CAROLINA COSTA DE ARAÚJO

Cephalopod biodiversity in the Southeastern Brazil Bight: early life stages and associated ocean processes

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Tese apresentada ao Instituto Oceanográfico da Universidade de São Paulo, como parte dos requisitos para obtenção do título de Doutora em Ciências, Programa de Oceanografia, área de Oceanografia Biológica.

Orientadora: Profa. Dra. Maria de los Angeles Gasalla

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RESUMO

ARAÚJO, Carolina Costa de. **Biodiversidade de cefalópodes na Plataforma Continental Sudeste do Brasil:** estágios iniciais de vida e processos oceanográficos associados. 2023. 105 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2023.

Os cefalópodes são comumente conhecidos como lulas, sépias e polvos e representam um importantes recursos pesqueiros em todo o mundo. Habitando quase todos os ecossistemas marinhos, os cefalópodes ocupam um nível trófico intermediário sendo considerados predadores oportunistas alimentando-se de uma variedade de peixes e crustáceos, além de serem importantes presas de peixes, mamíferos e aves marinhas. Crescimento rápido, ciclo de vida curto e forte plasticidade de história de vida refletem sua alta capacidade de resposta/sensibilidade às mudanças ambientais, particularmente durante os primeiros estágios da vida. Nesse sentido, estudos de distribuição e abundância de paralarvas na coluna de água têm sido considerados cruciais para o entendimento da biologia, áreas de desova e estrutura populacional de cefalópodes. O presente estudo investigou a abundância e a composição de paralarvas da Plataforma Continental Sudeste do Brasil (PCSB) revisitando uma coleção histórica de amostras de 1974 a 2010. O objetivo geral foi determinar padrões de longo prazo em processos oceanográficos que levam à flutuações na abundância e composição dos estágios iniciais da vida dos cefalópodes. Para tanto, este estudo foi dividido em três capítulos. No primeiro capítulo, a riqueza taxonômica de paralarvas foi avaliada e uma diversidade inédita de paralarvas oceânicas foi revelada em áreas da PCSB. No segundo capítulo, focado nas paralarvas de Argonautidae, uma interação de transporte plataforma e oceano aberto e ao longo da costa foi desvendada e sugerida como um dos principais contribuintes para a distribuição espacial e temporal dos estágios iniciais de vida dos cefalópodes na PCSB. O terceiro capítulo, explorando séries temporais através de análises multivariadas, descreveu uma assincronia temporal na abundância de conjuntos de paralarvas sobre a PCSB, potencialmente ligada à variabilidade multidecadal da temperatura e salinidade da superfície do oceano, bem como às oscilações climáticas globais. Juntos, esses estudos revelaram padrões de biodiversidade onde a abundância, composição e distribuição de paralarvas em áreas de plataforma estão intimamente associados com a dinâmica oceanográfica da PCBS. Processos oceanográficos como meandros e vórtices da Corrente do Brasil, eventos de ressurgência costeira de Cabo Frio e jatos de ressurgência que fluem para o sul e ao longo da costa por centenas de quilômetros são características-chave que influenciam tanto a diversidade quanto a abundância de assembleias de paralarvas na plataforma continental da PCBS. Cada um desses processos pode afetar distintamente a distribuição das paralarvas, uma vez que podem variar espacialmente e temporalmente (variabilidade sazonal e interanual). Finalmente, as principais suposições sobre a ecologia e o comportamento das paralarvas no presente estudo foram baseadas em uma amostragem multidecadal e em grande escala espacial usando a coleção histórica do ColBio-IOUSP, que forneceu propiciou insights entendimentos que poderiam ser subestimados em estudos direcionados a variações sazonais ou interanuais.

Palavras-chave: Paralarva, dinâmica oceânica, Plataforma Continental Sudeste do Brasil, análise de séries-temporais.

ABSTRACT

ARAÚJO, Carolina Costa de. **Cephalopod biodiversity in the Southeastern Brazil Bight:** early life stages and associated ocean processes. 2023. 105 f. Tese (Doutorado) – Instituto Oceanográfico, Universidade de São Paulo, São Paulo, 2023.

Cephalopods are commonly known as squid, cuttlefish and octopus and represent a major targeted fisheries resource worldwide. Inhabiting almost all marine ecosystems, cephalopods occupy an intermediate trophic level being considered opportunistic predators feeding on a variety of fishes and crustaceans and important preys of fishes, mammals and seabirds. Their rapid growth, short lifespans and strong life-history plasticity reflect their high responsiveness/sensitivity to environmental changes, particularly during early-life stages. In this regard, surveys of paralarvae abundance and distribution in the water column have been considered crucial to understand the biology, spawning areas and population structure of cephalopods. The present study investigated the abundance and composition of paralarvae from the continental shelf of the Southeastern Brazil Bight (SBB) by revisiting a historical collection of samples from 1974 to 2010. The overarching goal was to determine long-term patterns in oceanographic processes leading to fluctuations in the abundance and composition of cephalopods early life stages. For this purpose this study was divided into three chapters. In the first chapter, the taxonomic richness of paralarvae was assessed and an unprecedentedly high diversity of oceanic paralarvae was revealed in shelf areas of the SBB. In the second chapter, focused on Argonautidae paralarvae, an interplay of cross-shelf and along-shore transport was untangled and suggested as major contributor to spatial and temporal distribution of the cephalopods early life stages over the SBB shelf. The third chapter exploring multivariate time-series depicted a temporal asynchrony in the abundance of paralarvae assemblages over the SBB potentially linked to multi-decadal variability of ocean's surface temperature and salinity as well as global climate oscillations. Taken together, these studies revealed biodiversity patterns where the abundance, composition and distribution of paralarvae over shelf areas are intimately associated with the oceanographic dynamics of the SBB. Processes such as meanders and eddies of the Brazil Current, coastal upwelling events of Cape Frio and upwelling jets that flow southwards and along-shore for hundreds of kilometers are key features driving both diversity and abundance of paralarvae assemblages in the continental shelf of the SBB. Each of these processes may distinctively affect the distribution of paralarvae, since they might vary both spatially and temporally (seasonal and interannual variability). Finally, major assumptions about paralarvae ecology and behavior in the present study were based on a multi-decadal and large spatial scale sampling using the ColBio-IOUSP historical collection, which provided insights that could be underrated in studies targeting seasonal or interannual variations.

Keywords: Paralarvae, ocean dynamics, Southeastern Brazil Bight, Biodiversity, long-term variability.

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1 GENERAL INTRODUCTION

1.1 CEPHALOPODS' BIOLOGICAL TRAITS AND EARLY LIFE STAGES

Cephalopods, commonly known as squid, cuttlefish and octopus, have a unique set of biological characteristics and play a pivotal role in almost all marine ecosystems (e.g. Boyle and Boletzky 1996). In the marine food web, they occupy an intermediate trophic level and are considered opportunistic predators feeding on a variety of fishes and crustaceans. In retrospect, cephalopods represent important preys of fishes, mammals and seabirds (Santos and Haimovici 1998; 2001; 2002; Piatkowski et al. 2001; Staudinger 2006). Despite being very diverse, most cephalopods share common life traits such as short life span (2 to 4 years in average; most cephalopods are single breeders and die soon after reproduction) and fast growth rate (i.e. achieving maturity after one winter) (Boyle 1983; 1987; Boyle and Rodhouse 2005; Rodhouse 2010; Robin et al., 2014). From egg to spawning adults, they undertake a series of transitions, which involve radical changes in the organism and its relationship with the environment (Robin et al., 2014). For instance, the transition egg to paralarvae is characterized either by discrete morphological differences relative to adults (e.g. ommastrephids) or massive behavioral differences from a planktonic post hatching to nektonic or benthic adulthood (e.g. octopus) (Boletzky 1977).

Owing to their rapid growth, short lifespans, and strong life-history plasticity, cephalopods are highly responsive to environmental changes, generally resulting in significant seasonal and inter-annual fluctuations in population abundances (Boyle and Rodhouse 2005). These fluctuations may affect the entire ecosystem dynamics (André et al., 2010) and trends in cephalopod fisheries catch (Caddy and Rodhouse 1998; Rodhouse et al., 2014). For example, anthropogenic climate change effects such as ocean acidification may negatively impact cephalopod survival (Rodhouse et al., 2014). Conversely, early evidence using time-series fisheries data from 1953 to 2013 suggests that cephalopod populations have proliferated in response to a changing oceanic environment: with both abiotic (e.g. temperature increase) and biotic (e.g. competition pressure) factors being considered potential drivers of variation (Doubleday et al., 2016). Nonetheless, ocean warming will likely result in complex biological, physiological and behavioral changes (Pecl and Jackson 2008), particularly for cephalopods early life stages. Recent studies in benthic octopus have shown a higher thermal sensitivity in embryos than subadults and adults (Uriarte et al., 2012). It is well known that both the environment within the embryo and the surrounding oceanographic conditions (e.g.

oxygenation, temperature and salinity; Strathmann and Strathmann 1995; Uriarte et al., 2012; Sen 2005) are of utmost importance for survival and hatching success (Robin et al., 2014).

The present study is focused on paralarvae, firstly introduced by Young and Harman (1988), or the planktonic early stages of cephalopods between hatchling and subadults. In general, paralarvae have a similar morphology as compared to subadult and adult individuals. However, the changes occurring in the transition from paralarva to subadult are subtle relative to growth rates or morphological aspects (e.g. proboscis in ommastrephid) and should be identified for each family, since it does not involve ecological or habitat changes in all species (Shea and Vecchione 2010). Once hatched, paralarvae undergo a critical transition between endogenous to exclusively exogenous feeding, becoming active predators on other zoopplankton, and their exposure to specific environmental conditions will determine the recruitment success. Temperature, for instance, is known to positively affect the growth rates of paralarvae, shortening the transition to a subadult phase (e.g. Iglesias et al., 2004; Imamura 1990; Villanueva 1995). Nutrition is another crucial factor that might influence the development of early stages in cephalopods. The interplay between abiotic and biotic conditions for paralarvae is thus largely dictated by changes in oceanographic conditions, including currents, mixing, fronts, coastal upwelling, and primary productivity/competitive pressure (Waluda and Rodhouse 2006).

Despite the few studies addressing the spatiotemporal distribution of cephalopods early-life stages, increasing attention has been given to the influence of oceanic circulation on paralarvae population abundance during the last decades, particularly in areas where they represent major fisheries resources such as in Portugal and Spain (González et al. 2005; Moreno et al, 2009; Pierce et al., 2010; Otero et al. 2016). Such information is central to understand paralarvae dispersal behavior, recruitment success and population variability with major ecological and fisheries implications.

1.2 THE GLOBAL IMPORTANCE OF CEPHALOPODS FOR FISHERIES AND THEIR RESPONSES TO CLIMATE CHANGE

Cephalopods importance as targeted fisheries resource continues to rise each year with annual landings estimated at 2 million tons in 1980 to 4 million tons in 2010 (2 to 4% of global annual landings), generating a multi-billion dollar per year business (FAO 2020; Sea Around Us 2020). These figures of large-scale stock assessments are likely underestimated because landings from artisanal fisheries are not generally recorded or quantified (Boyle and Rodhouse

2005). In any case, a stock collapse of cephalopods as fisheries resources will lead to considerable ecological and economic impacts, especially for local communities depending on small-scale artisanal fishery.

In recent years, long-term trends in cephalopods abundance have been evaluated both locally and globally in the context of anthropogenic-induced climate change (Doubleday et al., 2016; van der Kooij et al., 2016; Xavier et al., 2016; Pang et al., 2018; Jin et al., 2020; Le Marchand et al., 2020; Lima et al., 2020; Schickele et al., 2021). Early estimates have reported a global trend of cephalopods' proliferation (Doubleday et al., 2016), and more recent predictions have shown a potential capacity of cephalopods to expand their distribution towards the pole (e.g. Xavier et al., 2016; Le Marchand et al., 2020; Lima et al., 2020). Notably, ocean warming could represent a plausible driver for these trends by accelerating cephalopods' lifecycles. In addition, global depletion of fish stocks, relieving cephalopods from predation and competitive pressure, could have played a major role for the growth of cephalopod populations (Caddy and Rodhouse 1998). These global trends, however, might also vary locally. For instance, in Europe, where cephalopods represent an important fisheries resource, future projections in ocean warming scenarios predict contrasting environmental suitability for cephalopods distribution: unfavorable in the Mediterranean Sea and the Bay of Biscay, whereas favorable in the North and Baltic Seas (Schickele et al., 2021).

In contrast to tradition fishery approaches for exploitation management (e.g. "long-lived" finfish), cephalopods stock estimations are very distinct as the most relevant commercial species live up to 1 year and reproduce only once (Boyle and Rodhouse 2005). Cephalopods stocks reflect their short lifecycles, high turnover of generations, variable growth rates and extended spawning, and thus the potential biomass of any cephalopod population is extremely difficult to access since there is no overlap between successive generations (Boyle and Boletzsky 1996). Despite their great resilience against fluctuations (e.g. ability to exploit available food resources and to overcome efficiently short adverse environmental events), cephalopods populations are volatile and vulnerable to large deviations in biological and physical variables, particularly during the paralarva phase. Thus long-term assessment of the spatial and temporal variability of early life stages in the water column may contribute to our understanding of cephalopods recruitment dynamics, abundance and habitat distribution. The understanding of these complex interactions is still incipient, but potentially critical to manage cephalopods stocks appropriately, influencing their sustainable exploitation and economic importance (Piatkowski, 1998; Rodhouse 2014).

1.3 THE SOUTH BRAZIL BIGHT AS STUDY AREA

Over the past 50 years, landings of cephalopods in South America have increased steadily particularly due to production in Peru and Argentina, with Brazil representing only a minor portion of the worldwide cephalopod consumption (Ospina-Alvarez et al., 2022). In Brazil, cephalopods represent a bycatch of sardine purse-seine and shrimp trawl fisheries, although small-scale targeted squid fisheries operate in periods of the year when other resources are low (Perez et al., 2002). In addition, squids are also targets of hand-jigging and artisanal fishers mainly during summer, when they often aggregate to spawn (Rodrigues and Gasalla, 2008). With the decline in trawl fisheries since the 80's (Haimovici et al., 2006), there exists a growing demand for cephalopod as fisheries resource (Vidal et al., 2013). The present study is focused on the southeastern Brazil, more specifically the South Brazil Bight (SBB) from Cape Frio (22°S) to Cape Santa Marta Grande (28°S), where the loliginid species *Doryteuthis plei* (Blainville, 1823) and the São Paulo squid *D. sanpaulensis* (Brackoniecki, 1984) are main targets of commercial fisheries (Gasalla et al., 2005; Perez et al., 2005; Rodrigues and Gasalla, 2008).

The SBB represents an 1100 km long stretch of the Brazilian coastline. The continental shelf may be divided into inner, mid and outer shelf shelves, with approximate depth ranges of <50, 50–100 and 100–200 m, respectively (Castro et al., 2006; 1998). The bottom topography between the mid- and outer shelves is smooth, and the shelf-edge located at the 200 m isobath (Mahiques et al., 2010). Whereas the shelf extends up to 230 km off Santos to the 200 m isobath, which is considered the offshore bathymetric limit of the SBB, in the northern and southernmost sectors, the continental shelf is relatively narrow (50–70 km wide) (Mahiques et al., 2010). These latitudinal differences are crucial for water masses circulation and thereby primary productivity distinctions between these sectors.

A peculiar feature of the SBB relative to other western boundary subtropical counterparts is the larger width of its continental shelf, particularly in the central sector, with ca 180 miles separating the coast and the shelf-edge (Brandini et al., 2018). Northerly and northeasterly winds from the western side of the South Atlantic Subtropical High regulate the water circulation in the mid and outer shelves (Satyamurty et al., 1998; Wainer et al., 2006). On the inner shelf, the continental runoff from small rivers and lagoons causes density discontinuities and buoyancy advection (Castro, 2014). The inner- and mid-shelf waters from the SBB are dominated by the less saline Coastal Water (CW, < 20 °C; < 35 psu) (Castro et al., 1998). In the southern sector of the SBB, the Brazilian Coastal Current (BCC) transports a substantial volume of less saline inner- and mid-shelf waters mixed with sub-Antarctic and coastal waters from the La Plata River northward as far as 24–25°S (de Souza and Robinson, 2004). On the outer-shelf, the Brazil Current flowing southwards along the shelf break at velocities ranging from 15 to 50 $cm.s^{-1}$ (Loder et al., 1998; Silveira et al., 2000), consists of the warm salty oligotrophic Tropical Water (TW, > 20 °C; > 36 psu) followed by the deeper nutrient-rich South Atlantic Central Water (SACW, 6–20 °C, 34.6–36 psu), which is the main thermocline below the TW (Castro et al., 1998). Coastal upwelling events of the oceanic SACW may occur seasonally driven by persistent northeastern winds as observed off Cape Frio (23°S) and Cape Santa Marta (28°S) (Valentin et al., 1987; Castello et al., 1997).

