

# Distribution patterns of loliginid squid paralarvae in relation to the oceanographic features off the South Brazil Bight (22°–25°S)

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## Abstract

Loliginid squids constitute marine resources of increasing importance in shelf ecosystems off the coast of South Brazil. However, the existing information and knowledge about the occurrence of early-life stages and causes of distributional patterns are insufficient. Here, we have revisited Brazilian historical plankton samples obtained from 11 oceanographic surveys to identify paralarvae and their abundances over time. The study area and time period cover the region between Cabo de São Tomé (22°S) and Cananéia (25°S) at depths down to 200 m from 1991 to 2005. Of the 246 paralarvae quantified, ~50% were identified to the genus or species level, including *Doryteuthis* spp. (*D. sanpaulensis* and *D. plei*), *Lolliguncula brevis* and a single specimen of *Pickfordiateuthis pulchella*. Paralarval occurrence and abundance peaked in different areas and were associated with distinct oceanographic conditions: *D. sanpaulensis* occurred in the northern region associated with cold waters and upwelling events, *D. plei* occurred primarily in the southern region of the study area and in warmer waters, and *L. brevis* was found in shallow and low salinity waters in the estuarine region off the coast of Santos. Overall, the highest abundance of paralarvae occurred in the nearshore, northernmost areas during summer, and this can be associated with the observed retention mechanisms caused by local circulation, seasonal upwelling, the intrusion of nutrient-rich waters, and spawning peaks. The present study provides new information and evidence for loliginid patterns in the area that may potentially be useful for better understanding the recruitment patterns and fishery assessments of squid populations.

## KEYWORDS

cephalopods, early-life stages, historical marine archives, Loliginidae, oceanographic surveys

## 1 | INTRODUCTION

Recent studies have emphasized the importance of ecological time-series datasets to assess the status of marine ecosystems and develop better tools for effective management measures (Koslow & Couture, 2015; Koslow & Davison, 2016). Investigations focused on cephalopod paralarvae in coastal and oceanic ecosystems have been scarce compared to those focused on fish larvae. However, knowledge of early-life stages and their relation to oceanographic

conditions is the basis for understanding the mechanisms responsible for the distribution, recruitment and variability of resources. Cephalopod paralarvae are usually rare in plankton samples, possibly due to inappropriate sampling methods and taxonomic uncertainties (Boyle & Rodhouse, 2005), but this is also likely due to specific characteristics, such as patchy distributions (González et al., 2005; Haimovici, Piatkowski, & Santos, 2002), and their ability to avoid plankton nets (Hanlon, Hixon, Turk, Lee, & Yang, 1985; Vecchione, 1987). Some successful studies on paralarval distribution have shown the role of

stratification, vertical structures and oceanographic processes, such as pycnocline and mixed-layer depth and upwelling events (González et al., 2005; Moreno dos Santos, Piatkowski, Santos, & Cabral, 2009; Otero et al., 2016; Röpke, Nellen, & Piatkowski, 1993; Vidal, Haimovici, & Hackbart, 2010). Moreover, the El Niño Southern Oscillation has been noted to be among the influences; e.g., Zeidberg & Hamner (2002) inferred El Niño is a factor in the increased abundance of *Loligo opalescens* in the Southern California Bight.

Loliginid squids are important fishery resources and play a significant ecological role in the South Brazil Bight (SBB) (Gasalla, Rodrigues, & Postuma, 2010) and in other coastal marine ecosystems (Boyle & Rodhouse, 2005; Piatkowski, Pierce, & Cunha, 2001; Pierce & Guerra, 1994; Rodhouse, 2005). In Brazil, the most widely studied species are *Doryteuthis plei*, *Doryteuthis sanpaulensis* and *Lolliguncula brevis*, with the first genus corresponding to the most abundant coastal cephalopods (Gasalla et al., 2005; Haimovici & Perez, 1991). *Doryteuthis* spp. have been caught by industrial (shrimp-trawling) and coastal small-scale fisheries (hand-jigging) (Gasalla, Postuma, & Tomás, 2005; Perez, 2002; Perez, Aguiar, & Oliveira, 2002; Postuma & Gasalla, 2010, 2014; Rodrigues & Gasalla, 2008). In contrast, *L. brevis* is caught as an incidental bycatch by shrimp fisheries, but has no commercial value (Zaleski, 2005, 2010). These three species appear to spawn throughout the year, with peaks during the summer months (Andriquetto & Haimovici, 1996; Costa & Fernandes, 1993b; Perez, Aguiar, & Oliveira, 2002; Rodrigues & Gasalla, 2008; Zaleski, 2005, 2010), thus producing several micro-cohorts (Perez et al., 2002).

In such a context, the present study aims to investigate the distribution of loliginid paralarvae in relation to the primary oceanographic features and processes in the continental shelf off the SBB based on plankton samples that were obtained from historical oceanographic surveys.

## 1.1 | Study area

The SBB region is influenced by mesoscale variability of the Brazil Current (BC) and seasonal coastal upwellings. The circulation is dominated by the BC that flows southward along the continental slope. The change in the coastline orientation at the cape region of Cabo Frio from

NE–SW to almost E–W and the shelf narrowing induce a meandering current, thus favoring the occurrence of coastal upwelling (Campos, Gonçalves, & Ikeda, 1995). The topography and coastline orientation promote the proximity of BC water masses toward the coast, thus improving the upwelling efficiency in the region (Cerdeira & Castro, 2014).

The BC transports two water masses, a salty and oligotrophic Tropical Water (TW) in the upper mixing layer and cold and nutrient-rich South Atlantic Central Water (SACW) in the lower layers. A third water mass exists aside from TW and SACW, the Coastal Water (CW), which results from the mixing of those two masses in the inner shelf with waters from continental discharge (Castro & Miranda, 1998).

The seasonal variability of the BC, which is caused by mesoscale processes (meanders and eddies), is an important mechanism of the dispersion and retention of nutrients and larval transport (Franco, Muelbert, & Mata, 2006). During the summer, wind stress from the northeast pushes surface waters offshore, following the Ekman transport, leading to bottom intrusions and an upwelling of the SACW that increases the local biological productivity. In winter, cold frontal systems invert the wind stress from northeast to southwest, the SACW retreats toward the slope and the water column becomes homogeneous (Campos, Gonçalves, & Ikeda, 1995; Castro & Miranda, 1998).

