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Community Structure and Spatiotemporal Dynamics of the Zooplankton in the South Brazilian Bight: A Review



Miodeli Nogueira Jr. and Frederico P. Brandini

Abstract The South Brazilian Bight (23–28.5°S; SBB) is a typical western boundary current system with a wide shelf and which has high ecologic and economic importance, supporting nationally important fishing grounds. Away from the coastal areas, the planktonic production is mostly controlled by regenerative processes prevailing in the oligotrophic Tropical Water (TW) of the Brazil Current, enriched by the advection of the nutrient-rich South Atlantic Central Water (SACW). About 790 zooplanktonic invertebrate species have been recorded, what is an underestimate considering that most meroplanktonic and some holoplanktonic taxa are largely unstudied. An inshore-offshore gradient is clear. Zooplankton abundance and biomass are typically higher in more coastal areas, diminishing offshore as the influence of the oligotrophic TW increases, while the diversity has the inverse tendency. The cold and nutrient-rich SACW intrusions certainly are the most relevant mesoscale physical feature over the shelf of the SBB, increasing considerably the primary production and subsequently zooplankton abundance and production. Indeed, available data suggest that the intrusions of the SACW and their strength are an important factor influencing both seasonal and interannual variability in zooplankton diversity, biomass, abundance, production, and size-spectra. While the distributional patterns of most of the dominant groups in relation to the main water masses are relatively well-known, little is known about the life strategy, trophic interactions, physiological responses, and the impact of the main physical processes on these populations. In this review, we also emphasize the need for process-oriented studies along SBB with spatiotemporal scales relevant to the main physical events in order to better understand the zooplankton dynamics and their role in the regional fishery production.

Keywords Zooplankton · Composition · Dynamics · South Brazilian Bight

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1 Introduction

The South Brazilian Bight (23–28.5°S, SBB) is a typical western boundary current system with a wide shelf that may reach up to ca. 200 km wide (Fig. 1). It is part of a transitional zone between subtropical and temperate domains (Lohrenz and Castro 2005; Longhurst 2006). The SBB hosts a large biodiversity and is the most productive Brazilian continental shelf region, supporting important fishing grounds with fish catches >200,000 tons/year (MPA 2011), emphasizing its economic and ecologic importance. The main targeted species is the Brazilian sardine *Sardinella brasiliensis* (MPA 2011). This species is primarily planktivorous (e.g., Dias et al. 2004), as is the case of many other economically important fish species from the SBB (e.g., Kurtz and Matsuura 2001; Soares and Vazzoler 2001) and elsewhere. Even though several adult fish do not eat plankton directly, the survivorship of their larvae and consequently their recruitment rates

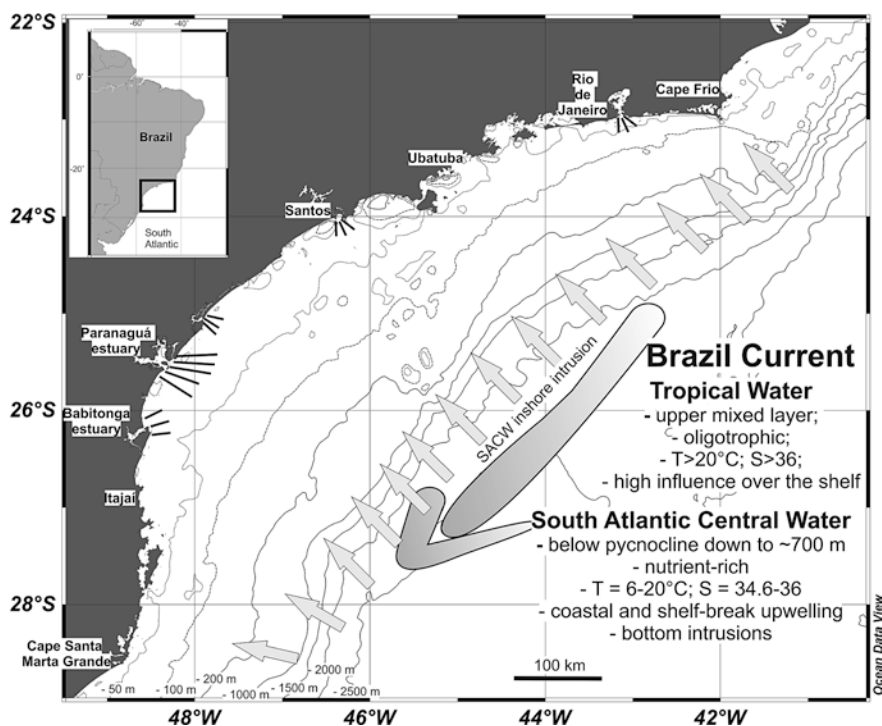


Fig. 1 Map of the South Brazilian Bight showing the main oceanographic features, such as the Brazil Current (large arrow) with the Tropical Water in the upper layer and the South Atlantic Central Water below along with its wind-driven inshore intrusions, and the main sources of continental drainage (solid lines). The Coastal Water is not shown, but it occupies mainly the shallow shelf (<50 m isobath) and has a variable signature with low salinity (<34) because of the mixing of continental runoff and the other two water masses. Generated using Ocean Data View 4.7.10 software (Schlitzer 2017)

