyraena* ***spp.***
  - Family Gempylidae
  - Family Scombridae

            Acanthocybium solandri (Cuvier, 1831)
            Euthynnus aletteratus (Rafinesque, 1810)
            Katsuwonus pelamis (Linnaeus, 1758)
            Scomberomorus sp.
            Thunnus spp.
        Family Nomeidae
    Other Pleuronectiformes
        Family Bothidae
            Bothus ocellatus (Agassiz,1831)
            Engyophrys senta Ginsburg, 1933
        Family Paralichthydae
            Citharichthys cf. spilopterus Gunther, 1862
            Citharichthys sp.
            Syacium papillosum (Linnaeus, 1758)
        Family Cynoglossidae
            Symphurus sp.
    Other Tetraodontiformes
        Family Balistidae
            Balistes capriscus ***Gmelin, 1788***
        Family Monacanthidae
            Stephanolepis hispidus (Linnaeus, 1766)
        Family Ostracidae
            Lactophrys trigonus (Linnaeus, 1758)
        Family Tetraodontidae
            Sphoeroides sp1
            Sphoeroides sp2
        Family Diodontidae
            Diodon hystrix Linnaeus, 1758
        Family Molidae
            Ranzania laevis (Pennant, 1776)

The abundance of the family groups of fish larvae is given in Table I. During the four periods, 80% of the total larvae taken represented eight characteristics families in increasing order of abundance: Scombridae (0.6%), Carangidae (1.6%), Paralepididae (2.7%), Bothidae (3.3%), Gonostomatidae (5.6%), Scaridae (7.5%), Gobiidae (21%) and Myctophidae (37.7%). Five families (Gadidae, Macrouridae, Monacantidae, Evermannelidae and Scombrolabracidae) were collected only in Period 4. The total number of larvae collected during Period 1 was less as that of the other three cruises. In this Period was observed the lowest taxon number.

In relation to habitat of adult fish groups, four dominant fish groups were recognized in the tropical Atlantic Ocean: epipelagic fish, mesopelagic fish, demersal fish and coral-reef-associated fish. Levels of abundance of mesopelagic fish larvae (Myctophidae and Gonostomatidae) were highest during Period 2 and Period 4. For other family (Paralepididae) levels of abundance were highest for Period 3, decreased in Period 2 and Period 4, and were at a minimum during Period 1. Abundance of Gobiidae (coral-reef-associated fish) was at a peak in Period 2, followed by Period 4 and Period 1. Bothidae family (Demersal fish larvae) were most abundant during Period 2 and Period 3. For the Scaridae family, a peak in larval abundance was observed during Period 3. Levels of abundance of families of epipelagic fish larvae (Caragidae and Scombridae) were very low during investigated periods.

SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF FISH LARVAE

Fish larvae showed a rather heterogeneous distribution with density at each station ranging from 0.5 larvae per 100 m^3 to 2000 larvae per 100 m^3. A general trend was observed towards lower density at oceanic stations, with abundance generally not more than 20 larvae per 100 m^3. Higher densities were found at stations located close to the Saint Peter and Saint Paul Archipelago (30 to 350 larvae per 100 m^3), Brazilian North Chain (40 to 750 larvae per 100 m^3) and Fernando de Noronha Archipelago (40 to 550 larvae per 100 m^3) during Periods 1, 2 and 3. Some stations located in the South continental shelf showed densities ranging

TABLE I

Family groups represented in ichtyoplankton samples collected in the west tropical Atlantic Ocean. Abundance is a sum of larvae from all positive stations and % is a percentage of total abundance.