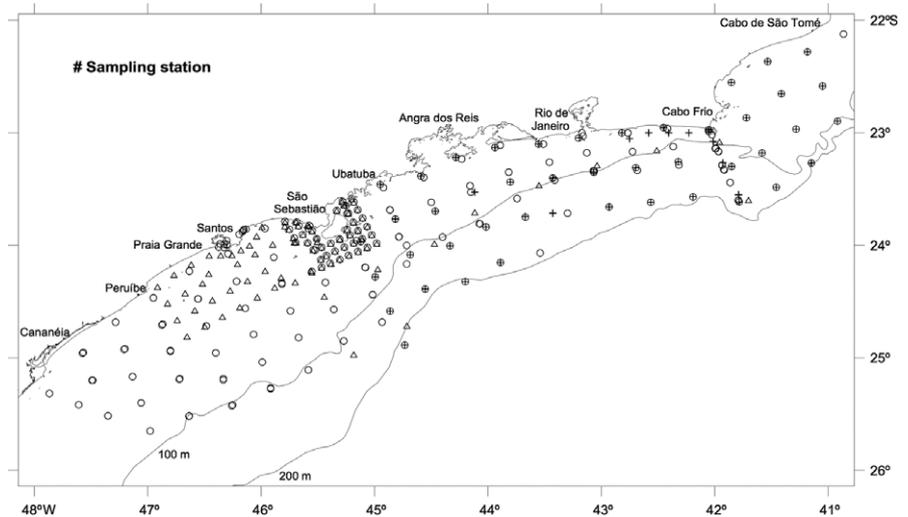
## 2 | MATERIALS AND METHODS

### 2.1 | Sampling

A collection of 644 samples from historical plankton surveys (Table 1) deposited at the Biological Collection “Prof. E. F. Nonato” - ColBIO (Oceanographic Institute, University of São Paulo) was examined to identify the distribution and abundance of Loliginidae paralarvae off the Southeastern Brazil Bight between Cabo de São Tomé (22°S) and Cananéia (25°S) down to 200 m in depth (Figure 1). From January 1991 to September 2005, 11 oceanographic cruises were undertaken during summer, spring and winter on board the research vessels “W. Besnard” and “Albacora”, using a ‘Bongo’ and ‘multi-plankton sampler’ (MPS), and each sample was obtained using 333 µm mesh sizes. The samples were collected using oblique (from near bottom to surface) and stratified (at 10–20 m intervals) hauls at

**TABLE 1** Plankton sampling summary of oceanographic cruises performed between 1991 and 2005

Cruise	Area	Date	R/V	Net type	Haul type	No. samples (Bongo/MPS)
SARDINHA-1	23°–25°S	12/1991	R/V. Prof. W. Besnard	Bongo	Oblique	71
SARDINHA-2	23°–25°S	01/1993	R/V. Prof. W. Besnard	Bongo	Oblique	70
OPISS-1	24°S	02/1994	R/V. Prof. W. Besnard	Bongo	Oblique	43
OPISS-2	24°S	10/1997	R/V. Prof. W. Besnard	Bongo	Oblique	43
PADCT-1	23°–25°S	11/1997	R/V. Prof. W. Besnard	Bongo	Oblique	11
DEPROAS-1	23°S	02/2001	R/V. Prof. W. Besnard	Bongo/MPS	Oblique/Stratified	16/63
DEPROAS-2	23°S	07/2001	R/V. Prof. W. Besnard	Bongo/MPS	Oblique/Stratified	19/46
DEPROAS-3	22°–24°S	01/2002	R/V. Prof. W. Besnard	Bongo/MPS	Oblique/Stratified	49/58
DEPROAS-4	22°–24°S	08/2002	R/V. Prof. W. Besnard	Bongo/MPS	Oblique/Stratified	47/47
ECOSAN-3	24°5'S	01/2005	R/V. Prof. W. Besnard	Bongo	Oblique	11
ECOSAN-H1	24°–25°S	09/2005	R/V. Albocara	Bongo/MPS	Oblique/Stratified	36/14



**FIGURE 1** Map of the study area and sampling sites between Cabo de São Tomé and Cananéia from 1991 to 2005. Open circles, summer stations; crosses, winter stations; triangles, spring stations

~2 knots for periods of 10 min. To estimate the filtered water volume, calibrated flowmeters were used and mounted on the net mouth apertures. All samples were preserved in 4% borax-buffered formaldehyde and were prepared using seawater. Oceanographic data, such as temperature and salinity, were obtained at each station from CTD casts near the bottom.

## 2.2 | Laboratory analysis

Paralarvae from the family Loliginidae were sorted based on diagnostic features, such as the eye being covered by a transparent cornea membrane, a bullet-shaped body form with well developed terminal fins, ventral arms ( $IV > I$ ) and tentacles (Hanlon et al., 1992; Jereb & Roper, 2010). Loliginid paralarvae were identified to the lowest taxonomic level possible based on McConathy, Hanlon & Hixon (1980), Vecchione (1982), Hanlon et al. (1992), Barón (2003) and Vidal, Marian & Martins (2013), according to the number of chromatophores on the cheek patch area (Vecchione & Lipiński, 1995) and dorsal mantle. The dorsal mantle length (DML) was obtained as established by Roper & Voss (1983) using the AXIOVISION 4.8 software on a computer connected to a scientific digital camera (Axiocom Erc 5s) installed on a Discovery V8 Zeiss stereomicroscope. Damaged individuals and/or those with inverted mantles were not measured.

## 2.3 | Statistical analysis

Generalized linear models (GLM), using the R software (R Development Core Team, 2005), were used to verify the relationships between the occurrence and inferred abundance of loliginid paralarvae (response variable) and environmental factors (continuous independent variable). The GLMs were performed using a two-step procedure, as proposed by Moreno et al. (2009) (i) presence/absence data were analyzed with a logistic regression model using the logistic link, and (ii) abundance data were analyzed using a gamma regression model with the log link. The presence/absence and abundance data were analyzed in response to the following explanatory variables:

depth, latitude, sea surface temperature and salinity, depth temperature and salinity, month and year. Generalized Additive Models (GAMs) were used to visualize the nonlinear relationships between response variables (presence/absence and abundance) and continuous (environmental) variables. These models fit data without requiring a specific mathematical model to describe the non-linearity between response and continuous variables (Crawley, 2005). To verify the influence of abiotic variables on the abundance of paralarvae identified to the species level, a redundancy analysis (RDA) (Rao, 1964; Van den Wollenberg, 1977) was performed using the CANOCO 4.5 software (Ter Braak & Smilauer, 2002). Prior to the RDA, the abundances and environmental variables were transformed [ $\ln(x + 1)$ ] to homogenize variances and reduce the asymmetry (Diekmann, Nellen, & Piatkowski, 2006). Subsequently, a Hellinger transformation was applied to the abundance data (Legendre & Legendre, 1998). A Monte Carlo permutation test was used to investigate the significance of the relationship between the abundance and environmental variables. To verify the significant differences between the DML obtained from Bongo and the MPS nets during the summer, spring and winter, the Mann–Whitney and Kruskal–Wallis tests were used, respectively.

## 2.4 | Hydrographic data

Temperature and salinity profiles were used to identify water masses, as defined by Campos et al. (1995), Castro and Miranda (1998), Castro, Lorenzetti, Silveira, & Miranda (2006), and Cerda & Castro (2014). To verify the existence of thermal stratification in the water column, a stratification parameter  $\Delta T$  was calculated using the following equation:

$$\Delta T = \frac{T_s - T_b}{|D_{T_s} - D_{T_b}|}, \quad (1)$$

where  $T_s$  is surface temperature,  $T_b$  is bottom temperature,  $D_{T_s}$  is depth of surface temperature and  $D_{T_b}$  is depth of bottom temperature.

### 3 | RESULTS

Overall, 246 loliginid paralarvae were found in 89 bongo samples and nine MPS samples. Nevertheless, ~50% were identified to the species level. The identified paralarvae included *Doryteuthis* spp. (*D. plei*  $n = 39$  and *D. sanpaulensis*  $n = 75$ ), *L. brevis* ( $n = 6$ ) and *Pickfordiateuthis pulchella* ( $n = 1$ ).

