

Brazilian Marine Biodiversity

Paulo Yukio Gomes Sumida
Angelo Fraga Bernardino
Fabio Cabrera De Léo *Editors*

Brazilian Deep-Sea Biodiversity

 Springer

Brazilian Marine Biodiversity

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Foreword

The deep sea is the widest ecosystem on Earth and has been long recognized as a research frontier in marine sciences. The logistical challenges to study offshore ecosystems, sometimes located kilometers below the sea surface, are tremendous and require significant investment that limits sampling on those areas. Therefore, we know very little about the biodiversity and ecological processes in the deep sea, especially along the Brazilian margin. However, our limited knowledge on the Brazilian margin's biodiversity contrasts with the high industrial and commercial interests on living and non-living resources provided by deep-sea ecosystems. Slope sediments, submarine canyons, cold seeps, organic falls, deep-water corals, and seamounts host unique biological assemblages and are directly or indirectly important to food provision (e.g., fishing) and climate regulation, and may hold rare biotechnological products. As a result of the rich resources, vast areas of the deep-sea Brazilian margin have been historically explored for fish, oil and gas, and other commodities, likely impacting a variety of deep-sea habitats at scales and intensity yet undetermined.

The deep Brazilian margin has an incredible geological heterogeneity with many special seafloor features that occur on other continental margins. Latitudinal changes in marine productivity, oceanographic conditions, and biological communities result in very distinct biological assemblages at regional and bathymetric scales, some of which have been studied in detail. In this book, we attempted to review the available scientific literature on the Brazilian deep-sea biodiversity associated with its many special geological and biological features, and to present an updated synthesis of their ecology, conservation, and future research needs.

There are no extensive reviews about the deep-sea Brazilian biodiversity. Similar reviews on this topic have been made by Levin and Gooday (2003)¹, where they reviewed the biological and oceanographic characteristics of the deep Atlantic Ocean with limited data from the Brazilian Economic Exclusive Zone. This book

¹Levin LA, Gooday AJ (2003) The deep Atlantic Ocean. In: Tyler PA (ed) *Ecosystems of the world*, vol. 28: *Ecosystems of the deep sea*. Elsevier, Amsterdam, pp 111–178.

expands that review with several new data on deep-sea assemblages from Brazil's EEZ produced in the last two decades, many of which was only available in Portuguese.

In this book, the current knowledge of marine benthic biodiversity along the Brazilian deep sea below the 200 m isobath (marking the transition from shelf-break into the slope) is reviewed, together with a review on the circulation of deep-water masses along the Brazilian continental margin and abyssal plain (Silveira et al. Chap. 2). Slope ecosystems, submarine canyons, and recently discovered chemosynthetic ecosystems are presented, with their benthic diversity, microbial and fish assemblages described (De Leo et al. Chap. 3, Shimabukuro et al. Chap. 5, Signori et al. Chap. 6, Melo et al. Chap. 7). Environmental settings of associated ecosystems are described, including vulnerable deep-sea coral reefs highlighting their biological and ecological relevance in face of current anthropogenic impacts and future threats (Kitahara et al. Chap. 4). Among those threats, Perez et al. (Chap. 8) summarize how decades of fishing and the offshore exploration for mineral resources have greatly expanded on the deep-sea Brazil slope and the threats that vulnerable benthic ecosystems are facing.

We expect that this book will be used by many students, scholars, and the wide public that share their interests in the deep sea. It is a tremendously rich ecosystem in terms of living species, with unique importance to global climate and to humanity, and from where many historical tales have originated in the past.

Sao Paulo, SP, Brazil
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Abbreviations

ANP	Brazilian National Petroleum Agency
AVISO	Satellite Altimetry Data
BNC	Brazilian Northern Coast
GPR	Ground Penetrating Radar
SLR	Sea-Level Rise
SRTM	Shuttle Radar Topography Mission
DHN	Brazilian Hydrographic Authority
DTM	Digital Terrain Model
ITCZ	Intertropical Convergence Zone
INMET	Brazilian National Institute of Meteorology
REBIO	Brazilian Federal Biological Reserve
CONAMA	National Environmental Council
SBE	Southern Brazil Marine Ecoregion
ENSO	El-Nino Southern Oscillation
MPA	Marine Protected Areas
IBAMA	Brazilian Environmental Agency
MMA	Brazilian Ministry of the Environment
EEZ	Economic Exclusive Zone
RGR	Rio Grande Rise

Project Acronyms

RADAM	Amazonas Radar Project
PROMAR	Research Program in Marine Sciences
GLOBESAR	NE Para and Coastal Plain Bragança Project
MADAM	Mangrove Dynamics and Management Project
RECOS	Millennium Institute Project
PIATAM	Potential Environmental Impacts of Petroleum Project
ReBentos	National Benthic Habitats Network (Sisbiota-CNPq)
GERCO	Brazilian National Coastal Management Project
PNGC	Brazilian National Plan of Coastal Management
REVIZEE	Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone
TALUDE	Research Project on the Brazilian Continental Slope
DEPROAS	Research Project on the Southeastern Continental Shelf
HABITATS	Research Project on the Deep-Sea Campos Basin

Chapter 1

An Introduction to the Brazilian Deep-Sea Biodiversity



Paulo Yukio Gomes Sumida , Fabio Cabrera De Leo,
and Angelo Fraga Bernardino

Deep-sea ecosystems are vast and remote and sustain a significant number of marine species globally. The total number of described eukaryotic marine species is ~226,000 according to data from the World Register of Marine Species (WoRMs, Appeltans et al. 2012). For benthic species in particular, modelling studies and estimates based on the accumulation rate of species per area in deep-sea sediments may increase benthic macrofaunal richness to over millions of species (Grassle and Maciolek 1992; Snelgrove and Smith 2002). As a result, the deep sea significantly contributes to global and regional species diversity pools, with high ecological as well as economic importance (Smith et al. 2008).

Given the large dimensions of the Brazilian coastline and extended jurisdictional area, a large part of the Brazilian Economic Exclusive Zone lies in deep waters. The heavy use of this area by the fishing and oil and gas industries, as well as other potential new uses, like deep-sea mining, calls for more intense scientific research (Bernardino and Sumida 2017). A better mapping and understanding of the Brazilian deep sea may reveal potential areas for conservation and novel ways for the sustainable use of deep-ocean resources.

The Brazilian continental margin was first mapped in the late 1960s and 1970s (Perez et al. [this volume](#), Chap. 8). In essence, this benchmark project identified the

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main geological and climatic processes responsible for shaping the current configuration of the Brazilian continental margin. Recent efforts combining worldwide datasets on satellite altimetry and high-resolution multibeam seafloor bathymetry have improved the spatial resolution of seabed geomorphological features across nearly all ocean basins (Harris and Whiteway 2011; Harris et al. 2014). This global effort has identified 29 general geomorphological features based on criteria defined by the International Hydrographic Organization (Fig. 1.1). The relative contributions of each of those features, which broadly include continental shelf, slope, submarine canyons, abyssal plains and hills, seamounts, guyots, sills, escarpments,



Fig. 1.1 Main geomorphological features on Brazil's continental margins. GIS database available through Blue Habitats (www.bluehabitats.org), an initiative supported by United Nations Environment Program (UNEP). Brazil's Economic Exclusive Zone (EEZ) boundaries are overlaid in red (GIS shapefile from Marine Regions Gazetteer, <http://www.marineregions.org/>). For a complete overview of the entire South Atlantic, refer to Figure 10 in Harris et al. (2014)

ridges, and trenches, are given in terms of percent area of seafloor coverage for the eight major ocean regions (Harris et al. 2014).

The Brazilian Economic Exclusive Zone (EEZ) has a total area of ca. 3.6 million km² and ranked 11th in size worldwide. Brazil has claimed an extension of its EEZ within the context of the UNCLOS (United Nation Convention on the Law of the Sea) policy framework, of an additional 0.96 million km² based on a newly delimited continental shelf boundary. This extends Brazil's EEZ to ~4.5 million km², moving the country to the 8th position of the worldwide largest EEZs (LEPLAC project). A recently claim over the Rio Grande Rise area may increase it even further to 5.7 million km², which would give Brazil sovereignty over potential areas for mining base metals and rare earth elements (Montserrat et al. 2019). The potential for exploitation of this area has made the Brazilian Government to nominate it as the “Blue Amazon,” as a comparison with the largest rainforest of the planet. The deep Brazil's Continental Margin provides a wide range of habitats for deep-sea benthic communities, with near 600,000 km² between 200 and 3000 m (Table 1.1). It is noteworthy that almost 2/3 of Brazil's EEZ region is comprised of deep seafloor features that occur beyond the continental shelf at depths over 200 meters, revealing that deep-sea ecosystems are prevalent over Brazil's EEZ. The continental shelf, which by definition extends down to the 200 m depth, has nearly 775,000 km² in area corresponding to roughly 21% of Brazil's EEZ (Table 1.1).

In the South Atlantic, the Brazilian Continental Margin belongs to a tectonically passive-type margin with a typically wide (> 100 km) continental shelf (De Leo et al. [this volume](#), Chap. 3). The shelf is wider on the equatorial NE-N margin, reaching its widest point along the Amazon deltaic fan (> 200 km; Nittrouer and DeMaster 1986). The deep-sea slope of the Brazilian margin is influenced by four

Table 1.1 Total area, % area, and number of most prominent geomorphological features on Brazil's Continental Margin (within its EEZ boundaries) and deep-sea ecosystems

Deep-sea ecosystem	Geomorphological feature and political boundaries	Total Area in km ² (within BR EEZ)	% Area	No. of features
	Continental shelf	774,563	20.5	–
Bathyal (200 to 3000 m)	Slope	484,961	13.3	–
	Terrace	61,171	1.7	–
	Submarine canyons	52,668	1.4	161
Abyssal (> 3000 m)	Continental rise	1,450,047	40	–
	Abyssal plain	1,074,834	29.6	–
	Submarine fans	177,492	4.9	2
	Seamounts	88,629	2.2	123
	Guyots (flat-top seamount)	51,799	1.4	13
	Ridges	44,519	1.2	30
	Spreading ridges	54,020	1.4	1
	EEZ (200 nm)	3,646,514	100	1

Data extracted from Harris et al. (2014). + Sum of % area of all geomorphological features surpasses 100% as some of the features overlap in space (e.g., Sao Paulo Plateau overlaps in area with the slope and continental rise). Extended Continental Shelf area claimed by Brazil was not included

main water masses with distinct flow directions: i) the South Atlantic Central Water (SACW; $T = 18\text{ }^{\circ}\text{C}$ to $6\text{ }^{\circ}\text{C}$) flowing northward between 300 and 550 m depth, ii) Antarctic Intermediate Water (AAIW, $T = 6\text{ }^{\circ}\text{C}$ to $2\text{ }^{\circ}\text{C}$) flowing northward between 550 and 1200 m depth, iii) North Atlantic Deep Water (NADW, $T = 4\text{ }^{\circ}\text{C}$ to $2\text{ }^{\circ}\text{C}$) flowing southward between 1200 and 3500 m, and iv) Antarctic Bottom Water (AABW, $T < 2\text{ }^{\circ}\text{C}$) flowing northward below 3500 m (De Madron and Weatherly 1994; Campos et al. 1995; Silveira et al. [this volume](#), Chap. 2). Although not often recognized, deep-sea water masses greatly influence continental shelf and coastal marine ecosystems by increasing the productivity and dynamics of biological assemblages along the Brazilian shelf. Upwelling events and episodic intrusions of the SACW lead to increases in pelagic productivity and change benthic assemblage composition, increasing its abundance and biomass (Sumida and Pires-Vanin 1997; Castro et al. 2006; Sumida et al. 2005; Yoshinaga et al. 2008; Quintana et al. 2015). Deep-sea water masses thus offer an important source of nutrients to shelf waters, especially along oligotrophic regions of the NE and Eastern Brazil margin. Water masses and bathymetric gradients in productivity also greatly influence benthic assemblages on the slope off Brazil's margin (Bernardino et al. 2016; Lavrado et al. 2017a, b,) that are further detailed in this book (De Leo et al. [this volume](#), Chap. 3).

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Chapter 2

Water Masses and Oceanic Circulation of the Brazilian Continental Margin and Adjacent Abyssal Plain



Ibson Carlos Almeida da Silveira, Dante Campagnoli Napolitano, and Igor Uchôa Farias

Abstract This chapter presents an overview of the water masses and oceanic circulation of the Brazilian Continental Margin (BCM) and the adjacent abyssal plain. Six major water masses compose the stratification over 5000 m of water column in the Southwestern Atlantic: the Tropical Water (the surface water TW, 0–150 m), the South Atlantic Central Water (the pycnoclinic water SACW, 150–500 m), the Antarctic Intermediate Water and the Upper Circumpolar Water (the intermediate waters AAIW and UCPW, 500–1300 m), the North Atlantic Deep Water (the deep water NADW, 1300–3500 m), and the Antarctic Bottom Water (the bottom water AABW, > 3500 m). The Lower Circumpolar Water (LCPW) may be also considered as an upper limb of the AABW and therefore characterized as such. These water masses are transported either equatorward or poleward by an intricate system of western boundary currents. There are three major current systems within the BCM limits. The Brazil Current (BC) system extends from 14°S to about 40°S and closes the South Atlantic Subtropical Gyre. This current starts as a weak 2 Sv ($1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$) jet transporting only TW at 15°S and exits the BCM as a jet with a vertical extent of more than 1000 m, transporting 25 Sv of TW, SACW, AAIW, and UCPW. Along its southward path, the BC develops large meanders and eddies, which may neck off and form vortical rings shed to more interior portions of the gyre. The North Brazil Undercurrent/North Brazil Current (NBUC/NBC) is the western boundary system which closes the Equatorial Gyre (14°S–6°N). This current system is more intense than that of the BC, with core speeds greater than 1 m s^{-1} and transports of 30–35 Sv. Unlike the BC, the NBUC presents its core at depths between 150 and 250 m. In its path toward the northern hemisphere, the current undergoes a series of retroreflections, at which it loses volume to the Tropical Atlantic interior and gains volume from shallower branches of South Equatorial Current (SEC). As a result, the NBUC loses its pycnoclinic core and becomes the surface-intensified

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NBC. This latter jet crosses the equator transferring TW, SACW, and AAIW to the northern hemisphere. Its large inertia inhibits the formation of large meanders and eddies while attached to the Brazilian continental slope. The only known exception is the recently described Potiguar Eddy at 4°S, an anticyclonically rotating permanent lens of SACW. The third current system is due to the Deep Western Boundary Current (DWBC), the main component of the Atlantic Meridional Overturning Circulation. This current flows southward along the Americas' continental border and reaches the BCM as a NADW-transporting, 20Sv deep jet. It exits the BCM as a 40 Sv jet after being fed by distinct interior sources of volume and recirculations. The AABW flow is not organized as a jet. Its northward motion occurs along the whole region of interest as a northward sluggish flow rubbing itself against the ocean floor of the abyssal plain.

Keywords South Atlantic Subtropical Gyre · Water masses · Western boundary currents · Brazil Current · North Brazil Current · Deep Western Boundary Current · Meanders · Eddies

2.1 Preamble

This chapter aims to present a brief description of the state of the art of the regional physical oceanography of the Brazilian Continental Margin (BCM) and adjacent abyssal plain. This text is inspired on the iconic work of Stramma and England (1999), which pioneered in presenting the water masses and oceanic circulation combining climatological hydrography and a validated numerical simulation of the South Atlantic. Here, we look further into the BCM using the same approach. The World Ocean Atlas climatology (WOA13; Locarnini et al. 2013; Zweng et al. 2013) is used to describe the water masses in terms of the temperature, salinity, density, dissolved oxygen, and nutrients. A validation on the Mercator Ocean (Toulouse, FR) GLORYS2V4¹ reanalysis was conducted through comparison of horizontal patterns, vertical extension, volume transports, and intraseasonal variability of the major ocean currents with information from the literature. All plots of horizontal velocity and vertical patterns presented in this chapter are derived from the reanalysis aforementioned, which time series spanned from 1993 to 2015.

¹The GLORYS2V4 outputs can be downloaded from http://marine.copernicus.eu/services-portfolio/access-to-products/?option=com_csw&view=details&product_id=GLOBAL_REANALYSIS_PHY_001_025

2.2 Water Masses

The vertical distribution of water masses in the Southwestern Atlantic Ocean changes along the South American continental border. A total of seven water masses can be identified throughout the South Atlantic Basin, each one occupying specific depths and latitudinal ranges over the Brazilian Continental Margin (BCM) and adjacent abyssal plain (Fig. 2.1). They are from surface to the ocean floor: the Tropical Water (TW), the South Atlantic Central Water (SACW), the Antarctic

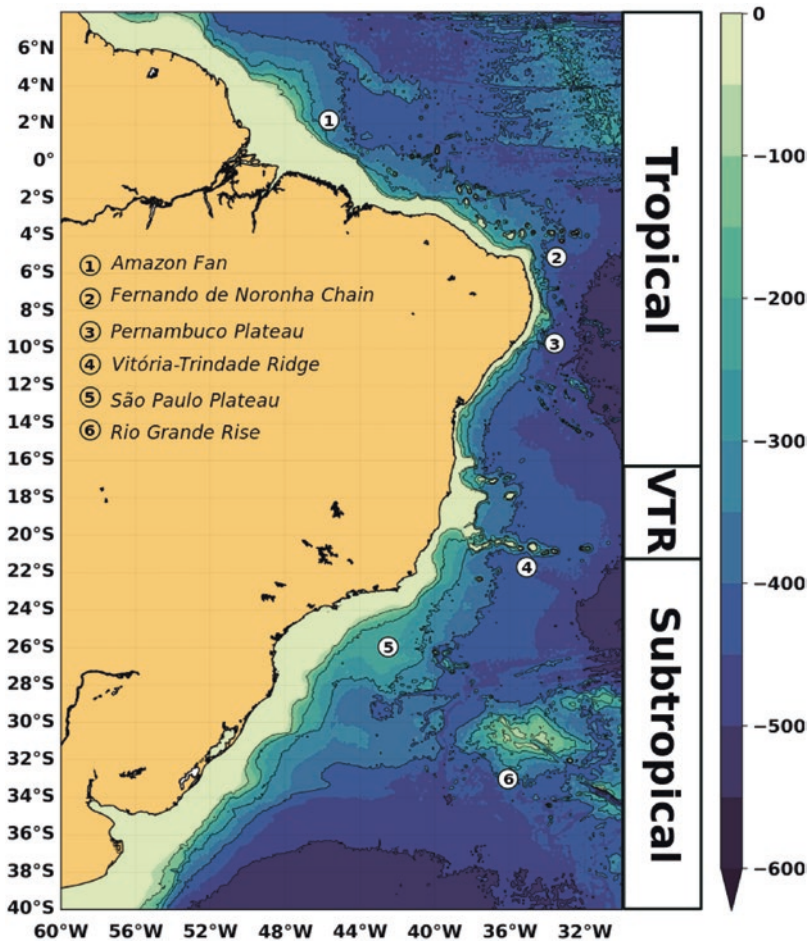


Fig. 2.1 The Brazilian Continental Margin, the adjacent abyssal plain and relevant bottom features (numbers). The Vitória-Trindade Ridge (VTR) is the region which naturally delimits the tropical and the subtropical portions of the margin and represents northern limit reached by the Upper Circumpolar Water (UCPW). Bathymetric data (indicating color palette on the right) from 1 Arc-Minute Global Relief Model (ETOPO 1; Amante and Eakins 2009)

Intermediate Water (AAIW), the Upper Circumpolar Water (UCPW), the North Atlantic Deep Water (NADW), the Lower Circumpolar Water (LCPW), and the Antarctic Bottom Water (AABW).

The surface TW presents the highest values of temperature and salinity of the water column (Emilsson 1961). The salinity maximum is most commonly found at subsurface, which led several authors to name it as “Subsurface Maximum Salinity Water” (Reid 1989) or “Salinity Mode Water” (Mémery et al. 2000). Near its origin site in the Tropics, the SACW is characterized by the largest variation of temperature and salinity due to its position at pycnocline level (Tomczak and Godfrey 1994). The intermediate and deep waters normally cannot be distinguished solely by their thermohaline properties. The oxygen-rich AAIW is characterized by the water column salinity minimum (Wüst 1935; Reid et al. 1977). The UCPW is identified by an oxygen minimum associated with a local silicate maximum (Mémery et al. 2000). AAIW and UCPW are the intermediate water masses of the Southwestern Atlantic. The deep NADW, which enters the Brazil Basin conserving its properties from its original source waters in the North Atlantic (Schott et al. 2005), is described here as a single water mass and is characterized by high values of oxygen and temperature, by a secondary water column salinity maximum, and by low local levels of nutrients (Maamaatuaiahutapu et al. 1994). The LCPW presents local low oxygen and high nutrient levels (Tsuchiya et al. 1994). The AABW is also nutrient rich, but is slightly fresher and colder than the LCPW. A more detailed description of these water masses can be found in Reid (1989), Tsuchiya et al. (1994), Stramma and England (1999), Mémery et al. (2000), and Silveira et al. (2000a). The LCPW and AABW density values are virtually indistinguishable from each other within the Brazil Basin (Mémery et al. 2000). Peterson and Stramma (1991) and Stramma and England (1999) considered the LCPW as simply the upper limb of the AABW. For these reasons, in this chapter, it will also be considered bottom waters within the BCM as solely AABW, where the LCPW is the lightest of the sources which form the densest water mass of the South Atlantic Ocean.

The Vitória-Trindade Ridge (VTR) – a nearly west-east seamount chain centered at about 20.5°S – is a notable topographic feature adjacent to the BCM and is set in this chapter to delimit the equatorial-tropical (hereafter referred as tropical) from the subtropical portions of the BCM and adjacent abyssal plain (Fig. 2.1). The tropical water column on the BCM may be distinguished by the absence of the UCPW, which has the VTR surroundings as its northern limit (Tsuchiya et al. 1994). The tropical BCM water mass structure is composed by the TW, SACW, AAIW, NADW, and AABW. While the former four water masses are transported by the western boundary current systems, the latter is driven by the bathymetric variations and spreads throughout the ocean floor over the continental rise and the adjacent abyssal plain. The subtropical BCM water mass structure consists of the vertical stack of the TW, SACW, AAIW, UCPW, NADW, and AABW. The circumpolar water reaches the Southwestern Atlantic carried by the Antarctic Circumpolar Current (ACC) through the Drake Passage (Piola and Gordon 1989). The UCPW, in particular, is transported by the ACC equatorward-flowing branch which borders the continental slope and is known as the Malvinas Current (MC; Talley 2011). The MC collides

with the Brazil Current (BC) at about 40°S, causing the UCPW to be advected eastward by the South Atlantic Current (SAC; Stramma and Peterson 1990) and to recirculate counterclockwise at the deepest portion of the South Atlantic Subtropical Gyre (Reid 1989; Stramma and England 1999).

Table 2.1 presents the water density ranges at which the water masses occur in the tropical and subtropical portions of the BCM. The values are presented in terms of density anomalies (σ_t), i.e., the total density subtracted by 1000 kg m⁻³. Moreover, in order to compare densities within a water column, which extends from the surface to more than 4000 m, the density computation is referenced at a nearby standard isobaric level (0 dbar, 1000 dbar, 2000 dbar, or 4000 dbar). In other words, the referenced density calculation is conducted as moving water parcels (with given temperature and salinity value) adiabatically to a referenced pressure level (Stewart 2008). The reader should be aware of the numerical correspondence between pressure in decibars (dbar) and depth in meters, which allows the use of both interchangeably.

Scattered climatological (WOA13) temperature-salinity (T-S) diagrams for both tropical and subtropical portions of the BMC are presented in Fig. 2.2. The characteristic “inverted-S shape” of the South Atlantic TS-Diagram is clearly noted in both panels of Fig. 2.2. A warmer TW in the tropical region and a fresher AAIW in the subtropical BCM are clearly observed. These differences in the TS Diagrams are due to the proximity of these water masses to their formation sites in the Tropical South Atlantic and in the southern limb of the Subtropical Gyre, respectively.