	Period 1		**Period 2**		**Period 3**		**Period 4**	
Taxon	Abundance	%	Abundance	%	Abundance	%	Abundance	%
ANGUILLIFORMES	30	1.01	109	1.83	93	1.98	75	1.34
Clupeidae	0	0.00	6	0.10	16	0.34	2	0.04
Engraulidae	2	0.07	21	0.35	8	0.17	1	0.02
Osmeridae	0	0.00	7	0.12	7	0.15	8	0.14
STOMIIFORMES	0	0.00	0	0.00	3	0.06	0	0.00
Gonostomatidae	99	3.33	438	7.37	244	5.19	300	5.36
Photichthyidae	7	0.24	16	0.27	4	0.09	122	2.18
Stomiidae	1	0.03	11	0.19	22	0.47	11	0.20
Melanostomiidae	22	0.74	19	0.32	19	0.40	37	0.66
Idiacanthidae	0	0.00	2	0.03	0	0.00	4	0.07
Scopelarchidae	0	0.00	14	0.24	48	1.02	23	0.41
Paralepididae	56	1.89	94	1.58	236	5.02	145	2.59
Evermannellidae	0	0.00	0	0.00	0	0.00	11	0.20
Neoscopelidae	0	0.00	0	0.00	11	0.23	1	0.02
Myctophidae	631	21.25	2205	37.11	1866	39.73	2619	46.82
Gadidae	0	0.00	0	0.00	0	0.00	3	0.05
Macrouridae	0	0.00	0	0.00	0	0.00	17	0.30
Bregmacerotidae	10	0.34	14	0.24	26	0.55	30	0.54
Ophidiidae	2	0.07	8	0.13	21	0.45	27	0.48
Carapidae	0	0.00	0	0.00	2	0.04	0	0.00
LOPHIFORMES	0	0.00	0	0.00	2	0.04	0	0.00
Ceratioidei	9	0.30	10	0.17	14	0.30	16	0.29
Exocoetidae	3	0.10	6	0.10	6	0.13	8	0.14
Hemiramphidae	0	0.00	5	0.08	9	0.19	13	0.23
Holocentridae	7	0.24	7	0.12	5	0.11	24	0.43
Syngnathidae	3	0.10	2	0.03	1	0.02	4	0.07
Fistularidae	0	0.00	1	0.02	1	0.02	3	0.05
Dactylopteridae	5	0.17	10	0.17	0	0.00	6	0.11
Scorpaenidae	0	0.00	0	0.00	1	0.02	2	0.04
Triglidae	0	0.00	1	0.02	0	0.00	0	0.00
Cottidae	0	0.00	6	0.10	0	0.00	0	0.00
PERCIFORMES	7	0.24	2	0.03	25	0.53	28	0.50
Percoidei	1	0.03	10	0.17	11	0.23	26	0.46
Echeneidae	0	0.00	0	0.00	0	0.00	0	0.00
Serranidae	11	0.37	36	0.61	9	0.19	50	0.89
Priacanthidae	6	0.20	14	0.24	15	0.32	11	0.20
Apogonidae	5	0.17	52	0.88	1	0.02	25	0.45
Carangidae	12	0.40	90	1.51	146	3.11	65	1.16
Bramidae	10	0.34	21	0.35	20	0.43	30	0.54
Lutjanidae	0	0.00	3	0.05	23	0.49	20	0.36
Gerreidae	1	0.03	20	0.34	16	0.34	1	0.02
Cotiidae	0	0.00	0	0.00	0	0.00	0	0.00
Monacantidae	0	0.00	0	0.00	0	0.00	5	0.09

TABLE I (continuation)

	Period 1		**Period 2**		**Period 3**		**Period 4**	
Taxon	Abundance	%	Abundance	%	Abundance	%	Abundance	%
Haemulidae	2	0.07	74	1.25	158	3.36	85	1.52
Sparidae	0	0.00	1	0.02	1	0.02	2	0.04
Sciaenidae	0	0.00	0	0.00	1	0.02	0	0.00
Pomacanthidae	0	0.00	4	0.07	7	0.15	6	0.11
Pomacentridae	0	0.00	20	0.34	2	0.04	6	0.11
Mugilidae	0	0.00	2	0.03	2	0.04	0	0.00
Sphyraenidae	0	0.00	3	0.05	7	0.15	0	0.00
Labridae	18	0.61	71	1.20	33	0.70	81	1.45
Scaridae	385	12.97	299	5.03	588	12.52	181	3.24
Blennioidei	0	0.00	19	0.32	0	0.00	5	0.09
Blenniidae	0	0.00	10	0.17	0	0.00	3	0.05
Callionymidae	15	0.51	64	1.08	68	1.45	103	1.84
Gobiidae	1017	34.25	1582	26.63	423	9.01	1059	18.93
Acanthuridae	44	1.48	10	0.17	9	0.19	13	0.23
Scombrolabracidae	5	0.17	0	0.00	0	0.00	0	0.00
Gempylidae	11	0.37	16	0.27	34	0.72	32	0.57
Scombridae	25	0.84	32	0.54	71	1.51	27	0.48
Scombrolabracide	0	0.00	0	0.00	0	0.00	15	0.27
Nomeidae	13	0.44	49	0.82	75	1.60	16	0.29
PLEURONECTIFORMES	1	0.03	0	0.00	5	0.11	0	0.00
Bothidae	101	3.40	297	5.00	181	3.85	68	1.22
Paralictidae	10	0.34	21	0.35	0	0.00	56	1.00
Cynoglossidae	0	0.00	4	0.07	3	0.06	0	0.00
Balistidae	4	0.13	4	0.07	7	0.15	0	0.00
Monacanthidae	0	0.00	5	0.08	0	0.00	0	0.00
Ostracidae	0	0.00	0	0.00	7	0.15	0	0.00
Tetraodontidae	5	0.17	8	0.13	6	0.13	10	0.18
Diodontidae	0	0.00	6	0.10	12	0.26	3	0.05
Molidae	0	0.00	2	0.03	0	0.00	1	0.02
Not identified	378	11.35	76	1.28	66	1.41	40	0.72
Total	2969	100.00	5941	100.00	4697	100.00	5594	100.00
No. of taxa	38		56		55		56	