#### 3.1 | Horizontal distribution

In general, loliginid paralarvae occurred between 7 and 100 m isobaths throughout the study area (Figure 2). The most frequent loliginid paralarvae in the samples was *D. plei* (5.5%). Table 2 summarizes the seasonality and spatial distribution of the Loliginidae species and the information about the depth, temperature (SST) and superficial salinity (SSS) where such data were found.

#### 3.2 | *Doryteuthis plei*

In general, *D. plei* paralarvae were primarily found in the study area between 25 and 65 m isobaths (Figure 3). During summer cruises, the horizontal distribution was limited to the southernmost area between São Sebastião Island (24°S) and Cananéia (25°S) (Figure 3a), with the highest abundances around São Sebastião Island being associated with higher SST (24.8–27.8°C, Table 2) and stratified waters formed by CW, SACW and TW. During spring and winter cruises, *D. plei* paralarvae were present (Figures 3b,c) and were associated with the lowest SST (Table 2) and homogenized waters formed by the CW.

#### 3.3 | *Doryteuthis sanpaulensis*

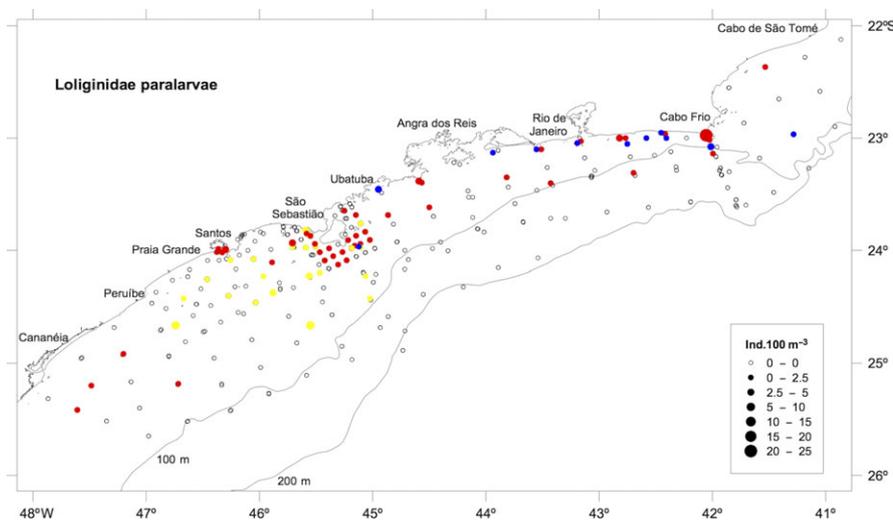
*Doryteuthis sanpaulensis* paralarvae occurred in the northernmost area between Cabo Frio (23°S) and São Sebastião Island (24°S) (Figure 4). During summer cruises, *D. sanpaulensis* was concentrated in Cabo Frio (23°S) (Figure 4) between 40 and 45 m isobaths and was associated with cold SST (14.7–23.8°C, Table 2) and homogenized and thermally

stratified waters formed by SACW and SACW-TW, respectively. The highest abundances (15.8 and 24.7 paralarvae.100 m<sup>-3</sup>) were found in the same stations close to Cabo Frio, where samples were taken at 3-day intervals. In the first collection, a stratified water column with strong intrusions of cold and nutrient-rich waters (Figures 5 and 6) was observed, but in the second collection, a homogenous water column formed by the SACW was detected, most likely due to upwelling. This phenomenon caused a 56% increase in the abundance of *D. sanpaulensis*. During the spring surveys, paralarvae occurred close to São Sebastião Island (24°S) (Figure 4) and were associated with stratified waters formed by the SACW and TW, whereas in the winter surveys, paralarvae were found to be associated with homogenized waters formed by the CW, SACW and TW.

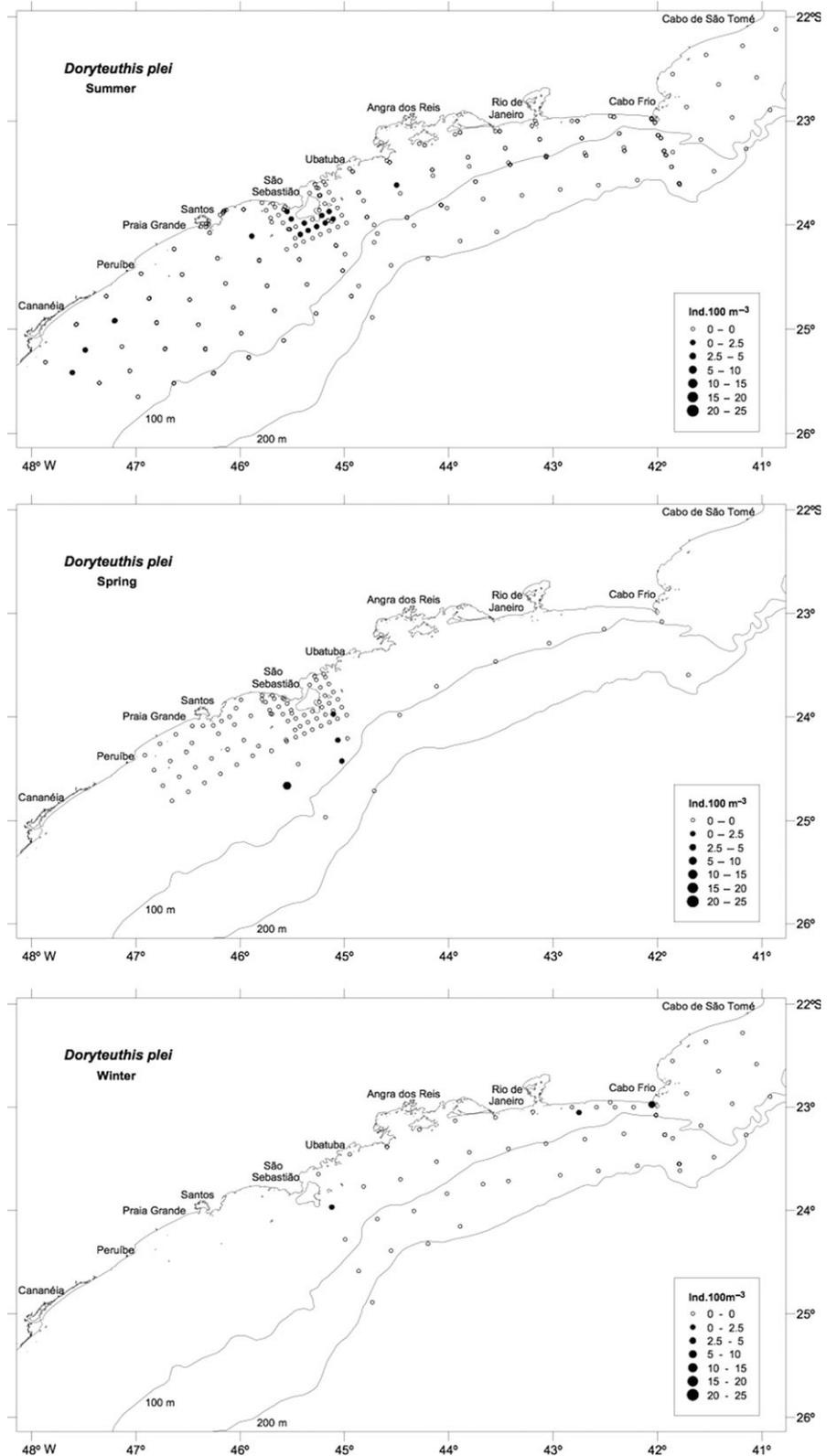
**TABLE 2** Summary of seasonality, spatial distribution, and oceanographic and biological characteristics

