



# Biodiversity of cephalopod early-life stages across the Southeastern Brazilian Bight: spatio-temporal patterns in taxonomic richness

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## Abstract

The diversity patterns of cephalopod early-life stages on the continental shelf of Southeastern Brazilian Bight (SBB, 22–25°S) were investigated using a historical plankton archive of 22 oceanographic cruises carried out from 1974 to 2010. From 874 plankton samples, 438 were positive for cephalopod paralarvae ( $n = 2116$ ), which were identified to the lowest taxonomic level possible, totaling 15 taxa belonging to 11 families. Richness and diversity indexes (Shannon-Wiener, Simpson, Pielou's evenness) revealed a cross-shelf gradient, independent of season and latitude. Abundance  $k$ -dominance curves were consistent with this depth-related trend, resulting in high values of  $k$ -dominance for the inner shelf during both summer and winter. Two major assemblages were identified by cluster analyses: an inner shelf and a mid-outer shelf. During summer, the inner shelf assemblage was composed of neritic Loliginidae Lesueur, 1821 and epipelagic Argonautidae Tryon, 1879, while in winter, benthic Octopodidae Orbigny, 1840 replaced Argonautidae in importance. These data reveal a remarkable difference in Argonautidae and Octopodidae paralarvae abundance, suggesting a seasonal reproductive pattern for these cephalopods in the SBB. Mesopelagic Enoploteuthidae Pfeffer, 1900 and Ommastrephidae Steenstrup, 1857 characterized the mid-outer shelf assemblages both in summer and winter. Although based on a higher taxonomic level, the distribution of cephalopod paralarva families reflected not only oceanographic patterns of the SBB but also their adaptations and reproductive strategies. In particular, the cross-shelf gradient in cephalopod biodiversity reflects a more dynamic oceanographic conditions in inner shelf compared with mid-outer shelf ecosystems.

**Keywords** Diversity · Paralarvae · Continental shelf · Squid · Octopus

## Introduction

Cephalopods are key components of marine food webs both as predator and prey (Santos and Haimovici 1998,

2002; Piatkowski et al. 2001; Boyle and Rodhouse 2005; Staudinger 2006; Gasalla et al. 2010; Rodhouse et al. 2014; Arkhipkin et al. 2015). They also represent important fishery resources worldwide (Jereb and Roper 2010), with the oceanic ommastrephid, neritic loliginid squids, and octopodids being the most commercially exploited cephalopods (Jereb and Roper 2010; Arkhipkin et al. 2015). Cephalopods are semelparous with a short life cycle (1–2 years) and plasticity in their life histories, responding rapidly to changes in environmental conditions (Boyle 1990; Boyle and Boletzky 1996; Pecl et al. 2004; Boyle and Rodhouse 2005; Pecl and Jackson 2008; Postuma and Gasalla 2010, 2014). Spatial and temporal fluctuations in abundance, distribution range, and diversity can therefore provide important clues about ecosystem alterations. Most investigations have been focused on cephalopod population dynamics relative to local and regional oceanographic process (e.g., González et al. 1997; Dawe et al. 2000; Anderson and Rodhouse 2001; Waluda

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et al. 2001). Although essential to assessment of stocks and management, cephalopod diversity patterns are relatively less studied.

While quite diverse in morphology, development, and behavior (Postuma and Gasalla 2015; Vecchione et al. 2017), the number of living cephalopod species is considered relatively low, with fewer than 1000 species described thus far (Jereb and Roper 2010). Interestingly, recent studies have been suggesting a hump-shaped distribution for cephalopod diversity in worldwide continental margins. Shelf-break areas are consistently associated with the maximum in cephalopod diversity, coinciding with optimal habitat conditions (e.g., higher environmental energy availability and productivity of subsurface and shallow waters, < 200 m) that promote high diversification rates (Rosa et al. 2008a, b; Keller et al. 2016). Other factors may influence patterns in cephalopod diversity such as the closely associated primary and secondary productivity cycles and low seasonal amplitude of these cycles observed in oligotrophic and warm oceanic areas, e.g., Mediterranean Sea (Rosa et al. 2008a; Keller et al. 2016).

On the Southern Brazilian shelf (22–34°S), the taxonomic composition of cephalopods is relatively well known; data is available from museum collection archives, trawl fishing prospects and fishery records and analysis of stomach contents (Palacio 1977; Costa and Haimovici 1990, Haimovici and Perez 1991; Costa and Fernandes 1993a; Haimovici et al. 1994; Haimovici 1998; Santos and Haimovici 2001, 2002; Vaske Jr and Pereira da Costa 2011). The Southern Brazilian shelf is dominated by loliginid squids (*Doryteuthis* spp. Naef, 1912) and benthic octopodids (*Octopus* spp. Cuvier, 1797 and *Eledone* spp. Leach, 1817) (Juanicó 1979; Haimovici and Andrigueto-Filho 1986; Haimovici et al. 1989; Haimovici and Perez 1991; Gasalla et al. 2005a, b; Perez et al. 2005; Martins and Perez 2008). The continental slope and adjacent waters are dominated by oceanic squids in the families Ommastrephidae (*Illex argentinus* Castellanos, 1960) and Enoploteuthidae (*Abralia* spp. Gray, 1849) (Haimovici et al. 1995; Santos and Haimovici 1998). In Brazil, the most exploited cephalopod species in fisheries are *D. plei* Blainville, 1823, *D. sanpaulensis* Brakoniecki, 1984, *O. vulgaris* Cuvier, 1797, and *I. argentinus* (e.g., Costa and Haimovici 1990; Haimovici and Andrigueto 1986; Gasalla et al. 2005a; Perez et al. 2005).

All commercially important cephalopods have a planktonic early-life stage, called “paralarva” (Young and Harman 1988). The cephalopod paralarvae are rare in plankton samples due to both patchy distribution and inappropriate sampling methods (González et al. 2005; Haimovici et al. 2002). Given the scarcity of cephalopod paralarvae in plankton samples, it is not surprising that the majority of studies about cephalopod diversity involve adults rather than paralarvae. Interestingly, cephalopod diversity patterns have been linked to seasonality of oceanographic conditions in the Gulf of California (De Silva-

Dávila et al. 2015). The distribution of cephalopod paralarvae in the Southeastern Brazilian Bight (SBB) also appears to be associated with regional mesoscale variability, as described by the few studies performed in the area (Santos and Haimovici 2007; Vidal et al. 2010; Araújo and Gasalla 2018).