from 50 to 150 larvae per 100 m^3, during Periods 2 and 4.

Distribution patterns of families among each of the periods are shown in Figures 5 and 6. During Period 3 the highest densities of Brothidae larvae were found at ocean area between F. Noronha Archipelago and Saint Peter and Saint Paul Archipelago, but the Brazilian North Chain stations also showed relatively high density during Period 2 (Figure 5). Carangidae larvae were collected more frequently near the coast. The stations with the highest densities of Carangidae larvae during Periods 2 and 3 were found along the shelf break (Figure 5). Gobiidae larvae during Period 1 were concentrated over the Brazilian North Chain and F. Noronha Archipelago and only a small number of them were collected at open ocean stations (Figure 5). Larvae of Gonostomatidae were found

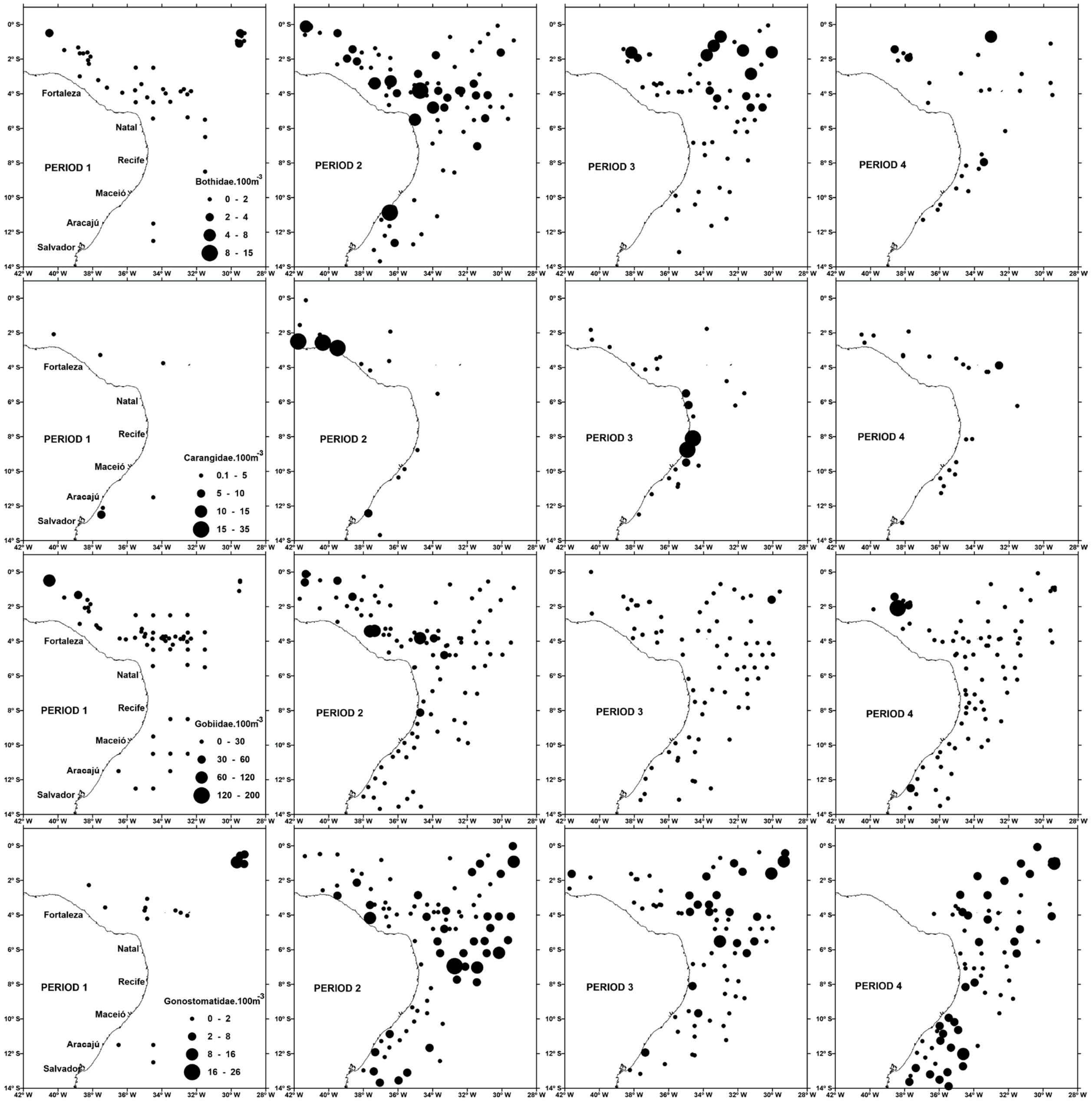

Figure 5 - Distribution and density (larvae.100m^{-3}) of the fish larvae families (Bothidae, Carangidae, Gobiidae and Gonostomatidae) in the west tropical Atlantic Ocean.

predominantly at open ocean stations during Periods 2, 3 and 4 and some at the continental margin (Figure 5). Myctophidae larvae were collected at open ocean stations with higher density over the Brazilian North Chain and F. Noronha Archipelago during Period 3 and Period 4, but also were collected at coastal stations with higher density between Natal and Salvador on Period 2 and Period 4 (Figure 6). Paralepididae larvae were collected at open ocean stations during all four periods, with higher density in the adjacent area to Saint Peter and Saint Paul Archipelago during Period 3 (Figure 6). The distribution patterns of the larvae Scaridae were similar during all four