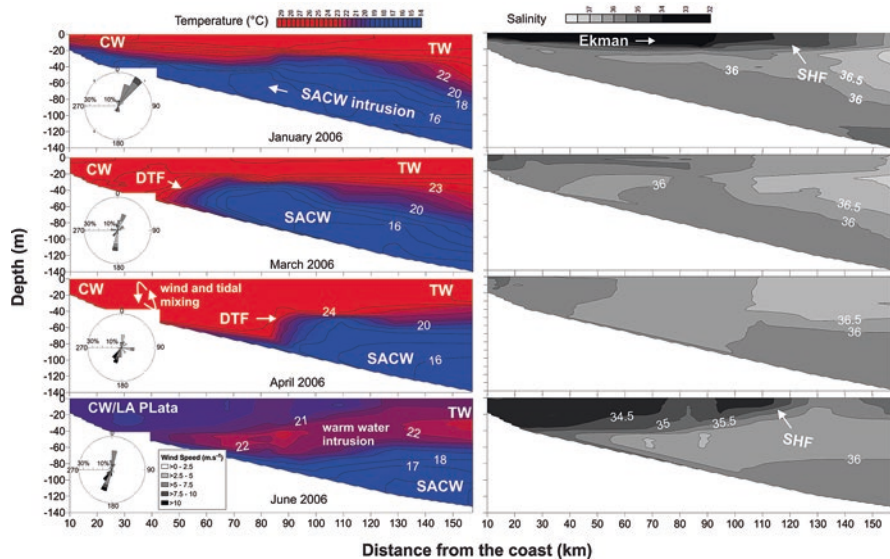
are greatly dependent on the availability of their planktonic food (Matsuura et al. 1992; Dias et al. 2004). Thus, the knowledge of zooplankton variability is important to understand the ecosystem functioning and its ecological patterns as well as to fisheries management, providing important information about the energy flow in marine communities (Montú et al. 1997). In the present study, we provide synoptic information on diversity, structure, and temporal variability of invertebrate zooplankton from the SBB in relation to the main water masses and oceanographic processes taking place over the shelf (Fig. 1).

2 Hydrography and Circulation Patterns

Several authors have described the general physical oceanographic characteristics of the SBB (e.g., Lohrenz and Castro 2005; Castro et al. 2005, 2006; Cerda and Castro 2014; Brandini et al. 2007, 2014). The overall circulation over the shelf follows the worldwide pattern of western boundary current systems, as part of the South Atlantic Anticyclonic Subtropical Gyre. The Brazilian Current (BC) originates at *ca* 10°S and flows southward near the continental slope through all the SBB until it meets the Malvinas Current, forming the Brazil–Malvinas Confluence Zone southward the SBB, between 33°S and 38°S, where a complex frontal system with cyclonic eddies and water column stabilization support high biological production (e.g., Brandini et al. 2000). On the SBB, the upper mixed layer in mid- to outer-shelf is dominated by warm (>20 °C), saline (>36), and oligotrophic Tropical Water (TW) of the BC (Figs. 1, 2, and 3). This water mass is formed as a consequence of the intense solar radiation and excess of evaporation, characteristic of tropical and subtropical oceans. Below the TW is the South Atlantic Central Water (SACW), formed by subsidence at the Subtropical Convergence, with temperatures varying from 6 to 18 °C and salinities from 34.6 to 36. The Coastal Water (CW) with lower salinities (<34) results from the mixing of TW and/or SACW with local continental drainage, and it occupies most of the shallow shelf. It is characterized by high seasonal and geographical physical-chemical fluctuations according to geomorphology, local precipitation and river discharge (Castro et al. 2006).

Most of the SBB's shelf area is dominated by one of these water masses or a mixture of them (Figs. 2 and 3); CW tends to dominate the inner shelf (Fig. 3a, b), and TW with the SACW below dominate the outer-shelf and offshore (Fig. 3c, d). A stable thermocline separates the TW and SACW, while the surface haline front (SHF) and the deep thermal front (DTF) separate the CW and TW and CW/TW and SACW, respectively (Castro et al. 2005, 2006; Brandini et al. 2014). These boundaries are dynamic and change their position mainly driven by the wind regime pattern which tends to be seasonal (Fig. 2).

During spring-summer northeasterly winds tend to dominate and CW is pushed offshore by surface Ekman transport with SHF reaching more than 100 km offshore (Fig. 2). This results in the onshore intrusions of the cold SACW (and the consequent



displacement of the DTF inshore) which provide important nutrient input and also enhance light conditions over the shelf by increasing the ratio between the depth of the euphotic and upper mixing zone, thus increasing considerably phytoplankton growth and production (Brandini et al. 2007, 2014). The particularities of the intrusions may change interannually and with latitude throughout SBB, depending mostly on wind conditions and interactions with local topography, respectively. For instance, in some locations with relatively shorter shelf such as Cape Frio and Cape of Santa Marta Grande, the SACW may reach the surface (Matsuura 1986; Castro et al. 2005, 2006; Cerda and Castro 2014; see Fig. 3), while in most other sites of the SBB, the intrusion fertilizes the euphotic zone and may reach the inner shelf areas (Fig. 2 and 3), but due to the larger continental shelf and gentle slope, it typically does not reach the surface (Brandini et al. 2007, 2014; Cerda and Castro 2014; Nagata et al. 2014).

These differences are clear comparing, for instance, the vertical temperature and salinity profiles of shallow waters (50 m) off Cape Frio and Itajaí (Fig. 3a, b). In the former, in December 2001 and November 2002, temperature was low (17–19 °C) in the surface, reaching <15 °C below 20 m, while the salinity was nearly homogeneous vertically 35.2–35.5 (Fig. 3b), denoting the SACW influence through the water column. Off Itajaí in January 2006, water column was very stratified both in temperature and salinity in the 50 m isobath (Fig. 3a, b); the lower temperature near the bottom indicates the influence of the SACW only in this depth stratum, whereas the lower salinities in the surface layer indicate the high influence of CW in the upper layer, with the SHF positioned offshore (Fig. 2).

During winter, shelf waters tend to overturn vertically (Fig. 2) due to tidal circulation and Ekman convergence of outer-shelf waters driven by southerly winds, and therefore the SHF and DTF reverse, being placed inshore and offshore, respectively. Also, the winter predominance of southwest winds shifts the offshore BMCZ northward, transporting subantarctic and less saline waters ($T = 4\text{--}15\text{ }^{\circ}\text{C}$, $S = 33.5\text{--}34$) from the Argentinian shelf, along with a coastal branch greatly dominated by the continental drainage of the La Plata River basin which may reach the southernmost shelf areas of the SBB (Brandini 1990; Castro et al. 2005, 2006). For instance, temperature and salinity were vertically homogeneous both off Cape Frio and Itajaí shallow waters during winter (Fig. 3a, b), in both cases highly influenced by the CW but colder and less saline off Itajaí due to influence of the La Plata Plume (Brandini et al. 2014).