Family, species	Area	Depth. (m)	SST (°C)	SSS	N
<i>Loliginidae</i>					
Summer	22.37–25.42	7–113	14.7–28.4	27.3–36.0	178
Spring	23.76–24.66	18–61	19.5–23.0	31.2–35.4	38
Winter	22.95–23.97	14–100	20.2–22.9	33.1–35.9	29
<i>Doryteuthis sanpaulensis</i>					
Summer	22.98–23.10	40–45	14.7–23.8	34.5–35.5	66
Spring	23.98–24.20	53–61	22.4–22.5	35.1–35.3	3
Winter	22.95–23.97	28–60	20.2–22.6	33.1–35.7	6
<i>Doryteuthis plei</i>					
Summer	23.62–25.42	25–65	24.8–27.8	33.2–35.1	23
Spring	23.98–24.66	30–46	20.3–23.0	33.9–35.0	8
Winter	22.98–23.97	25–60	20.2–22.6	33.1–35.9	8
<i>Lolliguncula brevis</i>					
Summer	23.99–24.02	7–13	25.6–25.7	27.3–32.1	5
Spring	24.09	25	20.3	31.2	1

SST (°C), sea surface temperature; SSM, sea surface salinity; N, number of paralarvae.



**FIGURE 2** Horizontal distribution and abundance of Loliginidae paralarvae from 1991 to 2005 between Cabo de São Tomé and Cananéia. Red circles: summer catches, blue circles: winter catches, yellow circles: spring catches and open circles: no catch. [Colour figure can be viewed at wileyonlinelibrary.com]

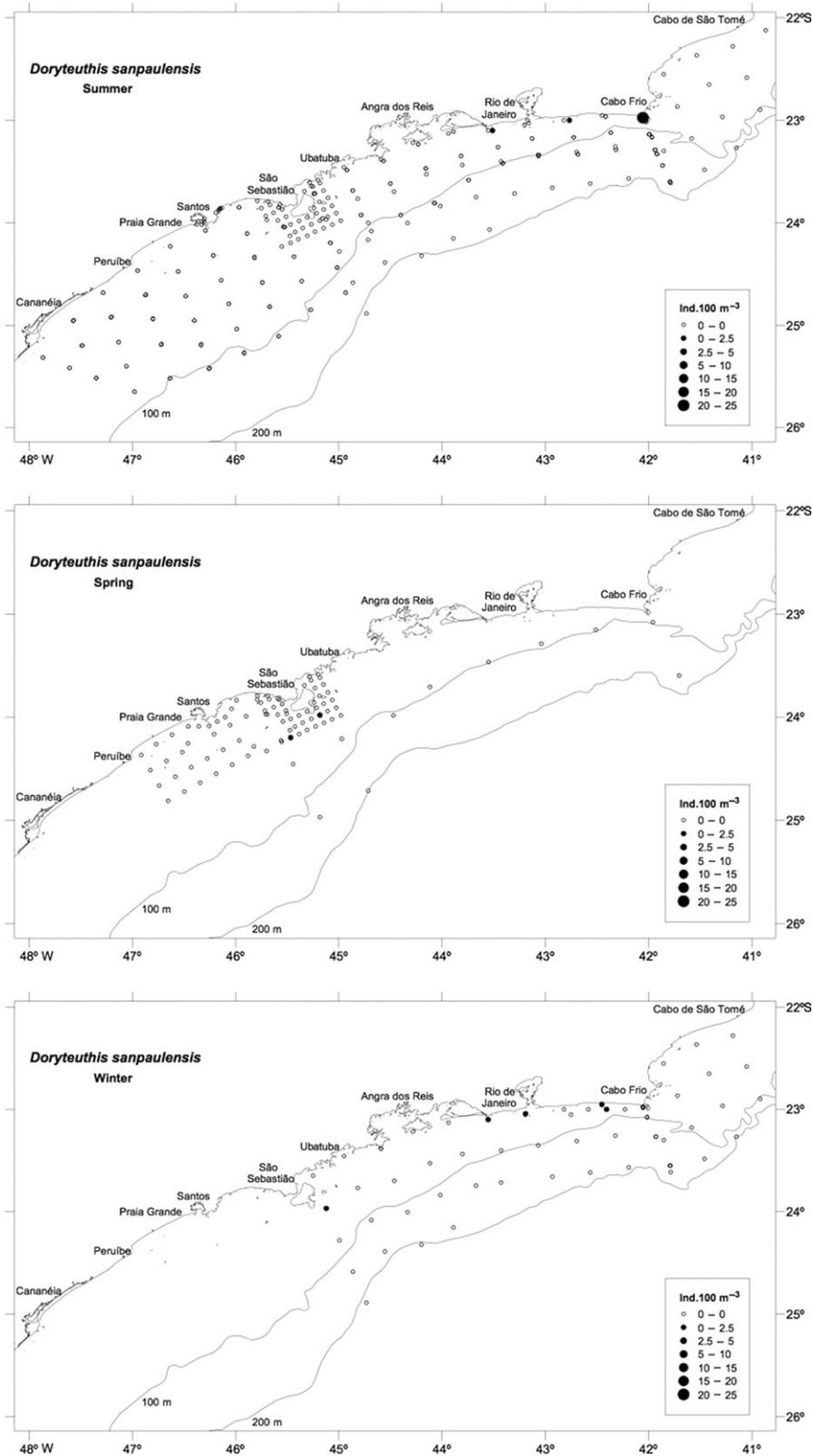


**FIGURE 3** Horizontal distribution and abundance of *Doryteuthis plei* from 1991 to 2005 between Cabo de São Tomé and Cananéia

### 3.4 | *Lolliguncula brevis*

*Lolliguncula brevis* paralarvae were restricted to the estuarine region of Santos (24°S) and found in shallow waters between 7 and 25 m

isobaths (Figure 7). *Lolliguncula brevis* was associated with an SST of approximately 25°C and 20°C during summer and spring, respectively, low salinity waters (27.3–32.1) and a homogeneous water column formed by the CW.



