PATTERNS OF DISTRIBUTION AND ABUNDANCE OF LARVAL PHOSICHTHYIDAE (ACTINOPTERYGII, STOMIIFORMES) IN SOUTHEASTERN BRAZILIAN WATERS

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ABSTRACT

Horizontal and vertical distribution patterns and abundance of larval phosichthyids were investigated from oblique and depth-stratified towns off Southeastern Brazilian waters, from São Tomé cape (41°W.; 22°S.) to São Sebastião island (45°W.; 24°S.). The sampling was performed during two cruises (January/2002 - summer; August/2002 - winter). Overall 538 larvae of Phosichthyidae were collected during summer and 158 in the winter. Three species, *Pollichthys mauli, Vinciguerria nimbaria* and *Ichthyioccoccus* sp. occurred in the area, but *Ichthyioccoccus* sp. was extremely rare represented by only one specimen, caught in the oceanic region during the summer. Geographically, larval were concentrated in the oceanic region, and vertically distributed mainly between the surface and 80 m depth in the summer and winter. Larvae were more abundant during the night, performing a diel vertical migration in the water column. The results suggest that the meandering and eddies of Brazil Current play important role on the transport and distribution patterns of larval phosichthyids over the oceanic and neritic area in the Southeastern Brazil.

RESUMO

Padrões de distribuição horizontal e vertical e abundância de larvas de peixes de Phosichthyidae foram examinados a partir de arrastos oblíquos e estratificados em águas do Sudeste Brasileiro, entre cabo de São Tomé (41°W.; 22°S.) e a ilha de São Sebastião (45°W.; 24°S.). A amostragem foi realizada durante dois cruzeiros (Janeiro/2002 - verão; Agosto/2002 - inverno). Foi coletado um total de 538 larvas de Phosichthyidae durante o verão e 158 no inverno. Três espécies, *Pollichthys mauli, Vinciguerria nimbaria* e *Ichthyioccoccus* sp. ocorreram na área, mas Ichthyioccoccus sp. foi extremamente rara representada somente por uma larva, capturada na região oceânica durante o verão. Geograficamente, as larvas estiveram concentradas na região oceânica e verticalmente entre a superfície e 80 m de profundidade nos cruzeiros de verão e inverno. As larvas foram mais abundantes durante a noite, apresentando uma migração vertical diária na coluna d'água. Os resultados sugerem um importante papel dos meandramentos e vórtices da Corrente do Brasil no transporte e padrões de distribuição das larvas dos Phosichthyidae nas áreas oceânica e nerítica do sudeste brasileiro.

Descriptors: Phosichthyidae, Larval fish, Distribution, Tropical water mass, Brazil current.
Descritores: Phosichthyidae, Larva de peixe, Distribuição, Massa de água tropical, Corrente do Brasil.

INTRODUCTION

Phosichthyidae are mesopelagic fishes, known as lightfishes due to the bioluminescence produced by special cells (photophores) located along the ventral region of the body (FAHAY, 1983; SCHAEFER et al., 1986). These fishes are also known for performing active diel vertical migration (CLARKE, 1971) from the mesopelagic to the epipelagic zones. Mesopelagic fish are dominant in the oceanic region both in number of species and individuals, and represent one of the most important links in the food chain in the marine ecosystem (TORTONESE, 1970; LOEB, 1979). They are important in the diet of pelagic predators such as *Coryphaena hippurus*, *Alepisaurus ferox*, *Alopias pelagicus* and *Thunnus albacares* (ZAVALA - CAMIN, 1978; MOTEKI et al., 2001) and are recognized as contributing to the distribution of tuna in the water column (MARCHAL; LEBOURGES, 1996; LEBOURGES-DHAUSSY et al., 2000). They feed on zooplankton, squid and other fish (LERMAN, 1986).

Larvae of mesopelagic fishes occur all year round in high abundance, mainly in the offshore region (MATSUURA et al., 1980). Phosichthyidae

species are oviparous and pelagic spawning, with planktonic eggs and larvae (SANZO, 1930, 1931; AHLSTROM; COUNTS, 1958; AHLSTROM; BALL, 1984). The planktonic fish eggs and larvae can be transported in the sea by oceanic circulation, so that their distribution and abundance are affected by many biological processes including ontogeny, the concentration and varied size of their food, intra and inter specific competition, and physical processes in the water column such as temperature, light intensity, oceanic fronts, tides, winds, currents, upwelling, thermoclines and haloclines (BLAXTER, 1973; LASKER, 1975; LOEB, 1979; HEMPEL, 1979; FORTIER; LEGGETT, 1983; PHONLOR, 1984; NEILSON; PERRY, 1990).

　　　　Acknowledge of the distribution patterns of larval fish and of environmental factors is very important for the understanding of the ecological processes that influence larval abundance in the ocean (BRODEUR; RUGEN, 1994). Studies have shown that Phosichthyidae larvae are distributed, preferentially, in the oceanic region, in warm and saline waters, with higher abundance between 0 and 100 m depth, in the Gulf of California, the East China Sea, off the coasts of Japan, Angola and in the Canary Islands (AHLSTROM, 1959; OZAWA, 1976; JOHN et al., 2001; RODRIGUEZ et al., 2004; FUKUI; KURODA, 2005; OKAZAKI; NAKATA, 2007; MOYANO et al., 2009). Some studies undertaken in

Brazilian waters, *e.g.* BONECKER AND HUBOLD (1990); NONAKA ET AL. (2000) and BONECKER ET AL. (2006), have shown that Phosichthyidae larvae occur mainly in the offshore region, their distribution being associated with cold water in the Abrolhos region (Bahia) but with a warmer water mass and mixed water in the southernmost area. However, information in the literature about the distribution of this group in Brazil is still scant. The present study aims to investigate the horizontal and vertical distribution and the abundance of Phosichthyidae larvae in relation to environmental factors in the region between São Tomé cape and São Sebastião island, in southeastern Brazil.

MATERIAL AND METHODS

　　　　Two cruises were carried out off southeastern Brazil by the R/V "Prof. W. Besnard", from São Tomé cape (41°W.; 22°S.) to São Sebastião island (45°W.; 24°S.). The sampling plan for the summer cruise (January, 2002) covered 72 oceanographic stations distributed on 14 transects (R1 to R14) and that for the winter cruise (August, 2002) 66 stations on 13 transects (R1 to R13), the station interval was 20 nautical miles (Fig. 1). The collection was performed in all the periods of day (dawn, day, dusk and night).
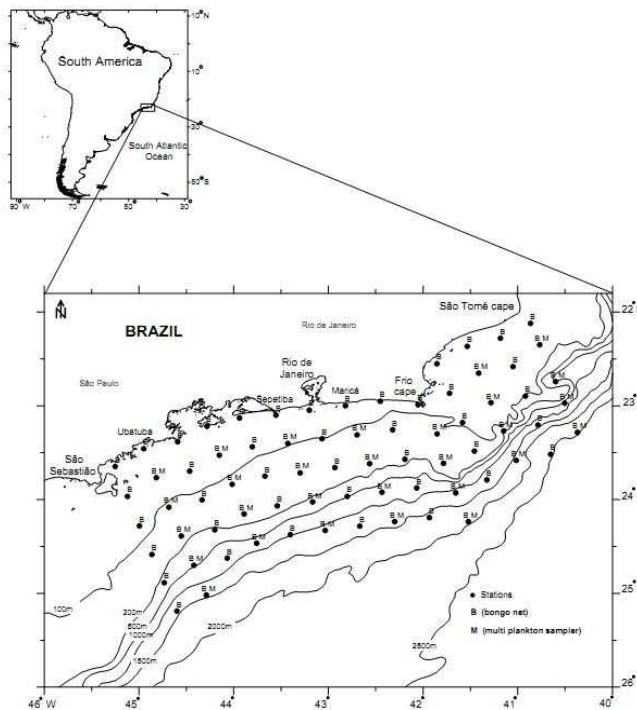

Fig. 1. Map of sampling stations performed in January/2002 and August/2002 between São Tomé cape (Rio de Janeiro) and São Sebastião island (São Paulo) in the southeastern coast of Brazil. Where there is letter **B** refers to ichthyoplankton collection stations with bongo net and **M** with multi plankton sampler.

