



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

Carolina C. Araújo^{1,2} · Maria A. Gasalla^{1,2}

Received: 15 October 2018 / Revised: 20 May 2019 / Accepted: 5 June 2019
© Senckenberg Gesellschaft für Naturforschung 2019

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

Communicated by M. Vecchione

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s12526-019-00980-w>) contains supplementary material, which is available to authorized users.

✉ Carolina C. Araújo
carolinaaraujo86@usp.br

Maria A. Gasalla
mgasalla@usp.br

¹ Graduate Program in Oceanography, Oceanographic Institute, University of São Paulo, São Paulo, Brazil

² Fisheries Ecosystems Laboratory, Oceanographic Institute, University of São Paulo, São Paulo, Brazil

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 Eupoloteuthidae (*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- μ m mesh size) towed obliquely surface-bottom-surface at \sim 2 knots

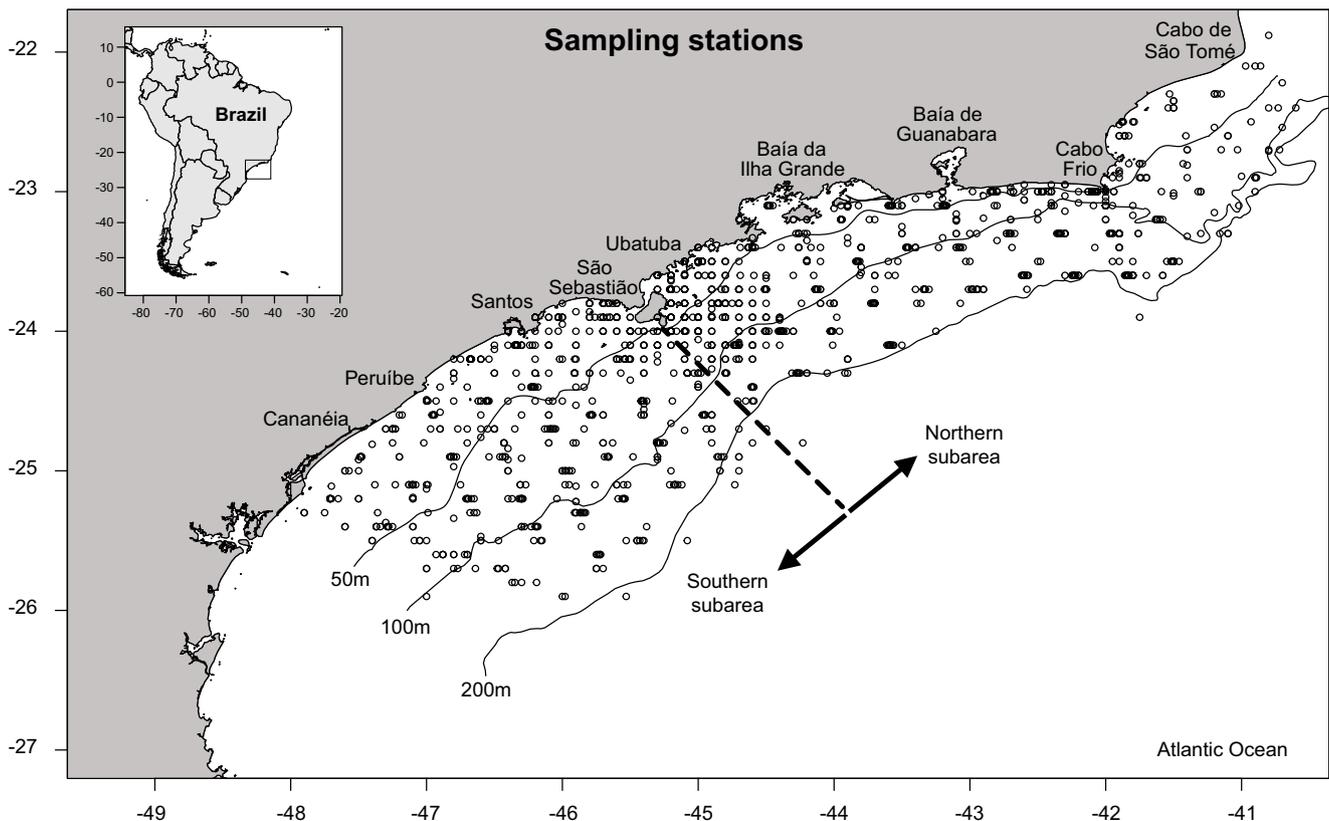


Fig. 1 Area with the sampling sites between Cabo de São Tomé and Cananéia surveyed from 1974 to 2010. The study area was further subdivided in two northern and southern subareas according to Katsuragawa et al. (2014)

(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 m³ 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 (μm)	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