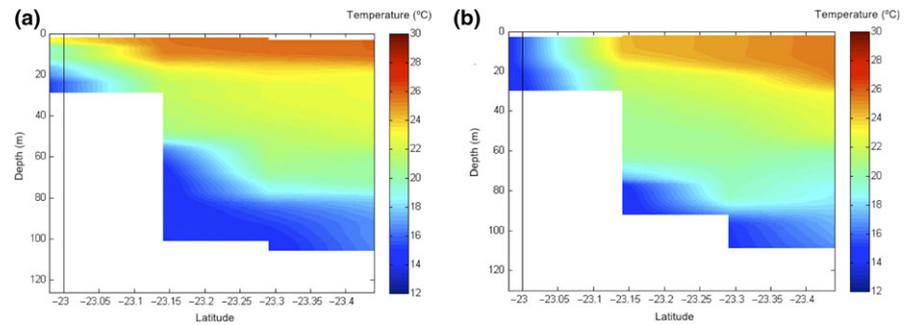
**FIGURE 4** Horizontal distribution and abundance of *Doryteuthis sanpaulensis* from 1991 to 2005 between Cabo de São Tomé and Cananéia

### 3.5 | Vertical distribution

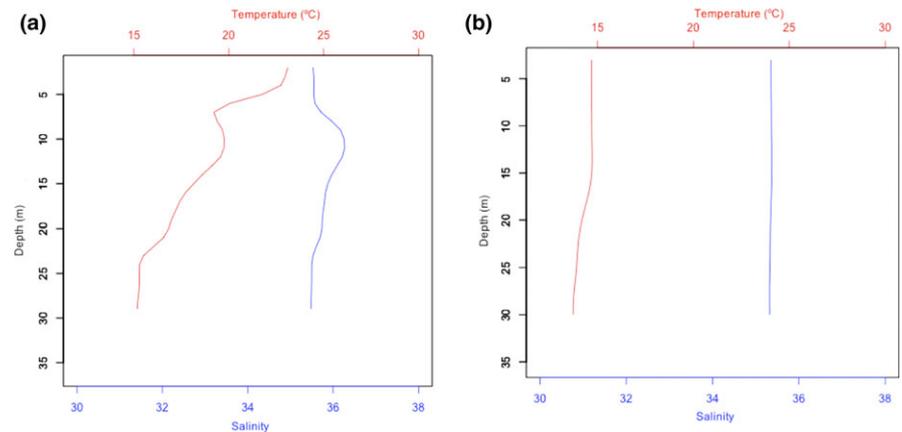
A total of 38 paralarvae were caught in nine of the 145 MPS samples. Samples were collected at depths between 0 and 100 m, but the paralarvae occurred exclusively at depths of less than 40 m

(Figure 8). During summer, the paralarvae were associated with homogenous waters formed by the SACW and below the thermocline in stratified water columns with the presence of TW at the surface and SACW in deeper layers. Moreover, the highest abundance was observed close to the bottom of a coastal station (40 m). During

**FIGURE 5** Vertical distribution of temperature in February 2001 in the Cabo Frio region. The black line across the graph represents the sample area, first sample (a), and second sample (b). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 6** Vertical profile of temperature and salinity in February 2001 in the Cabo Frio region. First sample (a) and second sample (b). [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



spring and winter, it was not possible to identify a consistent vertical distribution pattern, but we could observe the presence of paralarvae at depths <20 m (Figure 8).

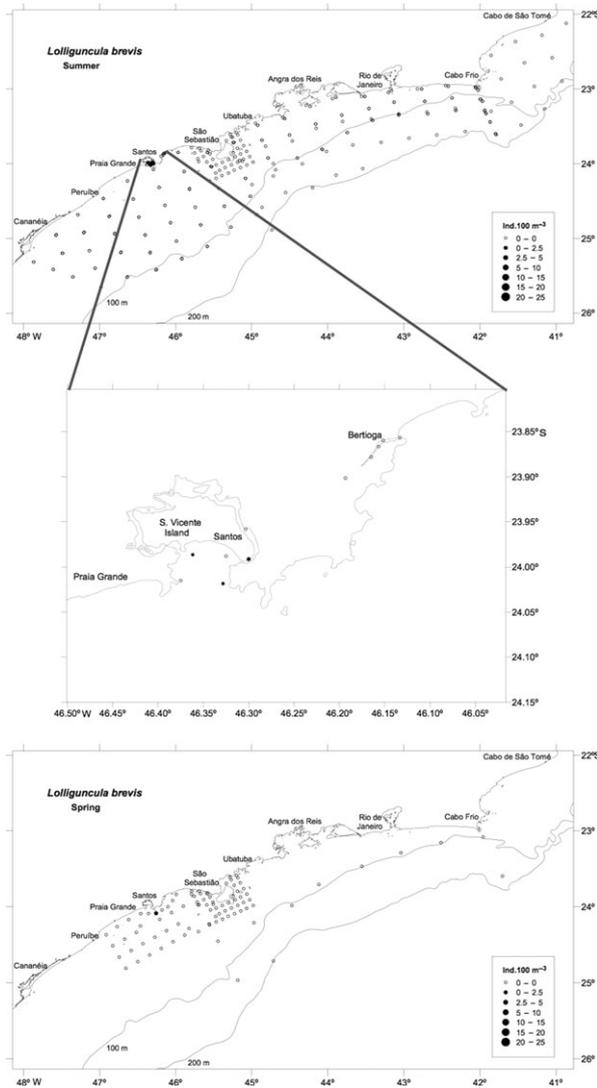
### 3.6 | Dorsal mantle length

The DML of 155 paralarvae were determined, but approximately 90 paralarvae were not measured due to inverted mantles. In general, the DML of paralarvae ranged from 1.1 to 6.3 mm ( $2.6 \pm 0.9$ ,  $n = 155$ ). The DML of paralarvae collected with a Bongo net ranged from 1.1 to 6.3 mm ( $2.5 \pm 1.0$ ,  $n = 127$ ), and that obtained with a MPS ranged from 1.6 to 4.7 mm ( $2.8 \pm 0.8$ ,  $n = 28$ ). The differences between the DML obtained using these two nets ( $U = 1404.5$ ,  $p = .08276$ ) were not significant. Therefore, the measurements obtained from both nets were pooled to verify possible seasonal differences. Nevertheless, no significant seasonal (summer, spring and winter) differences were found ( $\chi^2 = 3.2206$ ,  $gl = 2$ ,  $p = .1998$ ). *Doryteuthis plei* and *D. sanpaulensis* paralarvae showed similar ranges of DML, 1.5 to 4.6 mm ( $2.5 \pm 0.8$ ,  $n = 36$ ) and 1.6 to 4.5 mm ( $2.9 \pm 0.6$ ,  $n = 54$ ), respectively. The paralarvae *L. brevis* were smaller than the *Doryteuthis* species, ranging from 1.3 to 2.2 mm ( $1.7 \pm 0.5$ ,  $n = 4$ ). There was no clear pattern of DML distribution. However, during the summer months, most paralarvae measured between 1.5 and 3.0 mm (Figure 9), but during spring, the paralarvae were at their smallest, mostly ranging from 1.3 to 1.9 mm (Figure 10), and larger during the winter (Figure 11).

### 3.7 | Generalized linear models

The GLM results (Table 3) showed the importance of SST, depth and month in explaining the presence/absence of paralarvae. The best-fitted GLM model indicated that the SST was the most significant explanatory variable according to the AIC criterion (Table 3). The GAM plot from the model (Figure 12a) indicated a positive relationship with the SST from 20°C to 26°C, approximately. It was possible to observe that the presence of paralarvae is associated with shallow waters of approximately 20 m and 60 m (Figure 12b). Moreover, this model reflects the importance of seasonality to the presence of paralarvae. The best-fitted abundance model showed the influence of the SST, month, year and thermal stratification parameter, with the last being the most significant explanatory variable (Table 4). In contrast, the SST was the most important variable in the model ( $F$  and Chi-squared test, Table 3). The model indicates that the highest abundance of paralarvae is correlated with the coldest waters (Figure 13).