The present study was designed to examine patterns in the distribution and diversity of cephalopod paralarvae in continental shelf waters collected from 1974 to 2010 and to relate these trends to oceanographic processes of the SBB.

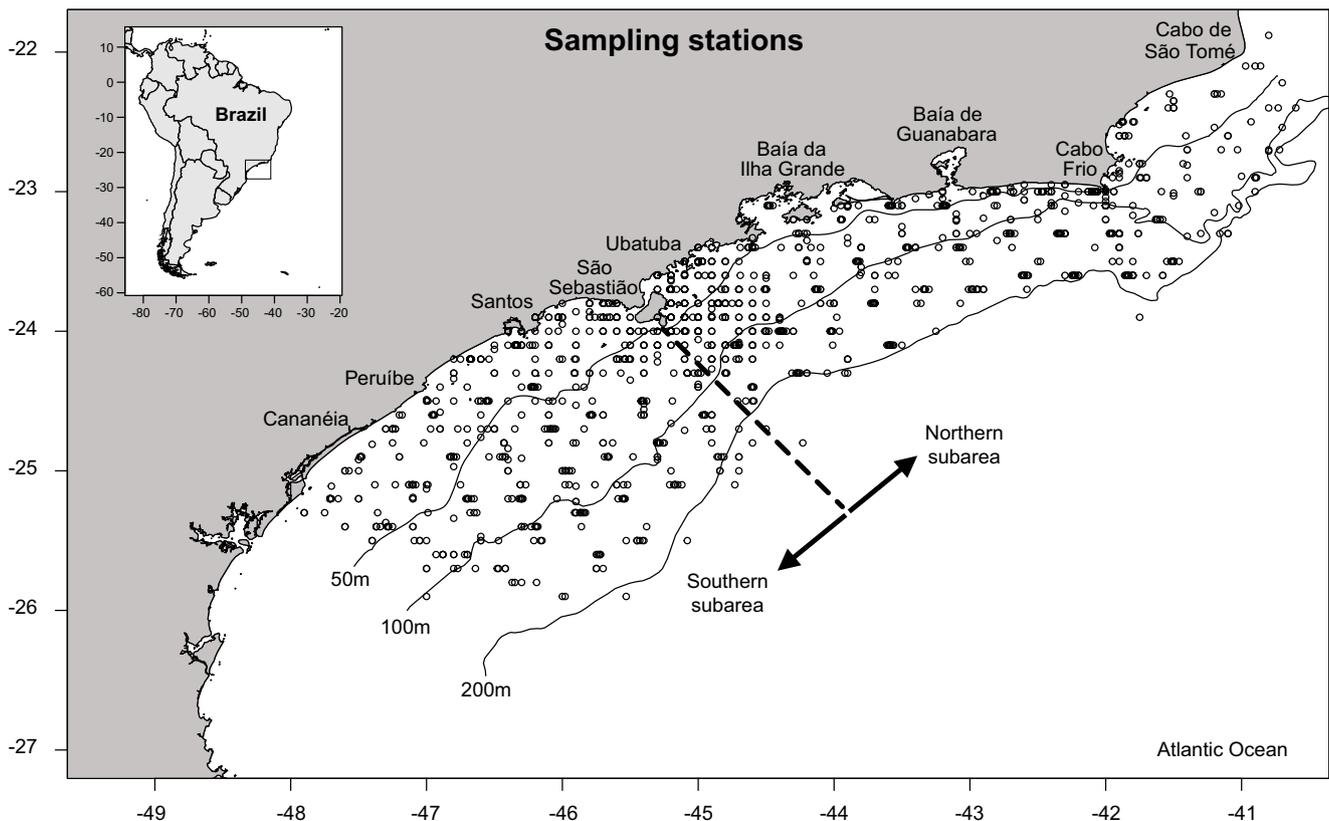
## Material and methods

### Study area

The study area comprises the continental shelf of the northernmost SBB between Cabo Frio (23°S) and Cananéia (25°S) (Fig. 1). The SBB is influenced by mesoscale circulation of the Brazil Current (BC). The region is characterized by three water masses: the salty and oligotrophic Tropical Water (TW) in the upper mixing layer (200 m) of the BC, the cold and nutrient-rich South Atlantic Central Water (SACW) flowing below TW as the thermocline portion of the BC, and the Coastal Water (CW), low-salinity water resulting from the mixing of fresh water from small-sized to medium-sized estuaries along the SBB with the TW and SACW (Campos et al. 1996, 2000; Castro and Miranda 1998; Silveira et al. 2000). While the BC flows southward along the continental slope, there is a strong north-to-south variability in oceanographic conditions in the SBB (Castro and Miranda 1998). The regional features driving meridional gradients in oceanographic conditions are an abrupt change in the coastline direction at Cabo Frio (from NE–SW to E–W) and continental shelf extension 50 km off Cabo Frio and 230 km off Santos (Fig. 1) (Castro and Miranda 1998; Mahiques et al. 2004). These meridional gradients are associated with mesoscale features typical of the BC (e.g., SACW upwelling and subsurface intrusions, coastal waters excursions onto oceanic areas, meanders, and eddies) that are considered critical for larval dispersion and/or retention in the SBB (Matsuura 1996; Franco et al. 2006; Yoshinaga et al. 2010; Martins et al. 2014).

### Sampling

A total of 874 plankton samples were collected during 22 cruises from 1974 to 2010 (Table 1), covering the majority of the shelf (up to 200 m) along the SBB between Cabo de São Tomé (22°S) and Cananéia (25°S) (Fig. 1). Plankton samples were obtained on-board several research vessels, “Prof. W. Besnard”, “Atlântico Sul,” and “Albacora”, using bongo nets (0.6 m mouth diameter; 333 and 505- $\mu$ m mesh size) towed obliquely surface-bottom-surface at  $\sim$ 2 knots



**Fig. 1** Area with the sampling sites between Cabo de São Tomé and Cananéia surveyed from 1974 to 2010. The study area was further subdivided in two northern and southern subareas according to Katsuragawa et al. (2014)

(Smith and Richardson 1977). The maximum sampling depth was 10 m off bottom. Calibrated flowmeters were placed at each net mouth aperture to estimate the filtered water volume. All samples were fixed in 4% borax-buffered formaldehyde in seawater and preserved in the Biological Collection “Prof. E. F. Nonato” (ColBIO) at the Instituto Oceanográfico, Universidade de São Paulo, Brazil.