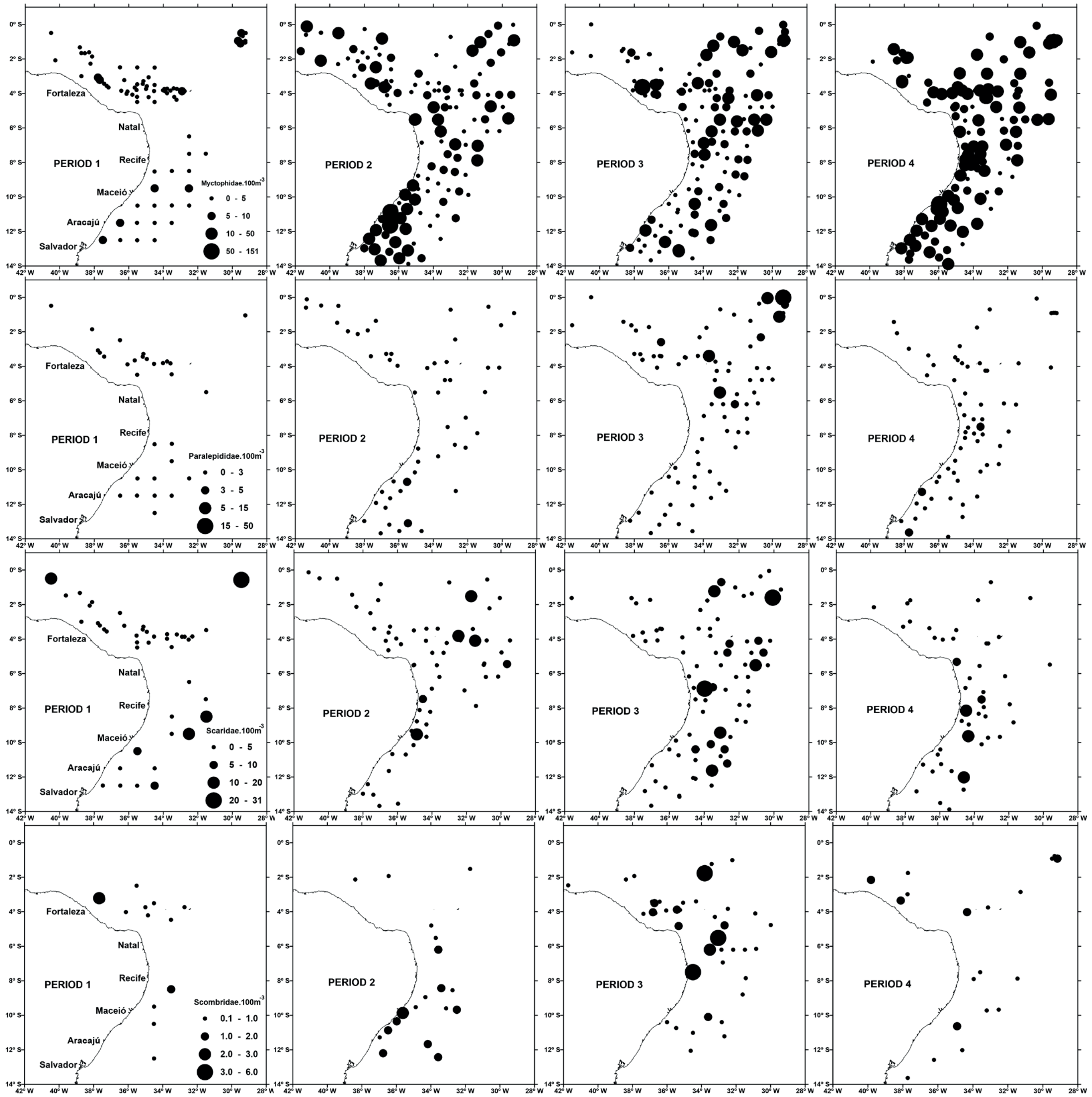

Figure 6 - Distribution and density (larvae.100m^{-3}) of the fish larvae families (Myctophidae, Paralepididae, Scaridae and Scombridae) in the west tropical Atlantic Ocean.

periods, with higher density at open ocean stations (Figure 6). Most of the Scombridae larvae were collected at coastal stations between Maceió and Aracajú during Period 2 and at open ocean stations during Period 3 (Figure 6).

CORRELATIONS BETWEEN ICHTHYOPLANKTON AND OCEANOGRAPHIC FACTORS

The CCA used environmental information to constrain a reciprocal averaging ordination between taxa and respective samples. Eigenvalues, measures of importance for CCA axes that may vary between zero and one, ranged from 0.087 for CCA 4 to

TABLE II
Result from canonical correspondence analysis (CCA) of 1946 cases of family occurrence in 526 collections from west tropical Atlantic Ocean.

Axes	1	2	3	4	Total Inertia
Eigenvalues:	0.651	0.453	0.139	0.087	3.197
Species-environment correlations:	0.785	0.629	0.544	0.493	
Cumulative percentage variance					
of species data:	15.5	19.2	19.9	30.4	
of species-environment relation:	51.9	87.4	94.5	98.9	
Sum of all eigenvalues:					3.197
Sum of all canonical eigenvalues:					1.33

0.651 for CCA 1 (Table II). The eigenvalues were moderately high for the first two axes, whereas CCA axes 3 and 4 were relatively low (i.e. < 0.2). Species-environment correlations were high for all four CCA axes, ranging from 0.785 for CCA 1 to 0.493 for CCA 4.

The combined sum of canonical eigenvalues (1.33) was equal 41% of that for the unconstrained eigenvalues (3.197), showing the effect of building environmental relationships into the CCA model. The low weighted correlation coefficients of the environmental variables indicated that there were not collinear variables (Table III). This result is important because multicollinear variables must be deleting from the analysis.

The plot of CCA species scores illustrates their dispersion pattern and the plot of oceanographic variables vectors illustrates the directions and strengths of environmental relationships within the first two dimensions of the CCA ordination.

Environmental variables correlated most strongly with CCA 1 included Depth. Another suite of environmental variables correlated best with CCA 2, including Temperature, Salinity, Phytoplankton biomass and Zooplankton biomass (Figure 7). Thus, families with low values on CCA 2 occurred mostly at high salinity and temperature stations, whereas families with high values on CCA 2 occurred mostly at high Phytoplankton biomass and Zooplankton biomass stations. The families that had high values on CCA 1 occurred in greater depths.