Offshore, seasonal and latitudinal variations are less pronounced with the typical tropical vertical profile of temperature and salinity with warm (>20 °C) and saline (>36) waters in the upper layer (Fig. 3c, d), typically under TW influence, and cold waters of the SACW below through the year. Relatively lower temperatures and salinity in the surface layer off Itajaí at the 130 m isobath during winter is resultant from the influence of the Plata Plume River (Brandini et al. 2014). The meandering of the Brazil Current along the continental slope and cyclonic eddies may lead to shelf-break upwellings of the SACW (Castro et al. 2005, 2006).

3 Zooplankton from South Brazilian Bight

3.1 Diversity and Association with Water Masses

About 790 invertebrate zooplanktonic species have been recorded at SBB. This number certainly is an underestimate, considering that (i) all meroplanktonic taxa and some holoplanktonic ones such as ctenophores, amphipods, euphausiaceans, turbellarians, polychaetes, and ostracods are largely unstudied and that (ii) there is a continuous discovery of new species (e.g., Bersano and Boxshall 1994; Nogueira Júnior et al. 2013) or records for the area (e.g., Campos and Vega-Pérez 2004; Carvalho and Bonecker 2008; Nogueira Júnior et al. 2016).

As observed in other pelagic coastal and oceanic systems, copepods are the most abundant and diverse taxa, representing ~33% of all invertebrate zooplanktonic species recorded at SBB (Fig. 4). Copepods are followed by cnidarians (~30%) and other crustaceans (mero + holoplankton = ~19%). However, the potential diversity of larval benthic crustaceans, polychaetes, and many other invertebrate taxa, such as mollusks and echinoderms, is gigantic. Each of these taxa have thousands of known species worldwide, most of them with planktonic larvae but which have not been described yet and are particularly understudied at the SBB. Amphipods are also locally understudied, only analyzed in details by Lima and Valentin (2001a).

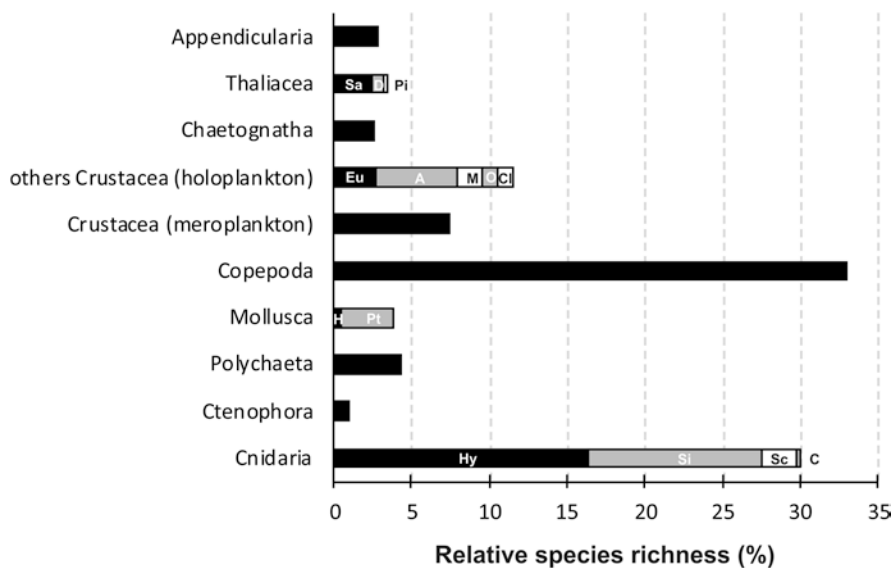


Fig. 4 Percentage of zooplankton species recorded at South Brazilian Bight according to main taxonomic groups. (Data from Lopes et al. (2006) complemented with recent new species and records up to 2015). Total number of species = 790. Hy hydromedusae, Si Siphonophorae, SC Scyphozoa, C Cubozoa, Pt Pteropoda, H Heteropoda, Eu Euphausiacea, A Amphipoda, M Mysidacea, O Ostracoda, Cl Cladocera, Sa Salpida, D Doliolida, Pi Pyrosomatida

The diversity of planktonic ostracods recorded (Fig. 4) is quite low (7 species) when compared to the 124 species recorded in the whole South Atlantic (Angel 1999). This taxon is locally understudied, and publications with specific or at least generic identifications of planktonic marine ostracods from the SBB are rare (Rocha 1983; Valentin 1980), although they may reach high abundances of up to 7600 ind m⁻³ (Valentin et al. 1987). Regardless, many planktonic ostracod species often dwell close to the bottom or live at depths greater than 200 m with considerably fewer species occurring over the shelf (Deevey 1974). The groups with lesser numbers of species are the pyrosomes and cubomedusae (2 species each). These taxa are also understudied in Brazil (Carvalho and Bonecker 2008; Nogueira Júnior and Haddad 2008), but unlike meroplanktonic larvae, amphipods, and ostracods, pyrosomes and cubomedusae are not very diverse, with only six species each recorded in whole South Atlantic (Esnal 1999; Carvalho and Bonecker 2008; Gershwin and Gibbons 2009; Oliveira et al. 2016).