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

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

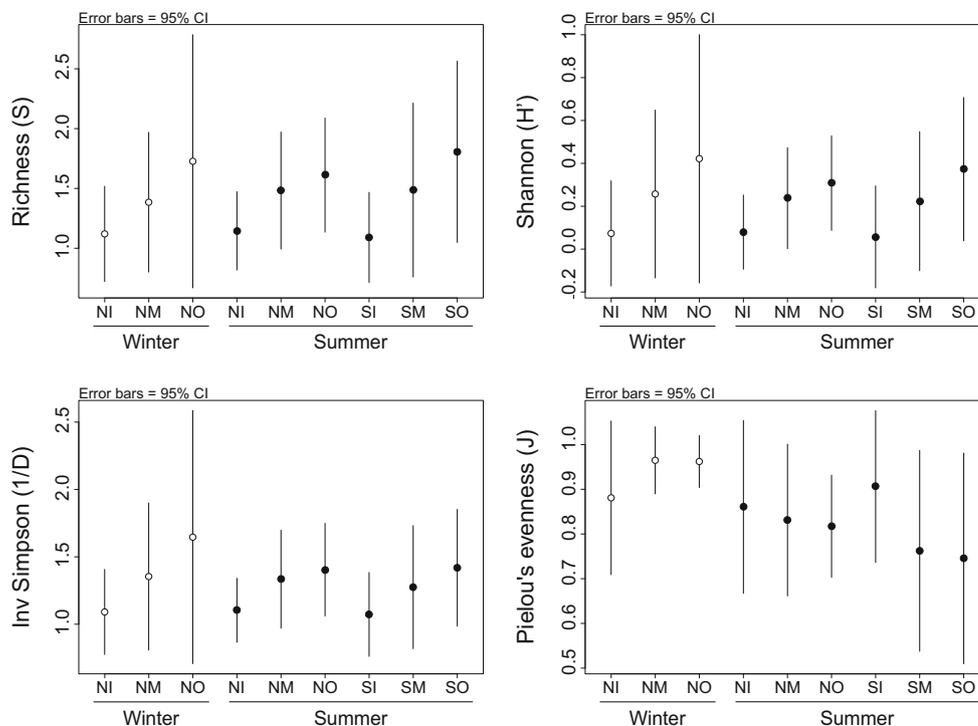
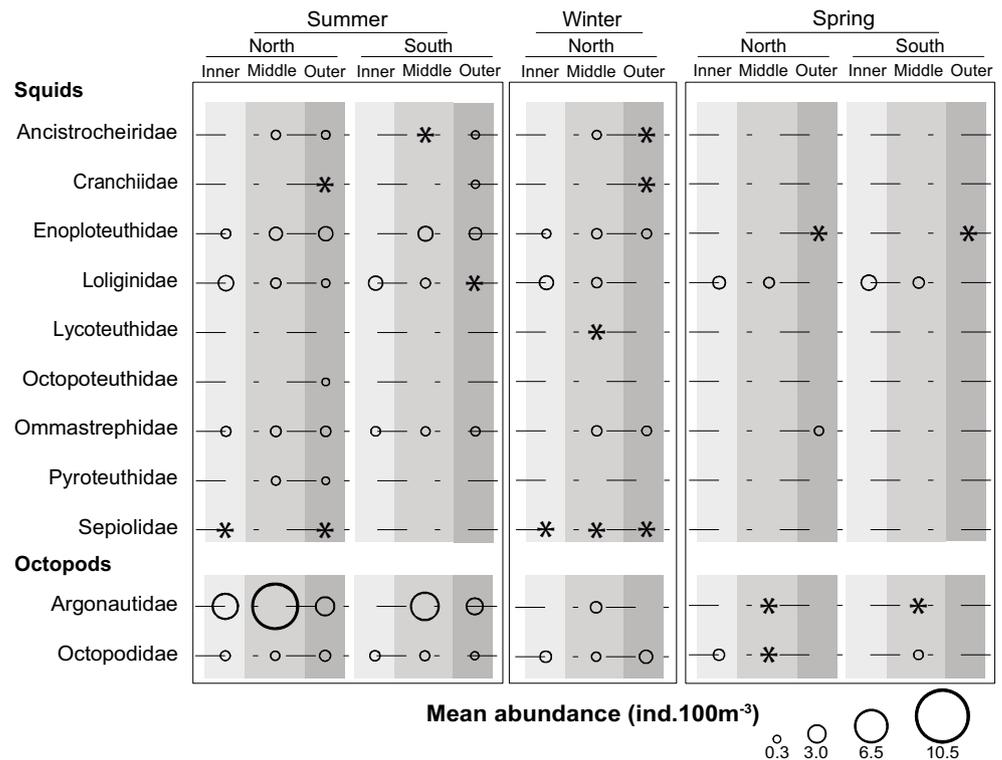


Fig. 3 Mean abundance of cephalopod paralarvae in the northern sector of the SBB between 1974 and 2010 during summer, winter, and spring. The star symbols (*) represent just one occurrence and horizontal dashed lines were used to facilitate data visualization of family abundance throughout the sampling periods



ANOSIM analysis between bathymetric zones during both summer and winter. These distinctions were mainly related to differences between inner shelf and both middle and outer shelves (Table 4). In general, the Global R values were lower in summer than in winter and highest between inner and outer shelves.

Guided by the results from ANOSIM, a SIMPER analysis was performed to identify taxon contribution to dissimilarity between bathymetric zones (Table 5). This analysis revealed Loliginidae as the main contributor to dissimilarity observed for the inner shelf versus both middle and outer shelves during summer (35–38%) and winter (48–50%). During summer, Enoploteuthidae and Argonautidae (each accounting for ca. 30%) contributed to the dissimilarity between middle and outer shelves. During winter, however, Enoploteuthidae and Ommastrephidae accounted together for > 50% of the average dissimilarity between the middle and outer shelves (Table 5).

Abundance k -dominance curves are displayed in Fig. 7 for both summer and winter, indicating a trend of higher diversity of families in middle and outer shelves relative to the inner shelf. During summer, Loliginidae and Argonautidae together contributed almost 90% of total abundance in the inner shelf (Fig. 7a). In contrast, Loliginidae alone contributed ca. 90% of total abundance in the inner shelf during winter, which is reflected in the curve's shape (Fig. 7b) indicating a higher dominance pattern than the summer. The k -dominance curves for middle and outer shelves were similar during summer with three families (Argonautidae, Enoploteuthidae, and

Loliginidae) accounting for ca. 80% of total abundance (Fig. 7a). In winter, a higher dominance pattern was observed in outer shelf relative to middle shelf (Fig. 7b).

