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Influence of ocean dynamics on the route of argonauts in the Southeastern Brazil Bight

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ABSTRACT

Argonauts (Cephalopoda: Argonautidae), also known as *'paper nautilus'*, are epipelagic octopuses that are believed inhabit the open ocean despite being rarely encountered alive. Previous studies on the early-life stages of cephalopods have reported unexpectedly high abundances of argonauts in continental shelf areas of the Southeastern Brazilian Bight (SBB). Based on this finding, we explored the potential ocean dynamics driving both seasonal and interannual argonaut paralarvae occurrence in the SBB shelf. A historical archive of plankton samples (n = 884) collected during 22 survey cruises between 1974 and 2010 covering the northern portion of the SBB was used. Spatiotemporal analysis combining environmental variables and horizontal and vertical abundance maps indicated that high frequency of argonaut paralarvae mostly occurred during summer with a high interannual variability. Horizontal and vertical maps revealed that they were mainly transported from the open ocean into the shelf by the onshore intrusion of water masses promoted by meanders and eddies of the offshore Brazil Current. Furthermore, argonaut occurrence in the southern shelf areas was remarkably influenced by the coastal jet originating from upwelling in the northern SBB. These results suggest that argonauts may be used as indicators of mesoscale processes. The present study provides a novel hypothesis for the route of argonauts from the pelagic realm to the continental shelf.

1. Introduction

Argonauts (Argonautidae Tryon, 1879) are epipelagic cosmopolitan octopuses occurring in tropical and temperate seas and show sexual dimorphism (Boyle and Rodhouse, 2005). They are also called "paper nautilus," for their thin, laterally compressed shell secreted by the females that acts as a brood chamber for egg-laying (Boyle and Rodhouse, 2005; Finn 2018) and a hydrostatic structure to attain neutral buoyancy (Finn 2018; Finn and Norman, 2010).

An adult female can be up to 15 times larger than a male (Guerra et al., 2002). Males are tiny (<15 mm total length), planktonic, and their third arm hectocotylizes within a thin pocket (Boyle and Rodhouse, 2005). Argonauts are believed to inhabit open-ocean pelagic habitats (Boyle and Rodhouse, 2005), but live organisms can be rarely observed. However, their ecological importance to the pelagic realm is frequently observed as the stomach contents of top predators (Roper et al., 1984; Staudinger et al., 2013) and occasional mass strandings (Norman, 2000). Argonautid mass strandings appear to be associated with atypical oceanographic and meteorological conditions, as observed along the Shimane Prefecture coast (western Japan Sea) (Okutani and Kawaguchi, 1983), the Uruguayan coast (southwestern Atlantic) (Demichelli et al., 2006), and southeast Tasmania (Grove, 2014; Grove and Finn, 2014). Comparatively little information is available about the biology and oceanic distribution of Argonautidae paralarvae. Forty-six specimens of *Argonauta nodosus* with mantle length (ML) of 2–9 mm were reported from the southwestern Atlantic at fairly shallow depths (43 and 125 m) off the southern Southeastern Brazilian Bight (SBB) (Vidal et al., 2010). Furthermore, an unusually high abundance (n = 960) of Argonautidae paralarvae was observed in continental shelf waters of the northern SBB (Araújo and Gasalla, 2019). These studies suggest the relevance of the continental shelf in the SBB for the life cycle of argonauts, which are commonly reported from the stomach of demersal and pelagic fish, marine mammals, and birds in this area (Santos and Haimovici, 2002; Vaske Jr and Castello, 1998; Vaske-Júnior and Rincón-Filho, 1998). Although governed by the Brazil Current (BC), a weak western boundary current, the SBB is influenced by intense mesoscale activity (Silveira et al., 2008). These include seasonal coastal upwelling off Cabo Frio and meanders and eddies from the BC (Castro and Miranda, 1998; Campos

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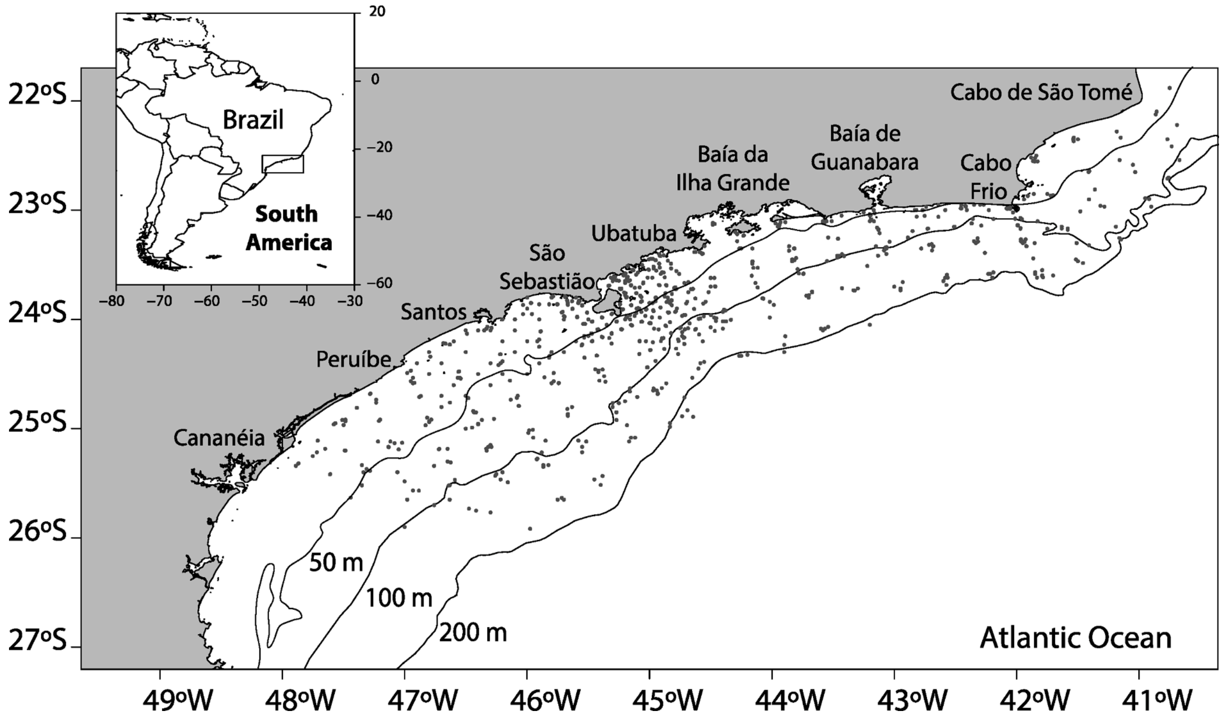

Fig. 1. Study area and sampling sites between Cabo de São Tomé and Cananéia.

et al., 2000), which may induce localized cross-shelf transport of the epipelagic larvae (Yoshinaga et al., 2010; Katsuragawa et al., 2014; Namiki et al., 2017; Araújo and Gasalla, 2019). This study aims to explain the relatively high abundance of Argonautidae paralarvae in continental shelf areas of the SBB. We investigated a historical collection of samples from 22 research cruises conducted from 1974 to 2010 in both summer and winter in the SBB, which were analyzed along with the temperature and salinity of surface and subsurface waters to describe the seasonal and interannual distribution of Argonautidae paralarvae in the SBB. We propose that the mesoscale features of BC aid in the transport of Argonautidae paralarvae from oceanic to continental shelf waters of the SBB.

