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Integrative Approach to Assess Benthic Ecosystem Functioning on the Southwest Brazilian Continental Shelf

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Abstract

Continental shelf is a highly dynamic system controlled by water mass interactions, biogeochemical processes, and biological production of organic matter. Climatic and hydrological processes originate large variability in many scales of time and space that are responsible for its typical unsteady status, mainly at shallower depths. The southeastern Brazilian continental shelf is an important economic area that houses the commercial Port of Santos, the Petrobras oil terminal in São Sebastião, and fishery activities. This concise chapter explores the relationships of the benthic community structure facing a complex physical environment allied to human influences. It is built on previous studies developed in the southeast Brazilian continental shelf from the past 25 years. The shelf benthic system is governed by seasonal pulses of primary production promoted by the South Atlantic Central Water bottom intrusion and coastal upwelling allied to the passage of winter cold fronts. Self-structuring benthic community is achieved by the mobility of the organisms, feeding activity, and biogenic transformation of the habitat due to bioturbation.

Keywords: water circulation, organic matter flux, community structure, biodiversity, anthropogenic influence, southeast Brazilian continental shelf, southwestern Atlantic

1. Introduction

Continental shelf is an extraordinary place for life in the oceans and vital for life support for the planet. Extended periods under high autotrophic biomass and primary production make the area the most productive in the oceans. Despite occupying an area of about 8.9% of the world's ocean, coastal ecosystems generate nearly 25% of the global biological productivity and more than 90% of total fish catch. Seasonal wind-driven water masses promote intense suspension of bottom sediments with consequent rapid return of nutrients to the euphotic zone. Here, the physical transport and biogeochemical transformation processes affect the fluxes of nitrogen and carbon into and out of the system. The relative shallowness of the shelf facilitates the recycling process and is the structural cause of the high biomass found. Indeed, the major part of the atmospheric

carbon fixation through photosynthesis occurs in potentially fertile shelves where it becomes incorporated to pelagic and benthic organisms besides bottom detritus.

Continental shelf surrounds every continent and represents the submerse extension of the land. With shallow seas associated forms a dynamic transitional system between the shoreline and deep sea. Width is variable and dependent on local topography with some areas more extensive than others. Mean values are about 70–80 km, and oceans with passive continental margins, like the Atlantic Ocean, present broader shelves than those of active tectonic margins, as the Pacific Ocean. In Brazil, the equatorial northernmost Amazon Shelf is about 330 km wide, whereas in the northeast coast, on parallel 14°S, the narrowest shelf is about 10 km wide [1].

The shelf is a low-sloping platform, with gradients lower than 1:1000 (1 m of decline for 1000 m of extension). However, local variability occurs due to the presence of canyons, valleys, and channels formed mainly during glacial and interglacial periods when sea level fluctuated. The coastline is the landward limit of the shelf that increases in depth to about 100–200 m where the gradient abruptly changes to about 1:40 forming the slope. The shelf break marks the offshore limit of the continental shelf.

Shelves can be divided into different areas according to distance from the coast. Generally, two areas are present, the inner or coastal shelf and outer or external shelf. Sometimes, depending on the shelf's width and hydrological regime, a middle region may appear between the two. The shelf division occurs due to differences in topography, hydrology, or sediment type, and there is no abrupt change between habitats when the frequent species overlap.

Climatic and hydrological processes act intensively on the shelf in several scales of time and space, and consequently, the environment is highly dynamic. Another important characteristic is that stability increases with distance from the coast and depth. Depth is a driving factor, but many others contribute to coastal instability as the seasonal change in temperature and salinity, water mass circulation, waves and storms, type of sediments, rivers inflow with chemical and geochemical alterations, and light. For benthic communities, the type of sediment, food availability, and benthopelagic coupling are essential among other biological and environmental interactions.

Sediments present in shelves are continental in origin and transported mainly by rivers but also by glaciers and winds. Light intensity may extend down 200 m, favoring photosynthesis and plant growth in both the water column and at the sea bottom, with consequent abundance and diversity of benthic life. Also important are the nonliving resources on the seabed such as the oil and gas resources. A great part of the petroleum production nowadays has been drawn out from the shelf.

The loss of marine diversity is higher in shallow coastal areas as a result of conflicting uses of coastal habitats [2]. It is closely connected with ocean pollution and acidification and results from man's interference. More than 50% of the human population lives near the coast, and the intense development of cities and use and abuse of marine waters and bottoms threaten the integrity of shelf systems. Sustainable usage of marine shelf systems continues to be imperative in addition to the living resource management. The pressing need for estimating the species diversity has been a significant asset for conservation programs, and several and useful tools were developed in the last few decades for that. Taxonomic sufficiency [3] and biotic indices among others allow a rapid diversity and structural assessment of the benthic communities of tropical and subtropical areas scarcely studied [4].

2. The southeast Brazilian continental shelf: physical environment and nutrient sources

The Brazilian coastline extends for more than 8500 km along the South American continent. It goes from the country's equatorial north to the temperate south, between latitudes 4°N and 34°S, and represents one of the world's longest continental coasts. Narrow in the northeast (c.a. 10 km at 14°S) and wide in the southeast (c.a. 180 km), coastal shelf presents a variety of ecosystems and habitats that brings expressive biodiversity and endemism to the region. Mangroves, coastal lagoons, and coralline calcareous algal reefs are important ecosystems of the coast, but marine sediments by far provide the largest area for benthic plants and animals. Indeed, after the ocean water column, marine sediments constitute the second biggest habitat on the planet.