As reference for the physical and chemical properties of the six water masses, which composes the water column of the Southwestern Atlantic, we present the

Table 2.1 Ranges of referenced density and depths of each water mass in the BCM and adjacent abyssal plain for their equatorial-tropical (T) and subtropical (S) portions. Values were compiled from Stramma and England (1999), Mémery et al. (2000), Silveira et al. (2000a), and Schott et al. (2005)

Water mass	Ref. dens. range (kg m ⁻³) ^a	Depth range (m)
Tropical Water	< 24.50 σ_0 (T) < 25.60 σ_0 (S)	0–150
South Atlantic Central Water	24.50–26.90 σ_0 (T) 25.60–26.80 σ_0 (S)	150–500
Antarctic Intermediate Water	26.90 σ_0 –32.15 σ_1 (T) 26.08 σ_0 –32.00 σ_1 (S)	500–1000
Upper Circumpolar Water	Not Present (T) 32.00 σ_1 –36.90 σ_2 (S)	1000–1300
North Atlantic Deep Water	32.15 σ_1 –45.90 σ_4 (T) 36.90 σ_2 –45.87 σ_4 (S)	1300–3500
Antarctic Bottom Water	> 45.90 σ_4 (T) > 45.87 σ_4 (S)	3500–bottom

^aDensity σ indices indicate that this quantity is referenced at the following isobaric levels: **0** (at the surface for TW, SACW, and AAIW), **1** (at 1000 dbar for UCPW), **2** (at 2000 dbar for NADW), **4** (at 4000 dbar for LCPW and AABW). Referenced density is expressed as the excess density amount relative to 1000 kg m⁻³, i.e., in “ σ_t ” units, a traditional notation in Physical Oceanography

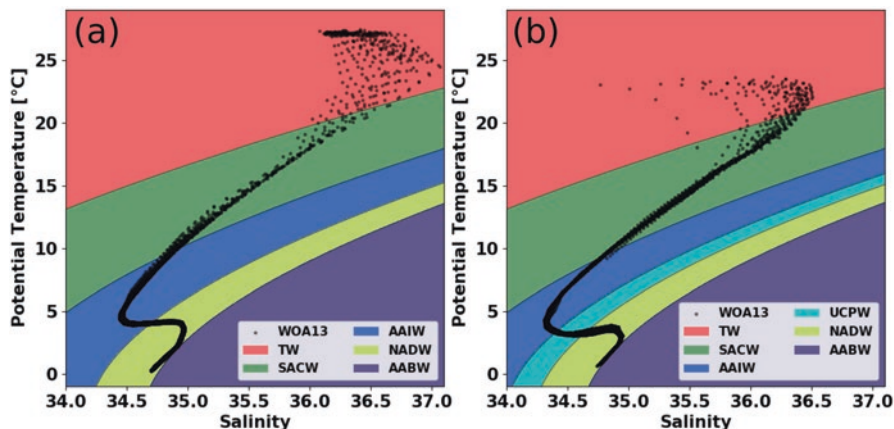


Fig. 2.2 TS-Diagrams for the (a) tropical (following Schott et al. 2005) and (b) subtropical (following Stramma and England 1999) portions over the Brazilian Continental Margin. Temperature (T) and salinity (S) data are from the World Ocean Atlas (WOA13) database (Locarnini et al. 2013; Zweng et al. 2013; Garcia et al. 2014a, b). The color coding indicates the different water masses in the region: Tropical Water (red), South Atlantic Central Water (green), Antarctic Intermediate Water (blue), Upper Circumpolar Water (cyan), North Atlantic Deep Water (yellow), and Antarctic Bottom Water (purple)

Table 2.2 Primary source water types of the physical and chemical properties for the six water masses which compose the water column in the Southwestern Atlantic. The information is based on Silveira et al. (2015), who gathered and compiled historical data from the literature as well as from in situ data at the formation site of the TW

Water mass	Temp. (°C)	Sal. (g kg ⁻¹)	Oxygen (ml l ⁻¹)	Phosphate (μmol l ⁻¹)	Nitrate (μmol l ⁻¹)	Silicate (μmol l ⁻¹)
Tropical Water	26.81	37.12	4.19	0.02	1.10	2.04
South Atlantic Central Water	16.26	35.80	5.13	0.51	6.14	5.12
Antarctic Intermediate Water	3.90	34.20	5.33	1.94	27.13	20.48
Upper Circumpolar Water	2.50	34.55	4.17	2.25	29.69	51.20
North Atlantic Deep Water	3.50	34.94	6.23	1.74	24.16	22.52
Antarctic Bottom Water	1.00	34.72	5.56	2.04	30.72	103.42

indices of temperature, salinity, dissolved oxygen, phosphate, nitrate, and silicate at their supposed formation site. Table 2.2 consists on an adaptation of the literature information gathered and presented by Silveira et al. (2015). The values for the TW were original to the authors' own research at the maximum salinity water generation site. The temperature and salinity values refer to an average of the water types in their subduction region.

As previously mentioned in this section, below the AAIW, water masses are difficult to distinguish using only thermohaline properties. The classical water masses analysis, such as the one detailed in Mamayev (1975), associates the core of the water masses to vertices on the T-S curve or specifically in the South Atlantic case,

to the inflection points on the “inverted-S” shape at the TS-Diagram. However, the circumpolar waters are not associated to these maxima or minima on this curve. Zemba (1991) proposed a simple qualitative identification of the circumpolar waters using nutrients and dissolved oxygen. Figure 2.3 exhibits Cartesian plots of dissolved oxygen and silicate structure in the x-axis and density anomalies referenced to 2000 m (σ_2) in the y-axis, i.e., a sort of “vertical” profile of dissolved oxygen (O_2) and silicate (SiO_4) in isopycnal coordinates. The signature UCPW in terms of oxygen minimum (silicate maximum) is absent (present) in the tropical (subtropical) portions of the BCM. Moreover, possible effects of biological activity and mixing are noticed in the AAIW oxygen content from the subtropical to tropical curves, where depleted values in the tropics are observed (Figure 2.3a).

The AAIW is transported equatorward as part of the subpycnoclinic circulation along the BCM. In the subtropical region, the oxygen maximum of the whole water column is found within the NADW domain ($\sim 37.0 \sigma_2$) and located below the UCPW minimum. Silicate concentrations, displayed in Figure 2.3b, show a continuous increase within the AAIW portion of the water column in the tropics which

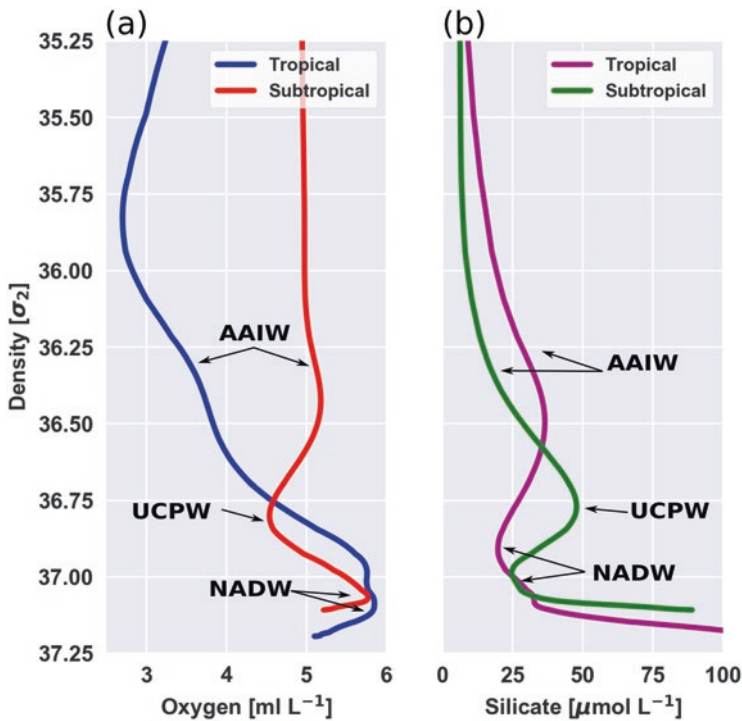


Fig. 2.3 Comparison of the intermediate and deep-water masses properties [(a) oxygen and (b) silicate] along a density gradient (σ_2) for the tropical and subtropical portions over the Brazilian Continental Margin. AAIW, Antarctic Intermediate Water; UCPW, Upper Circumpolar Water; NADW, North Atlantic Deep Water. Data from the World Ocean Atlas (WOA13) database (Locarnini et al. 2013; Zweng et al. 2013; Garcia et al. 2014a, b)

coincides with the oxygen minimum. The lowest SiO_4 concentrations of the profile are associated with the NADW and mirrors its oxygen maximum. While the relative higher silicate levels are noted in the tropics in relation to the subtropics could be attributed to remineralization, here it is speculated that the disappearing of the circumpolar water signal around the VTR latitude (Tsuchiya et al. 1994) is linked to topographic mixing (Garabato et al. 2004; Nikurashin et al. 2013) generated by the seamount chain. Such mixing may mask the UCPW characteristics within the greater volume of AAIW.

Unlike all other water masses over the BCM, the AABW is not associated with any western boundary current. The bottom water spreads through the bottom of the whole South Atlantic, covering a fair share of the abyssal plain and being severely constrained by topography.

2.3 Western Boundary Currents

The so-called upper ocean comprises the mixed layer, the seasonal pycnocline, and the permanent pycnocline (Cronin and Sprintall 2009). These three portions of the water column encompass about the first 1000–1300 m of the ocean and are related to the surface (TW), the pycnocline (or central, SACW), and the intermediate (AAIW and UCPW) water masses, respectively. Those bodies of water are transported by a complex system of western boundary currents, all of which border the continental slope and rise. Two main upper-ocean current systems occur along the BCM: the subtropical Brazil Current (BC) and the tropical North Brazil Current (NBC).

Below the permanent pycnocline, the NADW is carried poleward by the Deep Western Boundary Current (DWBC). This deep jet has its origin just south of the Labrador Sea and crosses the whole Atlantic Ocean before reaching the Southern Ocean (Talley 2011). The DWBC represents the deep part of the Atlantic Meridional Overturning Circulation (AMOC; Rintoul 1991). The sluggish AABW flow consists of the lowest part of the AMOC and opposes the DWBC, transporting the bottom water towards the Arctic. The surface, pycnoclinic, and intermediate parts of the AMOC greatly modify the upper ocean, majorly the wind-driven western boundary currents. These three AMOC components lead to the formation of an intricate pattern of current inversions with depth, which strengths the NBC and weakens the BC.

The mean circulation patterns along the whole BCM and adjacent abyssal plain are presented at the core depths of the water masses discussed in Sect. 2 of this chapter, namely, the TW (Fig. 2.4), SACW (Fig. 2.5), AAIW (Fig. 2.6), NADW (Fig. 2.7), and AABW (Fig. 2.8). The color background of each map corresponds that of the water mass bands of the TS diagrams exhibited in Fig. 2.2.

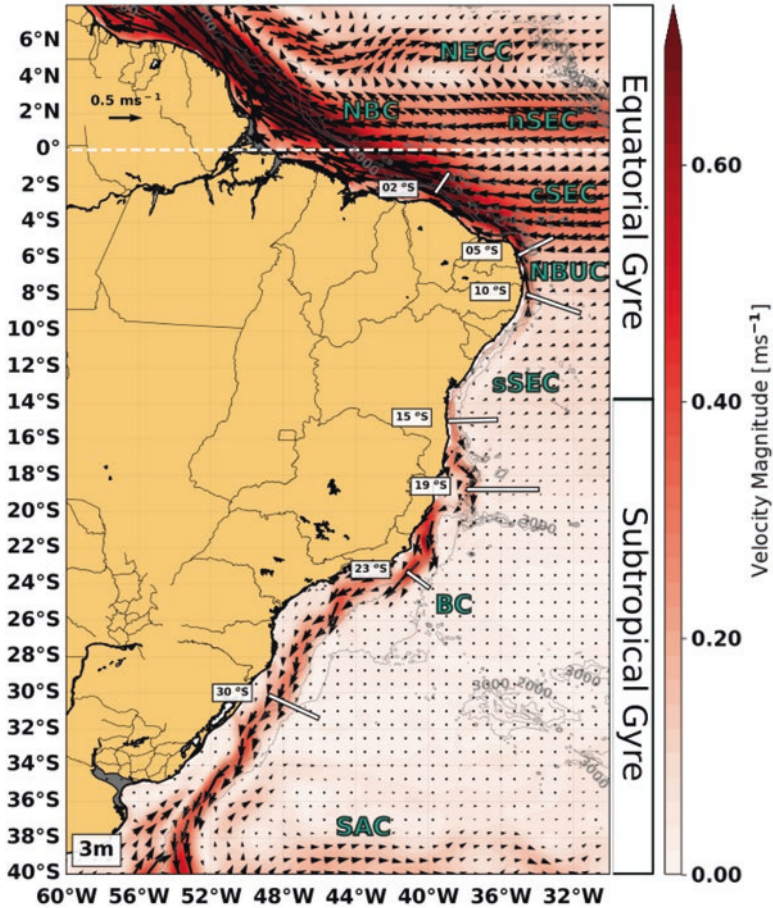


Fig. 2.4 Mean circulation pattern in the Tropical Water (TW) domain (3 m) along the Brazilian Continental Margin (BCM). The white bars represent selected transect positions for which vertical sections will be exhibited ahead on the chapter. The acronyms for the main currents stand for the following: SAC South Atlantic Current, BC Brazil Current, NBUC North Brazil Undercurrent, NBC North Brazil Current; *s,c,nSEC* southern, central, and northern branches of the South Equatorial Current; and NECC North Equatorial Countercurrent. The color coding (red) for the velocity magnitude field agrees with the one presented in Fig. 2.2

2.3.1 The Brazil Current System

Once credited to the bifurcation of the South Equatorial Current (SEC) surface layer at Cape São Roque (5.5°S), Stramma (1991) imputed that the BC formation occurs due to the impinging southernmost SEC (hereafter sSEC) branch at about 15°S, off the Brazilian Eastern coast. Silveira et al. (1994) showed that another SEC branch, the central one (cSEC), indeed reaches Cape São Roque, but adds its entire transport to feed the NBC. The apparent divergence is due to Ekman drift currents south of

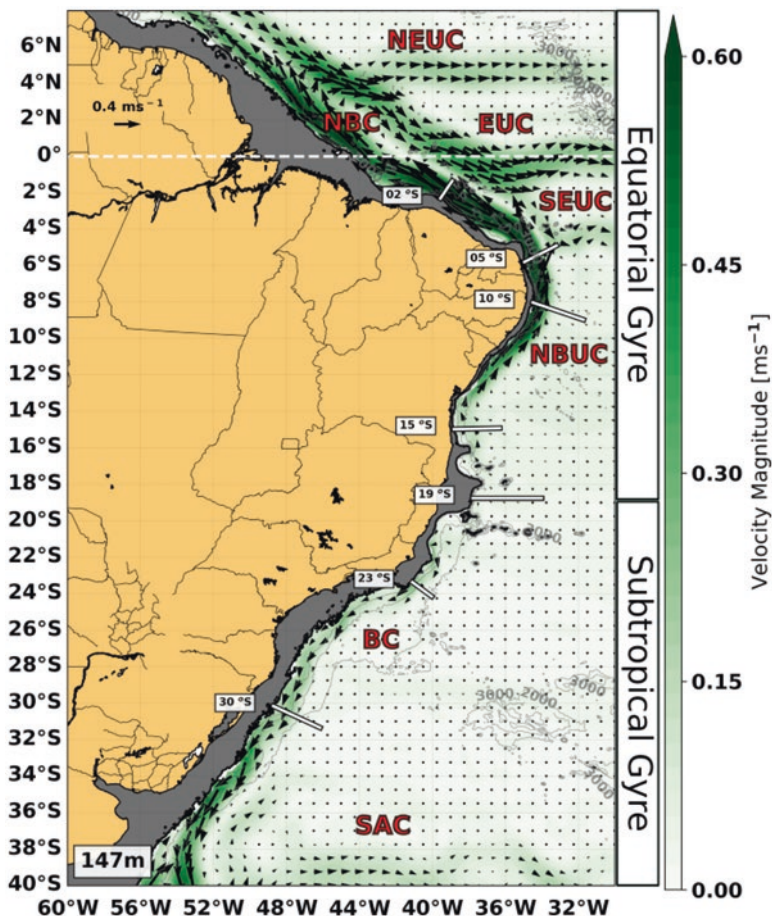


Fig. 2.5 Mean circulation pattern in the South Atlantic Central Water (SACW) domain (147 m) along the Brazilian Continental Margin (BCM). The white bars represent selected transect positions for which vertical sections will be exhibited ahead on the chapter. The acronyms for the main currents stand for the following: SAC South Atlantic Current, BC Brazil Current, NBUC North Brazil Undercurrent, NBC North Brazil Current, SEUC South Equatorial Undercurrent, EUC Equatorial Undercurrent, NEUC North Equatorial Undercurrent; and NECC North Equatorial Countercurrent. The color coding (green) for the velocity magnitude field agrees with the one presented in Fig. 2.2

the region (Richardson and Reverdin 1987). Rodrigues et al. (2007) conducted the most in-depth study about the southern SEC branch to date. The latter authors built their own temperature-salinity seasonal climatology and employed a multilayer numerical model to show that the sSEC bifurcation presents a robust annual cycle, varying from about 10°S in the austral summer to about 15°S in the austral winter.

Soutelino et al. (2011) examined data from high-resolution synoptic cruises at the BC origin site and validated global numerical simulations to describe that the

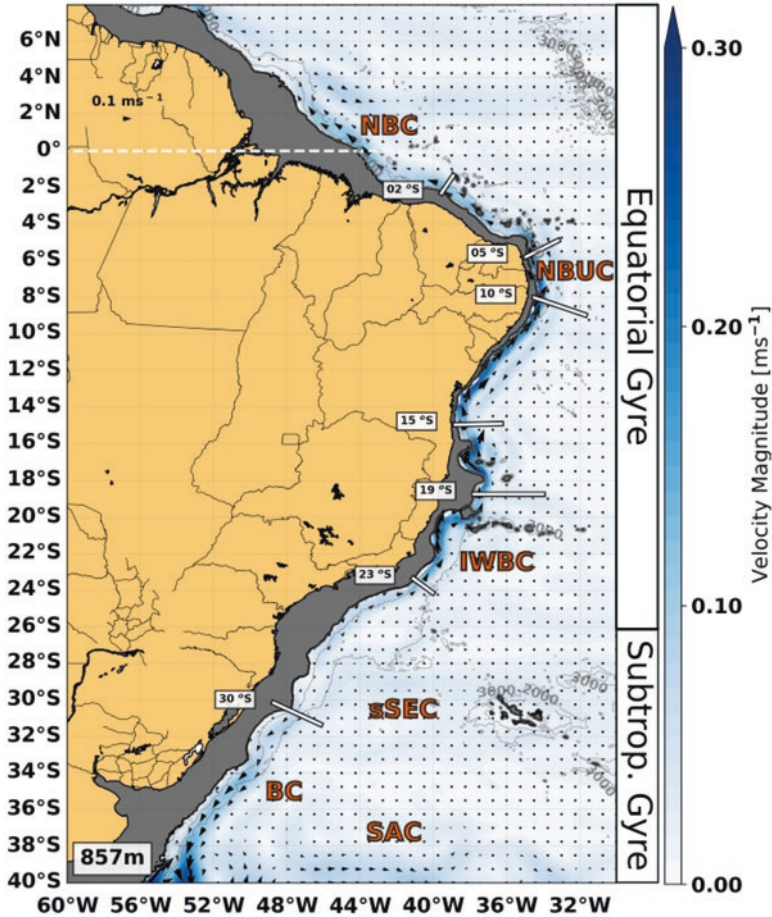


Fig. 2.6 Mean circulation pattern in the Antarctic Intermediate Water (AAIW) domain (857 m) along the Brazilian Continental Margin (BCM). The white bars represent selected transect positions for which vertical sections will be exhibited ahead on the chapter. The acronyms for the main currents stand for the following: SAC South Atlantic Current, BC Brazil Current, IWBC Intermediate Western Boundary Current, NBUC North Brazil Undercurrent, NBC North Brazil Current. The color coding (blue) for the velocity magnitude field agrees with the one presented in Fig. 2.2

BC is a shallow jet transporting TW only and rarely exceeding 2 Sv ($1 \text{ Sv} = 10^6 \text{ m}^3 \text{ s}^{-1}$) just south of the sSEC bifurcation, as shown here in Fig. 2.9. Beginning its path poleward along the eastern margin, the BC is forced to contour a convoluted shelf break between 16°S and 21°S due to the presence of the Royal Charlotte and Abrolhos Banks. As result, three large quasi-stationary, quasi-permanent anticyclones are formed: the Ilhéus Eddy (IE), the Royal Charlotte Eddy (RCE), and the Abrolhos Eddy (AE). The presence of these vortical features led the authors to propose that the BC is eddy-dominated at its origin site and called into question whether the current is, in fact, continuously flowing north of the VTR (Fig. 2.10). A

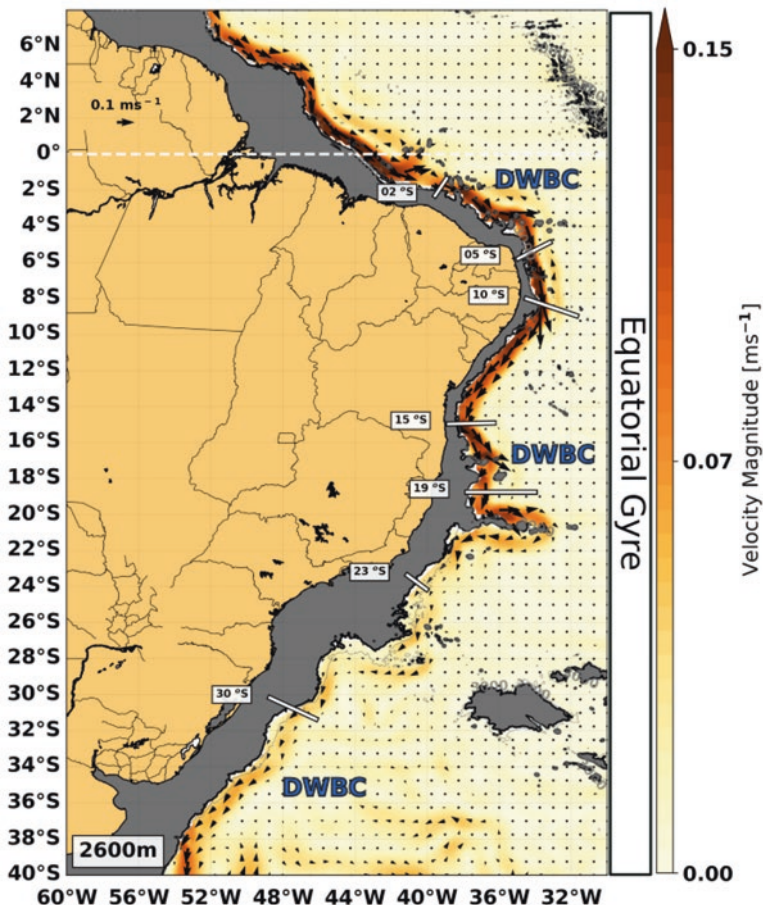


Fig. 2.7 Mean circulation pattern in the North Atlantic Deep Water (NADW) domain (2600 m) along the Brazilian Continental Margin (BCM). The white bars represent selected transect positions for which vertical sections will be exhibited ahead on the chapter. The acronym for the main currents stands for the following: *DWBC* Deep Western Boundary Current. The color coding (yellow) for the velocity magnitude field agrees with the one presented in Fig. 2.2

follow-up study carried out by the same authors employed numerical process modeling to verify that despite the eddies' formation be a result of hydraulic control, baroclinic (or vertical-shear) instability plays a secondary role and is responsible for eddy growth, subsequently causing them to detach from the BC axis.

At the VTR surroundings, the BC interacts with rough topography, generating submesoscale eddies and filaments, which are currently a “hot topic” within the ocean sciences due to the biogeochemical implications that accompany them. The VTR crossing and a “running-out-of-boundary” force the BC to sharply turn cyclonic (Evans et al. 1983; Napolitano et al. 2019). This large cyclonic loop and the reattachment latitude seem to be controlled by the BC transport (Fig. 2.10).

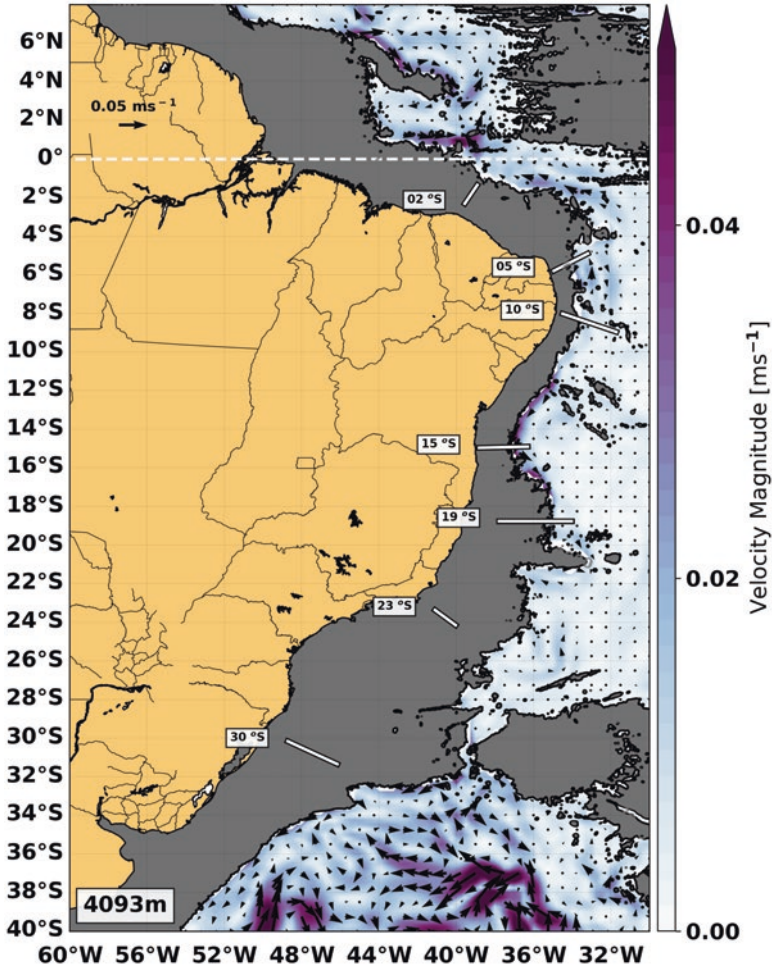


Fig. 2.8 Mean circulation pattern in the Antarctic Bottom Water (AABW) domain (4093 m) along the Brazilian Continental Margin (BCM). The white bars represent selected transect positions for which vertical sections will be exhibited ahead on the chapter. No organized continuous flow is observed. There is a general equatorward motion at this level. Occasional velocity strengthening is due to topographic constraints. The color coding (purple) for the velocity magnitude field agrees with the one presented in Fig. 2.2

Occasionally, the cyclonic loop leads to the formation of a fourth quasi-stationary feature related to the BC, the Vitória Eddy (VE). Unlike the other three, this one is a cyclone, which was described during the World Ocean Circulation Experiment (WOCE) by Schmid et al. (1995). Later, Gaeta et al. (1999) showed that the nutrient concentration and the primary productivity within the VE domain was at least twice those of the oligotrophic surrounding waters. Such an increase would be due to the quasi-geostrophic upwelling characteristic of a cyclonic feature.

