Spatial and temporal variability of larval fish assemblages in the central region of the Brazilian Exclusive Economic Zone (12–22°S)

Márcia Salustiano de Castro (contact author)
Cristina de Oliveira Dias
Ana Cristina Teixeira Bonecker

Email address for contact author: mscastro@biologia.ufrj.br

Departamento de Zoologia
Instituto de Biologia
Centro de Ciências da Saúde
Universidade Federal do Rio de Janeiro
Bloco A
Ilha do Fundão
21941-590, Rio de Janeiro, Brazil

Abstract—We evaluated spatial and temporal variations in larval fish assemblages occurring off the central coast of Brazil. Study material was collected during 3 oceanographic cruises (1999–2000) in the spring, winter, and autumn. Oblique hauls were sampled from 329 stations, and 88 families and 130 species were identified. The surveys recorded higher abundances of larval fish on the continental shelf during the winter, and diversity increased from coastal to oceanic waters. Furthermore, larval fish abundance showed a negative relationship with local depth in the 3 sampling periods, with the greatest abundances associated with shallower stations at the continental shelf. Myctophidae and Scaridae larvae showed the highest abundances in the oceanic region near the Abrolhos and Royal Charlotte Banks and on the Vitória Seamount in the Vitória-Trindade Ridge. The oceanic and seamount regions' high salinity (spring) and temperature (winter) were the best predictors of diversity and equitability. This study improved the knowledge of larval fish assemblages and their distribution in a coast-ocean gradient at different times of the year. It may also contribute to future studies aimed at understanding the influence of environmental variables on these organisms and the connectivity between different environments.

Introduction

The substantial morphological diversity and duration of the development stages of fish species suggest the existence of several adaptations to survive planktonic life (Moser and Smith, 1993; Cruz et al., 2016). The plankton stage varies from 47 to 93 d for Atlantic fish species and depends on the species and environmental conditions (Endo et al., 2019).

Although there is considerable variability in developmental cycles, many fish species use the same reproductive strategy of having planktonic larvae, resulting in the larvae co-occurring in time and space. Moser et al. (1987:98) define *assemblages* as "groups of taxa that occur together relatively frequently and are consistently part of each other's environment." Therefore, assemblages are groups of taxa with similar temporal and spatial distribution patterns.

The composition of assemblages partly depends on adult distributions and spawning seasonality (Souza and Mafalda, 2019; Daudén-Bengoa et al., 2020; Mwaluma et al., 2021). Hydrographic features such as water masses and currents also play an important role in the formation, maintenance, and regulation of larval assemblages and adult populations (e.g., Beckley et al., 2019; Santana et al., 2020; Compaire et al., 2021). In addition, physical and topographic features affect the spatial and seasonal distribution patterns of larval assemblages (Muhling and Beckley, 2007). In the oceanic region (area beyond the continental slope), seamounts and oceanic islands are topographic features that may affect larval assemblages (Harris et al., 2020). Seamounts have high primary productivity, which supports increased secondary production and attracts other organisms. These organisms, attracted by food availability, feed in these areas, leading to an increase in energy transfer to higher trophic levels and the carbon flux to greater depths (Lima et al., 2020; Bridges et al., 2021). Upwelling in oceanic waters can be induced by seamounts interacting with ocean currents (Annasawmy et al., 2020; Roberts and Ternon, 2020; Santana et al., 2020). These environments are habitats for pelagic, mesopelagic, and benthopelagic fish, which contribute to the formation of larval assemblages in the adjacent oceanic waters (Lima et al., 2020; Campanella et al., 2021).

Several studies worldwide have identified different larval fish assemblages and, when possible, sought to relate their occurrence with environmental conditions (e.g., Marancik et al., 2005; Olivar et al., 2012; Bonecker et al., 2017). Most studies on ichthyoplankton in Brazil were carried out in estuaries or adjacent coastal regions (Bonecker et al., 2019a; Lima et al., 2020; Alegretti et al., 2021; Bonecker et al., 2022). There are few studies on larval fish assemblages in the oceanic waters of Brazil, and most are theses or reports of monitoring programs (e.g., Nonaka et al., 2000; Bonecker et al., 2012; Stocco and Joyeux, 2015; Bonecker et al., 2017, 2019b; Souza and Mafalda, 2019). Most studies in Brazilian oceanic waters focused on a limited number of fish families (e.g., Castro and Bonecker, 2005, 2006; Barros et al., 2007; Campos et al., 2010; Castro et al., 2010). To fill in knowledge gaps and provide more information for future connectivity studies, we identified larval fish species along the Brazilian coast between 12°S and 22°S. This study aimed to answer 2 questions: (1) are there differences in the distribution of the abundance, composition, diversity, and equitability of fish larvae during 3 specific periods (spring 1998, winter 1999, and autumn 2000)? (2) If so, how are these differences affected by water temperature, salinity, and local depth?

Materials and methods

The central region of the Brazilian Exclusive Economic Zone is delimited in the north by Real River (12°S) and in the south by São Tomé Cape (22°S). This region has unusual topographic and oceanographic features due to the presence of seamounts and oceanic islands (Fig. 1A). Local topography supports the meandering of the Brazil Current and the formation of vortices in this region (Silveira et al., 2000; Palóczy et al., 2014). Abrolhos Bank and Vitória-Trindade Ridge act as physical barriers to the Tropical Water (TW) transported by the Brazilian Current that flows southward, resulting in vortices, meanders, and upwelling movements (Palóczy et al., 2014). Notably, Vitória-Trindade Ridge comprises approximately 30 shallow seamounts (depths <50 m) (Stocco and Joyeux, 2015).

This area has oligotrophic characteristics (Valentin et al., 2006) and is dominated by 3 water masses: TW, South Atlantic Central Water (SACW), and Coastal Water (Venancio et al., 2014; Castro Filho et al., 2015). Silveira et al. (2000) characterize the first 2 water masses as follows: TW—water temperature higher than 20.0°C and salinity higher than 36.0; and SACW—water temperature between 6.0°C and 20.0°C and salinity between 34.6 and 36.0. Venancio et al. (2014:242) reported that "[Coastal Water] and TW have the same temperature range but the [Coastal Water] is characterized by lower salinities than the TW, as a result from the mixing of shelf waters and continental drainage." In addition to these water masses, which dominate in the upper water column, there are also the Antarctic Intermediate Water (temperature between 3.0°C and 6.0°C and salinity between 34.2 and 34.6), Upper Circumpolar Deep Water (temperature between 3.3°C and 3.5°C and salinity between 34.4 and 34.6), and North Atlantic Deep Water (temperature between 3.0°C and 4.0°C and salinity between 34.6 and 35.0) (Silveira et al., 2000; Silveira, 2007).

Three oceanographic cruises were conducted during the spring of 1998 (from October to December), winter of 1999 (from May to July), and autumn of 2000 (from March to May), totaling 329 stations (Fig. 1, B–D). Oblique hauls were performed with a bongo net (330-µm and 500-µm mesh) during the day and at night in spring (57 d and 51 nights) and autumn (52 d and 56 nights) and only at night in winter. On the winter cruise, a concurrent exploratory fishing project conducted during daylight hours precluded plankton sampling except at night. Nets were towed from the surface to 200 m depth or 1 m above the bottom at shallower stations. Sampling stations were located over the continental shelf (depths <200 m), in the oceanic region (depths >200 m), and in the seamounts region (shallow depths in the oceanic region). Sampling followed the recommendations of Smith and Richardson (1977).

Two digital flowmeters (General Oceanics Inc, Miami, FL) were used to estimate the filtered water volume, and samples were immediately preserved in buffered formalin. Temperature and salinity data were obtained using a CTD Sea-Bird SBE19-03 SeaCAT Profiler (Sea-Bird Scientific, Bellevue, WA) from 3 depths: 20 m, 100 m, and 200 m. Temperature-salinity plots were created to identify water masses present in the area for each sampling period.

Only larval fish collected with the 330-µm mesh net were used in this study, and abundances (larvae/100 m^3) were determined using the volume of water filtered. Fish larvae were identified to the lowest possible taxon according to the methods of Bonecker and Castro (2006), Richards (2006), and Bonecker et al. (2014), among others. Larval fishes were classified as pelagic, mesopelagic, or demersal according to the habitats of the adults (Richards, 2006; Froese and Pauly, 2022). Classification followed Betancur-R et al. (2017) and Fricke et al. (2022). Damaged or very small larvae lacking diagnostic characters were grouped as unidentified. All identified specimens were deposited in the Integrated Zooplankton and Ichthyoplankton Laboratory of the Federal University of Rio de Janeiro collection.

The relative abundance (RA) was estimated as follows:

$$RA=(N\times 100)/n, \tag{1}$$

where N = the total number of individuals of a taxon in a sample; and
n = the total individuals of all taxa in the sample.

The RA values were classified following Lobo and Leighton (1986): dominant (≥50%), abundant (30–49.9%), low abundant (9.9–29.9%), and rare (<10%). The frequency of occurrence (FO) of each species was calculated as follows:

$$FO=(S\times 100)/p, \tag{2}$$

where S = the number of samples in which a taxon occurs; and
p = the total number of samples.

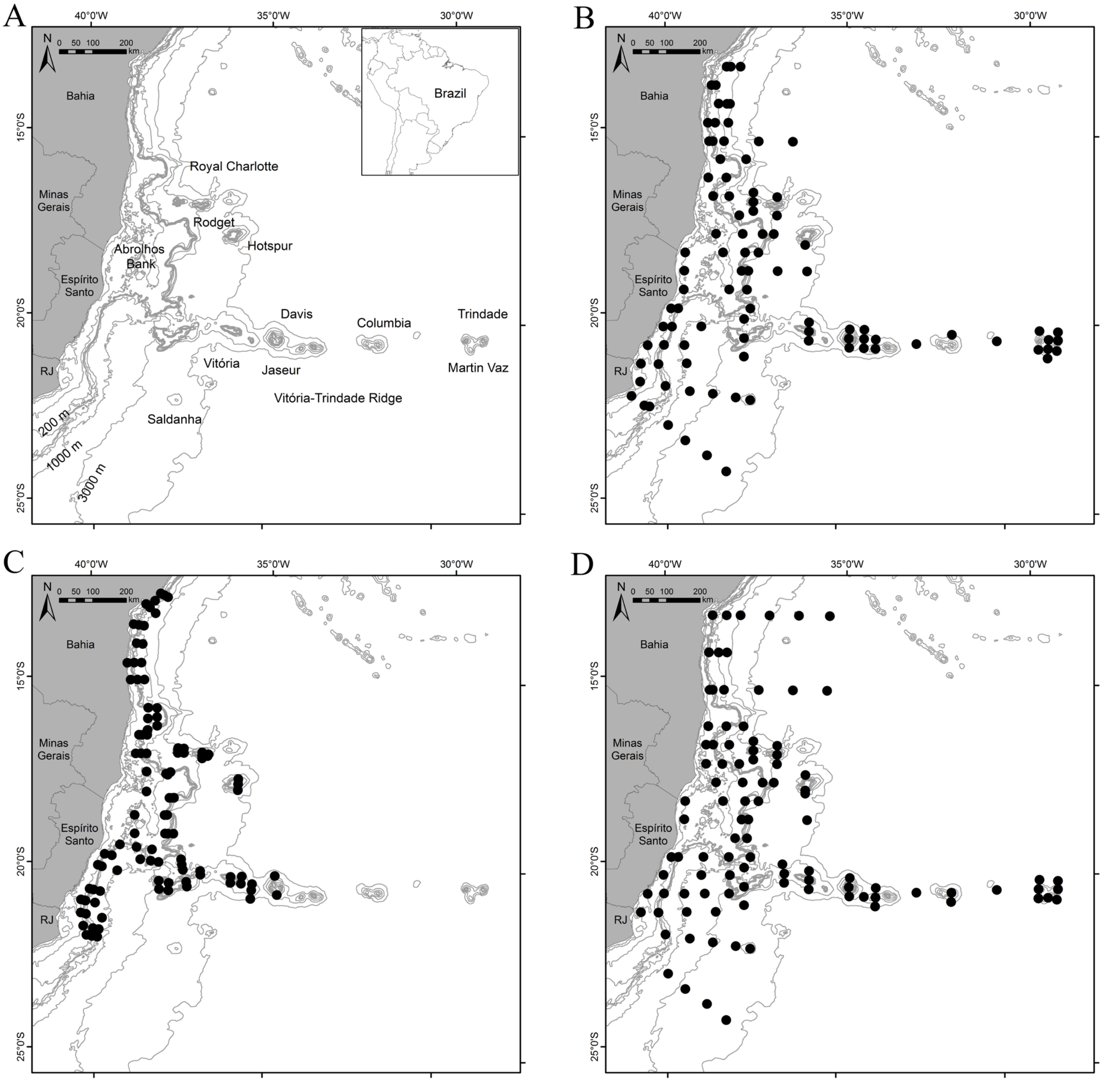

Figure 1

Map of the study area showing the main geographical features (gray depth contour lines) and (**A**) the sampling stations (black circles) during the (**B**) spring, (**C**) winter, and (**D**) autumn cruises. Stations are located in the central region of the Brazilian Exclusive Economic Zone (12–22°S). Oblique hauls were performed over the area to 200 m depth.