3.1.1 Cnidarians

Among hydromedusae, the holoplanktonic *Liriope tetrphylla* is the most ubiquitous, being the commonly dominant species in the shallow to mid-shelf under CW influence with densities up to 930 ind m⁻³ along with the occurrence of many other meroplanktonic, usually less abundant, species (Vannucci 1963; Nagata et al. 2014; Nogueira Júnior et al. 2014). High biomass of the scyphomedusa *Lychnorhiza lucerna* occurs in shallow coastal areas (<15 m), with recorded wet weight up to 6.4 kg km⁻² (Nogueira Júnior and Haddad 2017). Besides very abundant, this large jellyfish (>30 cm in bell diameter) is edible and may be commercially exploited as exportation product for human consumption, especially to Japan and China (Nagata et al. 2009), and may serve as shelter for other organisms such as young fishes, crabs, and shrimps (Nogueira Júnior and Haddad 2005; Martinelli Filho et al. 2008). Medusae from TW of the Brazilian Current are typically holoplanktonic like *Aglaura hemistoma*, *Solmundella bitentaculata*, and *Rhopalonema velatum*, the former commonly being the most abundant, with densities offshore typically not exceeding 10 ind m⁻³ (Vannucci 1957, 1963; Nogueira Júnior et al. 2014, 2015). In upwelling areas of Cape of Santa Marta Grande, the meroplanktonic hydromedusae *Olindias sambaquiensis* and *Rhacostoma atlanticum* are extremely abundant, with the latter representing up to 68% of the macrozooplankton carbon biomass (Mianzan and Guerrero 2000), both also occurring in areas dominated by CW (Vannucci 1951a; Nogueira Júnior and Haddad 2017). The holoplanktonic *Solmaris corona* is also found with relative high densities (up to 84 ind m⁻³) associated with SACW in offshore regions (Nogueira Júnior et al. 2014).

Siphonophores are usually more oceanic, with only a few species like *Muggiaea kochii*, *Diphyes bojani*, and *Nanomia bijuga* occurring abundantly in coastal areas. High diversity and abundance of siphonophores is found typically offshore in the upper layer of the BC. *M. kochii* tend to dominate under CW influence, where they may reach abundances of 140 colonies per cubic meter, while *D. bojani* and

Abylopsis spp. (mainly *A. tetragona*) in mid- to outer-shelf with densities typically <25 colonies per 10 cubic meters, and mainly *Chelloglyphes appendiculata* and *Eudoxoides spiralis* in oceanic areas under direct influence of BC (Cordeiro and Montú 1991; Nogueira and Oliveira 1991; Nagata et al. 2014; Nogueira Júnior et al. 2014, 2015). Other common siphonophores associated with TW offshore include *Enneagonum hyalinum*, *Eudoxoides spiralis*, *Eudoxoides mitra*, *Lensia* spp., and *Sulcoleolaria* spp., commonly in lower densities.

3.1.2 Ctenophores

Since only a few species of ctenophores (mainly smaller forms of *Beroe* spp.) may be routinely fixed and preserved with success (but see Sullivan and Gifford 2009; Engel-Sorensen et al. 2009), studies on ctenophores are generally scant. This is especially true for Brazilian ecosystems where these ctenophores, although common, are among the least-studied marine animals (Oliveira et al. 2007, 2016). Only 13 species of planktonic ctenophores have been recorded thus far (Oliveira et al. 2016). *Mnemiopsis leidyi* and *Beroe ovata* are common and occasionally abundant in coastal and estuarine areas (Oliveira et al. 2007; Nogueira Júnior et al. 2018). In offshore areas over the shelf abundances are low (<1 ind m⁻³), and small-sized (<10 mm high) *Beroe* sp. perform diel vertical migration through the thermocline (Nogueira Júnior et al. 2015).

3.1.3 Mollusks

Gastropod and bivalve larvae may be quite abundant on some situations, mostly in the shallow shelf dominated by CW and off estuaries influenced by river plumes with densities peaking around 1000–2000 ind m⁻³ (Valentin et al. 1987; Codina 2003). Among pteropods, *Creseis virgula* dominates the shelf TW, while *Limacina trochiforme* characterizes oceanic TW (Resgalla and Montú 1994; Resgalla 2008). *Creseis acicula* and *Limacina* spp. are quite abundant at Cape Frio with densities up to 13,600 ind m⁻³ (Valentin et al. 1987). *Cavolinia inflexa*, *Clio pyramidata*, and *Hyalocylis striata*, contrary, are widely distributed (Montú et al. 1997). Heteropods are commonly less abundant with dominance of *Atlanta* spp. in the northern SBB (Valentin et al. 1987). The heteropod *Firoloida desmarestia* was formally recorded only by Vannucci (1951b) near Trindade Islands. It is not abundant (<0.1 ind 10 m⁻³) but is moderately common offshore in the upper layer under TW influence and can be considered an indicator of this water mass offshore (MNJ, unpublished data).

3.1.4 Crustaceans

Due to the high diversity found at TW, 150–200 copepod species may be found in a typical cross-shelf transect and offshore areas (Lopes et al. 2006). Most of the coastal species are small-sized. The dominant copepods under CW influence

typically include *Acartia lilljeborgi*, *Paracalanus quasimodo*, *Parvocalanus crassirostris*, *Pseudodiaptomus acutus*, *Euterpina acutifrons*, *Labidocera fluviatilis*, *Ditrichocorycaeus amazonicus*, *Oncaea waldemari*, *Oithona hebes*, and *Oithona oswaldocruzi*, and these species may reach thousands and up to tenths of thousands ind m^{-3} (Valentin et al. 1987; Eskinazi-Sant'Anna and Björnberg 2006; Miyashita et al. 2009; Brandini et al. 2014; Melo Júnior et al. 2016). *Lubbockia squillimana* and *Paraeucalanus sewelli* are typically oceanic but may also occur in shallow waters, probably due to TW and SACW influences (Miyashita et al. 2009). Many of the coastal species are restricted to estuaries and the inner shelf, disappearing under influences of oceanic oligotrophic waters (Sartori and Lopes 2000).