A CTD (conductivity-temperature depth profiler) cast provided hydrographic data for each station. The temperature-salinity diagrams (T-S) provided the identification of water masses (EMÍLSSON, 1961; MIRANDA, 1985).

Two sampling methods were used to collect ichthyoplankton: 1) oblique tows with a 61 cm bongo fitted with 0.333 and 0.506 mm mesh nets (SMITH; RICHARDSON, 1977), of which only samples from the 0.333 mm mesh net were used in the present study; and 2) stratified tows with a 1 m^2 multi-plankton sampler (MPS), equipped with 5 nets of 0.300 mm mesh size, to target 20 m depth layers. The volume of water filtered was measured with a flowmeter mounted at the mouth of each net. Plankton samples were preserved aboard in 4% buffered formalin seawater.

Larvae were examined under a stereomicroscope and the identification of Phosichthyidae species was based on descriptions from the literature (AHLSTROM; COUNTS, 1958; GREY, 1964; FAHAY, 1983, 2007; WATSON, 1996; BONECKER et al., 2006; RICHARDS, 2006). The occurrence frequency of larvae (%) was calculated based on the Guille (1970) expression: [F = (Ni/Nt).100)] Where, F = occurrence frequency, Ni = the number of positive stations of the taxonomy category i, and Nt = the total number of stations. Abundance of larvae (larvae.m^{-2}) of bongo samples was estimated to represent the horizontal distribution, using Tanaka (1973) expression: [Y = (d.x) V^{-1}] where Y = number of larvae per m^2 of sea surface, d = depth of haul (m), x = number of larvae taken on sampling, and V = volume of filtered water (m^3) measured by flowmeter. Larval density (larvae.100m^{-3}) of MPS, describing larval distribution in different layers, was calculated by the ratio between the number of larvae taken in the sample and the volume of water filtered (m^3) as measured by flowmeter, multiplied by 100 (HENSEN, 1887).

Larvae were measured by a digitizing tablet, a stereomicroscope equipped with a drawing tube, and the size-frequency distributions obtained for 0.5 mm classes, and were categorized as belonging to the preflexion, flexion, or postflexion stage, according to the state of notochord flexion (AHLSTROM; BALL, 1954). The body length (BL) of the preflexion and flexion larvae was measured from the tip of the snout to the end of the notochord (equivalent to notochord length, NL), and of postflexion larvae from the tip of the snout to the posterior edge of the developing hypurals (equivalent to standard length, SL).

Based on previous studies (KATSURAGAWA; MATSUURA, 1992; LOPES et al., 2006), the study area was divided into three sub-areas parallel to the coast: a) coastal (from the coast to the 100 m isobath); b) intermediate (from 100 m to 200 m isobaths), and c) oceanic (deeper than the 200 m isobath). The non-parametric Mann-Whitney U-test was used to evaluate differences in larval abundance and density as between summer and winter and the different sub-areas. Differences between layers were examined by using a Kruskal-Wallis test and Dunn test *a posteriori* (ZAR, 1999). A multivariate statistical analysis (Redundancy Analysis - RDA), in the CANOCO software package (TER BRAAK; SMILAUER, 2002), was used to investigate the contribution of the environmental factors to the distribution and density of larvae and their respective development stages. A Monte Carlo test was used to test the significance of the contribution of the environmental variables to the biological data.

RESULTS

Oceanographic Conditions

The mean water temperature for all the study area, from surface to 200 m depth, was significantly higher (Mann-Whitney U-test, $P < 0.0001$) in the summer (20.33°C; sd = 3.79) than in the winter (20.28°C; sd = 2.73). Concerning the salinity, the mean observed during the summer was 36.24 (sd = 0.63) and that during the winter 36.14 (sd = 0.73), indicating significantly greater salinity in the summer according to a Mann-Whitney U-test ($P < 0.0001$) (Table 1).

During the summer the water column was strongly stratified, ranging from 24.31°C (sd = 2.21) at the 0-20 m layer to 19.62°C (sd= 2.90) at the 80-100 m layer. A significant difference was observed between the upper layers (0-40m) and the 60-100 m layer (Kruskal-Wallis test, $P < 0.05$). On the other hand, during the winter the water column was relatively homogeneous, with the temperature ranging from 22.63°C (sd = 0.82) at the 0-20 m layer to 20.22°C (sd = 2.53) at the 80-100 m layer (Table 1). The salinity of the water column was homogeneous, no significant differences being observed between layers in the summer and winter (Kruskal-Wallis test, $P > 0.05$). In the summer, the salinity presented mean = 36.37 (sd = 0.57) at the 0-20 m layer and 36.33 (sd = 0.58) at the 80-100 m layer and in the winter, mean = 36.08 (sd = 0.85) at the 0-20 m layer and 36.49 (sd = 0.56) at the 80-100 m layer.

Geographically, during the summer, the oceanic waters was significantly warmer (mean = 21.08°C, sd = 3.59) than the coastal waters (mean = 19.37°C sd = 4.01) and intermediate waters (mean = 19.30°C, sd = 3.72) (Mann-Whitney U-test, $P < 0.0001$), but during the winter, the coastal (mean = 20.84°C, sd = 1.95) and oceanic regions (mean = 20.53°C, sd = 2.85) were significantly warmer than the intermediate region (mean = 19.65°C, sd = 2.76)

(Mann-Whitney U-test, $P < 0.0001$). The salinity was significantly lower (Mann-Whitney U-test, $P < 0.0001$) in the coastal region (mean = 35.68, sd = 0.62), than in the intermediate (mean = 36.03, sd = 0.54), and oceanic regions (mean = 36.48, sd = 0.56) during the summer and the same occurred in the winter (mean = 35.39, sd = 0.94 in the coastal; mean = 36.05, sd = 0.49 in the intermediate and mean = 36.47, sd 0.57 in the oceanic regions) (Table 2).

The T-S diagrams (Fig. 2) indicated the influence and interactions of three water masses in the area: Tropical Water (TW), South Atlantic Central Water (SACW) and Coastal Water (CW). The Tropical water mass occupied the layer between the surface and 100 m depth, mainly in the oceanic region. In the deep layer (> 100m depth) values below 18°C and salinity between 35 and 36 were registered, indicating the presence of the SACW mass. The SACW was also found at the surface in the coastal region, between Frio cape and Guanabara bay (RJ) region, indicating a coastal upwelling event. In the southern coastal area the temperature was about 20°C and salinity 34 during both summer and winter, indicating the presence of a CW mass.

Table 1. Temperature (°C) and salinity registered during the summer and winter in southeastern Brazilian waters. Minimum, maximum, mean and standard deviation (sd) estimated for the water column (from surface to 200 m depth) and strata sampled by multi-plankton sampler (from zero to 100 m depth).