### Laboratory analysis

Cephalopod paralarvae were separated from the plankton samples and identified to the lowest taxonomic level possible (according to Table 2) based on Sweeney et al. (1992), Vecchione et al. (2001), and Zaragoza et al. (2015). Data analyses were constrained to family level, the lowest taxonomic level to which the majority of specimens could be identified.

### Data analysis

Cephalopod paralarvae abundance was standardized using the number of individuals per 100 m<sup>3</sup> of filtered water. According to previous studies (Mahiques et al. 2004; Miranda and Katsuragawa 1991), the study area was divided in two subareas as proposed by Katsuragawa et al.

(2014): north (from Cabo de São Tomé to São Sebastião Island) and south (from São Sebastião Island to Cananéia). These subareas were further subdivided into three bathymetric zones: inner shelf (< 50 m depth), middle shelf (50–100 m depth), and outer shelf (> 100 m depth). Thus, paralarva taxonomic composition was evaluated using samples classified according to subareas and bathymetric zones.

Diversity was assessed by richness (S), Shannon-Wiener (H'), Simpson (D), and Pielou's evenness (J') indexes using the vegan (Oksanen et al. 2010) and biodiversityR packages (Kindt and Coe 2005) in R software (R Development Core Team 2015).

Agglomerative hierarchical two-way cluster analyses were conducted to identify spatial presence-absence patterns of cephalopod paralarvae. For these analyses, the Sorensen distance measurement and a UPMGA clustering (unweighted pair group method with arithmetic mean) were applied using PC-ORD software 5.0 (MjM Software Design).

One-way analysis of similarity (ANOSIM) was used to test whether cephalopod paralarva composition differed significantly between assemblages defined a priori. The similarity percentage routine (SIMPER) was applied to the data to identify species contributing to formation

**Table 1** Plankton sampling summary encompassing oceanographic 22 cruises performed in the northern sector of the Southeastern Brazilian Bight (SBB) between 1974 and 2010

Cruise	Area	Date	Depth range (m)	Vessel	Type net	Mesh size ( $\mu\text{m}$ )	Haul type	No. of samples
ICTIO-1	Cabo Frio (RJ) to Cananéia (SP)	Nov Dec/1974	19 248	R/V Prof. W. Besnard	Bongo	300	Oblique	87
FINEP-1	Cabo Frio (RJ) to Cananéia (SP)	Nov Dec/1975	15 194	R/V Prof. W. Besnard	Bongo	300	Oblique	74
FINEP-5	Cabo Frio (RJ) to Cananéia (SP)	Dec/1976	18 183	R/V Prof. W. Besnard	Bongo	300	Oblique	65
PI-1	Ubatuba (SP)	Dec/1985	11 122	R/V Prof. W. Besnard	Bongo	300	Oblique	24
PI-2	Ubatuba (SP)	Jul/1986	13 122	R/V Prof. W. Besnard	Bongo	300	Oblique	28
PI-4	Ubatuba (SP)	Jul/1987	12 96	R/V Prof. W. Besnard	Bongo	300	Oblique	30
PI-5	Ubatuba (SP)	Dec/1987	12 133	R/V Prof. W. Besnard	Bongo	300	Oblique	9
PI-6	Ubatuba (SP)	Jul/1988	10 136	R/V Prof. W. Besnard	Bongo	300	Oblique	24
PI-7	Ubatuba (SP)	Dec/1988	42 136	R/V Prof. W. Besnard	Bongo	300	Oblique	5
SARDINHA-1	Cabo Frio (RJ) to Cananéia (SP)	Dec/1991	20 140	R/V Prof. W. Besnard	Bongo	300	Oblique	71
SARDINHA-2	Cabo Frio (RJ) to Cananéia (SP)	Jan/1993	16 134	R/V Prof. W. Besnard	Bongo	300	Oblique	71
OPISS-1	São Sebastião (SP)	Feb/1994	12 74	R/V Prof. W. Besnard	Bongo	300	Oblique	43
OPISS-2	São Sebastião (SP)	Oct/1977	12 76	R/V Prof. W. Besnard	Bongo	300	Oblique	43
PADCT-1	Cabo Frio (RJ) to Cananéia (SP)	Nov/1997	72 162	R/V Prof. W. Besnard	Bongo	300	Oblique	11
DEPROAS-1	Cabo Frio (RJ)	Feb/2001	36 161	R/V Prof. W. Besnard	Bongo	300	Oblique	16
DEPROAS-2	Cabo Frio (RJ)	Jul/2001	37 155	R/V Prof. W. Besnard	Bongo	300	Oblique	19
DEPROAS-3	Cabo de São Tomé (RJ) to São Sebastião (SP)	Jan/2002	14 197	R/V Prof. W. Besnard	Bongo	300	Oblique	49
DEPROAS-4	Cabo de São Tomé (RJ) to São Sebastião (SP)	Aug/2002	14 200	R/V Prof. W. Besnard	Bongo	300	Oblique	47
ECOSAN-3	Santos (SP)	Jan/2005	6 13	R/V Prof. W. Besnard	Bongo	300	Oblique	11
ECOSAN-H1	São Sebastião (SP) to Peruíbe (SP)	Sep/2005	14 60	R/V Albocara	Bongo	300	Oblique	36
ECOSAR-IV	Cabo de São Tomé (RJ) to Cananéia (SP)	Jan Feb/2008	21 112	R/V Atlântico Sul	Bongo	505	Oblique	27
ECOSAR-V	Cabo Frio (RJ) to Cananéia (SP)	Nov/2008	21 110	R/V Atlântico Sul	Bongo	505	Oblique	44
ECOSAR-VII	Cabo Frio (RJ) to Cananéia (SP)	Jan/2010	20 111	R/V Atlântico Sul	Bongo	505	Oblique	40

of each assemblage. Family abundances were  $\log(x + 1)$  transformed prior to analysis and similarity matrices were based on Bray-Curtis distance measurements. Abundance  $k$ -dominance curves were used to display

graphically cumulative abundance as a function of family rank in different assemblages. Analyses of similarity and  $k$ -dominance curves were performed using PRIMER-6 software.