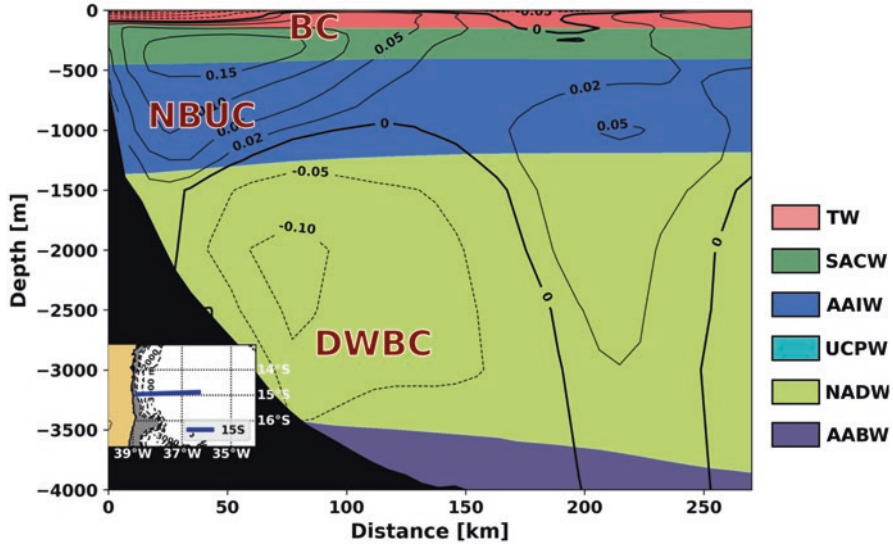


Fig. 2.9 Vertical section of a transect at 15°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The Brazil Current (BC) is depicted as a shallow flow occupying only the upper 150 m and transporting only Tropical Water (TW) southward. Underneath it, NBUC almost completely formed, transporting South Atlantic Central Water (SACW) and Antarctic Intermediate Water (AAIW) in the opposite direction. The layer of deep water exhibits a section of a large, asymmetric anticyclone of the Deep Western Boundary Current (DWBC)

Arruda et al. (2013) and Arruda and Silveira (2019) explored the dynamics of the coupling between the AE, north of the VTR, and the VE, accommodated within the Tubarão Bight (TB) (Fig. 2.10) at the southern flank of the Abrolhos Bank. The cyclonic VE and the anticyclonic AE form a dipole structure. There are two very distinct modes of variability of the AE-VE interaction. The first one is the most common situation where the VE is weaker than the AE. In this case, the VE is pushed north by the AE, it is shed by the BCM, and it crosses the VTR by orbiting the AE (Fig. 2.11a). If it is not destroyed in the process, it may reach the eastern flank of the Abrolhos bank and then keep propagating north, as predicted in the numerical experiments by Campos (2006). The second mode of variability occurs, as reported by Arruda and Silveira (2019), when the VE and AE have about the same strength and the BC gets locked between them (Fig. 2.11b). In this case, the dipole propagates as an entity in the southeastern direction and having the Besnard Bank (Fig. 2.11b) in its center. Strong shelf break upwelling is observed and the BC acts as a jet which extrudes the blend of surface and upwelled waters toward the open ocean. This upwelled plume can be tracked for more than 400 km away from the coast by its chlorophyll-a signature. This phenomenon very likely presents relevant biogeochemical processes associated with it.

The BC cyclonic loop reaches the shelf break at 21°S on average. The BC, as depicted by Silveira et al. (2004, 2008) and Lazaneo et al. (2020), extends from the

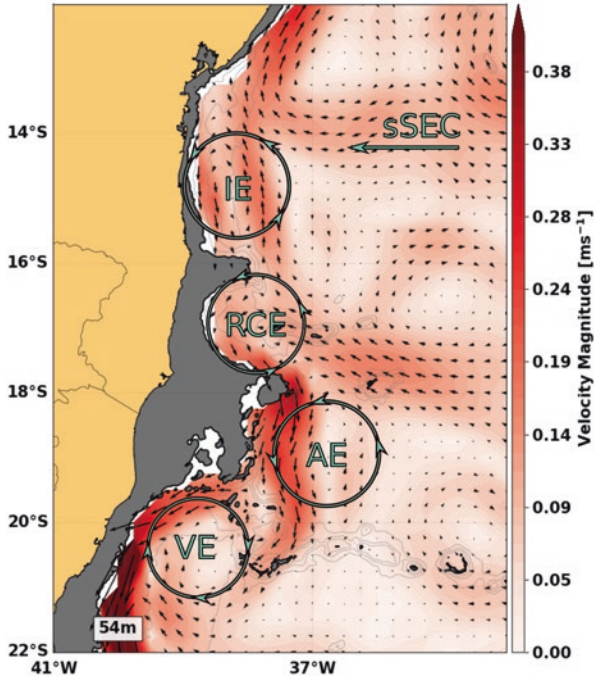


Fig. 2.10 The surface bifurcation of the southern branch of the South Equatorial Current (sSEC) and the origin of the “eddy-dominated” Brazil Current (BC). The map depicts the three anticyclones trapped in-between topographic features of the eastern Brazilian Continental Margin (BCM): the Ilhéus Eddy (IE), the Royal Charlotte Eddy (ECE), and the Abrolhos Eddy (AE). A fourth quasi-stationary cyclonic feature is the Vitória Eddy (VE) that docked in the Tubarão Bight (TB) bottom feature

surface down to 350–500 m, has width of 100–120 km, and carries 5–10 Sv of TW and SACW (Fig. 2.12). Peak velocities observed in situ can reach 0.7 m s^{-1} (Silveira et al. 2000a). The thickening of the BC south of the VTR has been addressed by Stramma and England (1999) and, in more detail, by Rodrigues et al. (2007) as consequence of the impinging sSEC at pycnocline level. According to the former authors, the VTR serves as the axis of this bifurcation and the southward-flowing branch adds SACW water to the BC as it triples its transport.

At Cape São Tomé (22°S) and Cape Frio (23°S) (Fig. 2.13), the BC develops meandering activity and eddy shedding. These meanders are always cyclonic and unstable, presenting a unique feature: they intensively grow oceanward, mostly not propagating north or south (Fig. 2.13). First described by Mascarenhas et al. (1971), these meanders were more thoroughly investigated in this century. Silveira et al. (2000a, 2004) described the shedding and their vertical structure. Silveira et al. (2008), Calado et al. (2006, 2008), Mano et al. (2009), and Rocha et al. (2014) addressed their dynamics and showed that the primary mechanism causing the growth is baroclinic instability even though barotropic (or horizontal shear)

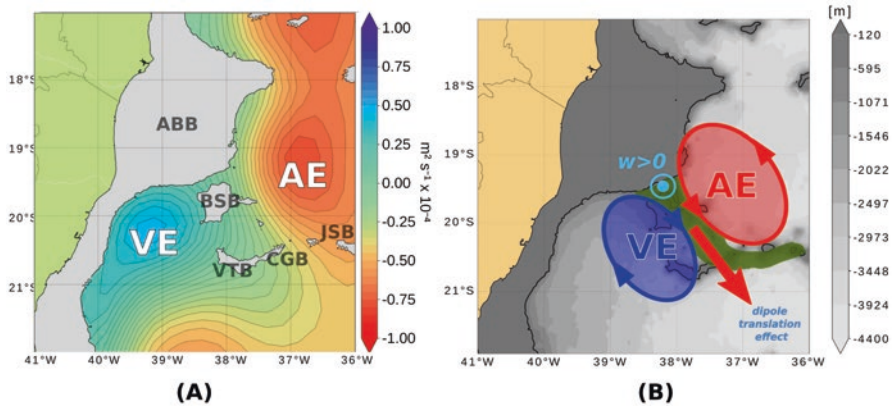


Fig. 2.11 The Vitória Eddy (VE) - Abrolhos Eddy (AE) dipole: **(a)** as depicted from sea surface (SSH) contours from the AVISO data set, distributed by the Copernicus Marine Environment Monitoring Service (CMEMS) at L4-level processing 1 with 0.25° of horizontal resolution; **(b)** as a schematic representation of the dipole moving southeastward, causing shelf-break upwelling at the Abrolhos Bank (ABB) eastern tip and advecting the upwelled waters (in green) towards the ocean interior with the Besnard Bank (BSB) as its center. Arruda and Silveira (2019) used sea color images to show that the plume had a higher chlorophyll-a signature than its surroundings. The Vitória Bank (VTB), Congress Bank (CGB), and Jaseur Bank (JSB) are other features that the Brazil Current (BC) has to overcome in the Vitória Trindade Ridge (VTR)

instability plays a supporting role after the growth has initiated. The unstable meanders present peak velocities exceeding 1.2 m s^{-1} . Moreover, as the growth occurs only in the cross-shelf direction, it can induce coastal divergence, which in turn enhances the coastal upwelling around the two capes (Calado et al. 2010; Palóczy et al. 2014). Organic matter is exported to the outer portions of the continental margin. No study about the ocean snow associated with the meander growth has been conducted so far.

As the Cape São Tomé meander grows, it may neck off and separate from the BC. Mill et al. (2015) analyzed 9 years of a satellite-derived sea surface temperature series to estimate that 2.5 events of unstably growing meanders occur per year. In their series, 72% of the unstable meanders end up reabsorbed by the BC. Only about 28% of these meanders are shed and become isolated rings, with 10% propagating south and 18% moving north. The authors also reported that the northward-moving rings can reach the Tubarão Bight, interact with the BC cyclonic loop and favor the VE formation or intensification. Those rings are detected due to the colder temperatures registered at the trapped waters inside them. The colder water is entrained by the eddy at shelf levels. These colder coastal waters are due to the coastal upwelling off Cape São Tomé. The eddy-trapping effect also captures nutrients and organisms from over the shelf. Pereira et al. (2019) carried out a simple theoretical study, which showed that once the eddy is shed, the vortical feature is capable of sustaining the plankton community inside it. This is due to an imbalance between upwelling on its leading edge and downwelling on its trailing edge, as the ring moves

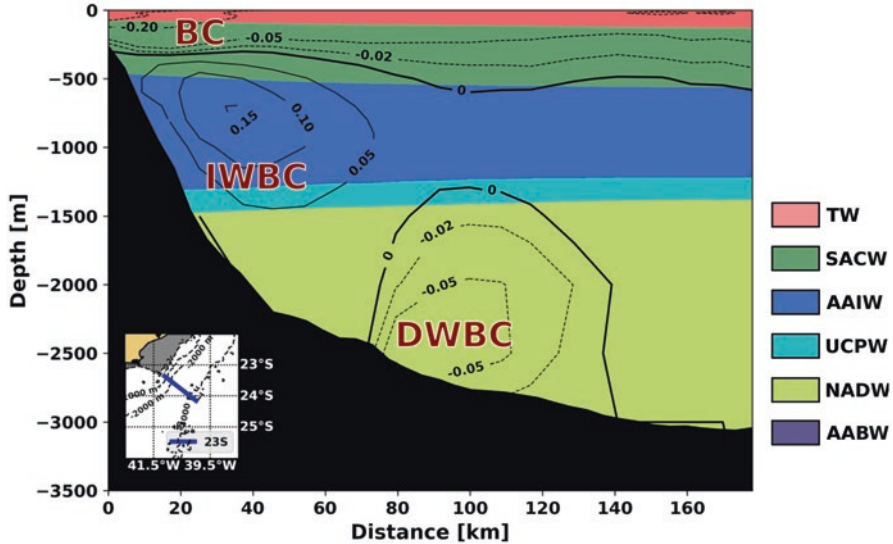


Fig. 2.12 Vertical section of a transect at 23°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The Brazil Current (BC) occupies the upper 380 m of the water column and transports Tropical Water (TW, in red) and South Atlantic Central Water (SACW, in dark green) southward. Underneath it, IWBC is depicted transporting Antarctic Intermediate Water (AAIW, in blue) and Upper Circumpolar Water (UCPW, in cyan) northward. The Deep Western Boundary Current (DWBC) is observed below 1500 m and carries North Atlantic Deep Water (NADW, in light green) toward the Antarctic Divergence

northward, which favors ascending velocities. Campos et al. (2000) pioneered in showing that BC meanders favored upwelling as they propagate along the shelf break. However, Pereira et al. (2019) considered a ring, where the coastal water supply is shut down by the necking-off process instead. They also used a simple nutrient-phytoplankton-zooplankton model to support their ideas and to explain the persistent higher chlorophyll content of those features, as depicted from sea color satellite images.

Further south, within the Santos Bight (23°S – 28°S; Fig. 2.13), another branch of the SEC feeds the BC in its way south. The subpycnoclinic sSEC bifurcates and adds AAIW to the BC (Böebel et al. 1999) at latitudes higher than 28°S. This additional contribution of volume deepens the current yielding a jet with 1500 m vertical extension (Rocha et al. 2014) and growth in volume transport (Schmid and Majumder 2018). This deep BC transports more than 18 Sv of TW, SACW, and AAIW (Stramma and England 1999; Schmid and Majumder 2018). This configuration is seen in Fig. 2.14, the BC and DWBC are virtually merged as one, and the whole water column in the western boundary layer flows poleward (Zemba 1991).

The “Santos Bifurcation,” as Böebel et al. (1999) named the subpycnoclinic sSEC bifurcation, sets up another important and unique feature of the BCM: the Intermediate Western Boundary Current (IWBC, see Fig. 2.12). This current was first predicted by Stommel (1965) as the intermediate response to the AMOC. The

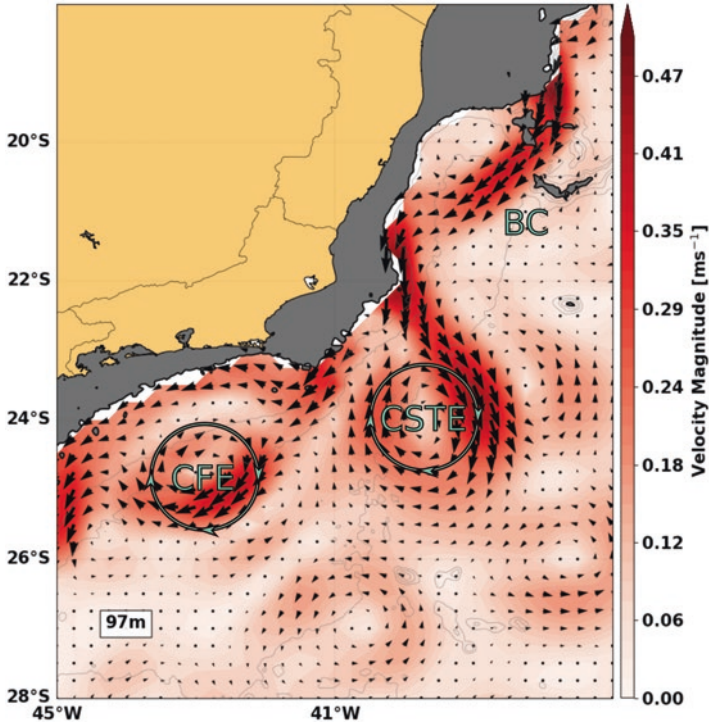


Fig. 2.13 An event of the baroclinically unstable, quasi-stationary Brazil Current (BC) meanders off Cape São Tomé (22°S) and Cape Frio (23°S). The so-called Cape São Tomé Eddy (CSTE) can neck off and form a vortical ring, which can be either reabsorbed by the BC or propagate offshore from its formation site, such as the Cape Frio Eddy (CFE) that is in this snapshot

IWBC flows equatorward carrying about 6 Sv of intermediate waters, namely, the AAIW and the UCPW, over its ~1200 m depth (Silveira et al. 2008). As the IWBC reaches the Tubarão Bight (21°S), it recirculates cyclonically, forming a stationary (and virtually steady) intermediate eddy (Legeais et al. 2013; Costa et al. 2017; Napolitano et al. 2019).

The southernmost portion of the BC is a region of high energy dissipation. From the Santos Bight, the warm and salty poleward current jet flows continuously until it encounters an equatorward current transporting cold and nutrient-rich waters. As aforementioned, at ~38°S, the MC collides with the BC forming an offshore jet, which is characterized by intense meandering, eddy-rich region. The Brazil-Malvinas Confluence is indeed one of the greatest dissipators of eddy kinetic energy in the globe (Maamaatuaiahutapu et al. 1994; Artana et al. 2019). The BC separation from the continental margin occurs in a convoluted manner: it retroflects by means of a large anticyclone and a spatially damped wave pattern toward the interior of the South Atlantic basin (Campos and Olson 1991; Silveira et al. 1999). The retroflection anticyclone is shed recurrently and represents a form of exporting organic matter and organisms from the subtropical gyre to subpolar water (Gordon

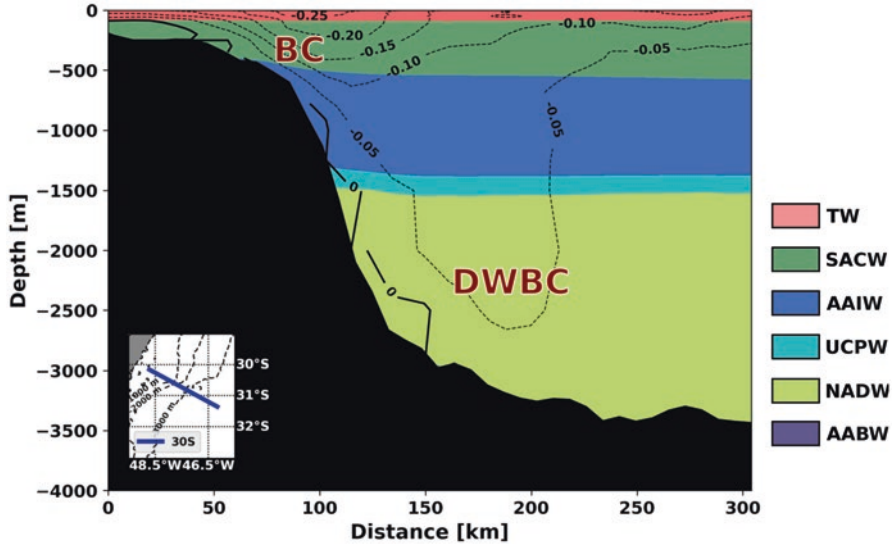


Fig. 2.14 Vertical section of a transect at 30°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The Brazil Current (BC) occupies the upper 1200 m of the water column and transports Tropical Water (TW, in red) and South Atlantic Central Water (SACW, in dark green) poleward and Antarctic Intermediate Water (AAIW, in blue), and Upper Circumpolar Water (UCPW, in cyan) equatorward. The Deep Western Boundary Current (DWBC), which carries North Atlantic Deep Water (NADW, in light green), virtually melds with the BC, yielding a 3000 m water column flowing southward

and Greengrove 1986). Reciprocally, the adjacent cyclone grows and is shed, but since its core is filled with subpolar water, it brings nutrients, organisms, and organic matter from subantarctic regions to the BC domain (Piola et al. 2000; Saraceno et al. 2004). The meandering jet initially form at the BCM site by both BC and MC splits as the former contours the Zapiola Rise from the north, and the latter from the south (Saraceno et al. 2004). The current formed and which closes the southern border of the South Atlantic Subtropical Gyre is known the SAC (Gordon 1981; Stramma and Peterson 1990).

2.3.2 The North Brazil Current System

The equator-flowing branch of the sSEC bifurcation at pycnoclinic level joins the underlying AAIW volume flux just north of the VTR (< 20°S). The IWBC crosses the ridge through two main passages between: (1) the Besnard and Vitória Banks and (2) the Congress and Jaseur Banks (Fig. 2.11). As mentioned in the previous section, the IWBC extends from 500 to about 1200 m. By adding the pycnoclinic northward-flowing bifurcated SEC branch, a new current is generated as it extends from 200 m to the base of the permanent pycnocline. This equatorward flow opposes

the shallow BC between 15°S and 20°S. Soutelino et al. (2013) considered this current a “North Brazil Undercurrent (NBUC) precursor.” The circulation pattern at the level of the NBUC core is shown in Fig. 2.5.

The NBUC was first described by the works of Silveira et al. (1994) and Stramma et al. (1995), and it is characterized as a fully developed and organized jet just north of the surface sSEC bifurcation, at about 15°S (in annual average terms). It transports about 30 Sv of TW, SACW, and AAIW equatorward in the upper 1200 m of water column (Schott et al. 2005). The NBUC presents a velocity core at the pycnocline (150–200 m, Stramma et al. 1995) and can be tracked by the salinity maximum observed just above it (Silveira et al. 1994). At 8°S, Fig. 2.15 captures an NBUC which is about 100 km wide, more than a 1000 m thick, and has peak velocities exceeding 0.8 m s⁻¹ at the pycnocline.

North of 5°S, the NBUC retroflects at subpycnoclinic level, forming a counter-current, which crosses the entire Tropical Atlantic in nearly zonal fashion, the South Equatorial Undercurrent (SEUC) (Fig. 2.16), as reported by Cochrane et al. (1979), Molinari et al. (1981), Silveira et al. (1994), and Schott et al. (1995). This retroflection, which is the southernmost of the four NBUC/NBC retroflections, will go through its path to the Caribbean (Figs. 2.16 and 2.17) and is probably linked to the veering of the BCM from a nearly meridional to a northeast-southwest orientation at Cape Calcanhar (~ 5°S; Fig. 2.1). As shown in Fig. 2.16, the current overshoots

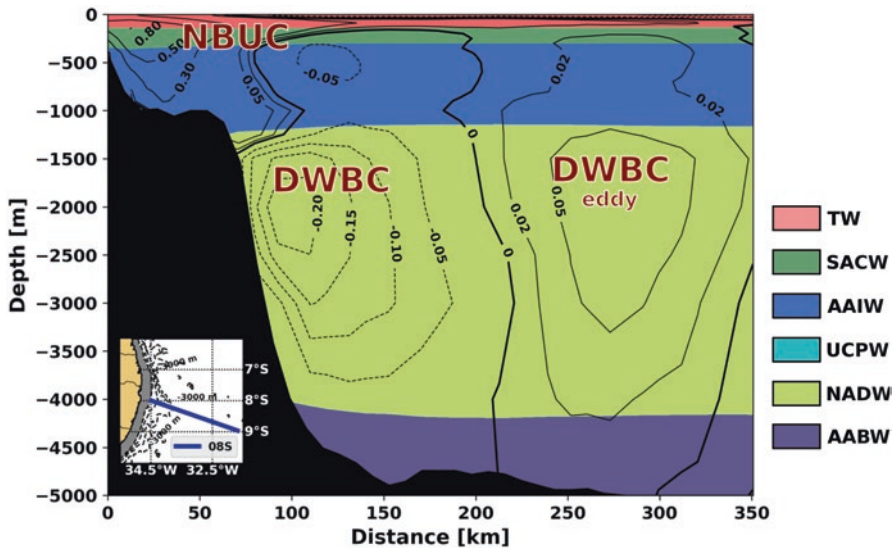


Fig. 2.15 Vertical section of a transect at 8°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The North Brazil Undercurrent (NBUC) is confined to the Pernambuco Plateau (~10°S) limits and has a vertical extension of more than 1000 m. The current transports Tropical Water (TW), the South Atlantic Central Water (SACW), and Antarctic Intermediate Water (AAIW) equatorward. The layer of deep water exhibits a section of a large, asymmetric anticyclone of the Deep Western Boundary Current (DWBC) heading poleward

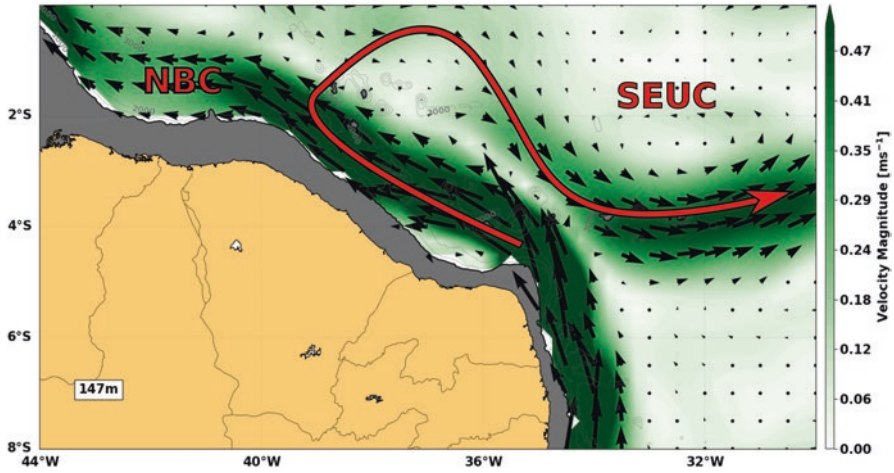


Fig. 2.16 Detail of the southernmost retroflexion of the North Brazil Undercurrent (NBUC) at about 5° S to feed the North Equatorial Undercurrent (NEUC) within the South Atlantic Central Water (SACW) domain

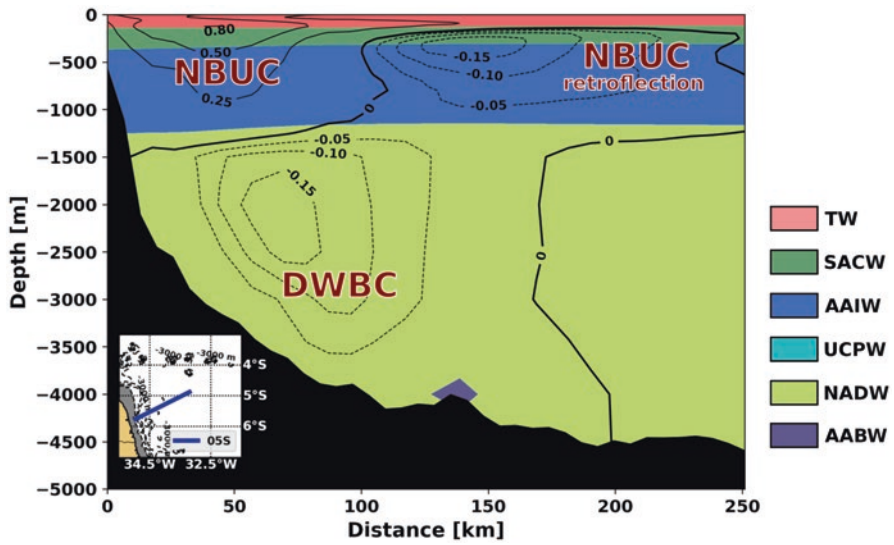


Fig. 2.17 Vertical section of a zonal transect at 5° S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The North Brazil Undercurrent (NBUC) southernmost retroflexion has two lobes with velocities of opposite direction. The oceanic lobe is weaker and feeds the North Equatorial Undercurrent (NEUC), indicating that only part of the NBUC jet loses volume due to the cyclonic loop. The NBUC transports Tropical Water (TW), the South Atlantic Central Water (SACW), and Antarctic Intermediate Water (AAIW) equatorward. The Deep Western Boundary Current (DWBC) is observed underneath the NBUC, adjacent to the continental slope and within the North Atlantic Deep Water (NADW) domain

its separation latitude of 4°S , suggesting that this phenomenon happens as consequence of the western boundary curvature and less intense velocities (if compared to the NBUC core) at lower SACW levels. On the other hand, upper SACW layers of the NBUC overcome Cape Calcanhar and recirculate anticyclonically at the Potiguar Bight (3°S – 5°S). This feature was recently described by Krelling et al. (2020) as a stationary and permanent NBUC frontal meander of elliptical form: the Potiguar Eddy ($\sim 4^{\circ}\text{S}$; Fig. 2.5). The NBUC surface layers are also able to contour Cape Calcanhar and reattach to the continental margin as they march equatorward.