The FO values were classified following the method of Matteucci and Colma (1982): very frequent (present in ≥70% of the samples), frequent (present in 40–69.9% of the samples), infrequent (present in 10–39.9% of the samples), and sporadic (present in <10% of the samples).

The heterogeneity of variances of environmental and biotic data was verified using Levene's test, and normality was tested using the Shapiro–Wilk test (Legendre and Legendre, 2012). To estimate whether sampling only at night in winter may have affected our results, we tested for differences in abundance and diversity index between day and night during spring and autumn using the Mann–Whitney U test. Our a priori assumption was that abundance would differ between day and night, mainly reflecting daytime net avoidance, but the number of taxa might or might not differ between day and night. In fact, neither abundance nor number of taxa differed significantly between day and night. Kruskal–Wallis nonparametric correspondence analyses (Kruskal and Wallis, 1952) were done to determine whether there were significant differences in temperature (at 20 m, 100 m, and 200 m depth), salinity (at 20 m, 100 m, and 200 m depth), local depth, larval fish abundances, diversity, and equitability (Zar, 2010) among the sampling periods. The threshold of statistical significance was 0.05 in all analyses. We used a post-hoc multiple comparisons test (2-tailed) to identify significant differences between the means of the categories. These analyses were performed using Statistica 7.0 (StatSoft Inc., Tulsa, OK).

The subsequent analyses (diversity, equitability, analysis of similarities, cluster, and similarity of percentages) were performed using the Plymouth Routines Multivariate Ecological Research package, vers. 6.1 (Clarke and Warwick, 2001; Clarke and Gorley, 2006).

The Shannon–Wiener diversity (H′) and equitability (J′) indices were calculated using individuals identified to species, or genus if there was only one taxon, in the larval fish assemblages (Legendre and Legendre, 2012).

The analysis of similarities test was used to assess whether the larval fish assemblage structure differed among the 3 sampling periods (188 species×320 samples).

A hierarchical agglomerative clustering analysis with group-averaging linking was carried out from a Bray–Curtis index of dissimilarity to verify the formation of clusters in each sampling period. Abundances were transformed using log(x+1) to reduce internal variance and compare the relevant descriptors to the objectives of this study. The matrices were formed by the sampling stations and fish taxa (spring 1998: 119 taxa and 102 sampling stations; winter 1999: 146 taxa and 112 stations; autumn 2000: 99 taxa and 106 stations). An analysis of the similarity profile was used to group statistically similar sampling stations with their species composition, testing the null hypothesis that there is no difference in the structure of the assemblages in the study area. The similarity of percentages test was used to identify the taxa that contributed most to the similarity and dissimilarity among the groups identified in the cluster analyses.

The influence of environmental parameters on the structure of larval fish assemblages in each sampling period was tested using generalized linear models with a gamma family and the function link=log. The descriptors were total larval fish abundance, diversity, and equitability, whereas the environmental parameters (temperature at 20 m, salinity at 20 m, and local depth) were used as predictor variables. The temperature and salinity obtained at 20 m were selected to include the shallowest stations in this analysis (continental shelf and seamounts), as this depth is common to all sampling stations. In addition, there is a well-mixed surface layer above 20 m depths (Cardoso and Dourado, 2014), and we decided to exclude data obtained at depths greater than 20 m.

Initially, a full model was designed using all the variables, and then biologically logical models were constructed containing fewer variables. The Akaike information criterion corrected for small sample sizes (AICc) was used to select the best model. The model with the lowest AICc was considered the most plausible for describing the data, and the importance of alternative models was estimated from the difference in AICc between the model and the best model (ΔAICc). Notably, models with a difference in ΔAICc values ≤2 were also considered plausible (Burnham and Anderson, 2002). Generalized linear models were performed in R (vers. 3.6.3; R Core Team, 2020) using the HH (Heiberger and Holland, 2015) and MuMIn packages (Bartoń, 2020).

Results

Environmental data

Temperature varied from 13.6°C to 24.1°C in spring, 14.4°C to 27.3°C in winter, and 14.3°C to 28.5°C in autumn (Table 1). Salinity varied from 34.4 to 37.9 in spring, 35.4 to 37.6 in winter, and 35.3 to 37.9 in autumn (Table 1).

The temperature and salinity at 20 m were significantly different among the 3 sampling periods ($P<0.05$). Temperatures in spring were different from those in winter and autumn. Salinities in winter were significantly different from those in spring and autumn. Temperatures at 100 m varied between spring and winter ($P=0.0075$), whereas the salinity values showed variation in the 3 periods ($P=0.0439$). At 200 m, temperatures did not vary among the 3 periods ($P=0.0516$), but the salinity values in spring differed from those in the winter and autumn ($P=0.0019$).

Temperature-salinity plots showed that during the 3 cruises, TW was mainly in the upper 100 m, and SACW was registered at 200 m. Nevertheless, TW reached 200 m and SACW reached 100 m in some sampling stations (Fig. 2, A–C).

During the 3 periods, the highest water temperatures at depths of 20 m and 100 m were observed north of the Abrolhos Bank, and the lowest values were found close to the Espírito Santo and Rio de Janeiro coasts. Temperatures below 20°C near the Rio de Janeiro coast showed the presence of SACW at a depth of 100 m in the 3 sampling periods. Temperatures at 20 m and 100 m varied little between the continental shelf and the oceanic and seamount regions in the 3 periods. At 200 m depths, slightly cooler temperatures occurred at stations closer to the coast, with SACW observed near Abrolhos Bank and the Rio de Janeiro coast.

At 20 m, the lowest salinities were close to the Rio de Janeiro coast and the highest were north of Abrolhos Bank in all seasons. At 100 m and 200 m depths, the lowest salinities were near the Rio de Janeiro coast and the highest were north of Abrolhos Bank in autumn and winter. Similar to temperature, salinity values at 20 m and 100 m varied little between the continental shelf and the oceanic and seamount regions. However, at 200 m depths, slightly lower salinity values were measured over the continental shelf.

Table 1

Minimum (Min) and maximum (Max) temperature (°C) and salinity values obtained at 20 m, 100 m, and 200 m depths during spring 1998, winter 1999, and autumn 2000 in the in the central region of the Brazilian Exclusive Economic Zone.

	Depth					
	20 m		100 m		200 m	
	Min	Max	Min	Max	Min	Max
Temperature (°C)						
Spring 1998	15.6	27.4	14.7	24.8	13.6	20.5
Winter 1999	22.5	27.3	18.8	26.8	14.4	19.4
Autumn 2000	18.4	28.5	16.8	25.6	14.3	21.0
Salinity						
Spring 1998	35.7	37.9	35.4	37.3	34.4	36.8
Winter 1999	36.1	37.6	36.1	37.6	35.4	36.3
Autumn 2000	35.4	37.9	35.8	37.3	35.3	37.7

Larval fish abundances

Although larval abundance and size frequency structure would normally be expected to differ between day and night sampling, mainly reflecting daytime net avoidance by larger larvae, the results of the Mann–Whitney U test found no significant difference in larval abundance and diversity between day and night. Therefore, subsequent analyses combined day and night sampling with nighttime sampling.

Larval fish abundance at each station in the 3 periods was low (<100 larvae/100 m^3), except for higher values obtained over the continental shelf. Abundance was highest during winter, with a maximum value of 405 larvae/100 m^3 (Fig. 3, A–C). Abundances were significantly different ($P<0.05$) among the 3 sampling periods ($P<0.05$), and the values in winter were higher than those in spring and autumn.

Larval assemblages

We observed 88 families, 130 species, and 53 taxa identified to genus in the study area (Suppl. Table 1). More demersal families (52) were collected compared to epipelagic (16) and mesopelagic (20) families, but in general, mesopelagic taxa were most abundant.

Most taxa were classified as rare because their RA was lower than 10% (Suppl. Table 1). Myctophidae larvae were classified as abundant in all 3 seasons but were much less abundant in spring and winter than in autumn (Suppl. Table 1). Meanwhile, Engraulidae and Scaridae were most abundant during winter and autumn, respectively.

Most taxa were classified as sporadic because their frequency of occurrence was low, with occurrences in <10% of the samples collected in each sampling period (Suppl. Table 1). During the spring, Myctophidae larvae were classified as very frequent; Paralepididae, darter goby (*Ctenogobius boleosoma*), and Scaridae were classified as frequent; and 29 families occurred infrequently. Phosichthyidae, Paralepididae, Myctophidae, Bregmacerotidae, darter goby, Scaridae, and Serranidae were classified as very frequent in winter. During this period, Sternoptychidae, Synodontidae, Ophidiidae, Apogonidae, Carangidae, and Labridae were frequent, whereas one order and 20 families were less frequent (Suppl. Table 1). During autumn, myctophids, darter goby, and Scaridae were very frequent; Gonostomatidae, Paralepididae, Carangidae, and Serranidae were frequent; and Anguilliformes and 14 families were less frequent (Suppl. Table 1).

Myctophidae were almost absent from continental shelf stations in spring but were present in autumn and winter (Fig. 4, A–C). Although abundances were low in the study area, the highest values in winter were on the continental shelf off the Espírito Santo and Bahia coast. Scaridae larval abundances were also low, and they were absent from many stations in spring (Fig. 5A). Abundances were highest in winter near the Abrolhos and Royal Charlotte Banks (Fig. 5B) and in autumn (Fig. 5C) near Royal Charlotte Bank and Vitória Seamount in the Vitória-Trindade Ridge.