**Table 2** Taxonomic list of cephalopod paralarvae collected with bongo net in the northern sector of the SBB between 1974 and 2010 during summer, winter, and spring

## Class Cephalopoda

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Subclass Coleoidea Bather, 1888
Superorder Decabrachia Boettger, 1952
Order Sepiida Zittel, 1895
Family Sepiolidae Leach, 1817
<i>Heteroteuthis</i> sp. (Rüppell, 1844)
Order Myopsida Orbigny, 1841
Family Loliginidae Lesueur, 1821
<i>Doryteuthis plei</i> (Blainville, 1823)
<i>Doryteuthis sanpaulensis</i> (Brakoniecki, 1984)
<i>Lolliguncula brevis</i> (Blainville, 1823)
<i>Pickfordiateuthis pulchella</i> Voss, 1953
Order Oegopsida Orbigny, 1845
Family Ancistrocheiridae Pfeffer, 1912
<i>Ancistrocheirus lesueurii</i> (Orbigny, 1842)
Family Cranchiidae Prosch, 1847
Family Enoploteuthidae Pfeffer, 1900
<i>Abralia</i> spp. Gray, 1849
<i>Abraliopsis</i> spp. Joubin, 1896
Family Lycoteuthidae Pfeffer, 1908
Family Octopoteuthidae Berry, 1912
<i>Octopoteuthis</i> sp. Rüppell, 1844
Family Ommastrephidae Steenstrup, 1857
<i>Illex</i> spp. Steenstrup, 1880
<i>Ommastrephes bartramii</i> (Lesueur, 1821)
<i>Sthenoteuthis pteropus</i> (Steenstrup, 1855)
Family Pyroteuthidae Pfeffer, 1912
Superorder Octobrachia Fioroni, 1981
Order Octopodida Leach, 1818
Suborder Incirrita Grimpe, 1916
Family Argonautidae Tryon, 1879
<i>Argonauta</i> spp. Linnaeus, 1758
Family Octopodidae Orbigny, 1840
<i>Octopus</i> spp. Cuvier, 1797
<i>Octopus defilippi</i> Verany, 1851

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## Results

### Taxonomic composition

A total of 2116 cephalopod paralarvae were found in 438 plankton samples. Paralarvae were from 15 taxa belonging to 11 families (Table 2). Argonautidae was the most abundant family, while Enoploteuthidae Pfeffer, 1900 and Loliginidae were the most frequent (Table 3).

The values for richness (S) and diversity indices ( $H'$  and  $1/D$ ) were highest towards the outer shelf in winter and

summer in both subareas, while values for equitability ( $J'$ ) were highest in winter and in both middle and outer shelves (Fig. 2).

### Abundance and distribution

Figure 3 displays mean abundance of paralarva families according to season (summer, winter, and spring), latitude (north and south), and bathymetric zones (inner, middle, and outer shelves). Paralarva distribution showed high diversity in families associated with middle and outer shelves, independent of season or latitude. We note that there were no research cruises in the southern subarea during winter.

The inner shelf assemblage was dominated by paralarvae of the neritic families Loliginidae, represented mainly by *Doryteuthis plei* and *Doryteuthis sanpaulensis* (data not shown), and Octopodidae Orbigny, 1840. These two families occurred nearly in all seasons and in both northern and southern subareas. Interestingly, the epi-mesopelagic families Argonautidae, Enoploteuthidae, and Ommastrephidae Steenstrup, 1857 also occurred in the inner shelf, but their distribution was mostly constrained to the northern subarea during summer. In winter, apart from Loliginidae and Octopodidae, Enoploteuthidae and Sepiolidae Leach, 1817 also occurred in the inner shelf of the northern subarea.

In contrast to the inner shelf, assemblages from middle and outer shelves were similar in terms of diversity (Fig. 2). The middle shelf was dominated by epipelagic Argonautidae, especially during summer. Enoploteuthidae, Ommastrephidae, Octopodidae, and Ancistrocheiridae Pfeffer, 1912 were frequent in middle and outer shelves, both during summer and winter. The mesopelagic families Cranchiidae Prosch, 1847; Octopoteuthidae Berry, 1912; Pyroteuthidae Pfeffer, 1912; and Sepiolidae were restricted to middle and outer shelves and the northern subarea.

Given the low number of paralarvae collected during spring surveys compared with other seasons (Table 2; Fig. 3), statistical analyses were exclusively performed for winter and summer (see below).

### Assemblages

A two-way cluster analysis applied to presence-absence of paralarvae was performed with the most frequent families during summer in both northern and southern subareas and during winter in northern subarea (Figs. 4, 5, and 6). In the northern subarea during summer, there was a clustering of middle and outer shelves as a single group characterized by the presence of Ommastrephidae and Enoploteuthidae, together with Argonautidae occurring mainly in the middle shelf (Fig. 4). The inner shelf is distinguished from middle and outer shelves due to the presence of Loliginidae and Octopodidae (Fig. 4). A similar pattern of presence-absence

**Table 3** Taxonomic composition, number of individuals ( $n$ ), frequency of occurrence (FO%) and depth range of cephalopod paralarvae collected with bongo net in the northern sector of the SBB between 1974 and 2010 during summer, winter and spring