The southeast Brazilian continental shelf (SBCS), or south Brazil bight (SBB), is one out of six characteristic physical environments found in the Brazilian continental shelf and the most studied (**Figure 1**). Its coastal limit lies between 23°S and 28.5°S approximately, and the inner, middle, and outer shelves are present on the extensive sea floor and separated by slight declines from each other. Broadly, sediments are distributed in strips along the coastline. Terrigenous bottoms predominate on the inner shelf in contrast with the outer shelf where carbonate sediments are the principals. Inner shelf and proximal bottoms of middle shelf are composed by sand, but near 70 m a sharp change occurs on the middle shelf due to the presence of a large deposit of silt and clay. Based on the bottom topography [5] and benthic macrofauna distribution [6], the north shelf of the southern Brazil bight was divided into two major areas, inner and outer shelf, separated by the 50 m isobath due to the strong coupling of macrofauna and sedimentary variables. Such division is valid for benthic animals with restricted locomotion and lifestyle dependent on geochemical characteristics of sediment grains.

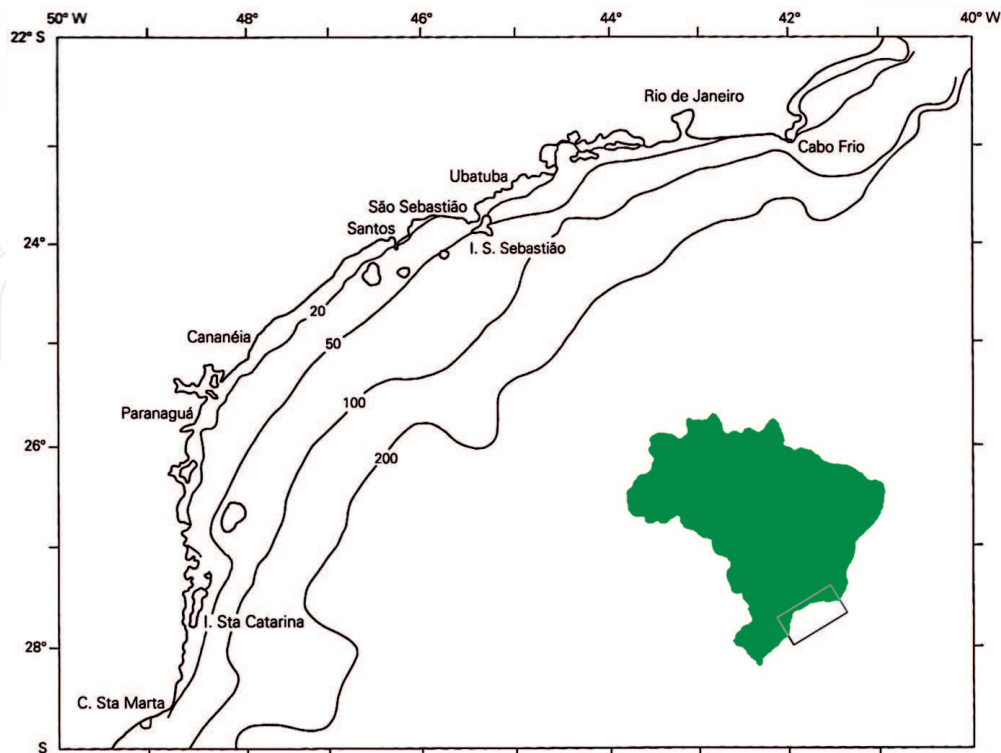


Figure 1. Location of the southeast Brazilian continental shelf. The isobaths depict the broad shelf configuration and the geographic position of the studied sites.

In the major part of the southeast Brazilian continental shelf, water movement is driven in different time scales by wind, the Brazil Current (BC), and tides [1]. The Brazil Current is part of the southward branch of the South Equatorial Current when it approaches the coast of South America between 7 and 17°S [7]. It flows southwestward along the shelf break to the Subtropical Convergence, between 33 and 38°S. In wider shelves the Brazil Current approximates to the coastline and fills at least outer shelf [1].

The Brazil Current transports three water masses with characteristic thermo-haline properties that interact along the shelf and shelf break according to the large-scale wind field: Tropical Water (TW), relatively warm ($T > 20^{\circ}\text{C}$) and salty ($S > 36$); South Atlantic Central Water (SACW), relatively cold ($T < 20^{\circ}\text{C}$) and low saline ($S < 36$); and Coastal Water (CW), warm and low saline ($T > 20^{\circ}\text{C}$ and $S < 36$) [8].

Tropical Water occupies the surface of the Tropical South Atlantic and is known as oceanic or offshore water. South Atlantic Central Water is oceanic in origin and formed by subduction of surface waters of the Subtropical Convergence. After a complex flow, it reaches the Brazilian coast most probably at Cabo de São Tomé (22°S) from which it is transported southwestward by the Brazil Current. It flows along the slope and can reach the shelf to compensate the Ekman transport of surface waters offshore caused by northeast winds. Winds are intense in the austral summer when South Atlantic Central Water intrudes from slope to shelf shallower depths in a cross-shelf transport. Continental waters (from rivers, estuarine plumes) mix with South Atlantic Central Water and Tropical Water resulting in the Coastal Water predominant on the inner shelf [1].

The Brazil Current presents also meandering and formation of mesoscale eddies (nearly around 100 km in diameter) in its frontal edge that facilitates the ascension of nutrients from deep areas and causes upwelling at the shelf break, with the consequent fertilization of large areas of outer shelf. When this process occurs, the regenerated production characteristic of oligotrophic open seawaters is temporarily substituted by new production based on input of new nutrients to the area. Besides the shelf break resurgences, coastal upwellings occur near to the coast and have local effects only. It is caused by northeast winds that when strong and intense deviate the surficial waters to offshore with the consequent ascension of water rich in nutrients from the South Atlantic Central Water. The most studied coastal resurgence in the southeast Brazil bight is that of Cabo Frio shelf (23°S), north of Rio de Janeiro State. Here shelf is narrow (nearly 90 km wide) and steep, which facilitates local water resurgence. As wind-driven the shelf upwelling of SACW is more recurrent and constant in the period from austral late spring to early autumn.