The SBB represents the most productive shelf province of the Brazilian margin due to the fertilization by frontal systems occurring simultaneously in different places and seasons (Brandini et al., 2018). Measurements of primary production range from 0.04 to 0.32 $mgC.m^{-2}.d^{-1}$ in the inner shelf and from 0.13 to 45 $mgC.m^{-2}.d^{-1}$ in mid- and outer shelves of the SBB (Brandini 1990; Gaeta and Brandini, 2006; Gonzalez-Rodriguez et al., 1992; Metzler et al., 1997; Brandini 1988), with an average rate of 0.24 $mgC.m^{-2}.d^{-1}$ (Gaeta and Brandini, 2006). Of note, the influx of nutrients in to the lower euphotic zone (1–5% light) is caused by SACW advection driven by a range of physical processes. On the inner-shelf, prevailing northeasterly winds during summer season result in SACW upwelling particularly in Cape Frio, where associated phytoplankton blooms are frequently observed (Valentin et al., 1987). Conversely, southwesterly winds associated with cold fronts discontinue upwelling events preventing them to occur year-round (Castro et al., 1998; 2006; Cerda and Castro 2014). Although less biologically studied, SACW plumes from Cape Frio upwelling front are frequently observed 300-400 km southwards, flowing along the coastline (Lorenzzetti and Gaeta, 1996; Gouveia et al., 2021). Over the shelf-break, SACW upwelling is induced by both bottom topography and hydrodynamic instabilities such as cyclonic eddies and meandering of the BC (Campos et al., 2000; Calado et al., 2006), and may locally affect the biological production (Yoshinaga et al., 2010; Namiki et al., 2017). Coastal and shelf edge SACW upwelling are crucial to the SBB biological productivity leading to episodic events of new production that replace the otherwise oligotrophic scenario of this province (Metzler et al., 1997; Brandini et al., 1998; 2018).

1.4 PRIMARY AIMS OF THE PRESENT STUDY AND BRIEF CHAPTERS' DESCRIPTION

Although the oceanographic dynamics of the SBB is relatively well studied both physically (e.g. Cerda and Castro, 2014) and biologically (particularly primary production [e.g. Carbonel and Valentin 1999; Brandini et al., 2018], zooplankton [e.g. Lopes et al., 2006] and fish larvae [e.g. Katsuragawa et al., 2014]), the distribution of cephalopods early life stages and its relationship with the oceanic dynamics from the study are still poorly understood. Despite limited in numbers of publications, there exist relevant literature available in this topic (Martins and Perez, 2006; Vidal et al., 2010; Araújo and Gasalla, 2017). Nonetheless, the present study represents the first attempt to investigate long-term changes in cephalopods distribution over the SBB, by revisiting a historical collection of samples from 1974 to 2010. The main objectives of the study are:

1. To verify major oceanographic features driving the paralarvae diversity over the continental shelf of the SBB (Chapter 1);
2. To evaluate long-term argonauts paralarvae abundance in the SBB, and it's relationship with oceanic dynamics of the region (Chapter 2);
3. To apply exploratory multivariate analyses aimed at exploring major abiotic driving factors affecting paralarvae assemblages over the SBB in a large scale time series study (Chapter 3).

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2 BIODIVERSITY OF CEPHALOPOD EARLY-LIFE STAGES ACROSS THE SOUTHEASTERN BRAZILIAN BIGHT: SPATIO-TEMPORAL PATTERNS IN TAXONOMIC RICHNESS (CHAPTER 1)

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Abstract

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

Keywords: Diversity, Paralarvae, Continental shelf, Squid, Octopus

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

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

On the Southern Brazilian shelf (22–34°S), the taxonomic composition of cephalopods is relatively well known; data is available from museum collection archives, trawl fishing prospects and fishery records and analysis of stomach contents (Palacio 1977; Costa and Haimovici 1990, Haimovici and Perez 1991; Costa and Fernandes 1993a; Haimovici et al. 1994; Haimovici 1998; Santos and Haimovici 2001, 2002; Vaske Jr and Pereira da Costa 2011).

The Southern Brazilian shelf is dominated by loliginid squids (*Doryteuthis* spp. Naef, 1912) and benthic octopodids (*Octopus* spp. Cuvier, 1797 and *Eledone* spp. Leach, 1817) (Juanicó 1979; Haimovici and Andrigueto-Filho 1986; Haimovici et al. 1989; Haimovici and Perez 1991; Gasalla et al. 2005a, b; Perez et al. 2005; Martins and Perez 2008). The continental slope and adjacent waters are dominated by oceanic squids in the families Ommastrephidae (*Illex argentinus* Castellanos, 1960) and Enoploteuthidae (*Abralia* spp. Gray, 1849) (Haimovici et al. 1995; Santos and Haimovici 1998). In Brazil, the most exploited cephalopod species in fisheries are *D. plei* Blainville, 1823, *D. sanpaulensis* Brakoniecki, 1984, *O. vulgaris* Cuvier, 1797, and *I. argentinus* (e.g., Costa and Haimovici 1990; Haimovici and Andriguetto 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.

2.2 MATERIAL AND METHODS

2.2.1 Study area

The study area comprises the continental shelf of the northernmost SBB between Cabo Frio (23°S) and Cananéia (25°S) (Fig. 1-1). 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. 1-1) (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).

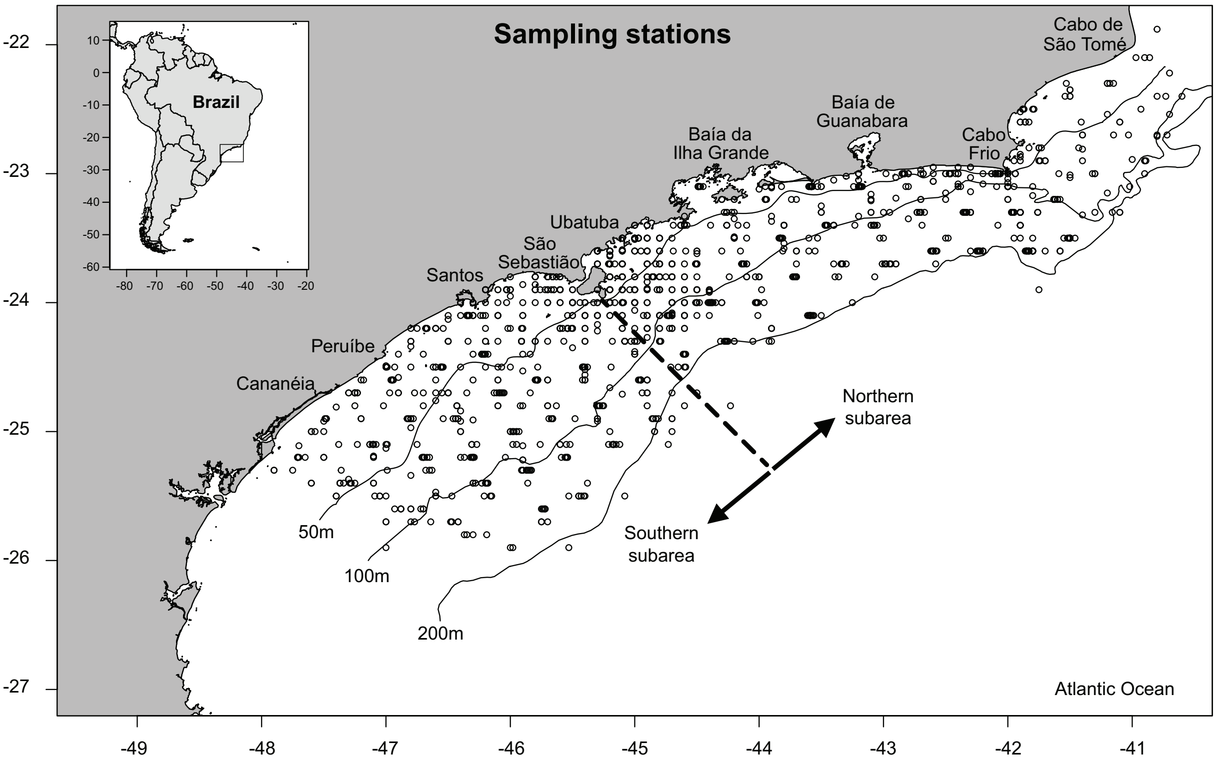

Figure 1-1. Area with the sampling sites between Cabo de São Tomé and Cananéia surveyed from 1974 to 2010. The study area was further subdivided in two northern and southern subareas according to Katsuragawa et al. (2014).

2.2.2 Sampling

A total of 874 plankton samples were collected during 22 cruises from 1974 to 2010 (Table 1-1), 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. 1-1). Plankton samples were obtained onboard several research vessels, “Prof. W. Besnard”, “Atlântico Sul,” and “Albacora”, using bongo nets (0.6 m mouth diameter; 333 and 505-µm mesh size) towed obliquely surface-bottom-surface at ~ 2 knots (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.

2.2.3 Laboratory analysis

Cephalopod paralarvae were separated from the plankton samples and identified to the lowest taxonomic level possible (according to Table 1-2) 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.

2.2.4 Data analysis

Cephalopod paralarvae abundance was standardized using the number of individuals per 100 m^3 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

Table 1-1. 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
	Cabo Frio (RJ) to			R/V Atlântico				

ECOSAR-VII	Cananéia (SP)	jan/2010	20–111	Sul	Bongo	505	Oblique	40

(SIMPER) was applied to the data to identify species contributing to formation 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.

2.4 RESULTS

2.3.1 Taxonomic composition

A total of 2116 cephalopod paralarvae were found in 438 plankton samples. Paralarvae were from 15 taxa belonging to 11 families (Table 1-2). Argonautidae was the most abundant family, while Enoploteuthidae Pfeffer, 1900 and Loliginidae were the most frequent (Table 1-3). 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. 1-2).

2.3.2 Abundance and distribution

Figure 1-3 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.

Table 1-2. 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
          - *Heteroteuthis* sp. (Rüppell, 1844)
      - Order Myopsida Orbigny, 1841
        - Family Loliginidae Lesueur, 1821
          - *Doryteuthis plei* (Blainville, 1823)
          - *Doryteuthis sanpaulensis* (Brakoniecki, 1984)
          - *Lolliguncula brevis* (Blainville, 1823)
          - *Pickfordiateuthis pulchella* Voss, 1953
      - Order Oegopsida Orbigny, 1845
        - Family Ancistrocheiridae Pfeffer, 1912
          - *Ancistrocheirus lesueuri* (Orbigny, 1842)
        - Family Cranchiidae Prosch, 1847
        - Family Enoploteuthidae Pfeffer, 1900
          - *Abralia* spp. Gray, 1849
          - *Abraliopsis* spp. Joubin, 1896
        - Family Lycoteuthidae Pfeffer, 1908
        - Family Octopoteuthidae Berry, 1912
          - *Octopoteuthis* sp. Rüppell, 1844
        - Family Ommastrephidae Steenstrup, 1857
          - *Illex* spp. Steenstrup, 1880
          - *Ommastrephes bartramii* (Lesueur, 1821)
          - *Sthenoteuthis pteropus* (Steenstrup, 1855)
        - Family Pyroteuthidae Pfeffer, 1912
    - Superorder Octobrachia Fioroni, 1981
      - Order Octopodida Leach, 1818
        - Suborder Incirrita Grimpe, 1916
          - Family Argonautidae Tyron, 1879
            - *Argonauta* spp. Linnaeus, 1758
          - Family Octopodidae Orbigny, 1845
            - *Octopus* spp. Cuvier, 1797
            - *Octopus defilippi* Verany, 1851

Table 1-3. Taxonomic composition, number of individuals (N), frequency of occurence (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**		

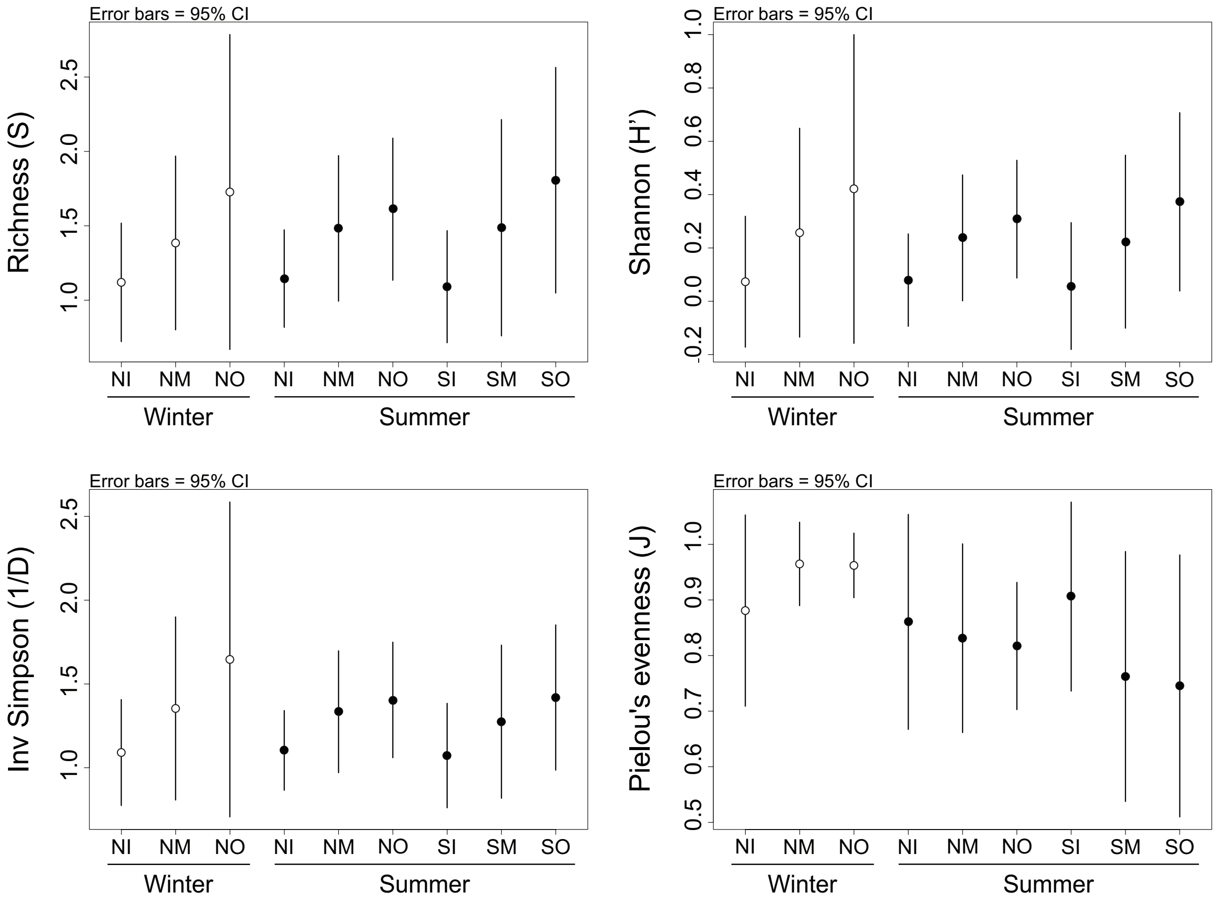

Figure 1-2. Mean and 95% confidence intervals of family-level diversity indexes for each subarea and bathymetric zone. N = northern subarea; S = southern subarea; I = inner shelf; M = middle shelf; O = outer shelf