2. Material and methods

2.1. Study area

The study area encompasses the continental shelf of the northern SBB between Cabo de São Tomé (22° S) and Cananéia (25° S) (Fig. 1). Circulation in the SBB continental shelf is primarily driven by the mesoscale variability of the BC (Silveira et al., 2000; Rocha et al., 2014), along with local and remote winds (Castelao and Barth, 2006), tides, and baroclinic pressure gradients (Castro et al., 2006; Palma and Matano, 2009). Here, the BC flows southward along the continental slope and is composed of oligotrophic Tropical Water (TW; >20 °C and salinity > 36) in the upper 200 m and the cold and nutrient-rich South Atlantic Central Water (SACW; <20 °C and salinity < 36) below the TW (200–500 m) as the pycnocline portion of the BC (Campos et al., 1996; Silveira et al., 2000). The SBB continental shelf is also influenced by Coastal Water (CW), a low-salinity water resulting from the mixing of freshwater from small-to medium-sized estuaries along the SBB with the TW and SACW (Castro and Miranda, 1998; Emílsson, 1961; Silveira et al., 2000).

This area is characterized by meridional gradients in primary production, reflecting the abrupt change in coastline direction from NE–SW to E–W at Cabo Frio (23° S) and differences in continental shelf width (from 50 km off Cabo Frio to 230 km off Santos; Fig. 1). The peculiar shelf morphology (coastline orientation and topography) at Cabo Frio combined with prevailing northeast winds during summer promote the Ekman transport of surface waters offshore, favoring intrusion of SACW toward the inner shelf, resulting in coastal upwelling off Cabo Frio (Cerda-Amor, 2004; Castelao and Barth, 2006). Atmospheric cold fronts, which are more intense during winter, reverse the Ekman transport to the coast, and the SACW retreats towards the shelf break (Castelao and Barth, 2006; Emílsson, 1961; Matsuura, 1985; Stech and Lorenzzetti, 1992). Phytoplankton blooms commonly observed as a consequence of SACW upwelling in coastal areas off Cabo Frio (Valentin, 1984; Gonzalez-Rodriguez et al., 1992) are considered key factors supporting the productivity of regional fisheries, particularly sardines (Matsuura, 1996). In contrast to Cabo Frio, primary production in the SBB continental shelf is considered to be under an oligotrophic regime, with a strong nutrient depletion in the euphotic zone associated with the TW (Metzler et al., 1997).

The SBB also undergoes intense interaction between shelf and open-ocean dynamics (Calil et al., 2021) that are critical for larval dispersion and/or retention (Matsuura, 1996; Franco et al., 2006; Yoshinaga et al., 2010; Martins et al., 2014; Namiki et al., 2017; Brandini et al., 2018). The BC diverts eastward at Cabo Frio owing to the change in coastline direction resulting in meandering of the BC with occasional generation of mesoscale eddies (Calil et al., 2021). These eddies may impact the continental shelf by promoting subsurface intrusion of the SACW from the open ocean, which may contribute to the export of coastal surface waters offshore (Calado et al., 2006; Campos et al., 2000; Silveira et al., 2004; Yoshinaga et al., 2010) (). Additionally, while centered at Cabo Frio, the upwelling front is frequently observed in association with southward-flowing cold-water jets along the SBB shelf, which may stretch hundreds of kilometers south of Cabo Frio (Calil et al., 2021; Carbonel, 1998; Lorenzzetti and Gaeta, 1996; Yoshinaga et al., 2010). These coastal upwelling jets are finally advected southwestward to areas deeper than 200 m at ~ 24° S (São Sebastião Island), potentially due to the combined effects of offshore cyclonic eddies and coastal currents (Calil et al., 2021). The complex mesoscale features that influence the interactions of local coastal and ocean ecosystems in the SBB shelf are still poorly understood (Valentin et al., 1987; Franco et al., 2006; Lopes et al., 2006; Yoshinaga et al., 2010; Martins et al., 2014; Namiki et al.,

Table 1
Summary of sampling parameters encompassing the 22 cruises performed in the northern sector of the Southeastern Brazilian Bight (SBB) between 1974 and 2010.

Cruise	Month	Year	Number of stations	Local depth
ICTIO-1	Nov/Dec	1974	87	19–248
FINEP-1	Nov/Dec	1975	74	15–194
FINEP-5	Dec	1976	73	18–183
PI-1	Dec	1985	27	11–122
PI-2	Jul	1986	28	13–122
PI-4	Jul	1987	30	12–96
PI-5	Dec	1987	9	12–133
PI-6	Jul	1988	24	10–136
PI-7	Dec	1988	5	42–136
SARDINHA-1	Dec	1991	71	20–140
SARDINHA-2	Jan	1993	70	16–134
OPISS-1	Feb	1994	43	12–74
OPISS-2	Oct	1997	43	12–76
PADCT-1	Nov	1997	11	72–162
DEPROAS-1	Feb	2001	16	36–161
DEPROAS-2	Jul	2001	19	37–155
DEPROAS-3	Jan	2002	49	14–197
DEPROAS-4	Aug	2002	47	14–200
ECOSAN-3	Jan	2005	11	6–13
ECOSAN HIDRO-1	Sep	2005	36	14–60
ECOSAR-IV	Jan/Feb	2008	27	21–112
ECOSAR-V	Nov	2008	44	21–110
ECOSAR-VII	Mar	2010	40	20–111

2017; Favero et al., 2017; Brandini et al., 2018).

2.2. Sampling

Horizontal occurrence patterns and interannual variability of Argonautidae paralarvae were analyzed based on 884 plankton samples collected during 22 survey cruises between 1974 and 2010 (Table 1), covering the northern SBB shelf along (Fig. 1). Samples were obtained onboard the research vessels, “Prof. W. Besnard” and “Atlântico Sul”, using Bongo nets and Multi Plankton Sampler (MPS). The Bongo nets (0.6 m mouth diameter; 333 and 505 µm mesh size) and MPS (333 µm mesh size) were towed obliquely in the order of surface-bottom-surface at ~ 2 knots (Smith and Richardson, 1977) and in five horizontal layers (0–20, 20–40, 40–60, 60–80 and 80–100 m). The maximum sampling depth was 10 m at the bottom of the shallow stations. Calibrated flowmeters were placed at the mouth apertures of each net to estimate the volume of filtered water. 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. Environmental variables, such as temperature and salinity, were obtained at each station from Nansen bottles and reversing thermometers until 1988, after which a Conductivity, Temperature, and Depth profiler (CTD) was used.

2.3. Data analysis

Paralarvae were obtained from the plankton samples and identified at the family level based on Sweeney et al. (1992) and Vecchione et al. (2001).

Argonautidae paralarvae abundance was calculated as the number of individuals per 100 m^{-3}, using flowmeter information (Moreno et al., 2009).

Temperature and salinity data were plotted on horizontal distribution maps using the geostatistical interpolation technique of ordinary kriging.

2.4. Quotient analysis

Single-parameter quotient analysis (SPQ) was used to characterize the habitat of the argonautid paralarvae corresponding to the “preferred”, “tolerated”, and “avoided” ranges of surface and subsurface temperatures (10 m), salinity, local depth, and distance from the coast.

The horizontal distribution maps and SPQ analysis were performed using R software (R Core Team, 2020).

3. Results

A total of 2168 argonautid paralarvae were obtained from the 146 plankton samples, majority of which (2136 paralarvae) were collected during summer cruises (Table 2).