Season	Stratum	Temperature °C				Salinity			
		minimum	maximum	mean	sd	minimum	maximum	Mean	sd
Summer	0-200 m	13.08	27.64	20.33	3.79	33.42	37.24	36.24	0.63
	0-20m	15.52	26.51	24.31	2.21	34.65	37.01	36.37	0.57
	20-40m	13.77	26.39	22.29	3.46	35.20	37.09	36.50	0.52
	40-60m	13.53	26.15	21.26	3.35	35.22	37.23	36.52	0.56
	60-80m	13.08	25.18	20.21	3.29	35.18	37.24	36.42	0.61
	80-100m	14.15	23.67	19.62	2.90	35.31	37.24	36.33	0.58
Winter	0-200 m	14.11	24.54	20.28	2.73	33.12	37.39	36.14	0.73
	0-20m	20.44	24.45	22.63	0.82	33.88	37.39	36.08	0.85
	20-40m	19.31	24.48	22.51	1.05	34.10	37.39	36.42	0.75
	40-60m	17.87	24.54	21.79	1.75	34.29	37.39	36.61	0.59
	60-80m	16.57	23.63	20.99	2.10	35.72	37.38	36.60	0.48
	80-100m	15.68	23.13	20.22	2.53	35.57	37.37	36.49	0.56

Table 2. Temperature (°C) and salinity registered during the summer and winter by region in southeastern Brazilian waters. Minimum, maximum, mean and standard deviation (sd) estimated for the water column (from surface to 200 m depth).

| Season	region	Temperature °C				Salinity			
		minimum	maximum	mean	sd	minimum	maximum	mean	Sd
Summer	Coastal	13.53	27.64	19.37	4.07	33.42	37.18	35.68	0.62
	Intermediary	13.08	26.61	19.30	3.72	34.92	37.17	36.03	0.54
	Oceanic	13.26	26.54	21.08	3.59	35.22	37.24	36.48	0.56
Winter	Coastal	14.11	23.67	20.84	1.95	33.12	37.04	35.39	0.94
	Intermediary	14.58	23.48	19.65	2.76	34.19	37.07	36.05	0.49
	Oceanic	14.21	24.54	20.53	2.85	35.35	37.39	36.47	0.57
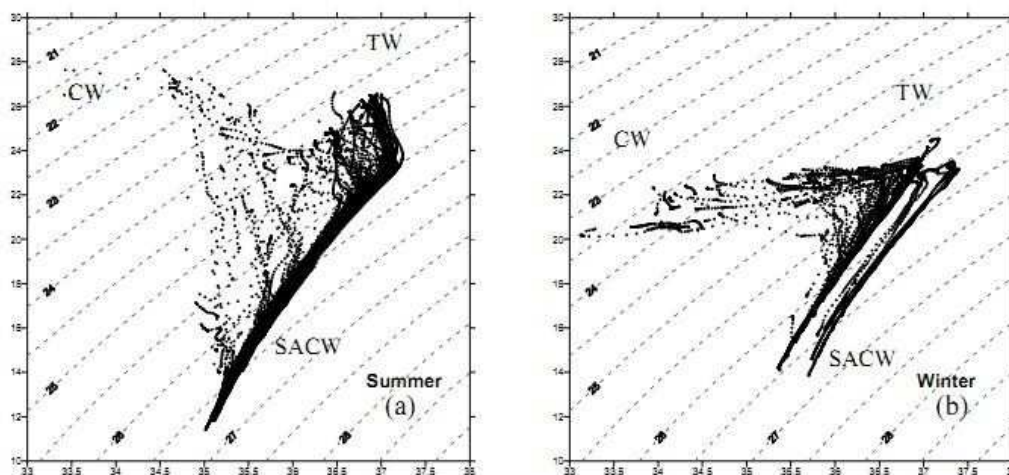
Fig. 2. Temperature-Salinity diagrams (T-S) of the total oceanographic stations realized during the summer (a) and winter (b) cruises, in 2002. Where TW refers to Tropical Water mass (>20°C and >36), SACW refers to South Atlantic Central Water mass (<20°C e salinity between 35 and 36) and CW refers to Coastal Water mass (>20°C and <34).

Larval Abundance and Horizontal Distribution
Bongo Net Samples

A total of 411 (summer) and of 139 (winter) larvae of Phosichthyidae were collected with the bongo net. These amounts corresponded to *ca.* 2% of the total fish larvae sampled each season (14,379 in the summer and 7,828 in the winter). Two phosichthyid species occurred in the samples, *Pollichthys mauli* and *Vinciguerria nimbaria*, *P. mauli* being predominant (62% of total Phosichthyidae in the summer and 54% in the winter). Larval *V. nimbaria* accounted for 25% of total phosichthyids in the summer and 45% in the winter.

The occurrence frequency of *P. mauli* was 50% in the summer and 45% in the winter. No significant difference was recognized in the abundance between these seasons (mean = 2.64 larvae.m^{-2}; sd = 7.42, in the summer and mean = 0.95 larvae.m^{-2}; sd = 2.61, in the winter) (Mann-Whitney U-test, $P > 0.05$). Larvae were widely distributed in the study area, but higher abundance was observed in the intermediate sub-area in the summer (102.65 larvae.m^{-2}), followed by the oceanic sub-area (85.29 larvae.m^{-2}), while in the coastal sub-area the abundance was significantly lower (1.82 larvae.m^{-2}) (Kruskal-Wallis test, $P < 0.05$). In the winter, higher abundance was estimated in the oceanic region (36.56 larvae.m^{-2}), followed by the intermediate sub-area (22.70 larvae.m^{-2}), both significantly different from the coastal region (3.71 larvae.m^{-2}) (Kruskal-Wallis test, $P < 0.05$) (Fig. 3).

The occurrence frequency of *V. nimbaria* was higher in the summer (29%) than in the winter (22%), but no significant difference was observed in the abundance between the seasons (mean = 1.08 larvae.m^{-2}; sd = 2.79, in summer and mean = 0.82 larvae.m^{-2}; sd = 1.92, in the winter) (Mann-Whitney U-test, $P > 0.05$). Concerning the horizontal distribution, the result suggests that higher larval concentrations either for *P. mauli* or *V. nimbaria* tended to be observed far offshore (Fig. 3). The larval concentrations were significantly higher in the oceanic region (50.56 larvae.m^{-2} in the summer and 38.80 larvae.m^{-2} in the winter) than in the coastal region (1.72 larvae.m^{-2} in the summer and 0.48 larvae.m^{-2} in the winter) (Kruskal-Wallis test, $P < 0.05$).

Larval Density and Vertical Distribution - MPS Samples

A total of 127 (summer) and of 19 (winter) larvae of Phosichthyidae were collected with MPS. Three species were identified: *P. mauli*, *V. nimbaria* and *Ichthyioccoccus sp.*, but *Ichthyioccoccus sp.* was extremely rare with only one specimen caught in the 20-40 m depth layer in the oceanic region during the summer. Larval *P. mauli* predominated in summer (65% of total Phosichthyidae), whereas *V. nimbaria* larvae were predominant in the winter (57% of total Phosichthyidae). *P. mauli* occurred at 60% of the oceanographic stations on the summer cruise and 14% in the winter, but the summer mean density of 3.37 larvae.100m^{-3} (sd = 7.25) was not significantly different from that observed in the winter of 0.33 larvae.100m^{-3} (sd = 1.61) (Mann-Whitney U-test, $P > 0.05$).
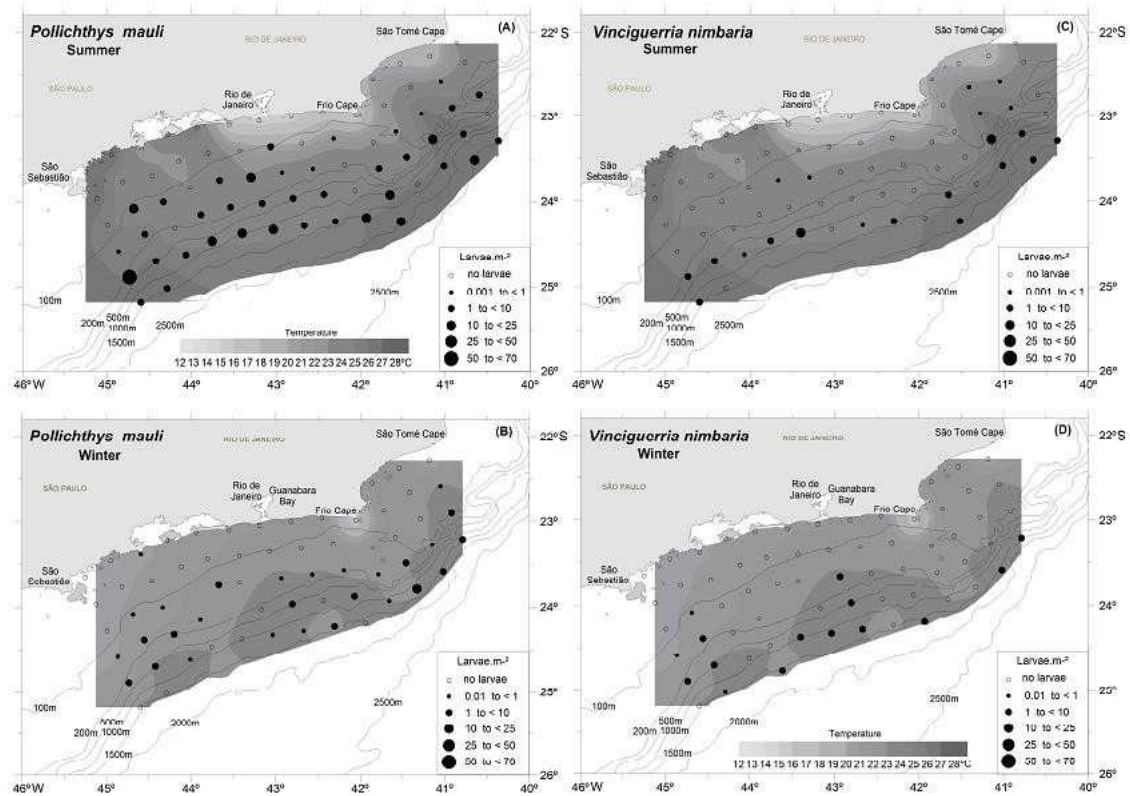
Fig. 3. Horizontal distribution of *Pollichthys mauli* in the summer (a) and in the winter (b); horizontal distribution of *Vinciguerria nimbaria* larvae during the summer (c) and winter (d) cruises in 2002, between São Tomé cape (RJ) and São Sebastião island (SP). Where **N** is the total number of larvae collected and the abundance larvae is estimated in larvas.m^{-2}. Temperature registered to 10 m depth.