The cSEC reaches the BCM at about 5°S and adds its entire transport to the NBUC. The sSEC is surface intensified with typical thickness of about 400 m (Silveira et al. 1994). This water volume strengthens the NBUC velocities in the upper layers. This is the opposite of what is observed in the NBUC subpycnoclinic layers, where transport decreases because of the volume losses associated with the 4°S subpycnoclinic retroflexion (Silveira et al. 1994). The NBUC vertical structure off Rio Grande do Norte and Ceará states ($\sim 3^{\circ}\text{S}$ – 6°S) depicts a jet with two velocity cores: a stronger one at surface and a weaker at pycnocline level (~ 200 m). Such pattern marks the transition of the NBUC to the NBC.

North of 2°S , the NBC/NBUC jet retroflects its upper pycnoclinic waters, as seen in Fig. 2.5, which undergoes a large anticyclonic loop which invades the northern hemisphere and bounces back to feed the eastward Equatorial Undercurrent (EUC, Goes et al. 2005). This retroflexion “erases” the pycnoclinic velocity core from the western boundary jet. The fully-formed NBC borders the Amazon shelf as a surface intensified current carrying 35 Sv (Fig. 2.18). It then faces its third retroflexion, forming a 400 km separation anticyclone at subpycnoclinic level, which is commonly referred in the literature as the Amazon Anticyclone (Cochrane et al. 1979; Bruce et al. 1985; Johns et al. 1990; Silveira et al. 2000b). This retroflexion feeds another nearly zonal countercurrent, the North Equatorial Undercurrent (NEUC). However, unlike its southern hemisphere counterpart at 4°S (seen in Figs. 2.15 and 2.16), this retroflexion can be unstable and can shed large anticyclonic rings. In the process of necking off the retroflexion bulge, the NBC subpycnoclinic layers are distended northward. According to Wilson et al. (2002), the rings formed in this process can be either solely subsurface rotating lenses or deep features, occupying the upper 1200 m of water column or more.

The fourth and northernmost NBC retroflexion occurs at about 6° – 8°N , therefore north of the BCM, and comprises surface and upper pycnocline waters. This retroflexion feeds the North Equatorial Countercurrent (NECC) which is the zonal jet that closes the so-called Equatorial Gyre (Mayer and Weisberg 1993). Its importance relies on the fact that anticyclones pinching off from the retroflexion lobe represent a mechanism of exporting upper-ocean waters from the southern to the northern hemisphere. The phenomenon is part of the AMOC upper limb (Johns et al. 1990; Fratantoni et al. 1995; Silveira et al. 2000b; Jochum and Malanotte-Rizzoli 2003).

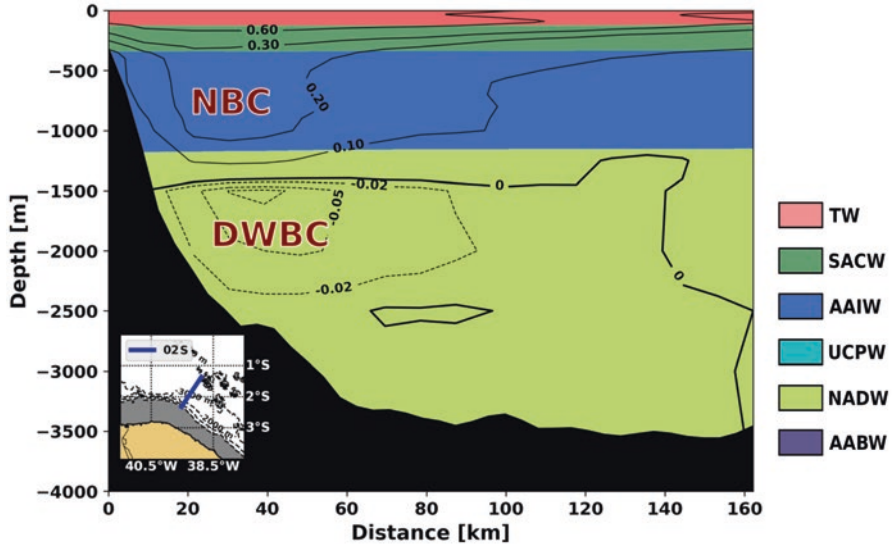


Fig. 2.18 Vertical section of a zonal transect at 2°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The surface-intensified North Brazil Undercurrent (NBC) will cross the equator with this vertical structure, a regular western boundary current. The NBC transports Tropical Water (TW), the South Atlantic Central Water (SACW), and Antarctic Intermediate Water (AAIW) and closes the Equatorial Gyre. The poleward-flowing Deep Western Boundary Current (DWBC) is observed underneath the NBC, adjacent to the continental slope and within the North Atlantic Deep Water (NADW) domain

2.3.3 The Deep Western Boundary Current

The DWBC is a formidable deep current which occupies the western boundary layer. The DWBC is formed just south of the Labrador Sea (70°N) and crosses the whole Atlantic Ocean carrying NADW towards the south pole (Tomczak and Godfrey 1994; Talley 2011). Once at that Southern Ocean, it upwells at the Antarctic Divergence (~60°S) and joins the ACC. Hence, the Atlantic Ocean exports NADW to the other two oceans via ACC. Therefore, it is necessary for the Atlantic Ocean to import upper-ocean and bottom waters to balance its mass and volume due to the NADW loss (Fig. 2.7). These outflows and inflows set up the AMOC, where the DWBC is in its main expression (Talley 2011; Wefer et al. 2012).

The DWBC enters the South Atlantic (Fig. 2.18), and consequently the BCM domain, carrying 20 Sv of NADW (Schott et al. 1993) poleward as part of the AMOC with velocities up to 0.2 m s⁻¹ (Fischer and Schott 1997). According to Dengler et al. (2004), the DWBC flows south-eastward along the South American continental slope and rise and veers southward just north of 5°S. The current then faces the Fernando de Noronha Seamount Chain (Fig. 2.1), which forces the DWBC jet to bifurcate during the crossing (Schott et al. 2003; Rhein and Stramma 2005). South of 5°S, the current is fully reattached to the slope and rise. By these latitudes,

slow and broad recirculations increase the DWBC transport which can reach virtually 40 Sv at 5°S (Schott et al. 2005).

As described by Dengler et al. (2004), between 8°S and 9°S, the DWBC has to contour the Pernambuco Plateau (Figs. 2.1 and 2.15). The abrupt change in the BCM orientation causes the current to meander and to break up in large, 400 km radius deep anticyclones. According to the same authors, these large eddies propagate southward along the Brazilian Eastern margin with typical translation speeds of 0.05 m s⁻¹. Figures 2.15 and 2.19 show a DWBC ring within the limits of the NADW. These anticyclones transport ~40 (25) Sv in their inner (outer) lobes (Schott et al. 2005). The difference in strength between the lobes was thought to be an artifact of the sampling strategy by Dengler et al. (2004) and Schott et al. (2005). However, it is more likely that this asymmetry is a result of an underlying residual DWBC flow.

The DWBC eddies flows poleward until reaching the Abrolhos Ridge (17°S) and the Hotspur Seamount (18°S) where they are destroyed (see Fig. 2.19). The DWBC deflects east by the presence of the VTR, as described by Garzoli et al. (2015). According to these authors, part of the DWBC carrying about 70% of its transport finds its way through the VTR passage between Seamount Columbia (~32°W) and Trindade Island (~29°W). This portion veers cyclonically just south of the VTR, reattaching the current to the western boundary, and flows poleward, as seen here in

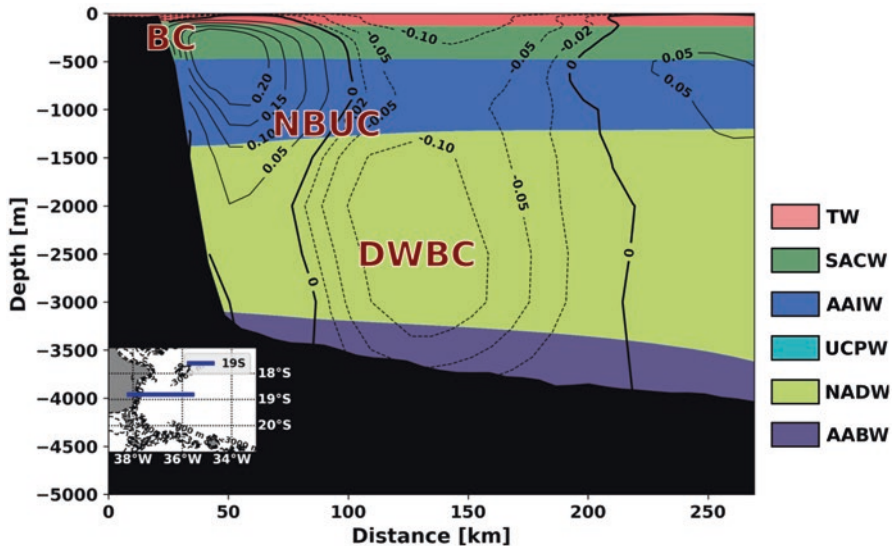


Fig. 2.19 Vertical section of a transect at 19°S (see Figs. 2.4, 2.5, 2.6, 2.7, and 2.8 for its position on the map). The Brazil Current (BC) is depicted as a shallow flow occupying only the upper 150 m and transporting only Tropical Water (TW) southward. Underneath it, NBUC almost completely formed, transporting South Atlantic Central Water (SACW) and Antarctic Intermediate Water (AAIW) in the opposite direction. The layer of North Atlantic Deep Water (NADW) exhibits the southward flowing Deep Western Boundary Current (DWBC)

Fig. 2.7. The same authors affirmed that the other 30% crosses the Atlantic Basin zonally and attaches itself to the eastern boundary. Very little is known in terms of the DWBC mesoscale variability between 20°S and 35°S to date. Meinen et al. (2012) reported variations on the DWBC transport at 34.5°S as large as the mean value of about 40 Sv from an inverted echo sounder array.

2.3.4 A Brief Synthesis

The BCM and adjacent abyssal plain has unique current and water mass set up among all western boundary current regimes in the world. Six boundary currents and six main water masses contribute to this rich, yet far from known system, responsible for motor biological ecosystems through all water column. Figure 2.20 presents a schematic synthesis of boundary currents and water masses along the whole BCM and adjacent abyssal plain. The thickness of the arrows is proportional to the volume transport. The meridional representation aims to give the reader a global sense of the currents' vertical shear and change in current direction, as well as of the formation sites associated with the divergence of the sSEC bifurcations.

It is clear that geostrophic currents greatly affect the pelagic communities. At last, it is worth mentioning that ocean dynamics may interfere in benthic communities as well in a great number of processes. Spatial distribution as well as temporal fluctuations in the structure of benthic communities are intrinsically connected not only the biotic factors, but also to hydrographic properties (e.g., temperature and salinity) and hydrodynamics (e.g., ocean currents, turbulence) (Gray 2002;

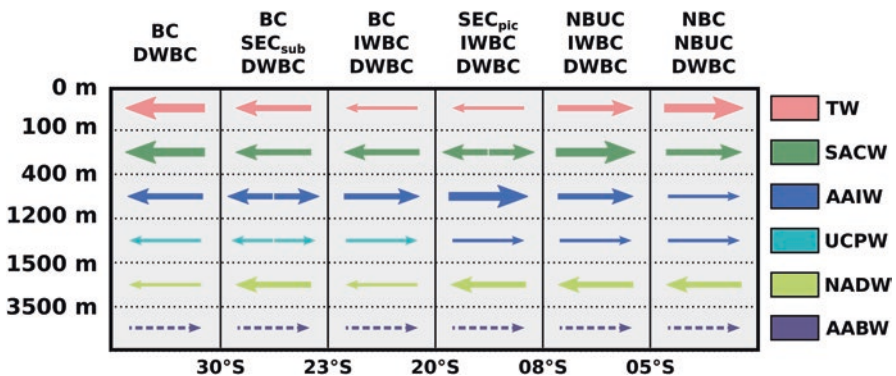


Fig. 2.20 Summary of currents and water masses along the Brazilian Continental Margin (BCM). SEC_{pic}, SEC at pycnoclinic level; SEC_{sub}, SEC at subpycnoclinic level. Arrows pointing right represent equator flow, whereas arrows pointing left represent poleward flow. The width of each arrow represents the relative intensity of the current. The colors represent, respectively: Tropical Water (red), South Atlantic Central Water (green), Antarctic Intermediate Water (blue), Upper Circumpolar Water (cyan), North Atlantic Deep Water (Yellow), and Antarctic Bottom Water (purple). (Adapted from Sousa 2017)

Piepenburg 2005). Ocean currents may transport or favor the settlement of those organisms, especially in the larval stage (Scheltema 1986). Pineda et al. (2009) also exemplify ocean current interference with benthos, namely, favoring/hindering of predation and food availability, physical larval transport causing a change in their behavior, and interaction with the substrate increasing/decreasing its availability.

Before concluding, we must address the predicted changes in a warming ocean both in hydrodynamic and hydrographic properties. Using climate models, several studies have been conducting projections on global circulation due to climate change. Since the conditions of the Ocean Current systems of the region can dictate the composition, structure, and abundance of benthic communities, climate change may play an important role in altering the current parameters in the South Atlantic Ocean and, consequently, the BCM.

Pontes et al. (2016) suggest that the increasing trend global warming via greenhouse effect may alter the volume transport of the ocean current system in the South Atlantic mainly due to the climatological wind regime according with the compiled outputs of 19 climate models from the Coupled Model Intercomparison Project phase 5 (CMIP5). A weakening of the net transport in the upper oceans compensated by the decreasing of transport in the deep circulation, whereas the BC tends to accelerate in the portion between the 30 ° and 40 °S based on an 80-year projection (Pontes et al. 2016). The acceleration of global circulation due to the intensification of surface winds over the past 20 years is already confirmed by Hu et al. (2020) that used several sources of observations, model reanalysis, and model simulations. Toste et al. (2018) also used the CMIP5 to describe a northward displacement of the BC region of formation as well as an increase of 1.4 °C of the mean values of sea surface temperatures in the next 80 years. It is important to highlight that those projections are based solely on simulations. Nevertheless, changes in the global ocean circulation and the marine ecosystem due to global warming are impending.

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Chapter 3

Continental Slope and Submarine Canyons: Benthic Biodiversity and Human Impacts



Fabio Cabrera De Leo, Angelo Fraga Bernardino,
and Paulo Yukio Gomes Sumida 

Abstract The Brazilian Continental Margin hosts a diverse deep seafloor landscape including vast areas of sedimented slopes, submarine canyons, reef-forming and solitary cold-water corals, methane seeps and pockmarks, seamounts, and guyots. The vast biodiversity associated with deep-sea benthic habitats remain largely undescribed with only a few, mostly descriptive, research programs established in the S and SE margins beginning in the late 1990s. These programs, in particular the REVIZEE – Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone – focused primarily on inventorying species lists and standing stock biomass of commercially exploited species to generate guidelines for a nationwide resource management strategy for Brazil’s EEZ. The poorly described nature of Brazil’s deep-sea habitats and benthic fauna can be clearly illustrated if we consider that only 4 (2.5%) out of 161 existing submarine canyons had benthic communities sampled and investigated to this date. Another indication of a poorly described deep-sea biodiversity along the Brazilian margin is verified by the limited number of species occurrence records for the SW Atlantic in the Ocean Biogeographic Information System (OBIS) database, representing only 0.06% of the global deep-sea species occurrence records below 500 m. Most deep-sea biodiversity currently described in Brazil comes from sedimented slopes and from upper to mid slope depths in the S-SE margin. Currently, sampling efforts remain largely concentrated on Campos and Santos Basins, and in the context of baseline and environmental impact assessments (EIAs) contracted by the oil and gas industry. Very few

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studies have dealt with cold-water coral communities, and virtually none has investigated seamount faunas deeper than 150 m. Only very recently, reports have described deep-sea faunas associated with pockmarks, methane seeps, and naturally occurring organic falls (all focus of other chapters in this book). Therefore, the current knowledge on Brazil's deep-sea fauna comes largely from soft-bottom benthic meio- and macroinfaunal communities. Overall depth-related distributional patterns of benthic assemblages on the slope are in relatively good agreement with patterns found for the N Atlantic, with high species diversity and biomass found on the upper slope as well as near upwelling areas on the SE margin. Also, species richness of combined macro- and megabenthos decreases from the SE towards the S margin, spanning 15° of latitude South (i.e., 21–34°S). The peer-reviewed scientific literature describing Brazil's Margin deep-sea environments remains scant, with the majority of recent findings and data repositories still inaccessible from the general public, and available only through gray-literature reports from various baseline and EIA assessments. Currently, the human impact footprint on Brazil's Margin is derived mostly from the oil and gas and deep-water fishing industries, with no systematic studies to date addressing the negative impacts of these activities on the various deep-sea habitats. Future human-related impacts on Brazil's Margin deep-sea biodiversity will also come from long-term climate change effects (predominantly ocean acidification) in accordance with modeling studies, from the offshore oil and gas industry, and potentially from deep-sea mining.

Keywords Continental slope · Submarine canyons · Brazilian margin · Benthic biodiversity · EEZ · Human impacts

3.1 Introduction

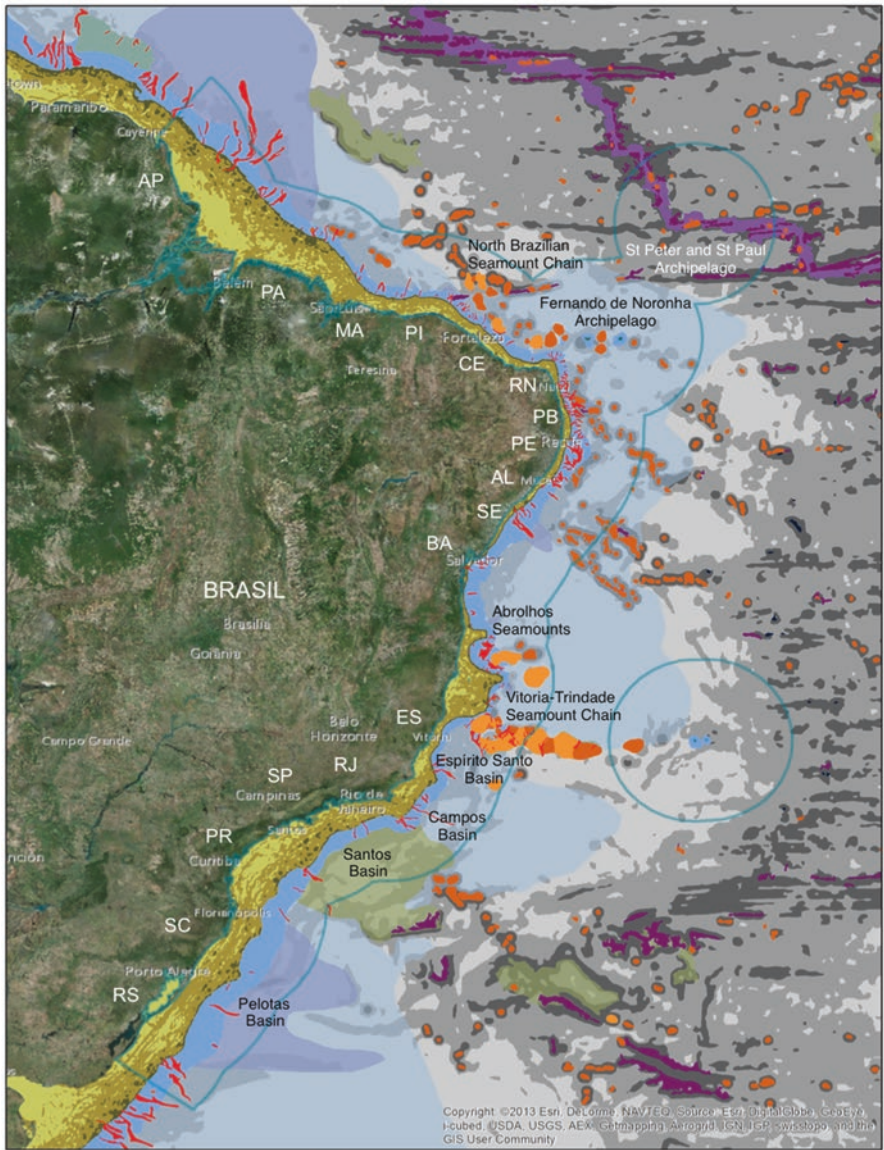
The continental margin is one of the most extensive marine landscapes within Brazil's Economic Exclusive Zone (EEZ) and supports a wide range of marine ecosystems and mineral resources. However, despite its ecological, social, and economic importance, the Brazilian deep margin is among the least studied and monitored marine ecosystems. At depths below 200 m, a number of ecosystems hosting unique biological communities thrive under low temperatures, high hydrostatic pressure, and overall low organic input. The deep-sea assemblages on continental margins have been widely recognized as important to overall ecosystem health and function, with increasing vulnerability to human impacts (Ramirez-Llodra et al. 2010, Levin and Sibuet 2012). Despite their unique importance, our knowledge of the biodiversity, ecosystem function, and overall health of Brazil's deep-sea ecosystems have historically been limited to taxonomic studies in areas of particular commercial or industrial interest. Here we review the published literature on deep-sea ecosystems of the Brazilian continental margin and their associated biological communities with focus on benthic organisms. We also evaluate the

vulnerability of deep-sea ecosystems with respect to ongoing and future anthropogenic activities and impacts, describing a few already implemented strategies in resource and ecosystem management, and future desired conservation strategies.

Brazil has a large deep-sea continental margin (hereafter called Brazil's Margin, Sumida et al. [this volume](#), Chap. 1, Fig. 1.1), which hosts a number of typical benthic ecosystems that are typical of other continental margins worldwide (Fig. 3.1). Soft-sediment slopes, frame-building deep-water corals, cold seeps, submarine canyons, sponge beds, and hard-bottom cliffs are among the geological and biological substrates occurring on Brazil's margin. Although clearly understudied, there are over 160 submarine canyons on Brazil's Margin, with remarkable and extensive canyon systems near the Amazon delta in the north, and off the Rio de La Plata river in the southern margin (Nittrouer and DeMaster 1986). Some shelf-incising canyons connect the shelf-break to the deep slope often reaching 2000 m depth. Seamounts and guyots (flat top seamounts) are also relatively abundant features on the eastern and northern margins, although contributing to a small percentages of total Brazil's EEZ (Fig. 3.1 and Table 1.1 in Sumida et al. [this volume](#), Chap. 1). At the Eastern margin, the Vitória-Trindade Seamount Chain is the longest seamount chain in the South Atlantic, which is located along a transform fault with previous volcanic origin (Skolotnev et al. 2010). At the northern margin, the Fernando de Noronha archipelago, the St. Peter and St. Paul rocks, and the North Brazilian Seamount Chains are also distinctive topographic features (Fig. 3.1). A total of 123 seamounts and 13 guyots occur in Brazil's margin, with virtually no information available on their associated deep-sea ecology. The Vitória-Trindade Seamount chain has been generally characterized with respect to its biological (benthic) communities, however only at the upper 150 m (O'Hara et al. 2010).