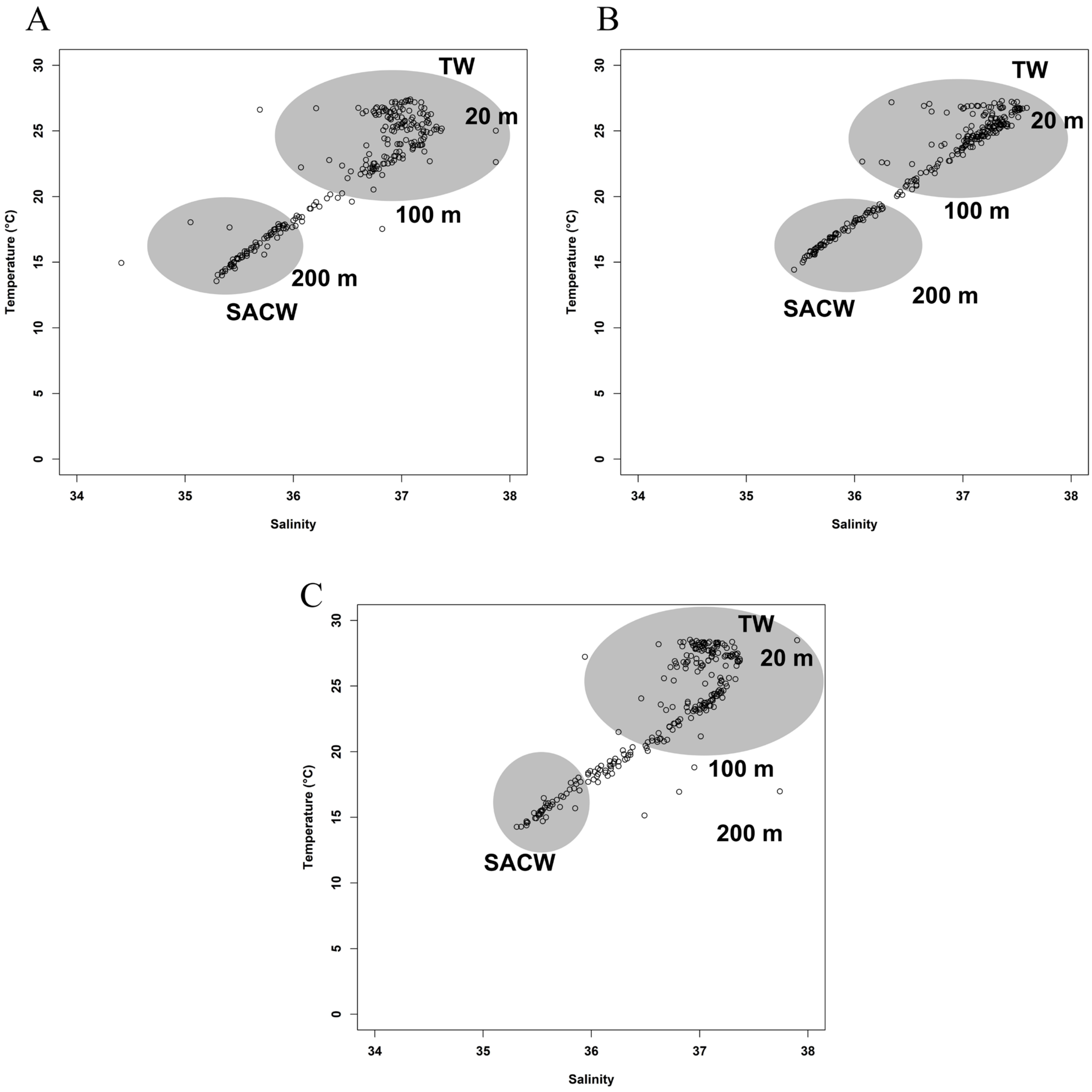

Figure 2

Temperature-salinity diagrams showing the water masses found during (**A**) spring 1998, (**B**) winter 1999, and (**C**) autumn 2000 at 3 depths in the central region of the Brazilian Exclusive Economic Zone. The water masses are the Tropical Water (TW) and South Atlantic Central Water (SACW).

Ecological indices

The diversity varied from 0.47 to 3.99 during spring, 0.51 to 3.66 in winter, and 0.73 to 3.18 in autumn. During the spring and winter, respectively, 40% and 70% of diversity values were greater than 2.00 (Fig. 6, A and B). During autumn, diversity values were distributed evenly across the study area (Fig. 6C). However, diversity varied significantly among the sampling periods (*P*<0.05), and the higher values in winter differed from those in spring and autumn.

Equitability varied from 0.20 to 1.00 during spring,

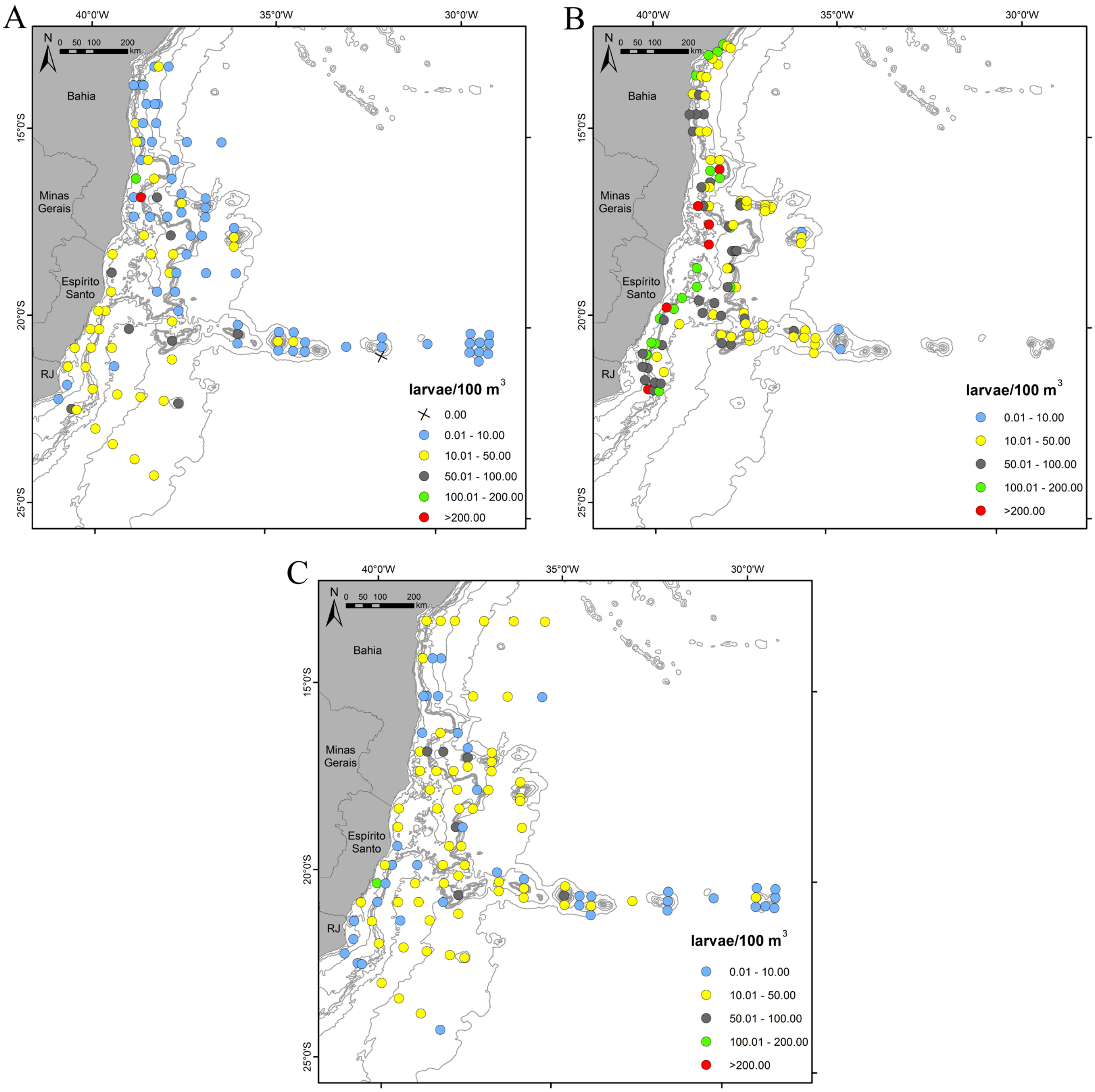

Figure 3

Map showing larval fish abundances (circles) during (**A**) spring 1998, (**B**) winter 1999, and (**C**) autumn 2000 in the central region of the Brazilian Exclusive Economic Zone. The × mark indicates the absence of larvae at that station. Solid gray lines indicate depth contours in meters.

from 0.17 to 1.00 in winter, and from 0.40 to 1.00 in autumn, reflecting the diversity results. Values obtained during the 3 sampling periods were significantly different ($P<0.05$). The equitability index showed differences in the evenness of taxa abundances in many of the sampling stations.

Spatial and temporal variations in larval fish assemblages

The analysis of similarities test showed that larval fish assemblages varied significantly among the 3 sampling periods (Global $R=0.201$, significance level=0.1%). The cluster analysis of the spring samples showed 15 station

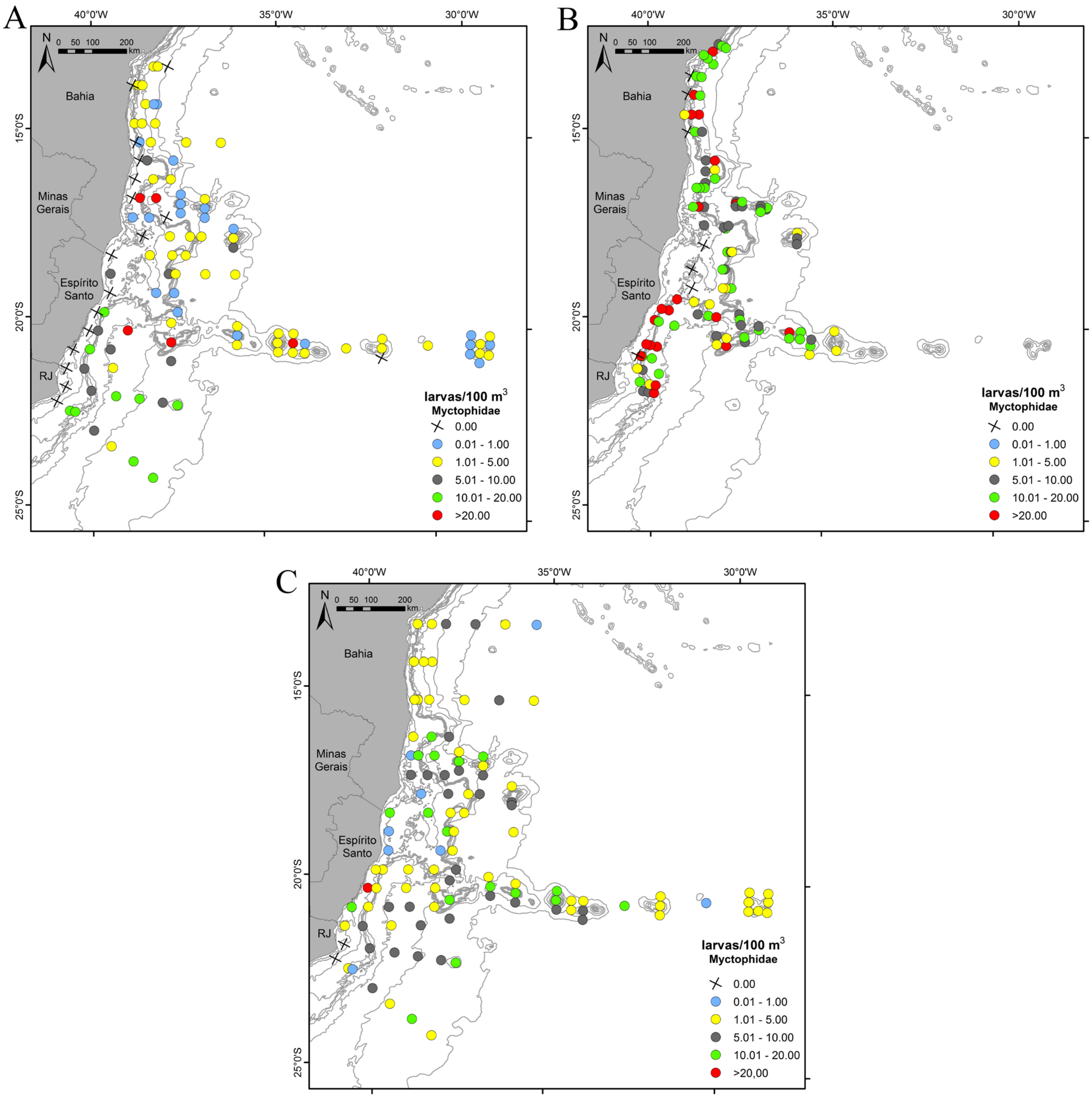

Figure 4

Map showing the distribution of Myctophidae larval abundance (circles) during (**A**) spring 1998, (**B**) winter 1999, and (**C**) autumn 2000 in the central region of the Brazilian Exclusive Economic Zone. The × mark indicates the absence of larvae at that station. Solid gray lines indicate depth contours in meters.

groups (Fig.7A, groups A–O). The similarity of percentages analysis showed that larvae distributed in the oceanic, mesopelagic, and coral reef areas made the largest contribution to assemblages in the oceanic region (Table 2). The groups formed by samples from the oceanic and seamount regions had greater contributions of larvae from oceanic and coral reef families. In the continental shelf assemblage, the largest contribution was from coastal taxa, whereas in the assemblage that included the continental shelf, oceanic, and seamount stations, the largest contributions were from coastal and coral reef taxa (Table 2).