Larval *P. mauli* occurred in all layers sampled in the summer, with higher density estimated in the 60-80 m layer (mean of 6.87 larvae.100m^{-3}; sd = 11.41). In the winter, larvae occurred only between 20 and 60 m depths, of which the 20-40 m layer was extremely poor with only 2 larvae collected, whereas the mean density estimated for the 40-60 m layer was 1.16 larvae.100m^{-3} (sd = 2.84) but no significant difference was observed between layers in either season (Kruskal-Wallis test, $P > 0.05$) (Figs 4 and 5).

The occurrence frequency of larval *V. nimbaria* was 25% on both the cruises, based on the MPS collections. Larval abundance in the summer was 0.84 larvae.100m^{-3} (sd = 3.51) and in the winter 0.51 larvae.100m^{-3} (sd =3.04), no significant difference being recognized in the density between seasons (Mann-Whitney U-test, $P > 0.05$). This species was absent in the 80-100 m layer in both seasons. Higher density was estimated in the surface layer (0-20 m) in the summer (mean = 1.33 larvae.100m^{-3}, sd = 3.27)

and from 20 to 40 m depth in the winter (mean = 1.65 larvae.100m^{-3}, sd = 6.21), no significant differences being observed among layers (Kruskal-Wallis test, $P > 0.05$) (Figs 4 and 6).

Larval Length Frequency

The size of *P. mauli* larvae ranged from 3 to 25 mm, indicating the presence of all the early developmental stages. About 60% were in postflexion (>7 mm SL) in the summer and winter. The larvae of 3-5 mm NL were in preflexion stage and 5-7 mm SL in the flexion stage. Although no significant (Mann-Whitney U-test, $P > 0.05$) differences were observed in the size-frequency larvae among regions, in general larvae larger than 15 mm SL tended to occur predominantly in the shallower stations of the intermediate sub-area, while the smaller larvae (3-4 mm NL) occurred in the oceanic region, mainly in the summer. The most frequent size classes in the oceanic

region were of 5.75 and 6.25 mm in the summer and of 4.75 and 6.25 mm in the winter. In the intermediate sub-area the 5.75 and 9.25 mm size classes predominated in the summer, and the 10.75 mm class predominated in the winter (Fig. 7).
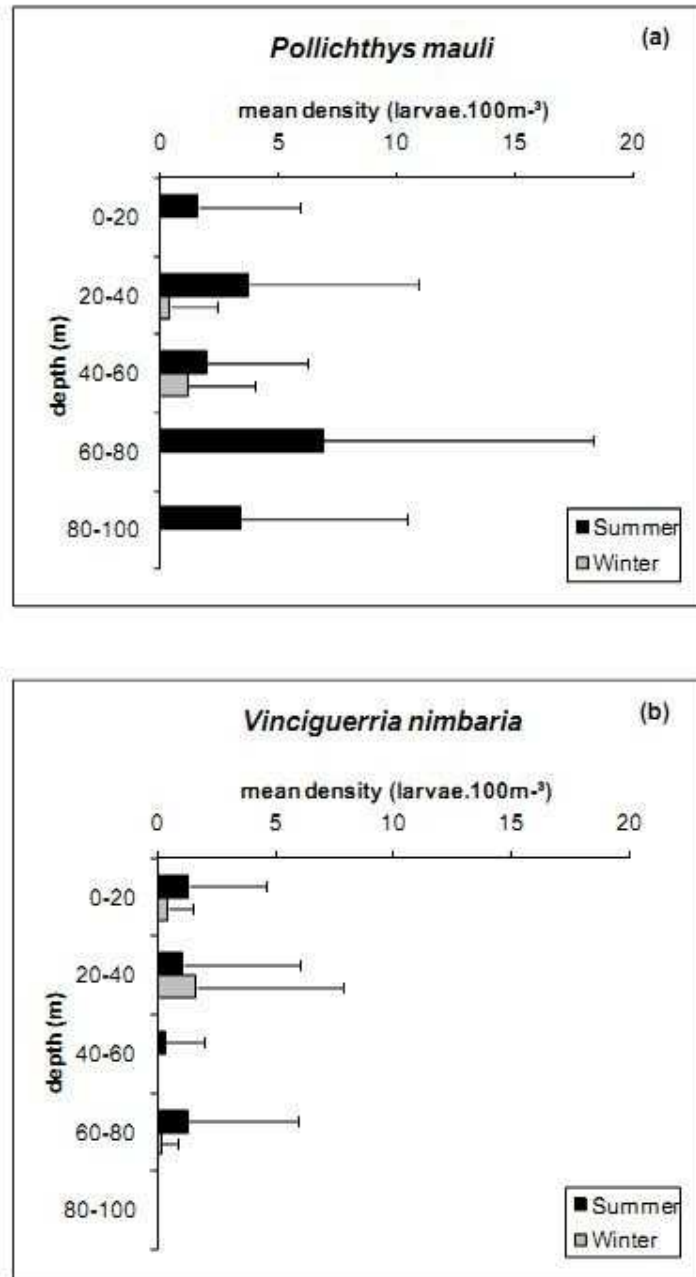