Copepods associated with the TW, such as *Acrocalanus longicornis*, *Calanopia americana*, *Clausocalanus furcatus*, *Farranula gracilis*, *Haloptilus*, *Mecynocera*, and *Candacia* among others, are commonly more abundant in the upper mixed layer (Björnberg 1963, 1981; Lopes et al. 1999; Brandini et al. 2014). Among these, *C. furcatus* commonly is the dominant species; this small-sized copepod is typically oceanic and known to be well-adapted to thrive successfully in oligotrophic waters, producing more offspring under lower food concentrations (Mazzochi and Paffenhöfer 1998; Brandini et al. 2014). Species typical from the SACW include *Heterorhabdus*, *Euatideus*, *Temeropia*, *Haloptilus* spp., *Centropages violaceus*, *Ctenocalanus vanus*, and *Calanoides carinatus* (Valentin 1989). Most of this species disappear shortly after upwelling or mixing events, except for the two latter which persist and are commonly used as indicator of SACW presence on the shelf (Björnberg 1963, 1981; Valentin 1984a, b, 1989). *C. vanus* typically dominate the mid-shelf during SACW intrusion periods, usually accumulating in the deep chlorophyll maximum layer, but its populations may persist throughout the seasons (Brandini et al. 2014).

Cladocerans are essentially neritic, with higher concentrations near the coast (Muxagata and Montú 1999), being particularly common in the upper mixed layer reaching densities up to ca. 2000 ind m^{-3} (Rocha 1982; Valentin et al. 1987; Miyashita et al. 2011; Domingos-Nunes and Resgalla 2012; Brandini et al. 2014). Parthenogenetic reproduction is the main reproductive strategy of SBB cladoceran populations allowing a rapid populational growth under favorable conditions, and thus population variations are accentuated, and abundance pulses over the shelf are commonly observed (Resgalla and Montú 1993; Miyashita et al. 2011). In shallow coastal waters, *Pseudevadne tergestina* and *Penilia avirostris* are the most common and abundant, particularly under stratified conditions due to bottom intrusions of the SACW (Rocha 1982; Valentin 1984a, b; Miyashita et al. 2010, 2011; Brandini et al. 2014). *Pleopsis polyphemoides* is a CW indicator, frequently associated with estuarine waters (Valentin et al. 1987; Resgalla and Montú 1993; Miyashita et al. 2011), and when associated with *Evadne nordmanni* and *Pleopsis schmackeri* differentiates thermal conditions of summer and winter, respectively, on South Brazilian Shelf (Resgalla 2008). *Evadne spinifera* characterizes the oceanic TW (Resgalla and Montú 1993; Resgalla 2008) but also may occur in the inner shelf in low abundance and frequency (Miyashita et al. 2011). *Podon intermedius* is a cold-water species, typically associated with SACW intrusions (Rocha 1982; Miyashita et al. 2011).

Most mysids tend to be more common in coastal and estuarine areas (Murano 1999). They may reach high concentrations at surf zone of sandy beaches, where *Metamysidopsis elongata atlantica* may reach high densities (up to 3500 ind m⁻³) and biomass, dominating the zooplankton (Bersano 1994; Ávila et al. 2009). In contrast, euphausiids are more common over the shelf-break and oceanic areas, especially the adult forms of some dominant species such as *Euphausia similis*, *E. recurva*, *E. lucens*, and *Thysanoessa gregaria* (Montú et al. 1997). Species like *Euphausia recurva*, *E. americana*, *E. hemigiba*, *Stylocheiron* spp., *Thysanopoda* spp., and *Nematobrachion flexipes* are typical of warm waters and indicate the influence of BC over the shelf (Lansac-Tôha 1991).

Two species of holoplanktonic decapods of the genus *Lucifer* are common, *L. faxoni*, most common, is typically more coastal, while *L. typus* occurs in areas of mixed CW/TW in salinities higher than 36 (Brandão et al. 2015), although both species also occur on TW offshore until near the Mid-Atlantic Ridge (~15°W, Marafon-Almeida et al. 2016). Hyperiid are understudied in the SBB, and the unique comprehensive survey found 40 species and densities up to ca. 160 ind m⁻³, with *Lestrigonus bengalensis* and *Simorhynchotus antennarius* dominating, the former typical from the CW and usually absent from salinities >36 of the TW, and both also may occasionally be associated with siphonophores and/or salps (Lima and Valentin 2001a, b).

3.1.5 Chaetognaths

Chaetognaths are important predators and usually considered good water mass indicators. *Parasagitta friderici* is associated with waters of lower salinities (Nogueira Júnior et al. 2018) and considered typical of CW, where it commonly is the most abundant species, along with *Parasagitta tenuis* reaching densities usually smaller than 250 ind m⁻³ (Almeida Prado 1961, 1968; Liang 2002); however at Cape Frio chaetognath densities up to 2600 ind m⁻³ have been reported, and *Flaccisagitta enflata* is typically the dominant species (Valentin et al. 1987). This later species also typically dominates the TW over the shelf along with the less abundant *Ferosagitta hispida*, *Serratosagitta serratodentata*, *Flaccisagitta hexaptera*, *Pterosagitta draco*, and *Krohnitta pacifica* which are typical of oceanic TW, while *Krohnitta subtilis*, *Decipisagitta decipiens*, and *Pseudosagitta lyra* are typical from SACW (Almeida Prado 1968; Liang and Vega-Pérez 1994, 2002; Montú et al. 1997; Liang 2002; Resgalla 2008).

3.1.6 Appendicularians

A little more than 20 species of appendicularians have been recorded over the SBB, with *Oikopleura longicauda* being the dominant species (Tundisi 1970; Sinque 1982), particularly in the upper mixed layer where it may reach densities up to ca. 1100 ind m⁻³ (Miyashita and Lopes 2011). *O. fusiformis* also reaches

high densities at CW, and *Fritillaria pellucida* is more abundant at SACW intrusions. Other species such as *O. rufescens*, *F. borealis*, and *F. pellucida* are typical of shelf and slope waters, and *O. albicans*, *O. cophocerca*, and *F. formica* are predominantly from oceanic waters (Montú et al. 1997). Appendicularians have high secondary production on SBB inner shelf equaling to 77% of the copepod production (Miyashita and Lopes 2011).