Water masses dynamics linked to the presence of vortices of local and meso-scales are in great part responsible for water column fertilization with direct impact on planktonic and benthic shelf communities. Waters acting on southeast Brazil bight are a result of the three water masses mixed in variable volumes. Coastal Water plus the seasonal intrusion of South Atlantic Central Water coastal wards enhance abundance and diversity of biological communities on the shelf as they feed from the new production at the base of the euphotic layer, a labile and fresh organic matter colonized by heterotroph bacteria. SACW is rich in minerals from deep water and when breaks the thermocline during its ascending to surface, reaches the photosynthetic layer and fertilizes shelf from bottom to mid-waters. The biological consequence is an expressive primary production and improvement of the local food web.

Continental fertilization of seawater comes from medium- or small-sized outflows that contribute to the low saline waters of the inner shelf. Large rivers or estuaries are absent in the southeast Brazil coast (SBB). The coastal lagoon system of

Cananeia in south SBB and Santos Estuary in the central part are important freshwater local inputs. Coastal currents are parallel to the coast, mainly northeast directed, and can be intensified in speed by winds of cold fronts more frequent and stronger during austral winter. These fronts can resuspend bottom sediments and bring the particulate organic matter to the water column promoting the recycling of nutrients and enhancement of the benthopelagic coupling. Wind is the main forcing agent on water circulation in SBB, while tidal currents have a negligible influence [1].

According to the characteristics and dynamics of the water masses present, hydrographic fronts may occur on inner and outer shelves. The front is the water masses interface with distinct physical, chemical, and biological characteristics. The presence of SACW in contact with Coastal Water and Tropical Water in the euphotic zone configures a frontal zone. Also, fronts are horizontal gradients of temperature and salinity formed due to differences in depth, wind direction and intensity, and water density, among others. Detection of thermal fronts, for instance, can help to identify zones of ecological importance for marine fauna and to better understand habitat dynamics as a function of its spatial and temporal extent and variability [9]. Evidence of the influence of thermodynamic fronts on benthic megafauna living in central and northern southeast Brazil bight will be presented later in this chapter.

On the southeast Brazil bight, the inner side of the Deep Thermal Front tidal circulation maintains a mixed layer from surface to bottom in contrast with the side outward from the front that is constantly stratified. Especially in summer, when the offshore SACW intrudes coastward, the physical stratification is enhanced though the shelf. As a consequence of the two-layered water column establishment, the changing of substances and organisms between the surface and the seafloor is inhibited. The 20°C isotherm indicates the limit beyond that South Atlantic Central Water dominates the shelf bottom layer. Similar to temperature, salinity has the Shelf Hyaline Front (SHF) originated between the coastal low saline-mixed waters and the stratified high saline waters from South Atlantic Coastal Water and Tropical Water on the outermost shelf.

The shelf eutrophication promoted by the upwelling of deep water is intermittent and more frequent in summer. During winter SACW retreats to the shelf break more often due to the change in the direction of prevailing winds. In this case, the shelf's bottom is filled with the warm less enriched Coastal Water, while the oligotrophic Tropical Water dominates at the surface.

To summarize, the southern Brazil bight has oligotrophic upper waters (Coastal Water and Tropical Water) in most parts of the shelf in the absence of an external source of nutrients. When the environment is perturbed by SACW intrusion, rich in nutrient salts, an increase in phytoplankton biomass occurs due the presence of new species better adapted to compete in the new condition. On the inner shelf, phytoplankton biomass data are in the range of coastal oligo-mesotrophic areas, and values between 0.16 and 6.42 mg Chl-a m⁻³ were observed for São Sebastião shelf and similar neighboring places [20]. The presence of cross-shelf intrusions, meanderings, and resurgences of SACW permits entrance of new nutrients at the base of euphotic layers of both inner and middle shelves in summer and outer shelf in the winter. The chlorophyll maximum layer is formed in subsurface following the SACW superior limit. The continental shelf is then fertilized in summer by large autotrophic plankton, mainly diatoms, and local primary production frequently enhances several times. In the stratified waters of Ubatuba shelf, the maximum value of chlorophyll-a equal to 14.7 mg m⁻³ was found at 18 m depth in the SACW, which is 13 times higher than that obtained at the surface in the Coastal Water [10]. Another example is that of the Vitoria Eddy, Abrolhos Bank, where the increase of nutrients from deep water turns the area nearly 40% more productive than that out of the vortex [11]. The deep chlorophyll maximum (DCM) layer may reach several