Discussion

Studies focusing on distribution of cephalopod paralarvae from Brazilian coastal and oceanic waters are scarce. The present study investigated paralarva distribution patterns and diversity in the northern sector of the SBB, covering shelf waters from Cabo de São Tomé (22°S) to Cananéia (25°S) (Fig. 1; Table 1). An important oceanographic feature of the study area is the change in coastline orientation at Cabo Frio from NE–SW to roughly E–W, along with a narrow shelf that favors the occurrence of seasonal coastal upwelling (Campos et al. 1995). Prevalent northeast winds during the summer and spring move surface waters offshore, via Ekman transport, resulting in the upwelling of SACW and consequent phytoplankton blooms that are commonly observed in this region (Valentin 1984; Gonzalez-Rodriguez et al. 1992). During winter, cold frontal systems invert the wind stress from NE to SW. Consequently, SACW retreats towards the slope and TW and CW dominate the upper water column of the continental shelf (Campos et al. 1995; Castro and Miranda 1998). Furthermore, the steep topography and coastline orientation of Cabo Frio bring BC water masses closer to the coast, enhancing upwelling efficiency and allowing unique mesoscale features to

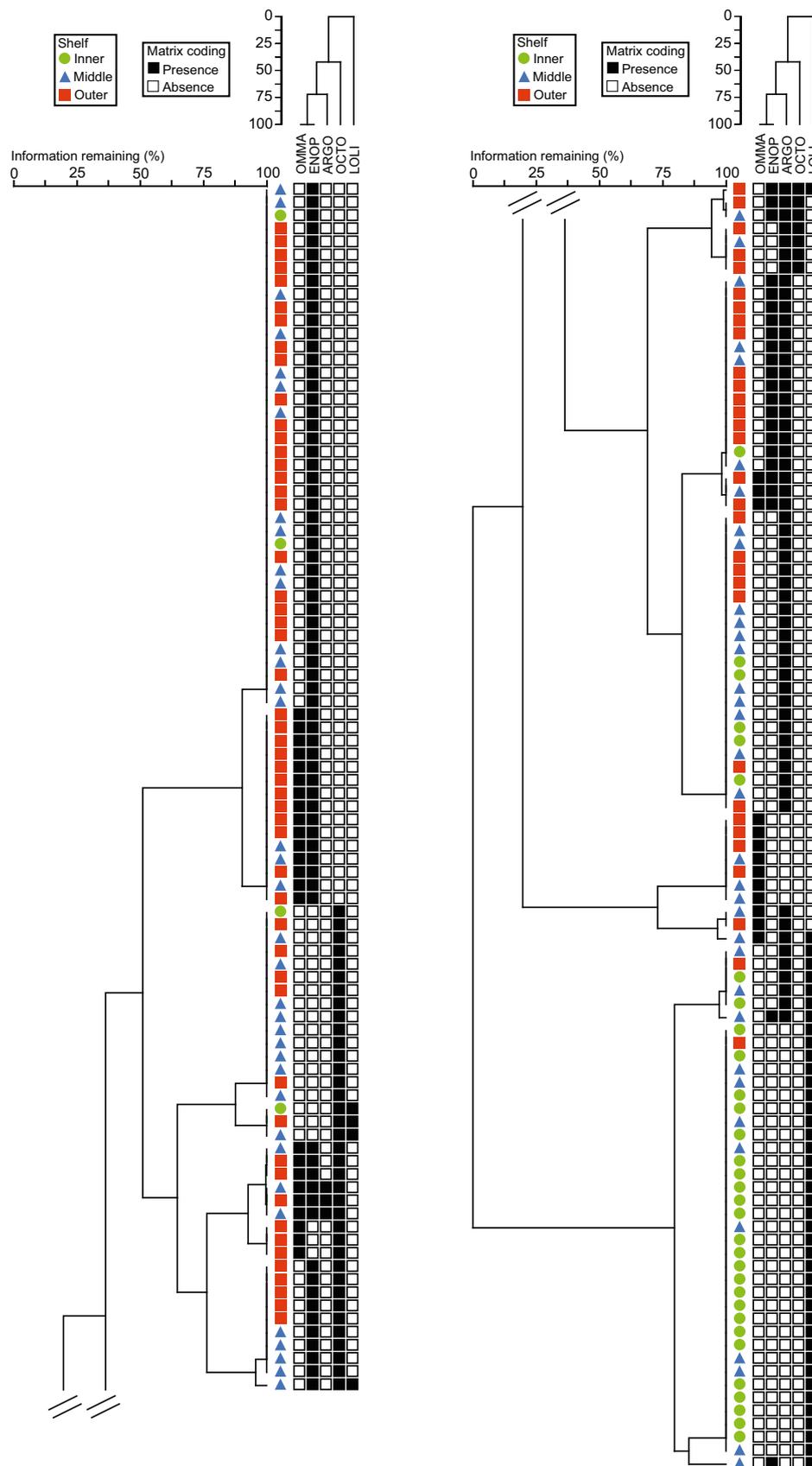


Fig. 4 Two-way presence-absence cluster of cephalopod paralarvae collected in northern subarea during summer in inner, middle, and outer shelves. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; OCTO = Octopodidae; LOLI = Loliginidae

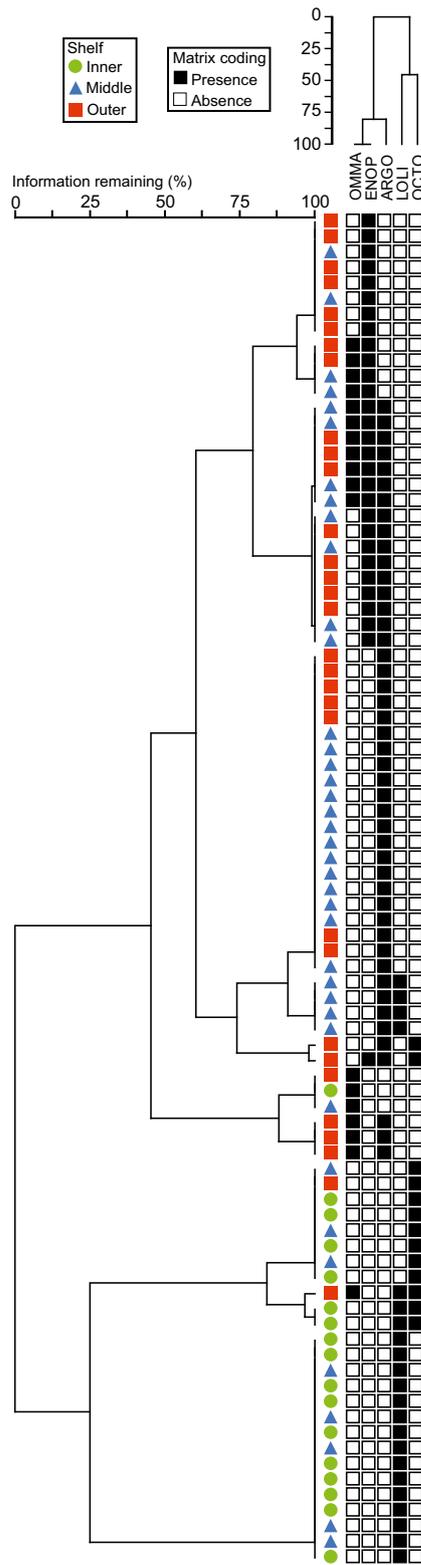


Fig. 5 Two-way presence-absence cluster of cephalopod paralarvae collected in southern subarea during summer in inner, middle, and outer shelves. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; LOLI = Loliginidae; OCTO = Octopodidae