Fig. 4. Mean density of *P. mauli* and *V. nimbaria* fish larvae estimated to each layer sampled by multi plankton sampler (MPS) in the oceanographic stations, during the summer and winter cruises, in 2002. The density is expressed in larvae.100m^{-3} and error bars are standard deviation about the mean density.
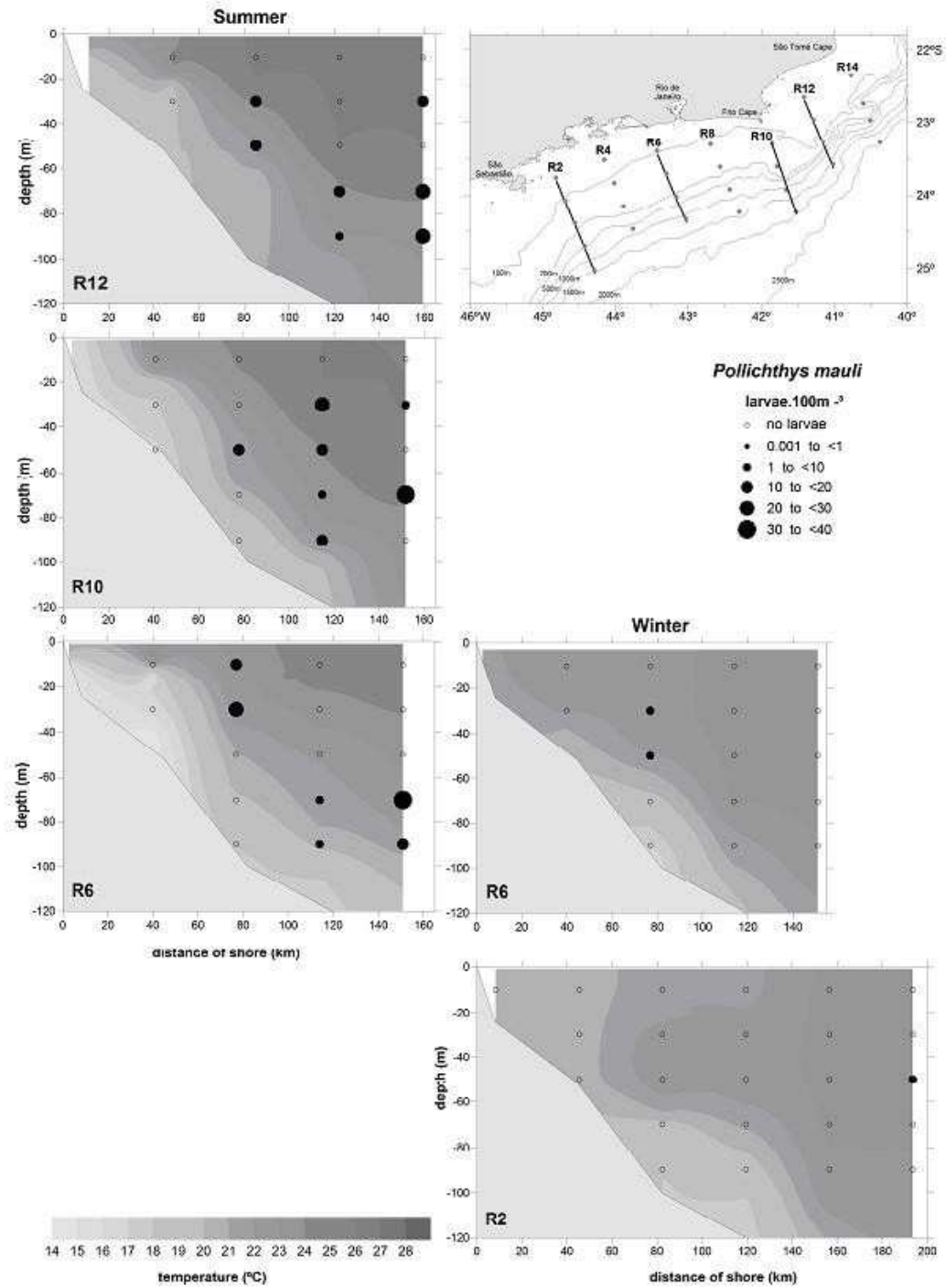
Fig. 5. Vertical profiles of temperature (°C) and vertical distribution of *P. mauli* larvae on transect perpendicular to Brazilian coast (R) during the summer and winter, 2002. The density is expressed in larvae.100m⁻³.
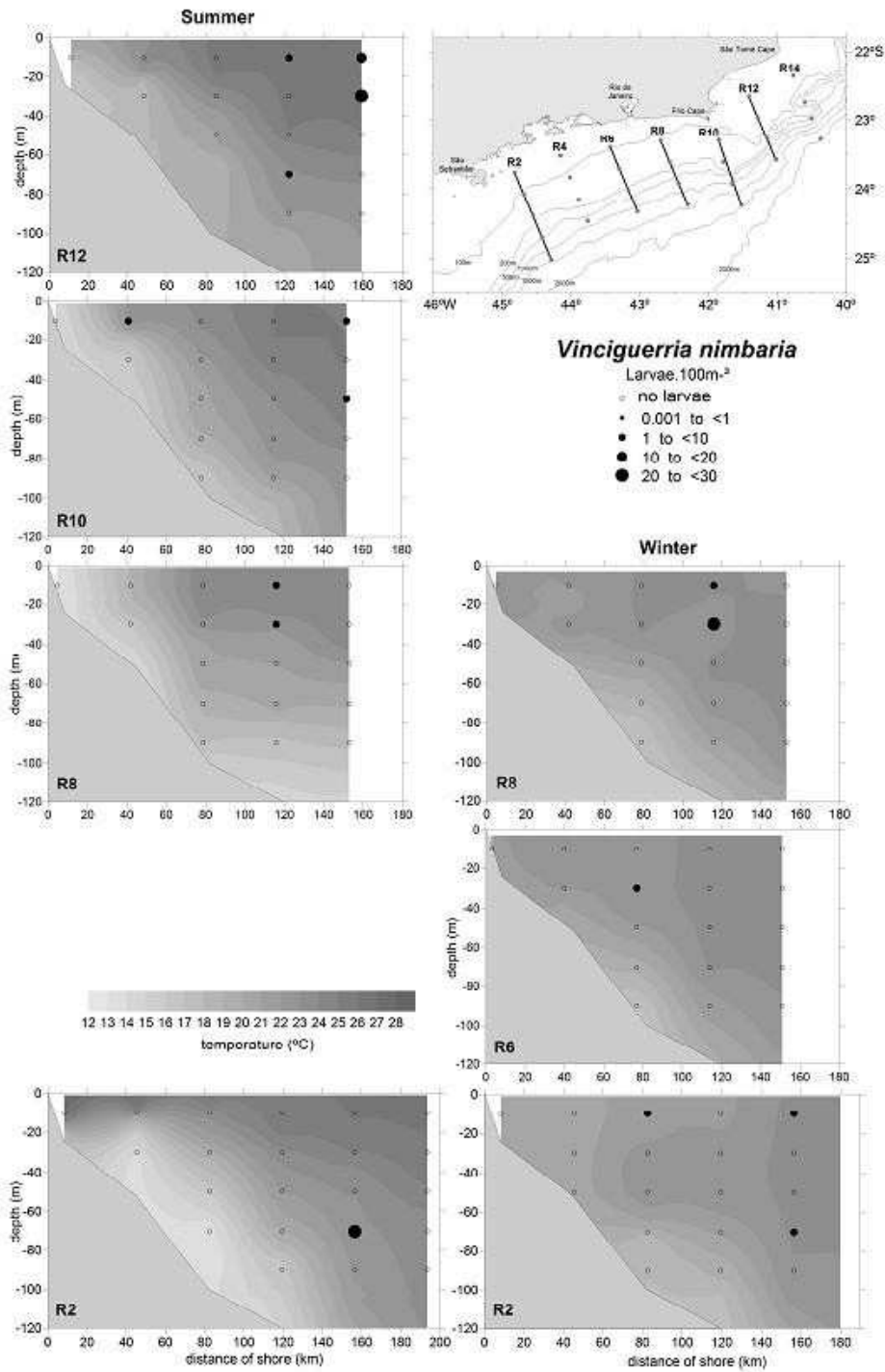
Fig. 6. Vertical profiles of temperature (°C) and vertical distribution of *V. nimbaria* larvae on transect perpendicular to Brazilian coast (R) during the summer and winter, 2002. The density is expressed in larvae.100m⁻³.

In the water column, *P. mauli* larvae in preflexion were collected more frequently between 40 and 100 m, while, postflexion larvae were more frequent between the surface and 20 m, these data suggesting an ontogenetic vertical movement of larvae (Fig. 8).