Distinctive patterns of dispersion in space occurred for the various ecological groups with respect to the important environmental variable. Bothidae and Gobiidae were positively correlated with second CCA axes, appearing mostly at high phytoplankton biomass and zooplankton biomass. Scaridae, Scombridae and Gonostomatidae were positively correlated with first CCA axes, occurring mostly at deep offshore stations. Carangidae was negatively correlated with first and second CCA axes, predominantly occurring at low phytoplankton biomass and zooplankton biomass and at inshore stations. Myctophidae and Paralepididae were negatively correlated with second CCA axes, predominantly occurring at higher salinities and water temperature (Figure 7).

DISCUSSION

According to temperature and salinity results, the study area presented typical characteristics of tropical regions, with high salinity and temperature, low thermal oscillation. Consequently, this area is known to be oligotrophic with a low concentration of nitrates, chlorophyll-*a* biomass, and primary production (Queiroz et al. 2015, Souza et al. 2013, Ekau and Knoppers 1999).

Such characteristics may be explained by the existence of a warm surface layer above a colder and

TABLE III
Weighted correlation matrix from CCA.

Longitude	1.0000					
Latitude	0.1484	1.0000				
Station Depth	0.4239	-0.0334	1.0000			
Temperature	-0.0461	-0.0136	-0.0334	1.0000		
Salinity	-0.1670	-0.3340	-0.1127	-0.0430	1.0000	
Secondary Biomass	0.0286	0.2898	0.1005	-0.0120	-0.1424	1.0000
	Longitude	Latitude	Station Depth	Temperature	Salinity	Secondary Biomass

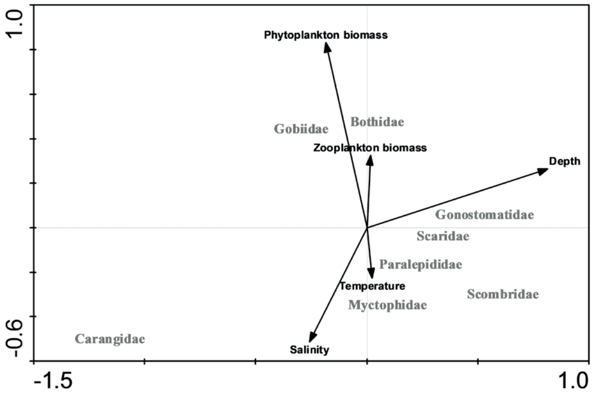

Figure 7 - Biplot of the species scores and important environmental correlation vectors in the first two canonical correspondence analysis dimensions.

denser sub-surface layer, which creates a permanent thermocline. This tends to inhibit the upward flow nutrient of rich deeper layers, restricting primary production in surface waters (Travasso et al. 1999).

The biological parameters showed a remarkable spatial variability for tropical oceanic regions. A gradient of phytoplankton biomass, zooplankton biomass and fish larvae density were observed in all studied periods, with lower concentrations in the South area (oceanic) and higher concentrations in the North area (seamounts and islands). Coastal areas between Rio Grande do Norte and Ceará and between Pernambuco and North Bahia also had high fish larvae density. The role of seamounts and oceanic islands in fishery production is well known to fishermen, since they cause remarkable concentrations of commercially valuable species, as a result of the enhancement process (Fonteneau 1991). Araujo and Cintra (2009) indicate that the interaction of currents with the topography of the St. Peter and St. Paul Archipelago can cause physical processes such as the production of vortices, disturbances of thermohaline structure and possible mechanisms of local upwelling. Queiroz et al. (2015) found variations in depths at which the thermocline starts in the Saint Peter and Saint Paul Archipelago that allows input of the richest water at the base of the photic layer.

The distribution of seamount ichthyoplankton was first considered by Nellen (1974), who reported that the larvae of two 'topographically associated' fish species were more abundant over Great Meteor Seamount than in the surrounding North Atlantic waters. Lessa et al. (1999) observed aggregation of fishes around and close to the Saint Peter and Saint Paul Archipelago, particularly large flying fishes as well as tunas and local fisheries on tunas and bentho-pelagic species, suggest the maintenance of higher biomass in this region in comparison to adjacent waters.