Although argonautid paralarvae were found along the entire continental shelf of the study area (Fig. 2), a remarkable distinction was observed between the northern portion (between Cabo Frio (23° S) and São Sebastião (24° S)) and the southern portion (south of São Sebastião). In the northern portion, argonautid paralarvae occurred close to the coast at depths < 50 m, whereas they were predominantly associated

Table 2
Summary of Argonautidae paralarvae occurrence for all cruises from 1974 to 2010 in the continental shelf between Cabo Frio (22° S) and Cananéia (25° S). Abundance, mean abundance and standard deviation (sd) of paralarvae are given in ind.100 m^{-3}.

Cruise	Month	Year	Number of stations	Positive stations	FO(%)	N	Abundance	Mean abundance	sd	Local depth range (m)
ICTIO-1	Nov/Dec	1974	87	27	31.0	106	0.35–5.28	0.51	1.05	57–248
FINEP-1	Nov/Dec	1975	74	6	8.1	11	0.28–1.56	0.06	0.26	84–147
FINEP-5	Dec	1976	73	31	42.5	656	0.38–60.67	4.89	11.24	35–148
PI-1	Dec	1985	27	13	48.1	850	0.98–83.27	15.41	24.83	32–122
PI-2	Jul	1986	28	–	–	–	–	–	–	–
PI-4	Jul	1987	30	8	26.7	23	0.56–5.11	0.61	1.33	72–96
PI-5	Dec	1987	9	4	44.4	18	0.78–6.89	1.94	2.78	64–126
PI-6	Jul	1988	24	3	12.5	3	0.41–0.70	0.07	0.19	58–84
PI-7	Dec	1988	5	4	80.0	315	9.88–202.96	47.8	86.92	42–136
SARDINHA-1	Dec	1991	71	11	15.5	16	0.51–1.85	0.15	0.41	52–114
SARDINHA-2	Jan	1993	70	1	1.4	1	0.50	–	–	108
OPISS-1	Feb	1994	43	1	2.3	2	1.27	0.03	0.19	72
OPISS-2	Oct	1997	43	–	–	–	–	–	–	–
PADCT-1	Nov	1997	11	2	18.2	3	0.84–1.67	0.23	0.54	72–78
DEPROAS-1	Feb	2001	16	1	6.3	7	3.70	–	–	40
DEPROAS-2	Jul	2001	19	–	–	–	–	–	–	–
DEPROAS-3	Jan	2002	49	15	30.6	109	0.48–31.28	2.06	5.91	32–197
DEPROAS-4	Aug	2002	47	2	4.3	3	0.40–1.97	0.05	0.29	60–69
ECOSAN-3	Jan	2005	11	–	–	–	–	–	–	–
ECOSAN HIDRO-1	Sep	2005	36	–	–	–	–	–	–	–
ECOSAR-IV	Jan/Feb	2008	27	11	40.7	32	0.29–4.68	0.64	1.12	29–106
ECOSAR-V	Nov	2008	44	–	–	–	–	–	–	–
ECOSAR-VII	Mar	2010	40	6	15.0	13	0.43–1.80	0.13	0.4	57–105

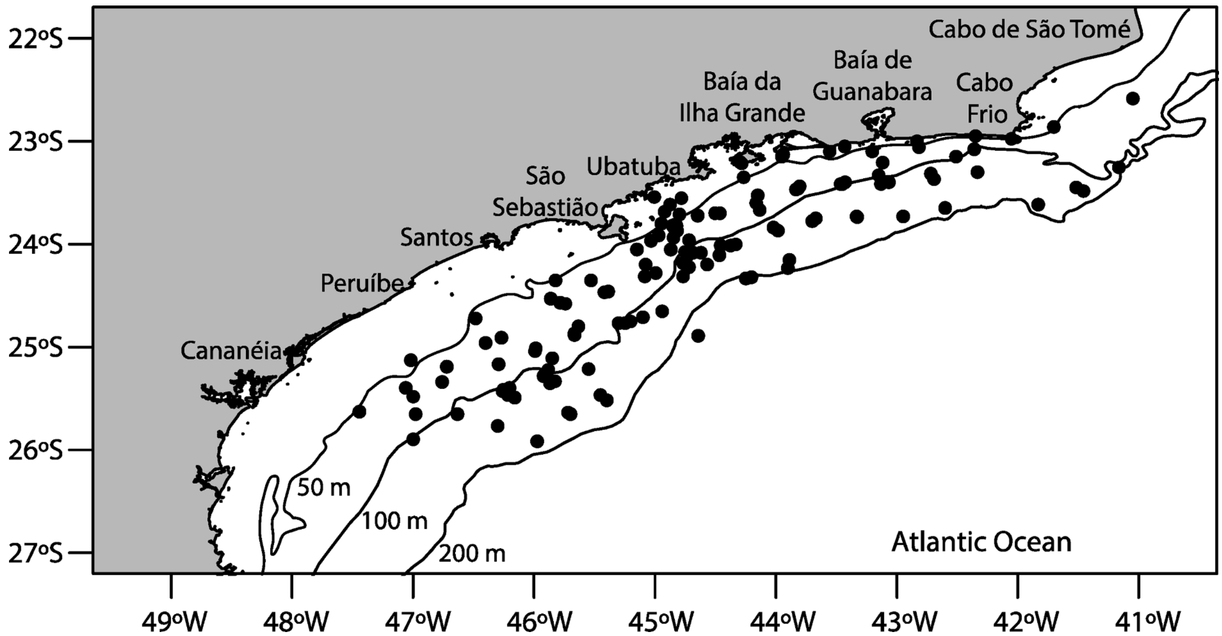

Fig. 2. Horizontal distribution of Argonautidea paralarvae between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer for the study period.

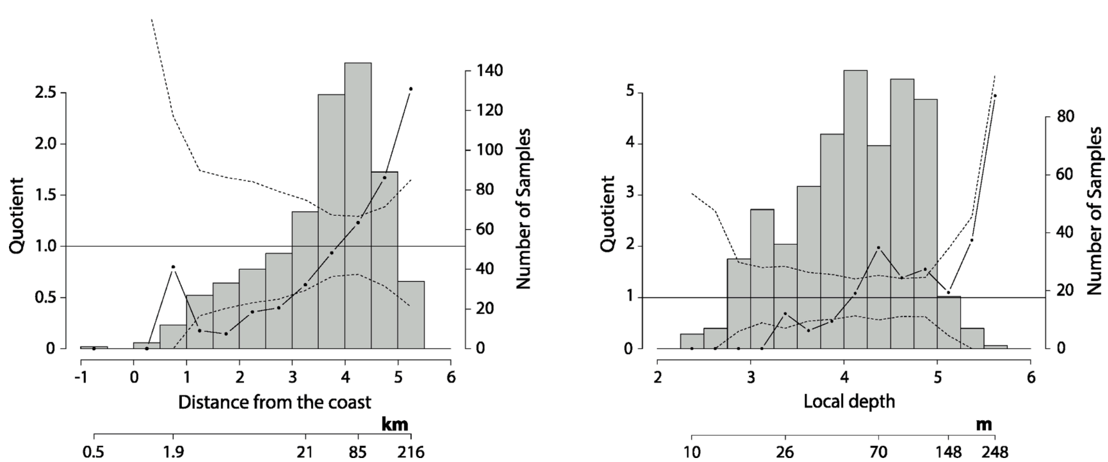

Fig. 3. Single parameter quotient (SPQ) analysis for the local depth (natural logarithms in m) and distance from coast (natural logarithms in km) of Argonautidae paralarvae occurrence in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer for the study period. Histograms represent the number of stations within each bin of the covariate, the dashed-dotted line represents the paralarvae abundance quotient value. The horizontal line represents the null hypothesis of evenly distributed paralarvae and the dashed lines represent its upper and lower confidence intervals.

with the middle shelf (50–200 m) in the southern portion (Fig. 2).