The length of *V. nimbaria* larvae ranged from 3 to 23 mm, indicating the presence of all the early stages. More than 45% of the larvae were in postflexion. The length in the preflexion stage ranged from 3 to 6 mm NL, and in the flexion stage from 6 to 8 mm SL. So that specimens > 8 mm SL were in postflexion. The predominant size classes during the summer in the oceanic sub-area were those of 5.75 and 6.25 mm, and in the intermediate sub-area were of 4.75 and 6.25 mm. During the winter the predominant size classes were of 4.25 and 5.75 mm in the oceanic region and 4.75 mm and 6.75 mm in the intermediate region, but no significant differences were found in the size-frequency larvae among regions in either season (Mann-Whitney U-test, $P > 0.05$) (Fig. 7). *V. nimbaria* larvae in preflexion were collected more frequently between 60 and 80 m, while postflexion larvae were

more frequent between the surface and 20 m and from 20 to 40m depth, there being no significant difference in the size-frequency larvae among layers (Kruskal-Wallis test, $P > 0.05$) and no clear ontogenetic vertical movement because the number of larvae was very low.

Diel Variation

Larval *P. mauli* occurred during all periods of the day (dawn, day, dusk and night), but *V. nimbaria* was absent at dusk. No significant differences were observed among periods, but abundance was higher at night than in the other periods for the two species in both seasons (Kruskal-Wallis test, $P > 0.05$).

In the water column, *P. mauli* larvae occurred in higher density in the upper layer (0-60 m) during the night but in the 60 to 80 m layer the density was high during the day in the summer and at dawn in the winter. In the deepest layer (80-100 m) a greater density of larvae was estimated but no significant difference was observed (Kruskal-Wallis test, $P > 0.05$) (Fig. 9).
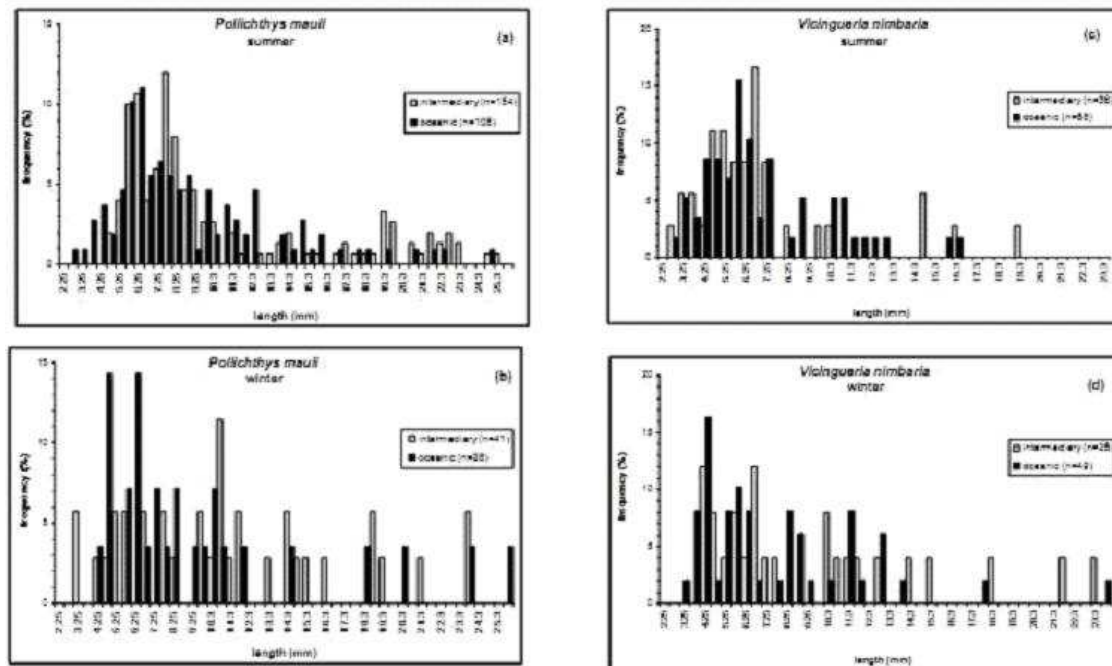

Fig. 7. Frequency – size class distribution of *P*. mauli during the summer (a) and winter (b) and *V. nimbaria* larvae in the summer (c) and winter (d) in the intermediary and oceanic region, in 2002.
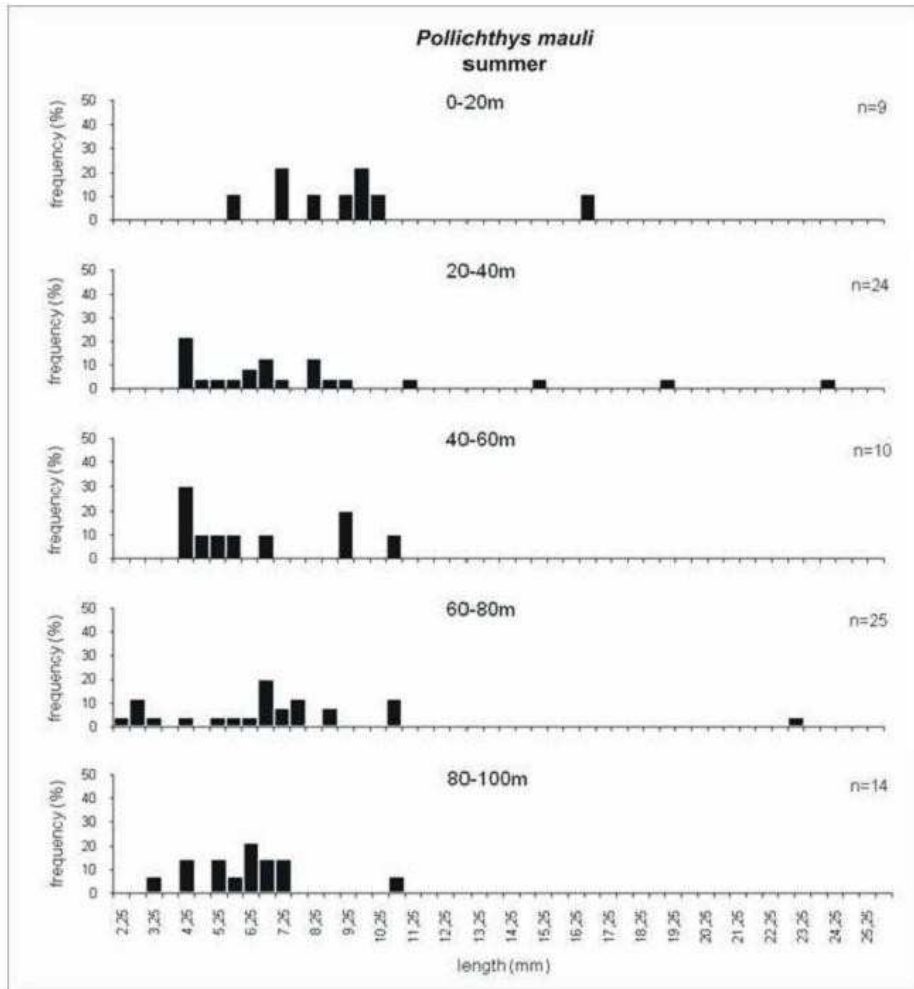
Fig. 8. Frequency – size class distribution of *P*. mauli larvae in the layers sampled by MPS net, during the summer in 2002. The *n* is the number of larvae collected.
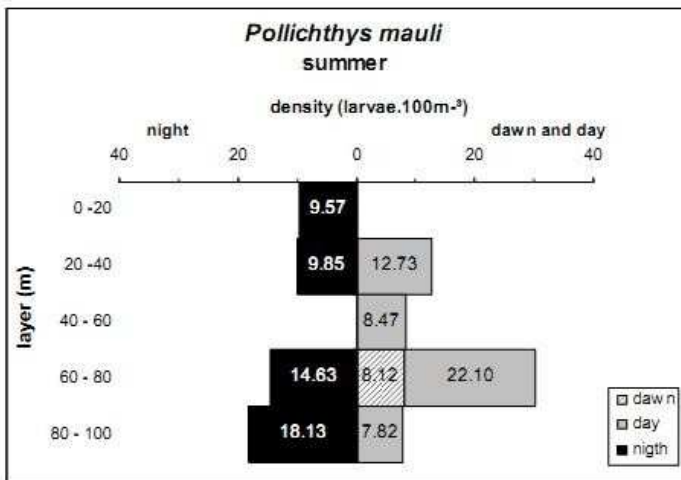

Fig. 9. Vertical distribution of *P. mauli* density larvae (larvae.100m-³) in the layers sampled in the periods of the day, during the summer in 2002.