3.1.7 Thaliaceans

The salp *Thalia democratica* is the most ubiquitous species, being widely distributed over shelf, coastal, and offshore areas (Tavares 1967; Valentin and Monteiro-Ribas 1993; Amaral et al. 1997; Nogueira Júnior et al. 2015), occasionally reaching estuarine waters in salinities down to 21 (Nogueira Júnior et al. 2018). This opportunist species has high asexual reproduction rates (Esnal and Daponte 1999), forming huge aggregates that may exert negative impact over the recruitment of pelagic fishes (Matsuura et al. 1992; Katsuragawa et al. 1993; Resgalla et al. 2001) by depleting resources from the water column. The doliolids *Doliolum nationalis* and *Dolioletta gegenbauri* are the most common in the CW and TW over the shelf (Tavares 1967), with abundances up to 1000 ind m⁻³ (Valentin et al. 1987), with gonozooids being particularly abundant in the upper mixed layer and phorozooids over the deep chlorophyll maximum layer (Nogueira Júnior et al. 2015). High biomass of *Salpa fusiformis* over the shelf can be observed associated with the SACW intrusions (Nogueira Júnior and Brandini, unpublished data). Other species like *Brooksia rostrata*, *Ihlea punctata*, *Riteriella retracta*, and *Cyclosalpa polae* may be found over the shelf at much smaller concentrations (Amaral et al. 1997; Esnal and Daponte 1999), the former typically associated with TW (Nogueira Júnior and Brandini, unpublished data).

3.2 Abundance and Biomass Distribution

An inshore-offshore gradient in the zooplankton abundance, biomass and diversity is typical over the whole SBB. While abundance and biomass are higher in more coastal areas diminishing offshore as the influence of the oligotrophic TW increases, the diversity has the inverse tendency (Katsuragawa et al. 1993; Vega-Pérez 1993; Lima and Valentin 2001a; Resgalla et al. 2001; Lopes et al. 2006; Brandini et al. 2014). Although data from different studies may vary considerably due to latitudinal, interannual differences and also due to different sampling strategies such as sampling frequency and mesh size (e.g., Miyashita et al. 2009), generally higher zooplankton abundance and biomass are associated with CW, decreasing in other water masses independently of the season, and higher diversity is associated with the TW (e.g., Valentin 1984a; Valentin and Monteiro-Ribas 1993; Lopes et al. 2006; Brandini et al. 2014; Nogueira Júnior et al. 2014, 2015).

For instance, zooplankton biovolume and copepod biomass of up to 1.7 ml m^{-3} and 100 mg C m^{-3} , respectively, have been reported from shallow waters off Cape Frio, while offshore the values were $<0.1 \text{ ml m}^{-3}$ (Nogueira and Oliveira 1991) and $<10 \text{ mg C m}^{-3}$ (Dias et al. 2015). Off Ubatuba, biovolumes also are commonly $>1 \text{ ml m}^{-3}$ and up to 6 ml m^{-3} in shallow waters and much lower ($<0.5 \text{ ml m}^{-3}$) in offshore areas ($>100 \text{ m}$ isobaths, Vega-Pérez 1993; Codina 2003). A high variability has been reported through different years, with high concentrations (up to 38 ml m^{-3}) occasionally also found in mid- to the outer-shelf mostly due to the massive presence of salps (Katsuragawa et al. 1993) which are typically oceanic (see above). Similarly, further south of the SBB, average biovolumes between 1977 and 1990 reached $>1 \text{ ml m}^{-3}$ in coastal areas and typically lower values ($<0.25 \text{ ml m}^{-3}$) offshore, with differences more pronounced during summer and autumn (Resgalla et al. 2001). Copepod biomass off Ubatuba may reach up to ca. 100 mg DW m^{-3} , but more commonly is $<30 \text{ mg DW m}^{-3}$ (Melo Júnior et al. 2016), with summer averages around 7.3 mg C m^{-3} (Miyashita et al. 2009). Zooplankton abundances over the shallow shelf are typically $>2000 \text{ ind m}^{-3}$, and concentrations of tenths of thousands ind m^{-3} have commonly been reported with up to ca. $100,000 \text{ ind m}^{-3}$, while offshore of the 100 m isobath densities are typically $<1000 \text{ ind m}^{-3}$, and commonly lower, occasionally reaching up to 1700 ind m^{-3} (Vega-Pérez 1993; Schettini et al. 1998; Valentin 1984a, b; Valentin et al. 1987; Sartori and Lopes 2000; Miyashita et al. 2009; Brandini et al. 2014; Dias et al. 2015).

A few exceptions to these general patterns of decreasing abundance and increasing diversity toward offshore include (i) the tendency of some taxa to have higher diversity and abundance in coastal and estuarine waters, mostly those somehow associated to the seafloor such as meroplanktonic hydromedusae, mysids, and decapod larvae (Nogueira Júnior 2012; Nogueira Júnior et al. 2014; Miyashita and Calliari 2014; Brandão et al. 2015; Nogueira Júnior et al. 2018), and (ii) some typically oceanic taxa such as euphausiaceans, salps, and siphonophores tend to have higher abundances over the mid- to outer-shelf and shelf-break (Valentin and Monteiro-Ribas 1993; Amaral et al. 1997; Esnal and Daponte 1999; Gibbons et al. 1999; Nogueira Júnior et al. 2014).

Horizontally, higher zooplankton concentrations are usually associated with areas under continental drainage influence, like off Guanabara, Cananéia, and Paranaguá Bays (Vannucci and Almeida Prado 1959; Resgalla et al. 2001; Lopes et al. 2006; Nagata et al. 2014; Brandão et al. 2015). Areas subjected to the upwelling (Valentin 1984a, b, 1989; Valentin and Monteiro-Ribas 1993) or bottom intrusions (Miyashita et al. 2009, 2011; Brandini et al. 2014) of the SACW also typically tend to have high seasonal zooplankton concentrations. The dynamics of the SACW movements certainly is the most relevant mesoscale physical feature over the shelf of the SBB (Castro et al. 2005, 2006; Cerda and Castro 2014) impacting biological communities (Miyashita et al. 2009, 2011; Brandini et al. 2014). Either coastal and shelf-break upwelling or bottom intrusion of the SACW causes enrichment over the shelf and shelf-break (Brandini et al. 1997, 2014), increasing considerably the primary production and subsequently zooplankton abundance, biomass, and production (Guenther et al. 2008; Miyashita et al. 2009, 2011; Brandini et al. 2014; Marcolin et al. 2015).