The fish larvae in the west Tropical Atlantic Ocean were produced by a diverse collection of fish family. The high diversity of 72 taxa is characteristic of the tropical marine ecosystem and similar taxonomic richness of larval fish is known from the eastern tropical Pacific (Ahlstrom 1971, 1972) and the Gulf of Mexico (Richards et al. 1993). Many species do not have vertical migratory behavior, thereby changes in species composition at 150 m would be possible by active vertical circulation in the water column above the seamount summit (Diekmann et al. 2006).

The dominant taxonomic groups (family) from the four periods showed a distinct temporal pattern in abundance. The overall larval abundance of Period 2 was the highest. The Myctophidae larvae abundance was highest during Periods 2 and 4 with high water temperature. Myctophid fish in the temperate and subtropical seas are known to spawn mainly from late winter to summer, coinciding with the seasonal peak of zooplankton production in the area (Doyle et al. 1993). Variable patterns have been observed at Southeast Hancock Seamount, where the larvae abundance of two species of the Myctophidae larvae, *Maurolicus muelleri* and *Pseudopentaceros wheeleri* varied seasonally, being more abundant over the seamount than the surrounding waters in summer (Boehlert 1988).

Among the Bothidae, the larval abundance of *Bothus ocellatus* was highest in eriods 2 and 3. Another species (*Engyophrys senta*) also showed relatively high values in Period 2 and insignificant in other periods. With the Carangidae, the larval abundance of *Decapterus punctatus* was highest during Periods 1 and 3, while Period 2 was lower abundance. The larval abundance of *Chloroscombrus chrysurus* was highest during Period 2. *Selene setapinnis, Selene vomer* and *Elagatis bipinnulata* were less abundant in all periods. Few studies have reported a high abundance of *S. setapinnis*, ranging from 0.2% to 2% of collections in the southern Atlantic off the Brazilian coast (Campos et al. 2010, Souza and Mafalda Jr. 2008). Flores-Coto and Sanchez-Ramirez (1989) found *S. setapinnis* comprised 6.1% of collections and were most abundant in warmer months in the southern Gulf of Mexico. This is in contrast with results of other studies in the Gulf of Mexico, which have typically found *C. chrysurus* to be the dominant species (Ditty et al. 2004, Flores-Coto and Sanchez-Ramirez 1989, Aprieto 1974). Costa et al. (2005) examined carangid distributions in a semi-enclosed bay in southeastern Brazil and found *C. chrysurus* abundance and biomass was significantly related to decreased salinity and shallow water depths.

A Conceptual model of the fish larvae assemblage in the Brazil tropical oceanic zone is presented in Figure 8. Events such as larval drift, vertical migration and upwelling might be responsible for the formation, maintenance and breakdown of this high standing stock. Topography upwelling causes an increase of nutrient availability in the subsurface waters and increase of phytoplankton growth, the first larval stages might find enough food to develop. Fish tend to spawn on specific sites that are associated with favorable nursery areas (Figure 8).

During vertical migration, larvae of mesopelagic fish are transported by the prevailing current-system during their night-time ascent and the larvae of epipelagic, demersal and coral-reef-associated fish drift with the surface current, gradually displacing to form the oceanic assemblage the tropical Atlantic.

Larval fish distribution in the west tropical Atlantic Ocean varied over time and among sampling locations. Larvae of mesopelagic (Myctophidae, Gonostomatidae and Paralepididae) and coral-reef-associated groups (Scaridae and Gobiidae) were sampled at open ocean stations. In offshore areas, diversity may be increased by mesopelagic and bathypelagic species, which are distributed in the water column according to the abundance of their potential prey (Moser and Smith 1993) and depth of the thermocline (Longhurst 1985). According to Nonaka et al. (2000) and Diekmann et al. (2006), pelagic species belonging to the Myctophidae, Gonostomatidae, Paralepididae, Phosichthyidae and Exocoetidae are dominant in the oceanic assemblage. Gonostomatidae have a circumglobal distribution (Briggs 1960, Fahay 1983) and usually have high species richness in oceanic samples (Moyano et al. 2009, Moyano and Hernández-León 2011). The wide larval distribution, especially

Gobiidae, might be a consequence of a high larval drift from the coral-reef area where massive spawning occurs (Mafalda Jr. and Rubín 2006).

Larvae of Carangidae (epipelagic) were collected more frequently near the coast. Nonaka et al. (2000) studying larval fish assemblages of the Abrolhos Bank region found a neritic assemblage composed of pelagic fish, such as the Clupeidae, Engraulidae, Carangidae, and Bregmacerotidae. Coastal regions adjacent to estuaries present favourable conditions for the development of fish species that use these areas as nursery and protection for their eggs and larvae.