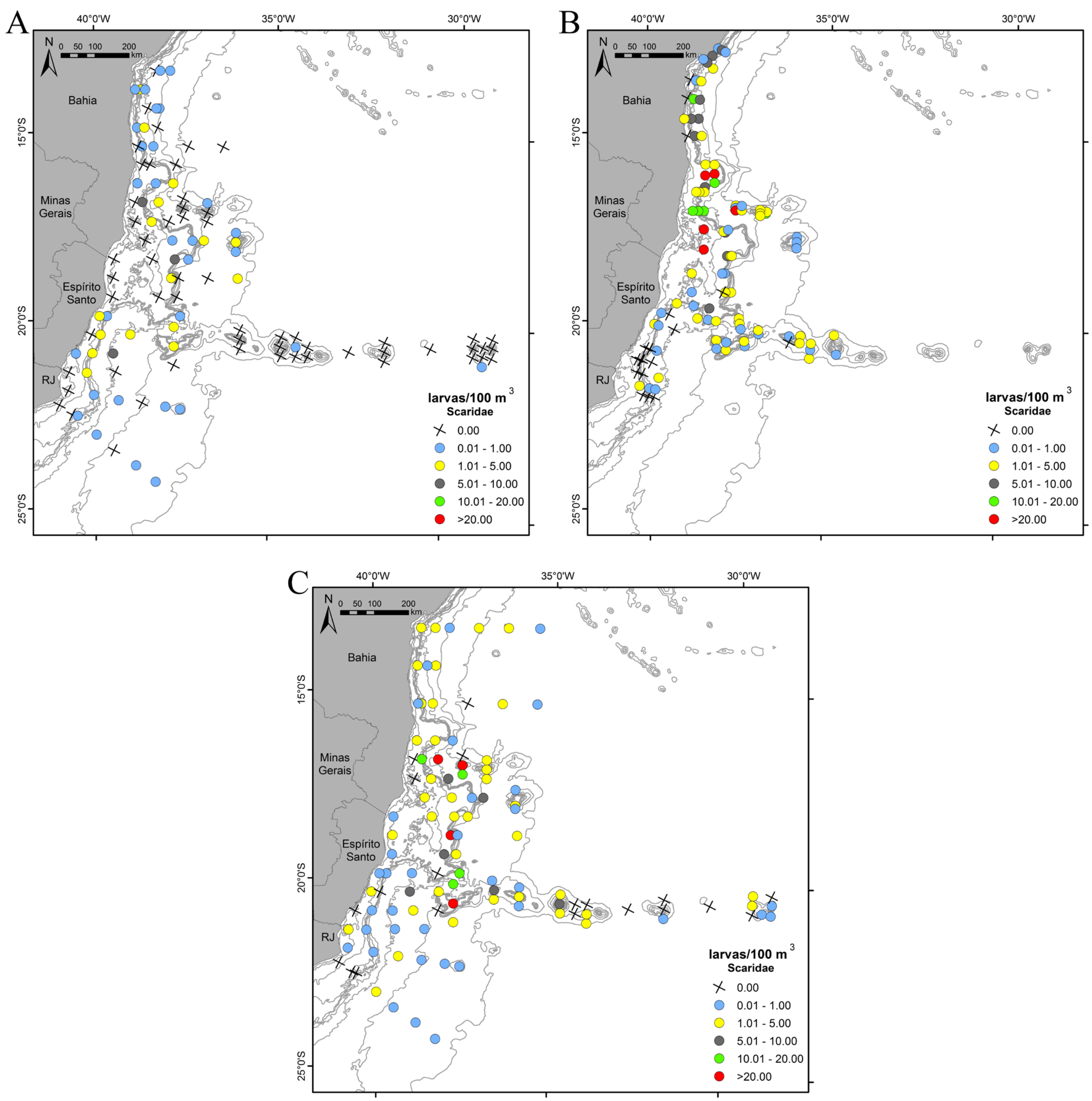

Figure 5

Map of the distribution of Scaridae larval abundance during the (**A**) spring 1998, (**B**) winter 1999, and (**C**) autumn 2000 in the central region of the Brazilian Exclusive Economic Zone. The × mark indicates the absence of larvae at that station. Solid gray lines indicate depth contours in meters.

In winter, 15 assemblages also were found (Fig. 7B, groups A–O). Assemblages from the continental shelf had a greater contribution of larvae from coastal families and other families common in coral reefs, with the occasional presence of mesopelagics (Table 3). Coral reef larvae dominated the continental shelf and seamount assemblage (Table 3). The assemblage that included ocean and seamount stations had a greater contribution of larvae from mesopelagic and coral reef families. Mesopelagic taxa dominated the continental shelf–oceanic assemblage, whereas reef families dominated the assemblage that included the continental

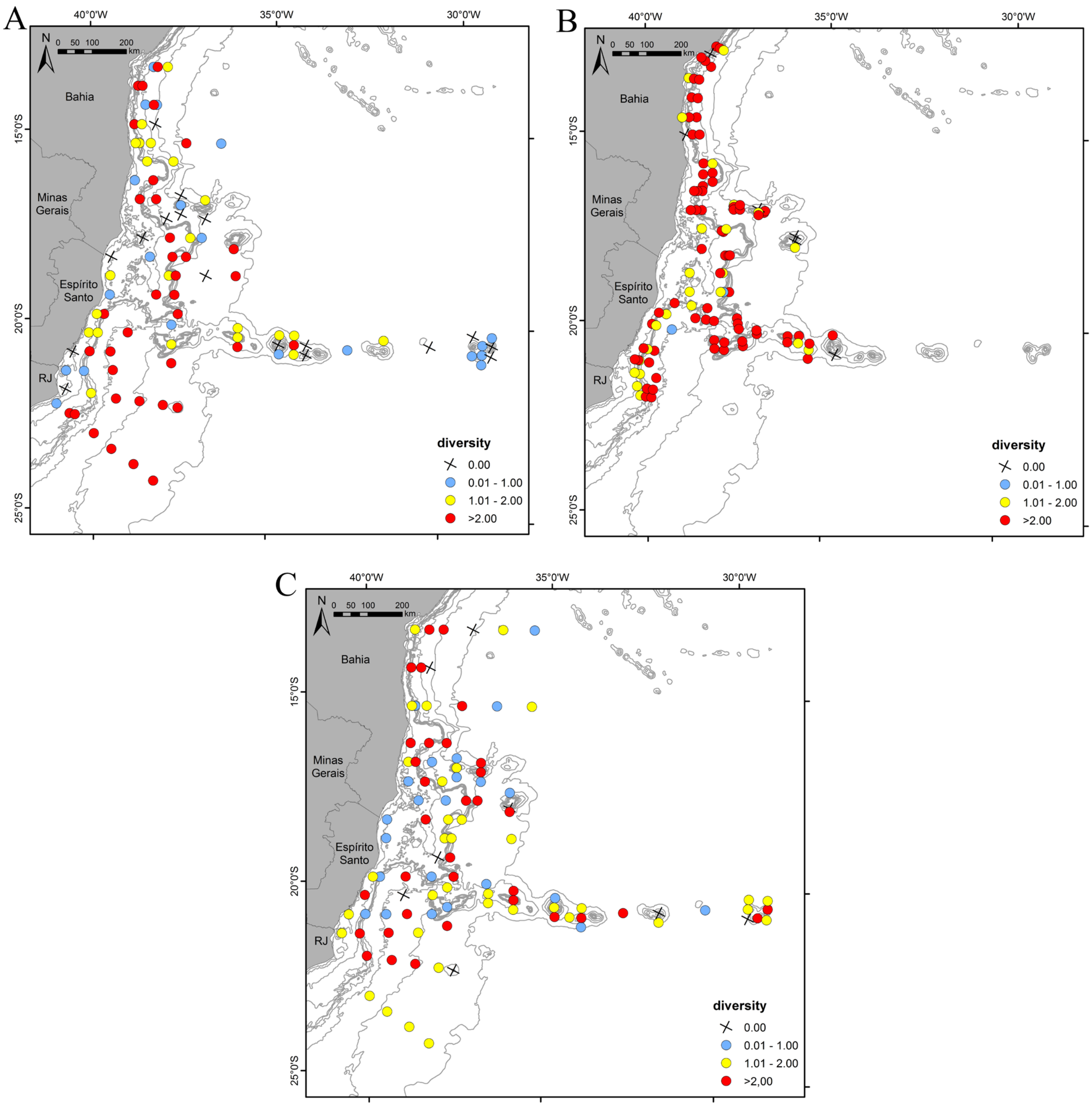

Figure 6

Map showing the distribution of larval diversity values during (**A**) spring 1998, (B) winter 1999, and (**C**) autumn 2000 in the central region of the Brazilian Exclusive Economic Zone. The × mark indicates the absence of larvae at that station. Solid gray lines indicate depth contours in meters.

shelf, oceanic, and seamount stations. Finally, mesopelagic and coral reef families contributed the most to the oceanic assemblages.

During autumn, no significant difference in larval fish assemblages was observed (Fig. 7C). Scaridae larvae dominated most stations (71%). Notably, 2 sampling stations separated from the others were represented only by larval topside lanternfish (*Notolychnus valdiviae*) (Myctophidae) and *Eustomias* sp. (Stomiidae). The lack of Scaridae and Callionymidae also contributed to the dissimilarity between these sampling stations and the others (Fig. 7C).

Table 2

Results of the similarity of percentages analysis showing the contribution of species to the differences among the groups formed in the cluster analysis during spring 1998 in the central region of the Brazilian Exclusive Economic Zone.

Group A Average similarity: 20.29%		Group B Average similarity: 17.88%		Group C Average similarity: 12.33%	
Taxa	%	Taxa	%	Taxa	%
Myctophum nitidulum	80.86	*Sudis atrox*	42.23	Scorpaenidae	79.03
Cyclothone alba	19.14	*Euthynnus alletteratus*	37.94	*Sigmops elongatus*	10.48
		Thunnus thynnus	13.18	*Ranzania laevis*	10.48
Group D Average similarity: 23.87%		**Group E Average similarity: 27.75%**		**Group F Average similarity: 18.43%**	
Taxa	%	Taxa	%	Taxa	%
Labridae	67.98	*Coryphaena hippurus*	64.59	*Dactylopterus volitans*	100
Myripristis jacobus	13.95	Ophidiidae	35.41		
Cyclothone braueri	11.46				
Group G Average similarity: 29.67%		**Group H Average similarity: 49.02%**		**Group I Average similarity: 33.55%**	
Taxa	%	Taxa	%	Taxa	%
Cyclothone braueri	41.60	*Maurolicus stehmanni*	31.97	*Pollichthys mauli*	25.77
Pollichthys mauli	22.89	*Myctophum nitidulum*	17.24	Scaridae	22.15
Lepidophanes guentheri	22.89	*Pollichthys mauli*	15.04	*Maurolicus stehmanni*	19.14
Sudis atrox	12.61	*Myctophum affine*	12.26	*Bregmaceros atlanticus*	14.48
		Bothus ocellatus	7.64	*Hygophum reinhardtii*	8.11
		Lestidium atlanticum	4.84	*Cyclothone alba*	4.26
		Scaridae	4.14		
Group J Average similarity: 31.34%		**Group K Average similarity: 24.68%**		**Group L Average similarity: 23.03%**	
Taxa	%	Taxa	%	Taxa	%
Callionymidae	32.91	*Pollichthys mauli*	31.64	Scaridae	77.42
Scorpaenidae	17.86	*Hygophum reinhardtii*	31.64	Callionymidae	11.50
Lestidium atlanticum	15.57	*Bothus ocellatus*	14.81	Apogonidae	2.24
Pollichthys mauli	13.68	Ophidiidae	12.55		
Lampanyctus sp.	5.94				
Sudis atrox	5.48				
Group M Average similarity: 43.56%		**Group N Average similarity: 30.17%**		**Group O Average similarity: 43.82%**	
Anchoa januaria	100.00	Taxa	%	Taxa	%
		Apogonidae	42.82	Scaridae	25.10
		Labridae	35.63	Scorpaenidae	20.74
		Haemulidae	4.85	Callionymidae	15.48
		Ophidiidae	3.84	Apogonidae	14.41
		Bothus ocellatus	3.66	*Chloroscombrus chrysurus*	8.88
				Labridae	5.74

Influence of environmental conditions on larval fish assemblages

Among the competing generalized linear models, the most plausible model indicated that total larval fish abundance was mainly related to depth, with a negative relationship in the 3 sampling periods and a positive or negative relationship with temperature and salinity depending on the sampling period (Table 4). Salinity (spring 1998; positive relationship) and temperature (winter 1999; positive relationship) were the best predictors of diversity, while salinity was positively related to equitability during spring 1998 (Table 4).