Off Cape Frio the relation of SACW upwelling with zooplankton dynamics was relatively well-studied in different spatiotemporal scales (e.g., Valentin 1984a, b, 1989; Valentin et al. 1987; Valentin and Monteiro-Ribas 1993; Lopes et al. 1999; Guenther et al. 2008). In the downwelling phase, a microbial structure prevails with dominance of pico- and nanophytoplankton and high contribution of bacterioplankton and microzooplankton. During upwelling, microplankton, mostly diatoms, and mesozooplankton, mostly copepods, are the main producers and consumers, respectively, characterizing an herbivorous, more productive, food web (Guenther et al. 2008). During downwelling, mesozooplankton is dominated mostly by *Paracalanus parvus*, *Temora turbinata*, and *Pseudevadne tergestina*, while during the upwelling the two latter species decrease in abundance, while zooplankton biomass is dominated by opportunistic herbivores including *Paracalanus parvus*, *Oikopleura longicauda*, *Thalia democratica*, *Calanoides carinatus*, and *Ctenocalanus vanus*, and the main carnivore is the chaetognath *Flaccisagitta enflata*. These herbivores can achieve high growth rates induced by pulses of autotrophic microplankton biomass, typical of upwelling areas (Valentin 1984a, b, 1989; Valentin et al. 1987; Guenther et al. 2008). After maximum period, there is the appearance of herbivores, predators, and eventually detritivores (*Ctenocalanus vanus*, *Creseis acicula*, *Penilia avirostris*, *Doliolum* spp., *Eucalanus* spp.), detritivores and omnivores (*Temora stylifera*, *Centropages furcatus*, *Euterpina acutifrons*, *Microsetella* sp., *Conchoecia* spp., and *Oithona plumifera*), and carnivores like *Flaccisagitta enflata*, siphonophores, and copepods of the families Euchaetidae, Candacidae, and Pontellidae (Valentin 1989). The zooplankton biomass in this area is high, with mean annual dry weight of 66 mg m^{-3} , typically $<50 \text{ mg m}^{-3}$ during the downwelling phase and up to $>200 \text{ mg m}^{-3}$ associated to the SACW upwelling (Valentin 1984b; Valentin et al. 1987).

In the central and south parts of the SBB, copepod abundance and biomass is considerably higher during SACW intrusion periods, apparently due to enhanced food for the dominants *Oncaea waldemari*, *Oithona plumifera*, and *Ctenocalanus vanus*, the two latter clearly vertically concentrated at the deep chlorophyll maximum layer (Katsuragawa et al. 1993; Vega-Pérez 1993; Miyashita et al. 2009; Brandini et al. 2014). Off São Paulo shallow shelf, the SACW intrusion contributed more to the increase in copepod production than the plume of the small Santos Bay (Miyashita et al. 2009). Similarly, the cladocerans *Penilia avirostris*, *Pseudevadne tergestina*, and *Evadne spinifera* typically increase their abundance in inner-to mid-during intrusions of the SACW (Miyashita et al. 2011; Brandini et al. 2014), as well as abundance and biomass of appendicularians, dominated mostly by *Oikopleura longicauda* (Miyashita et al. 2011). Differently, coastal hydromedusae tend to have reduced distribution and abundance during SACW intrusion (Nogueira Júnior et al. 2014). Although SACW intrusions support a general increase in zooplankton abundance and biomass, it has been suggested that the high dominance of small copepods and cladocerans indicate the intrusions do not last long enough to sustain the development of large organisms, with longer generation times (Marcolin et al. 2015).

The dynamics of water mass changes and fertilization processes in the region are wind-driven which are typically seasonal (e.g., Castro et al. 2005, 2006; Brandini et al. 2014; Cerda and Castro 2014) leading to seasonal changes in the zooplankton assemblages of the SBB. The general tendency is that zooplankton abundance and biomass over the shelf peaks between December and March, associated with periods of the SACW intrusion, with minimum values during autumn-winter when the water column is vertically mixed and SACW influence is restricted to offshore (Matsuura et al. 1980, Resgalla et al. 2001; Miyashita et al. 2009, 2011; Miyashita and Lopes 2011; Brandini et al. 2014; Marcolin et al. 2015; Melo Júnior et al. 2016). This seasonal pattern is recurrent and has been observed for different taxonomic groups such as copepods (Lopes et al. 1999; Sartori and Lopes 2000; Brandini et al. 2014), decapod larvae (Fehlauer and Freire 2002; Koettker and Freire 2006; Marafon-Almeida et al. 2008), heteropod mollusks (Resgalla and Montú 1994), hydromedusae (Vannucci 1963), siphonophores (Nogueira Júnior et al. 2014), and ichthyoplankton (Matsuura 1996; Godefroid et al. 1999). Multi-year data suggest that the intrusions of the SACW and their strength over the inner shelf is an important factor influencing both seasonal and interannual variability in zooplankton diversity, abundance, biomass, and size-spectra (Katsuragawa et al. 1993; Vega-Pérez 1993; Marcolin et al. 2015; Melo Júnior et al. 2016).