The SPQ analysis indicated that argonautid paralarvae tolerated local depths between ~ 26 and 248 m, preferring 70–148 m isobaths (Fig. 3), corresponding to the middle shelf. Distances > 85 km from the coast were preferred, corresponding to the middle and outer shelves. Sites near the coast (<21 km) were avoided (Fig. 3).

Figs. 4 and 5 display the horizontal distribution of argonautid paralarvae during summer cruises, along with surface and subsurface water temperatures (0 and 10 m, respectively). These data indicate a remarkably high interannual variability in argonautid paralarvae abundance despite the prevalence of SACW subsurface intrusion or upwelling in the Cabo Frio region. The highest paralarvae abundance was observed in FINEP-5 and DEPROAS-3 cruises, while the lowest occurred in FINEP-1 and SARDINHA-2 cruises, with both occurring during SACW upwelling at Cabo Frio. Interestingly, a high frequency was observed during the ICTIO-1 cruise, in the absence of SACW upwelling off Cabo Frio. Although the distribution of argonautid paralarvae cannot be correlated to the coastal upwelling off Cabo Frio, the data indicate a close association between the paralarvae abundance and a southward-flowing relatively low-temperature plume derived from the Cabo Frio region. With the exception of the ICTIO-1 cruises, this "cold" plume (better defined as an upwelling coastal current resulting from SACW upwelling off Cabo Frio; Cerda and Castro 2014) reached areas within the southern portion of the study area. However, it diluted southward of São Sebastião Island (i.e., warmer temperatures relative to the northern portion) and drifted offshore towards southwest. The importance of this upwelling coastal current for the transport and distribution of argonautid paralarvae in the study area can be illustrated by at least three major features: 1) highest abundances observed in the FINEP-5 cruise followed the exact pattern of this current (i.e., southeast and southwest in the northern and southern portions, respectively); 2) second highest abundances observed in the DEPROAS-3 cruise were associated with the southern front of this current; and 3) intermediate abundances in the southern portion were exclusively related to the middle and outer shelves, whereas abundance was extremely low in the inner shelf.

Further studies were conducted to better understand the possible

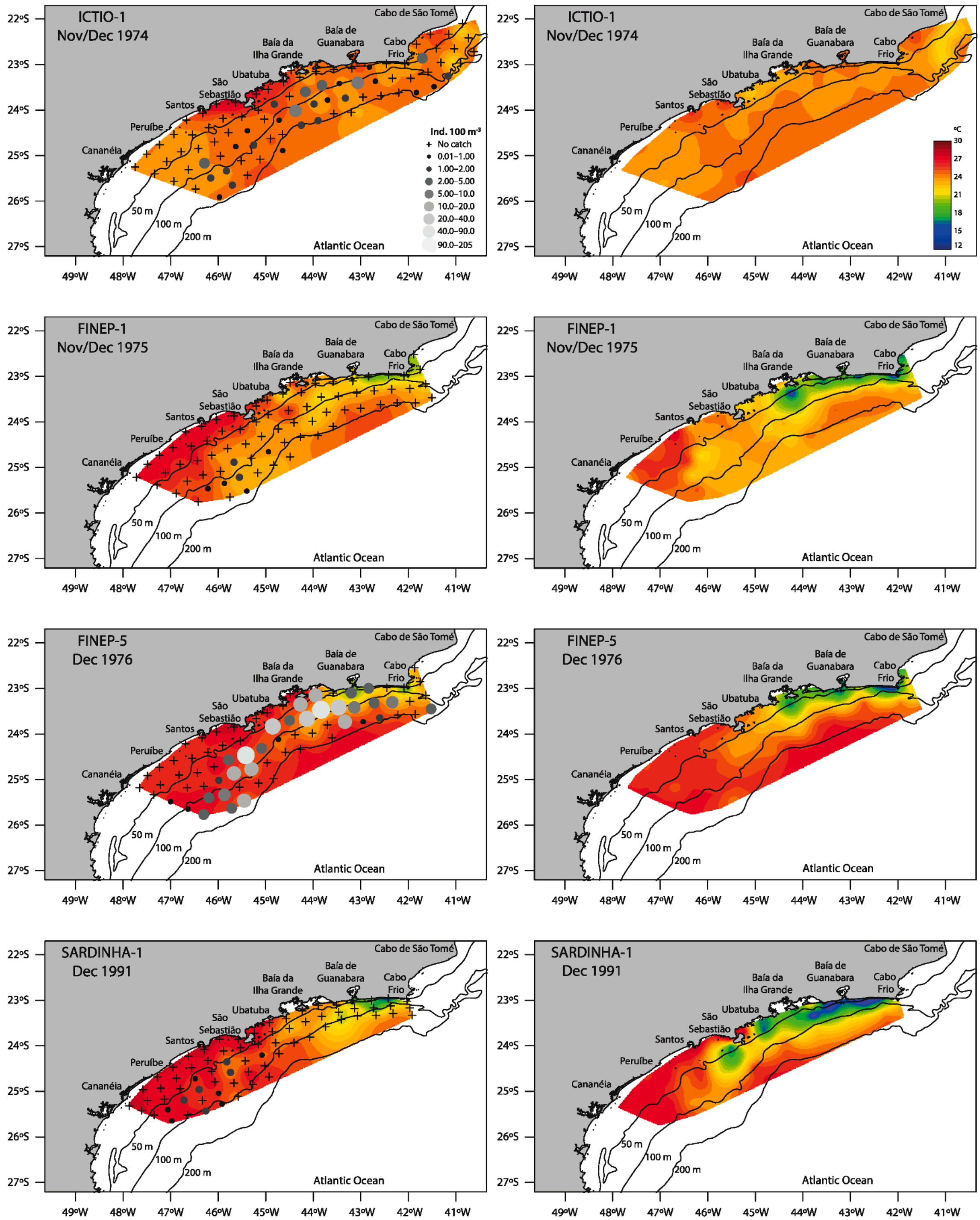

Fig. 4. Horizontal distribution of Argonautidae paralarvae abundance and surface temperature on left and subsurface temperature (10 m) on right in the in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer from 1974 to 1991.

roles of mesoscale features in the transport of argonautid paralarvae over shallow waters of the SE Brazilian shelf. Projeto Integrado (PI) comprised the summer and winter cruises in 1985, 1987 and 1988 (Table 1) in the Ubatuba region, northward to São Sebastião Island, the data from which revealed a marked seasonal trend in argonautid paralarvae abundance (Fig. 6). The highest abundances were recorded during summer cruises and were associated with low temperatures in the subsurface waters; lower abundance of paralarvae were observed in winter when water temperatures were comparatively warmer. Furthermore, samples from an MPS collected during cruises DEPROAS-1 and DEPROAS-3 were used to verify the vertical distribution of argonautid paralarvae relative to the major water masses during SACW upwelling at Cabo Frio. It should be noted that the samples from DEPROAS-1 were collected from a single transect visited on three consecutive days. The data revealed that the paralarvae from DEPROAS-1 (Fig. 7) were associated with the shallowest station, and corresponded to SACW upwelling. The highest abundances were observed in a transect in DEPROAS-3, likely owing to a counterclockwise rotating eddy in the shelf areas (Gouveia et al., 2021). In the latter transect of DEPROAS-3, the paralarvae distribution did not follow a defined pattern, and was observed in the surface TW, subsurface SACW, and the thermocline (Fig. 8).