The São Paulo Plateau and the Campos and Santos Basins are the most well-mapped and studied areas in the Brazilian margin in terms of seafloor geomorphology and physical oceanography as well as of benthic and pelagic standing stock biomass and overall biodiversity. Most oceanographic studies to date have been carried out in the S-SE Brazilian margin, which is near several research and academic institutions that have been funded through collaborative and interdisciplinary programs devoted to study deep-sea communities at shelf break and slope depths (Sumida and Pires-Vanin 1997; De Leo 2013; Amaral and Rossi-Wongtschowski 2004; Capítoli and Benvenuti 2004; Capítoli and Benvenuti 2006, Bernardino et al. 2016; Lavrado et al. 2017a, b). Additionally, those basins have historically concentrated Brazil's largest offshore oil and gas operations, and therefore most seafloor mapping and environmental monitoring programs occurred there through industry funding. In the early 2000s, additional international petroleum companies have initiated their activities in Brazil and started funding their own exploration and production activities, spurring new deep-sea monitoring initiatives (Machado et al. 2004; Schreiner et al. 2008, 2009; de Almeida and Kowsmann 2014).

In the Southwest Atlantic, limited funding and logistical constraints such as the lack of availability of research-devoted deep submergence vehicles (i.e., ROVs and submersibles) have contributed to a significantly reduced sampling effort of deep-sea marine biodiversity when compared to other well-studied Atlantic basins to the



- | | | | |
|------------------------|--------------|-----------------|---------|
| Shelf - high profile | Hadal canyon | shelf valley | rise |
| Shelf - medium profile | guyot | rift valley | terrace |
| Shelf - low profile | seamount | glacial trough | trench |
| Slope | bridge | trough | plateau |
| Abyss - mountains | sill | ridge | |
| Abyss - hills | escarpment | spreading ridge | |
| Abyss - plains | | fan/apron | |

Fig. 3.1 Seafloor geomorphological features along Brazil's EEZ (green-line polygon). Inner and outer continental shelf, light and dark green; slope, blue; submarine canyons, red; seamounts, dark orange, guyots, light orange; submarine fans, purple; continental rise, light blue. (Brazil's states with ocean borders: AP, Amapá; PA, Pará; PI, Piau; MA, Maranhão; CE, Ceará; RN, Rio Grande do Norte; PB, Paraíba; PE, Pernambuco; AL, Alagoas; SE, Sergipe; BA, Bahia; ES, Espírito Santo; RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RG, Rio Grande do Sul)

North (Sumida and Pires-Vanin 1997; Levin and Gooday 2003). In spite of these limitations, a few large-scale deep-sea biodiversity assessments have allowed sampling efforts along the deep slopes along the Brazilian margin (Netto et al. 2005; Bernardino et al. 2016; Lavrado et al. 2017a, b). In the next sections, we describe the current knowledge available on deep-sea benthic community studies, summarizing overall community structure, abundance, and biodiversity patterns in areas of the slope.

3.2 Biodiversity of the Deep-Sea Margin

The biodiversity of the deep ocean is notoriously less studied when compared to highly accessible and more thoroughly sampled coastal and continental shelf areas (Smith et al. 2008; Thurber et al. 2014). Perhaps for this reason there is still a heated debate in the scientific literature as if deep-sea biodiversity is higher, comparable, or lower than in shallow water and terrestrial environments (Hessler and Sanders 1967; Grassle and Maciolek 1992; Gray 1994). Nonetheless, the scientific community seem to agree upon the existence of high levels of species diversity in the deep-sea besides harsh environmental conditions that include low temperatures, high-pressure, absence of light and very limited autochthonous primary productivity (Rex and Etter 2005; McClain and Schlacher 2015).

Globally, nearly ~1.3 million marine species occurrence records from 158,000 unique sampling coordinates, and depths between 500 and 10,897 m, have been catalogued by the Ocean Biogeographic Information System (OBIS, www.iobis.org; Fig. 3.2a). This number represents a modest 3% of all records of marine species (excluding Bacteria, Archaea, Fungi, Plantae, and Protozoa) when shallow coastal and shelf areas are also considered. This is not surprising considering that only 1% of the deep ocean, including the seafloor and the deep pelagic realm, has been sampled (Webb et al. 2010; Appeltans et al. 2012). For the Brazilian Continental Margin below 500 m and extending to the EEZ border (seafloor and water column combined), an even more modest number of approximately 26,000 unique species occurrences have been catalogued in the OBIS database, which is only 0.06% of the global deep-sea occurrence records below 500 m depth (Fig. 3.2b). Albeit those numbers are likely an underestimation of species records along Brazil's deep-sea margin, as not all species occurrences have been entered in the OBIS database, they still highlight the limited number of studies reporting deep-sea marine biodiversity along Brazil's deep margin.

Following international conventions, Brazil has started to address its deep-sea continental margin diversity in early 1990s through the REVIZEE program (Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone). This program intended to map and quantify resources (biological, mineral) and the marine biodiversity within Brazil's EEZ, an area of 3.5 million km². The REVIZEE program was a landmark for deep-sea exploration of Brazil's upper slope (200–800 m) and provided the first broad scale publicly available

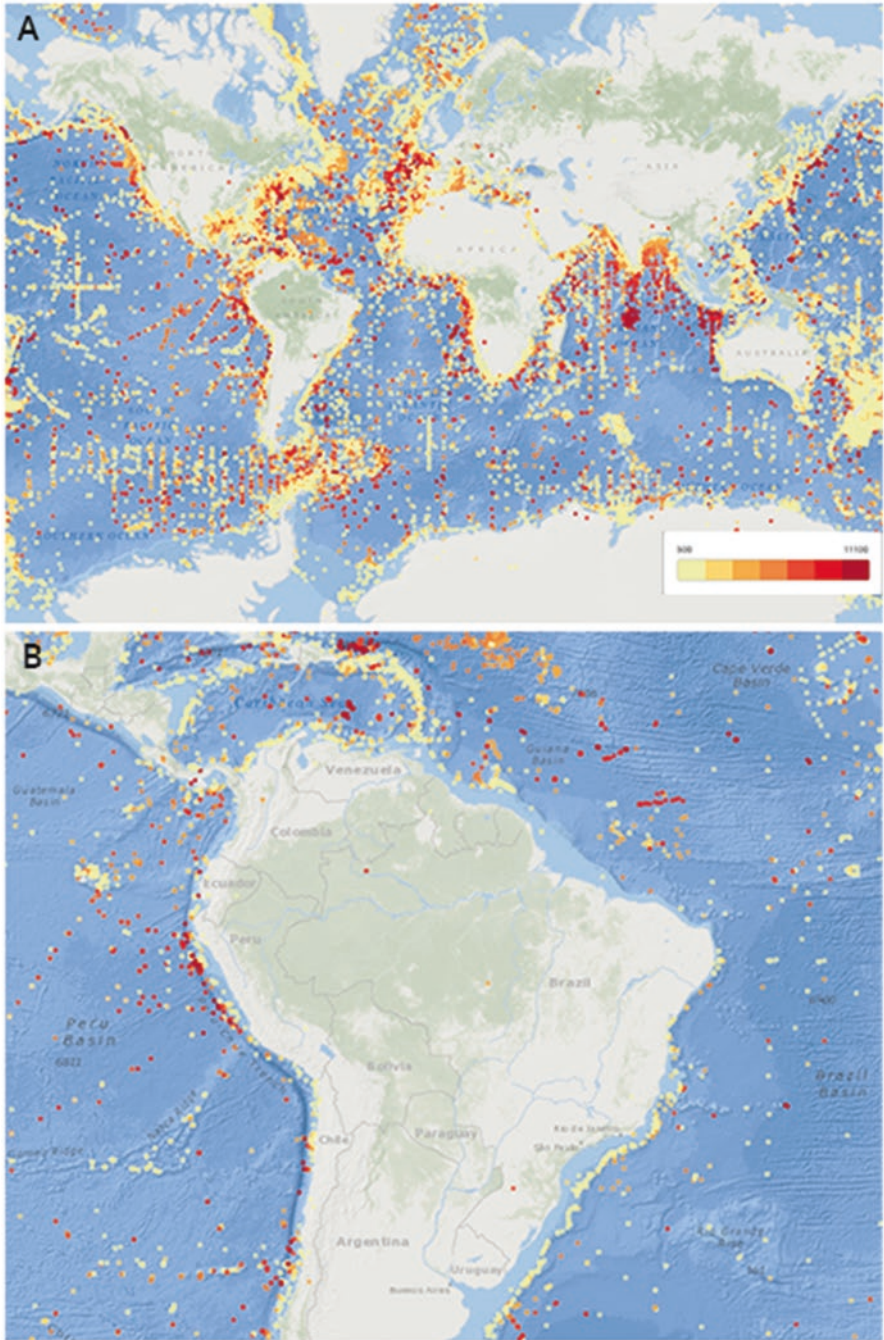


Fig. 3.2 Unique positions with species occurrence records currently in the Ocean Biogeographic Information System (OBIS) database, at depths ranging from 500 to 10,897 m (maps provided by D. Appeltans, IOC-UNESCO). (a) Worldwide records. (b) Records off Eastern and Western South America highlighting the low number of catalogued deep-sea species occurrences off the Brazilian Continental Margin. Color-coded legend represents number of occurrence records

scientific assessment of deep-sea benthic and demersal biodiversity in the South Atlantic (Amaral and Rossi-Wongtschowski 2004; Bernardes et al. 2005a, b; Perez et al. [this volume](#), Chap. 8). Despite the extensive geographical coverage of that sampling program, the temporally discrete and fragmentary nature of the sampling (sometimes only a single sample in each station) precluded robust ecological analyses. Additionally, taxonomic descriptions were typically limited given the concentrated sampling effort, thus spatial patterns and estimates of total species richness remained unresolved. Nevertheless, the scope of the REVIZEE program was mostly centered in drawing a first baseline assessment of overall benthic abundance and diversity by large taxonomic groups, for the purpose of establishing future biomass stock assessments (of commercially important species) and monitoring strategies (see Perez et al. [this volume](#), Chap. 8).

Given its abundant offshore oil and gas reservoirs, the Campos Basin on the SW Atlantic is a well-studied deep-sea basin off Brazil with respect to its seafloor biodiversity and natural resources. Exploration and production licenses since the mid-1990s have been allowing both baseline and monitoring studies to gather data on soft-bottom benthic fauna (Costa et al. 2015), with a few studies addressing the biodiversity of cold-water coral communities (Cavalcanti 2013; Cavalcanti et al. 2017; Arantes et al. 2009), and the impacts associated with offshore drilling operations (Netto et al. 2009; Santos et al. 2009; Lavrado et al. 2017a, b). Other basins with recent interest in offshore oil and gas exploration have also been moderately investigated, with a few studies addressing overall environmental and ecosystem health (Carreira et al. 2010; Bernardino et al. 2016). From the abovementioned baseline and monitoring initiatives, much of the described benthic species record inventories and geographic ranges remain mostly available through technical reports, with a very small fraction published in the peer-reviewed scientific literature.

3.2.1 Slope Benthic Ecosystems

3.2.1.1 Patterns of Faunal Abundance and Species Richness

Global spatial and temporal patterns in deep-sea species diversity related to latitudinal and bathymetric gradients have been constrained for several ocean basins (Rex 1983; Carney 2005). Although most sampling efforts have concentrated in continental margins and ocean basins of the North Atlantic, Northeast and Northwest Pacific, and Indian Oceans, overall bathymetric patterns of benthic diversity in the South Atlantic continental margin share some commonalities with patterns observed worldwide (Levin et al. 2001; Levin and Gooday 2003; Carney 2005; Rex et al. 2005; Menot et al. 2010). Off Brazil, broad latitudinal and bathymetric benthic abundance and biomass patterns were derived from the “REVIZEE-Southern Margin” program, where sampling was stratified by depth (< 100, 100–200; 200–300; 300–500, and > 500 m) and latitudinally covering at least three deep-sea basins, including Campos, Santos, and Pelotas. The program collected 131,369

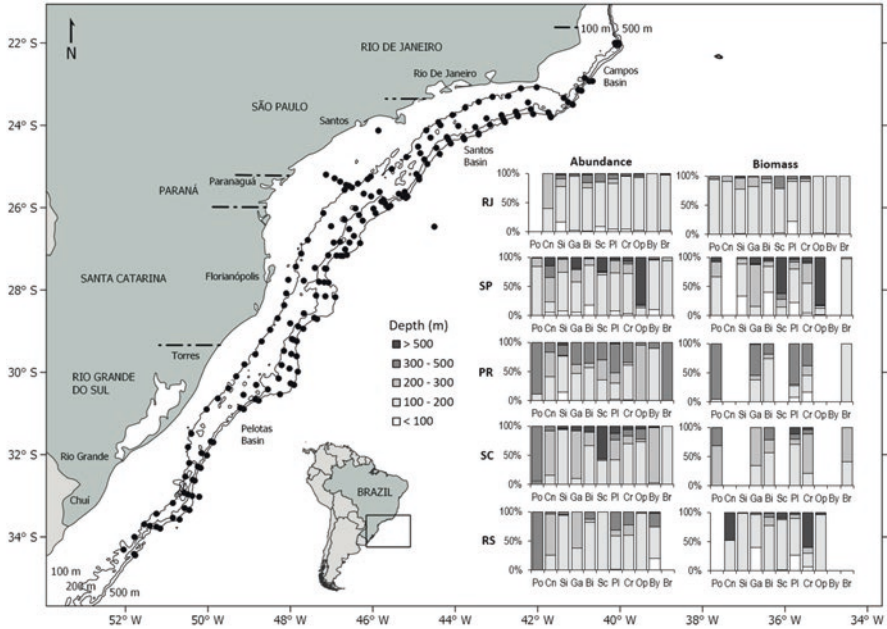


Fig. 3.3 Map with sampling grid of REVIZEE program along Brazil's S and SE margin. Bar charts represent combined macro and megabenthic relative abundances by main taxonomical groups (left) and biomass (right) in different depths. Po, Porifera; Cn, Cnidaria; Si, Sipuncula; Ga, Gastropoda; Bi, Bivalvia; Sc, Scaphopoda; Pl, Polychaeta; Cr, Crustacea; Op, Ophiuroidea; By, Bryozoa; Br, Brachiopoda. RJ, Rio de Janeiro; SP, São Paulo; PR, Paraná; SC, Santa Catarina; RS, Rio Grande do Sul. (Modified from Amaral and Rossi-Wongtschowski 2004)

individuals of macro- and megabenthos distributed among 28 higher taxa, and 1035 species and morpho-species combined (Amaral and Rossi-Wongtschowski 2004). Fish species were excluded from the analysis, and faunal abundance and biomass data were presented by combining samples from three remote samplers (van Veen grabs, box-corers, and a beam trawls) within a single station. Results were always presented for the most frequent and abundant higher taxonomic groups: Porifera, Cnidaria, Sipuncula, Gastropoda, Bivalvia, Scaphopoda, Polychaeta, Crustacea, Ophiuroidea, Bryozoa and Brachiopoda (Fig. 3.3). Overall, the program described a rich benthic fauna with higher abundances occurring in muddy and fine sand substrates with low biogenic carbonate contents.

Off Campos Basin, a very small proportion of the benthic relative abundance and biomass were associated with depths below 300 m. However, this basin received a considerably smaller sampling effort during the REVIZEE program when compared to the other regions. Further south, the remaining basins had specific taxa with high relative abundances and biomass in the 300–500 and > 500 m depth strata. In Santos Basin in particular, Scaphopoda and Ophiuroidea were relatively abundant at >500 m; and in some areas, Porifera, Brachiopoda, and Scaphopoda had high relative abundances at 300–500 m. Finally, in Pelotas Basin, Porifera was

abundant at 300–500 m, while Cnidaria dominated at >500 m. In general, no clear bathymetric patterns of relative abundance were evident for most megabenthic groups (Fig. 3.3). However, there were notable differences in benthic community structure at a higher taxa level across deep-sea basins, with Porifera, Ophiuroidea, Bryozoa, and Brachiopoda predominant off Santos Basin, whereas Crustacea were dominant on Campos Basin and Cnidaria, Gastropoda, and Scaphopoda abundant in Pelotas Basin.

Multivariate clustering and ordination analysis revealed that the most important environmental variables driving these broad-scale community structure patterns were related to seafloor sediment heterogeneity. Water mass parameters such as temperature, salinity, and dissolved oxygen did not have strong influence in determining faunal assemblages. This is likely due to the fact that the South Atlantic Central Water (SACW), flowing southward along the margin and overlying the seafloor at shelf-break and slope depths down to 500 m, has relatively homogeneous and stable conditions (Castro-Filho et al. 2015; Silveira et al. [this volume](#), Chap. 2). Faunal groupings, characteristic of Santos Basin slope, were correlated with more homogeneous seabed conditions, with sediments mostly composed by high mud and low carbonate contents. In Campos Basin shelf-break and slope, a unique and diverse assemblage was found associated with substrates composed of a mixture of coarse sands, gravel, and patches of fragmented branching calcareous algae and dead rhodoliths. Overall, more diverse assemblages were found in areas with medium-grain-sized sediments (Amaral and Rossi-Wongtschowski 2004).

A few other oceanographic research programs also collected somewhat sparse samples at shelf-break and slope depths in S-SE Brazil. The Oceanographic Institute of the University of São Paulo (IO-USP) studied benthic assemblages offshore Ubatuba (Santos Basin), from 130 to 600 m (Sumida and Pires-Vanin 1997). Sharp boundaries separating species assemblages along the bathymetric gradient were detected based upon 15 rectangular dredge tows, each 15 min in duration, up slope, and at 1 knot speed. Despite a total of 464 unique taxa being identified in the study, only 56 with higher occurrence frequencies were used in further community analysis. Clustering of species and canonical correspondence ordination analysis revealed that assemblages were tightly linked to different depth strata (Fig. 3.4). The authors discussed their results in light of previously established deep-sea faunal zonation patterns described for the North Atlantic at the benchmark Gay Head-Bermuda transect (Grassle et al. 1979; Rex 1981). In particular, Sumida and Pires-Vanin (1997) suggested the 500 m isobath as the upper limit of true deep-sea fauna in the area. However, they also highlighted some of the caveats related to the sparse nature of the sampling program (only 15 dredge tows in an area roughly of 0.01 km²), as well as with the lack of ground-truthing of seafloor sediment grain-sized and organic matter composition, both precluding strong inferences about environmental influences on benthic assemblages other than the pure bathymetric gradient.

The TALUDE Project coordinated by the Federal University of Rio Grande (FURG) was another initiative during the late 1980s that studied the distribution of benthic communities from the coastal inner shelf (11 m) to the upper slope (500 m) depths offshore the southern Brazilian margin (Pelotas Basin, Capítoli and Benvenuti

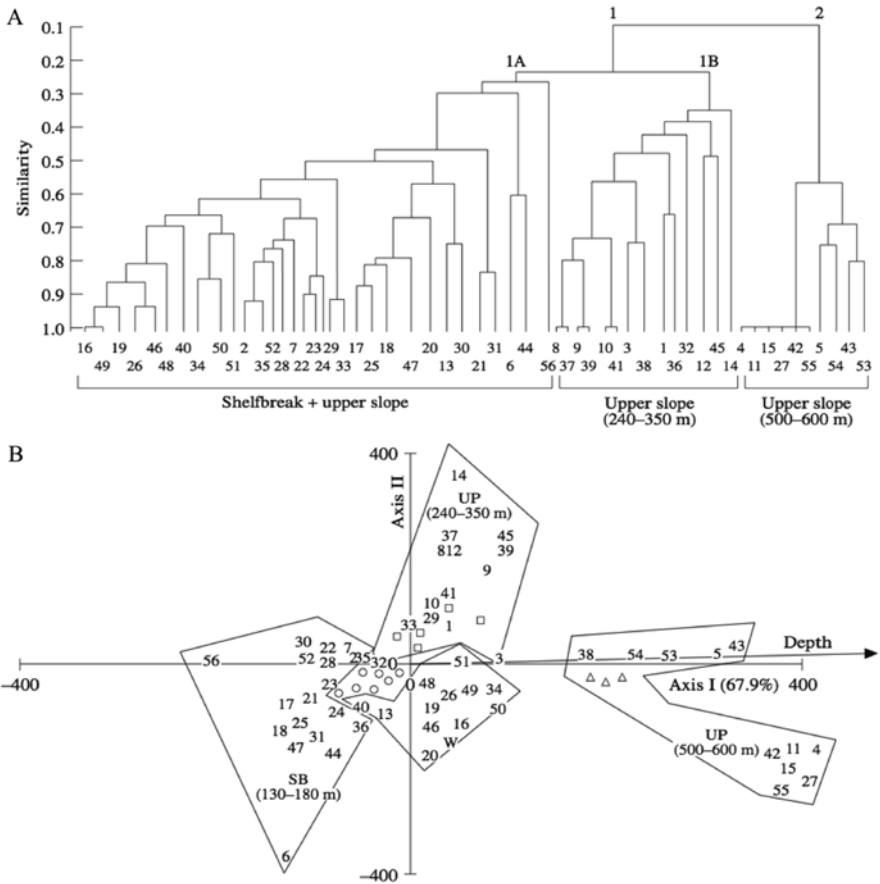


Fig. 3.4 (a) Cluster analysis output based on species presence-absence data from 15 rectangular dredge tows (UPGMA-Jaccard Similarity Coefficient – numbers 1–56 represent species with higher occurrence frequencies selected for the analysis) (b) Canonical Correspondence Analysis (CCA) showing main faunal groupings (SB, shelf break; UP, upper slope; W, wide bathymetric distribution). Circles, shelf break stations; squares, upper slope (240–350 m); triangles, upper slope (500–600 m). Modified from Sumida and Pires-Vanin (1997)

2004, 2006). The sampling program spanned from 1986 to 1993 and, similarly as the above example from Santos Basin, also employed a rectangular dredge, although with slightly smaller frame size (0.3 × 1 m), half the size of the cod end mesh (i.e., 5 mm), and much shorter tows, lasting only 2 min. A total of 127 stations were sampled, but only 14 with depths between 200 and 500 m. Even though the dataset in Capitoli and Benvenuti (2004, 2006) encompassed a wider bathymetric range and a larger sampling effort in the slope, the authors found lower species richness (320 species) off Pelotas compared to the Santos basin slope studied in Sumida and Pires-Vanin (1997). The authors suggested that at least for the SE-S Brazilian upper

continental slope, benthic macro- and megafauna species richness diminishes southwards from 21° to 34° of latitude South.

More recently, baselines of megabenthic and demersal fish assemblages were carried out on Campos Basin from shelf waters down to slope depths of 2000 m. Results were based on 42×15 m otter trawl hauls with a 6.3 m^2 effective net mouth area, with 18 hauls conducted over the slope (376–2030 m, Costa et al. 2015; Lavrado et al. 2017a; Fig. 3.5a). Overall, 452 species were recorded, with teleosts, crustaceans, and echinoderms representing 92% to the total number of taxa. Megabenthic density (Fig. 3.5b) and biomass peaked in the upper slope (300–500 m), despite the fact that sample effort was much smaller in this depth stratum due to the presence of rhodolith beds and hard bottoms including deep coral reefs (Table 3.1). Most abundant taxa at those depths were the sea urchin *Stylocidaris lineata* (330 ind.km^{-2}), penaeid shrimps *Penaeopsis serrata* (217 ind.km^{-2}) and *Parapenaeus politus* (104 ind.km^{-2}), and squat lobster *Agonida longipes* (112 ind.km^{-2}). At mid-slope depths (1000–1200 m), the megafauna was dominated by the shrimp *Benthescymus barletti* (216 ind.km^{-2}) and squat lobster *Munida microphthalma* (37 ind.km^{-2}). Finally, in the lower slope (1900–2000 m), the isopod *Acutiserolis coineauae* (77 ind.km^{-2}) and the ophiuroids *Ophiomusium eburneum* (32 ind.km^{-2}) and *Ophiosphalma* cf. *armigerum* (17 ind.km^{-2}) dominated the fauna (Costa et al. 2015). The benthic megafauna community structure was largely governed by water

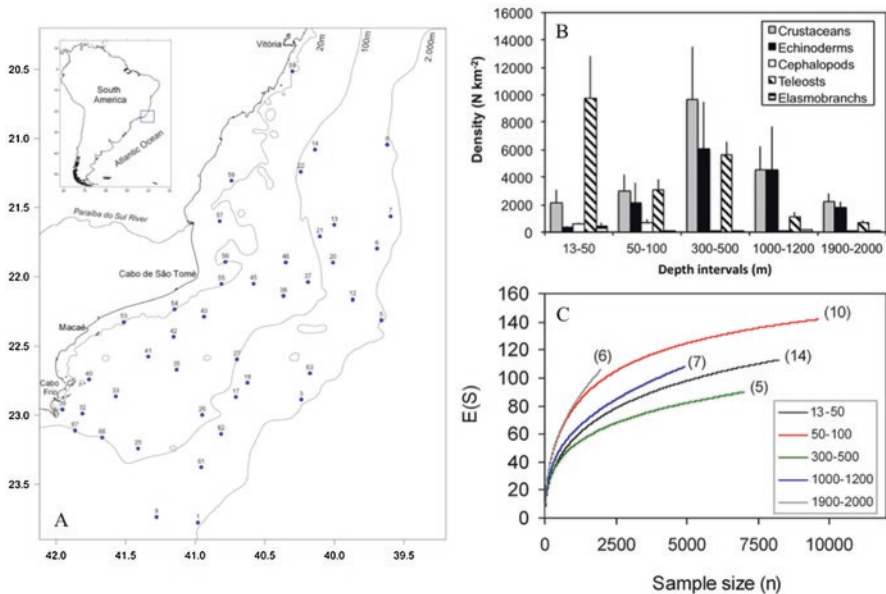


Fig. 3.5 Sampling grid (a), density (b), and individual-based (i.e., n = number of individuals) rarefaction curves of expected number of species $E(S)$ as a function of depth interval (c) of megabenthic communities off Campos Basin, Brazil (Modified from Costa et al. 2015). Numbers in parentheses on panel C indicate sampling effort, i.e., number of trawls

Table 3.1 Sampling effort (number of samples, trawling time, swept area, and species per hour), species richness and mean (\pm SE) biomass, density, diversity, and evenness of benthic megafauna on Campos Basin, Brazil (from Costa et al. 2015)

Depth (m)	13–50	50–100	300–500	1000–1200	1900–2000
Samples	14	10	5	7	6
Trawling time (h)	6.5	5.8	2.16	8.61	10.0
Swept area (km ²)	0.22	0.18	0.06	0.23	0.28
Species richness (S)	113	142	90	108	106
Biomass (kg)	734 \pm 191	417 \pm 201	804 \pm 184	267 \pm 90	53 \pm 13
Density (N.km ⁻²)	12,500 \pm 3323	7951 \pm 2421	20,191 \pm 4583	10,219 \pm 3519	4733 \pm 976
Diversity (H')	5.7 \pm 3	9.0 \pm 3	7.8 \pm 2	9.2 \pm 5	14.2 \pm 6
Evenness (J')	0.50 \pm 0.2	0.65 \pm 0.1	0.58 \pm 0.1	0.62 \pm 0.2	0.69 \pm 0.1
Species per hour	54 \pm 21	52 \pm 16	78 \pm 12	31 \pm 12	25 \pm 28

mass distributions along the slope with upper slope species occurring under the South Atlantic Central Water (SACW), mid slope bathed by the Antarctic Intermediate Water (AIA), and lower slope species by the North Atlantic Deep Water (NADW) (see Silveira et al. [this volume](#), Chap. 2). The authors discussed, however, that some of these depth zonation trends were biased by the relatively small size of the trawling nets, precluding, for example, the capture of large-sized benthopelagic fish from the families *Synaphobranchidae*, *Macrouridae*, *Moridae*, *Ophiidiidae*, and *Alepocephalidae*, known to occur in abundance both in the mid and lower slopes (Costa et al. 2007). Species rarefaction analysis revealed an increase of megafaunal species richness with depth along Campos Basin (Fig. 3.5c). The curves for both mid and lower slopes showed the steepest slopes of accumulation of expected number of species, even though having received nearly half of the sampling effort compared with the shallower sites. Nonetheless, none of the curves showed signs of reaching asymptotic values (Costa et al. 2015).