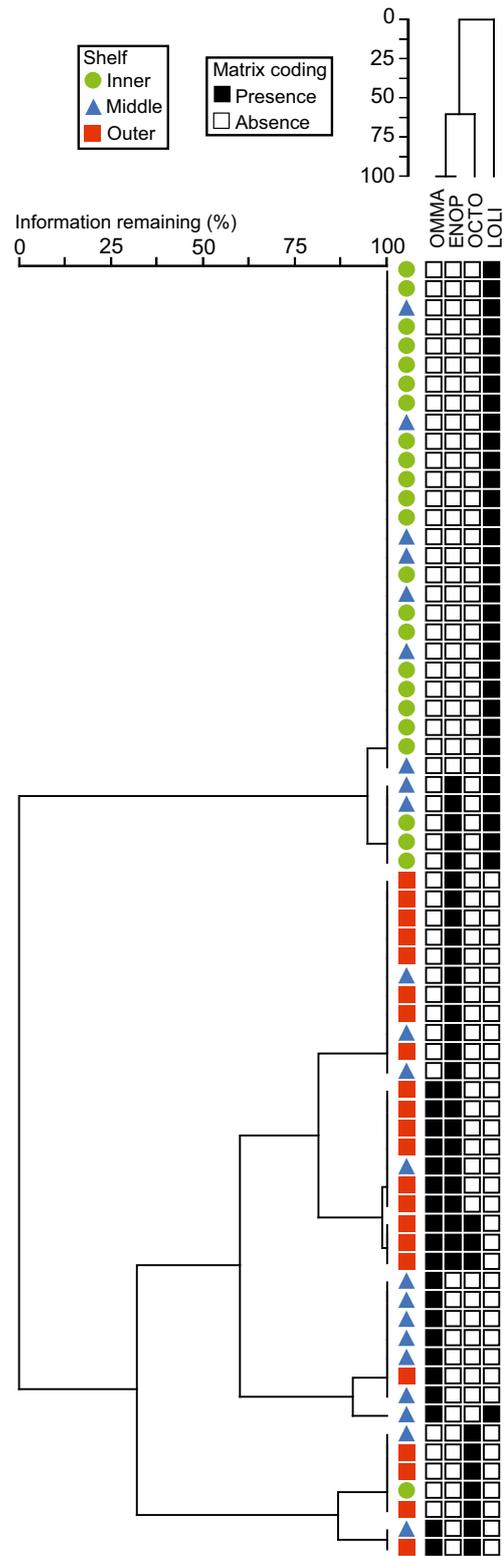


Fig. 6 Two-way presence-absence cluster of cephalopod paralarvae collected during winter in inner, middle, and outer shelves of the northern subarea. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; OCTO = Octopodidae; LOLI = Loliginidae

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, Enoplateuthidae, 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>
Enoplateuthidae	18.2	<u>26.4</u>	<u>32.6</u>	Enoplateuthidae	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

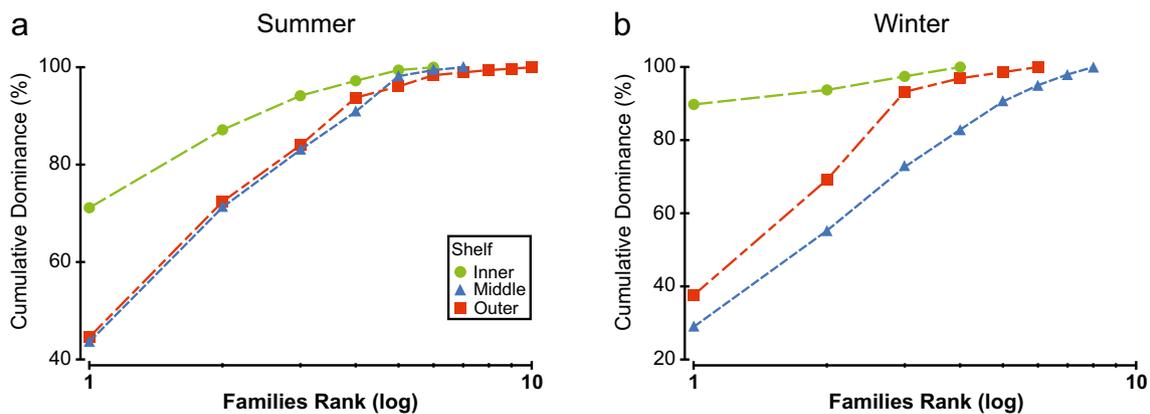


Fig. 7 Abundance k -dominance curves of bathymetric zones (inner, middle, and outer shelves). **a** Summer; **b** Winter

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 (Laptikhovsky 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.

Acknowledgments The authors are grateful to the responsible for the Biological Collection “Prof. E. F. Nonato” – ColBIO, Oceanographic Institute, University of São Paulo, for the plankton samples. We are also thankful to the Graduate Program on Oceanography from the University of São Paulo.

Funding This study was financed in part by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – CAPES/PROEX.

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.