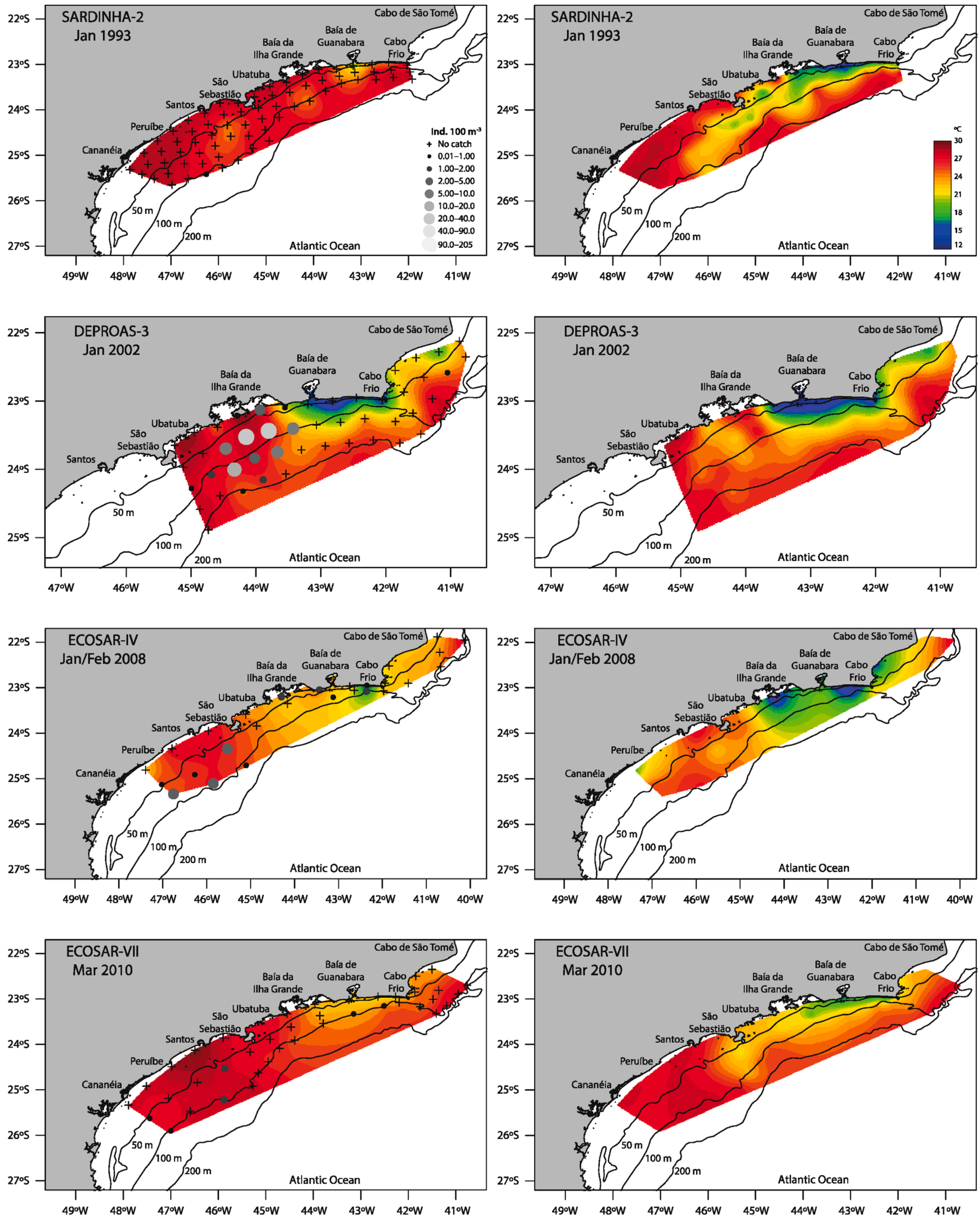

Fig. 5. Horizontal distribution of Argonautidae paralarvae abundance and surface temperature (left) and subsurface temperature (10 m, right) in the in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer during 1993–2010.

The SPQ analysis for surface temperatures showed no correlation with paralarvae occurrence, and a tolerance range of 16–28 °C was estimated. At the subsurface (10 m), the tolerance became 14–28 °C, concentrating at ~ 23 °C. Surface and subsurface temperatures of ~ 27 °C were avoided (Fig. 9). Surface salinity tolerance was 33–37, with a preference of 35–36, while values of ~ 34.5 were avoided. In the subsurface, tolerance was 34–37.5, with a preference of 35–35.5 (Fig. 9).

4. Discussion

The present study explains the occurrence of epipelagic argonautid paralarvae along the SBB continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) (Araújo and Gasalla, 2019). The historical data of 22 plankton surveys between 1974 and 2010 provided a broad perspective on the oceanographic processes that may influence the distribution and abundance patterns of early-life stages of Argonautidae in the study area. Our findings support the idea that mesoscale hydrodynamic processes, such as the upwelling front, coastal upwelling jets, meanders, and eddies from the BC, are crucial for the distribution of epipelagic argonautid paralarvae.

Argonaut paralarvae were recorded mainly during summer cruises compared with winter (Table 2). Even though distributed throughout