3.2.2 Submarine Canyons

Nearly 10,000 submarine canyons exist worldwide and occur predominantly along continental margins, covering a total area of 4.4 million square kilometers, or 1.2% of the entire ocean's seafloor (Harris et al. 2014). These abrupt topographic features are key in connecting shallow coastal areas to the deep sea by channeling and transporting sediments (Oliveira et al. 2007; Puig et al. 2014), organic matter (Vetter and Dayton 1998; De Leo et al. 2010, 2014), marine debris (Schlning et al. 2013), and pollutants (Paull et al. 2002). Canyons can focus kinetic energy of internal tides inducing vertical mixing (Zhao et al. 2012) and also trigger upwelling through the topographic steering of shelf currents (Hickey 1997; Allen and De Madron 2009), which in turn may enhance local primary productivity (Ryan et al. 2005) and zooplankton biomass (Macquart-Moulin and Patriiti 1996; Greene et al. 1988).

Additionally, the topographic focusing of zooplankton and micronekton biomass in submarine canyons often provide trophic subsidies to larger predator fish, marine mammals, and seabird species (Genin 2004; Moors-Murphy 2014). Furthermore, due to high-localized productivity in concert with extremely heterogeneous and complex seafloor habitats, high benthic biomass and biodiversity have also been reported for a range of temperate, tropical, and subtropical submarine canyons (Schlacher et al. 2007; McClain and Barry 2010; De Leo et al. 2010, 2014; Ramos et al. 2017).

A total of 161 submarine canyons have been identified along Brazil's continental margin based on global multibeam bathymetry and satellite altimetry databases (Harris et al. 2014, Table 3.2). According to Harris and Whiteway (2011), passive continental margins, as in the case of the Brazilian margin, host 15% less submarine canyons than active margins worldwide. Two types of submarine canyons occur along the Brazilian margin, "shelf-incising" canyons, which have their shallowest portion ("canyon head") intersecting with the edge of the continental shelf, and "blind" canyons, which are confined to the slope (Harris and Whiteway 2011). A third canyon type, "shelf-incising-connected with river-mouth," is absent from Brazil's margin. Canyons on passive margins are therefore less common and more interspaced, as in the case of Brazil's margin, with higher occurrences in the northern and eastern margins (Fig. 3.1, Table 3.2). Shelf-incising canyons are particularly abundant in northeastern Brazil, where the continental shelf reaches its narrowest point, with total number of canyons progressively diminishing towards the northern and southern margins, as the continental shelf progressively widens. At those extremes, with only a few exceptions, canyons are mostly disconnected from the shelf, i.e., "blind" canyons.

Table 3.2 Number, types and total area of submarine canyons along Brazil's Continental Margin⁺

BR margin region	Submarine canyon classification ⁺⁺	Total area in km ² (within BR EEZ)	No. of features	Studied (or sampled) canyons
North	Shelf-incising	8748	16	Amazon
	Blind	12,821	37	
Northeast/ East	Shelf-incising	10,364	24	Sao Francisco
	Blind	17,236	69	Brejo Grande, Rio Praúnas, Aroeira, Rio Doce
South	Shelf-incising	4398	4	Almirante Câmara*, Watu Norte*
	Blind	5241	11	Itapemirim, Grussaí*, Goitacazes
Total	Shelf-incising	23,510 (0.58)	44	
	Blind	35,298 (0.86)	117	

+ Data from Harris et al. (2014); ++ Harris and Whiteway (2011); * sampled with respect to benthic communities (da Fonsêca-Genevois et al. 2017; Lavrado et al. 2017a, b; Bernardino et al. 2019)

There are only a few studies describing the role of submarine canyons as organic matter corridors affecting deep-sea benthic fauna along Brazil's margin. Most of the studies to date have focused on aspects of late-quaternary sedimentary processes and associated physical circulation dynamics. On the equatorial margin, the Amazon canyon associated with the Amazon fan was one of the first studied canyon systems in Brazil (Damuth et al. 1983; Flood et al. 1991; Pirmez and Imran 2003). More recently, submarine canyon systems off the NE and E continental margins, including the São Francisco Canyon, and Brejo Grande Canyon complex, off Sergipe and Alagoas States, have also been studied predominantly under a geological context (Silva 2007; Figueiredo et al. 2011; Ribeiro 2016). Additionally, in Campos Basin, submarine canyon research has also historically focused on the genesis, sedimentary dynamics, and canyon seafloor stratigraphy, all driven by the oil and gas industry interested on deep-sea reservoirs (Machado et al. 2004).

Only very recently submarine canyons on the southeastern margin off Campos and Santos Basins have been investigated with respect to their ecological importance to overall continental margin biodiversity (benthos predominantly). The Almirante Câmara and Grussaí canyons on the Campos Basin (da Fonsêca-Genevois et al. 2017; Lavrado et al. 2017b) and the Watu Norte and Rio Doce canyons further north and off Espírito Santo have been sampled predominantly by means of box coring at depths ranging from 400 to 1300 m (Bernardino et al. 2019). In the Almirante Câmara and Grussaí canyons, macrofaunal abundance and biomass were reported to be comparatively higher than adjacent open slope areas mostly at mid-canyon depths (700–1000 m). Only the former canyon system showed higher macrofaunal abundance and biomass at the shallower sampled station (400 m; Bernardino et al. 2019). These results agree with previous studies that have demonstrated that organic enrichment or “canyon effects” are diluted towards the mouth of the canyons due to progressive consumption of labile organic matter by benthic communities at mid-canyon depths and with accumulation of refractory organic matter towards deeper areas (De Leo et al. 2012; 2014; Campanyà-Llovet et al. 2018; Leduc et al. 2020). Additionally, reduced benthic macro- and megafauna abundances towards the head of submarine canyons are thought to be related to increased physical disturbance by variable and stronger current regimes at shallower depths (Vetter et al. 2010; Paterson et al. 2011; De Leo et al. 2012, 2014).

Rarefaction species richness (ES-25) and Shannon diversity were indistinct between Almirante Câmara and Grussaí Canyons and respective adjacent slope ecosystems on Campos Basin. However, the abundance and relative taxon composition of benthic macrofaunal assemblages were very distinct between the two habitats, particularly at 1000 and 1300 m of depth, and also between each canyon. Two bivalve families, Yoldiidae and Thyasiridae, and one of Aplacophora (Prochaetodermatidae) occurred predominantly in both canyons, while the gastropod *Benthonellania coronata* was significantly more abundant in the open slope (Lavrado et al. 2017b). Additionally, carnivorous polychaetes and tanaids occurred in higher abundances in both canyons, and polychaetes from the family Amphinomidae, in particular *Paramphinome posterobranchiata*, an endemic species of Campos Basin, occurred in higher abundances in the slope. Amphinomid and

ampharetid polychaetes are also abundant on organic falls sampled on Campos and other deep-sea basins, suggesting that canyons may also act as a potential refuge for opportunist fauna (Bernardino et al. 2017; Barroso et al. 2018; Bernardino et al. 2019). These differences in community structure have also been reported in other continental margins, with marked canyon effects in species composition and dominance patterns caused by increased seafloor topography, sedimentary habitat heterogeneity and often much higher organic matter deposition in canyons (Vetter and Dayton 1998; Vetter et al. 2010; De Leo et al. 2010, 2014). In this study at Campos Basin in SE Brazil, the authors described that at larger spatial scales, water mass composition, total sedimentary organic carbon, phytodetritus (including chlorophyll-a and phaeopigments), grain size distribution – all parameters that highly covariate with depth – were the main drivers of the observed faunal zonation among upper, mid, and deep slope areas (Bernardino et al. 2016). At smaller spatial scales, the Almirante Câmara and Grussaí submarine canyons also played an important role in determining differences in benthic assemblage composition, particularly at upper and mid slope depths; and labile organic matter channeling and accumulating through these topographic features were assigned as the main drivers of benthic community structure (Carreira et al. 2017; Lavrado et al. 2017b).

The meiobenthos, with focus on nematodes, was also investigated in those same two canyon systems, but differently from the macrofauna did not exhibit significant changes in community composition between canyon and open slope (Fonsêca-Genovois et al. 2017). However, a few nematode genera, including *Leptosomatum*, *Nannolaimoides*, and *Trileptium* only occurred in the Grussaí Canyon, and *Glochinema* only in Almirante Câmara Canyon, suggesting that limited sampling may prevent a true understanding of deep-sea biodiversity patterns associated with submarine canyons. Particularly high densities and dominance of *Desmoderella* and *Cervonema* were observed at 400 m and 700 m, respectively, in Almirante Câmara Canyon. Similar to what was recorded for the macrobenthos, the total sedimentary particulate organic matter, phytopigments and grain-size heterogeneity were the main drivers of community structure. Overall, the total nematode taxa richness for the entire sampled region off Campos Basin (~100 km²) reached 243 genera from 41 families, and therefore much higher if compared to the Northeast Atlantic with 128 genera from 35 families (Tietjen 1984); and the East Atlantic with 79 genera from 24 families (Vanreusel et al. 1992). A total of 99 nematode genera occurred at Grussaí Canyon and 108 in Almirante Câmara Canyon, numbers that are relatively high and comparable with genus diversity observed in several other submarine canyon systems in the Northeast Atlantic, such as Cascais, Setúbal, and Nazaré Canyons off Portugal and Whittard Canyon off Ireland (Garcia et al. 2007; Ingels 2010; Ingels et al. 2009, 2011). Nematode densities were significantly higher in the shelf-incising Almirante Câmara Canyon in comparison with the “blind” Grussaí Canyon, perhaps indicating a stronger influence of organic matter accumulation and transport through the former system, with its head indenting the deep continental shelf.

The last decade (2010–2020) saw a rapid increase in the number of multidisciplinary research programs aiming at studying physical, geological, and biological processes in submarine canyons (Matos et al. 2018). New technologies, including

large networks of cabled observatory arrays, have allowed for the high-frequency monitoring of submarine canyon benthic habitats with respect to surface ocean variability, carbon flux, and pelagic-benthic coupling (Thomsen et al. 2017; Chauvet et al. 2018; De Leo et al. 2018). Furthermore, the recent interest in submarine canyon biodiversity and ecosystem function research grew due to increased human pressures on deep margin environments by direct exploitation of deep-water fisheries and oil and gas resources, and the prospecting for mineral and genetic resources (Levin and Sibuet 2012; Cordes et al. 2016; Fernandez-Arcaya et al. 2017). Since canyons often harbor highly productive, biodiverse, and structurally complex habitats such as cold-water coral mounds, sponge gardens, and cold seeps, they can be classified as Ecologically or Biologically Significant Marine Areas (EBSAs) or as Vulnerable Marine Ecosystems (VMEs). Both designations fall under United Nations' (UN) Convention of Biological Diversity (CBD 2008, COP9) and under UN's Food and Agriculture Administration (FAO 2009) established criteria implemented for the management and conservation of deep-sea habitats targeted by deep-water fisheries and offshore drilling (reviewed in Fernandez-Arcaya et al. 2017).

Submarine Canyons at the Brazilian margin, and in the South Atlantic more broadly, remain disproportionately understudied relative to other continental margins of the North Atlantic, Pacific, and Indian Oceans and in the Mediterranean Sea (Matos et al. 2018). As described above, only 4 submarine canyons in the SE margin, representing less than 2.5% of all Brazilian canyons, have received baseline studies to study benthic assemblages, with virtually no data addressing submarine canyon pelagic ecosystems. Therefore, there is a notorious gap in the exploration and understanding of this particular deep-sea habitat across the extensive Brazilian margin.

3.3 Human Impacts on Brazilian Continental Margins

3.3.1 Current Threats to Deep-Sea Ecosystems Off Brazil

A recent review study has established the temporal evolution in the extent and spectrum of human impacts affecting deep-sea ecosystems, revealing distinct but overlapping phases (Ramirez-Llodra et al. 2011). Until the early 1970s, direct human impacts in the deep sea were mainly related to waste disposal (i.e., sewage, dredge spoils, low-level radioactive waste, munitions, and pharmaceuticals) that caused presumably local impacts on continental slopes. In the following decades up to the present, technological development combined with a worldwide economic growth has led to a major shift in the nature and extent of human impacts on deep-sea ecosystems as a result of large-scale exploitation of living (i.e., fisheries; see Perez et al. *this volume*, Chap. 8) and nonliving (i.e., oil and gas) resources, which now occur at depths below 2000 m (Mengerink et al. 2014; Cordes et al. 2016). In addition to this marked transition, the current spectrum of human activities affecting deep-sea ecosystems is notably diverse, from microplastic residues deposited in

submarine canyons and abyssal sediments (Cauwenberghe et al. 2013; Fernandez-Arcaya et al. 2017), to the imminent threats posed by seabed mining on abyssal plains, seamounts, and mid-ocean spreading centers (Smith et al. 2008b; Mengerink et al. 2014). Therefore, perhaps not even the most remote deep-sea ecosystem may be completely unaffected by human influence today (Halpern et al. 2008; Sweetman et al. 2017). Below we provide a brief overview of current human activities with potential for impacting deep-sea ecosystems along the Brazilian Continental Margin. There is limited published information on the quantification of these human impacts on deep-sea ecosystems off Brazil, and for that reason we describe some of the known or modeled impacts from published literature on other continental margins.

3.3.1.1 Oil and Gas

The offshore oil and gas industry is of major importance to the Brazilian economy and currently over 70% of all oil and gas is produced from deep-sea reservoirs, with over 100 offshore platforms operating at depths from 200 to 2000 m (ANP 2015; Bernardino et al. 2020; see Chap. 8). The offshore oil production at reservoirs below 200 meters depth has increased by over 1000% between 2010 and 2014, compared to a 14% decrease of onshore production, raising great concerns about the impacts and conservation of deep-sea ecosystems along the slope (Almada and Bernardino 2017). Although the environmental regulations for licensing offshore platforms and pipelines have improved since its implementation in the 1980s, there are still important gaps in the regulatory framework process during the bidding rounds for new offshore developments in Brazil (Mariano and La Rovere 2007; Bernardino and Sumida 2017). As a consequence, a proper implementation of the environmental impact assessments (EIAs) required during the stages of seismic surveys, pipeline and platform installations, production, and decommission is often overlooked by the regulatory agencies.

There are limited published in situ assessments of the impact of offshore activities on nearby deep-sea sediments and associated benthic fauna within Brazil's margin. Modeling of plume dispersion as well as the characterization of chemical contamination by nonaqueous synthetic-based drilling muds have been experimentally evaluated at a single site at 900 m depth on Campos Basin (Pivel et al. 2009; Pozebon et al. 2009). The areal extent of contamination by hydrocarbons, arsenic and heavy metals based on a single drilling operation, was determined to be within 1 km of the drilling site (Fig. 3.6a). The physical and chemical impacts of the drilling mud on benthic meio- and macrofauna provided some contrasting results, with much more evident negative effects on meiofauna compared with macrofauna (Netto et al. 2009; Santos et al. 2009). The meiobenthos showed significant decreases in density and number of taxa, as well as in nematode density and richness (number of families and genera) just 1 month after drilling (Fig. 3.6c–d, Netto et al. 2009). Additionally, the relative abundances of nonselective deposit-feeding nematodes, particularly the genus *Sabatieria*, which is known to inhabit hypoxic and anoxic

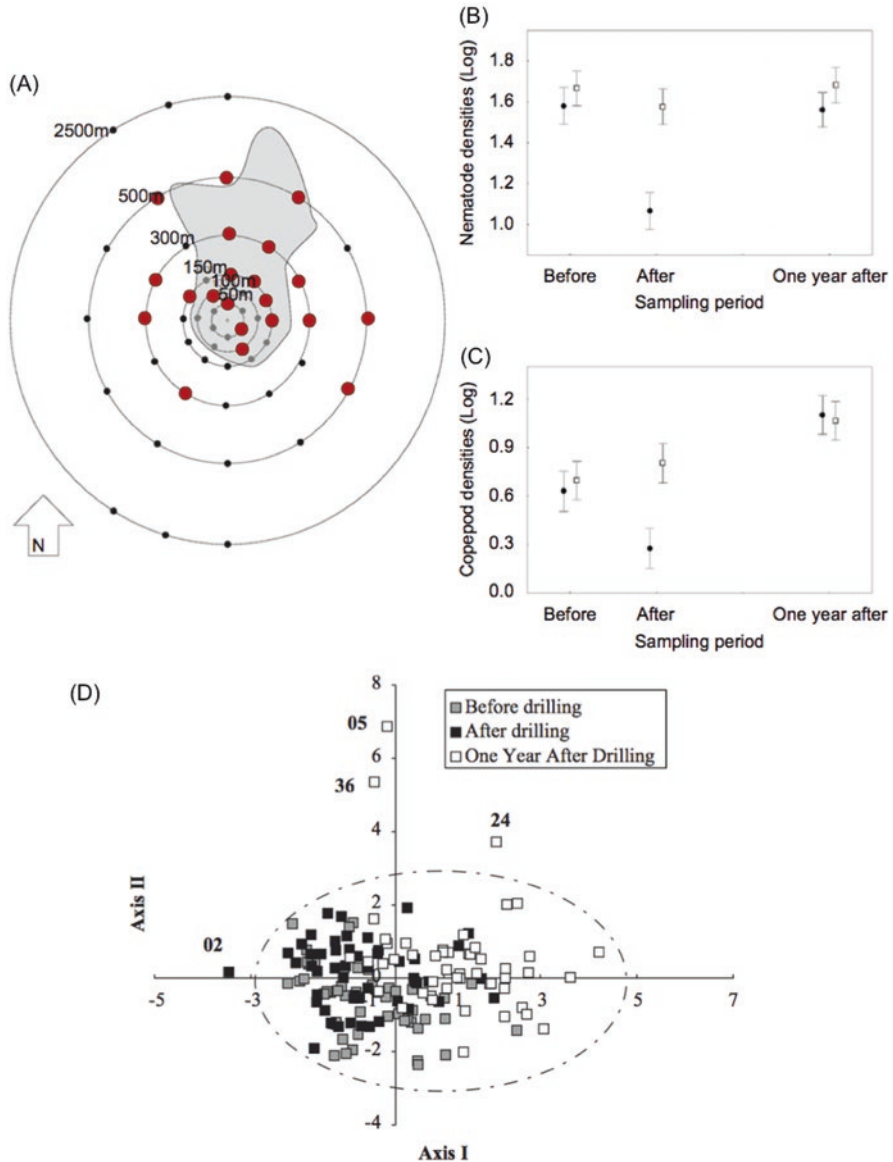


Fig. 3.6 (a) Modeled impacted area (shaded gray) for the discharge and deposition of the synthetic-based drilling mud cuttings at a Campos Basin site at 900 m depth (modified from Pivel et al. 2009). Small dots represent locations where chemicals (hydrocarbons, arsenic, and heavy metals) as well as benthic communities were sampled. Larger dots represent areas where meiofauna was most severely affected (Netto et al. 2009). Log-transformed mean and standard error for nematode (b) and copepod (c) densities before and 1 month and 1 year after drilling on impacted areas (circles) and non-impacted areas (squares) (Netto et al. 2009). (d) Principal Component Analysis (PCA) highlighting changes in macrofaunal community structure before 1 month and 1 year after drilling (after Santos et al. 2009)

environments (Soetaert and Heip 1995), increased significantly within this short post-impact period. Changes in meiofaunal assemblages persisted within 1 year after the drilling took place and were more marked in areas north of the drilling site, agreeing with the modeling studies that indicated a northward transport of the drill mud cuts (Netto et al. 2009). The authors suggested a predominant burial impact of the synthetic-based mud on the meiofauna, with a 12-month recover period to pre-impact conditions although changes in meiofaunal assemblages were still evident after 1 year (Netto et al. 2009).

For the macrobenthos, the same drilling experiment caused localized negative effects at sites located between 50 and 500 m from the drilling well (Santos et al. 2009). No significant changes in density, number of families, and functional groups related to drilling activities were observed at a control site located 2500 m away from the well. At the most impacted sites, macrofaunal densities decreased by 50–75% of pre-drilling values, and the number of families and of some faunal functional (feeding) groups, such as motile deposit-feeders, also were significantly reduced 1 month after drilling. The densities of discretely motile deposit-feeders, such as polychaetes from the *Paranoidae* and *Spionidae* families, exhibited four- to sixfold increases 1 year after drilling, showing evidence of strong recolonization (Santos et al. 2009). The observed changes in community structure (Fig. 3.6d) were poorly correlated with the chemical variables of the sediment, including the total linear petroleum hydrocarbons, unresolved complex mixture (UCM), and metals such as barium. The authors therefore suggested that the changes observed in macrofauna community structure were more related to indirect effects of the presence of drilling cuttings in the sediment, causing physical suffocation, changes in the particle size spectrum, organic enrichment, and oxygen depletion (Santos et al. 2009).

The Campos Basin is the most important deep-sea basin for offshore oil and gas production in Brazil. In this basin, there are over 11,000 km² of leased blocks below 200 m depth, covering a significant portion of the upper and mid slope between 200 and 1500 m (Almada and Bernardino 2017). The recent increase in the spatial footprint of exploration and exploitation activities of the oil and gas industry resulted in significant overlaps between leased areas and deep-sea ecosystems of high biological importance that fall under the EBSAs and VMEs framework definitions. These include cold-water coral reefs, submarine canyons, cold seeps, seamounts, and background soft sediments on the slope (Bernardino and Sumida 2017). There are records of significant *Desmophyllum pertusum* (former *Lophelia pertusa*) reef formations on the middle slope at Campos Basin (~600–800 m depth), some extending for over 40 km and with coral mounds reaching over 10 m height above the seabed (Viana et al. 1998). However, there is a considerable lack of information about the true spatial extent of the cold-water coral formations and its associated biodiversity on the basin. Most of the existing scientific literature is limited to descriptions of coral species occurrences along Brazil's margin and some studied deep-sea basins (Kitahara 2007; Pires 2007; Arantes et al. 2009; See Kitahara et al. [this volume](#), Chap. 4).

In some areas of Campos Basin, the spatial overlap between leased blocks and currently mapped deep-sea EBSAs and VMEs reach >80% in area (Almada and

Bernardino 2017). There is currently a very limited understanding of the basin-wide ecosystem health of those deep-sea ecosystems, and also their vulnerability to chronic and acute environmental impacts from the oil and gas industry, which have now accumulated decades of offshore exploration. In this context, Almada and Bernardino (2017) employed a systematic conservation planning approach (*sensu* Margules and Pressey 2000) and mapped the EBSAs along Campos Basin based on a hierarchical habitat classification using publicly available biological (macroben- thos and cold-water corals) and environmental databases (Cavalcanti 2013). Habitat mapping using abiotic surrogates of seabed geophysical and sedimentary character- istics (grain size and total organic carbon) were used to generate nested levels of habitat classes (Roff et al. 2003). Finally, after setting a target conservation goal of >30% for each defined seafloor EBSA habitat, a decision tree model based on the selection frequency of 5 km² planning units (PUs) was used to generate best conser- vation scenarios under a network of Marine Protected Areas (MPAs) (Fig. 3.7). Three simulated scenarios had distinct conservation performances for each EBSA along the margin and with variable interference with leased areas. In the third scen- ario, where EBSAs protection was restricted to within a 5 km buffer radius around currently operating offshore oil platforms, 93.6% of the solutions reached the 30% protection target (Fig. 3.7e–f). The best solution had an overlap of 5.5% between the conservation area (2330 km²) and leased blocks, and 1.6% of the PUs were highly important for conservation targets. Scenario 3 protected the largest area of cold- water coral reefs and canyons when compared to the unrestricted scenario 1, also with significant higher conservation success than scenario 2 (Almada and Bernardino 2017).