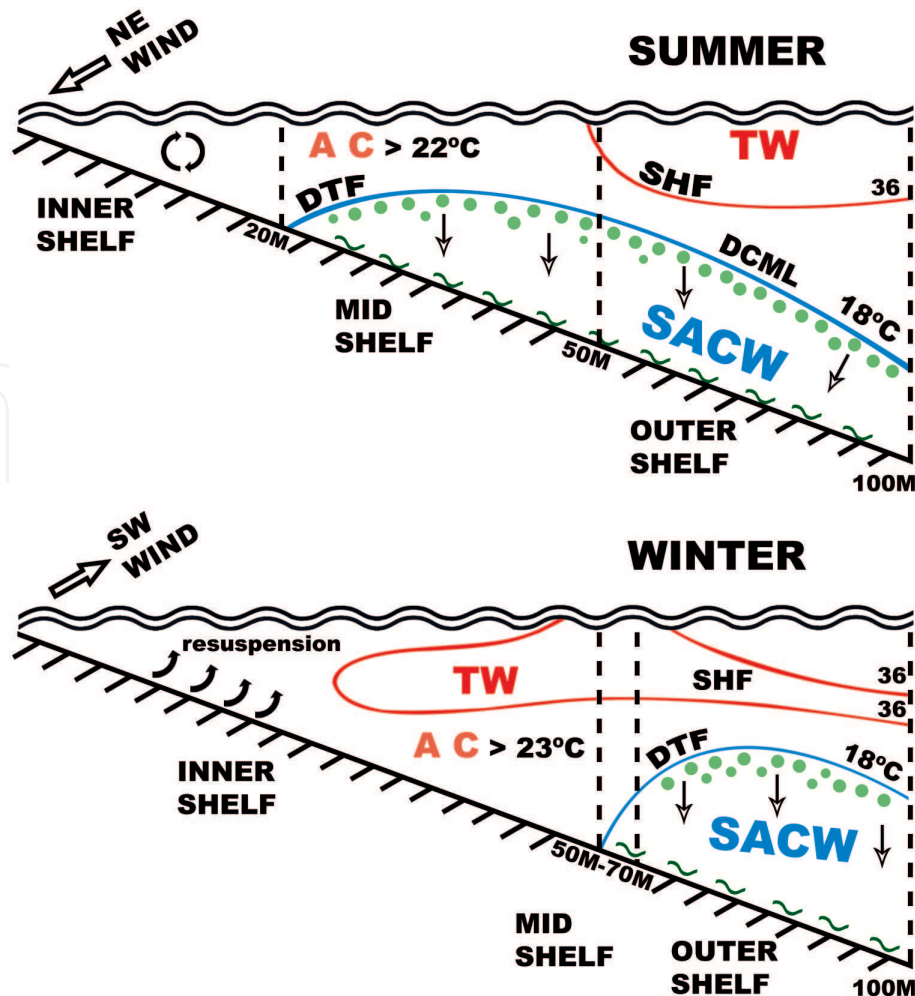


Figure 2. Diagrammatic model of the main physical and biological processes in the Southeast Brazilian continental shelf in summer and wintertime. Shelf division is based on seasonal hydrodynamics. AC = coastal water, SACW = South Atlantic central water, TW = tropical water, DTF = deep thermal front, SHF = surficial hyaline front, DCML = deep chlorophyll maximum layer, o = phytoplankton cells, ~ = detritus, ↓ = phytoplankton sinking and benthos enrichment, ↑ = resuspension of bottom sediments.

meters in thickness depending on wind force and shelf depth. The eutrophication benefits from wind strength for reaching shallower depths on the shelf. Also, in summer, more than one event can occur independently on the middle and outer shelves as was demonstrated offshore of Santa Catarina State, southern southeast Brazil bight [12]. New nutrients significantly improved carbon net biomass and exportation of organic matter to benthic system with a consequent increment of secondary production. A diagrammatic model of the biological and physical interactions for the southeast Brazilian continental shelf is presented in **Figure 2**.

3. Food supply to the benthic system

With the main mechanisms of shelf eutrophication understood, it was possible to estimate the quantity of organic matter on southeast Brazil bight fuelled to the sediments. Knowledge about the relationships between macrofauna and organic matter input is crucial for understanding the structure and dynamics of benthic communities. The role of the remote source of nutrients represented by the South Atlantic Central Water shelf intrusion has been studied intensively on southeastern Brazilian continental shelf in a multidisciplinary approach. In the São Sebastião Channel (SSC), NE São Paulo State, a clear relationship between high quantities of

fresh organic matter and SACW intrusion was observed on bottom sediments [13] and in the Cabo Frio resurgence as well [14].

The quality of sedimenting particles, however, is difficult to be evaluated due mainly to the complexity of intrinsic variables involved and the inexistence of a universal marker for quality. Prevailing oceanographic condition, depth, time and duration, concentration, and heterogeneity of organic content act directly on the organic matter constitution. Considering biomarkers, fatty acids, sterols, and isotopic composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have been frequently used nowadays besides chlorophyll-a and the relation between chlorophyll-a and phaeopigments. Lipid content stocks energy and brings to food high nutritional power and consequently is considered a good indicator of the quality of the particle ingested.

The organic matter concentration and its chemical composition contribute in regulating the metabolism and distribution of organisms as well as the biomass and diversity of communities. Differences in composition show, for instance, the source of the organic matter present on the shelf's bottom. In shallow shelf areas, detritus of continental origin dominates, whereas in middle and outer shelves, organic matter is mainly from oceanic waters.

The impact of food quality on benthic macrofauna communities was evaluated on the São Sebastião Channel (23°30' to 24°00' S; 45°05' to 45°30' W), São Paulo State, north of southeast Brazil bight [15]. The study searched for differences in species composition, vertical distribution, trophic habits, and bioturbation effects on benthic assemblages (alive bacterial biomass and polychaetes from meio- and macrofauna) submitted to two dissimilar oceanographic conditions, with and without South Atlantic Central Water influence. Different responses for each situation of food input based on fatty acid classes, particulate organic matter quality, and relative contribution of other sources of organic matter to the detritus pool are expected.

However, why do we work with polychaetes and why are there so many ecological studies focused on these animals? The answer is that they are frequently the most abundant infaunal component of macrofauna in sediments, representing 40–50% of the whole macrofauna on coastal and shallow areas of southeast Brazil bight [11]. A wide range of feeding habits and lifestyles give the species capacity to modify bottom deposits by bioturbation, changing geochemical processes such as oxygen and phosphate fluxes [16]. An important part of the benthic research developed on the southeastern Brazilian shelf has been accomplished employing polychaetes as a proxy of the total macrofauna.