Discussion

The water masses observed during the 3 sampling periods showed a permanent vertical stratification that is characteristic of this area (Andrade et al., 2004;

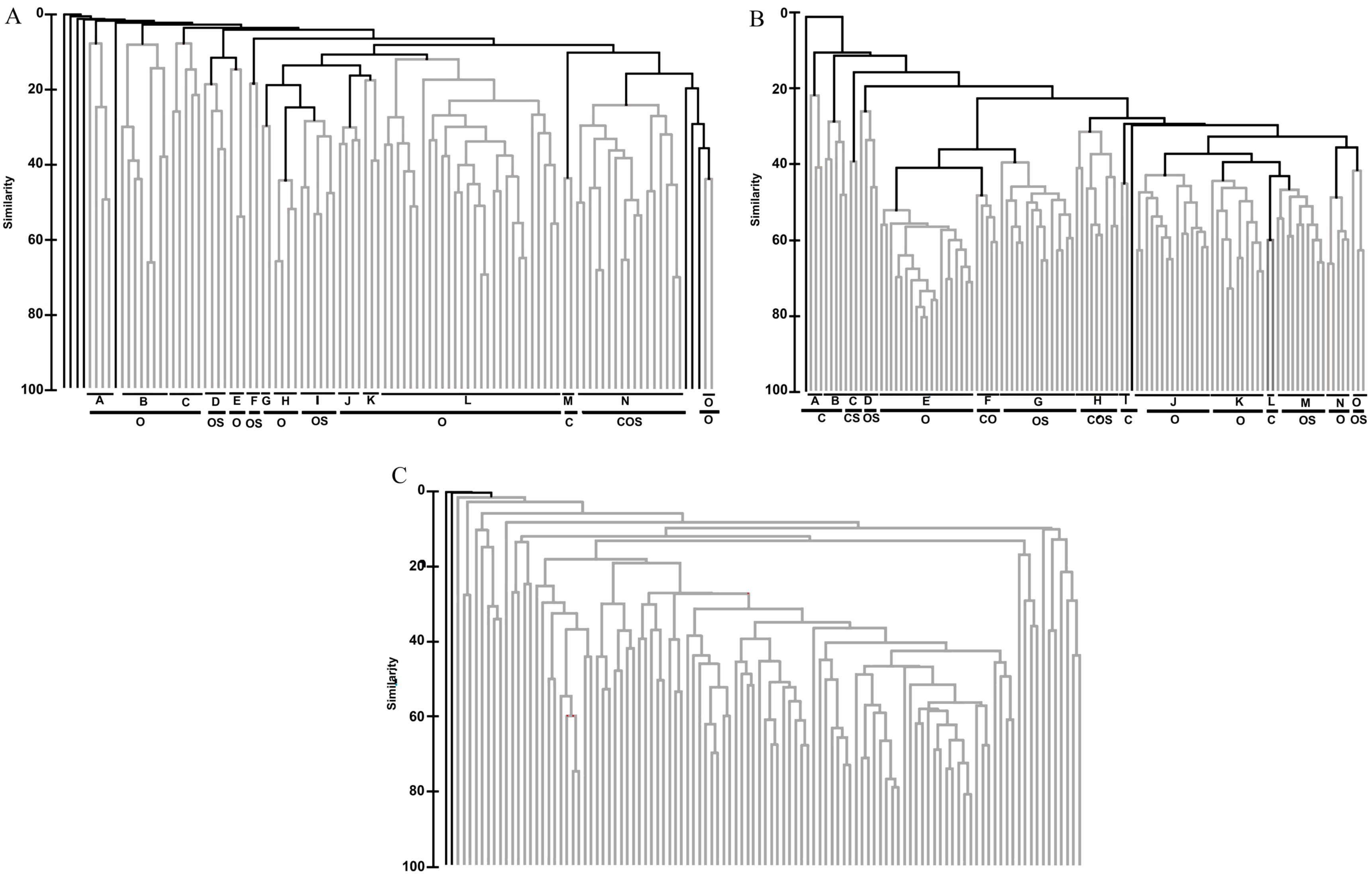

Figure 7

Cluster analysis showing similarities in the structure of larval fish assemblages in the central region of the Brazilian Exclusive Economic Zone during (**A**) spring 1998, (**B**) winter 1999, and (**C**) autumn 2000. Gray lines indicate groups that are significantly different. Letters on the first line of the *x*-axis represent the groups formed by sampling stations (A–O). Letters on the second line of the *x*-axis represent assemblages formed, including the continental shelf assemblage (C), oceanic assemblage (Oc), continental shelf and seamounts assemblage (CS), coastal shelf and oceanic assemblage (COc), oceanic and seamounts assemblage (OcS), and continental shelf, oceanic, and seamounts assemblage (COcS). Hierarchical agglomerative clustering was performed using the Bray–Curtis index of dissimilarity.

Table 3

Results of the similarity of percentages analysis showing the contribution of species to the differences among the groups observed during winter 1999 in the central region of the Brazilian Exclusive Economic Zone.

Group A Average similarity: 28.17%		Group B Average similarity: 32.72%		Group C Average similarity: 39.27%	
Taxa	%	Taxa	%	Taxa	%
Decapterus punctatus	47.49	*Engraulis anchoita*	56.78	Apogonidae	56.60
Trachurus lathami	23.63	*Chloroscombrus chrysurus*	10.97	Scaridae	25.20
Chloroscombrus chrysurus	10.20	*Sardinella aurita*	10.70	Labridae	18.19
Bregmaceros cantori	10.07	*Diplectrum radiale*	5.79		
		Scaridae	3.41		
		Syacium papillosum	2.72		

Group D Average similarity: 31.89%		Group E Average similarity: 58.69%		Group F Average similarity: 51.40%	
Taxa	%	Taxa	%	Taxa	%
Pollichthys mauli	56.40	*Maurolicus stehmanni*	37.03	*Maurolicus stehmanni*	50.62
Scaridae	43.60	*Pollichthys mauli*	25.47	*Pollichthys mauli*	43.31
		Bregmaceros atlanticus	13.27		
		Vinciguerria nimbaria	8.71		
		Lestrolepis intermedia	4.25		
		Lestidium atlanticum	3.13		

Group G Average similarity: 47.29%		Group H Average similarity: 38.36%		Group I Average similarity: 45.07%	
Taxa	%	Taxa	%	Taxa	%
Vinciguerria nimbaria	26.49	Scaridae	25.96	*Bregmaceros cantori*	38.68
Pollichthys mauli	21.86	*Diplectrum radiale*	17.51	*Vinciguerria nimbaria*	33.61
Lepidophanes guentheri	13.60	Labridae	14.71	Scaridae	27.71
Scaridae	10.83	Apogonidae	9.43		
Bregmaceros atlanticus	8.25	Ophidiidae	6.02		
Lestidium atlanticum	4.64	*Serranus* sp.	4.41		
Scorpaenidae	3.87	*Pollichthys mauli*	3.80		
Maurolicus stehmanni	2.88	*Decapterus punctatus*	2.77		
		Vinciguerria nimbaria	2.13		
		Mullidae	1.67		
		Scorpaenidae	1.58		
		Syacium papillosum	1.35		

Group J Average similarity: 46.93%		Group K Average similarity: 49.47%		Group L Average similarity: 59.97%	
Taxa	%	Taxa	%	Taxa	%
Scaridae	44.38	Scaridae	59.33	Scaridae	22.46
Vinciguerria nimbaria	18.50	Labridae	11.42	Labridae	18.55
Pollichthys mauli	15.53	*Vinciguerria nimbaria*	5.93	*Decapterus punctatus*	15.51
Labridae	7.95	Callionymidae	4.48	Scorpaenidae	10.57
Lepidophanes guentheri	4.78	*Lestrolepis intermedia*	4.12	Apogonidae	8.33
		Lampadena sp.	3.96	*Lepidophanes guentheri*	8.14
		Lepidophanes guentheri	2.40	*Lampadena* sp.	5.20
				Ophidiidae	5.20

Group M Average similarity: 50.28%		Group N Average similarity: 53.43%		Group O Average similarity: 48.71%	
Taxa	%	Taxa	%	Taxa	%
Scaridae	41.33	Scaridae	42.21	*Vinciguerria nimbaria*	28.87
Decapterus punctatus	14.19	Callionymidae	32.34	Scaridae	25.51
Pollichthys mauli	7.66	*Vinciguerria nimbaria*	14.44	Ophidiidae	15.98
Vinciguerria nimbaria	7.50	*Lestidium atlanticum*	5.55	*Lestrolepis intermedia*	11.53
Lepidophanes guentheri	5.17			Labridae	6.20
Labridae	4.30			*Lestidium atlanticum*	5.41
Apogonidae	4.02				
Lutjanidae	3.16				
Bregmaceros atlanticus	2.84				

Table 4

Results of generalized linear models used to examine the effect of environmental parameters on larval fish abundance, diversity, and equitability during the 3 sampling periods in the central region of the Brazilian Exclusive Economic Zone. Model selection based on Akaike information criterion (AIC) scores was used to determine the model with the most support. For each model, the AIC corrected for small sample sizes (AICc), the difference in AICc between the model and the best model (ΔAICc), and the weight (wi) are provided. An asterisk (*) indicates the model that best fits the data. The predictor variables were temperature (Tem, at 20 m), salinity (Sal, at 20 m), and local depth (Dep). The absence of a model for one of the sampling periods was due to the test not detecting biologically logical models.

Model	AICc	ΔAICc	wi
1 – Larval fish abundance			
Spring 1998			
(-) Tem/(-) Dep/(+) Sal*	101.17	0.00	0.96
Winter 1999			
(-) Dep/(-) Sal*	14.14	0.00	0.74
Autumn 2000			
(+) Tem/(-) Dep/(-) Sal*	45.98	0.00	0.51
(+) Tem/(-) Dep	46.17	0.18	0.46
2 – Diversity			
Spring 1998			
(+) Sal*	-24.98	0.00	0.43
(-) Tem/(+) Sal	-23.37	1.61	0.19
(-) Dep/(+) Sal	-23.12	1.87	0.17
Winter 1999			
(+) Tem*	-578.71	0.00	0.30
(+) Tem/(+) Sal	-577.43	1.28	0.16
(+) Dep/(+) Tem	-577.09	1.61	0.14
3 – Equitability			
Spring 1998			
(+) Sal*	-137.82	0.00	0.36

Bonecker et al., 2012). Other studies have also described the dominance of TW and SACW in the upper 200 m of the water column (Brandão et al., 2020; Santana et al., 2020). The upwelling of SACW in the Cabo Frio upwelling system (23–42°C) likely influenced lower temperatures observed near the Rio de Janeiro coast (Valentin, 2001). This upwelling center has 2 phases: the "upwelling phase from late September to March and a relaxation phase from April to early September" (Calil et al., 2021:1).