In conclusion, this initial exercise of defining potential deep-sea EBSA conser- vation areas should be repeated for other deep-sea basins offshore Brazil's continen- tal margin, where current and planned expansion activities of deep-water oil and gas exploration will continue to overlap with and pose potential threats to the Brazilian deep-sea biodiversity (Bernardino and Sumida 2017). More importantly, a transpar- ent process involving all stakeholders including industry, governmental regulatory agencies (ANP, IBAMA, MMA), research and academic institutions, nongovern- mental organizations, and the general public should be put in place in order to safe- guard the proper management of deep-sea mineral and biological resources. Such a plan has attained varying levels of success in other parts of the globe (Cordes et al. 2016).

3.3.1.2 Deep Water Fishing

The impacts of deep-water commercial fishing on Brazil's margin is discussed in much more detail in Perez et al. (*this volume*, Chap. 8).

Off the Brazilian margin deep-water fishing still occurs in the upper and lower slope, despite of the already fully and overexploited status of many of the commer- cially important stocks (Perez et al. 2009; Pezzuto et al. 2006). In spite of the still ongoing fishing activity, currently little information exists on the extent of the

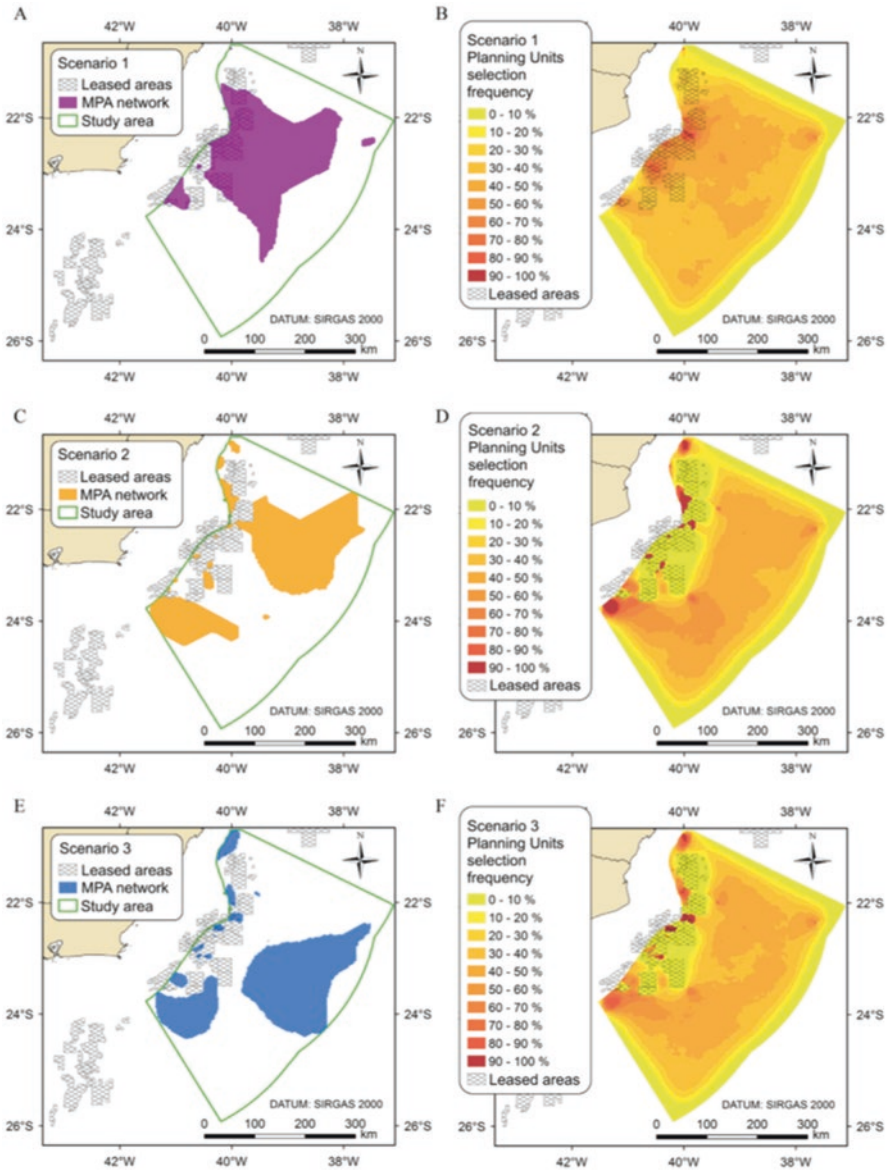


Fig. 3.7 Different scenarios of MPA network design offshore Campos Basin, Brazil (Modified from Almada and Bernardino 2017). (a) Scenario 1 with MPA Network overlapping current leased and production offshore blocks. (b) Frequency of selection of Planning Units (PU) for conservation in Scenario 1, with hot areas indicating areas of higher conservation value. (c). MPA Network on Scenario 2, completely avoiding current offshore blocks. (d). PU selection for this Scenario. (e) MPA Network selection of areas within leased blocks but with a 5-km buffer zone from each offshore platform and with higher cost of conservation within exploration areas. (f) PU selection frequency also indicated for scenario 3

impacts on seafloor communities and its biodiversity. In one of these studies, rare quantitative data showed absolute catches of non-targeted species (individuals per sampled net) ranging from 33 to 459,833 individuals for invertebrates, 41 to 23,954 elasmobranchs, 41 to 110,665 teleosts, and 8 to 711 turtles, cetaceans and birds combined (Perez and Wahrlich 2005). Qualitative data specifically from the trawling fleet reported 185 macro and mega invertebrate species captured as bycatch, including sponges, cnidarians, annelids, crustaceans, and echinoderms (Bastos 2004). To the best of our knowledge, no studies in Brazil have quantitatively addressed the impacts of deep-water fishing activities on benthic assemblages, ecosystem function, and overall biodiversity. Therefore, we believe this gap should be addressed in the near future in parallel with ongoing fisheries management strategies recently implemented (since 2008), which included establishment of total allowable catches, gear restrictions such as minimum mesh sizes, bycatch limits and fishing area, and season closures (Perez et al. 2009, [this volume](#), Chap. 8).

Globally, bottom trawling represents today the single most pervasive human activity affecting the deep seafloor and its benthic ecosystems (Ramirez-Llodra et al. 2011). At a global scale, most deep-sea bottom trawling occurs on sedimented slopes at the edges of continental margins, although at smaller spatial scales, seafloor topographic features such as seamounts and submarine canyons are also targeted, with particular negative effects on benthic habitat framework builders, such as sponge reefs and cold-water coral communities (Clark and Koslow 2007; Pierdomenico et al. 2018).

Direct effects of bottom trawling have been extensively reviewed and include scraping and ploughing of the substratum, sediment resuspension with a smothering impact on the fauna, destruction of non-target benthic species, and organic loading from the dumping of waste from at-sea processing (Auster et al. 1996; Collie et al. 2000). Documented indirect effects include post-fishing mortality and long-term trawl-induced changes in the benthos, such as reduced diversity, evenness and biomass, changes in community and trophic structure, and reduction of habitat heterogeneity (Jennings et al. 2001; Clark and Koslow 2007; De Leo et al. 2017). Additional long-term and widespread effects of trawling include changes in sedimentary processes. For example, dense sediment gravity flows can be triggered by the continuous dragging of heavy otter boards (often weighing up to 1.3 tonnes each) through soft muddy sediments (Palanques et al. 2006; Paradis et al. 2017). In particular, where entire trawler fleets concentrate their operations on the flanks or axis of submarine canyons, these trawl-induced sediment gravity flows can be transported, trapped along, and deposited in the canyon seafloor, smothering the benthic epi- and infauna (Puig et al. 2012). Such impacts, which have been compared to the effects of large-scale plowing of farmlands, integrated over decades of intense fishing activity, have caused a fourfold increase in natural sedimentation rates near submarine canyons in the Mediterranean, with a landscape-scale smoothing effect in the seabed topography (Puig et al. 2012). As a consequence, drastic changes in the physical properties of surficial sediments directly affect the dynamics of water-sediment chemical exchanges and substantially reduce the organic matter content

available for the epi- and infaunal benthic organisms (Puig et al. 2012; Martín et al. 2014).

Recent awareness campaigns exposing the general public to the negative impacts of bottom trawling on deep-sea ecosystems culminated with the European Commission's ban on trawling below 800 m in the North-East Atlantic. Furthermore, benchmark initiatives such as the Global Fishing Watch (<http://globalfishingwatch.org/>), a partnership program between nongovernmental organizations and Google, are making vessel automatic identification system (AIS) data publicly available, allowing the tracking of worldwide illegal and unreported fishing activity (including bottom trawling). The program still has limited data availability, only with the most recent 5 years of AIS data (as of December 2017). Nevertheless, for the Brazilian margin in particular, the observed spatial patterns in fishing activity for the last 4 years corroborates the known deep-water fishing operations described above, with concentrated fishing activity in the central, southeastern, and southern EEZ sectors, and sparse activity near seamount chains in the northern, northeastern, and eastern sectors (Fig. 3.8).

3.3.2 Future Threats by Climate Change and Seabed Mining

3.3.2.1 Climate Change

Climate change is likely to cause significant and widespread effects on bathyal and abyssal deep-sea communities in the coming decades (Ramirez-Llodra et al. 2011; Sweetman et al. 2017). Deep-sea observational studies have reported increasing temperatures in deep-water masses (Purkey and Johnson 2010), decreased dissolved oxygen concentrations (Stramma et al. 2010; Breitburg et al. 2018), reduced pH (Byrne et al. 2010), and altered particulate organic carbon (POC) flux to the seafloor (Smith et al. 2008a, 2013). As the ocean functions as a major sink for atmospheric CO₂, as well as for the heat generated from the planet's net greenhouse gas effect, it buffers the large-scale effects from climate change (Pachauri et al. 2014). However, this buffering capacity will be severely compromised if atmospheric CO₂ levels reach model predictions of 900 ppm by 2100, which are not far from the present-day ~410 ppm concentrations (Meinshausen et al. 2011).

According to a recent study based on shipboard observations, the abyssal ocean (below 2000 m) has taken up 19% of Earth's excess anthropogenic heat and 27% of anthropogenic carbon since the pre-industrial era (Talley et al. 2016). Modeling studies have shown that abyssal ecosystems are warming at rates of 0.01 to 0.1°C per decade (Purkey and Johnson 2010), with highest temperature changes predicted for the abyssal North Atlantic, Southern, and Arctic Oceans (Mora et al. 2013). Model predictions also show temperature increases of 3.6 °C for the bathyal Pacific, 4.4 °C for the Atlantic, and 3.7 °C for the Arctic (Mora et al. 2013). The warming of the ocean at its surface also has multiple cascading effects on processes such as solubility of O₂ from the atmosphere, nutrient regeneration and carbon export from

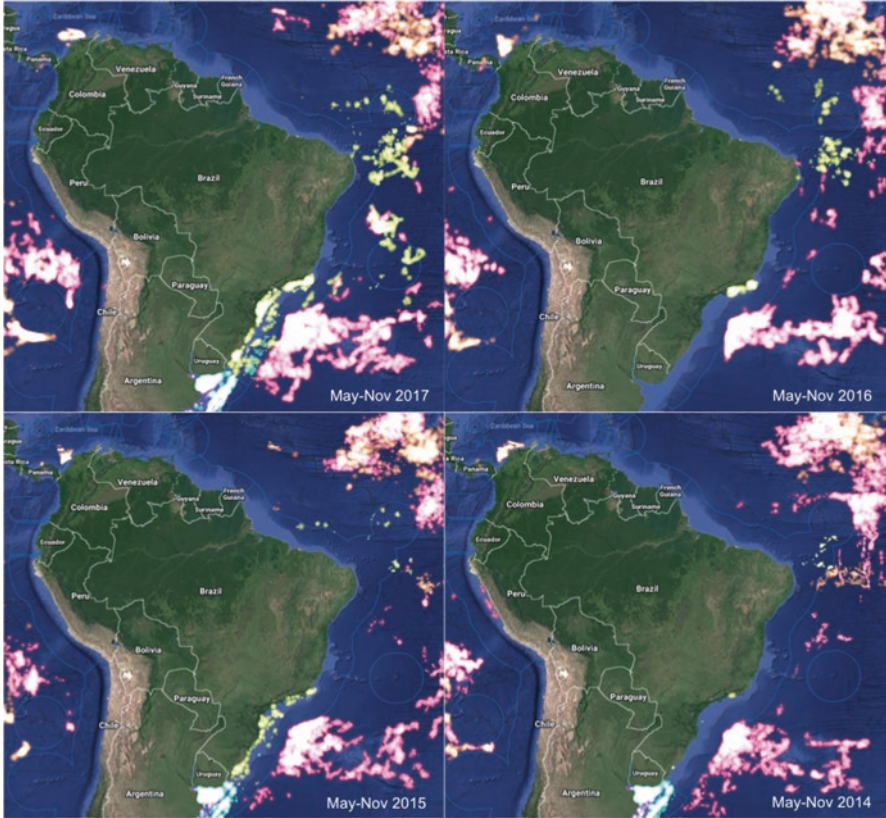


Fig. 3.8 Apparent fishing activity in Brazil's EEZ and beyond derived from vessel automatic identification system (AIS) data (source: Global Fishing Watch, <http://globalfishingwatch.org/map>). Color-coded are Brazilian fishing fleet, which includes chartered fleet (yellow), Japanese (orange), Spanish (pink), Uruguayan (green-bluish); Argentinean (purple)

the euphotic zone, and deep-water formation. Initially, thermal stratification will reduce vertical mixing and therefore prevent nutrient regeneration from deeper waters, with direct effects on primary productivity (Behrenfeld et al. 2006). Poor nutrient regeneration has led to shifts in phytoplankton communities from large fast-sinking diatoms to slow-sinking picoplankton (Bopp et al. 2005), and these shifts are predicted to directly influence in the decline of POC flux in the Pacific, Atlantic, and Indian Oceans, with up to 40 and 55% in POC flux reductions to the bathyal and abyssal regions of the Indian Ocean, respectively (Mora et al. 2013; Morán et al. 2015). Particularly the Pacific oceanic gyres and the equatorial upwelling zones will also be extremely affected, with up to 40% declines in POC flux (Sweetman et al. 2017). On the other hand, some areas along eastern boundary current systems (e.g., California and Peru) already show signs of localized increases in POC flux export, primarily triggered by observed enhanced upwelling-favorable wind-stress conditions (Jones et al. 2014).

Vertical thermal stratification combined with reduced O₂ solubility will promote widespread ocean deoxygenation, in particular in intermediate waters already affected by oxygen minimum zones (OMZs) (Keeling et al. 2010; Stramma et al. 2010). Existing long-term time-series observations already point to the expansion in volume of many OMZs over the past 50 years, particularly those along the eastern boundary current systems (Crawford and Peña 2013; Gilly et al. 2013). Additionally, results from modeling studies further predict bottom-water oxygenation reductions in the bathyal North Pacific, Atlantic, Arctic, and Southern Oceans by 0.7–3.7% by 2100 (Sweetman et al. 2017).

Ocean acidification is another major consequence of climate change whose effects are already measurable from surface ocean waters all the way to bathyal depths (Doney et al. 2009; Byrne et al. 2010). In the Pacific Ocean, for example, basin-wide changes in pH have been documented in waters as deep as 500 m, with increases of up to 0.03 pH units due to uptake of anthropogenic CO₂ – up to 50% of total increase if considering natural decadal variability in dissolved inorganic carbon (Byrne et al. 2010). Furthermore, modeling studies predict that up to 17% of the deep North Atlantic (below 500 m) could experience pH reductions of 0.2 units by 2100, affecting a large number of benthic biodiversity hotspots such as seamounts and submarine canyons (Gehlen et al. 2014).

Based on current knowledge on how deep-sea benthic communities and ecosystems respond to natural and human-induced environmental gradients, generalized predictions have been made with respect to benthic ecosystem structure and function under modeled extreme climate change scenarios (Smith et al. 2008a; Sweetman et al. 2017). For example, as temperatures increase in the deep-sea benthic boundary layer, biodiversity and body size are expected to decline concurrently with increases in metabolism (Fig. 3.9a). The expansion of oxygen minimum zones along some continental margins will have significant effects on deep-sea community structure and function, with macro- and megabenthic diversity, biomass, and sediment bioturbation decreasing over time, while habitat compression, carbon burial, nitrogen loss, and meiofaunal abundances will increase (Fig. 3.9b). Under increasingly acidic conditions resulting in the lowering of calcite and aragonite saturation states, deep-sea calcifying organisms such as cold-water corals, mollusks, and echinoderms will be particularly susceptible to predation due to thinner and weaker structures. Metabolism, energy demand, and shell dissolution will exponentially increase while overall calcifier taxa abundance and diversity will decline (Fig. 3.9c). The predictions ranging between 30% and 50% in POC flux reductions among some of the world's bathyal and abyssal regions will also severely impact benthic ecosystem structure and function, with overall reductions in biodiversity, abundance and biomass, nutrient cycling, and bioturbation, with a resulting reduction in the mixed layer depth. On the other hand, microbial biomass and its relative contribution to total carbon cycling will increase (Fig. 3.9d).

While the predicted impacts of climate change, particularly under extreme scenarios (weak to no mitigation), will affect deep-sea benthic communities at a global scale, bathyal and abyssal ecosystems in the SW Atlantic, particularly off the Brazilian Continental Margin, may experience a unique range of effects by 2100. In

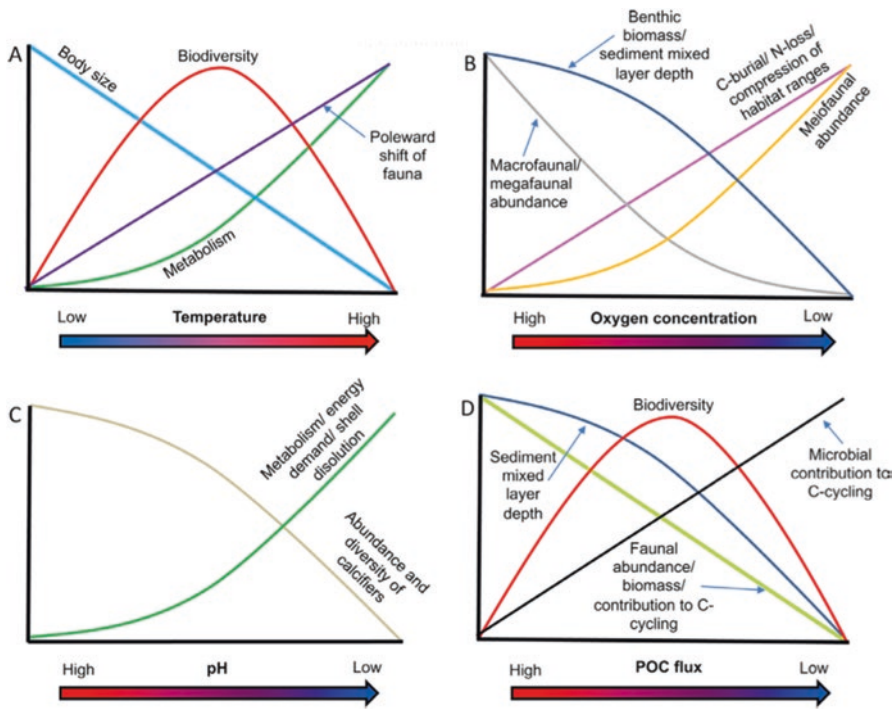


Fig. 3.9 Predicted effects of climate change on deep-sea benthic ecosystems (copyright: Elementa Science of the Anthropocene; Sweetman et al. 2017). Concept depictions showing how changes in temperature (a), oxygen (b), pH (c), and particulate organic carbon (POC) flux (d) may alter specific ecosystem properties of deep-sea benthic ecosystems

particular, the results from the modeling approach by Sweetman et al. (2017) predict that the SW Atlantic deep sea will also be impacted by deoxygenation, temperature increases, or significant changes in POC flux and potentially affected by ocean acidification with pH reductions of up to 0.3 units.

Current international and collaborative efforts advocating for deep-sea stewardship are defining priorities for long-term monitoring programs to address the “essential ocean variables” (EOVs) to be monitored consistently across the global ocean, and in particular to address climate change (Levin et al. 2019). In addition, some of these programs, such as the Deep Ocean Stewardship Initiative (DOSI, <https://www.dosi-project.org/>) and the Deep Ocean Observing Strategy (DOOS, <https://deep-oceanobserving.org/>) are having a central role in connecting the scientific community with a range of deep-sea stakeholders, and in particular with policy makers (Levin et al. 2019). We are working towards Brazil’s participation in those global efforts that would lead to research and monitoring programs aiming to evaluate the potential ecological effects of climate change also in the deep South Atlantic Ocean. These efforts will be key to validate predictions of environmental change with respect to the Brazil’s deep ocean ecosystems and its potential effects on biodiversity and associated ecological services.

3.3.2.2 Seabed Mining

Commercial deep seabed mining was, for at least four decades (1980s–2010s), unfeasible primarily due to technological constraints and overall economic unviability (Van Dover 2011). However, since the early 2000s, mining exploration licenses have been granted in marine areas within and beyond national jurisdictions following major technological breakthroughs by the mining industries and increasingly economic attractiveness (Levin et al. 2016; Jones et al. 2017). Existing deep-sea mineral resources (excluding oil and gas and methane hydrates, Bernardino et al. 2020) include manganese nodules occurring predominantly on abyssal plains, seafloor massive sulfides occurring in spreading ridges, cobalt-rich ferromanganese crusts on seamounts, and phosphorite deposits found along continental margins. All of these resources are known to occur within Brazil's EEZ (see Perez et al. [this volume](#), Chap. 8). To date deep-sea commercial-scale mining activities have not yet taken place in Brazil's margin.

Very little is known about short- and long-term environmental impacts associated with large-scale deep-sea mining activities. Most information available on the nature and extent of impacts on deep-seafloor habitats and biota comes from experimental mining operations conducted by industry and a few research programs and has concentrated mostly on abyssal manganese nodule provinces (reviewed in Jones et al. 2017). The estimated spatial footprint of impacts caused by future mining activities on manganese nodule fields of the Clarion Clipperton Fracture Zone (CCZ) in the Equatorial North Pacific are expected to reach 300–600 km² per year (Smith et al. 2008b; Wedding et al. 2013). This estimate takes in consideration the physical impacts of nodule and sediment removal of combined mining activities of all currently granted exploration blocks, with mining expected to start as early as 2025 (Wedding et al. 2013). This spatial footprint also considers the impacts of near-bottom and water column sediment plumes, expected to be generated from tailings from the mining head during extraction, and from sediments attached to nodules during lifting from the seabed, respectively (Oebius et al. 2001). Single-mining operations in abyssal settings are expected to generate sediment plumes that will disperse within 100 km and in any direction of the mining disturbance, and over timescales of 1–2 months (Ledwell et al. 2000; Thurnherr 2004).

A meta-analysis of post-mining disturbance experiment data showed that most benthic meio-, macro-, and megafauna experienced severe density reductions following up to 3–7 years after initial disturbance (Jones et al. 2017). Some specific groups, such as the sessile megafauna, showed no signs of recovery even after 7 years of the mining disturbance as this group depends heavily on the nodules as a substrate for attachment (Amon et al. 2016). Macrofaunal diversity and species richness may be significantly lower even after 7 years of the initial simulated mining disturbance (Thiel et al. 2001; Jones et al. 2017), evidencing the long lasting negative effects of deep-sea mining on biodiversity and ecosystem functions.