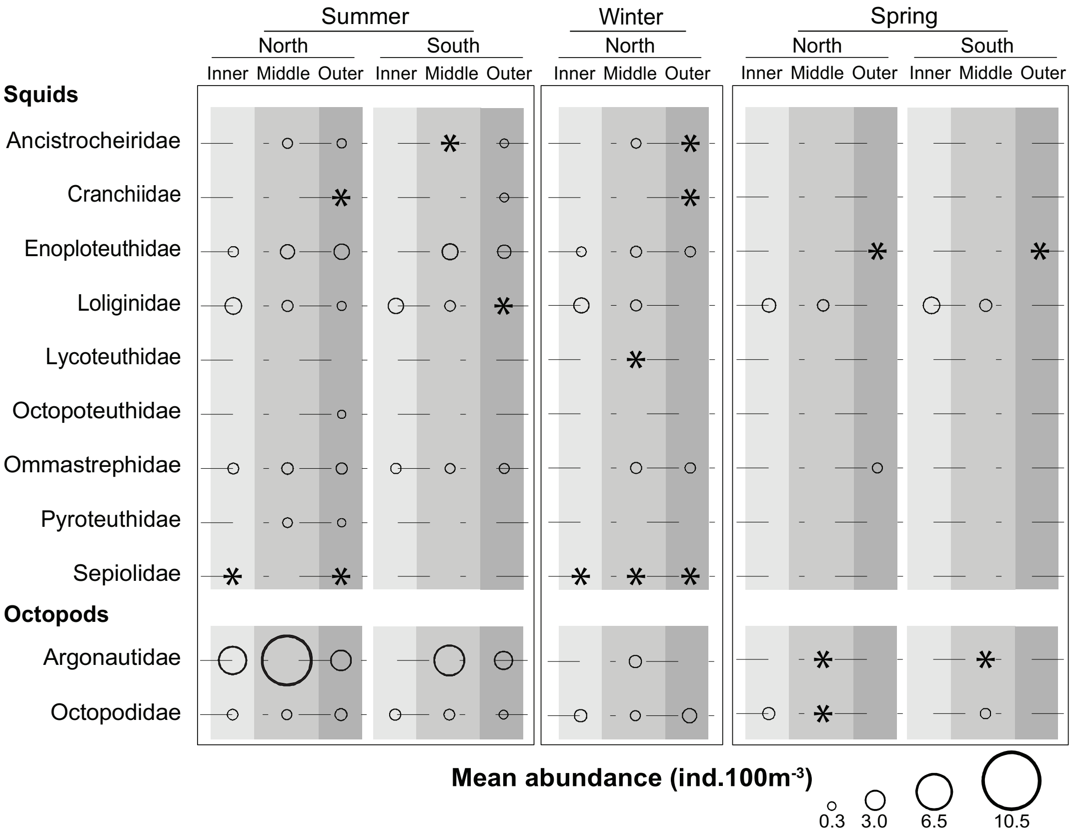

Figure 1-3. Mean abundance of cephalopod paralarvae in the northern sector of the SBB between 1974 and 2010 during summer, winter, and spring. The star symbols (*) represent just one occurrence and horizontal dashed lines were used to facilitate data visualization

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. 1-2). 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 1-2; Fig. 1-3), statistical analyses were exclusively performed for winter and summer (see below).

2.3.3 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. 1-4, 1-5, and 1-6). 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. 1-4). The inner shelf is distinguished from middle and outer shelves due to the presence of Loliginidae and Octopodidae (Fig. 1-4). A similar pattern of presence-absence was observed in the southern subarea during summer (Fig. 1-5).

Interestingly, a slight change in paralarva distribution was noticed during winter in the northern subarea, especially in the inner shelf (Fig. 1-6). 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.

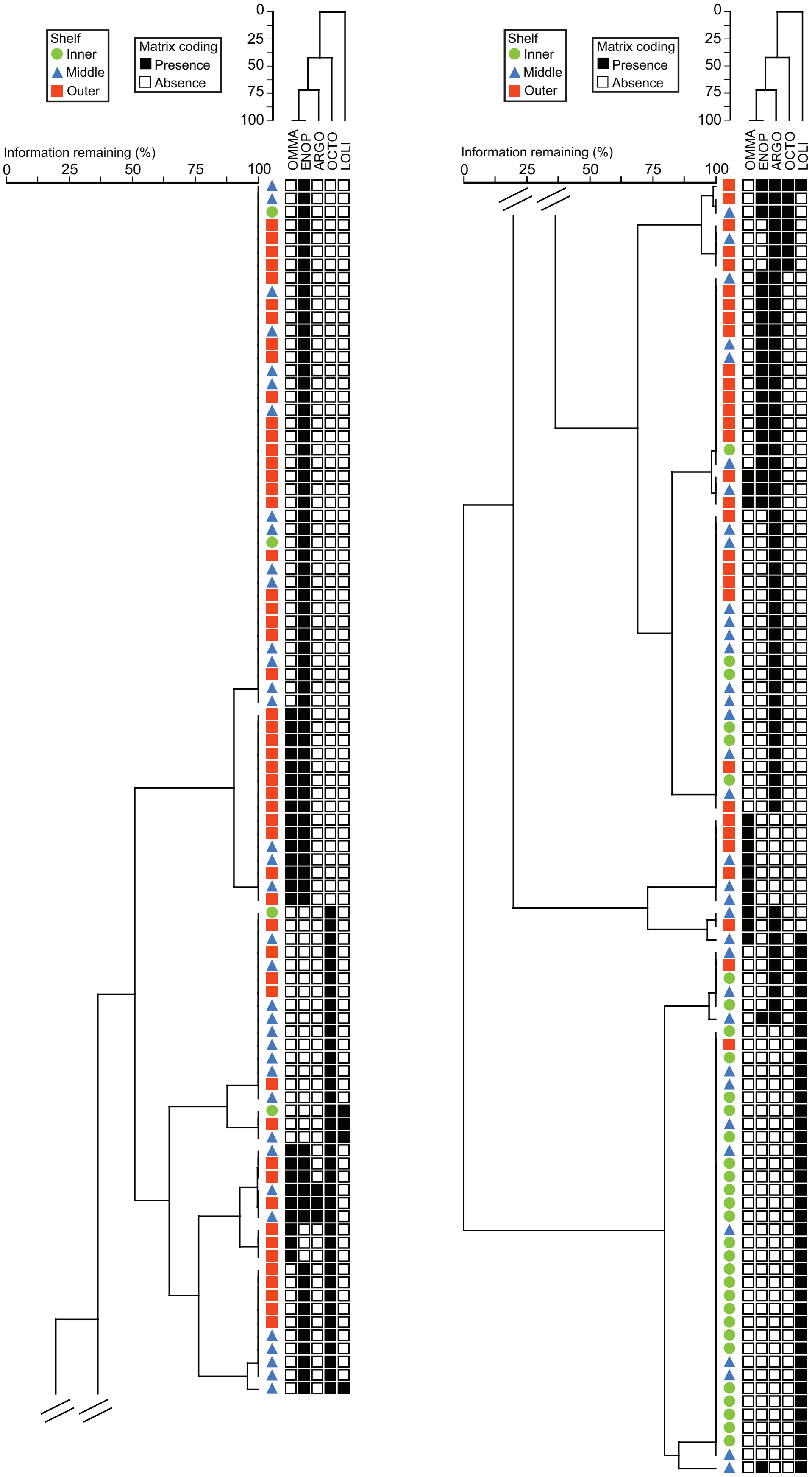

Figure 1-4. Two-way presence-absence cluster of cephalopod paralarvae collected in northern subarea during summer in inner, middle, and outer shelves.OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; OCTO = Octopodidae; LOLI = Loliginidae

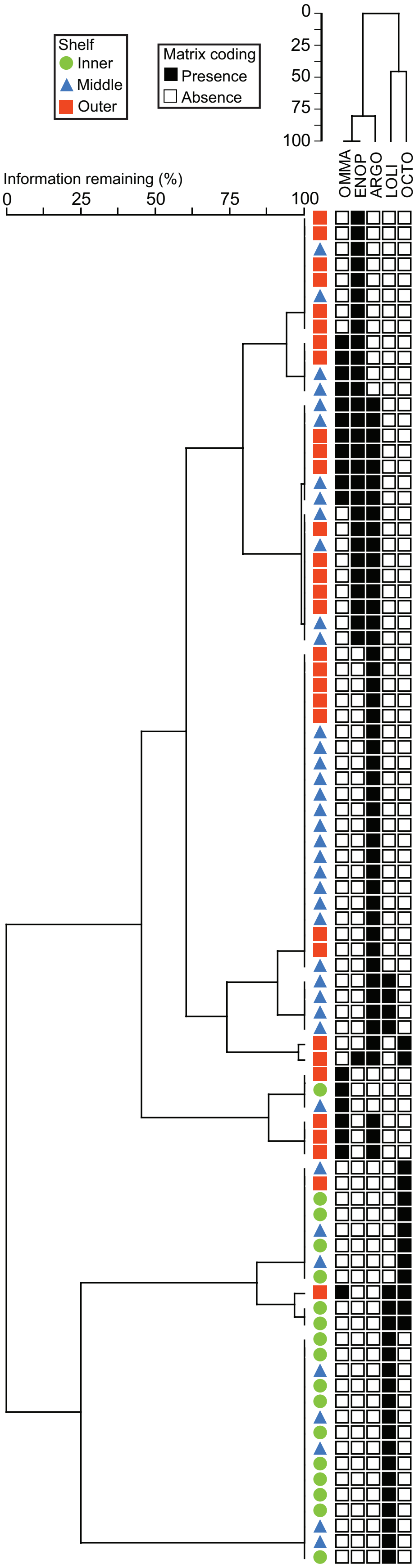

Figure 1-5. Two-way presence-absence cluster of cephalopod paralarvae collected in southern subarea during summer in inner, middle, and outer shelves. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; ARGO = Argonautidae; LOLI = Loliginidae; OCTO = Octopodidae

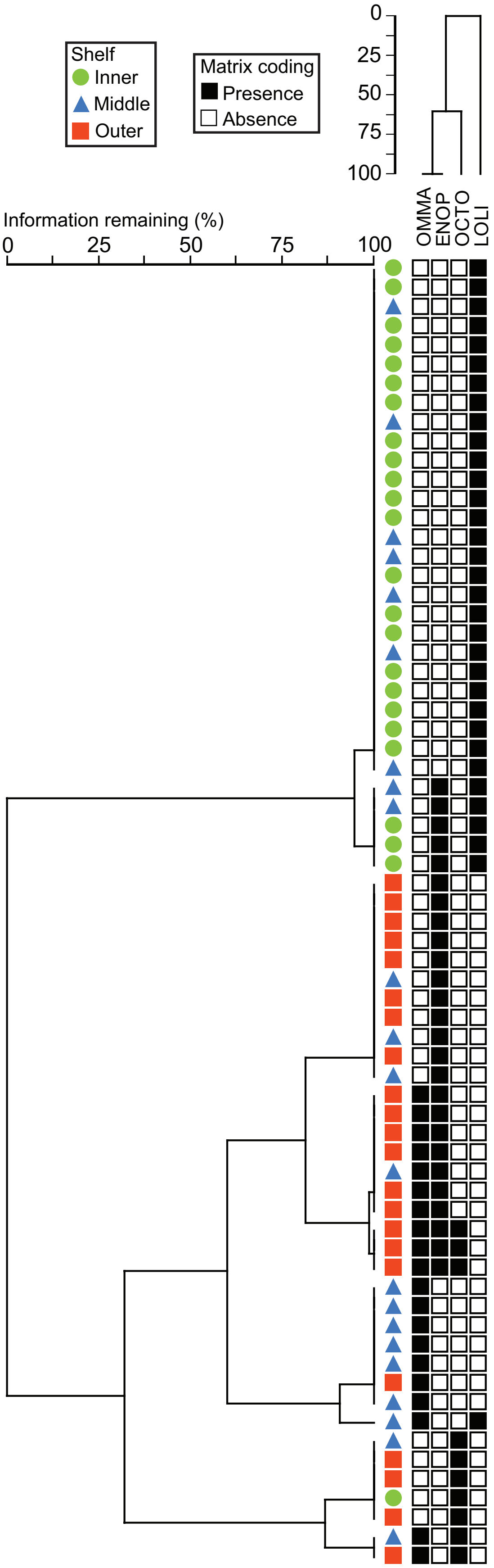

Figure 1-6. Two-way presence-absence cluster of cephalopod paralarvae collected during winter in inner, middle, and outer shelves of the northern subarea. OMMA = Ommastrephidae; ENOP = Enoploteuthidae; OCTO = Octopodidae; LOLI = Loliginidae

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 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 1-4). In general, the Global R values were lower in summer than in winter and highest between inner and outer shelves.

Table 1-4. 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 x South	R=0.02	-
Inner x Middle	R=0.15*	R=0.28*
Inner x Outer	R=0.39*	R=0.72*
Middle x Outer	R=0.05*	R=0.15*

**P < 0.05.*

Guided by the results from ANOSIM, a SIMPER analysis was performed to identify taxon contribution to dissimilarity between bathymetric zones (Table 1-5). 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 1-5).

Table 1-5. Dissimilarities (%) and taxon contribution (%) based on SIMPER analysis for bathymetric zones during summer and winter. Highest values are underlined.

	Summer				**Winter**		
	Inner x Middle	Inner x Outer	Middle x Outer		Inner x Middle	Inner x Outer	Middle x Outer
Average dissimilarity (%)	84,7	94,5	79,8	Average dissimilarity (%)	76,6	95,7	81,1
Taxon contribution (%)				Taxon contribution (%)			
Loliginidae	38,4	35,4	10,8	Loliginidae	50,2	47,81	17,05
Argonautidae	26,0	17,9	30,4	Ommastrephidae	15,7	13,11	22,56
Enoploteuthidae	18,2	26,4	32,6	Enoploteuthidae	12,5	22,14	28,88
Octopodidae	9,6	8,6	10,7	Ancistrocheiridae	7,0	-	8,01
Ommastrephidae	-	8,0	10,7	Octopodidae	5,1	11,53	14,28

Abundance k-dominance curves are displayed in Fig. 1-7 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. 1-7a). 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. 1-7b) 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. 1-7a). In winter, a higher dominance pattern was observed in outer shelf relative to middle shelf (Fig. 1-7b).

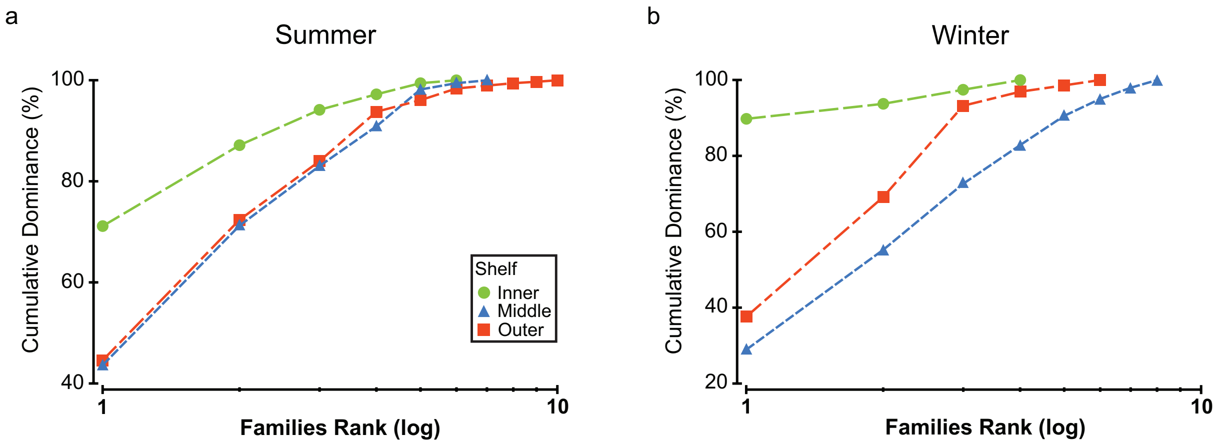

Figure 1-7. Abundance k-dominance curves of bathymetric zones (inner, middle, and outer shelves). a Summer; b Winter

2.4 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. 1-1; Table 1-1). 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 occur in the region (Cerda 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. 1-1; Lorenzzetti 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. 1-1, (for instance) a strong summer thermocline (20–50 m depth) may develop due to intrusions of SACW below CW, with a retreat of SACW towards the slope during winter (Castro-Filho et al. 1987). This subsurface intrusion of SACW over shelf areas from the northern portion of the study area can also fuel primary production during summer (Aidar et al. 1993; Braga and Müller 1998; Gaeta et al. 1999). In contrast to the northern area of the SBB, oligotrophic conditions prevail in shelf and open waters with a strong depletion of nutrients in the euphotic zone associated with TW (Metzler et al. 1997).