São Sebastião Channel is a peculiar area in the southeast Brazil bight inner shelf due to its geomorphology and hydrodynamic complexity. With nearly 25 m of length, it separates the continent from the large São Sebastião Island (SSI). The SSC with a width of 6–7 km and a depth of 20–25 m at the south and north entrances, respectively, narrows to about 2 km in the middle length where it is as deep as 45 m and curves northwest. It functions as a tunnel for winds from the open sea magnifying its strength. In the channel Coastal Water flows from the northeasternmost part of the year. Intense and strong winds in late spring and summer months promote SACW inflow through the channel's south entrance where a paleo-valley runs out on the island side. At this time a well-defined thermocline establishes in the water column with the two water masses running in the opposite direction, the warm low saline Coastal Water at the surface in SW direction and the cold saline South Atlantic Central Water on the bottom in a NE direction. The hydrology is more complex due to a counterclockwise vortex promoting the flow attenuation in the north insular side [17].

The main transport of sediments on São Sebastião Channel occurs from southwest to northeast with a tendency for more intense deposition of silt and clay along

the continental margin and middle part, places of low current speed. The existence of distinct sediment patches is one of the leading causes associated with the high benthic diversity found in the area [18]. Another critical factor to be considered is the chronic oil and sewage contamination present in the central narrower part of the channel due to the presence of the São Sebastião Harbor, the DTCS large oil terminal, and the Araçá sewage pipe responsible for discharges of a quarter of the urban sewage of São Sebastião city. Low current speed makes difficult the dispersion of contaminants that are deposited in the fine sediments below. The resulting effect is a change in the quality of the bottom environment. Analyses of total organic carbon (TOC) of sediments in the central area of SSC showed high values that are indicative of organic enrichment [19]. This condition associated with the sewage discharge and petroleum-derived hydrocarbon creates a eutrophic environment that puts the benthic species at risk of damage [4, 14]. Indeed, loss of abundance and diversity of species of the whole macrofauna were observed earlier in that area characterized by an unbalanced community [18]. So, although the waters of the São Sebastião Channel were described as meso-oligotrophic [20], the bottom can be considered eutrophic either by natural or by anthropogenic causes.

In the southeastern continental inner shelf, two mechanisms have been evoked to support the benthic communities along the year. One is associated with SACW bottom inflow and seasonal enhancement of the quantity and quality of benthic organic load. The other is present when Coastal Water is the only water mass flowing in the area. In shallow depths (<50 m) frequent and intense mixing occurs in the water column especially in winter months due to the passage of cold fronts. As the input of nutrients is low and constant, the quantity of organic particles is not a food stressor for the communities, but quality is. In these areas partially degraded organic detritus with lower nutritional capacity composes the bottom organic matter. In springtime 2004 only the relative deeper (15 m) north station on the São Sebastião Channel was under the South Atlantic Central Water influence, and the quantity of labile organic material peaked to $206.14 \mu\text{g g}^{-1}$, a value four times higher than those found at the same place in autumn under domination of Coastal Water [15]. On the non-upwelling scenario of the same shallow area, a rapid loss of the labile component occurred, and the major part of the organic matter is partially degraded and accumulated as pointed out by the high values of short-chain saturated fatty acids found [15]. An important aspect of the mid-water upwelling of SACW is that its effects on benthos enhancement lasts even after the water mass returns to offshore. The high quantity of the organic matter settled goes to the bottom subsurface layers due to the reworking of macrofauna. In that manner it stays available in the sediments for a few months [15, 21].

Organic matter quantity and quality is the primary driver for changes in the structure of benthic communities. However, besides the organic matter load, it is necessary to consider the trophic group structure and degree of faunal mobility in the sediments (or bioturbation) for a better understanding of the process. Benthic fauna work on the food particles through fractioning and moving them into the sediments and so making the smaller food parts available to the organisms in a constant action/reaction with the environment. Many studies have been developed in the area of São Sebastião, Ubatuba, and Santos shelves and north and central areas of the southeast Brazilian continental shelf, with species of total macrofauna [13, 19], polychaetes [15, 18], amphipod crustaceans [23], bacteria biomass, and meiofauna [21]. The results recognized the organic matter quality and quantity as the main determinants of the structure of benthic assemblages. The fauna seems to be not food-limited by the quantity of the organic particles loaded, but by their quality that can alter species composition, abundance, and diversity. The constant input and prevalence of local partially degraded organic detritus (refractory material)

in the sediments were shown to be significant and able to maintain the benthic assemblages on shallow coastal areas [15, 21]. On the other hand, places under the South Atlantic Central Water influence showed more abundant and diverse benthic communities that are most probably supported by the high proportion of recently produced planktonic organic matter present in the sediments [15, 18, 22].

The relationships between feeding mode and species mobility are complex, and their study helps to understand the functioning of benthic communities. In the São Sebastião and Santos shelves, several studies were conducted with polychaete and crustacean species to identify their trophic guilds and link them with sediment type and organic matter content [23, 24]. Five trophic groups are reported for the SBB shelf and recently were associated with four bioturbation categories, for a better understanding of the functional structure of polychaete assemblages in the São Sebastião Channel and vicinities [15]. In shallow places with predominance of local input of degraded organic material, as the São Sebastião Channel margins and other coastal areas, the diffusive mixing (rapid redistribution of the organic matter within the sedimentary column) is reported as the main process associated with dominance of the subsurface deposit feeders. The result is the disturbance of the whole sediment column by relatively high bioturbation rates. Species composition of the assemblages can vary along the year, but relevant functional changes were not observed in the system, i.e., different species may occur through time but play the same role. Large quantities of small opportunist species occurred in the São Sebastião Channel continental margin, like *Cossura candida*, together with mobile large Sternaspidae, as *Sternaspis capillata*, both subsurface deposit feeders but with different bioturbation behaviors. *C. candida* is a diffusive mixer, i.e., rapidly redistributes the organic matter within the sedimentary column, and *S. capillata* is a conveyor belt transporter, i.e., moves particles of sediment up to the surface during its subsurface feeding or burrow excavation. The species are characteristic of environments under intermediate stress condition [15], and the input of anthropogenic organic matter locally produced seems to support them.