The first two RDA canonical axes explained 99.7% of the total variance in the relationship between the species abundance and the environment variables (Table 4). The environmental variables explained 68.5% of the variance, and 62.5% was explained by axis 1. The first axis was explained by depth ( $r = -.83$ ) and SSS ( $r = 0.76$ ), but the second axis explained 37.2% of the variance from SST ( $r = -.55$ ) and latitude ( $r = -.55$ ). The RDA biplot (Figure 14) showed the distribution of three species influenced by different environmental variables. *L. brevis* paralarvae were associated with shallower waters and a lower SSS, contrary to what was observed



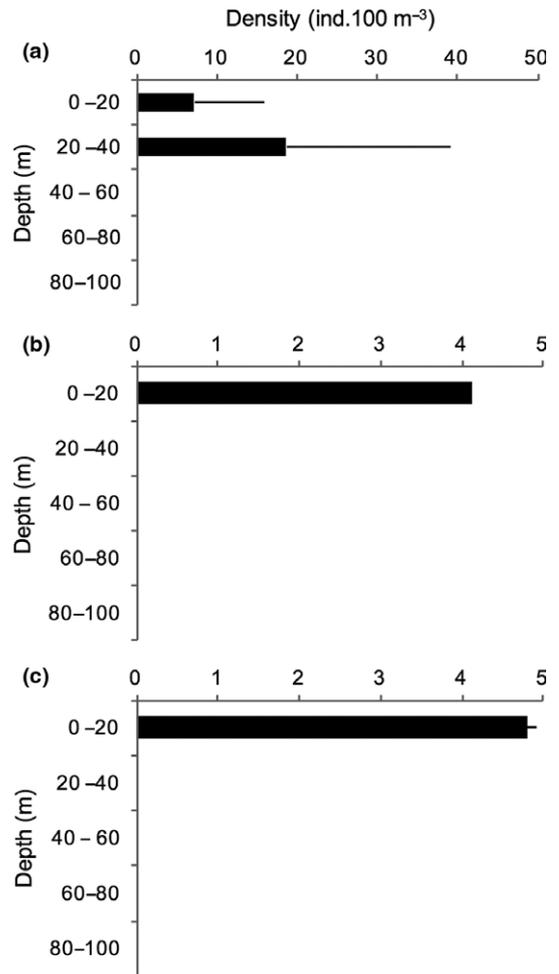
**FIGURE 7** Horizontal distribution and abundance of *Lolliguncula brevis* from 1991 to 2005 between Cabo de São Tomé and Cananéia

for *D. sanpaulensis* and *D. plei*. In relation to the horizontal distribution, *D. sanpaulensis* paralarvae occurred in the northernmost region and was associated with the lowest SST, whereas *D. plei* occurred primarily in the southernmost region and in warmer waters.

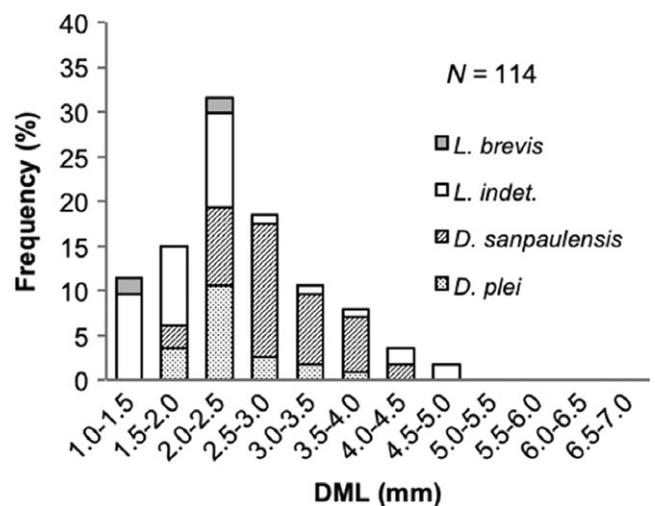
#### 4 | DISCUSSION

The identification of loliginid paralarvae to the species level is based on a chromatophore pattern due to similarity in shape. However, only half of the paralarvae were identified to the species level, most likely because old preserved plankton samples and/or those preserved in formaldehyde fixation exhibited damage to the chromatophore pattern (Nesis, 1999; Moreno et al., 2009).

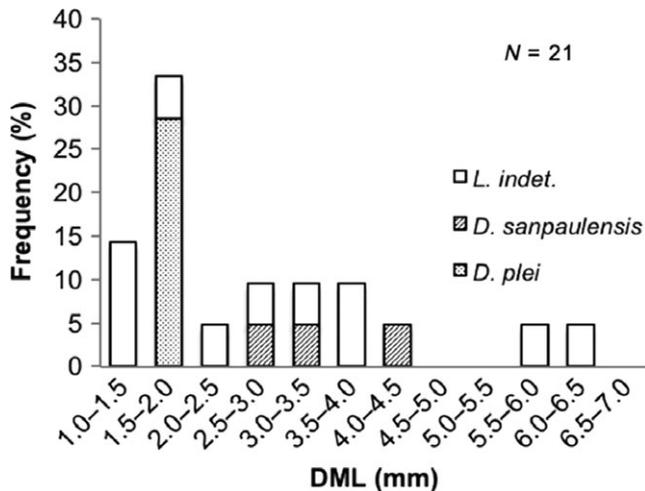
In the present study, it was possible to observe different distribution and abundance patterns of the loliginid paralarvae species. Although paralarvae occurred throughout the study area, they were found especially near the shore, a pattern observed among several



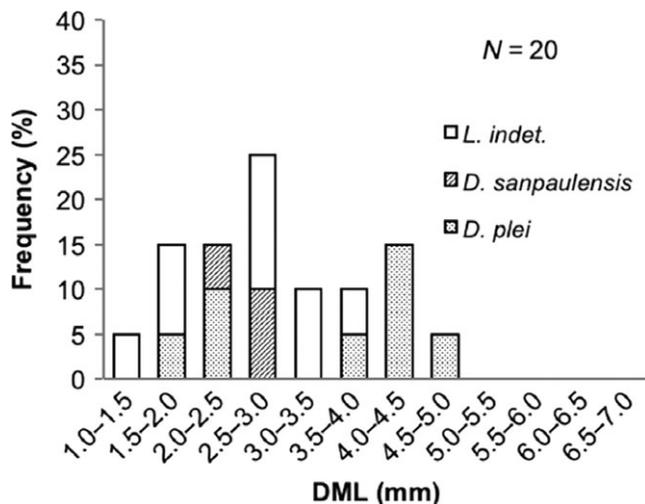
**FIGURE 8** Vertical distribution and abundance of paralarvae during summer (a), winter (b), and spring (c). Bars show the mean abundance (ind. 100 m<sup>-3</sup>), and error bars show the standard deviation



**FIGURE 9** Distribution of dorsal mantle length (mm) of loliginid paralarvae collected using Bongo nets and MPS during the summer periods, from 1991 to 2005, between Cabo de São Tomé and Cananéia



**FIGURE 10** Distribution of dorsal mantle length (mm) of loliginid paralarvae collected using Bongo nets and MPS during the spring periods, from 1997 to 2005, between São Sebastião and Peruíbe