In the present study, the distribution and diversity patterns of paralarvae in the SBB show a predominance of neritic families (Loliginidae and Octopodidae) in the inner shelf, but epipelagic and mesopelagic families (Argonautidae, Enoploteuthidae, and Ommastrephidae) in the middle and outer shelves. This cephalopod distribution pattern is a common feature found in continental margins worldwide (Clarke 1996). While the oceanographic conditions in northern and southern subareas of the SBB are notably different (see “Material and methods”), our findings did not reveal significant differences in paralarva composition for a latitudinal gradient (Table 4). However, a strong cross-shelf gradient was identified as the driving force for formation of paralarva assemblages during both summer and winter. More specifically, there is an increase in paralarva diversity from the inner towards the middle and outer shelves (Figs. 1-2 and 1-7).

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 1-1).

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 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; Lorenzzetti 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.

2.5 CONCLUSIONS

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

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3 INFLUENCE OF OCEAN DYNAMICS ON THE ROUTE OF ARGONAUTS IN THE SOUTHEASTERN BRAZIL BIGHT (CHAPTER 2)

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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.

3.1 INTRODUCTION

Argonauts (Argonautidea 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). Furthermore, an unusually high abundance 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 (Vaske and Castello, 1998, Vaske and Rincón-Filho, 1998, Santos and Haimovici, 2002f). 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 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, Araujo 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.

3.2 MATERIAL AND METHODS

3.2.1 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. 2-1). 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; >20ºC and salinity >36) in the upper 200 m and the cold and nutrient-rich South Atlantic Central Water (SACW; <20ºC and salinity <36) below the TW (200–500 m) as the pycnocline portion of the BC (Campos et al., 1996, 2000, 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 (Emilsson, 1961, Castro and Miranda 1998, 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. 2-1). 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 (Emilsson 1961, Matsuura 1985, Stech and Lorenzetti, 1992, Castelao and Barth, 2006). 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 (Campos et al., 2000, Silveira et al., 2004, Calado et al., 2006, 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 (Lorenzzetti and Gaeta 1996, Carbonel, 1998, Yoshinaga et al., 2010, Calil et al., 2021). 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., 2017, Favero et al., 2017, Brandini et al., 2018).

3.2.2 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. 2-1). 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.

3.2.3 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 100m^{-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.

3.2.4 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).

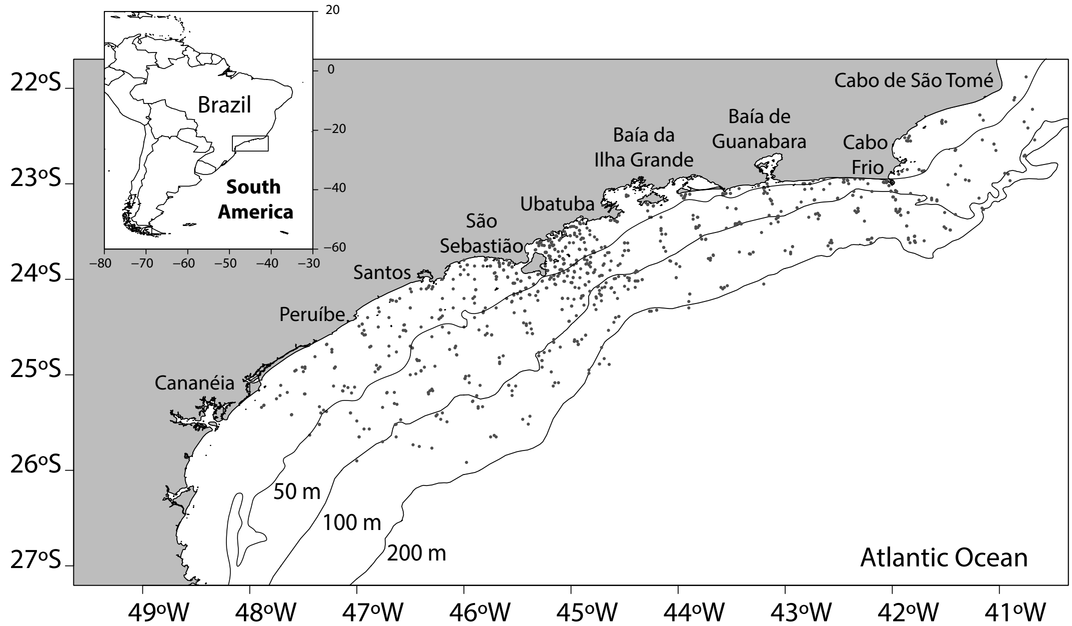

Figure 2-1. Study area and sampling sites between Cabo de São Tomé and Cananéia.

Table 2-1. 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

3.3 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 2-2).

Table 2-2. 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	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

Although argonautid paralarvae were found along the entire continental shelf of the study area (Fig. 2-2), 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 with the middle shelf (50–200 m) in the southern portion (Fig 2-2).

The SPQ analysis indicated that argonautid paralarvae tolerated local depths between ~26 and 248 m, preferring 70–148 m isobaths (Fig. 2-3), 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. 2-3).

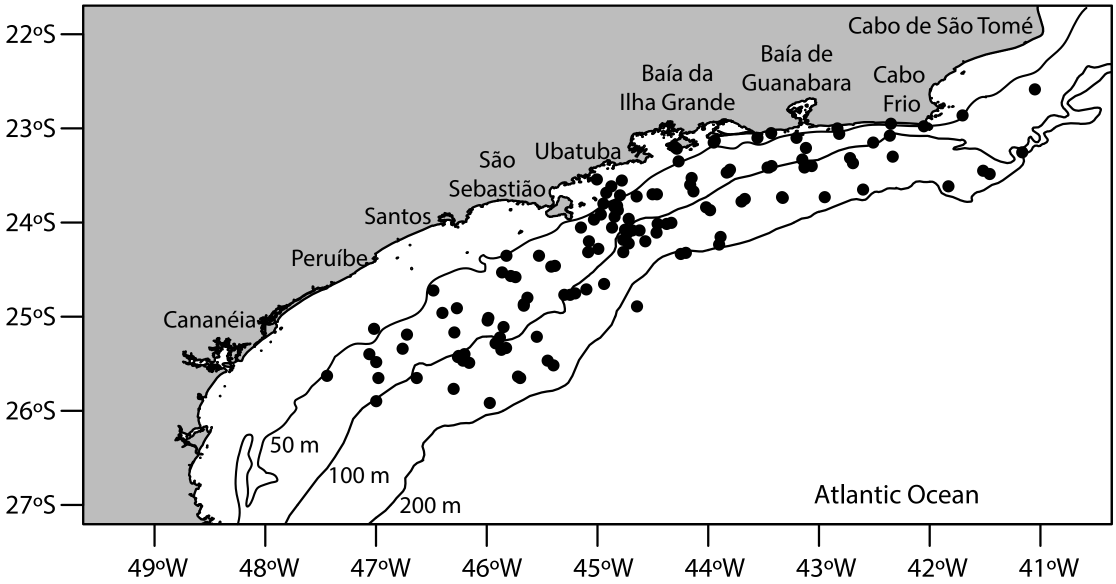

Figure 2-2. Horizontal distribution of Argonautidea paralarvae between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer for the study period.

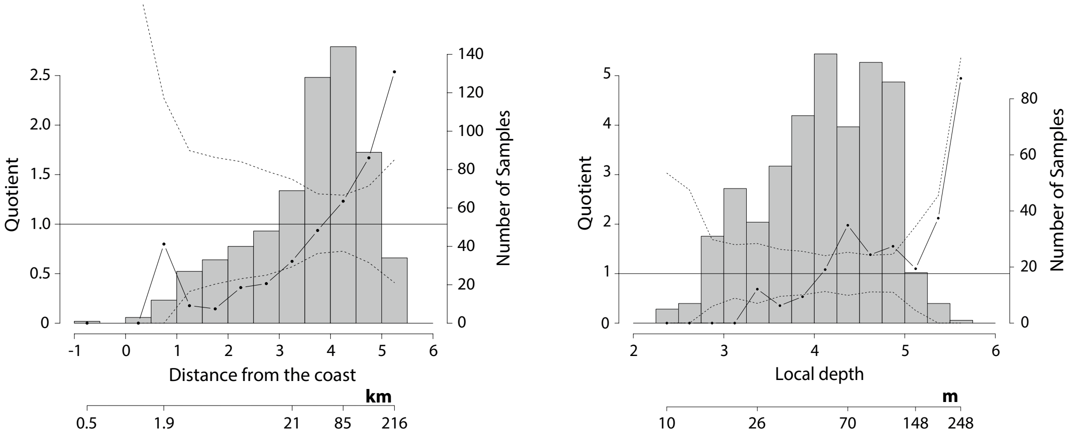

Figure 2-3. Single parameter quotient (SPQ) analysis for the local depth (natural logarithms in m) and distance from coast (natural logarithms in km) of Argonautidae paralarvae occurrence in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer for the study period. 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.

Figures 2-4 and 2-5 display the horizontal distribution of argonautid paralarvae during summer cruises, along with surface and subsurface water temperatures (0 and 10m, 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 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 2-1) in the Ubatuba region, northward to São Sebastião Island, the data from which revealed a marked seasonal trend in argonautid paralarvae abundance (Fig. 2-6). 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. 2-7) 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. 2-8).

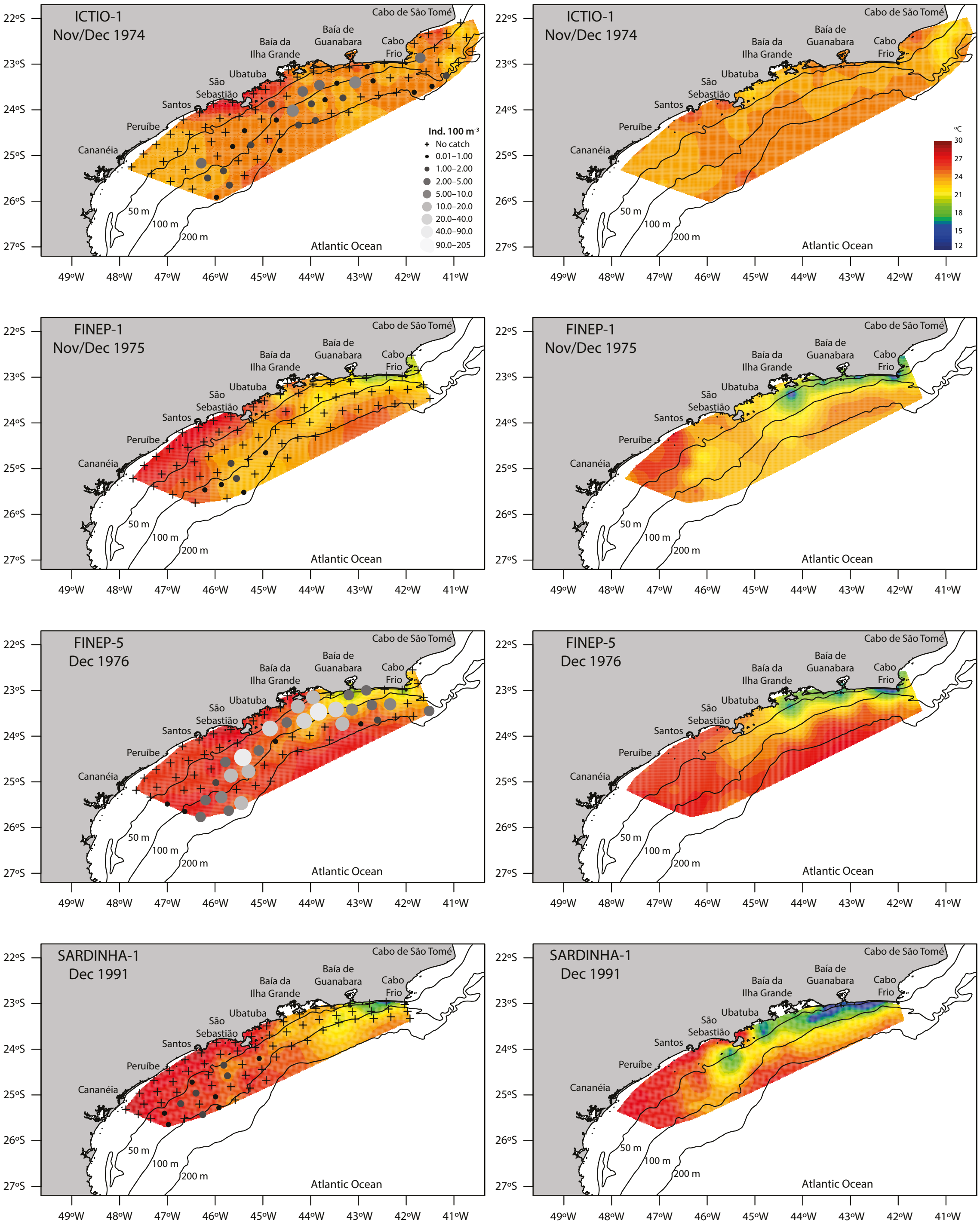

Figure 2-4. Horizontal distribution of Argonautidae paralarvae abundance and surface temperature on left and subsurface temperature (10 m) on right in the in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer from 1974 to 1991.

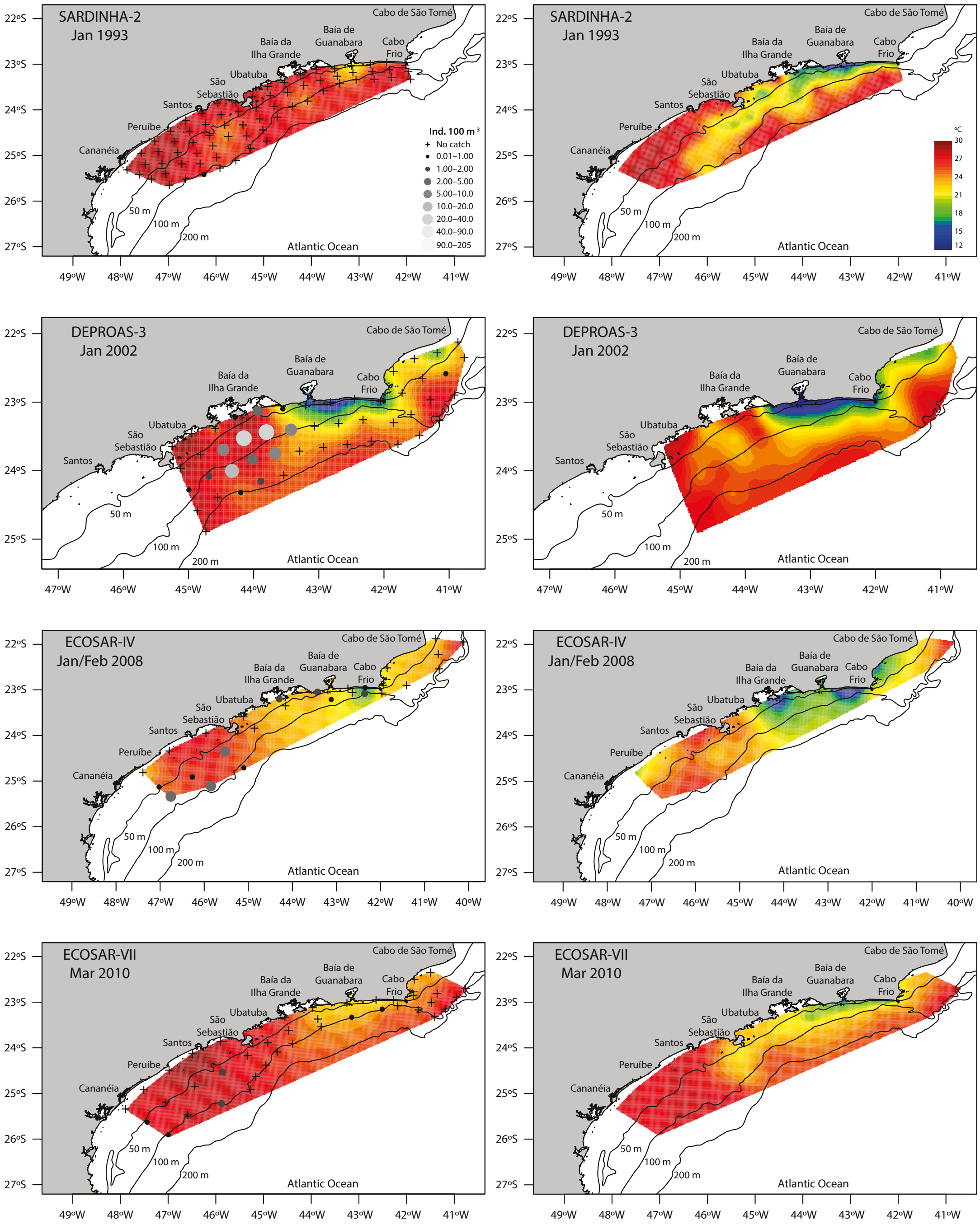

Figure 2-5. Horizontal distribution of Argonautidae paralarvae abundance and surface temperature (left) and subsurface temperature (10 m, right) in the in the continental shelf between Cabo de São Tomé (22º S) and Cananéia (25º S) during summer during 1993–2010.