References

- Aidar E, Gaeta SA, Giancesella-Galvão SMF, Kutner MBB, Teixeira C (1993) Ecosistema costeiro tropical: nutrientes dissolvidos, fitoplâncton e clorofila-a, e suas relações com as condições oceanográficas na região de Ubatuba. *Publ Esp Inst Oceanogr* 10: 9–43
- Anderson CIH, Rodhouse PG (2001) Life cycles, oceanography and variability: ommastrephid squid in variable oceanographic environments. *Fish Res* 54:133–143
- Araújo CC, Gasalla MA (2018) Distribution patterns of loliginid squid paralarvae in relation to the oceanographic features off the South Brazil Bight (22°–25°S). *Fish Oceanogr* 27:63–67
- Arkhipkin AI, Rodhouse PGK, Pierce GJ et al (2015) World squid fisheries. *Rev Fish Sci Aquacult* 23:92–252
- Bather FA (1888) Shell-growth in Cephalopoda (Siphonopoda). *Ann Mag Nat Hist* 6:289–310
- Berry SS (1912) A review of the cephalopods of western North America. *Bull Bur Fish Wash* 30:263–336
- Boettger CB (1952) Die Stämme des Tierreichs in ihrer systematischen Gliederung. *Abh Braunschweig Wiss Ges* 4:238–300
- Boyle PR (1990) Cephalopod biology in the fisheries context. *Fish Res* 8: 303–321
- Boyle PR, Boletzky SV (1996) Cephalopod populations: definition and dynamics. *Trans R Soc London B* 351:985–1002
- Boyle PR, Rodhouse PG (2005) *Cephalopods: ecology and fisheries*. Wiley-Blackwell, Oxford
- Braga ES, Müller TJ (1998) Observation of regeneration of nitrate, phosphate and silicate during upwelling off Ubatuba, Brazil, 23°S. *Cont Shelf Res* 18:915–922
- Brakoniecki TF (1984) A full description of *Loligo sanpaulensis*, Brakoniecki, 1984 and a redescription of *Loligo Gahi* d’Orbigny, 1835, two species of squid (Cephalopoda: Myopsida) from the Southwest Atlantic. *Bull Mar Sci* 34:435–448
- Brandini FP, Nogueira M, Simião M, Carlos Ugaz Codina J, Almeida Noernberg M (2014) Deep chlorophyll maximum and plankton community response to oceanic bottom intrusions on the continental shelf in the South Brazilian Bight. *Cont Shelf Res* 89:61–75
- Calado L, Gangopadhyay A, Silveira ICA (2006) A parametric model for the Brazil Current meanders and eddies off southeastern Brazil. *Geophys Res Lett* 33:L12602
- Campos EJD, Gonçalves JE, Ikeda Y (1995) Water mass structure and geostrophic circulation in the South Brazil Bight: summer of 1991. *J Geophys Res* 100:18537–18550
- Campos EJD, Ikeda Y, Castro BM, Gaeta SA, Lorenzetti JA, Stevenson MR (1996) Experiment studies circulation in the Western South Atlantic. *EOS Trans Am Geophys Union* 77:253–259
- Campos EJD, Velhote D, Silveira ICA (2000) Shelf break upwelling driven by Brazil Current cyclonic meanders. *Geophys Res Lett* 27: 751–754
- Carbonel C (1998) Modelling of upwelling in the coastal area of Cabo Frio (Rio de Janeiro, Brazil). *Braz J Oceanogr* 46:1–17
- Castellanos ZJA (1960) Una nueva especie de calamar argentino *Ommastrephes argentinus* sp. nov. (Mollusca: Cephalopoda). *Neotropica* 6:55–58