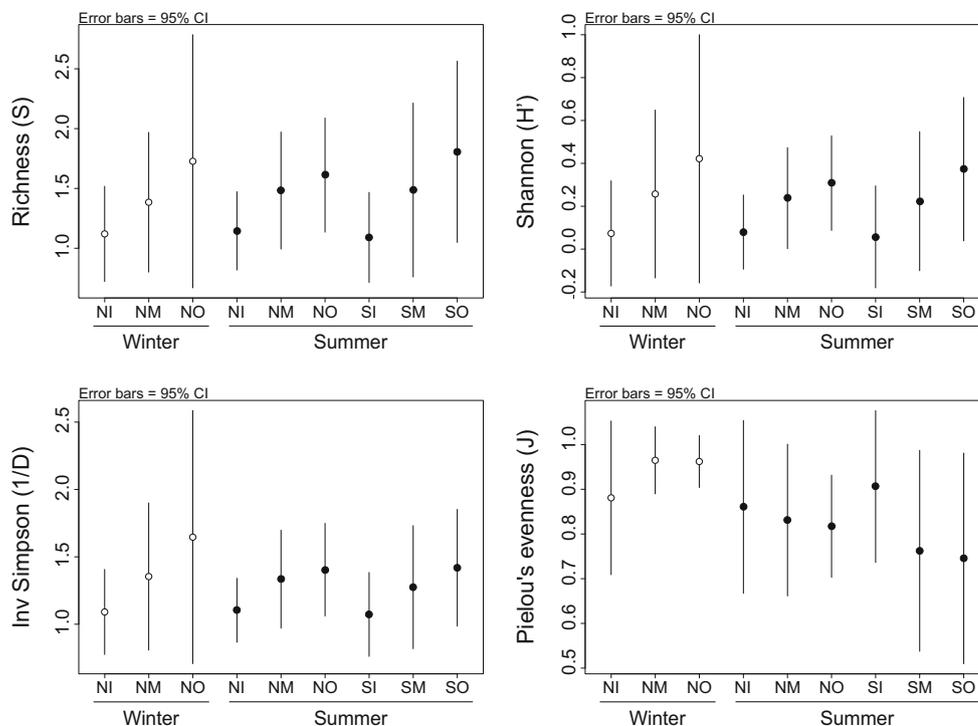
Taxonomy (family)	Summer			Winter			Spring		
	$n$	FO (%)	Depth range (m)	$n$	FO (%)	Depth range (m)	$n$	FO (%)	Depth range (m)
Superorder Decabrachia									
Undetermined	2	0.3	43–148	1	0.7	57	–	–	–
Ancistrocheiridae	21	2.2	60–197	7	4.1	72–155	–	–	–
Cranchiidae	4	0.3	43–120	2	0.7	130	–	–	–
Enoploteuthidae	493	22.3	32–201	35	17.6	38–200	4	2.2	120–162
Loliginidae	229	15.4	7–122	56	22.3	10–84	38	24.4	18–61
Lycoteuthidae	–	–	–	1	0.7	88	–	–	–
Octopoteuthidae	2	0.3	103–200	–	–	–	–	–	–
Ommastrephidae	104	9.6	34–201	28	13.5	52–200	1	1.1	123
Pyroteuthidae	4	0.8	89–201	–	–	–	–	–	–
Sepiolidae	2	0.3	43–120	3	2.0	22–153	–	–	–
Superorder Octobrachia									
Undetermined	5	0.6	37–100	–	–	–	–	–	–
Argonautidae	954	17.0	29–248	3	1.4	60–69	3	2.2	–
Octopodidae	82	9.7	7–201	27	6.8	29–200	5	5.6	21–99
Total	1902				163			51	

was observed in the southern subarea during summer (Fig. 5). Interestingly, a slight change in paralarva distribution was noticed during winter in the northern subarea, especially in the inner shelf (Fig. 6). The cluster of inner shelf samples was characterized by the presence of Loliginidae, while Octopodidae occurred mainly in the middle shelf. Nonetheless, as observed in summer, Ommastrephidae and

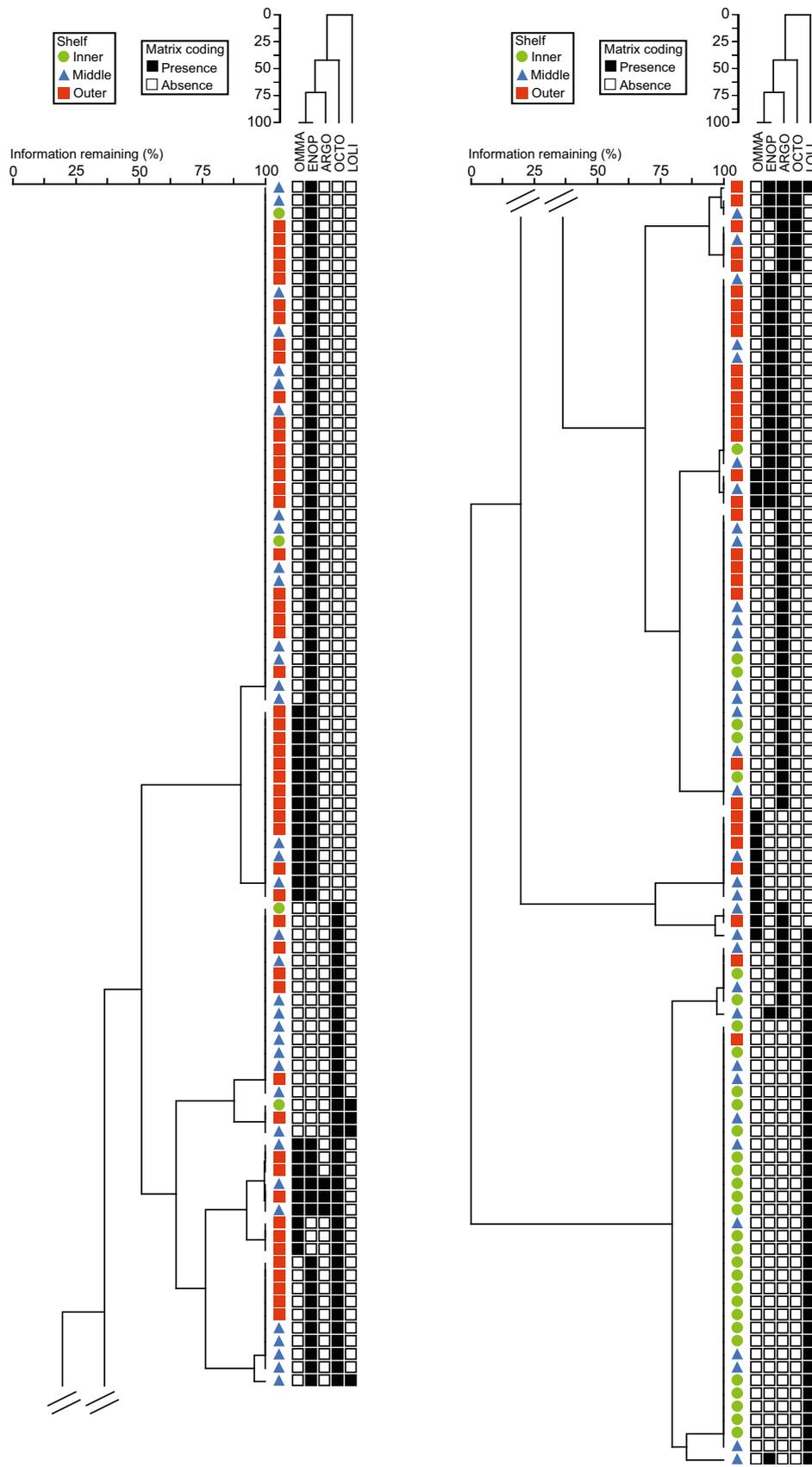
Enoploteuthidae characterized the cluster formed by middle and outer shelves samples.