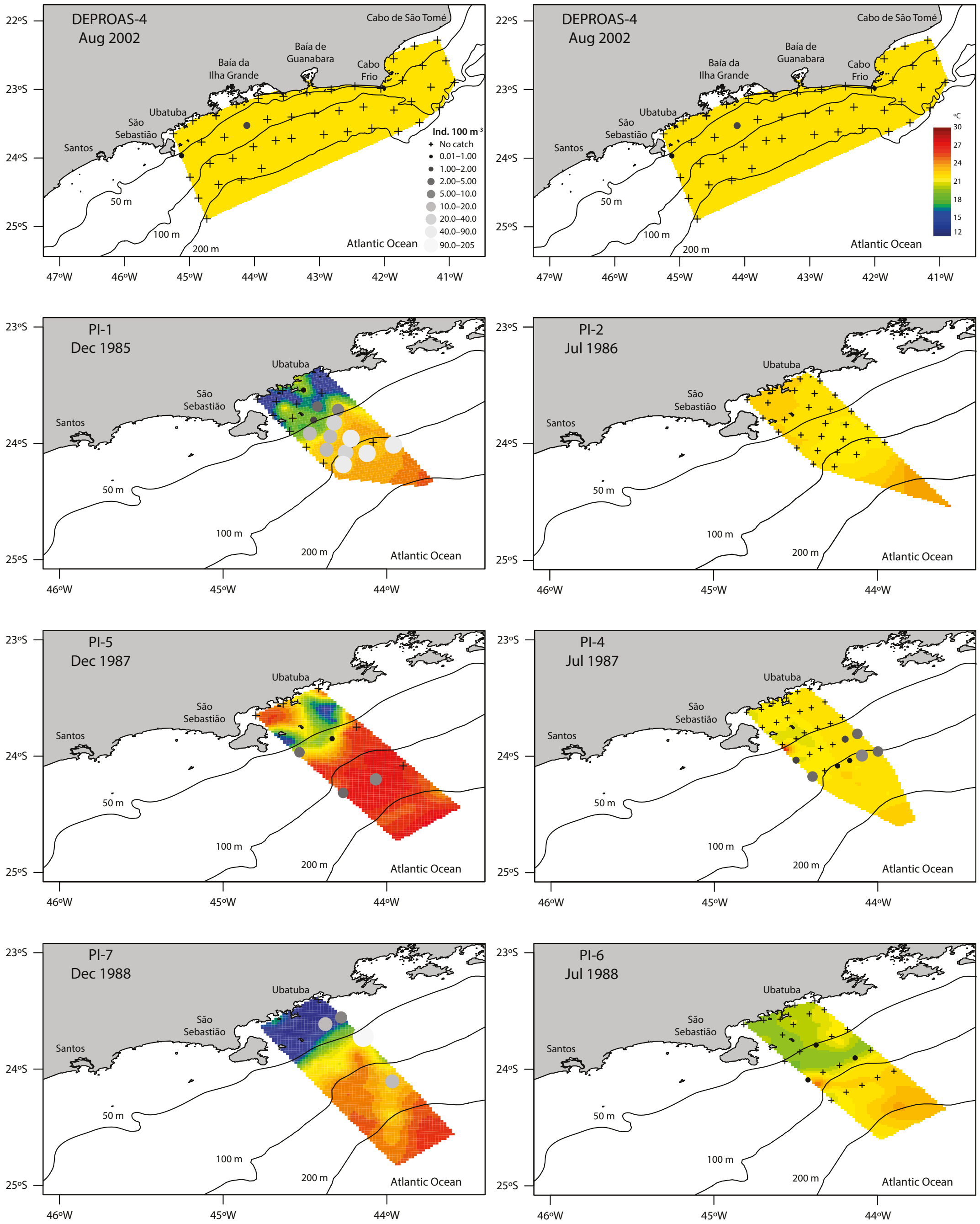

Figure 2-6. Horizontal distribution of Argonautidae paralarvae abundance and subsurface temperature (10 m) in the continental shelf of Ubatuba (23°5’ S) during summer (left) and winter (right) during 1985–1988.

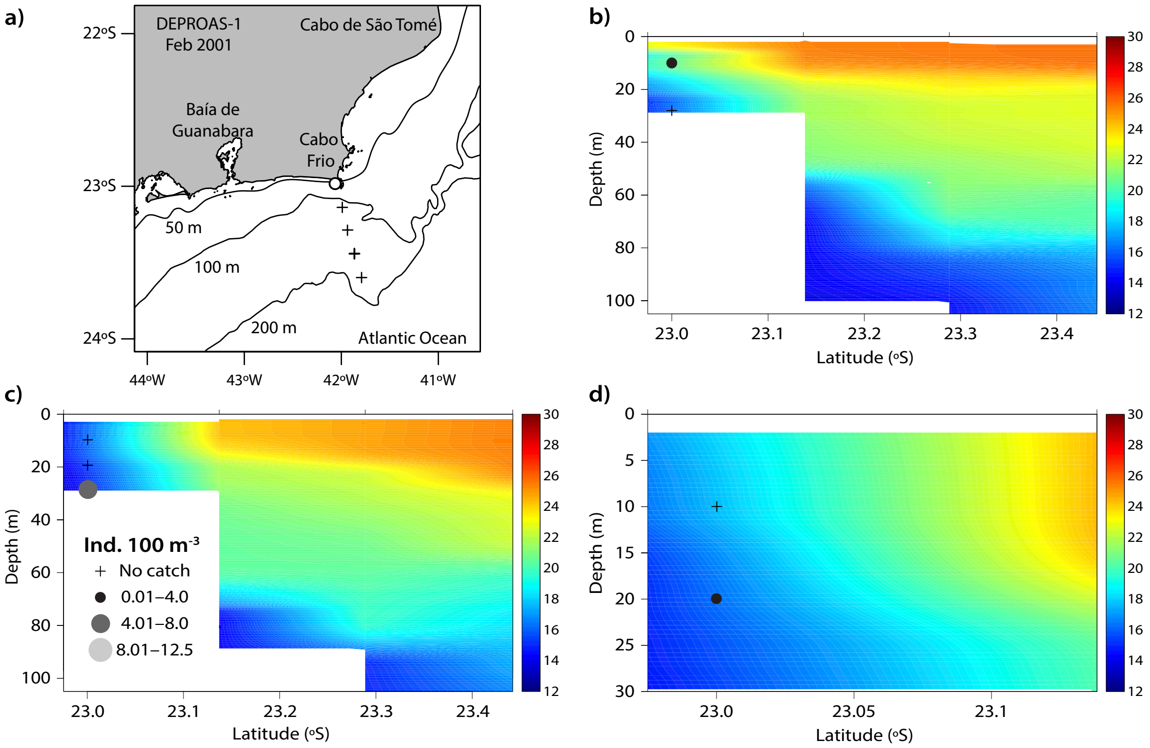

Figure 2-7. Vertical distribution of Argonautidae paralarvae abundance in the continental shelf of Cabo Frio (22° S) during summer in 2001. (a) Location of stations and transect (o = positive station); (b) vertical distribution on transect 1; (c) transect 2 and (d) transect 3.

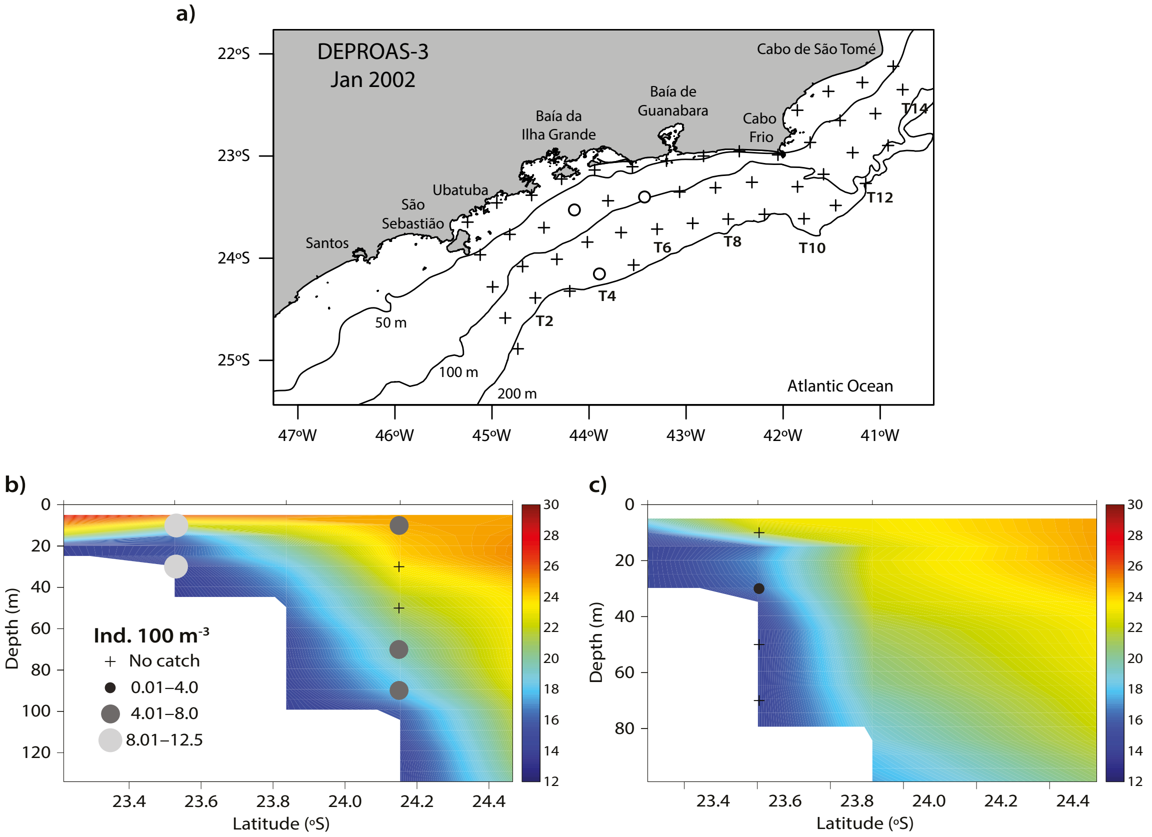

Figure 2-8. Vertical distribution of Argonautidae paralarvae abundance in the continental shelf between Cabo de São Tomé (22° S) and São Sebastião (23° S) during summer in 2002. (a) Location of stations and transects (o = positive station); vertical distribution on (b) transect T4 and (c) transect T6.

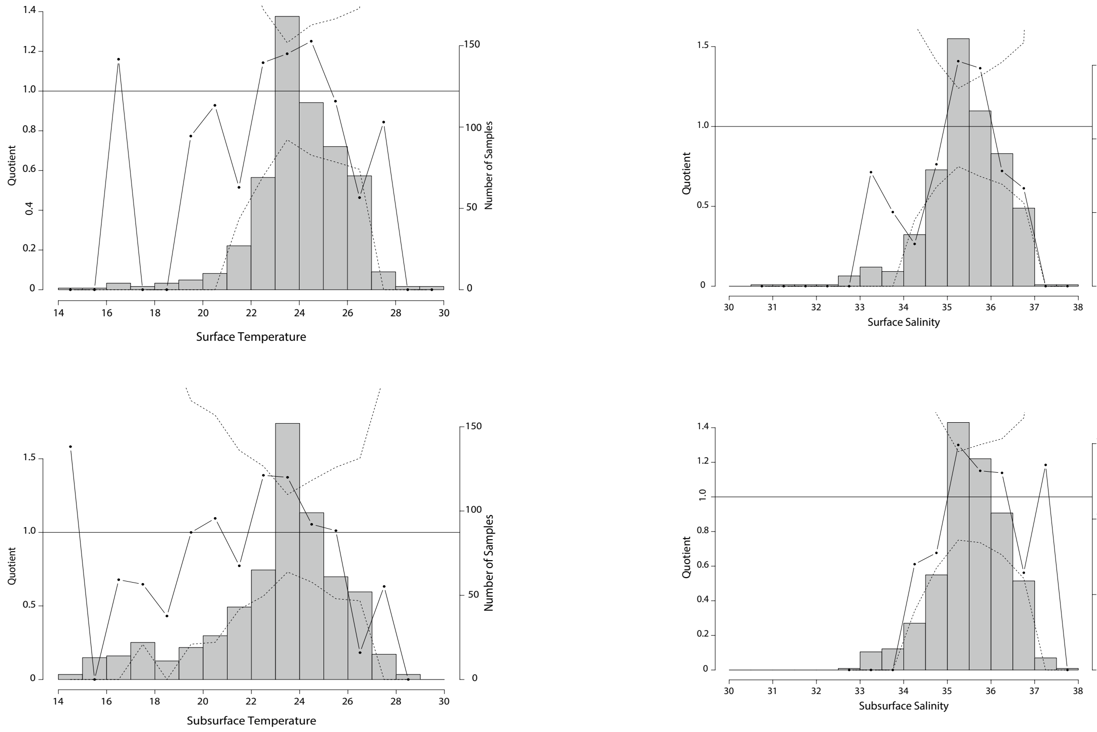

Figure 2-9. SPQ analysis for surface and subsurface temperature (°C) and salinity of Argonautidae paralarvae occurrence in the continental shelf between Cabo de São Tomé (22° S) and Cananéia (25° S) during summer during the study period. Histograms represent the number of stations within each bin of 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.

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. 2-9). 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. 2-9).

3.4 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 2-2). Even though distributed throughout the study area (Figs. 2-4, 2-5, and 2-6), 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 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. 2-8). 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 (Fig. 2-5 and 2-8). 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 (Figs. 2-7 and 2-8). 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. 2-4 and 2-5; -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. 2-6 -PI-1,2-5 and 2-7). 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.

3.5 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 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.

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4 LONG-TERM CHANGES OF CEPHALOPOD PARALARVAE ABUNDANCE IN THE CONTINENTAL SHELF OF THE SOUTHEASTERN BRAZIL BIGHT (22–25°S) (CHAPTER 3)

ABSTRACT

Cephalopods early life stages are very sensitive to environmental changes, particularly the paralarval stages that are critical to population dispersal and recruitment success. While seasonal and interannual variations in paralarvae abundance relative to oceanographic conditions have been relatively well studied, little attention has been given to long-term climate fluctuations in their composition and distribution. Here, a historical collection of plankton samples from 1974 to 2010 was used to investigate possible environmental drivers of multi-decadal paralarvae assemblages' distribution in shelf areas of the South Brazil Bight (SBB; 22–25°S). Exploratory multivariate analyses of time-series data indicated a well-defined segregation of neritic versus epi and mesopelagic assemblages. When biotic and abiotic variables were considered together, sea surface temperature was clearly identified as the main contributing factor. Moreover, further results from multiple factor analysis suggested salinity as the main driver for opposite responses of families within the neritic and mesopelagic assemblages (e.g. Loliginidae versus Octopodidae). The data series also revealed that a temporal asynchrony between Argonautidae and Loliginidae abundances, two of the most abundant paralarvae families from the study area, coincides with positive anomalies for the Southern Oscillation Index. Despite several limitations (e.g. lack of sampling continuity for some years or seasons, size and vertical distribution of paralarvae), this analysis identified potential oceanographic drivers impacting long-term dynamics of paralarvae abundance over the SBB, which may directly impact patterns of transport, dispersal and habitat shifts of cephalopods early life stages assemblages.