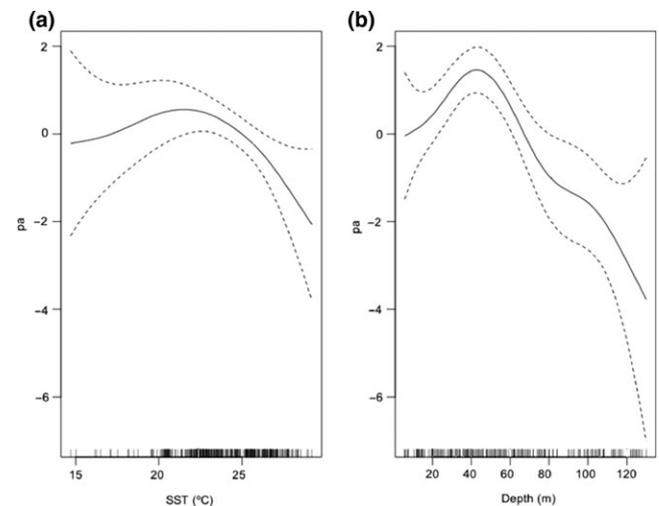
**FIGURE 11** Distribution of dorsal mantle length (mm) of loliginid paralarvae collected using Bongo nets and multi-plankton sampler during the winter periods in 2001 and 2002, between Cabo de São Tomé and São Sebastião

species of Loliginidae (*Doryteuthis pealeii* Vecchione, 1981; *L. brevis* Vecchione, 1991b; *Doryteuthis gahi* Rodhouse, Symon, & Hatfield, 1992; *Doryteuthis opalescens* Zeidberg & Hamner, 2002; *Loligo vulgaris* Piatkowski, 1998; González et al., 2005; Moreno et al., 2009; *D. plei* Martins & Perez, 2006; *Loligo forbesi* Piatkowski, 1998; *D. sanpaulensis* Vidal et al., 2010). Distribution patterns can be related to the distribution of adults because mature individuals move to shallow areas for reproduction and spawning (Rodrigues & Gasalla, 2008), when they are usually the target of fisheries (Postuma & Gasalla, 2010, 2014). According to Lipiński (1998), the concentration of mature cephalopods determines the distribution and abundance of paralarvae. Loliginid paralarvae in coastal waters are rare even where there are aggregations of reproduction and spawning (Collins, Yau, Boyle, Friese, & Piatkowski, 2002; Hatfield & Rodhouse, 1994; Sauer, 1995), suggesting some inefficiency in the

**TABLE 3** Summary of the best-fit GML models

Variable	AIC	LRT	$p(\text{Chi})$
Presence/absence			
Model: $pa \sim \text{SST} + \text{depth} + \text{month}$			
SST ( $df = 1$ )	362.07	6.09	.01
Depth ( $df = 1$ )	377.05	21.07	.00
Month ( $df = 7$ )	377.43	33.44	.02
Variable	AIC	F	$p(\text{Chi})$
Abundance			
Model: $\text{abundance} \sim \text{SST} + \text{tsp} + \text{month} + \text{year}$			
SST ( $df = 1$ )	327.68	266.12	$1.55e^{-03}$
tsp ( $df = 1$ )	311.16	69.72	$9.82e^{-03}$
Month ( $df = 1$ )	315.24	118.24	$9.00e^{-04}$
Year ( $df = 1$ )	313.65	99.31	$2.23e^{-03}$

AIC, akaike information criterion; F, statistic test; LRT, likelihood-ratio test;  $p(\text{Chi})$ , probability of Chi-squared test.



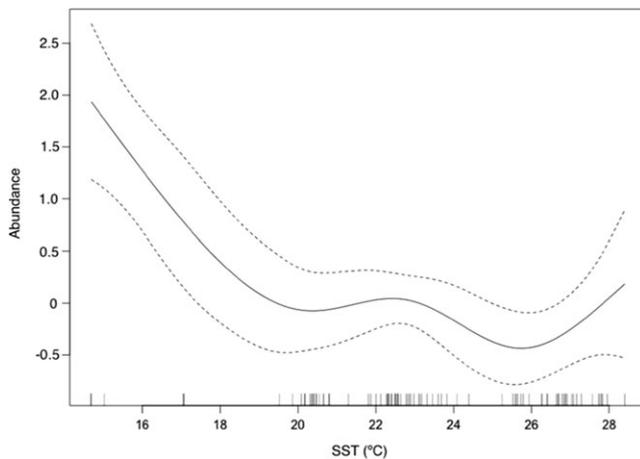
**FIGURE 12** Smoothing curve obtained using the GAM model fit to the SST (a), depth (b) and presence/absence of Loliginidae paralarvae from 1991 to 2005 in the region between Cabo de São Tomé and Cananéia

collection method, such as the length or mouth size of the net (Camarillo-Coop, Salinas-Zavala, Manzano-Sarabia, & Aragón-Noriega, 2011), speed and haul methods. A speed greater than 3.5 knots would probably decrease the net avoidance, and tows that are directed along the seabed might be more effective than the regular double oblique hauls, which is used on most ichthyoplankton cruises, as observed by Piatkowski (1998). Saito (1994) verified the efficiency of oblique tows, regardless of the net aperture size to catch *Ommastrephes bartamii* paralarvae, which may explain the low paralarvae occurrence in samples that were obtained using MPS nets and collected using horizontal tows. Some authors have highlighted the efficiency of different net types, such as using the surface manta net to collect ommastrephid paralarvae (Vecchione, 1999) and the epibenthic sled net to catch loliginid and sepiolid paralarvae (Bouali, Moreno, & Robin, 2009). Based on these findings and the scarcity of paralarvae among the samples in the present study, the efficiency of

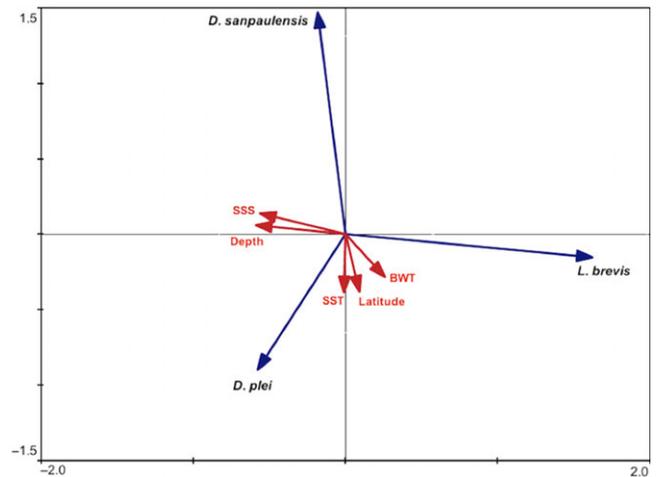
**TABLE 4** Results of the redundancy analysis (RDA) applied to paralarvae abundance and environmental variables

Variable	Correlations axis			
	1	2	3	4
Latitude	0.1291	-0.5505	0.0492	0.0000
Depth	-0.8289	0.0868	0.0451	0.0000
SST	-0.0138	-0.5548	-0.2111	0.0000
BWT	0.3641	0.4102	0.0918	0.0000
SSS	-0.7621	0.2014	0.1075	0.0000
Eigen values	0.428	0.255	0.002	0.226
Cumulative % variance of species data	42.8	68.3	65.5	91.0
Cumulative % variance of species -environmental relationship	62.5	99.7	100	0

SST (°C), sea surface temperature; SSS, sea surface salinity; BWT, bottom water temperature.