- Castro BM, Miranda LB (1998) Physical oceanography of the western Atlantic continental shelf located between 4°N and 34°S. In: Robinson R, Brink KH (eds) *The sea*. John Wiley and Sons, New York, pp 209–251
- Castro-Filho BM, Miranda LB, Miyao SY (1987) Condições hidrográficas na plataforma continental ao largo de Ubatuba: variações sazonais e em média escala. *Bol Inst Oceanogr* 35:135–151
- Cerda C, Castro BM (2014) Hydrographic climatology of South Brazil Bight shelf waters between São Sebastião (24°S) and Cabo São Tomé (22°S). *Cont Shelf Res* 89:5–14
- Clarke MR (1996) The role of cephalopods in the world's oceans. *Phil Trans R Soc London B* 351:979–1112
- Coelho LI, Muto EY, Marian JEAR, Soares LSH (2010) Contribuição ao conhecimento da dieta, atividade alimentar e reprodução de *Lolliguncula brevis* (Blainville, 1823) na região costeira de Santos (Estado de São Paulo). *Bol Inst Pesca* 36:225–236
- Costa PAS, Fernandes FC (1993a) Seasonal and spatial changes of cephalopods caught in the Cabo Frio (Brazil) upwelling system. *Bull Mar Sci* 52:751–759
- Costa PAS, Fernandes FC (1993b) Reproductive cycle of *Loligo sanpaulensis* (Cephalopoda: Lolliginidae) in the Cabo Frio region, Brazil. *Mar Ecol Prog Ser* 101:91–97
- Costa PAS, Haimovici MA (1990) Pesca de polvos e lulas no litoral do Rio de Janeiro. *Ciênc Cult* 42:1124–1130
- Cuvier G (1797) *Tableau élémentaire de l'histoire naturelle des animaux*. Baudouin, Paris
- Dawe EG, Coulburne EB, Drinkwater KF (2000) Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *ICES J Mar Sci* 57:1002–1013
- de Blainville HD (1823) *Memoire sur les especes du genre calamar (Loligo, Lamarck)*. *J Phys Chim Hist Nat* 96:116–135
- De Silva-Dávila R, Franco-Gordo C, Hochberg FG et al (2015) Cephalopod paralarval assemblages in the Gulf of California during 2004–2007. *Mar Ecol Prog Ser* 520:123–141
- Fioroni VP (1981) Die Sonderstellung der Sepioliden, ein Vergleich der Ordnungen der rezenten Cephalopoden. *Zool. Jahrb., Abt. Syst. Ökol. Geogr. Tiere* 108:178–228
- Franco BC, Muelbert JH, Mata MM (2006) Mesoscale physical processes and the distribution and composition of ichthyoplankton on the southern Brazilian shelf break. *Fish Oceanogr* 15:37–43
- Gaeta SA, Ribeiro SMS, Metzler PM, Francos MS, Abe DS (1999) Environmental forcing on phytoplankton biomass and primary productivity of the coastal ecosystem in Ubatuba region, southern Brazil. *Rev Bras Oceanogr* 47:11–27
- Gasalla MA, Perez JAA, Marques CA, Tomás ARG, Aguiar DC, Oliveira UC (2005a) *Loligo sanpaulensis* (Brakoniecki, 1984). In: Cergole M, Ávila-da-Silva AO, Rossi-Wongtschowski CLB (eds) *Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em exploração*. Instituto Oceanográfico – USP (Série documentos REVIZEE: Score Sul), São Paulo, pp 69–80
- Gasalla MA, Postuma FA, Tomás ARG (2005b) Captura de lulas (Mollusca: Cephalopoda) pela pesca industrial desembarcada em Santos: comparação após 4 décadas. *Braz J Aquat Sci Technol* 9:5–8
- Gasalla MA, Rodrigues AR, Postuma FA (2010) The trophic role of the squid *Loligo plei* as a keystone species in the South Brazil Bight ecosystem. *ICES J Mar Sci* 67:1413–1424
- González M, Sánchez P (2002) Cephalopod assemblages caught by trawling along the Iberian Peninsula Mediterranean coast. *Sci Mar* 66:199–208
- González AF, Trathan P, Yau C, Rodhouse PG (1997) Interactions between oceanography, ecology and fishery biology of ommastrephid squid *Martialia hyadesi* in the South Atlantic. *Mar Ecol Prog Ser* 152:205–215
- González F, Otero J, Guerra A, Prego R, Rocha F, Dale AW (2005) Distribution of common octopus and common squid paralarvae in a wind-driven upwelling area (Ria of Vigo, northwestern Spain). *J Plankton Res* 27:271–277
- Gonzalez-Rodriguez E, Valentin JL, André DL, Jacob SA (1992) Upwelling and downwelling at Cabo Frio (Brazil). *J Plankton Res* 14:289–306
- Gray JE (1849) *Catalogue of the Mollusca in the collection of the British Museum, part I: Cephalopoda antepedia*. British Museum, London
- Grimpe G (1916) *Chuniotheuthis*. Eine neue Cephalopodengattung. *Zool Anz* 46:349–359
- Haimovici M (1998) Cefalópodes. In: Seeliger U, Odebrecht C, Castello JP (eds) *Os ecossistemas costeiro e marinho do extremo sul do Brasil*. Ecoscientia, Rio Grande, pp 162–165
- Haimovici M, Andrigueto-Filho JM (1986) Cefalópodes costeiros capturados na pesca de arrasto do litoral sul do Brasil. *Arq Biol Tecnol* 29:473–495
- Haimovici M, Perez JAA (1991) Coastal cephalopod fauna of southern Brazil. *Bull Mar Sci* 49:221–230
- Haimovici M, Perez JAA, Costa PAS (1989) A review of cephalopods occurring in the waters of Rio de Janeiro state, Brazil with first record of four species. *Rev Bras Biol* 49:503–510
- Haimovici M, Perez JAA, Santos RA (1994) Class Cephalopoda Cuvier, 1798. In: Rios EC (ed) *Seashells of Brazil*. FURG, Rio Grande, pp 311–320
- Haimovici M, Vidal EAG, Perez JAA (1995) Larvae of *Illex argentinus* (Castellanos, 1960) from five surveys on the continental shelf of southern Brazil. *ICES Mar Sci Symp* 199:414–424
- Haimovici M, Piatkowski U, Santos RA (2002) Cephalopod paralarvae around tropical seamounts and oceanic islands off the north-eastern coast of Brazil. *Bull Mar Sci* 71:313–330
- Jereb P, Roper CFE (eds) (2010) *Cephalopods of the world an annotated and illustrated catalogue of species known to date. Volume 2, Myopsid and Oegopsid Squids*. FAO Species Catalogue for Fishery Purposes. FAO, Rome
- Joubin L (1896) Observations sur divers Céphalopodes. Première Note: *Abrialopsis pfefferi* (nov. gen. et spec.). *Bull Soc Scient Méd Ouest* 5:19–35
- Juanicó M (1979) Contribuição ao estudo da biologia dos cefalópodes Lolliginidae do Atlântico Sul Ocidental entre o Rio de Janeiro e Mar del Plata. Ph. D thesis, Universidade de São Paulo
- Katsuragawa M, Dias JF, Harari J, Namiki C, Zani-Teixeira ML (2014) Patterns in larval fish assemblages under the influence of the Brazil current. *Cont Shelf Res* 89:103–117
- Keller S, Bartolino V, Hidalgo M, Bitetto I, Casciaro L, Cuccu D et al (2016) Large-scale spatio-temporal patterns of Mediterranean cephalopod diversity. *PLoS One* 11:e0146469
- Kindt R, Coe R (2005) *Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies*. World Agroforestry Centre (ICRAF), Nairobi
- Laptikhovskiy VV (1999) Fecundity and spawning in squid of families Enoploteuthidae and Ancistrocheiridae (Cephalopoda: Oegopsida). *Sci Mar* 63:1–7
- Leach WE (1817) Synopsis of the orders, families and genera of the class Cephalopoda. *Zool Miscell* 7:373–376
- Leach WE (1818) Sur plusieurs espèces nouvelles de la classe des Céphalopodes et sur une nouvelle distribution systématique des ordres, familles et genres de cette classe. *J Phys Chim Hist Nat* 86:393–396
- Lesueur CA (1821) Description of several new species of cuttlefishes. *J Acad Nat Sci Phila* 2:86–101
- Linnaeus C (1758) *Systema naturae*. Laurentius Salvius, Stockholm
- Lopes RM, Katsuragawa M, Dias JF, Montú MA, Muelbert JH, Gorri C, Brandini FP (2006) Zooplankton and ichthyoplankton distribution on the southern Brazilian shelf: an overview. *Sci Mar* 70:189–202