Benthic assemblages behave differently in the presence of SACW's eutrophication. In such places, the major part of the species belongs to the conveyor belt transport category, that is, individuals that promote rapid movement of recently produced organic matter downward in the sediment. The procedure favors both surface deposit feeders and diffusive mixers equally by combining old and fresh organic matter. So, with the pulses of intense and high bottom eutrophication, a modification of the species composition occurs together with functional changing.

4. Benthic studies on the southeast Brazilian continental shelf

Between 1985 and 1988, a multidisciplinary oceanographic project was conducted on the São Paulo State northeastern shelf, by the Oceanographic Institute of the University of São Paulo, to understand the structure and functioning of the continental shelf system from the coast to offshore of Ubatuba, north-south Brazil bight [25]. The study detailed the complex hydrodynamics of the water masses and their role on the large episodic input of new nutrients to the shelf and the consequences on pelagic and benthic communities. It also established the founding knowledge about the functioning of the system based on a seasonal local trophic model. This project was the pioneer in southeast Brazilian shelf by assembling researchers of the many branches of oceanography to understand shelf functioning addressed by its physical, chemical, and biological characteristics. Some other multi- and interdisciplinary projects came along the following 25 years and contributed to improving the knowledge by answering questions opened at every study end.

Without any doubt, the central and north parts of the SBB, in front of São Paulo and Rio de Janeiro States, are the best areas studied. Along the long coastline, few geographical features can modify local sedimentary and hydrographic main processes with consequences on benthic communities' structure and distribution. The first one is the large São Sebastião Island, northeast São Paulo State, separated from the continent by a long narrow channel, the São Sebastião Channel that constitutes the second feature. The third modifier is the sudden east to the northeast inflection of coastline in front of Cabo Frio, northeast Rio de Janeiro State, with consequent expressive shelf narrowing (**Figure 1**). Another critical factor to the change in coastline is that caused by the opening of estuaries: the southern Cananea/Iguape lagoon system, the larger central Santos-São Vicente estuarine complex, and the northern Bertioga.

São Sebastião Island is an important geomorphologic marker of the coastline as it divides the adjacent shelf in northern and southern sectors. The northern sector is more complex due to the irregular littoral of many small bays and islands associated with the irregular isobaths outline. A clear difference exists between sediments from W to SW and N to NE of the island, with a predominance of fine and very fine sands in the southwest and muddy sediments (silt and clay) in the east and northeast. The SSI functions as a physical barrier to marine currents from S to SW linked to the passage of cold fronts in the winter and is a perennial source of sediments and detritus to the region. São Sebastião Channel is a particular area from the inner shelf and was divided into three sectors (central, south, and north) based on sediment type coupled to depth, channel wall declivity, quantity of suspension matter, and dominant hydrographic processes. Regarding Cabo Frio, the change in the direction of coastline in the area favors the approximation of the Brazilian Current to the continent and, associated with strong northeast winds, promotes the coastal upwelling of deep cold waters that modify local food quantity and quality to benthic assemblages, as explained earlier.

Reports on the importance of sediments for benthic species distribution are numerous in the literature. In the central and north parts of southeast Brazil, shelf studies of the megabenthos have shown that hydrothermal dynamics is the driver factor structuring the communities, whereas for macrofauna the variables associated with sediments are the most important. Megafauna is here defined as large organisms captured by fishnets, like crabs, shrimps, and sea stars, and macrofauna are those invertebrates $\geq 0.5\text{mm}$ length from both infauna and epifauna of almost all phyla. Except for Peracarida crustaceans (as isopods, tanaids, and amphipods) that protect their eggs and embryos in the ventral marsupium, most of the other benthic species are benthopelagic with initial free-swimming larval stages and posterior bottom settlement. Sediment is then required in the initial and crucial stage of the species life cycle. Some other organisms, as many shrimps are pelagic, but bottom dependent for feeding. On the other hand, several megabenthic species are large agile animals that need to move long distances for feeding and reproduction and, consequently, are affected by water motion. Recently attention has been paid in studying the role of thermohaline fronts on the habitat dynamics in function of its temporal and spatial extensions. One of these studies was developed in the Ubatuba shelf, SBB shelf, and later expanded to São Sebastião and Santos shelves. The results showed a constant temporal and spatial change of habitat between *Xiphopenaeus kroyeri* and *Portunus spinicarpus*, two coupled species linked to the South Atlantic Central Water deep thermal front.

X. kroyeri, also known as sea-bob or “camarão sete barbas,” is a penaeid shrimp with a length of 9–10 cm and a long curved rostrum distributed along the southeast Brazil bight coastal area, from Rio de Janeiro to Santa Catarina States. The species lives in shallow warm water (warmer than 20°C) 30 m in depth. The swimming

crab *P. spinicarpus* inhabits cold (below 20°C) deeper shelf water (from 50 to 70 m to shelf break) with populations extremely numerous at the 18°C isotherm in the South Atlantic Central Water frontal zone. Both species extend or diminish their spatial range of distribution seasonally according to the constant displacement of SACW [26]. Similar results obtained for other vicinal areas showed that the southeast Brazilian shelf is a dynamic habitat for megafauna species supported by plankton-benthic interactions coupled to physical forces as hydro-thermodynamics, winds, and tidal mixing, among the principals. The seasonal variation in abundance of both species on the three studied localities is presented in **Table 1**.

In Cabo Frio and Ubatuba, a study that lasted over 2 years was developed to compare the megabenthic community structure in relation to different physical processes that occur in those areas, the local upwelling in Cabo Frio and the mesoscale South Atlantic Central Water middle depth intrusion in Ubatuba [27]. Density, biomass, and species richness were evaluated on inner and outer shelves in the austral winter of 2001 and summer and spring of 2002. Substantial spatial and temporal changes occurred in species composition and dominance of key species on both areas and suggested the close linkage between megabenthic communities and water masses seasonal dynamics associated with differences in sediment type.