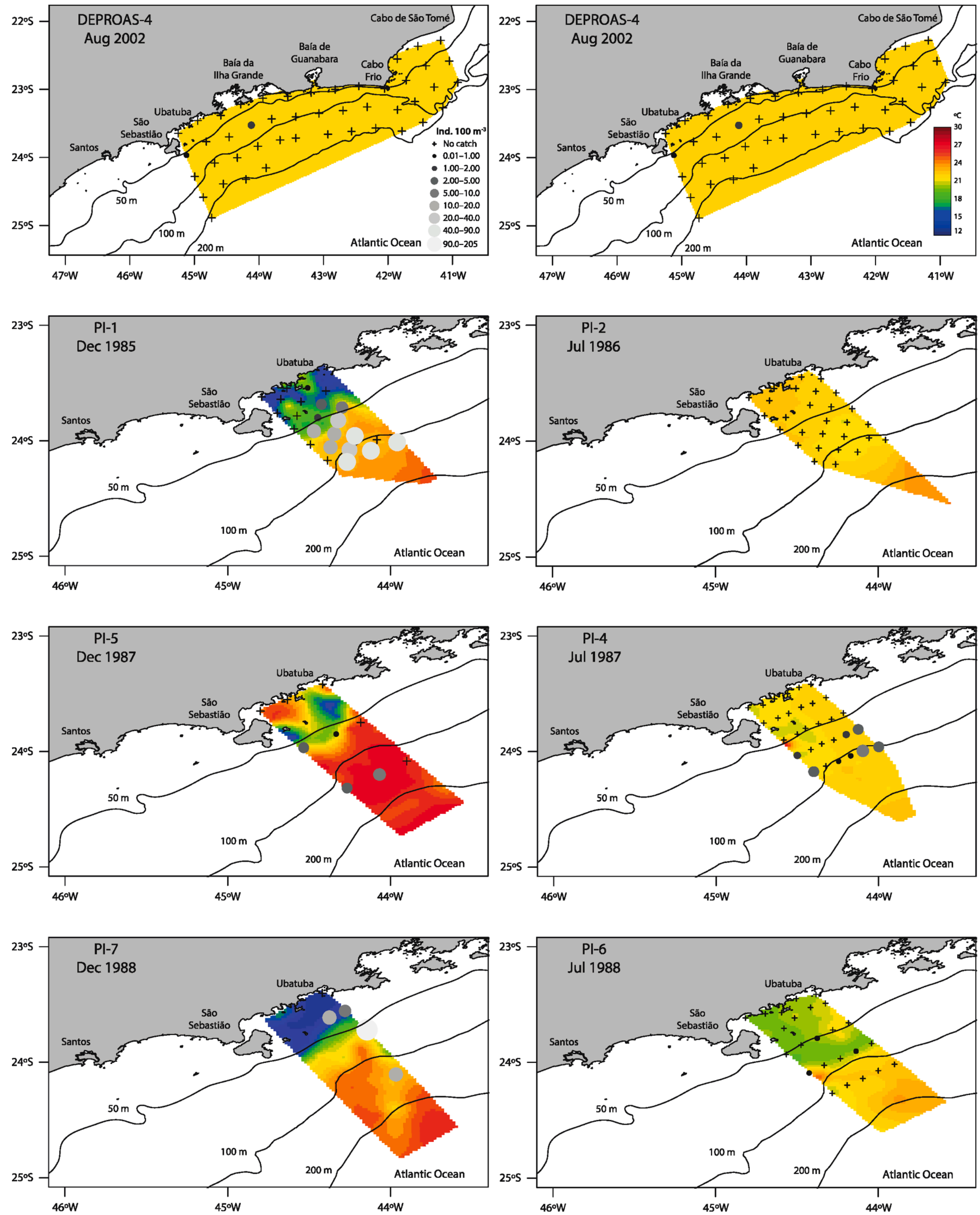

Fig. 6. Horizontal distribution of Argonautidae paralarvae abundance and subsurface temperature (10 m) in the continental shelf of Ubatuba (23°5′ S) during summer (left) and winter (right) during 1985–1988.

the study area (Figs. 4, 5, and 6), paralarvae occurrence was markedly concentrated in the middle and outer shelf areas south of São Sebastião Island (24° S). In contrast, a more homogenous horizontal distribution from the inner to outer shelf areas was observed towards north between Cabo Frio (22° S) and São Sebastião Island.

The higher abundance during summer compared to winter cruises suggests at least two possible explanations: the seasonal reproductive cycle of Argonautidae and the influence of mesoscale features over shelf areas during summer. Based on the distribution of Argonautidae in open ocean waters (Boyle and Rodhouse, 2005; Finn, 2013), the former explanation requires a year-round study to investigate the seasonal abundance of paralarvae in offshore waters rather than continental shelf areas. Although it is crucial to investigate the seasonality of the Argonautidae reproductive cycle, such studies do not explain the mechanisms by which paralarvae are transported to shallow shelf waters. The coastal upwelling system of Cabo Frio is remarkably seasonal and not only influences the local primary productivity (Gaeta and Brandini, 2006; Lopes et al., 2006; Brandini et al., 2018), but also the distribution of several planktonic larval species (Lopes et al., 2006; Yoshinaga et al., 2010; Katsuragawa et al., 2014; Namiki et al., 2017; Favero et al., 2017; Araújo and Gasalla, 2017; 2019). This coastal upwelling during summer is also linked to the intensity of meanders and eddies from the BC, which

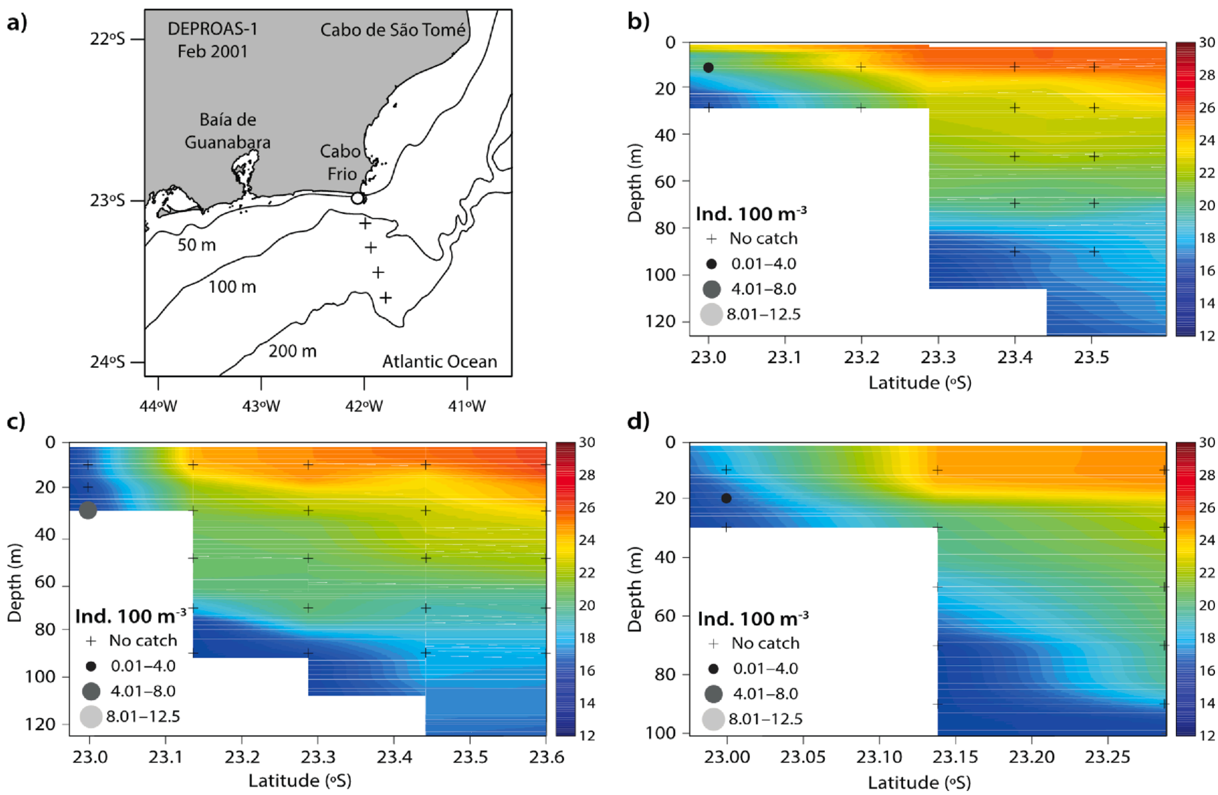

Fig. 7. Vertical distribution of Argonautidae paralarvae abundance in the continental shelf of Cabo Frio (22° S) during summer in 2001. (a) Location of stations and transect (o = positive station); (b) vertical distribution on transect 1; (c) transect 2 and (d) transect 3.

are neutralized by the increased northward-moving cold atmospheric fronts in winter (Gouveia et al., 2021). Thus, mesoscale features, such as coastal upwelling and meanders of the BC are plausible mechanisms by which these paralarvae are transported from open ocean waters to continental shelf areas during the summer months.