Although these SACW intrusions are the most important mesoscale physical forcing over the SBB typically leading to increased zooplankton abundance and biomass during warm stratified periods, other seasonal patterns can also be found including the absence of seasonal variations on chaetognaths off Santos and Cananéia (Almeida Prado 1968), and winter peaks as is the case of larval decapod abundance at Guanabara Bay entrance (Fernandes et al. 2002), copepod biomass in the São Sebastião Channel (Eskinazi-Sant'anna and Björnberg 2006), and occasionally off Ubatuba (Melo Júnior et al. 2016), and hydromedusae in the inner shelf of the central SBB (Nagata et al. 2014). These are usually related to complex hydrodynamic and meteorological processes that commonly occur during winter. It is not clear whether these winter increments represent an advection of shelf populations, concentrating in the inner shelf, an actual populational increase (Nagata et al. 2014; Melo Júnior et al. 2016), or a combination of both. During winter, the typically lower rainfalls decrease the volume of coastal water and carry shelf waters toward the coast, enhanced by the prevalent southeasterly winds and cold fronts, causing coastward advection and accumulation of the zooplankton (Nagata et al. 2014). Also, the cold fronts may lead to pycnocline erosion and particle resuspension (Gaeta et al. 1999; Castro et al. 2006), what could provide additional food sources for the plankton community growth (Melo Júnior et al. 2016). The combination and interaction of these factors, along with intra-regional variations in biotic factors such as food and predator type and concentration, may lead to irregular and unpredictable seasonal patterns, particularly for groups with complex life cycles (Nagata et al. 2014).

Smaller-scale variations (hours, days, weeks) also are substantial and may be wider than seasonal changes, particularly in coastal areas under strong tidal

influence, but have been less studied locally apart from a few studies inside estuaries (e.g., Ara 2002; Liang et al. 2003; Mendes et al. 2012), or in the inner shelf focused on the diel vertical migration (e.g., Moreira 1973, 1976a; Sinque 1982). The causes of these small-scale temporal fluctuations seem to be more linked to exchange of water masses, populations transfer, and trophic factors (Valentin 1989). Offshore over the shelf, a more physically stable environment, abundance, and community structure remained relatively constant throughout 48 h of sampling (Nogueira Júnior et al. 2015); however patch formation and horizontal variation have not been addressed.

These general spatiotemporal trends of the SBB zooplankton dynamics described above are comparable to other western boundary current systems, such as the South Atlantic Bight (Atkinson 1977; Atkinson et al. 1984; Paffenhöfer 1985; Paffenhöfer et al. 1984, 1994, 1995; Coston-Clements et al. 2009) and the Kuroshio Current System (Chern et al. 1990; Hsung-Yung and Yuh-ling 1992; Qiu 2001) which are subjected to seasonal, wind-driven oceanic intrusions and/or surface salinity fronts, whose dynamics largely control plankton diversity, composition, and abundance, except that the SBB shelf tends to be larger (up to ca. 200 km; Castro et al. 2005, 2006; Lohrenz and Castro 2005). Zooplankton abundances and composition of dominant species and/or genera from SBB also are similar to these other ecosystems, with tenths of thousands ind m^{-3} commonly found and up to $>100,000$ ind m^{-3} (Paffenhöfer et al. 1984, 1987, 1994, 1995; Toda 1989; Nakata et al. 2000; Kâ and Hwang 2011; Lo et al. 2012).

4 Final Remarks

The zooplankton community of the SBB is structured according to the water masses that shelter the dominant taxonomic groups, tending to have higher densities in more coastal areas and higher diversity in more offshore waters, under the influence of the TW. Onshore bottom intrusion of cold oceanic waters (SACW) over the shelf, although understudied, is one of the processes that most affect the planktonic communities over the SBB, hence affecting the nourishment of pelagic fish stocks, such as the Brazilian sardines and anchovies.

Taxonomy is among the most studied issue for the main zooplankton groups. Great gaps still exist, however, for the meroplankton as a whole, and some sporadically abundant holoplanktonic taxa such as ctenophores, ostracods, polychaetes, amphipods, euphausiids, and thaliaceans. Effort in this direction is being carried out with the descriptions of the larval stages of several decapods (e.g., Fransozo and Bertini 2003; Negreiros-Fransozo et al. 2003; Barros-Alves et al. 2013; Pantaleão et al. 2013; Alves et al. 2016) and the publication of an identification key for Brazilian ctenophores (Oliveira et al. 2007), for instance. The connection of zooplanktonic associations with different water masses is satisfactorily addressed, being one of the few ecological aspects relatively well-studied locally. We can predict with considerable confidence which are the main species in each major water mass. However, it is

still needed to intensify sampling efforts at the outer-shelf and shelf-break zones, especially associated with the frontal eddies and shelf-break upwellings associated with the BC meanders, as already pointed out a decade ago (Lopes et al. 2006).

Main gaps on marine zooplankton knowledge off Brazil, pointed out 20 years ago (Brandini et al. 1997), are still hampering a broader knowledge of the plankton community off the SBB. We still need (i) detailed analyses of the meroplankton taxonomy and spatiotemporal distributional patterns over the shelf; (ii) more studies on larval dispersion and recruitment in relation to meteorological, hydrographical, and biological behaviors; (iii) simultaneous studies coupling planktonic communities with the dominant oceanographic processes, including relevant vertical resolution and higher sampling frequency throughout the seasonal cycles; (iv) to know the small- and medium-scale temporal variations (hours, days, weeks) and the influence of physical and biological processes on this variability; and (v) detailed knowledge of population dynamics and life history of all taxa, as well as determination of metabolic rates and trophic interactions.

The general lack of studies on metabolism, physiology, and survivorship (but see, e.g., Moreira 1976b, 1978; Moreira and Vernberg 1978; Miyashita and Calliari 2016) of the main species along with the scattered data on secondary production (e.g., Miyashita et al. 2009; Miyashita and Lopes 2011; Melo Júnior et al. 2013) and trophic interactions (e.g., Vega-Pérez and Liang 1992; Liang and Vega-Pérez 1995; Vega-Pérez et al. 1996) does not allow adequate extrapolation of trophic models and energy flow through food chains. These are crucial information to understand the basic structure and functioning of the SBB ecosystem and, ultimately, shift the usual target species to an ecosystem-oriented fisheries management in one of the most important fishing zones among the Brazilian regional seas.

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