In the summer, larval stages of *V. nimbaria* were collected during dawn, day and night from the surface to 40 m but were more concentrated during the day in the 60-80 m layer. The highest larval density was estimated during the day between 20 and 40 m depth in the winter. No significant differences were found among the densities estimated for any of the layers (Kruskal-Wallis test, $P > 0.05$) and it was not possible to verify any diel vertical migration.

Environmental and Biological Relationships

The Redundancy analysis indicated that the seasons and the temperatures (axis 1: 34.5%; axis 2: 24.4%, respectively) were the most marked determining environment factors in the larval distribution of *P. mauli* and *V. nimbaria*, according to ontogenetic stage and diel variation (Monte Carlo, $P < 0.05$). The diagram of ordination showed a positive correlation between different development stages of *P. mauli* and the summer, when the larval density (larvae.100m^{-3}) presented its highest values, and a

correlation between *V. nimbaria* larvae and the winter, also observed in terms of the values of larval density (Fig. 9).

The preflexion stage of *P. mauli* and *V. nimbaria* presented a positive correlation to depth and a negative one to temperature. Larvae occurred mainly in the deeper layers (40 and 100 m) of the water column analyzed, where the temperature is lower. Postflexion larvae were more frequent between the surface and 20 m depth, presenting a negative correlation to depth and a positive one to temperature.

In relation to diel variation, both species were collected in greater density during the night on both summer and winter cruises. As *P. mauli* and *V. nimbaria* larvae in the postflexion stage presented a positive correlation to night, while preflexion and flexion larvae presented a negative correlation, we may suppose that the swimming abilities and the change in visual perception related to the stages of larval development, exercise an influence in the capture of the larvae.
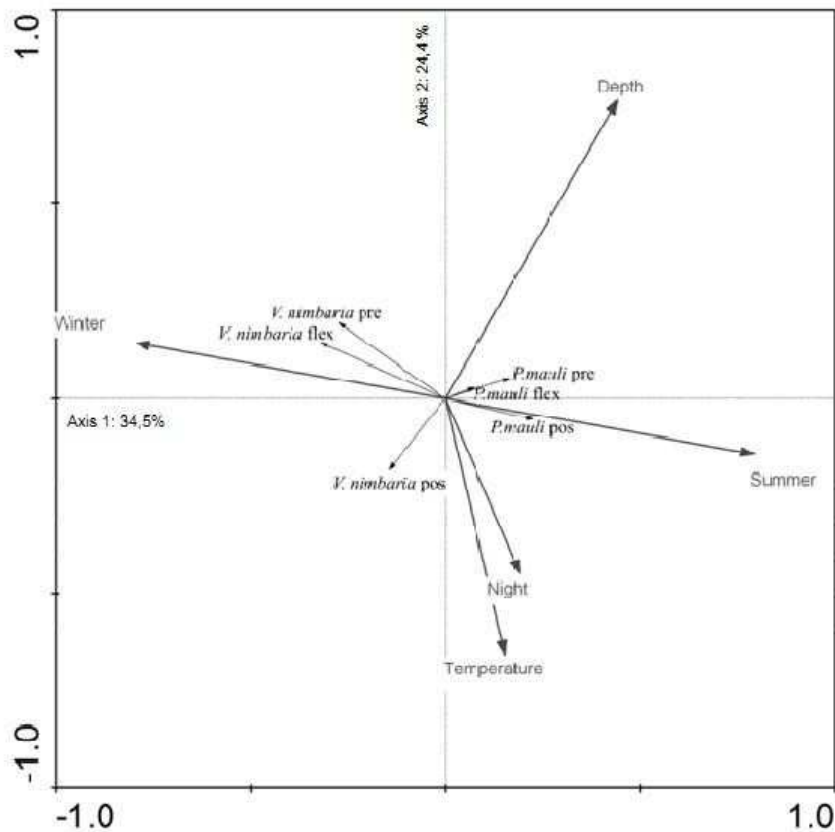

Fig. 10. RDA ordination plot of *P. mauli* and *V. nimbaria* in different development larval stages according to the state of notochord and environment factors that presented significant difference, according to Monte Carlo test ($P < 0.05$). *V. nimbaria* and *P. mauli* pre = *V. nimbaria* and *P. mauli* in preflexion stage, *V. nimbaria* and *P. mauli* flex = *V. nimbaria* and *P. mauli* in flexion stage and *V. nimbaria* and *P. mauli* pos = *V. nimbaria* and *P. mauli* in postflexion stage.

Larval *P. mauli* and *V. nimbaria* occurred throughout the study area, presenting their highest abundance values at those oceanographic stations located in the intermediate and oceanic sub-areas and distributed in the upper 100 m depth of the water column, where the Tropical Water (TW) mass was present. Probably larval distribution is related to the TW transported by the Brazilian Current.

DISCUSSION

Phosichthyidae species compose the mesopelagic group of fishes in the marine ecosystem but are not the dominant ones. The proportion of Phosichthyidae larvae (*ca.* 2% of total larvae collected) was relatively low in the present study, if one compares this result with the relative value of the other mesopelagic fish larvae, such as those of Sternoptychidae (*ca.* 15%) and Myctophidae (*ca.* 14%). However, this low proportion of occurrence of larvae is similar to that observed in other regions, *e.g.* off eastern Brazil (NONAKA et al., 2000), in the Gulf of California (AVALOS-GARCIA et al., 2003), the western North Pacific (SASSA; KONISHI, 2006) and on the shelf break of the East China Sea (OKAZAKI; NAKATA, 2007).

Although eight species of Phosichtyidae are known to inhabit southeastern Brazilian waters (MENEZES; FIGUEIREDO, 2003), only three species, *Pollichthys mauli* (POLL, 1953), *Vinciguerria nimbaria* (JORDAN and WILLIAMS, 1895) and *Ichthyococcus sp.*, were collected in the present study. The sampling method may influence the collection of some species due to the vertical migration to layers deeper than those attained by the bongo net. But studies indicate that the majority of fish larvae, even of the mesopelagic species, are distributed in the upper 200 m of the water column (*e.g.* LOEB, 1980; BRODEUR; RUGEN, 1994; SASSA et al., 2002). Larval *Ichthyioccoccus sp.*, that was extremely rare in the samples, is exceptional as it inhabits depths of from 200 to 500 m (SCHAEFER et al., 1986). According to BERNARDES et al. (2005), adult *Vinciguerria poweriae* and *Polymetme thaeocoryla* tend to be distributed in the southernmost Brazilian waters, far from the area of this present study. Perhaps the same pattern of geographical distribution of the larvae may explain the absence of these species in our results.

Larvae of *P. mauli* and *V. nimbaria* have been registered, by many authors, in the Atlantic, Pacific and Indian Oceans (SCHAEFER et al., 1986; RICHARDS, 2006; OKAZAKI; NAKATA, 2007; MOYANO et al., 2009, among others). In Brazilian waters these species have previously been reported on the eastern coast by BONECKER AND HUBOLD (1990). Both these species occurred in summer and

winter in the present study, but the occurrence of these larvae has also been reported in spring by BONECKER and HUBOLD (1990), and in autumn by NONAKA et al. (2000), suggesting that these species spawn all the year round.

Overall, abundance did not differ significantly between seasons for *P. mauli* or *V. nimbaria* larvae, but a slight trend to higher abundance was observed for both species in the summer. This result agrees with BADCOCK (1984) who observed a spawning peak of *P. mauli* during the summer in the Western North Atlantic and the Mediterranean Sea. On the other hand, STEQUERT et al. (2003) reported that *V. nimbaria* larvae are predominant all the year round and that this species spawns continuously throughout the year in the equatorial Atlantic Ocean.