4.1 INTRODUCTION

Cephalopods represent major targeted fisheries resource worldwide, currently ca. 2–4% of global annual landings (FAO 2020). They occupy an intermediate trophic level in marine ecosystems being considered opportunistic predators feeding on a variety of fishes and crustaceans and also important preys of fishes, mammals and seabirds (Piatkowski et al. 2001). A set of unique biological traits, including rapid growth, short lifespans and strong life-history plasticity make cephalopods highly responsive to environmental changes, particularly between the phases of egg mass, hatchling and pre-recruit juveniles (Rodhouse et al., 1992; Boyle and Boletzky 1996). For this reason, paralarval surveys are considered instrumental to understand the distribution, biology, spawning areas and population structure of cephalopod biodiversity (Piatkowski 1998; Boyle and Rodhouse 2005). Thus, investigating the paralarvae dynamics in relation to global climate change seems crucial to determine potential oceanographic patterns responsible for fluctuations in abundance of cephalopods early life stages.

Despite still at an emerging stage, some studies have attempted to verify paralarval distribution relative to large-scale climatic events such as the El Niño Southern Oscillation (ENSO). For instance, a study in the Southern California Bight has used a 30 years record of the market squid *Doryteuthis opalescens* paralarvae to show that ENSO anomalies were likely more linked to adult population than early life stages fluctuations in abundance (Perretti and Sedarat, 2016). In the same area, El Niño conditions from 2015 to 2016 resulted in extraordinarily low squid paralarval abundance, contrasting sharply with cool and productive La Niña conditions from 2011 to 2013 (Van Noord and Dorval 2017). More recently, Ruvalcaba-Aroche et al. (2022) have modeled the seasonal and interannual variations of the nursery habitat based on ommastrephid squid paralarvae collected between 2010 and 2017 in the tropical-subtropical convergence off Mexico (Gulf of California). These authors revealed that during La Niña conditions, potential nursery habitat did not vary interannually, whereas a clear change in nursery habitat was recorded during El Niño events.

In the present study area, the South Brazil Bight (22–28°S), few recent studies have addressed an integrative investigation of cephalopods early-life stages with local oceanography. Although key environmental drivers including coastal upwelling (Vidal et al., 2010; Araújo and Gasalla, 2017) and mesoscale eddies, meanders and upwelling plumes (Araújo and Gasalla, 2019; 2022) have been identified, the abundance of paralarvae was not integrated to multi-decadal fluctuations and large-scal climate indexes such as ENSO. A peculiar feature of the SBB relative to other western boundary subtropical counterparts is the larger width of its continental shelf, particularly in the central sector, with ca 180 miles separating the coast and the shelf-edge (Brandini et al., 2018). Northerly and northeasterly winds from the western side of the South Atlantic Subtropical High regulate the water circulation in the mid and outer shelves (Satyamurty et al., 1998; Wainer et al., 2006). Climate oscillations such as ENSO are known to influence not only patterns of precipitation in the southern Brazil (Grimm et al., 1998), but there exist some observational evidence linking sea surface temperature (SST) anomalies in the western South Atlantic to ENSO events (e.g. Lentini et al., 2001; Piola et al., 2018). Early observations by Martin et al. (1988) reported an increase in the frequency of coastal upwelling in Cape Frio (22°S) during the warm 1982 ENSO. Lentini et al. (2001) have also found out that negative SST anomalies at the Western Atlantic (22° to 42°S) corresponded to warm ENSO events from 1982 to 1994. More importantly, Matsuura (1996) provided the first biological evidence attributed to a possible link between local ENSO manifestation (expressed as an earlier cold SST anomaly during the 1976–1977 El Niño) and the 1977 Brazilian sardine recruitment failure in the SBB.

In this study, we have investigated long-term fluctuations in paralarvae abundance by revisiting a historical collection of plankton samples (from 1974 to 2010) over the SBB continental shelf (Figure 3-1). Here, an analysis of critical abiotic factors for larval dispersal such as surface and subsurface (10 m depth) temperature and salinity integrated selected climatic indexes such as the Southern Oscillation Index (SOI), Oceanic Niño Index (ONI) and the Tropical Southern Atlantic Index (TSA). The main objective was to apply exploratory multivariate analyses to identify the potential drivers of multi-decadal climatic fluctuations influencing the abundance and distribution of cephalopod early-life stages assemblages in the SBB.

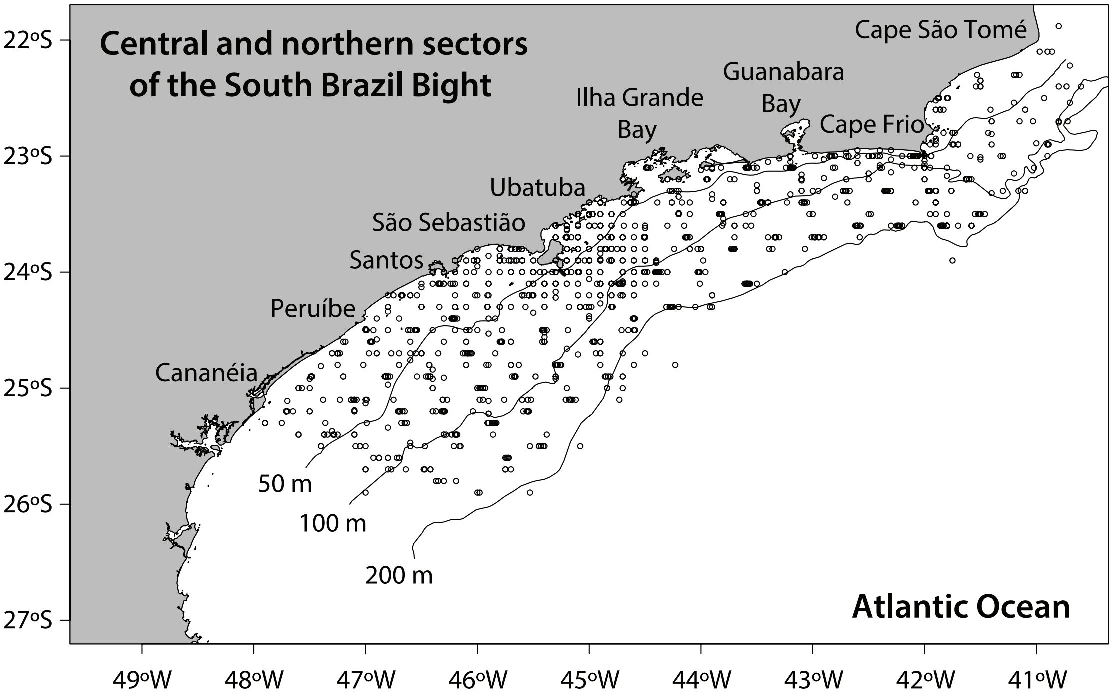

Figure 3-1. The study area encompasses the central and northern sectors of the SBB. Sampling stations over the continental shelf are shown together with the 50, 100 and 200 m isobaths.

4.2 MATERIAL AND METHODS

4.2.1 Study Area

The present study is focused on the continental shelf of the northern and central sectors of South Brazil Bight (SBB), i.e. from Cape Frio (22°S) to Cananéia (25°S), although the SBB extends south reaching the Cape Santa Marta Grande (28°S). The SBB represents 1100 km of the Brazilian coastline (Figure 1), and the continental shelf may be divided into inner, mid and outer shelf shelves, with approximate depth ranges of <50, 50–100 and 100–200 m, respectively (Castro et al., 2006; 1998). Whereas the shelf extends up to 230 km off Santos to the 2000 m isobath, which is considered the offshore bathymetric limit of the SBB, the continental shelf is relatively narrow (50–70 km wide) in the northern and southernmost sectors (Mahiques et al., 2010). These latitudinal differences are crucial for water masses circulation and thereby primary productivity distinctions between these sectors.

The inner- and mid-shelf waters from the SBB are dominated by the less saline Coastal Water (CW, < 20 °C; < 35 psu) (Castro et al., 1998). On the outer-shelf, the Brazil Current flowing southwards along the shelf break consists of the warm salty oligotrophic Tropical Water (TW, > 20 °C; > 36 psu) followed by the deeper nutrient-rich South Atlantic Central Water (SACW, 6–20 °C, 34.6–36 psu), which is the main thermocline below the TW (Castro et al., 1998; Silveira et al., 2000). On the inner shelf, the continental runoff from small rivers and lagoons causes density discontinuities and buoyancy advection (Castro, 2014). Prevailing northeasterly winds during summer season result in SACW upwelling, particularly in Cape Frio (northernmost sector of the study area), where associated phytoplankton blooms are frequently observed (Valentin et al., 1987). In the central sector, the influx of nutrients in to the lower euphotic zone (1–5% light) may be caused by SACW advection driven by a range of physical processes, including meanders and eddies of BC and persistent northeastern winds (Castro, 2014). Conversely, southwesterly winds associated with cold fronts discontinue SACW advection towards the shelf and prevents coastal upwelling events to occur year-round (Castro et al., 1998; 2006; Cerda and Castro 2014). Over the shelf-break, SACW upwelling is induced by both bottom topography and hydrodynamic instabilities such as cyclonic eddies and meandering of the BC (Campos et al., 2000; Calado et al., 2006), and may locally affect the biological production (Yoshinaga et al., 2010; Namiki et al., 2017). Although less biologically studied, SACW plumes from Cape Frio upwelling front are frequently observed 300-400 km southwards, flowing along the coastline (Lorenzzetti and Gaeta, 1996; Calil et al., 2021). Taken together, these dynamic features are crucial to the SBB biological productivity leading to episodic events of new production that replace the otherwise oligotrophic scenario of the SBB (Metzler et al., 1997; Brandini et al., 1988; 2018).

4.2.2 Data Collection and Laboratory Analysis

Cephalopod paralarvae were analyzed based on plankton samples collected in historical oceanographic surveys from 1974 to 2010 (Table 3-1), covering the northern of the South Brazil Bight (Figure 3-1) onboard the several research vessels, “Prof. W. Besnard”, “Atlântico Sul,” and “Albacora”. Plankton samples were obtained, following Smith and Richardson (1977), using bongo nets (0.6 m mouth diameter; 333 and 505-µm mesh size), towed obliquely surface-bottom-surface at ~ 2 knots, not exceeding 10 m off bottom. A calibrated flow meter was attached at each net mouth aperture to estimate the filtered water volume. Temperature and salinity data were obtained at each station from Nansen bottles and reversing thermometers until 1988, after which a conductivity-temperature-depth profiler (CTD) was used. The 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.

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

4.2.3 Abundance estimates

Mean annual values were calculated as the mean abundance (ind.100m^{-3}) of a specific paralarvae family in a given year. The samples collected in both summer and winter cruises from an year were pooled together to calculate the mean annual values.

4.2.4 Multivariate Analyses

Multiple Factor Analysis (MFA) is becoming a popular method to study the influence of several groups of variables on the same set of individuals (Escofier and Pagès, 1994; Pagès, 2014), and has been widely applied (Abdi et al., 2013), including in marine sciences. MFA is an extension of the principal component analysis (PCA), designed for situations where the same variables (matrix columns) are measured in the same grid cells (data rows) at various times (tables). By doing so, the variability in time is explicitly differentiated from the correlation structure among the variables, allowing a consistent estimation of variables' correlation structure in time and also to quantify the temporal variability around the average structure (Petitgas et al., 2018; Doray et al., 2018). In a single PCA sources of variability are pooled and thereby the temporal structure is less clearly identified than in MFA. For each year, data are organized as a time series of variables and grid cells, and the MFA proceeds as a double PCA. First, a PCA is applied to each yearly table, followed by a second PCA is applied on the global table generating a factorial space. The principal components of the MFA (Dimensions) are interpreted with those variables showing a good correlation with the components for a sufficiently large number of years (Petitgas et al., 2018). The MFA is subjected to the same limitations as PCA. That is, all variables must be valued in all grid cells and a large proportion of zeroes and/or very high values may affect variables' correlation. While, the abiotic data were standardized when required, a fourth root transformation was applied to biotic data (abundance of paralarvae) to reduce the effect of some high values on the correlations. The data analyses were performed using R (R Core Team 2022) with scripts provided by Dr. Saskia Otto, from Hamburg University, a partner of Mission Atlantic project. Therefore, the multivariate analysis was conducted under the context of Mission Atlantic case study, an European Comission H2020 funded Consortium led by DTU (Danish Technical University) where the University of São Paulo is engaged.

4.3 RESULTS

4.3.1 Cephalopod paralarvae composition

A total of 3438 paralarvae were found from 464 plankton samples. Paralarval identification resulted in 11 families (Table 3-1). The most abundant family was the epipelagic Argonautidae in terms of numbers and mean abundance (ind. 100m^{-3}), corresponding to more than 50% of all paralarvae. For the statistical analyses, the mean abundance of paralarvae per year was utilized.

Table 3-1. Cephalopod paralarvae assemblages mean abundance (ind. 100m^{-3}) per year.

Assemblages	**Families**	**1974**	**1975**	**1976**	**1985**	**1986**	**1987**	**1988**	**1991**	**1993**	**1994**	**1997**	**2001**	**2002**	**2005**	**2008**	**2010**
Epipelagic	Argonautidae	1.359	0.062	4.889	15.413	0.000	0.915	8.295	0.274	0.007	0.030	0.046	0.106	1.074	0	0.243	0.133
Neritic	Loliginidae	0.289	0.080	0.098	0.233	0.218	0.621	0.223	0.364	0.113	0.591	0.222	1.159	0.304	0.800	0.200	0.265
	Octopodidae	0.092	0.011	0.087	0.088	0.106	0.079	0	0.111	0.289	0.040	0.072	0.070	0.193	0.064	0.068	0.060
Mesopelagic	Ancistrocheiridae	0.013	0.025	0.000	0.095	0.023	0.049	0.020	0.004	0	0	0	0	0.014	0	0.012	0
	Cranchiidae	0.003	0	0	0	0	0	0.047	0.001	0	0	0	0	0	0	0	0.011
	Enoploteuthidae	0.307	0.045	0.675	0.540	0.023	0.062	0.262	0.282	0.440	0	0.035	0.500	0.369	0	0.274	0.653
	Lycoteuthidae	0.001	0	0	0	0	0.017	0	0	0	0	0	0	0	0	0	0
	Octopoteuthidae	0.001	0	0	0	0	0	0	0.001	0	0	0	0	0	0	0.006	0
	Ommastrephidae	0.081	0.016	0.169	0.117	0.000	0.111	0.166	0.074	0.075	0	0.013	0.140	0.177	0	0.020	0.126
	Pyroteuthidae	0.003	0	0.008	0	0	0	0	0.001	0	0	0	0	0	0	0.009	0
	Sepiolidae	0.005	0	0	0	0	0	0	0.008	0	0	0	0	0.039	0	0	0

4.3.2 Principal Component Analysis

The PCA was used to extract the dominant modes of variability in paralarvae families' abundance (biotic variable) during the time series sampling from 1974 to 2010 over the SBB. The two main components of the PCA jointly explained ca. 47.5% of the data variability (Figure 2). Notably, PC1 explaining 29.7% of data variance has segregated meso and epipelagic families with negative values (of note Ommastrephid, Enoploteutidae and Argonautidae) from the neritic families Loliginidae and Octopodidae that scored positively in PC1. Interestingly, Octopodidae was the most expressive family driving paralarvae assemblages with prominent negative values in PC2, together with minor contributions of Pyroteuthidae and Octopotheutidae. Positive values in PC2 were associated with Cranchiidae and Argonautidae, but to a lesser extent as compared to the magnitude of values observed for Octopodidae. Sampling years 2005 and 1994 were major drivers for paralarvae family distribution with positive values in PC1, whereas the year 1988, with striking high positive values, represented a critical component for assemblage definition in PC2.