The analysis of similarity (ANOSIM) showed no difference (Global  $R = 0.02$ ;  $P = 0.18$ ) between northern and southern subareas during summer, suggesting no major effects of latitude on the composition of paralarvae in the SBB. Conversely, pronounced differences were identified by

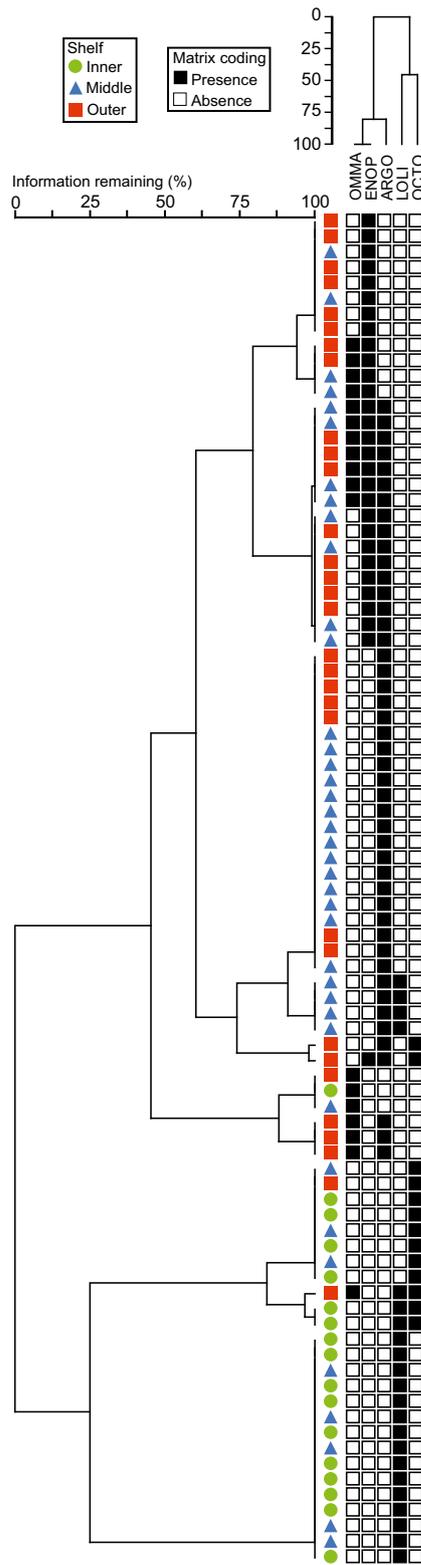
**Fig. 2** Mean and 95% confidence intervals of family-level diversity indexes for each subarea and bathymetric zone. N = northern subarea; S = southern subarea; I = inner shelf; M = middle shelf; O = outer shelf



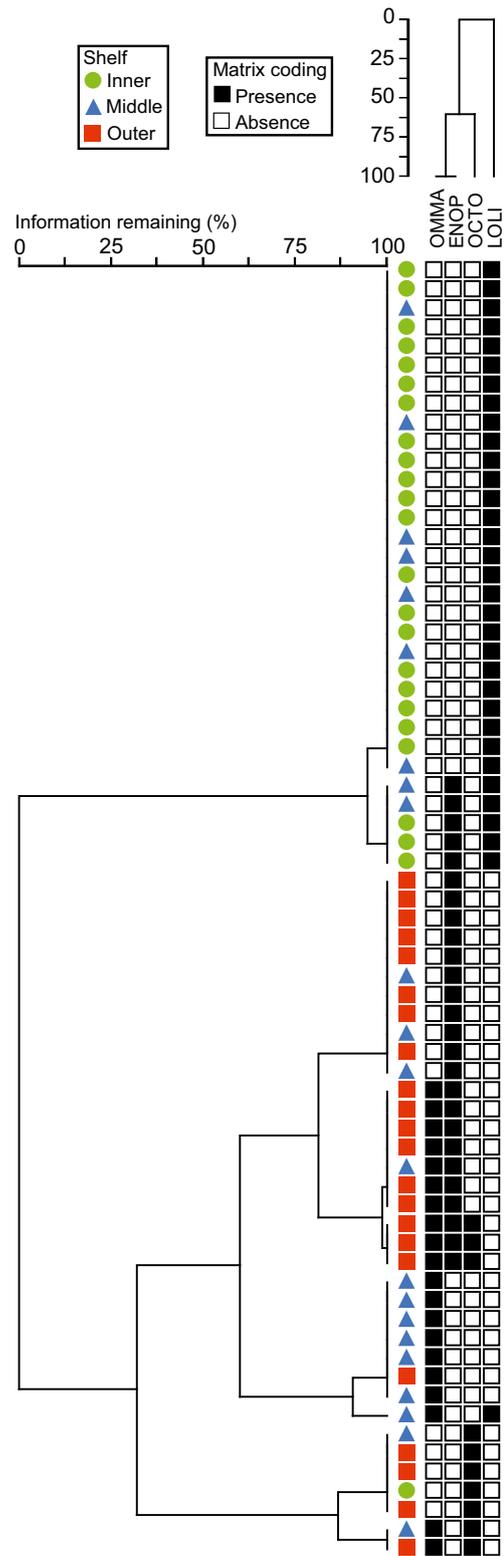




**Fig. 4** Two-way presence-absence cluster of cephalopod paralarvae collected in northern subarea during summer in inner, middle, and outer shelves. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; OCTO = Octopodidae; LOLI = Loliginidae



**Fig. 5** Two-way presence-absence cluster of cephalopod paralarvae collected in southern subarea during summer in inner, middle, and outer shelves. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; LOLI = Loliginidae; OCTO = Octopodidae



**Fig. 6** Two-way presence-absence cluster of cephalopod paralarvae collected during winter in inner, middle, and outer shelves of the northern subarea. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; OCTO = Octopodidae; LOLI = Loliginidae