Considering the inner shelf, diversity in Ubatuba was higher than in Cabo Frio, and both areas presented different species dominance also. In Cabo Frio the sea star *Astropecten brasiliensis* was the most abundant in all the periods sampled, even in the presence of SACW thermal front (Summers 2001 and 2002). *P. spinicarpus* appeared on the inner shelf driven by SACW thermal front, but only predominated on that area in spring 2002 (709 individuals/catch) when bottom temperature reached 13.5°C. However, in wintertime under the warm Coastal Water influence, the number of species increased from 10 to 22, and diversity increased from $H = 0.3$ to

Species	<i>Xiphopenaeus kroyeri</i>		<i>Portunus spinicarpus</i>		Water mass	
	Inner	Outer	Inner	Outer	Inner	Outer
Places	shelf	shelf	shelf	shelf	shelf	shelf
Ubatuba ¹						
Summer 1985	0	0	3281	5152	SACW	SACW
Winter 1986	5892	0	34	0	CW	SACW
São Sebastião ²						
Summer 1994	54	0	5	578	SACW	SACW
Winter 1997	385	0	11	407	CW	SACW
Santos ²						
Summer 2006	47	0	4	1675	SACW	SACW
Winter 2005	5413	0	0	1224	CW	SACW
Cabo Frio ³						
Summer 2002	0	0	43	0	SACW	SACW
Winter 2001	0	0	1	1968	CW	SACW

¹Pires [26].

²Non-published data.

³De Léo and Pires-Vanin [27].

SACW = South Atlantic Central Water, CW = Coastal Water.

Table 1.
 Seasonal distribution of the abundances of *Xiphopenaeus kroyeri* and *Portunus spinicarpus* according to the extension of the South Atlantic Coastal Water intrusion on the shelf.

1.3, with dominance of the crab *Leucippa pentagona* and the gastropod *Buccinanops cochlidium* (= *Buccinanops gradatum*) instead of shrimps, as presented in other parts of the southeastern Brazilian inner shelf. Regarding the outer shelves, differences in species composition between both places were also detected, despite their proximity (only 463 km distant) and permanent SACW influence. In this case, the contrast in sediment type explains the faunistic changes: Ubatuba has a sandy bottom (coarse and medium sands) at 100 m, whereas in Cabo Frio the sediment is silted at the same depth. The hydrodynamic characteristics associated with sediments are responsible for the major part of the shift on the structure of the communities of both areas. This is especially true for the slow-moving megabenthic species as the sea stars and anomuran crustaceans (*Munida irrasa*). As they feed mainly on local macrofauna living on sediments, the quantity and quality of the prey available for feeding depends on the sediment characteristics, as grain size and organic content [26].

Spatial distribution of the communities of benthic macrofauna has been usually related to seafloor characteristics, like topography, sedimentary texture, oxygen content, organic matter, and depth. Studies developed in the south Brazil bight have shown that besides those variables, the oceanographic and meteorological processes (as SACW intrusion and cold fronts, respectively) play an important role also. Spatial and temporal changes in the communities of macrofauna were intensely studied on the São Paulo State shelf, the central part of the SBB. Based on bottom topography, water circulation, sediment deposition, and sedimentary organic matter content, the area was characterized by three subareas: the northern Ubatuba and São Sebastião shelves [13, 25, 26], the central Santos shelf [24, 29] and the southern Cananeia/Iguape shelf. Since sediment was identified to be the structural driving factor for the macrobenthic communities, a detailed explanation of its distribution in the complex continental shelf of São Paulo becomes necessary. The presence near the coast of the large São Sebastião Island, associated with water fluxes from Santos, Peruíbe, and Bertioga estuaries, adds to the sedimentary system complexity.

The regional distribution of the superficial sediments indicated the presence of three regions. In the south region, corresponding to the continental shelf in front of the Peruíbe river mouth, the sediment presents an average diameter corresponding to fine sand with isolated silt patches. In the central portion of the area, the continental shelf of Santos has very fine and fine sands, which form the homogeneous bottom, with muddy sediments deposited in the deeper portions. In the north region, situated north of the São Sebastião Island, the deposition pattern is much more complex; in areas shallower than 60 m very fine sand interspersed with bands of fine sand predominate, while near to the coast, spots of medium and coarse sand overlay the bottom. The major part of the smaller grains is retained into the bays, but some quantity can be carried on the water surface layer by the Coastal Water during the South Atlantic Central Water bottom intrusion and deposited around the 50–60 m isobath at the middle shelf. Another shallow depositional environment is that at E/NE of the São Sebastião Island. The island functions as a shield to waves from the highly dynamic southern frontal systems by changing current direction and diminishing its velocity. Consequently, the finer sediments are deposited behind the island on an area known as “island shadow zone.” Considering the outer shelf of the three regions, there is a clear relation between increase of depth and decrease in the sediment granulometry; the 120 m isobath practically delimits the zone of the predominance of sand from that of muddy sediments [30].

Macrofauna of São Paulo continental shelf is numerous, diversified, and firstly distributed according to sedimentary characteristics. Polychaetes show up as the most numerous group collected accounting for 51% of total fauna on São Sebastião shelf [28]. Polychaetes and crustaceans Peracarida were studied to species level in order to understand benthic community structure and function [24, 31]. Working

with several benthic marine groups of invertebrates proved to be important for bringing consistency and generality to the results obtained. Broadly, density was significantly higher in sediments with a sufficient content of labile organic matter. Also, species richness was higher on the coarser sediments of the inner shelf, whereas diversity and evenness increase at sites of intermediate depths (40–50 m) on the middle shelf. In contrast, the outer shelf houses deepwater species that live preferentially in muddy sediments as deep as 70–80 m. As an example, the diversity of amphipods on the northern Ubatuba shelf decreased with the increase of sedimentary silt and clay, whereas abundance of the tube-dwellers follows the contrary [31], which shows the role of the muddy belt from the outer shelf for the shift in community composition along the shelf.