**FIGURE 13** Smoothing curve obtained using the GAM model fit to the SST and abundance of Loliginidae paralarvae from 1991 to 2005 in the region between Cabo de São Tomé and Cananéia

cephalopod paralarvae sampling might be strongly related to the species, specific swimming behavior and sampling method because the cruises were performed to collect larval fish, as observed by Piatkowski (1998), who examined 2,700 samples of 140 zooplankton and ichthyoplankton collections from historical plankton studies and found only 142 loliginid paralarvae. Due to the low occurrence in the MPS samples, it was not possible to identify a consistent vertical distribution pattern; however, previous studies showed a vertical distribution of loliginid paralarvae between the surface layers and a depth of approximately 70 m (Moreno et al., 2009; Roura et al., 2016; Vidal et al., 2010), which agreed with our observations. The year round occurrence of loliginid paralarvae can be associated with the reproductive strategy of increasing recruitment success, as suggested by O'Dor (1998). *Doryteuthis sanpaulensis* and *D. plei* spawn continuously but do so more intensely during the late spring and summer months, when remarkable intrusions of cold and nutrient-rich waters occur in the SACW (Andrighetto & Haimovici, 1996; Costa &

**FIGURE 14** Redundancy analysis (RDA) ordination diagram (biplot species-environmental). BWT, bottom water temperature; SSS, sea surface salinity; SST, sea surface temperature. [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Fernandes, 1993a,b; Perez, Aguiar, & Oliveira, 2002; Rodrigues & Gasalla, 2008). This reproductive pattern may expose the seasonal broods to different environmental conditions throughout the year, thus enhancing the chances of survival and the consequent recruitment (O'Dor, 1998). However, the seasonal hydrographic variation may affect paralarval survival (Martins, Camargo, & Gasalla, 2014). During winter and autumn, for example, the SACW retracts toward the shelf break, which decreases productivity and destratifies the water column (Emilsson, 1961; Matsuura, 1986). Moreover, larval transport models (Lagrangian particle-tracking Individual-Based Model) showed significant losses to the ocean and the shore during winter (Martins, Camargo, & Gasalla, 2014).

The greatest abundance of *D. plei* paralarvae around São Sebastião Island (SSI) during the summer months may be linked to spawning aggregations near shore, as reported by Postuma & Gasalla (2014), when the mature squid population becomes vulnerable to artisanal fishery. These aggregations were observed in shallow waters (5 to 20 m isobaths) in the north/northeast and south/southeast during the summer months, with peaks between February and March, and were associated with the warm SST (Postuma & Gasalla, 2014). During summer in the SSI, a strong vertical thermal stratification is observed that is caused by the intrusion of the SACW, which is responsible for local enrichment and stability in the water column (Castro et al., 2008). Furthermore, Katsuragawa, Dias, & Lopes (2008) observed a concentration of larval fish in the southeast, where the current system moving from southwest to southeast (Castro et al., 2008) and the presence of the island (Furtado, Barcellos, Conti, Rodrigues, & Mahiques, 2008) promote retention and concentration. Moreover, during the summer, egg capsules of *D. plei* were found on the muddy bottom at a depth of 20 m, close to the coast in the SSI region (Gasalla, Migotto, & Martins, 2011), which suggests that the region could be a potential spawning and nursery ground.

In the Cabo Frio region, upwelling occurs due to a set of mechanisms, such as coastal divergence (Ekman transport), topographic

effects, coastline orientation, the cyclonic meandering of the Brazil Current, and wind stress curl in all seasons but is stronger during spring/summer and weaker during autumn/winter (Campos, Velhote, & Silveira, 2000; Castelao & Barth, 2006; Castro & Miranda, 1998; Cerda & Castro, 2014; Rodrigues & Lorenzetti, 2001). These mechanisms increase the local productivity caused by intermittent intrusions of the nutrient-rich SACW. In the present study, it was possible to detect the influence of upwelling on the abundance of *D. sanpaulensis*, as evidenced by an increase of 56% after a recent upwelling event. The influence of upwelling on the distribution of *D. sanpaulensis* was previously observed in southern Brazil (Vidal et al., 2010), where the highest abundance occurred in coastal and mid-shelf waters with the presence of SACW. According to Rocha, Guerra, Prego, & Piatkowski (1999) and González et al. (2005), the presence/absence of upwelling is important to define the abundance and spatial distribution of *L. vulgaris* and *Octopus vulgaris* in Galician waters. Even so, lower temperatures decrease the growth rate and extend the period of the early stages (McInnis & Broenkow, 1978). Barón (2003) verified that the normal embryonic development of *D. sanpaulensis*, in northern Patagonia, is between 12°C and 23°C, which agrees with the results found in the present study. Additionally, *D. sanpaulensis* paralarvae occurred in a similar depth range to that where Costa & Fernandes (1993a,b) and Rodrigues & Gasalla (2008) found mature adults in the Cabo Frio region. Thus, based on the results in the present study, it is possible to infer that the Cabo Frio region can be an important area for collecting *D. sanpaulensis*.

The SBB, particularly in the ISS and Cabo Frio regions, seems to present three key processes (enrichment, concentration and retention) that combine to offer a favorable habitat for recruitment success. Moreover, the retention and concentration mechanisms may be important to confine the paralarvae in suitable areas and prevent offshore losses to adjacent waters, thus improving the survival rate and collection success. According to Martins et al. (2014), the circulation pattern on the SBB promotes the retention mechanisms on the shelf that are responsible for exposing the paralarvae to suitable conditions for survival, primarily during the summer, when the enrichment process occurs, thus favoring paralarval survival and, consequently, the success of collection.

Salinity and depth distinguished the distribution patterns of the *Lolliguncula* and *Doryteuthis* genera. The first occurred in areas associated with shallow and low salinity waters in the bay and coastal region near Santos, similar to that reported by Vecchione (1991a,b) in the coastal and estuarine waters of Louisiana. According to Vecchione (1991), *L. brevis* paralarvae do not seem to be as euryhaline as the adults, and this observation was verified in the present study. Although *L. brevis* paralarvae occurred in lower salinity waters (27.3–32.1) than did *Doryteuthis* spp. paralarvae (33.1–35.9), they were associated with higher salinity waters compared to the range where the adults were found (Perez & Zaleski, 2013). Latitude and SST were found to be the environmental features that were most important to differentiate the distribution pattern of the *D. sanpaulensis* and *D. plei*, which agrees with the distribution of known spawners in the study area (Coelho, Muto, Marian, & Soares, 2010; Costa &

Fernandes, 1993a,b; Juanicó, 1979; Postuma & Gasalla, 2010; Rodrigues & Gasalla, 2008).

The findings obtained provide new information on the loliginid early-life stages in the SBB area that will be potentially useful in the investigation of recruitment patterns. Overall, loliginid paralarvae species present different distribution patterns similar to those observed in the adult population strata, which coincide with the already known spawner distribution in the study area. Although spawning occurs throughout the SBB all year, the reproductive strategies seem to be linked to seasonal enrichment processes, such as intrusions of cold and nutrient-rich waters and coastal upwelling, that are responsible for enhancing local productivity, which favors survival, growth and recruitment of early-life stages.

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