Our results showed that the pattern of vertical distribution of *P. mauli* larvae differed with season, being widespread in all layers in the summer, but with a higher density in the 60-80 m layer, whereas in the winter larvae tended to concentrate in the 40-60 m layer. But the distribution of *V. nimbaria* did not overlap that of the former species and exhibited a preference for the 20-40 m layer both in the summer and in the winter. Muhling and Beckley (2007) undertook collections in south-western Australia from the surface to 1000 m depth; *Pollichthys* sp. larvae were caught only at 1000 m depth during the winter and *Vinciguerria* sp. were collected in layers below 40 m, and in greater density at 300 m depth. *V. nimbaria* larvae were collected in layers deeper than 50 m in the North Atlantic (GREY, 1964) and LOEB (1979, 1980) observed more occurrences of larvae (90%) between 25 and 75 m depth and collected the highest number of *V. nimbaria* larvae between 25 and 50 m in the North Pacific central gyre.

Diel vertical migration is known to occur in several groups of fish and their larvae, especially in species with light organs (CLARKE, 1971; NEILSON; PERRY, 1990; WATANABE et al., 1999). Our results indicated a tendency of *P. mauli* larvae to concentrate in the surface layer (0-20 m) during the night, and to occur in higher density in the 60-80 m layer during the day, indicating a movement of organisms in the water column during the day, but some larvae were observed at 80-100 m both at night and by day. This diel movement was not clear with regard to *V. nimbaria* larvae, but a vertical migration of adult *V. nimbaria* related to its feeding activity is known (MARCHAL and LEBOURGES, 1996; LEBOURGES-DHAUSSY et al., 2000; STEQUERT et al., 2003), so further studies are necessary to enable us to come to a conclusion regarding the behavior of *V. nimbaria* larvae.

Postflexion larvae were mainly associated with the night period, whereas preflexion and flexion

larvae were associated with other periods of the day. This fact may be related to the increase in the ability to move associated with growth. Postflexion larvae have greater swimming ability and are capable of migrate vertically, rising to the surface at night and descending to deeper layers during the day. Net avoidance associated with the development of the visual perception of the larvae (BLAXTER; HUNTER, 1982) may also have had some influence in the sampling of larger specimens during the day. SASSA and KONISH (2006) observed no clear ontogenetic vertical migration of jack mackerel larvae (*Trachurus japonicus*) with <3 mm standard length. According to those authors, migratory behavior tends to develop with the increased swimming ability of the larvae and greater intensity is observed in the vertical migration after the postflexion stage.

In the present study the early larval *P. mauli* (by 3 mm NL) was concentrated in the deeper layer (60-80 m) of the oceanic sub-area, whereas the postflexion larvae were found mainly near the surface (0-40 m) and in the intermediate sub-area. The postflexion larvae of *V. nimbaria* also had their peak distribution in the intermediate sub-area and in the surface (0-20 m) layer. The occurrence of preflexion larvae in layers deeper than 60 m was also observed by LOEB (1979) in the North Pacific Central gyre. These patterns of vertical distribution related to ontogeny may be strategically important to development during the early life stages, as food requirements, as well as the ability to detect prey, increase with the size of the larvae. In this case the presence of larger larvae in the upper surface layer, with higher prey abundance, must be advantageous for feeding. On the other hand, changes in oceanographic conditions, which vary according to the different layers of the water column, may affect the larval stages in other ways, for example by transporting them to more or less favorable areas (CHA et al., 1994).

The larval phosichthyids were, in some case, found in the TW-SACW interface. This pattern of distribution associated with the transition area of two water masses has also been observed in other regions. LOEB (1979, 1980) studying the vertical distribution of *Vinciguerria* collected in the mixing layer and Ahlstrom (1959) collected *V. lucetia* larvae in the mixed layer and above the thermocline in Baja California. In Brazil, BONECKER and HUBOLD (1990), observed the occurrence of *V. nimbaria* and *Vinciguerria* sp. associated with the mixture between TW and SACW.

Several works have shown that phosichthyids are distributed mainly in the oceanic region (e.g. OKAZAKI; NAKATA, 2007; MOYANO et al., 2009), although distribution in a shallower zone (50-100 m isobaths) has been reported in eastern Brazil (BONECKER; HUBOLD, 1990; NONAKA et al., 2000; BONECKER et al., 2006). In the case of the present study the environmental boundaries of both species appear to be in close association with the Tropical Water (TW), that embraces the oceanic but also the neritic area, at least as far as the mid-shelf. The overall picture of the present study area, from the hydrographic point of view, follows the classical description given in the literature for both seasons (CASTRO; MIRANDA, 1998; SILVEIRA et al., 2000; CASTRO et al., 2006; among others) and shows the interactions of the three water masses, TW, SACW, and CW. The shapes of the T-S diagrams of this study (Fig. 3) resemble the shape of those described by CASTRO and MIRANDA (1998) based on historical data. Among the many hydrographic features of the Southeastern Brazilian Bight, the perturbations of the Brazil Current flow in the form of meanders or eddies seem to be crucial to the spreading of the larvae of mesopelagic fish over the neritic area.

As the presence of early larvae indicates the proximity of the spawning ground (JONES, 2002), the spawning of *P. mauli* and *V. nimbaria* is probably concentrated in the deeper layers of the water column of the oceanic area, where the early larvae were found. After hatching, the larvae tended to expand their distribution, either vertically or geographically, as discussed above. Our findings that both species exhibited increased mean lengths in an offshore-coastal direction, supports the idea of their moving to the neritic area. This distribution must be favored by the meandering patterns or eddy activities (CASTRO; MIRANDA, 1998) which enhance the transport of larvae toward the mid-shelf. One of the benefits to the species is that, as the demand for food increases with larval growth, the movement from oligotrophic oceanic water to areas of higher concentration of prey organisms may contribute to the improvement of the larval condition as also therefore to the chance of success in surviving during early development.

The larval transport strategy, from oligotrophic to productive regions, has been accounted as important for mesopelagic species in other regions. For example, in an analysis of distribution patterns of larval myctophids in the transitional region of the western North Pacific, SASSA et al. (2004) discussed the role of hydrographic structures, such as the fronts and rings related to the Kuroshio and Oyashio current systems, in larval transport from spawning to nursery grounds. Concerning the phosichthyids of Southeastern Brazil, further studies are necessary to obtain information such as will enable us accurately to correlate the increment of age to distance offshore, as well as information on the speed at which those fish larvae can be transported within the system, in order to evaluate the use of the area as a nursery ground.

Another hydrographic feature important to the biological processes in southeastern Brazilian

waters is the intrusion of the SACW toward the coast in the bottom layer. The position of the bottom thermal front changes seasonally, being closer to the coast during summer and farther offshore during winter (CASTRO; MIRANDA, 1998), and depending on the strength of the SACW intrusion the coastal upwelling may occurs, mainly near Frio cape. The spawning strategies associated with these dynamic processes have already been intensively discussed (MATSUURA, 1996; LOPES et al., 2006), and it has been observed that the input of the nutrient rich cold water of the SACW contributes to the enhancement of primary productivity in the coastal area (LOPES et al., 2006). For some small pelagic fish species, such as sardine and rough scad, studies have shown a tendency of the peak spawning period to correspond to the period when the intrusion of SACW becomes more frequent, i.e., during spring and summer (MATSUURA et al., 1992; KATSURAGAWA et al., 2006). However, for the phosichthyids of the study area, apparently there is no direct dependence on the coastal events as no significant difference in larval abundance between summer and winter has been found, but rather these species seem to be opportunistic in taking advantage of the eddies as a way to spread throughout the neritic area, and thus improve the chance of finding the prey organisms. Further studies comparing the nutritional conditions of larvae collected in oceanic and coastal areas may contribute to an evaluation of the advantage of this distribution pattern.

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