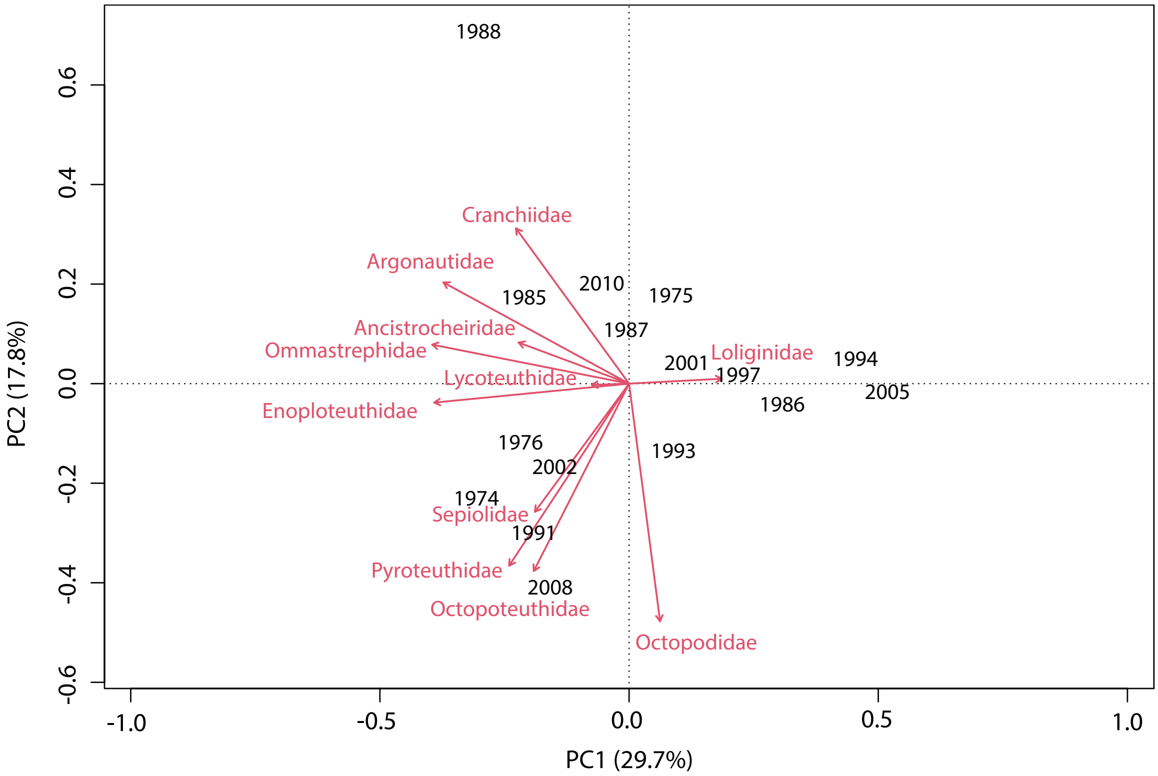

Figure 3-2. Principal component analysis (PCA) of the abundance of paralarvae families in the time series sampling in the SBB.

4.3.3 Multiple Factor Analysis

The MFA revealed a well-defined segregation of paralarvae families not only in response to abiotic factors such as temperature and salinity, but also to climate-based indexes SOI and ONI (Figure 3-3). The two main dimensions (Dim 1 and 2) explained jointly 38.8% of data variance. Displaying negative values in Dim 1, the neritic families were clearly separated from the epi and mesopelagic families that showed positive values in Dim 1. This remarkable segregation of paralarvae assemblages was to a great extent driven by temperature with negative scores in Dim 1, and to a lesser degree by ONI and SOI with opposing values in Dim 1. More specifically, Argonautidae, followed by Ancistrocheiridae, Cranchiidae and SOI displayed the highest positive scores in Dim 1, whereas temperature, ONI and Octopodidae the most negative values (Figure 4A).

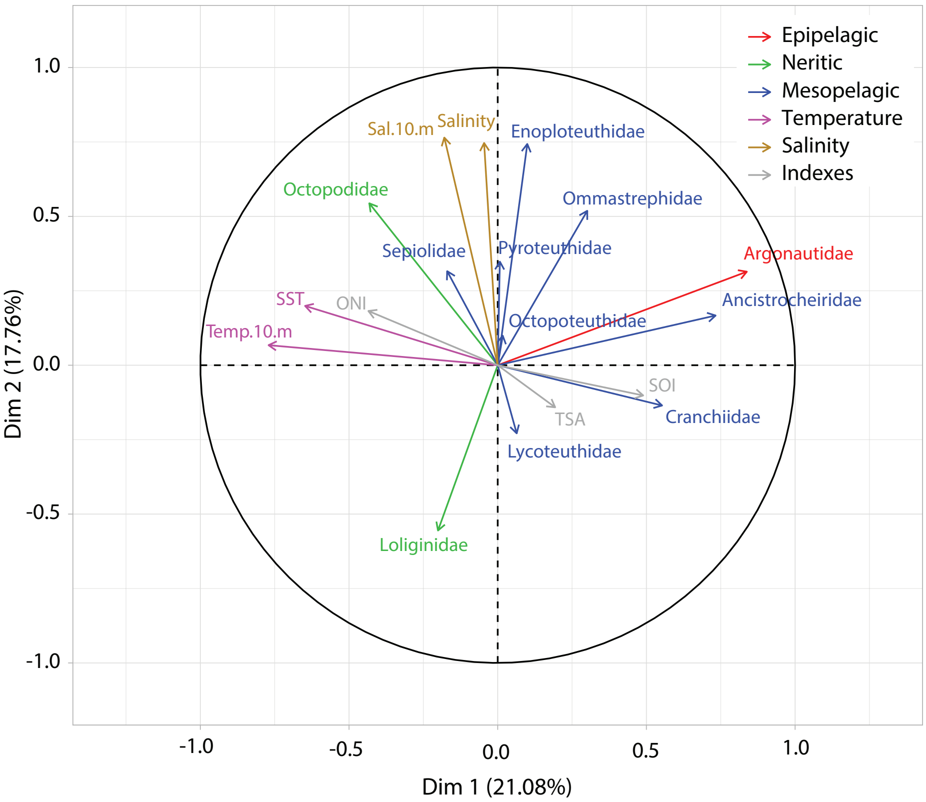

Figure 3-3. Multiple Factor Analysis (MFA) of the time-series data divided into categories: epi, mesopelagic and nertic paralarvae families, temperature and salinity, and climate indexes.

The Dim 2 in MFA was mostly driven by salinity. Displaying positive values in Dim 2, salinity contributed to the segregation of families within the neritic and mesopelagic assemblages (Figure 3-3). For the neritic families, while Octopodidae was clearly associated with salinity, Loliginidae displayed an opposite response with the lowest negative scores in

Dim 2 (Figure 3-4B). Although Enoploteuthidae and Ommastrephidae scored among the highest positive values in Dim 2, the magnitude of score values for the other mesopelagic families was relatively lower in this MFA component (Figure 3-4B).

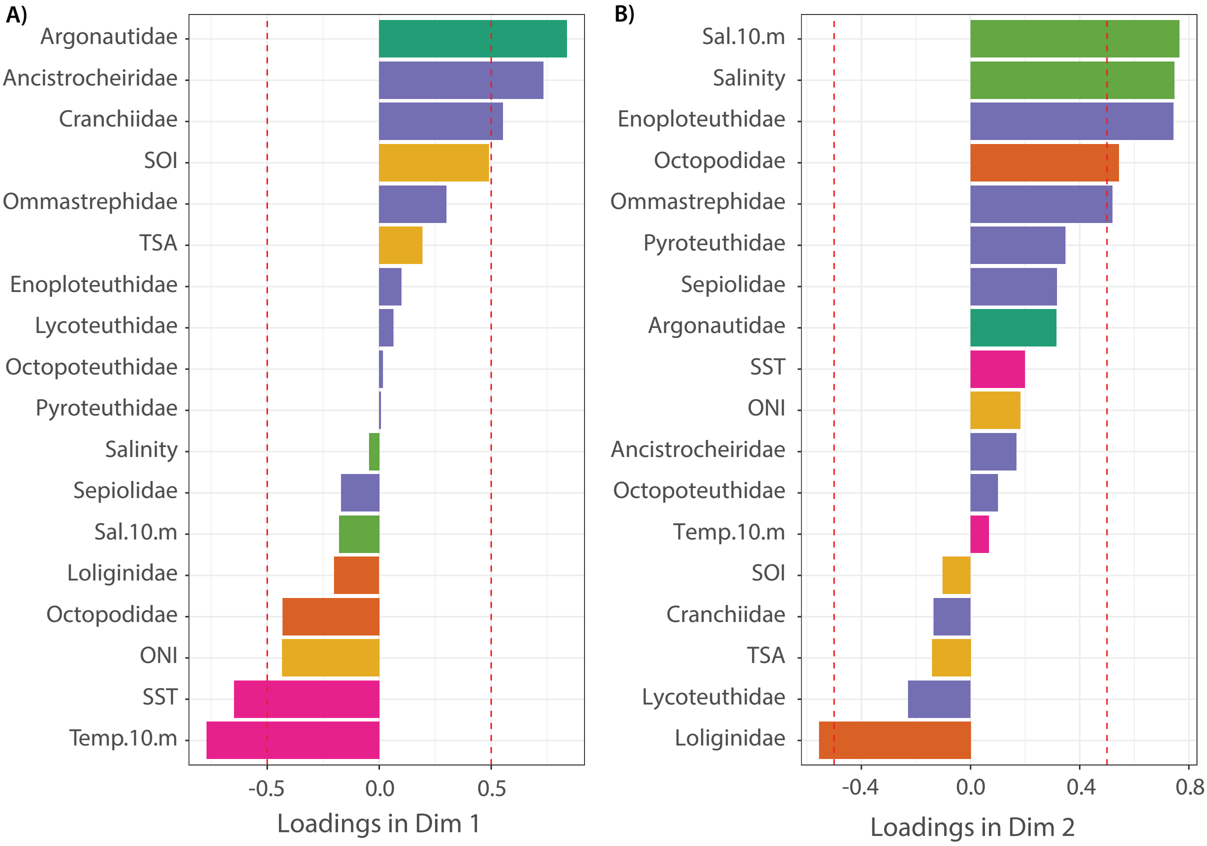

Figure 3-4. Individual contribution of each variable to Dim 1 (A) and Dim 2 (B) of the MFA. Variables were color-coded into epi, mesopelagic and neritic families (in dark green, blue and brown, respectively), salinity (light green), temperature (pink), and climate indexes (yellow).

4.3.4 Traffic Light Plot

A traffic light plot (TLP) was applied to explore the temporal trajectories of abiotic and biotic time series in the study area (Figure 3-5). The scores of each year in the two main dimensions of the MFA were overlapped with the TLP to assist in data interpretation, since Dim 1 and 2 revealed important clues on paralarvae assemblages and their relationship with abiotic parameters (Figure 3-5A and 3-5B, respectively). From this time series data, it is possible to infer that the year 1988 (an important factor in PC2; Figure 3-2) sets a boundary between mostly positive values in Dim 1 of the MFA before versus mostly negative Dim 1 values after 1988 (Figure 3-5A). This trend was associated with SOI positive anomalies linked to low water temperatures and relatively lower values for ONI and TSA indexes observed before 1988. Recall that the biological significance of Dim 1 in MFA was the segregation of neritic assemblages from meso and epipelagic families (Figure 3-3 and 3-4A). Nonetheless, the year 1988 corresponded to an abrupt shift in frequency of the paralarvae families Argonautidae and Ancistrocheridae, with higher frequencies observed before 1988, as well as for neritic assemblages, particularly Loliginidae, with opposite trends (i.e. higher frequencies after 1988).

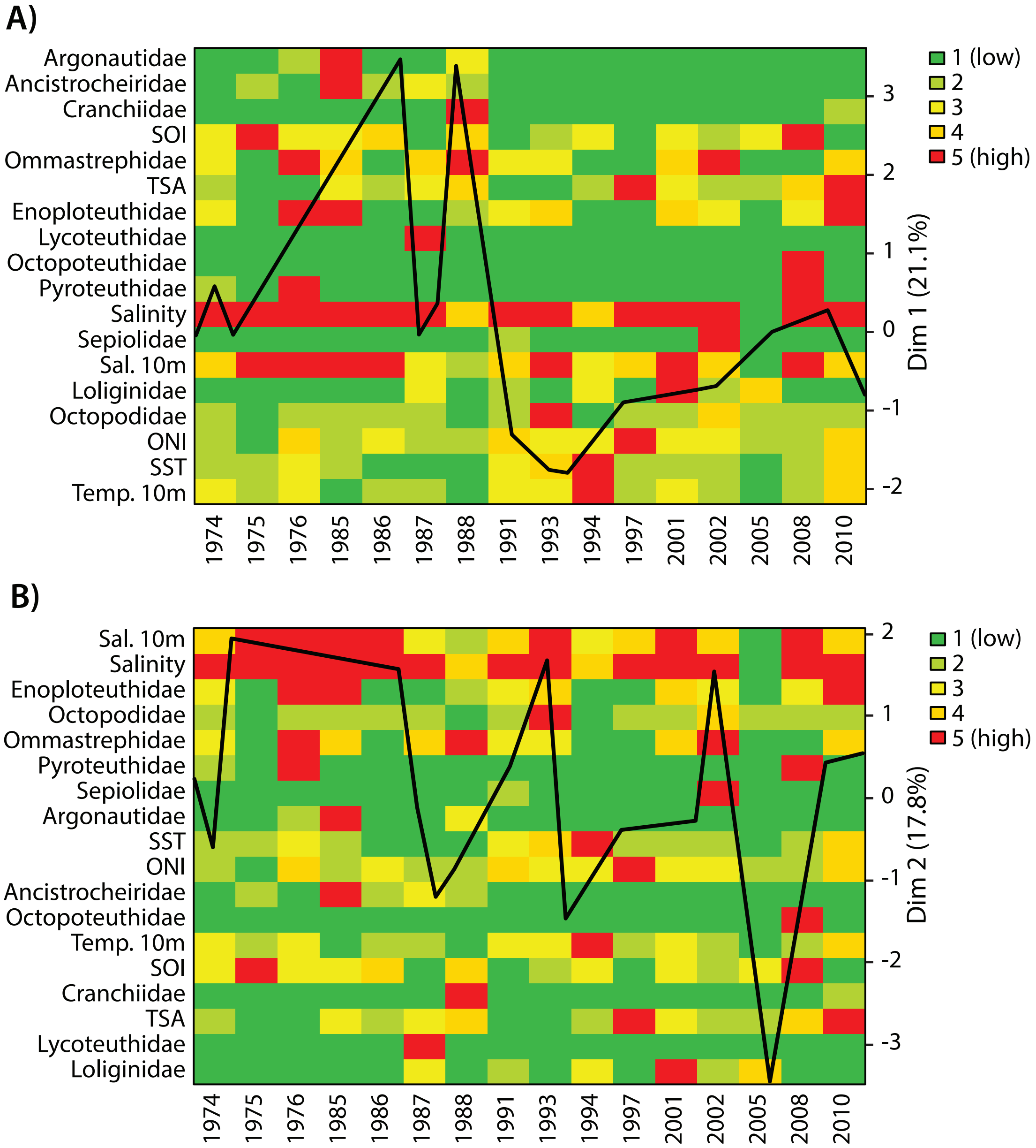

Figure 3-5. Traffic Light Plot (TLP) representing the temporal trajectories of biotic and abiotic parameters in the SBB. The variables were transformed into quintiles (red represents high values while green represents low values of the respective variable) and sorted according to Dim 1 (A) and Dim 2 (B) of the MFA. Hence, variables listed at the top are positively correlated to Dim 1 or 2, and vice versa.

Given its importance defining paralarvae assemblages, the Dim 2 of MFA was also overlapped with TLP (Figure 3-5B). The major abiotic driver for paralarvae assemblages definition in Dim 2 of MFA was salinity. Although less clear than Dim 1 (Figure 3-5A), the year 1988 marked a boundary between higher (before) and lower (after) frequencies of positive anomalies for salinity. Despite occurring throughout the time series, the frequency of occurrence of mesopelagic Enoplotheutidae and Ommastrephidae together with Octopodidae corresponded to positive anomalies in salinity (as evidenced in Figure 3-5B).

4.4 DISCUSSION

Our analysis revealed a strong multi-decadal asynchrony between key paralarvae assemblages of the SBB. Considering exclusively biotic parameters, the PCA showed a clear trend segregating neritic assemblages of cephalopods early life stages from epi and mesopelagic groups (families). This exact same trend was observable in the MFA (when abiotic parameters were overlaid to the distribution of paralarvae in PCA), which consistently revealed a positive association of temperature with neritic assemblages. The association of neritic families with high temperatures likely reflects the relative stability and year-round dominance of CW over the shelf (Castro, 2014). Conversely, both epi and mesopelagic assemblages inhabiting oceanic areas are highly dependent on the BC dynamics to reach shelf depths (Araújo and Gasalla, 2019; 2022). The latter studies have suggested two potential mechanisms for onshore parlarvae transport: 1) subsurface transport by SACW advection to the coast, eventually ensuing coastal upwelling; and 2) surface transport by meanders and eddies of the BC reaching shelf areas.