- Lorenzetti JA, Gaeta SA (1996) The Cape Frio upwelling effect over the South Brazil Bight northern sector shelf waters: a study using AVHRR images. *Int Arch Photogramm Remote Sens* 31:448–453
- Macedo-Soares LCP, Garcia CAE, Freire AS, Muelbert JH (2014) Large-scale ichthyoplankton and water mass distribution along the South Brazil Shelf. *PLoS One* 9:e91241
- Mahiques MM, Tessler MG, Ciotti AM, Silveira ICA, Sousa SHM, Figueira RCL, Tassinari CCG, Furtado VV, Passos RF (2004) Hydrodynamically driven patterns of recent sedimentation in the shelf and upper slope off Southeast Brazil. *Cont Shelf Res* 24:1685–1697
- Martins RS, Perez JAA (2008) Artisanal fish-trap fishery around Santa Catarina island during spring/summer: characteristics, species interactions and the influence of the winds on the catches. *Bol Inst Pesca* 34:413–423
- Martins RS, Camargo R, Gasalla MA (2014) The São Paulo shelf (SE Brazil) as a nursery ground for *Doryteuthis plei* (Blainville, 1823) (Cephalopoda, Loliginidae) paralarvae: a Lagrangian particle-tracking individual-based model approach. *Hydrobiologia* 725:57–68
- Matsuura Y (1996) A probable cause of recruitment failure of the Brazilian sardine *Sardinella aurita* population during the 1974/75 spawning season. *S Afr J Mar Sci* 17:29–35
- Metzler PM, Glibert PM, Gaeta SA, Ludlam J (1997) New and regenerated production in the South Atlantic off Brazil. *Deep Sea Res* 44:363–384
- Miranda LB, Katsuragawa M (1991) Estrutura térmica na região sudeste do Brasil (outubro/novembro 1988). *Publ Esp Inst Oceanogr* 8:1–14
- Moreno A, dos Santos A, Piatkowski U, Santos AMP et al (2009) Distribution of cephalopod paralarvae in relation to the regional oceanography of the western Iberia. *J Plankton Res* 31:73–91
- Naef A (1912) Teuthologische Notizen. 4. Die Gattungen der Loliginidae. *Zool Anz* 39:741–745
- Namiki C, Katsuragawa M, Napolitano DC, Zani-Teixeira ML, Mattos RA, Silveira ICA (2017) Hydrodynamically-driven distribution of lanternfish larvae in the Southeast Brazilian bight. *J Mar Syst* 170:115–133
- Oksanen J, Blanchet FG, Kindt R et al. (2010) Vegan: community ecology package. R package version 1.17–3. <https://www.cran.r-project.org>
- Orbigny Ad' (1835-1848) Histoire naturelle générale et particulière des céphalopodes acétabulifères vivants et fossiles. JB Baillière, Paris
- Otero J, González ÁF, Sieiro MP, Guerra Á (2007) Reproductive cycle and energy allocation of *Octopus vulgaris* in Galician waters, NE Atlantic. *Fish Res* 85:122–129
- Palacio, FJ (1977) A study of coastal cephalopods from Brazil with reference to Brazilian zoogeography. Ph. D thesis, University of Miami
- Pecl G, Jackson F (2008) The potential impacts of climate change on inshore squid: biology, ecology and fisheries. *Rev Fish Biol Fish* 18:373–385
- Pecl GT, Moltschanivskyj NA, Tracey SR, Jorda AR (2004) Inter-annual plasticity of squid life history and population structure: ecological and management implications. *Oecologia* 139:515–524
- Perez JAA, Aguiar DC, Oliveira UC (2002) Biology and population dynamics of the long-finned squid *Loligo plei* (Cephalopoda: Loliginidae) in southern Brazilian waters. *Fish Res* 58:267–279
- Perez JAA, Gasalla MA, Aguiar DC, Oliveira UC, Marques CA, Tomás ARG (2005) *Loligo plei*. In: Cergole M, Ávila-da-Silva AO, Rossi-Wongtschowski CLB (eds) Análise das principais pescarias comerciais da região Sudeste-Sul do Brasil: dinâmica populacional das espécies em exploração. Instituto Oceanográfico – USP (Série documentos REVIZEE: Score Sul), São Paulo, pp 62–68
- Pfeffer G (1900) Synopsis der oegopsiden Cephalopoden. *Mitteilungen der Naturhistorischen Museum in Hamburg* 17:147–198
- Pfeffer G (1908) Die Cephalopoden. *Nordisches Plankton* 2:9–116
- Pfeffer G (1912) Die Cephalopoden der Plankton-Expedition. *Ergebnisse der Plankton-Expedition der Humboldt* 2:1–815
- Piatkowski U, Pierce GJ, Cunha MM (2001) Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fish Res* 52:5–10
- Postuma FA, Gasalla MA (2010) On the relationship between squid and the environment: artisanal jigging for *Loligo plei* at São Sebastião Island (24°S) southeastern Brazil. *ICES J Mar Sci* 67:1353–1362
- Postuma FA, Gasalla MA (2014) Reproductive activity of the tropical arrow squid *Doryteuthis plei* around São Sebastião Island (SE Brazil) based on a 10-year fisheries monitoring. *Fish Res* 152:45–54
- Postuma FA, Gasalla MA (2015) Ethogram analysis reveals new body patterning behavior of the tropical arrow squid *Doryteuthis plei* off the São Paulo coast. *Biol Bull* 229:143–159
- Prosch V (1847) Nogle nye Cephalopoder, beskrevne og anatomisk undersøgte. *Kongelige Danske Videnskabernes Selskabs Skrifter* 1:53–72
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>
- Rodhouse PG, Pierce GJ, Nichols OC et al (2014) Environmental effects on cephalopod population dynamics: implications for management of fisheries. *Adv Mar Bio* 67:99–233
- Rodrigues AR, Gasalla MA (2008) Spatial and temporal patterns in size and maturation of *Loligo plei* and *Loligo sanpaulensis* (Cephalopoda: Loliginidae) in southeastern Brazilian waters, between 23°S and 27°S. *Sci Mar* 72:631–643
- Rosa R, Dierssen HM, Gonzalez L, Seibel BA (2008a) Large-scale diversity patterns of cephalopods in the Atlantic open ocean and deep sea. *Ecology* 89:3449–3461
- Rosa R, Dierssen HM, Gonzalez L, Seibel BA (2008b) Ecological biogeography of cephalopod molluscs in the Atlantic Ocean: historical and contemporary causes of coastal diversity patterns. *Glob Ecol Biogeogr* 17:600–610
- Roura A, Álvarez-Salgado XA, González AF, Greogori M, Rosón G, Otero J, Guerra A (2016) Life strategies of cephalopod paralarvae in a coastal upwelling system (NW Iberian Peninsula): insights from zooplankton community and spatio-temporal analyses. *Fish Oceanogr* 25:241–258
- Rüppell E (1844) Intorno ad alcuni cefalopodi del mare di Messina: lettera del Dr. Eduardo Ruppell di Frankfort sul Meno al Prof Anastasio Cocco Giornale del Gabinetto Letterario di Messina 5: 129–135
- Sakurai Y, Kiyofuji H, Saitoh S, Goto T, Hiyama Y (2000) Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. *ICES J Mar Sci* 57:24–30
- Santos RA, Haimovici M (1998) Trophic relationships of the long-finned squid *Loligo sanpaulensis* on the Southern Brazilian Shelf. *S Afr J Mar Sci* 20:81–91
- Santos RA, Haimovici M (2001) Cephalopods in the diet of marine mammals stranded or incidentally caught along southeastern and southern Brazil (21–34°S). *Fish Res* 52:99–112
- Santos RA, Haimovici M (2002) Cephalopods in the trophic relations off southern Brazil. *Bull Mar Sci* 71:753–770
- Santos RA, Haimovici M (2007) Composição de espécies, distribuição e abundância relativa de cefalópodes do ambiente pelágico da plataforma externa e talude superior da região Sudeste-Sul do Brasil. In: Bernardes RA, Rossi-Wongtschowski CLB, Madureira LS (eds) Prospecção pesqueira de espécies pelágicas de pequeno porte na Zona Econômica Exclusiva da Região Sudeste-Sul do Brasil, Instituto Oceanográfico – USP (Série documentos REVIZEE: Score Sul), São Paulo, pp 101–135
- Silva L, Vila Y, Torres MA, Sobrino I, Acosta JJ (2011) Cephalopod assemblages, abundance and species distribution in the Gulf of Cadiz (SW Spain). *Aquat Living Resour* 24:13–26