Studies that interpret ichthyoplankton structure in terms of adult characteristics often find spatially heterogeneous distribution of larvae that are attributable to adult characteristics (Gaughan et al. 1990, Yoklavich et al. 1992). Knowing geographical locations of spawning adults can also help explain spatial heterogeneity in ichthyoplankton structure (Rakocinski et al. 1995).

The commonalities and differences in species-environment relationships were exhibited in the the CCA plots. A gradient in temperature, salinity, phytoplankton biomass, zooplankton biomass and station depth was strongly correlated with changes in ichthyoplankton structure. The CCA plots demonstrated that Myctophidae and Paralepididae responded similarly with increased abundance at high salinities and temperatures. Bothidae and Gobiidae were more abundant at higher phytoplankton biomass and zooplankton biomass. Scaridae, Scombridae and Gonostomatidae displayed similar spatial arrangement in CCA plots, with higher abundances at deep offshore stations. Macedo-Soares et al. (2014) found that water masses were the main components that accounted for the composition of fish larval assemblages along the South Brazil Shelf. It is known that several fish species have their reproductive strategies adjusted for environmental factors such as surface currents. Meteorological and oceanographic conditions influence the feeding of organisms and eggs and

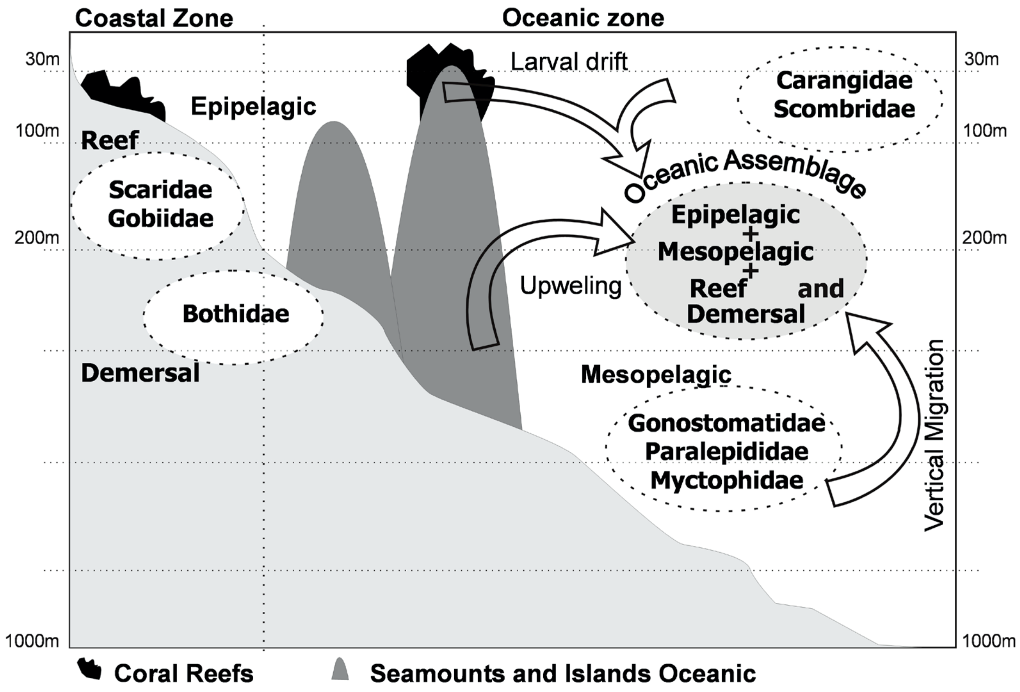

Figure 8 - Conceptual model of the fish larvae assemblage in the west tropical Atlantic Ocean.

larvae can be transported by currents (Freitas and Muelbert 2004). As a result, the reproductive success of fish is affected resulting in recruitment variability.

In conclusion, our study supports the hypothesis that in the west tropical Atlantic Ocean, temporal and spatial differences in both composition and abundance of ichthyoplankton appeared to be associated with differences in geological and environmental conditions.

ACKNOWLEDGMENTS

The authors express their thanks to Ministério do Meio Ambiente (MMA), Diretoria de Hidrografia e Navegação (DHN) and ANTARES oceanographical ship, for supporting this study though the program REVIZEE.

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