According to Dim 2 in MFA, neritic assemblages were clearly separated into Loliginidae and Octopodidae, with salinity identified as major environmental driver. The tolerance and sensitivity of cephalopods' early life stages to gradients in salinity have received very little attention and the available data are mostly focused on embryos (D'Aniello et al., 1989; Paulij et al., 1990; Sen, 2004; Cinti et al., 2004; Nabhitabhata et al., 2001). The salinity's optimum range for egg incubation and hatching for coastal cephalopods is relatively wide between 22 and 39 (Nabhitabhata et al., 2001). More recently, Castellano et al. (2017) have reported survival rates for *Octopus vulgaris* Type II paralarvae from the study area varying between 60–83%, 73–100% and 100% for salinities of 28, 30 and 37, respectively. Increased precipitation in summer months and thereby formation of estuarine plumes may result in salinity gradients across the inner shelf of the SBB (Castro, 2014). Strong El Niño events are known to enhance rainfall anomalies in summer months over the whole Southern Brazil (Grimm et al., 1998). Increased estuarine plumes over the shelf caused by rainfall could explain the negative association of Loliginidae with salinity (as observed in Dim 2 of MFA). However, the TLP results indicated an opposite pattern showing that Loliginidae was found in very low frequencies before the year 1988, albeit the high frequency of positive anomalies for SOI. Thus, it seems plausible to suggest that rainfall triggered outflow from small rivers and lagoons along the SBB may not chiefly influence the distribution of neritic assemblages. Conversely, oceanic fronts promoted by either BC intrusions into the shelf (via meanders and eddies) or SACW onshore advection may generate salinity gradient shifts in inner shelf waters, which are usually dominated by the less salty CW (Cerda and Castro, 2014). Thus the association of Octopodidae and mesopelagic Ommastrephidae and Enoploteuthidae with salinity in Dim 2 of the MFA could possibly be related to intrusions of salty oceanic waters into shelf areas.

Argonautidae scored negatively with temperature in Dim 1 of the MFA. The presence of this oceanic paralarvae in shelf areas of the SBB was shown to be associated with: 1) entrance via shelf-break mesoscale processes such as SACW upwelling events and meanders and eddies of BC in the northern sector of the SBB; 2) long distance (300–400 km) transport by upwelling plumes flowing southward and along-shore; and 3) offshore transport when upwelling plumes deviate southwestward around São Sebastião Island, in the central sector of the SBB (Araújo and Gasalla, 2022). From the latter study, it was possible to conclude that the presence of Argonautidae paralarvae in SBB shelf is likely related to the presence of SACW over the SBB.

The dynamics of SACW in the study area is regulated by northerly and northeasterly winds from the western side of the South Atlantic Subtropical High (Satyamurty et al., 1998; Wainer et al., 2006), and therefore may respond to large-scale climatic variations such as ENSO. Although exploratory, TLP results have revealed an opposite trend for high and low frequencies of Argonautidae and Loliginidae, respectively, linked to positive SOI events. In fact, negative anomalies in SST over the study area have been reported shortly before, during or right after the El Niño onset (Martin et al., 1988; Lentini et al., 2001), with dramatic biological consequences for fisheries in the SBB (Matsuura 1996). It is thus plausible to hypothesize that SOI events are linked to SACW onshore advection causing: 1) water column stratification in the shelf and/or 2) intensification of coastal upwelling events in the northernmost sector of the SBB. In either way, the presence of the cold and nutrient-rich SACW in the shelf generally leads to episodic events of new production that replace the otherwise oligotrophic scenario of the SBB shelf (Metzler et al., 1997; Castro, 2014; Brandini et al., 2018). Thus, a strong component of long-term paralarvae assemblage changes may be related to the competitive pressure in shelf waters of the SBB. That is, in periods of high biological productivity, competitive pressure may have played a role not only for the opposite responses

Argonautidae and Loliginidae to SOI positive anomalies, but also for the segregation of Loliginidae and Octopodidae within neritic assemblages (as observed in MFA).

The mesopelagic assemblages could be divided into three major groups regarding their temporal distribution. The first group consists of Sepiolidae, Pyroteuthidae, Octopoteuthidae and Lycoteuthidae, from which temporal dynamics were not strongly influenced by either sampling years or abiotic factors. For instance, these families seemed unresponsive to temperature, a major environmental driver for mesopelagic versus neritic assemblages separation in Dim 1 of the MFA. A slight positive association of Sepiolidae and Pyroteuthidae as well as a moderate negative association of Lycoteuthidae with salinity was observed in Dim 2 of the MFA. The second mesopelagic group consists of Ancistrocheiridae and Cranchiidae families from which temporal distribution resembled those for the epipelagic Argonautidae. Thus it is possible that SACW dynamics and positive scores for SOI might play a role in the temporal distribution of Ancistrocheiridae and Cranchiidae paralarvae over the SBB shelf, as previously discussed for Argonautidae. While rare families of paralarvae (with generally low abundances) represent the first and second groups, the mesopelagic assemblages are unexpectedly diverse in the SBB shelf areas (Araújo and Gasalla, 2019). The third mesopelagic group is composed by the relatively abundant Enoplotheutidae and Ommastrephidae families, which were moderately responsive to temporal variations in water temperature, but highly responsive to salinity, resembling the temporal dynamics of Octopodidae. Nonetheless, in contrast to Octopodidae, the mesopelagic Enoplotheutidae and Ommastrephidae inhabit the oceanic realm and their presence in shelf areas is likely governed by the dynamics of the warm and salty oligotrophic TW, the uppermost expression of the BC that flows along the shelf break in the SBB (Cerda and Castro, 2014).

This study has shown important patterns for understanding temporal variability although several limitations beyond the usually patchy distribution of cephalopods early life stages. Despite the relatively high numbers of individuals sampled throughout the years, size distribution and vertical profiles of paralarvae were not possible to be evaluated. Samples taken with bongo nets designed to collect fish larvae might not be ideal to assess paralarvae abundance across the water column (Piatkowski 1998; Araújo and Gasalla, 2017). Nonetheless, we believe that for non-abundant zooplankton such as cephalopod early life stages (Piatkowski 1998), the sampling design is sufficient to provide insights into their long-term ecology and distribution. In addition, the data used in this study lack continuity of sampling cruises for some years and seasons, which may interfere with statistical averaging in multivariate analyses. In this respect, we believe that multi-decadal dynamics in paralarvae distribution patterns might be more relevant for the most abundant than rare families.

4.5 CONCLUSIONS

In summary, using multivariate analyses and a unique long-term data set, we have showed a pronounced multi-decadal variability and abrupt transitions in paralarvae assemblages from the SBB. Temperature was identified as the main abiotic parameter consistently driving the segregation between neritic and oceanic paralarvae assemblages. Additional findings revealed temporal asynchrony between families within the neritic and mesopelagic assemblages in response to salinity. This exploratory approach to verify the impact of multi-decadal climate changes on paralarvae abundance further revealed that SOI positive anomalies were associated with high and low abundances of Argonautidae and Loliginidae, respectively, two of the most abundant paralarvae families in the SBB. It is important to recall that the loliginid species *Doryteuthis plei* (Blainville, 1823) and the São Paulo squid *D. sanpaulensis* (Brackoniecki, 1984) are main targets of commercial fisheries in the SBB (Gasalla et al., 2005; Perez et al., 2005; Rodrigues and Gasalla, 2008). Finally, this study highlights that the SBB peculiar oceanographic features relative to other western boundary systems play not only a crucial role for seasonal and interannual variations, but may also represent a potential factor for multi-decadal fluctuations in abundance of paralarvae assemblages.

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5 CONCLUSIONS AND FUTURE PERSPECTIVES

The overarching goal of the present study was to determine long-term patterns in oceanographic processes leading to fluctuations in the abundance and composition of cephalopods early life stages in the SBB. Three main conclusions emerged from this study: 1) there exists an unprecedentedly high diversity of oceanic paralarvae in the contintental shelf of the SBB, particularly represented by the mesopelagic assemblage, associated with the oceanographic dynamics of the area (Chapter 1); 2) a complex interplay of cross-shelf and along-shore transport chiefly contributes to the spatial and temporal distribution of oceanic Argonautidae early life stages over the SBB shelf (Chapter 2); and 3) multi-decadal variability of ocean surface temperature and salinity as well as global climate oscillations may potentially explain the temporal asynchrony among paralarvae assemblages over the SBB (Chapter 3). In this context, some general limitations of this study and further considerations are outlined below.

5.1 SAMPLE COLLECTION, SIZE DISTRIBUTION AND TAXA IDENTIFICATION

Due to the patchy distribution of cephalopods early life stages in the water column, assessment of paralarvae abundance in the ocean is somehow complex (Piatkowski 1998). In this context, sampling methods for paralarvae collection are not usually ideal to estimate their variability in abundance and composition across the water column. For instance, the majority of the samples used in this study were collected with bongo net that prevents the assessment of vertical profiles. Such limitations were previously discussed in detail (Araújo and Gasalla, 2017) and addressed in all Chapters of this thesis. Long-term and large spatial scale sampling as performed in the present study (using the ColBio-IOUSP historical collection) likely minimizes these sampling issues, and thus is believed sufficient to provide insights about paralarvae ecology and behavior and to derive valid inferences as compared to studies targeting seasonal or interannual variations.

Size distribution is considered crucial to understand paralarvae dispersal strategies as demonstrated in several studies (e.g. Perretti and Sedarat, 2016). In this study, size distributions of paralarvae were not taken into account, but the entire collection of sorted organisms is available and can be evaluated in future research. Another crucial feature that was also not examined in this study is the identification of paralarvae to the species level. In this respect, modern taxonomy using molecular techniques may be helpful in future investigations, in addition to morphological analysis. It is worth mentioning that most of the "old" plankton samples were preserved in formaldehyde, preventing the use of DNA for taxonomy. However, samples collected in cruises after the year 2000 used ethanol for preservation. Thus, there are still potential for applying either morphological or modern taxonomy in samples from this study. Recall that a single, but fundamental study by Salles et al. (2013) has set the southernmost limits of the distributional range of *Octopus vulgaris* to the southern Brazil (downstream of Rio de Janeiro) using analysis of mitochondrial markers. Further studies addressing either size distribution or species level of paralarvae used in this study will be critical to a better understanding of the main oceanographic features operating influencing cephalopods early life stages distribution over the SBB. In particular, these studies should focus on the high diversity of oceanic paralarvae families over shelf of the SBB (Araújo and Gasalla 2019) and the long-distance transport model recently suggested for argonautid paralarvae (Araújo and Gasalla 2019).

5.2 ON THE NEED FOR FURTHER EVIDENCE ON ALONG-SHORE AND CROSS-SHELF LARVAL TRANSPORT

In contrast to other western boundary subtropical systems, the SBB is relatively larger regarding the width of its continental shelf, particularly in the central sector, with ca 180 miles separating the coast and the shelf-edge (Brandini et al., 2018). Nonetheless, the continental shelf is relatively narrow (50–70 km wide) in the northern and southernmost limits of the SBB (Mahiques et al., 2010). The latter areas are seasonally impacted with coastal upwelling events driven by prevailing northerly and northeasterly winds, which fuel new production in surface waters (Valentin et al., 1987; Lopes et al., 2006; Cerda and Castro, 2014; Brandini et al., 2018). In concert with the latter data, paralarvae distribution is largely affected by the dynamics of coastal upwelling in the SBB (Vidal et al., 2010; Araújo and Gasalla, 2017; 2019; 2022).

In addition to coastal upwelling at the northern and southern limits of the SBB, intense and complex interactions between shelf and open ocean dynamics are frequently observed (Lorenzetti and Gaeta, 1996; Campos et al., 2000; Silveira et al., 2004; Calado et al., 2006; Cerda and Castro, 2014; Calil et al., 2021) and are deemed critical for larval transport. For instance, a number of studies have already depicted the role of BC meandering directly impacting the abundance of zooplankton in the SBB shelf (Yoshinaga et al., 2010; Namiki et al., 2017; Favero et al., 2017; Brandini et al., 2018; Araújo and Gasalla, 2019; 2022). Nevertheless, by using time series data of argonautid paralarvae abundance in the SBB, this study was the first to provide evidence for the importance of long-distance along-shore and cross-shelf larval transport by Cape Frio upwelling jets (Araújo and Gasalla 2022 in Chapter 2). The relevance of such long-distance transport of upwelled waters, from which nutrients become progressively depleted (Carbonel and Valentin, 1999), is yet to be validated for other zooplankton such as fish larvae using the same historical sample collection.

It must be stated that a set of samples available in ColBio collection could be highly relevant to provide complimentary data on paralarvae distribution over the SBB. Firstly, given the importance of oceanic assemblages to the shelf areas of the SBB, in particular the high abundance of Enoploteutidae, Ommastrephidae and Argonautidae, it would be ideal to examine samples from stations on the shelf-break or even deeper areas that were not covered in this study. This information could be central not only to understand variations in spatial and temporal distribution of oceanic assemblages, but also to verify whether neritic assemblages could possibly experience offshore transport as reported for meroplaktonic crustaceans (Yoshinaga et al., 2010).

Lastly, while our sampling design was limited to 25°S, the southernmost limit of the SBB is located at Cape Santa Marta Grande (28°S) and samples from this area are available at ColBio. The southern sector of the SBB is highly relevant to paralarvae research not only due to its coastal upwelling events (Vidal et al., 2010), but particularly owing to the presence of the Brazilian Coastal Current (BCC) (see discussion below). Little attention has been given to biological consequences of BCC over the SBB (Brandini et al., 2018), and virtually no information on paralarvae composition and abundance exists.

5.3 LONG-TERM VARIABILITY OF PARALARVAE ASSEMBLAGES

Cephalopods exhibit a unique set of biological traits such as extremely fast growth rates and rapid rates of turnover at the population level, and are renowned for their extreme flexibility and plasticity to environmental changes, largely reflecting in dramatic and direct responses of growth to temperature (Pecl and Jackson 2008). In a warming ocean scenario, a global proliferation of cephalopods has been reported (Doubleday et al., 2016), and more recent predictions have shown a potential capacity of cephalopods to expand their distribution towards the pole (e.g. Xavier et al., 2016; Le Marchand et al., 2020; Lima et al., 2020). While it would be logical to suggest that rising water temperatures is associated with faster growth rates and thereby accelerated turnover of populations, ocean warming will likely result in complex biological, physiological and behavioral changes (Pecl and Jackson 2008), particularly for cephalopods early life stages.

In Chapter 3, exploratory multivariate analyses of multi-decadal data on paralarvae abundance suggested both surface temperature and salinity as major driving factors influencing cephalopod early life stages assemblages in the SBB. In addition, the findings revealed that Argonautidae and Loliginidae display opposite responses to positive anomalies in the Southern Oscillation Index. Despite representing mostly a bycatch of fish and shrimp trawl fisheries, loliginid are the commercially relevant cephalopods for the SBB region (Perez et al., 2002; Gasalla et al., 2005; Perez et al., 2005; Rodrigues and Gasalla, 2008). Thus, understanding the long-term distribution of loliginid species may provide important clues about their sensitivity to the impacts of overfishing and/or abrupt climate change.

Although exploratory in nature, the temporal asynchrony between paralarvae assemblages reported in this long-term study needs further validation. For instance, expanding the analyses for samples collected in shelf break areas would certainly improve our current understanding about the long-term distribution of paralarvae assemblages over the SBB, in particular the temporal dynamics between onshore/offshore larval transport. The analysis of samples in the southern sector of the SBB (25–28°S) is another major gap left by this study. This region is frequently influenced by Brazilian Coastal Current (BCC, 18 °C; 32 psu) that flows northwards extending from south of Cape Santa Marta (28°S) reaching shelf areas well within the central sector of the SBB (Campos et al., 1999; Lentini et al., 2001). The BCC is a combination of Southern Brazil shelf waters with sub-Antarctic and coastal waters from the La Plata River (Brandini et al., 2018). Importantly, BCC intrusions into the SBB were reported as a seasonal phenomenon (more often occurring in winter months) presenting interannual variability possibly related to El Niño Southern Oscillation (Campos et al., 1999; Lentini et al., 2001) with dramatic effects on biological productivity (Ciotti et al., 19995). Given the absence of major river systems throughout the SBB, the long-term dynamics of the cold and low salinity BCC and its relationship with El Niño/La Niña events may chiefly influence the composition and abundance of paralarvae in the southern sector of the SBB.

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