Although upwelling regions are known to have high productivity (Eisele et al., 2021; Ramírez-Martínez et al., 2022), our data did not seem to be influenced by this as, in general, the study area was characterized by low larval fish abundance. The Brazilian central coast is characterized by oligotrophic waters, with low primary and fishery productivities and dominated by tropical waters transported southward by the Brazil Current (Bonecker et al., 2006a; Ciotti et al., 2007). This oligotrophic water most likely influenced the low abundances of fish larvae recorded in the study area. As expected, the highest larval abundance values were observed in the continental shelf, as these regions are usually more productive than the oligotrophic oceanic waters (Santana et al., 2020). Souza and Mafalda (2019) also found lower larval abundances towards oceanic waters in northeast Brazil, and Torres-Barajas et al. (2021) showed a similar pattern in Mexico.

Larval abundances generally increase during the hottest periods of the year (summer and spring) and decrease in winter (Nonaka et al., 2000). Although there was no significant difference between day and night abundances in spring and autumn, the higher abundances we observed in winter may reflect the influence of sampling only at night. Sampling at night commonly yields more larvae than sampling during the day in both coastal and oceanic regions (Olivar and Beckley, 2022; Ramírez-Martínez et al., 2022; Wang et al., 2022). Greater abundances of larvae observed during the night may be associated with larval vertical migration, with larvae moving from greater daytime depths to shallower depths at night (Bonecker et al., 2019c). However, because we sampled the entire water column where most larvae live both day and night, migration into or out of the sampling domain should have contributed minimally to the differences observed among sampling periods. Several authors in Brazil (e.g., Nonaka et al., 2000) and elsewhere (e.g., Funes-Rodríguez et al., 2002; Avalos-García et al., 2003) also recorded the seasonal change in the composition of larval assemblages.

Furthermore, larval fish assemblages during spring and winter revealed patterns of taxa distributions. Larger, older larvae, which have greater visual capacity and swimming abilities, often avoid capture from plankton nets during the day (Morse, 1989; Whitney et al., 2021). The size- or stage-frequency data are unavailable, and it was not possible to evaluate the influence of avoidance by larger larvae. However, the lack of a statistically significant difference in day versus night abundances in spring and autumn suggests that the effect of any net avoidance by larger, older larvae is minor.

The number of species identified (130) between Rio Real (12°S) and São Tomé Cape (12°S) is considered high compared to other larval fish studies in the same area (Nonaka et al., 2000; Stocco and Joyeux, 2015). Most of the taxa identified have already been recorded on the Brazilian coast, mainly as adults (Figueiredo et al., 2002; Menezes et al., 2003; Costa et al., 2005). However, there also were several first records for Brazilian waters: maurolicine Type Alpha, *Tiluropsis*, benttooth bristlemouth (*Cyclothone acclinidens*), nofin loosejaw

(*Photostomias guernei*), *Bregmaceros* n. sp., and deepwater pipefish (*Cosmocampus profundus*) (Harold and Johnson, 2003; Bonecker and Castro, 2006; Bonecker et al., 2006b). The range of the pipehorse (*Amphelikturus dendriticus*) was also extended to the Vitória coast in the Espírito Santo State. High numbers of taxa are characteristic of tropical marine environments (Nonaka et al., 2000; Katsuragawa et al., 2014), as observed in the Gulf of Mexico (Flores-Coto et al., 2000; Espinosa-Fuentes and Flores-Coto, 2004), the west coast of Mexico (Franco-Gordo et al., 2002), and Australia (Beckley et al., 2019).

The overall larval fish fauna included more demersal fish families than epipelagic or mesopelagic families, but mesopelagics, mainly Myctophidae, had more larvae than the others. It is common for some taxa to be dominant in ichthyoplankton assemblages (Katsuragawa et al., 1993). Notably, Myctophidae commonly dominate assemblages in studies in oceanic regions of the world (Echeverri-García et al., 2022). Analysis of similarities showed that the 3 sampling periods differed significantly. This result likely reflects a seasonal effect rather than a sampling effect because there were no significant differences between day and night abundances and diversities in spring and autumn. However, we cannot exclude the possibility that it is also partly a sampling artifact, as tows were conducted only at night during the winter. A potential contributor to an increased number of species at night may be the migration of mesopelagic taxa into or out of the upper water column. Loeb (1979:777) noted that larvae of most mesopelagic fish occur "within the upper several hundred meters of the water column" but also noted that in the California Current region, "the majority of species occurred within the mixed layer and upper thermocline." Therefore, as we sampled nearly the entire water column both day and night where most of these larvae live, migration into or out of the sampling domain is not likely to have contributed significantly to the observed differences among sampling periods. Continental shelf assemblages were formed mainly by coastal families, some reef-associated families, and some mesopelagic families that may have been associated with the upwelling of SACW. Coastal families with epipelagic and demersal habitats, such as Engraulidae, Clupeidae, and Gobiidae, are also common in other coastal areas (e.g., Marancik et al., 2005; Katsuragawa et al., 2014). The dominance of demersal and mesopelagic families in coastal and oceanic waters, respectively, was also recorded in the tropical eastern Indian Ocean (Beckley et al., 2019).

The oceanic assemblages were dominated by epipelagic and mesopelagic families, as expected, and by reef-associated families due to the presence of seamounts. Similar results were obtained in the Vitória-Trindade Seamount Chain (Stocco and Joyeux, 2015). Assemblages found in oceanic, seamount, and continental shelf environments had a greater contribution of mesopelagic, oceanic, and reef-associated families, a pattern seen in other studies. For example, Harris et al. (2020) found a dominance of mesopelagic families (e.g., Myctophidae and Gonostomatidae larvae) in an area of shallow seamounts in the southwest Indian Ocean, and Funes-Rodríguez et al. (2002) observed overlap among larvae from the 3 habitats in the eastern Pacific off Baja California, Mexico. This species overlap from different habitats can occur due to the fluidity of the pelagic environment, which allows larval dispersal and transport by currents (Crochelet et al., 2020).

Oceanic islands and seamounts are favorable environments for pelagic and demersal species that normally do not occur in oceanic regions (Boehlert and Mundy, 1993); moreover, "currents can ensure connectivity between them and with adjacent ecosystems" (Crochelet et al., 2020:2). Simon et al. (2022:558) state that "seamounts are important to the connectivity between the continental shelf and oceanic islands, in both ecological and evolutionary timescales." Upwelling and vortices can occur in seamount vicinities, increasing the primary productivity and zooplankton abundance and acting as hotspots for many benthic and pelagic organisms, including fishes (Stocco and Joyeux, 2015; Lima et al., 2020). However, little is known about the fish larvae in these ecosystems and whether these communities are distinct or "an extension of typical oceanic assemblages" (Harris et al., 2020:1). In our study in oceanic waters, the presence of larvae from reef-associated families (e.g., Scaridae, Labridae, Apogonidae) and those that have a more coastal distribution (e.g., Carangidae, Serranidae, Scorpaenidae, Gobiidae), in addition to the mesopelagic ones, suggests that seamounts support a wide range of fish families with different habitats.

The study area was characterized by high diversity values with significant seasonal variation. Although the greater diversity during winter may be related to the exclusively nighttime collections, this sampling effect likely had a minor influence on the observed results, as previously discussed. Another study on the Brazilian coast also observed an increase in diversity values in a seaward direction (Katsuragawa et al., 2014). The high diversity values we observed during the 3 study periods were most likely influenced by the habitat variability in the study area, with the presence of seamounts and coral reefs. The diversity values in our study were similar to those in Morocco and Mauritania (Arkhipov et al., 2022) and in the northern Aegean Sea (Kallianiotis et al., 2023). Diversity values were higher than the values observed in the northern Red Sea (Abu El-Regal, 2017), the Gulf of Alaska (Doyle et al., 2009), and the Gulf of Mexico (Meinert et al., 2020). However, comparisons are limited in the last study as the authors focused on the family level.

The results of the generalized linear model with the environmental parameters showed that the greatest larval abundances were associated with the shallower stations on the continental shelf. In contrast, greater salinity values, which are characteristic of the oceanic and seamount regions, were associated with the greatest diversities. Furthermore, equitability reflected the environmental stability of the oceanic region as it was positively associated with higher temperatures.

Conclusions

The larval fish assemblages varied seasonally and reflected the behavior and distributions of adults. Fish larvae abundances differed among the 3 sampling periods, and we observed the highest abundances in fish larvae in winter. Abundances were highest on the continental shelf where depths were shallow, with peaks in the oceanic region near Abrolhos Bank and on the Vitória Seamount in the Vitória-Trindade Ridge. We observed 6 assemblages in the study area: continental shelf assemblage; oceanic assemblage; continental shelf and seamounts assemblage; coastal shelf and oceanic assemblage; oceanic and seamounts assemblage; and continental shelf, oceanic, and seamounts assemblage. The distributions of Myctophidae and Scaridae larvae revealed the highest abundances in the oceanic region near the Abrolhos and Royal Charlotte Banks and on the Vitória Seamount in the Vitória-Trindade Ridge. Furthermore, diversity was higher in oceanic waters of high salinity and temperature. Our study provides information on larval fish assemblages in Brazil's tropical waters, from coastal to oceanic and seamount regions, and will contribute to future studies that evaluate larval fish dispersion.

Acknowledgments

We thank S. Bonecker for his comments on this manuscript, P. de Carvalho for making the maps, and G. Moser and W. Richards for their help in Myctophidae larvae identification. This study was supported by the Executive Committee, Interministerial Commission for Marine Resources, Ministry of Environment, Sectoral Plan for Marine Resources, and a Coordenação de Aperfeiçoamento de Pessoal de Nível Superior grant.

Literature cited

Abu El-Regal, M. A.
2017. Spatial and temporal distribution of larvae of coral reef fishes in northern Red Sea, Egypt. Iran. J. Fish. Sci. 16:1043–1062.

Alegretti, C. B., H. Grande, C. A. P. Namiki, R. H. Loose, and F. P. Brandini.
2021. A preliminary assessment of larval fish assemblages on artificial reefs in the nearshore southern Brazil. Ocean Coastal Res. v69:e21017. https://doi.org/10.1590/2675-2824069.21-002cba

Andrade, L., A. M. Gonzalez, J. L. Valentin, and R. Paranhos.
2004. Bacterial abundance and production in the southwest Atlantic Ocean. Hydrobiologia 511:103–111. https://doi.org/10.1023/B:HYDR.0000014033.81848.48

Annasawmy, P., J.-F. Ternon, A. Lebourges-Dhaussy, G. Roudaut, P. Cotel, S. Herbette, F. Ménard, and F. Marsac.
2020. Micronekton distribution as influenced by mesoscale eddies, Madagascar shelf and shallow seamounts in the south-western Indian Ocean: an acoustic approach. Deep-Sea Res., II 176:104812. https://doi.org/10.1016/j.dsr2.2020.104812

Arkhipov, A. G., F. V. Kolomeiko, and R. A. Pak.
2022. Assessment of the species diversity of ichthyoplankton in the northern part of the central eastern Atlantic. J. Ichthyol. 62:421–427. https://doi.org/10.1134/S0032945222020011

Avalos-García, C., L. Sánchez-Velasco, and B. Shirasago.
2003. Larval fish assemblages in the Gulf of California and their relation to hydrographic variability (autumn 1997–summer 1998). Bull. Mar. Sci. 72:63–76.

Barros, F. B. A. G., M. S. de Castro, and A. C. T. Bonecker.
2007. Description and distribution of the larvae of two species of Fistulariidae (Teleostei, Syngnathiformes) in the southeastern Brazil. Biota Neotrop. 7(1):bn03107012007. https://doi.org/10.1590/S1676-06032007000100014

Bartoń, K.
2020. MuMIn: multi-model inference. R package, vers. 1.43.17. [Available from https://CRAN.R-project.org/package=MuMIn, accessed April 2020.]

Beckley, L. E., D. Holliday, A. L. Sutton, E. Weller, M. P. Olivar, and P. A. Thompson.
2019. Structuring of larval fish assemblages along a coastal-oceanic gradient in the macro-tidal, tropical eastern Indian Ocean. Deep-Sea Res., II 161:105–119. https://doi.org/10.1016/j.dsr2.2018.03.008

Betancur-R, R., E. O. Wiley, G. Arratia, A. Acero, N. Bailly, M. Miya, G. Lecointre, and G. Ortí.
2017. Phylogenetic classification of bony fishes. BMC Evol. Biol. 17:162. https://doi.org/10.1186/s12862-017-0958-3

Boehlert, G. W., and B. C. Mundy.
1993. Ichthyoplankton assemblages at seamounts and oceanic islands. Bull. Mar. Sci. 53:336–361.