**Table 4** One-way analyses of similarity (ANOSIM) based on Bray-Curtis distance for cephalopod paralarvae between northern and southern subareas, and bathymetric zones (inner, middle, and outer shelves)

	Summer	Winter
Global effect	$R = 0.18^*$	$R = 0.39^*$
Group comparison		
North $\times$ south	$R = 0.02$	–
Inner $\times$ middle	$R = 0.15^*$	$R = 0.28^*$
Inner $\times$ outer	$R = 0.39^*$	$R = 0.72^*$
Middle $\times$ outer	$R = 0.05^*$	$R = 0.15^*$

\* $p < 0.05$ 

occur in the region (Cerdeira and Castro 2014). Alongshore variations in the vicinity of Cabo Frio include upwelling cells and plumes frequently observed south of Cabo Frio (until Baía de Guanabara), as well as northwards close to Cabo de São Tomé (Fig. 1; Lorenzetti and Gaeta 1996; Carbonel 1998). This mechanism of cross-shelf transport of water masses was defined by Calado et al. (2006) as coastal water excursions onto oceanic areas promoted by meanders of the BC. South of Cabo Frio, in shelf areas of Ubatuba (Fig. 1, (for instance) a strong summer thermocline (20–50 m depth) may develop due to intrusions of SACW below CW, with a retreat of SACW towards the slope during winter (Castro-Filho et al. 1987). This subsurface intrusion of SACW over shelf areas from the northern portion of the study area can also fuel primary production during summer (Aidar et al. 1993; Braga and Müller 1998; Gaeta et al. 1999). In contrast to the northern area of the SBB, oligotrophic conditions prevail in shelf and open waters with a strong depletion of nutrients in the euphotic zone associated with TW (Metzler et al. 1997).

In the present study, the distribution and diversity patterns of paralarvae in the SBB show a predominance of neritic families (Loliginidae and Octopodidae) in the inner shelf, but epipelagic and mesopelagic families (Argonautidae, Enoploteuthidae, and Ommastrephidae) in the middle and

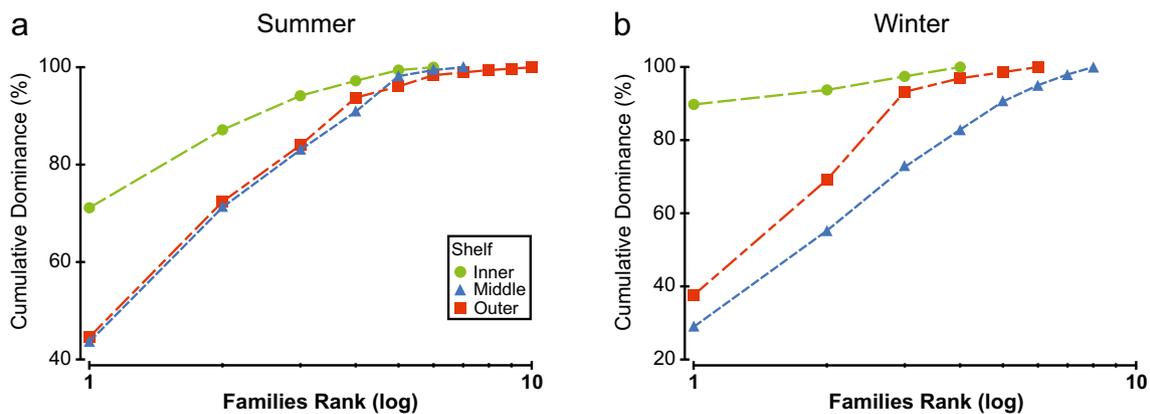
outer shelves. This cephalopod distribution pattern is a common feature found in continental margins worldwide (Clarke 1996). While the oceanographic conditions in northern and southern subareas of the SBB are notably different (see “Material and methods”), our findings did not reveal significant differences in paralarva composition for a latitudinal gradient (Table 4). However, a strong cross-shelf gradient was identified as the driving force for formation of paralarva assemblages during both summer and winter. More specifically, there is an increase in paralarva diversity from the inner towards the middle and outer shelves (Figs. 2 and 7).

Our findings are consistent with diversity of zooplankton and ichthyoplankton species increasing from coastal to oceanic waters in the Brazilian shelf (e.g., Lopes et al. 2006; Brandini et al. 2014; Katsuragawa et al. 2014; Macedo-Soares et al. 2014). The inshore to offshore increase in both zooplankton and fish larva diversity is generally attributed to distinct pelagic food-web structures of the mesotrophic CW and the oligotrophic waters of BC (e.g., Lopes et al. 2006). In addition, several mesoscale features related to BC circulation in the SBB (e.g., coastal upwelling, meanders, and eddies) are thought to contribute to this pattern (Lopes et al. 2006; Katsuragawa et al. 2014). The distribution of cephalopod paralarvae in the SBB also appears to be linked to the regional mesoscale variability as described by some studies (Santos and Haimovici 2007; Vidal et al. 2010; Martins et al. 2014; Araújo and Gasalla 2018). Relative to these previous investigations, here, the focus is to explain cross-shelf variability in paralarva diversity observed for the northern sector of the SBB with extended spatial and temporal sampling coverage (Table 1).

The diversity of adult cephalopods tends to increase from the coast to open waters (e.g., González and Sánchez 2002; Rosa et al. 2008a, b; Silva et al. 2011; Keller et al. 2016), and this pattern could be linked to adaptations required to inhabit the neritic environment. As highlighted by Boyle and Rodhouse (2005), all coastal forms are active, muscular, and strong-swimming, whereas none have the flaccid body and sluggish movements observed in mesopelagic and

**Table 5** Dissimilarities (%) and taxon contribution (%) based on SIMPER analysis for bathymetric zones during summer and winter. Highest values are underlined

	Summer			Winter			
	Inner $\times$ middle	Inner $\times$ outer	Middle $\times$ outer	Inner $\times$ middle	Inner $\times$ outer	Middle $\times$ outer	
Average dissimilarity (%)	84.7	94.5	79.8	Average dissimilarity (%)	76.6	95.7	81.1
Taxon contribution (%)				Taxon contribution (%)			
Loliginidae	<u>38.4</u>	<u>35.4</u>	10.8	Loliginidae	<u>50.2</u>	<u>47.81</u>	17.05
Argonautidae	<u>26.0</u>	17.9	<u>30.4</u>	Ommastrephidae	15.7	13.11	<u>22.56</u>
Enoploteuthidae	18.2	<u>26.4</u>	<u>32.6</u>	Enoploteuthidae	12.5	22.14	<u>28.88</u>
Octopodidae	9.6	8.6	10.7	Ancistrocheiridae	7.0	–	8.01
Ommastrephidae	–	8.0	10.7	Octopodidae	5.1	11.53	14.28