Several ecological models were constructed for the southeast Brazil bight with environmental parameters (grain size and angularity, organic matter quantity and quality, temperature, salinity, and depth, among the principals) and biological indicators (as abundance, biomass, diversity, evenness, feeding groups, behavioral groups, microbial biomass) to interpret the benthic species distribution on the shelf. Results demonstrated that the species are grouped into three main areas parallel to the coastline, forming communities with particular physical, sedimentary, and geochemical characteristics and controlled by different species. Three main groups of species characterized three benthic areas, the inner, the middle, and the outer shelf groups that delimit the coastal zone, the intermediary zone, and the deep zone. The most striking differences occur between the inner and outer shelf groups; the middle shelf functions as an ecotone with species from both areas.

The coastal zone (12 to 30–40 m) includes shallow warmwater species related to well-sorted and very fine sand bottoms with labile and refractory organic matter mixed, subjected to a strong hydrodynamics associated with water masses and cold fronts; density and diversity are generally high, and the fauna is composed mainly by r-strategists as *Prionospio dayi* (polychaete) and *Ampelisca paria* (amphipod). The deep zone (>70 m) sustains cold-water species living in poorly sorted silt and clay bottoms with high organic matter content; density is variable but frequently high. The robust correlation of density and evenness with depth indicates that the deep zone is a more stable environment than the coastal zone and frequently supports an abundant fauna that can reach densities of 958 individuals per m⁻² [28]. Some discriminant species here are the large carnivores *Sigambra* sp. and *Aglaophamus* sp., the subsurface deposit feeders *Petersenaspis capillata* and *Leitoscoloplos kerguelensis* (polychaetes) [29], and the burrowers *Pseudoharpina dentata*, *Urothoe* sp., and *Heterophoxus videns* (amphipods) [24]. On the other hand, as a transitional region, the intermediary zone is usually characterized by high values of species richness, diversity, and evenness besides chlorophyll-a content correlated with density, which indicates fresh organic matter input. These findings evidence the continuous organic load and enrichment of sediments in the area and no food limitation for the fauna. This is an unstable environment with annual ranges of temperature between 17.2 (summer) and 21°C (winter) as observed in Santos' shelf.

The coastal zone may present patches of finer sediments in front of river outflow or of physical coastal modifiers, as in the case of San Sebastião Island that creates a “shadow zone” behind. The accumulation of such very different sediments, muddy and rich in refractory organic matter, modifies the inner shelf bottom and creates a local environment with a new sedimentary process and particular geochemical properties. As a consequence, an abrupt change occurs and disrupts the sandy community pattern present in the rest of the area. This is the case of the shallow bottom in front of Peruíbe river mouth, south of Santos shelf. The community of the less saline muddy sediment (salinity of 34.6 to 35 in winter (2006) and 33.1 to 33.9 in summer (2007)) is characterized by *Mediomastus* sp. and *Magelona posterelongata*; the first

one is a subsurface deposit feeder and a conveyor belt transporter, and the second is an interface-feeder and surface depositor. Species of *Mediomastus* are always very abundant in systems constantly exposed to high organic load [29]. Indeed, the terrigenous input of detritus to coastal waters in São Paulo shelf is permanent and increases in summer, the period of more intense rains and with a fresh food supply associated with the South Atlantic Central Water intrusion. As an interface-feeder, *M. posterelongata* is stimulated just after the deposition of freshly organic matter [32], but is exceeded by the *Mediomastus* sp. that feed on the abundant and long-lasting degraded material [15, 29]. On the other hand, species of polychaetes of the sandy group were mostly tubicolous and surface-feeders and associated with the high content of chlorophyll-a and cold water in summer, which suggests pulses of fresh organic matter to those communities. The structure of the three shelf species groups just discriminated seems to be resilient and time-stable. Several ecological indices used, as well as the different size strata of benthic animals (macro- and megafauna) and different taxonomic groups used, indicated the existence of the same organization independent of species composition or season. When a shift of species occurs, as in the seasonal changes, the new species will play a similar functional role of the substituted, as observed for polychaetes in São Sebastião shelf.

5. Conclusion

The southern Brazilian continental shelf ecosystem is characterized by both high species diversity and complex biotic interactions among the component species. The region is physically controlled by the dynamics of three water masses. One of them, the South Atlantic Central Water intrudes from the shelf break to the coast seasonally bringing nutrients to the euphotic zone and, consequently, enhancing primary productivity. The thermal front formed in the frontal zone between South Atlantic Central Water and the shallow Coastal Water is responsible for the concentration of an extremely dense population of the swimming crab *P. spinicarpus* that moves according to the SACW dislodgment on the shelf. Density of macrofauna in south Brazilian bight is moderate and linked to seasonal pulses of labile organic matter in the middle and inner shelves and to water mixing processes that resuspend bottom sediments with old and fresh detritus for recycling. This suggests that the quality besides quantity of organic matter available as food in sediments is of great importance for structuring the macrobenthic communities. Biomass was usually low when compared to other similar environments elsewhere and probably is related to the characteristic mesotrophy of the shelf waters. Changes in macrofauna density and biomass seems to be independent of the periods of high food availability, but the differential quality of the sediments can change community species composition by differences in trophic habits and mobility behavior. Diversity is high, mainly on the middle shelf and outer shelf. Dominance of few species is a characteristic of the inner and outer shelf zones. The reciprocal interaction between sediments and species helps in maintaining the community dynamics through time.

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