Bonecker, A. C. T., and M. S. de Castro.
2006. Atlas de larvas de peixes da região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central, Ser. Livros 19, 214 p. Mus. Nac., Rio de Janeiro, Brazil.

Bonecker, A. C. T., D. R. Tenenbaum, E. Gonzalez-Rodriguez, R. Paranhos, and S. L. C. Bonecker.
2006a. Metodologia. *In* Características hidrobiológicas da região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central (J. L.Valentin, ed.), p. 13–19. Ideal Gráfica e Editora, Brasília, Brazil.

Bonecker, A. C. T., M. S. de Castro, C. Namiki, F. T. Bonecker, F. B. A. G. Barros, and W. M. Monteiro-Ribas.
2006b. Ictioplâncton. *In* Características hidrobiológicas da

região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central (J. L. Valentined, ed.), 141–159. Ideal Gráfica e Editora, Brasília, Brazil.

Bonecker, A. C. T., M. Katsuragawa, M. S. de Castro, E. A. P. Gomes, C. A. P. Namiki, and M. L. Zani-Teixeira.
2012. Larval fish of the Campos Basin, southeastern Brazil. Check List 8:1280–1291. https://doi.org/10.15560/8.6.1280

Bonecker, A. C. T., C. A. P. Namiki, M. S. de Castro, and P. N. Campos.
2014. Catálogo dos estágios iniciais de desenvolvimento dos peixes da bacia de Campos. Zoologia: guias e manuais de identificação séries, 295 p. Soc. Bras. Zool., Curitiba, Brazil.

Bonecker, A. C. T., M. Katsuragawa, M. S. de Castro, E. A. P. Gomes, C. A. P. Namiki, and M. L. Zani-Teixeira.
2017. Estrutura espacial e temporal da comunidade ictioplanctônica. *In* Ambiente pelágico: caracterização ambiental regional da Bacia de Campos, Atlântico Sudoeste (A. P. C. Falcão and D. L. Moreira, eds.), p. 207–245. Elsevier, Rio de Janeiro, Brazil.

Bonecker, A. C. T., M. S. de Castro, P. G. Costa, A. Bianchini, and S. L. C. Bonecker.
2019a. Larval fish assemblages of the coastal area affected by the tailings of the collapsed dam in southeast Brazil. Reg. Studies Mar. Sci. 32:100848. https://doi.org/10.1016/j.rsma.2019.100848

Bonecker, A. C. T., M. Katsuragawa, M. S. de Castro, C. Namiki, M. L. Zani-Teixeira, I. U. Farias, and I. C. A. da Silveira.
2019b. Seasonal variability of ichthyoneuston assemblage on the continental shelf and slope of the Southwest Atlantic Ocean, Brazil (20°–23°S). J. Appl. Ichthyol. 35:655–671. https://doi.org/10.1111/jai.13890

Bonecker, A. C. T., C. O. Dias, M. S. de Castro, P. F. Carvalho, A. V. Araujo, R. Paranhos, A. S. Cabral, and S. L. C. Bonecker.
2019c. Vertical distribution of mesozooplankton and ichthyoplankton communities in the south-western Atlantic Ocean (23°14′1″S 40°42′19″W). J. Mar. Biol. Assoc. U.K. 99:51–65. https://doi.org/10.1017/S0025315417001989

Bonecker, A. C. T., M. S. de Castro, C. O. Dias, F. Sá, G. N. Mill, R. D. Ghisolfi, and S. L. C. Bonecker.
2022. Monitoring of ichthyoplanktonic community at the Doce River mouth and adjacent marine region in southeast Brazil after Fundão dam collapse. J. Sea Res. 189:102284. https://doi.org/10.1016/j.seares.2022.102284

Brandão, M. C., C. A. E. Garcia, and A. S. Freire.
2020. Meroplankton community structure across oceanographic fronts along the South Brazil Shelf. J. Mar. Syst. 208:103361. https://doi.org/10.1016/j.jmarsys.2020.103361

Bridges, A. E. H., D. K. A. Barnes, J. B. Bell, R. E. Ross, and K. L. Howell.
2021. Benthic assemblage composition of south Atlantic Seamounts. Front. Mar. Sci. 8:660648. https://doi.org/10.3389/fmars.2021.660648

Burnham, K. P., and D. R. Anderson.
2002. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed., 488 p. Springer-Verlag, New York.

Calil, P. H. R., N. Suzuki, B. Baschek, and I. C. A. da Silveira.
2021. Filaments, fronts and eddies in the Cabo Frio coastal upwelling system, Brazil. Fluids 6:54. https://doi.org/10.3390/fluids6020054

Campanella, F., M. A. Collins, E. F. Young, V. Laptikhovsky, P. Whomersley, and J. van der Kooij.
2021. First insight of meso- and bentho-pelagic fish dynamics around remote seamounts in the South Atlantic Ocean. Front. Mar. Sci. 8:663278. https://doi.org/10.3389/fmars.2021.663278

Campos, P. N., M. S. de Castro, and A. C. T. Bonecker.
2010. Occurrence and distribution of Carangidae larvae (Teleostei, Perciformes) from the southwest Atlantic Ocean, Brazil (12–23°S). J. Appl. Ichthyol. 26:920–924. https://doi.org/10.1111/j.1439-0426.2010.01511.x

Cardoso, D. H., and M. Dourado.
2014. Modelagem unidimensional da camada limite oceânica durante a passagem de uma frente fria na região da confluência Brasil-Malvinas. Rev. Bras. Meteorol. 29:367–378. https://doi.org/10.1590/0102-778620120546

Castro, M. S. de, and A. C. T. Bonecker.
2005. Leptocephali collected off the eastern coast of Brazil (12°–23°S). Zootaxa 935:1–28. https://doi.org/10.11646/zootaxa.935.1.1
2006. Distribution of larval Stomiidae of the Brazilian central coast, southwest Atlantic Ocean (12°S–22°S). Zootaxa 1236:23–36. https://doi.org/10.11646/zootaxa.1236.1.2

Castro, M. S. de, W. J. Richards, and A. C. T. Bonecker.
2010. Occurrence and distribution of larval lanternfish (Myctophidae) from the southwest Atlantic Ocean. Zoologia 27:541–553. https://doi.org/10.1590/S1984-46702010000400006

Castro Filho, B. M., A. F. Pereira, A. de Caroli, H. F. Neto, G. C. A. Paschoal, I. C. A. da Silveira, and C. C. Amor.
2015. Correntes e massas de água na plataforma continental. *In* Meteorologia e oceanografía (R. P. Martins and G. S. Grossmann-Matheson, eds.), vol. 2, p. 189–252. Elsevier, Rio de Janeiro, Brasil.

Ciotti, A. M., E. Gonzalez-Rodriguez, L. Andrade, R. Paranhos, and W. F. Carvalho.
2007. Clorofila *a*, medidas bio-ópticas e produtividade primária. *In* Características hidrobiológicas da região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central (J. L.Valentined, ed.), 61–72. Ideal Gráfica e Editora, Brasília, Brazil.

Clarke, K. R., and R. N. Gorley.
2006. PRIMER v6: user manual/tutorial (Plymouth routines in multivariate ecological research), 190 p. PRIMER-E, Plymouth, UK.

Clarke, K. R., and R. M. Warwick.
2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd ed., 176 p. PRIMER-E, Plymouth, UK.

Compaire, J. C., P. Pérez-Brunius, S. P. A. Jiménez-Rosenberg, J. R. Outerelo, L. P. E. García, and S. Z. Herzka.
2021. Connectivity of coastal and neritic fish larvae to the deep waters. Limnol. Oceanogr. 66:2423–2441. https://doi.org/10.1002/lno.11762

Costa, P. A. S., A. S. Martins, and O. Olavo (eds.).
2005. Pesca e potenciais de exploração de recursos vivos na região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central, Ser. Livros 13, 247 p. Mus. Nac., Rio de Janeiro, Brazil.

Crochelet, E., N. Barrier, M. Andrello, F. Marsac, A. Spadone, and C. Lett.
2020. Connectivity between seamounts and coastal ecosystems in the southwestern Indian Ocean. Deep-Sea Res., II 176:104774. https://doi.org/10.1016/j.dsr2.2020.104774

Cruz, P. R., I. P. Affonso, and L. C. Gomes.
2016. Ecologia do ictioplâncton: uma abordagem cienciométrica. Oecol. Aust. 20:436–450. https://doi.org/10.4257/oeco.2016.2004.04

Daudén-Bengoa, G., S. P. A. Jiménez-Rosenberg, J. C. Compaire, L. P. Echeverri-García, P. Pérez-Brunius, and S. Z. Herzka.
2020. Larval fish assemblages of myctophids in the deep water region of the southern Gulf of Mexico linked to oceanographic conditions. Deep-Sea Res., I 155:103181. https://doi.org/10.1016/j.dsr.2019.103181

Doyle, M. J., S. J. Picquelle, K. L. Mier, M. C. Spillane, and N. A. Bond.
2009. Larval fish abundance and physical forcing in the Gulf of Alaska, 1981–2003. Prog. Oceanogr. 80:163–187. https://doi.org/10.1016/j.pocean.2009.03.002

Echeverri-García, L. P., G. Daudén-Bengoa, J. C. Compaire, S. P. A. Jiménez-Rosenberg, P. Pérez-Brunius, V. Ferreira-Bartrina, and S. Z., Herzka.
2022. Variability of fish larvae assemblages relative to mesoscale features in the deep water region of the southern Gulf of Mexico. Hydrobiologia 849:1471–1493. https://doi.org/10.1007/s10750-022-04797-w

Eisele, M. H., S. Madrigal-Mora, and M. Espinoza.
2021. Drivers of reef fish assemblages in an upwelling region from the eastern tropical Pacific Ocean. J. Fish Biol. 98:1074–1090. https://doi.org/10.1111/jfb.14639

Endo, C. A. K., D. F. M. Gherard, L. P. Pezzi, and L. N. Lima.
2019. Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. Sci. Rep. 9:8634. https://doi.org/10.1038/s41598-019-45042-0

Espinosa-Fuentes, M. L., and C. Flores-Coto.
2004. Cross-shelf and vertical structure of ichthyoplankton assemblages in continental shelf waters of the southern Gulf of Mexico. Estuar. Coastal Shelf Sci. 59:333–352. https://doi.org/10.1016/j.ecss.2003.09.006

Figueiredo, J. L., A. P. Santos, N. Yamaguti, R. A. Bernardes, and C. L. D. Rossi-Wongtschowski.
2002. Peixes da Zona Econômica Exclusiva da região sudeste-sul do Brasil: levantamento com rede de meia-água, 248 p. Imprensa Oficial do Estado, São Paulo, Brazil.

Flores-Coto, C., F. Flore-Hernández, F. Zavala-Garcia, V. Arenas-Fuentes, M. A. Monreal-Gómez, and D. A. Salas-de-León.
2000. Oceanic and neritic ichthyoplankton at the edge of the continental shelf in the southern Gulf of Mexico. Gulf Caribb. Res. 12:31–35. https://doi.org/10.18785/gcr.1201.04

Franco-Gordo, C., E. Godínez-Domínguez, and E. Suárez-Morales.
2002. Larval fish assemblages in waters off the central Pacific coast of Mexico. J. Plankton Res. 24:775–784. https://doi.org/10.1093/plankt/24.8.775

Fricke, R., W. N. Eschemeyer, and R. van der Laan (eds.).
2022. Eschmeyer's Catalog of Fishes: genera, species, references. [Available from http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp, accessed July 2022.]

Froese, R., and D. Pauly (eds.).
2022. FishBase, vers. 08/2022. [World Wide Web electronic publication.] [Available from http://www.fishbase.org, accessed August 2022.]