Three major summer scenarios have been derived from this study based on a strong interannual variability in the distribution of paralarvae. The first is related to the upwelling in Cabo Frio, which is associated with a high abundance of paralarvae (FINEP-5, DEPROAS-3, ECOSAR-IV). The second scenario is linked to upwelling associated with the relatively low FO of the paralarvae (FINEP-1, SARDINHA-1, SARDINHA-2, and ECOSAR-VII). The third scenario was only observed during a single cruise (ICTIO-1), and showed a relatively high FO of paralarvae over the entire study area in the absence of coastal upwelling. Thus, it is inferred that the occurrence of paralarvae in continental shelf areas is largely independent of SACW advection in Cabo Frio. Supporting data on the vertical distribution of paralarvae during coastal upwelling events in Cabo Frio and quotient analysis also indicated a weak association of Argonautidae with SACW and low temperatures. These findings are in contrast to the distribution of juveniles (mainly females) and mature males that occur at middle-shelf depths under the influence of SACW and high chl-a concentrations on the southern Brazilian continental shelf (28°09–29°56′ S) (Vidal et al., 2010). However, based on available data, the latter study revealed that early paralarvae (<3 mm ML), were found on the outer shelf associated with BC and TW. Thus, we suggest that the cross-shelf transport of epipelagic Argonautid paralarvae occurs via meanders and eddies from the BC rather than subsurface intrusions of SACW.

Several studies have evidenced the importance of meanders and eddies from BC in transporting planktonic larvae (Yoshinaga et al., 2010; Katsuragawa et al., 2014; Namiki et al., 2017). These mesoscale features were also recognized crucial to the early-life stages of cephalopods in other Western boundary systems such as in the Western Caribbean (Castillo-Estrada et al., 2020) and the Western North Atlantic Ocean (Vecchione et al., 2001). In the present study, one of the highest abundances of Argonautidae paralarvae was recorded at the southern border of the upwelling front during a strong coastal upwelling event off Cabo Frio (DEPROAS-3, Fig. 8). This event coincided with the presence of the BC over shelf areas south of Cabo Frio, mainly due to its meanders and eddies (Campos et al., 2000; Castelao and Barth, 2006; Palóczy et al., 2014), promoting the onshore transport of TW, and thereby lanternfish larvae, from open waters (Namiki et al., 2017). This mechanism can be considered as the most plausible explanation for the accumulation of Argonautidae paralarvae at the southern border of the upwelling front during DEPROAS-3 (Figs. 5 and 8). Owing to differences in the topography of the continental shelf in the study area, this mechanism can also be used to explain the higher FO of paralarvae closer to the coast in the northern (narrower shelf) portion than in the southern (wider shelf) portion. The dominance of the oceanic families Enoploteuthidae and Ommastrephidae in narrow continental shelf areas, suggesting cross-shelf paralarval transport, has been observed not only in Cabo Frio as compared to other regions of the SBB (Araújo and Gasalla, 2019), but also in the Mesoamerican Barrier Reef System, Western Caribbean (Castillo-Estrada et al., 2020). Interestingly, TW intrusion into shelf areas by meanders and eddies of BC may also promote cross-shelf larval transport in winter in the absence of coastal upwelling (Namiki et al., 2017). Thus, the relatively high FO of paralarvae in the third summer scenario may still be explained by TW intrusion, independent of coastal upwelling events. Additionally, paralarval transport to the inner shelf, i.e., outside the BC domain, might be facilitated by Ekman transport as winds are the main mechanism for current generation in these shallow areas.

Notably, DEPROAS-3 illustrates the initial phases of a strong coastal upwelling event in Cabo Frio, which is unique compared to other cruises

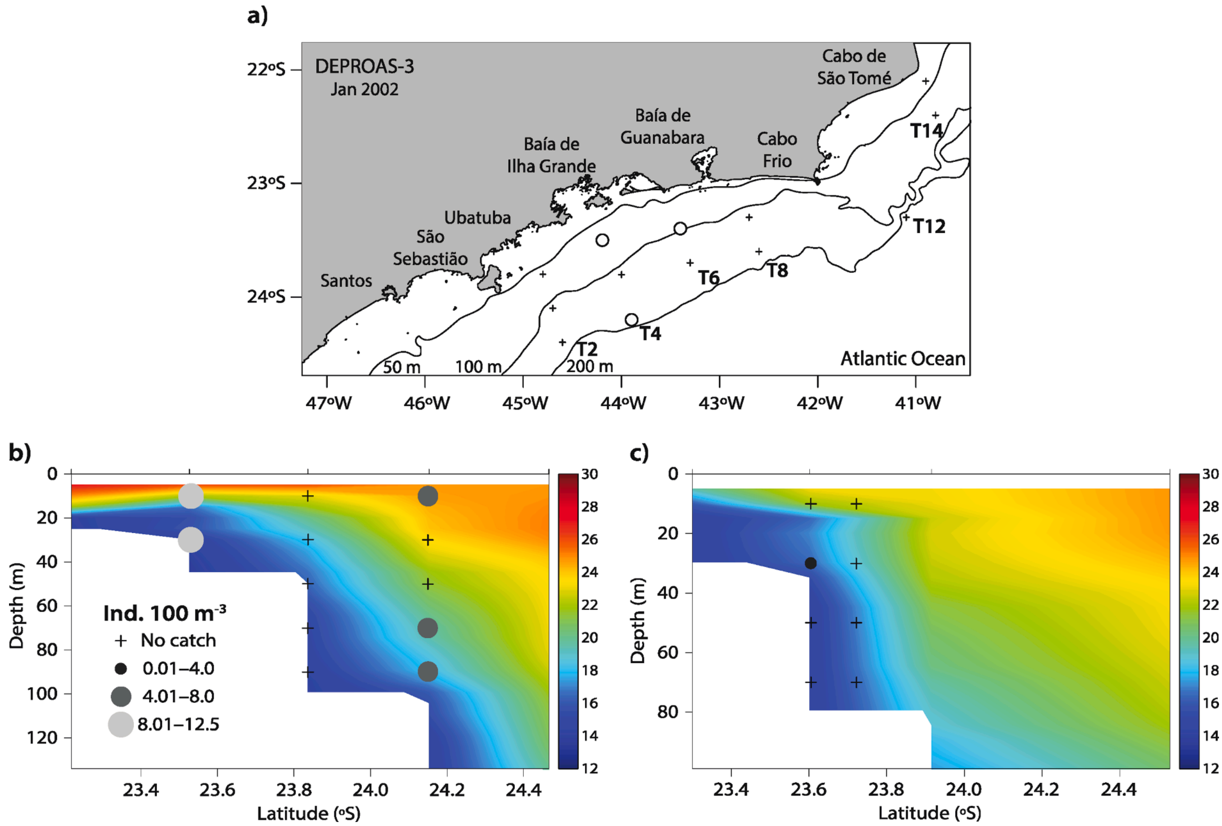

Fig. 8. Vertical distribution of Argonautidae paralarvae abundance in the continental shelf between Cabo de São Tomé (22° S) and São Sebastião (23° S) during summer in 2002. (a) Location of stations and transects (o = positive station); vertical distribution on (b) transect T4 and (c) transect T6.