**Fig. 7** Abundance  $k$ -dominance curves of bathymetric zones (inner, middle, and outer shelves). **a** Summer; **b** Winter

bathypelagic forms. Moreover, a tough corneal covering the eyes, as observed in incirrats, cuttlefish, and loliginid squid, reflects an evolutionary adaptation to protect the eyes from suspended sediments from coastal regions. Compared with adult cephalopods, less is known about cross-shelf gradients of paralarva diversity. According to our data, the high abundance of Loliginidae, Octopodidae, and Argonautidae in the inner shelf contributes to lower diversity of paralarvae relative to middle and outer shelves of the SBB.

It is rather surprising that the effects of both latitudinal and seasonal gradients of the study area were negligible compared with the cross-shelf gradient in paralarva diversity. As mentioned in the description of the study area, the BC circulation in the narrow shelf of the northern subarea is highly dynamic with frequent coastal upwelling, meanders, and eddies, while the wider southern subarea is relatively less influenced by these mesoscale features. The latitudinal gradient in the study area plays a major role not only in primary productivity of shelf waters (Metzler et al. 1997; Brandini et al. 2014) but also in zooplankton and larval distribution over the SBB (Matsuura 1996; Lopes et al. 2006; Katsuragawa et al. 2014; Namiki et al. 2017). Similarly, seasonal amplitudes in biological production from shelf areas of the SBB are linked to seasonal mesoscale variability of the BC (Castro and Miranda 1998; Cerda and Castro 2014), with higher productivity and biomass markedly associated with summer (Matsuura 1996; Sumida et al. 2005). Nonetheless, the distribution of paralarvae found by the present study seems to agree with an increase in diversity of adult cephalopods from coastal to open waters as observed worldwide (Rosa et al. 2008a, b; Keller et al. 2016). Apart from coastal adaptation of cephalopods (Boyle and Rodhouse 2005), other factors may contribute to the low diversity of paralarvae observed in inner shelf compared with open shelf waters of the SBB. These factors may include a combination of physical and behavior processes occurring in inner shelf areas such as annual variability in winter cold front intensity (Stech and Lorenzetti 1992), upwelling and subsurface intrusion of SACW (Castro and

Miranda 1998; Cerda and Castro 2014), and reproductive strategies.

Despite the strong cross-shelf gradient in diversity pattern, our findings also revealed conspicuous features of paralarva distribution in the SBB. For instance, there is no clear seasonal pattern of distribution for Loliginidae and Enoploteuthidae, two of the most important families contributing to assemblage's formation in inner and middle/outer shelves, respectively. While Loliginidae are known to spawn throughout the year with peaks associated with summer in the SBB (Costa and Fernandes 1993b; Perez et al. 2002; Rodrigues and Gasalla 2008; Coelho et al. 2010; Postuma and Gasalla 2014), no regional information is available for Enoploteuthidae. Most octopods found by our study belong to the genera *Octopus* (data not shown), which are known to reproduce year-round worldwide (Otero et al. 2007; Moreno et al. 2009). For instance, in the Iberian Peninsula, the distribution of *Octopus* is more tightly connected to the upwelling dynamics than their spawning period (Moreno et al. 2009; Roura et al. 2016). Similarly, no clear seasonal pattern was observed for octopod paralarvae in the present study. These paralarvae appeared more frequently in inner shelf during summer, however, and in middle shelf areas during winter. This distribution pattern agrees well with the seasonal intrusions of SACW over the SBB. That is, SACW displacement towards the coast under prevalent NE winds of summer may favor the retention of octopod paralarvae in neritic zones. SACW returns to the shelf break during winter, coinciding with the occurrence of Octopodidae paralarvae in middle shelf.

The occurrence of epipelagic and mesopelagic paralarvae, such as Argonautidae, Enoploteuthidae, and Ommastrephidae in the inner shelf (notably during summer and mainly in the northern subarea), suggests their link to frontal processes of BC. In this respect, mechanisms that promote the intrusion and/or retention of paralarvae in inner shelf areas are highlighted as follows: meanders of BC, upwelling and subsurface intrusions of SACW, and southward coastal cold-water plumes advected from Cabo Frio (e.g., Castro-Filho et al. 1987; Lorenzetti and Gaeta 1996; Cerda and Castro

2014). The presence of mesopelagic ommastrephid paralarvae in the shelf might be associated with their habit of spawning gelatinous egg masses at the pycnocline in offshore waters, returning to the shelf along with frontal processes and/or rising to surface waters where hatchlings grow and feed (Sakurai et al. 2000). A reproductive strategy similar to the Ommastrephidae is believed to be adopted by the Enoploteuthidae (Laptikhovskiy 1999). Information about life cycle and distribution of Argonautidae is scarce in the SBB. In the southern sector of the SBB, Argonautidae paralarva densities were associated with middle shelf waters (ca. 70 m) coinciding with a subsurface chlorophyll maximum that corresponded to the boundaries between TW and SACW (Vidal et al. 2010). Our data revealed a remarkable difference in argonaut paralarva abundance between summer and winter, suggesting a seasonal reproductive pattern for these cephalopods in the SBB.

## Conclusion

Although based on a higher taxonomic level, remarkable patterns in distribution of paralarvae provided important information about diversity of cephalopods in the SBB. The paralarva families Loliginidae, Octopodidae, Argonautidae, Enoploteuthidae, and Ommastrephidae contributed significantly to define cephalopod assemblages in the study area. Our findings were that diversity of cephalopods did not reflect oceanographic conditions such as latitudinal gradients that chiefly influence the biological productivity of the SBB. However, some families such as Argonautidae and Octopodidae displayed a marked seasonal pattern in distribution. In this study, increased paralarva diversity towards the open ocean suggests a more dynamic inner shelf relative to middle and outer shelves. Given the ecological importance and relevance for fisheries, further studies are required to understand the nature of paralarvae assemblages in the SBB.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements, if applicable.

**Data availability** The datasets generated during the current study are available from the corresponding author on reasonable request.

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