Funes-Rodríguez, R., C. Flores-Coto, A. Esquivel-Herrera, M. A. Fernández-Alamo, and A. Gracia-Gásca.
2002. Larval fish community structure along the west coast of Baja California during and after the El Niño event (1983). Bull. Mar. Sci. 70:41–54.

Harold, A. S., and R. K. Johnson.
2003. Bregmacerotidae. *In* The living marine resources of the western central Atlantic. Volume 2: bony fishes part 1 (Acipenseridae to Grammatidae) (K. E. Carpenter, ed.). FAO Species Identification Guide for Fishery Purposes and American Society of Ichthyologists and Herpetologists Special Publication No. 5, p. 1003–1004. FAO, Rome.

Harris, S. A., M. Noyon, F. Marsac, P. Vianello, and M. J. Roberts.
2020. Ichthyoplankton assemblages at three shallow seamounts in the South West Indian Ocean. Deep-Sea Res., II 176:104809. https://doi.org/10.1016/j.dsr2.2020.104809

Heiberger, R. M., and B. Holland.
2015. Statistical analysis and data display: an intermediate course with examples in R, 2nd ed., 898 p. Springer, New York.

Kallianiotis, A. A., N. Kamidis, A. Tselepides, and I. E. Batjakas.
2023. Spatiotemporal and environmental dynamics of abundances and diversity of larval fish in artificial reef edge habitats of Kitros, Pieria (Northern Aegean Sea, Eastern Mediterranean). J. Mar. Sci. Eng. 11(1):40. https://doi.org/10.3390/jmse11010040

Katsuragawa, M., Y. Matsuura, K. Suzuki, J. F. Dias, and H. L. Spach.
1993. O ictioplâncton ao largo de Ubatuba, SP: composição, distribuição e ocorrência sazonal (1985–1988). Publção Esp. Inst. Oceanogr., S. Paulo 10:85–121.

Katsuragawa, M., J. F. Dias, J. Harari, C. Namiki, and M. L. Zani-Teixeira.
2014. Patterns in larval fish assemblages under the influence of the Brazil current. Cont. Shelf Res. 89:103–117. https://doi.org/10.1016/j.csr.2014.04.024

Kruskal, W. H., and W. A. Wallis.
1952. Use of ranks in one-criterion variance analysis. J. Am. Stat. Assoc. 47:583–621. https://doi.org/10.1080/01621459.1952.10483441

Legendre, P., and L. Legendre.
2012. Numerical ecology. *In* Developments in environmental modelling, 3rd ed., vol. 24, 990 p. Elsevier, Amsterdam, The Netherlands.

Lima, M. J., I. Sala, and R. M. A. Caldeira.
2020. Physical connectivity between the NE Atlantic seamounts. Front. Mar. Sci. 7:238. https://doi.org/10.3389/fmars.2020.00238

Lobo, E., and G. Leighton.
1986. Estructuras comunitárias de las fitocenosis planctónicas de lós sistemas de desembocaduras de rios y esteros de La zona Central de Chile. Rev. Biol. Mar. Oceanogr. 22:1–29.

Loeb, V. J.
1979. Vertical distribution and development of larval fishes in the North Pacific Central Gyre during summer. Fish. Bull. 77:777–793.

Marancik, K. E., L. M. Clough, and J. A. Hare.
2005. Cross-shelf and seasonal variation in larval fish assemblages on the southeast United States continental shelf off the coast of Georgia. Fish. Bull. 103:108–129.

Matteucci, S. D., and A. Colma.
1982. Metodología para el estudio de la vegetación. Secr. Gen. Organ. Estados Am., Programa Reg. Desarro. Cient. Tecnol., Ser. Biol. Monogr. 22, 77 p.

Meinert, C. R., K. Clausen-Sparks, M. Cornic, T. T. Sutton, and J. R. Rooker.
2020. Taxonomic richness and diversity of larval fish assemblages in the oceanic Gulf of Mexico: links to oceanographic conditions. Front. Mar. Sci. 7:579. https://doi.org/10.3389/fmars.2020.00579

Menezes, N. A., P. A. Buckup, J. L. de Figueiredo, and R. L. de Moura (eds.).
2003. Catálogo das espécies de peixes marinhos do Brasil, 160 p. Mus. Zool. Univ. São Paulo, São Paulo, Brazil.

Morse, W. W.
1989. Catchability, growth, and mortality of larval fishes. Fish. Bull. 87:417–446.

Moser, H G., and P. E. Smith.
1993. Larval assemblages and oceanic boundaries. Bull. Mar. Sci. 53:283–289.

Moser, H G., P. E. Smith, and L. E. Eber.
1987. Larval fish assemblages in the California Current region, 1954–1960, a period of dynamic environmental change. CalCOFI Rep. 28:97–127.

Muhling, B. A., and L. E. Beckley.
2007. Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. J. Plankton Res. 29:967–983. https://doi.org/10.1093/plankt/fbm072

Mwaluma, J., N. Ngisiang'e, M. Osore, J. Kamau, H. Ong'anda, J. Kilonzi, M. Roberts, E. Popova, and S. C. Painter.
2021. Assemblage structure and distribution of fish larvae on the North Kenya Banks during the Southeast Monsoon season. Ocean Coastal Manag. 212:105800. https://doi.org/10.1016/j.ocecoaman.2021.105800

Nonaka, R. H., Y. Matsuura, and K. Suzuki.
2000. Seasonal variation in larval fish assemblages in relation to oceanographic conditions in the Abrolhos Bank region off eastern Brazil. Fish. Bull. 98:767–784.

Olivar, M. P., and L. E. Beckley.
2022. Latitudinal variation in diversity and abundance of mesopelagic fishes associated with change in oceanographic variables along 110°E, south-east Indian Ocean. Deep-Sea Res., II 198:105053. https://doi.org/10.1016/j.dsr2.2022.105053

Olivar, M. P., A. Bernal, B. Molí, M. Peña, R. Balbín, A. Castellón, J. Miquel, and E. Massutí.
2012. Vertical distribution, diversity and assemblages of mesopelagic fishes in the western Mediterranean. Deep-Sea Res., I 62:53–69. https://doi.org/10.1016/j.dsr.2011.12.014

Palóczy, A., I. C. A. da Silveira, B. M. Castro, and L. Calado.
2014. Coastal upwelling off Cape São Tomé (22°S, Brazil): the supporting role of deep ocean processes. Cont. Shelf Res. 89:38–50. https://doi.org/10.1016/j.csr.2013.09.005

R Core Team.
2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Available from https://www.R-project.org, accessed August 2020.]

Ramírez-Martínez, G. A., A. Giraldo, M. Rivera-Gómez, and G. Aceves-Medina.
2022. Daily and monthly ichthyoplankton assemblages of La Azufrada coral reef, Gorgona Island, Eastern Tropical Pacific. Reg. Studies Mar. Sci. 52:102378. https://doi.org/10.1016/j.rsma.2022.102378

Richards, W. J. (ed.).
2006. Early stages of Atlantic fishes: an identification guide for the western north Atlantic. Volumes 1 and 2, 2640 p. CRC Press, Boca Raton, FL.

Roberts, M. J., and J.-F. Ternon.
2020. The MADRidge project—a major contribution to IIOE2-WIOURI focussing on three shallow seamounts and their pelagic ecosystems in the vicinity of the Madagascar Ridge. Deep-Sea Res. II 176:104817. https://doi.org/10.1016/j.dsr2.2020.104817

Santana, J. R., A. E. S. F. Costa, D. Veleda, S. H. L. Schwamborn, P. O. Mafalda Jr., and R. Schwamborn.
2020. Ichthyoplankton community structure on the shelf break off northeastern Brazil. An. Acad. Bras. Cienc. 92(2):e20180851.

Silveira, I. C. A.
2007. O Sistema Corrente do Brasil na Bacia de Campos, RJ. Ph.D. diss., 160 p. Univ. São Paulo, São Paulo, Brazil. [Available from Universidade de São Paulo, Rua Praça do Relógio 109, Bloco L Térreo, 05508-050, São Paulo, Brazil.]

Silveira, I. C. A., A. C. K. Schmidt, E. J. D. Campos, S. S. Godoi, and Y. Ikeda.
2000. A Corrente do Brasil ao largo da costa leste brasileira. Rev. Bras. Oceanogr. 48:171–183. https://doi.org/10.1590/S1413-77392000000200008

Simon, T., H. T. Pinheiro, S. Santos, R. M. Macieira, Y. S. S. Ferreira, G. Bernardi, L. A. Rocha, S. R. Floeter, C. E. L. Ferreira, and J.-C. Joyeux.
2022. Comparative phylogeography of reef fishes indicates seamounts as stepping stones for dispersal and diversification. Coral Reefs 41:551–561. https://doi.org/10.1007/s00338-021-02178-8

Smith, P. E., and S. L. Richardson.
1977. Standard techniques for pelagic fish egg and larva survey. FAO Fish. Tech. Pap. 175, 100 p. FAO, Rome.

Souza, C. S., and P. O. Mafalda Jr.
2019. Large-scale spatial and temporal variability of larval fish assemblages in the tropical Atlantic Ocean. An. Acad. Bras. Cienc. 91(1):e20170567. https://doi.org/10.1590/0001-3765201820170567

Stocco, L. B., and J.-C. Joyeux.
2015. Distribution of fish larvae on the Vitória-Trindade Chain, southwestern Atlantic. Check List 11(2):1590. https://doi.org/10.15560/11.2.1590

Torres-Barajas, C. E., M. C. Navarro-Rodriguez, L. Kelly-Gutiérrez, and R. Flores-Vargas.
2021. Variación espacio-temporal de las densida-des de las especies ictioplanctónicas y su relación con la temperatura y salinidad en Bahía de Banderas, México. Acta Pesq. 7(14):34–50.

Valentin, J. L.
2001. The Cabo Frio upwelling system, Brazil. *In* Coastal marine ecosystems of Latin America. Ecological studies, vol. 144 (U. Seeliger and B. Kjerfve, eds.), p. 97–105. Springer, Berlin, Germany.

Valentin, J. L., R. Paranhos, B. C. M. T. Faro, and A. S. M. Gonzalez.
2006. Massas d'Água. *In* Características hidrobiológicas da região central da Zona Econômica Exclusiva brasileira. Doc. REVIZEE/SCORE Central (J. L. Valentin, ed.), p. 21–29. Ideal Gráfica e Editora, Brasília, Brazil.

Venancio, I. M., A. L. Belem, T. H. R. dos Santos, M. do R. Zucchi, A. E. G. Azevedo, R. Capilla, and A. L. S. Albuquerque.
2014. Influence of continental shelf processes in the water mass balance and productivity from stable isotope data on the southeastern Brazilian coast. J. Mar. Syst. 139:241–247. https://doi.org/10.1016/j.jmarsys.2014.06.009

Wang, Y.-C., S.-C. Tsai, and W.-Y. Chen.
2022. Diel vertical distribution patterns of pelagic fish larvae in Yilan Bay, Taiwan. J. Mar. Sci. Technol. 29(6):6. https://doi.org/10.51400/2709-6998.2557

Whitney, J. L., J. M. Gove, M. A. McManus, K. A. Smith, J. Lecky, P. Neubauer, J. E. Phipps, E. A. Contreras, D. R. Kobayashi, and G. P. Asner.
2021. Surface slicks are pelagic nurseries for diverse ocean fauna. Sci. Rep. 11:3197. https://doi.org/10.1038/s41598-021-81407-0

Zar, J. H.
2010. Biostatistical analysis, 5th ed., 944 p. Prentice Hall, Upper Saddle River, NJ.

Cite as: Castro, Márcia Salustiano de, Cristina de Oliveira Dias, and Cristina Teixeira Bonecker. 2024. Spatial and temporal variability of larval fish assemblages in the central region of the Brazilian Exclusive Economic Zone (12–22°S). *In* Early Life History and Biology of Marine Fishes: Research inspired by the work of H Geoffrey Moser (J. M. Leis, W. Watson, B. C. Mundy, and P. Konstantinidis, guest eds.), p. 233–252. NOAA Professional Paper NMFS 24. https://doi.org/10.7755/PP.24.17