(Figs. 7 and 8). For instance, during FINEP-5 and ECOSAR-IV cruises that showed relatively high abundances of paralarvae (first summer scenario), the upwelling event was relatively more mature with the development of a southward coastal upwelling jet flowing along-shore (Lorenzzetti and Gaeta, 1996;Carbonel, 1998; Yoshinaga et al., 2010; Cerda and Castro, 2014;Calil et al., 2021). However, supporting the mechanism of onshore larval transport with TW intrusion south of the upwelling front, the highest abundances were registered on the southern fringes of the coastal upwelling jets. Consistent accumulation of paralarvae in the southern borders of the upwelling front (DEPROAS-3) or jets (FINEP-5 and ECOSAR-IV), and early and late expressions of the Cabo Frio upwelling events suggest that both features may represent effective barriers preventing cross-shelf larval transport from open waters to shallow shelf areas. The cross-shelf barrier imposed by upwelling fronts or jets may also explain the low frequencies of Argonautidae paralarvae associated with relatively cold waters and the generally low paralarval abundances in the northern portion of the study area during continuous coastal upwelling off Cabo Frio (second summer scenario).

The second summer scenario was associated with overall low paralarvae FO. First, the low abundance of paralarvae may be attributed to the upwelling jets, which act as barriers and hinder direct transport from TW into shelf areas. Second, this low abundance may be the result of dilution as these jets travel long distances to reach the southern portion of the study area, where they deviate offshore and flow southwestwards. Argonautidae paralarvae occurred consistently in the southern fringes of these long-distance travelling upwelling jets, and can be related with their occurrence in the middle and outer shelf areas (Figs. 4 and 5; FINEP-1, SARDINHA-1, and ECOSAR-VII). Long-distance advection of Argonautidae paralarvae by the coastal upwelling jets may also explain their relatively high frequencies in coastal areas off Ubatuba during summer, as observed due to SACW in subsurface waters (Fig. 6 -PI-1,5 and 7). Thus, long-distance transport by south-moving upwelling jets may play a major role in the recruitment of Argonautidae in the SBB shelf.

The oceanographic processes discussed above influence paralarvae survival by allowing their development in higher productivity areas compared to the open ocean. However, in addition to mesoscale transport mechanisms, abundances may also be related to their aggregation tendency (chain formation) (Nesis, 1977). The reason for chain formation in Argonautidae is unclear, and several hypotheses have been proposed for it, e.g., shared swimming among individuals (Voss and Williamson, 1971), increased visual appearance of females reduces the mating effort for males (Rosa and Seibel, 2010), their benthic origin, which intrinsically associates their lifestyle with a substratum (Rosa and Seibel, 2010). Chain formation can also be a special adaptation of argonaut females for passive floating during egg laying and hatching (Nesis, 1977). Chain formation by females could explain the elevated abundance of paralarvae in the shelf areas of SBB. However, it is worth mentioning that females were not observed in the studied samples probably because of the sampling method used in this study.

5. Conclusions

This study explains the influence of oceanographic processes for an unusually high abundance of Argonautidae paralarvae in continental shelf waters of the SBB, especially during the summer months. Our data suggest that the net cross-shelf transport of Argonautidae paralarvae from open waters to shelf areas is related to the onshore intrusion of TW promoted by meanders and eddies of the BC, particularly in the northern portion of the study area. The upwelling front off Cabo Frio and the resultant south-moving coastal upwelling jet prevent onshore TW intrusion into shelf areas, functioning as physical barriers for cross-shelf larval transport. However, upwelling jets can act as effective highways for long-distance larval transport from Cabo Frio to the southern

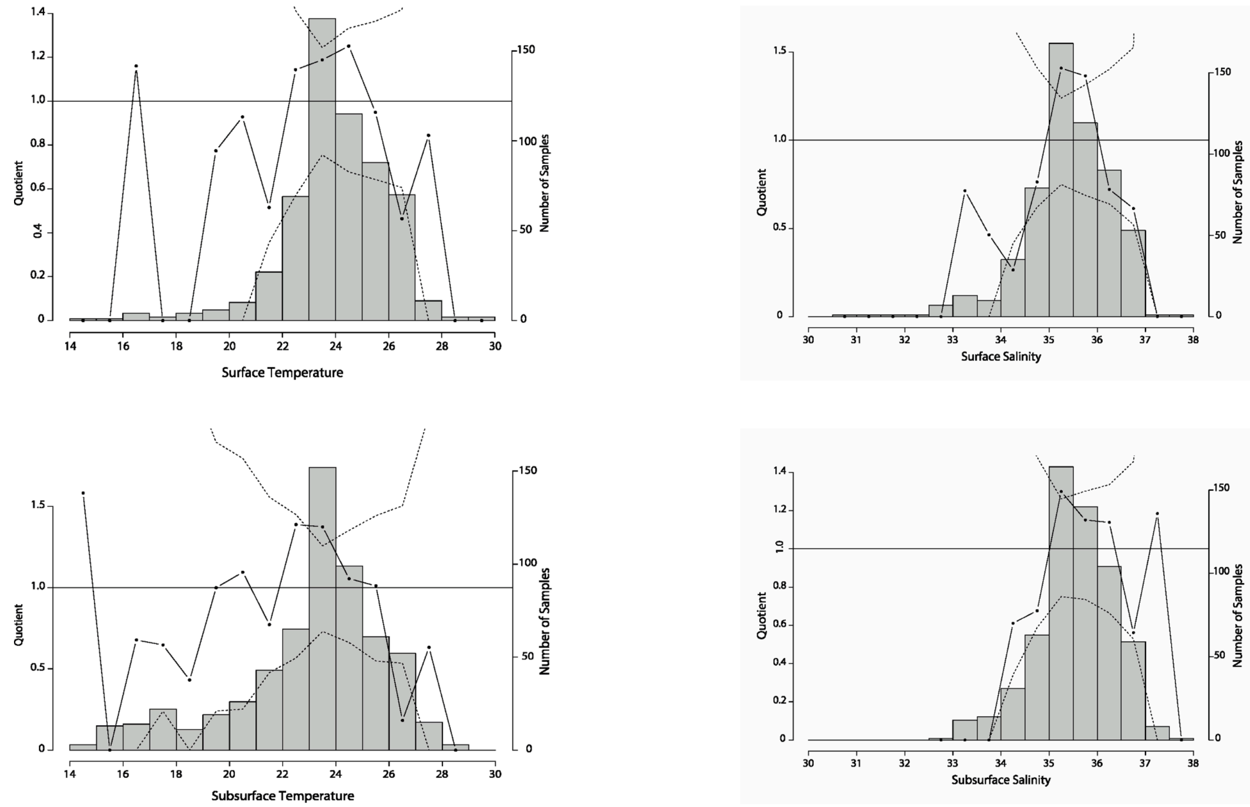

Fig. 9. SPQ analysis for surface and subsurface temperature (°C) and salinity of Argonautidae paralarvae occurrence in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer during the study period. Histograms represent the number of stations within each bin of the covariate, dashed-dotted line represents the paralarvae abundance quotient value. The horizontal line represents the null hypothesis of evenly distributed paralarvae and the dashed lines represent its upper and lower confidence intervals.

portions of the SBB, where they diverge offshore towards the southwest. Although representing only a snapshot of both paralarval abundance and oceanographic conditions at a given location and time of year, the findings of this study may contribute to a better understanding of the distribution of Argonautidae paralarvae and other epipelagic larval species in the SBB. The importance of mesoscale processes of the BC, especially meanders and the coastal upwelling jet, for the distribution and reproductive strategies of Argonautidae in the SBB are still uncertain, and require further large-scale studies.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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