- Silveira ICA, Schmidt ACK, Campos EJD, Godoi SS, Ikeda Y (2000) A Corrente do Brasil ao Largo da Costa Leste Brasileira. *Rev Bras Oceanogr* 48:171–183
- Smith PE, Richardson SL (1977) Standard techniques for pelagic fish egg and larvae surveys. *FAO Fish Tech Pap* 175:1–100
- Staudinger MD (2006) Seasonal and size-based predation on two species of squid by four fish predators on the Northwest Atlantic continental shelf. *Fish Bull* 104:605–615
- Stech JL, Lorenzetti JA (1992) The response of the South Brazil Bight to the passage of wintertime cold fronts. *J Geophys Res* 97:9507–9520
- Steenstrup J (1855) Kjaeber af en kolossal Blaeksprutter. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling 5/6: 199–200
- Steenstrup J (1857) Oplysning om en ny art af blaeksprutter, *Dosidicus eschrichtii*. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling, 185 1/2:11–14
- Steenstrup J (1880) De Ommatostrephagtige blaeksprutter indbyrdes forhold. Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling 73–110
- Sumida PYG, Yoshinaga MY, Ciotti AM, Gaeta SA (2005) Benthic response to upwelling events off the SE Brazilian coast. *Mar Ecol Prog Ser* 291:35–42
- Sweeney MJ, Roper CFE, Mangold KM, Clarke MR, Boletzky SV (1992) Larval and juvenile cephalopods: a manual for their identification. *Smithson Contrib Zool* (513):1–282
- Tryon GW (1879) Argonautidae. In: Tryon GW (1883) *Manual of conchology, structural and systematic: with illustrations of the species* 1:133–141
- Valentin JL (1984) Spatial structure of the zooplankton community in the Cabo Frio region (Brazil) influenced by coastal upwelling. *Hydrobiologia* 113:183–199
- Vaske Jr T, Pereira da Costa FA (2011) Lulas e polvos da costa brasileira. UFC LABOMAR-UNISANTA Fortaleza
- Vecchione M, Roper CF, Sweeney MJ, Lu CC (2001) Distribution, relative abundance and developmental morphology of paralarval cephalopods in the Western North Atlantic Ocean. *NOAA Tech Rep NMFS* 152:1–54
- Vecchione M, Jorgensen EM, Sakurai Y (2017) Editorial: recent advances in the knowledge of cephalopod biodiversity. *Mar Biodivers* 47: 619–620
- Verany JB (1851) Cephalopodes de la Méditerranée. In: *Mollusques Méditerranéens observés, décrits figurés et chromo-lithographiés d'après nature sur de modèles vivants*. *Genes* 1:1–137
- Vidal EAG, Haimovici M, Hackbart CS (2010) Distribution of paralarvae and small juvenile cephalopods in relation to primary production in an upwelling area off southern Brazil. *ICES J Mar Sci* 67:1346–1352
- Voss GL (1953) A new family, genus and species of myopsid squid from the Florida Keys. *Bull Mar Sci* 2:602–609
- Waluda C, Rodhouse PG, Podestá GP et al (2001) Surface oceanography of the inferred hatching grounds of *Illex argentinus* (Cephalopoda: Ommastrephidae) and influences on recruitment variability. *Mar Biol* 139:671–679
- Yoshinaga MY, Sumida PYG, Silveira ICA, Ciotti AM, Gaeta SA, Pacheco LFCM, Koettker AG (2010) Vertical distribution of benthic invertebrate larvae during an upwelling event along a transect off the tropical Brazilian continental margin. *J Mar Syst* 79:124–133
- Young RE, Harman RF (1988) Larva, paralarva and subadult in cephalopod terminology. *Malacologia* 29:201–207
- Zaragoza N, Quetglas A, Moreno A (2015) Identification guide for cephalopod paralarvae from the Mediterranean Sea. *ICES Coop Res Rep* 324: 1–91
- Zittel, KA von (1895). *Grundzüge der Paläontologie (Paläozoologie)*, I Abteilung, Invertebrata. Oldenburg. Druck und Verlag von R. Oldenburg, München und Leipzig

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.