Looking into the future, potential industrial-scale mining of cobalt-rich ferromanganese crusts at the Rio Grande Rise region (Fig. 3.10) should therefore adopt scientifically sound guidelines for sustainable exploitation and only be implemented

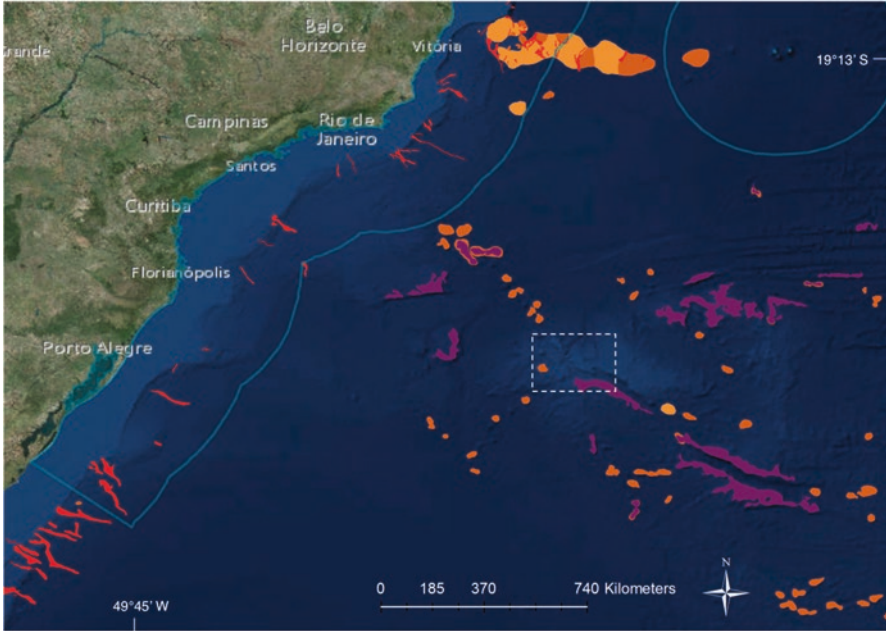


Fig. 3.10 Area of the Rio Grande Rise (dashed white rectangle) where the Brazilian Geological Survey (CPRM) has been granted a 15-year exploration license by the International Seabed Authority (ISA), to prospect cobalt-rich ferromanganese crusts in the deep seabed (boundaries just illustrative, and map with real claim boundaries available at ISA's website). However, the Brazilian Government has recently requested the expansion of its EEZ to include the RGR. Seabed geomorphology from Harris et al. (2014): submarine canyons, red; seamounts, dark orange, guyots, light orange; ridges, purple. Green line represents Brazil's EEZ boundaries. Refer to Fig. 8.1 in Chap. 8, for a detailed picture of the spatial distribution of all mineral resources along the entire Brazilian margin

after careful evaluation of the potential impacts on deep-sea biodiversity, in particular due to the existence of a large cluster of seamounts in the region. Recent spatial planning strategies in the context of cobalt-rich ferromanganese crust mining near seamounts have recommended that mining sites should (i) be less than 2 km in linear extent, (ii) be distributed in multiple depth strata in a single seamount, and (iii) be interspaced by distances greater than 10 km between seamounts (Schlacher et al. 2013). The arguments behind these recommendations are primarily based on high benthic fauna turnover along depth gradients and at spatial scales smaller than 2 km, resulting from extreme high seamount habitat heterogeneity (Schlacher et al. 2007, 2013). The issues related to the jurisdiction and regulatory frameworks and conservation planning for potential future mining of deep-sea mineral resources in Brazil are discussed in Perez et al. (this volume, Chap. 8).

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Chapter 4

Brazilian Deep-Sea Corals



**Marcelo Visentini Kitahara, Ralf Tarciso Silva Cordeiro,
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Abstract The Brazilian Continental Margin (BM) hosts one of the most poorly known deep-water fauna in the world, especially those referred to as habitat forming such as scleractinians and octocorallians (*Cnidaria: Anthozoa*). In waters deeper than 150 m, these anthozoans are the framework builders for coral reefs and coral gardens. Together, these habitats host the highest diversity of metazoans on the external shelf and slope. Although only a few surveys have been dedicated to the study of these organisms in the BM, it is known that *Desmophyllum pertusum* (former *Lophelia pertusa*), *Solenosmilia variabilis*, and *Madrepora oculata* form extensive reefs especially on the southern and southeastern regions. In the same way, Octocorallia representatives, such as those of the families Priminoidae, Clavulariidae, Plexauridae, Alcyoniidae, Isididae, Coralliidae, and Paragorgiidae, also have great ecological importance at the BM and are particularly abundant at the northern and northeastern continental shelves and slope. In order to set a baseline for future research, the present chapter provides a historical review of the studies of these anthozoans from the BM, including a list of all records and their geographical and depth distributions. Based on part of these records, the BM distributional modeling

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of these organisms is predicted using habitat suitability models, which suggest that carbonate saturation state, temperature, dissolved oxygen, and particulate organic carbon are the main factors structuring habitat suitability along the BM. In addition, a comprehensive review of the studies focusing on reproduction of the main species occurring at the BM, a key process for the maintenance and renewal of coral populations and, therefore, design of marine protected areas, as well as the human-based impacts imposed to the habitats structured by these species, are provided.

Keywords Scleractinia · Octocorallia · Distribution · SDM · Reproduction · Anthropogenic impacts

4.1 Deep-Sea Corals

Ubiquitous to all oceans, the phylum Cnidaria (*gr. cnidos* = “stinging nettle”) is among the most basal metazoan group in the tree of life, with plausible fossil records dating back from the pre-Cambrian (ca. 580 Ma – Chen et al. 2002). Cnidarians have only two tissue layers (ectoderm and endoderm) resulting in a very simple body plan. As its name suggests, all representatives of this group contain stinging cells (cnidocytes), used for defense and prey capture. The vast majority of cnidarians are restricted to the marine realm, although a few species are known to occur in freshwater (e.g., the Cnidaria genera *Hydra* spp., *Craspedacusta* spp., *Limnacadium* spp., *Calposoma* spp., *Polypodium* spp., *Cordylophora* spp.). The approximately 11,000 extant representatives of the phylum are divided into 2 subphyla: *Anthozoa* and *Medusozoa*. Besides other characteristics, these two cnidarian lineages are differentiated mainly by the lack of the medusa stage and presence of a circular mitochondrial genome (Bridge et al. 1992) in *Anthozoa*, which is most likely to be the ancestral state of the phylum (Schuchert 1993; Bridge et al. 1995; Kayal and Lavrov 2008).

Having the same name as the subphylum to which it belongs, the class *Anthozoa* is the largest cnidarian group, embracing nearly 7,000 extant species that are traditionally divided into two subclasses (Octocorallia and Hexacorallia). Octocorallians are animals in which each polyp has eight pinnately branched tentacles and eight complete mesenteries (Han et al. 2010). On the other hand, most hexacorallians typically have tentacles and mesenteries in a sixfold symmetry at least in one of their ontogenetic stages.

Contrary to the popular belief, coral “reefs,” defined as biogenic, long-lived, three-dimensional, self-sustained structures that change hydrodynamics, locally trapping sediment and providing habitat for many other species (Roberts et al. 2009), are not restricted to shallow waters. On the contrary, there is a vast body of evidence that some deep-water anthozoans fulfill these ecological and geological

criteria (Roberts et al. 2009). Thus, deep-sea reef ecosystems are known from all oceans, being the most common framework engineers the scleractinians (stony corals), octocorallians (sea fans, sea pens, gorgonians), sponges, and stylasterids (lace corals). Within these groups, the present chapter will cover those pertaining to Anthozoa (i.e., Scleractinia and Octocorallia).

4.1.1 Hexacorallia Scleractinia

The Hexacorallia comprises six extant orders, of which only the Scleractinia produces aragonitic secretions resulting in a continuous skeleton. Among extant scleractinian species, nearly 40% live in waters deeper than 50 m (Cairns et al. 1999; Cairns 2007a) and are often referred to as cold- or deep-water corals. With reference to the presence/absence of unicellular photosynthetic dinoflagellates (*Symbiodinium* spp.) within the gastroderm, scleractinians can be categorized in three ecological types that are independent of taxonomy: zooxanthellate, azooxanthellate, and facultative. The zooxanthellae are unicellular photosynthetic dinoflagellates that are considered to be symbionts, assisting the corals in nutrient production through photosynthetic activities, and typically have average densities of $1-5 \times 10^6$ per square centimeter in zooxanthellate coral tissue (Drew 1972; Kawaguti and Nakagama 1973). In brief, the zooxanthellae provide fixed carbon compounds to the coral host, enhancing calcification and facilitating elemental nutrient fluxes (Pearse and Muscatine 1971; Barnes and Chalker 1990; D'Elia and Wiebe 1990; for zooxanthellae diversity, see Marcelino and Verbruggen 2016). In turn, the host coral polyp provides a protected environment and a steady supply of carbon dioxide for the zooxanthellae photosynthesis (Davies 1984). The obligate nature of the symbiotic relationship geographically restricts the vast majority of zooxanthellate scleractinians to tropical regions with shallow (usually less than 90 m), warm, and clear waters (Stanley 2006).

In contrast, azooxanthellate corals do not live in association with photosynthetic dinoflagellates, being considered heterotrophic. This group is reported from off continental Antarctica (Cairns 1982) to the Arctic Circle (Roberts et al. 2009), and among its representatives, some colonial and solitary species are considered cosmopolitan in distribution (e.g., *Madrepora oculata*, *Enallopsammia rostrata*, *Stenocyathus vermiformis* – Fig. 4.1). Furthermore, the fact that they are not dependent on symbionts enables azooxanthellate corals to thrive in aphotic regions. Although most species commonly occur between 200 and 1000 m (Cairns 2007a), some are able to inhabit waters as deep as 6,300 m (Keller 1976), with temperatures as low as -1 °C (Vaughan and Wells 1943). However, some are restricted to shallow waters (e.g., *Tubastraea diaphana*) and some are known only from waters deeper than 3,800 m (e.g., *Fungiacyathus pseudostephanus*).

Despite exceptions are known, most azooxanthellate corals are solitary (Cairns 2007a) and have large polyps, whereas the vast majority of zooxanthellate corals are colonial (highly integrated corallites), and have small polyps. Such correlation

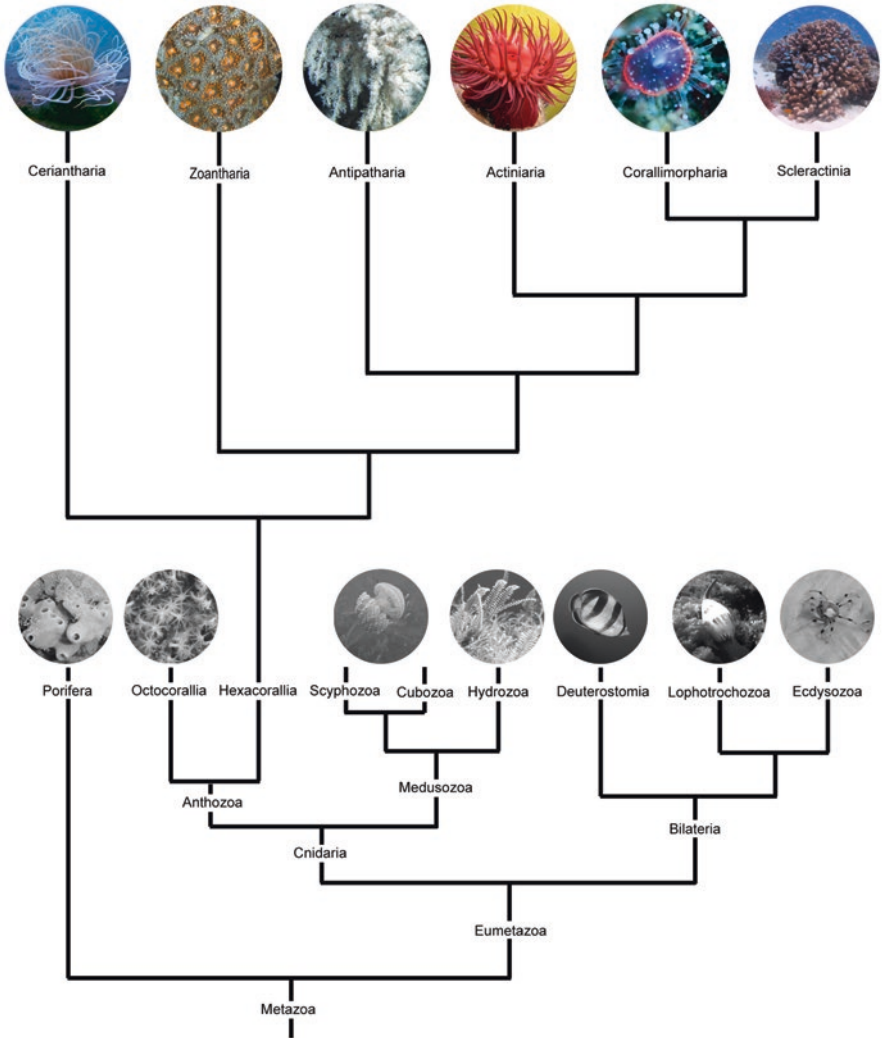


Fig. 4.1 General relationships within metazoans (bottom cladogram) and among hexacorallians (top cladogram). The position of the Ceriantharia has been in debate during the last few years (see Stampar et al. 2014)

(colonial/symbiotic vs. solitary/asymbiotic) is thought to be an evolutionary response by shallow-water species to the symbiotic relationship (Stanley and Swart 1995), in which onset is believed to be within the Triassic around the Tethys Sea (Frankowiak et al. 2016). Supporting this idea, a rough comparison shows that most shallow-water zooxanthellate species tend to form colonies with morphologies that increase light exposure (e.g., laminar, foliaceous, massive, branching – see Stanley

2006), whereas most colonial azooxanthellate species have morphologies that tend to enhance “filtering” capabilities (e.g., anastomotic, fan shape).

The third “ecological type,” the facultative group, consists of species that have the ability to enter symbiotic relationships with photosynthetic dinoflagellates when in adequate environmental conditions, although this association can be lost or drastically reduced when environmental conditions become disadvantageous (e.g., increase in turbidity, season) without negative impacts for the coral host (Dimond and Carrington 2008). However, such flexibility is quite rare; to date only 11 species are recognized as facultative (Cairns et al. 1999).

Altogether, the Scleractinia is considered to be the most recent evolutionary stage within the Hexacorallia (Brugler and France 2007) (Fig. 4.1), forming some of the most complex habitats in the oceans (i.e., coral reef) and sustaining some of the most diverse ecosystems on the planet (Rogers 1999; Dower and Perry 2001; Reed 2002). According to Veron (2011), it is not yet possible to estimate the proportion of marine species occupying coral reefs, although the diversity of most metazoan phyla peaks in shallow-reef habitats.

4.1.2 *Octocorallia*

The subclass Octocorallia corresponds to the largest monophyletic group of cnidarians, hitherto with 47 families, about 370 genera, and between 3,100 and 3,400 species (McFadden 2007; Pérez et al. 2016). The uncertainty on an exact number of species is mainly related to several taxa in need of revision. Nonetheless, relationships between higher taxa within the clade are still discussed (McFadden et al. 2010). These animals are consistently grouped together by having polyps with eight tentacles, eight complete mesenteries (McFadden 2007), and mostly by possessing tentacles flanked by pinnules (Alderslade and McFadden 2007).

Except for one solitary species, *Taiaroa tauhou*, all octocorals are modular colonial organisms (Bayer and Muzik 1976), some reaching 5 (Watling et al. 2013) or even 10 m in height (Smith 2001). Polyps within a colony may be monomorphic (only autozooids) or dimorphic (autozooids and siphonozooids) (Bayer 1973), all interconnected by a network of canals or by a common coenenchyme from which they arise (Sánchez 2004).

They usually have a discontinuous skeleton, formed by microscopic calcareous elements, immersed in their soft tissue (coenenchyme), named sclerites (Cairns and Bayer 2009). These elements, originated from the ectoderm, strengthen the colonies and are involved in defense against predation and abrasion (West 1998). The presence, shape, size, and distribution of sclerites within an octocoral are characters upon which the traditional taxonomy relies on (Bayer et al. 1983). Besides the sclerites, horny or calcareous axes and even aragonitic skeletons may be present.

Currently, despite not well supported by molecular evidence (McFadden et al. 2010), Octocorallia is composed of three morphologically distinct orders: Helioporacea, Pennatulacea, and Alcyonacea. The first is the only group having

continuous aragonitic skeletons, comprising five extant species (Miyazaki and Reimer 2015). Pennatulacea embraces around 225 species and have unbranched colonies, with a primary axial polyp (oozoid) differentiated in a bulbous peduncle for anchorage in soft bottoms, and secondary dimorphic polyps (Williams 2011). Finally, Alcyonacea is the most diverse order, representing more than 1/3 of all species within the subclass, showing several growth forms, being monomorphic or dimorphic, and having the widest bathymetric and geographic ranges (Cairns 2016; Pérez et al. 2016).

As observed on scleractinians, shallow-water and mesophotic octocorals show symbiosis with zooxanthellae (Cordeiro et al. 2015b), but unlike hexacorals, octocorals are rarely addressed in the literature in terms of their existence or facultative symbiosis. In the Atlantic, shallow-water octocorals are mainly represented by gorgonians (the so-called alcyonaceans with supporting axes), whereas in the Indo-Pacific the soft corals are dominant (alcyonaceans lacking supporting rigid axes) (Pérez et al. 2016).

Despite their richness in shallow waters, at least 75% of the octocorals described so far are deep-sea species (Cairns 2007b). This percentage is probably higher since many taxa were described in recent years and sampling is still limited globally (Pante and France 2010; Pante and Watling 2011; Cairns 2016; Cordeiro et al. 2017; Cairns and Cordeiro 2017; Moore et al. 2017). For instance, some regions known as centers of diversity for coral species, such as the Malay Archipelago (Indo-Pacific) and the Gulf of Mexico, are still poorly known in terms of deep-sea octocoral richness (Cairns and Bayer 2009; Pérez et al. 2016).

4.2 Brazilian Deep-Sea Corals

Although some national (such as the Project Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone – REVIZEE; see Amaral and Rossi-Wongtschowski 2004; Perez et al. [this volume](#), Chap. 8) or regional research programs have improved our knowledge on the Brazilian deep-sea fauna, the vast majority of studies focusing on anthozoans from this environment were driven by collections made “by chance”. Additionally, the limited number of Cnidarian taxonomists, the large deep-sea area, limited resources, and the few sampling expeditions resulted in a highly underestimated number of deep-sea octocorallians and scleractinians along the Brazilian continental margin.

Nevertheless, onboard observers on deep-water industrial fisheries reported that several areas of the Brazilian EEZ, especially along the southeastern and southern margin, harbor abundant and diverse coral communities (e.g., Perez and Wahrlich 2005; Kitahara 2009). In these reports, several deep-water coral species, including Scleractinia, Octocorallia, and Antipatharia (see Loiola 2007; Cordeiro et al. 2012) were accidentally sampled as by-catch. Within these areas, the main deep-water coral reef framework builders are the scleractinians *Desmophyllum pertusum* (former *Lophelia pertusa*), *Solenosmilia variabilis*, and *Madrepora oculata* (Castro

et al. 2006; Kitahara 2007; Pires 2007). However, it is important to note that there are slight differences between the deep-water reefs between the southern and southeastern Brazilian margin. On the southern slope, these ecosystems appear to be more continuous if compared to those from the southeastern margin. In the latter, which is the most studied region in terms of framework builders and the only area on Brazil's margin studied by ROVs imaging and geophysical mapping (see Cavalcanti et al. 2017), there are thousands of potential reef targets ranging from 1 to over 2,800 m long that potentially harbor live corals and associated organisms (Cavalcanti et al. 2017). According to Pires et al. (2016) and Cavalcanti et al. (2017), the main framework builders on the S and SE deep-sea margins are *S. variabilis*, *D. pertusum*, *Enallopsammia rostrata*, and *M. oculata*, and some Octocorallia representatives of the families Priminoidae, Clavulariidae, Plexauridae, Alcyoniidae, Isidiidae, Coralliidae, and Paragorgiidae.

The northern and northeastern Brazilian margins are the least studied regions in terms of deep-sea fauna. Recent studies revealed the presence of corals off the continental shelf under the influence of the Amazon river plume in areas previously considered to be unfavorable for the occurrence of these organisms (Cordeiro et al. 2015b; Moura et al. 2016), with records still limited to shallow and mesophotic depths. However, records of *M. oculata*, *S. variabilis*, and *D. pertusum* below the 250 m isobath (at 9, 3, and 17°S, respectively) indicate that deep-water reefs might be more common in these regions than previously thought (Pires et al. 2016, see also Sect. 4.3, Fig. 4.5 and recent data by Cordeiro et al. 2020). It is also important

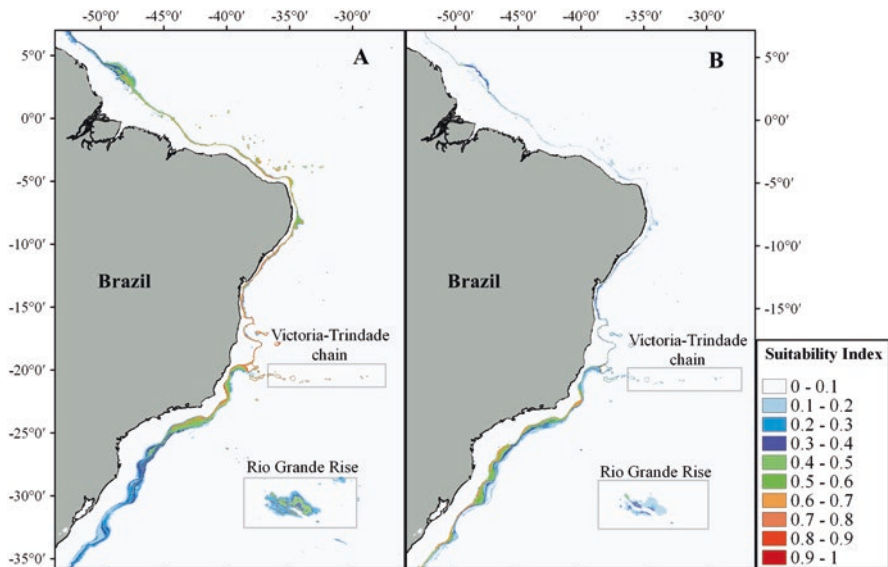


Fig. 4.5 Deep-water azooxanthellate Octocorallia (a) and Scleractinia (b) habitat suitability distribution in the Brazilian continental slope. Suitability Index could take values between 0 and 1, with higher values indicating higher habitat suitability to the deep-water coral group

to note that the Brazilian offshore islands are likely to have favorable environmental conditions for deep-water scleractinians and octocorallians (see Sect. 4.3), of which some have already been reported to Vitória-Trindade seamount chain (Pires et al. 2016), and more recently *M. oculata* has been found at nearly 110 m deep at São Pedro and São Paulo Archipelago (Rocha, personal communication), a location where other solitary species were also observed (Fig. 4.2).

4.2.1 History of the Study of the Deep-Water Scleractinians from Brazil

The scientific research on the Brazilian deep-water coral fauna began in the end of the nineteenth century. At that time, de Pourtalès (1874) studied the zoological material collected during the RV *Hassler* expedition, describing *Rhizosmilia maculata* (as *Bathycyathus maculatus*) from the Abrolhos archipelago (Eastern Brazil), and *Sphenotrochus auritus* from Cabo Frio (SE Brazil). In the same publication, the

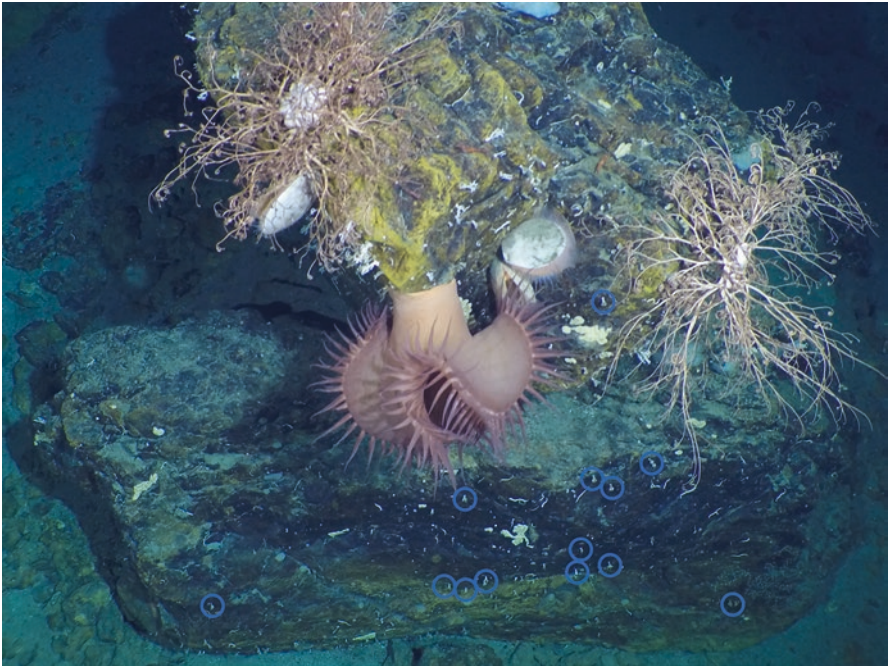


Fig. 4.2 Boulder inhabited by an anemone, echinoderms, mollusks, and several solitary scleractinian corals (some encircled in blue) on the São Pedro e São Paulo Archipelago at 110 m depth. Image ALUCIA AL170602 Cruise to San Peter and San Paul's Rock, June 19 to July 8, 2017

azooxanthellates *Tethocyathus cylindraceus*, *Cladocora debilis* (as *Cladocora patriarca*), and *Madracis asperula* were also reported to Brazil, of which the former two species to Cabo Frio and the latter to the Bahia State. During the following 100 years, ten additional studies on the azooxanthellate coral fauna were published, resulting in five new species occurrences to Brazilian waters – *Deltocyathus halianthus* (Lindström 1877), *Astrangia solitaria* and *A. rathbuni* (Vaughan 1906), *Madracis brueggemanni* (Gardiner 1913), and *Phyllangia americana* (Laborel 1970). At the same time, other studies on this fauna reported new distributional records (Moseley 1881; Squires 1959; Tommasi 1970; Laborel 1970; Wells 1973; Leite and Tommasi 1976). Within these studies, the reported deep-water scleractinian species were *D. halianthus*, *Madrepora oculata*, *Madracis pharensis*, *Fungiacyathus symmetricus*, *Stephanocyathus diadema*, *Deltocyathus italicus*, *Desmophyllum dianthus*, *Cladocora debilis*, *Desmophyllum pertusum* (as *Lophelia pertusa*), *Solenosmilia variabilis*, *Dasmosmilia lymani*, *Stenocyathus vermiformis*, *Trochocyathus* sp., *Deltocyathus calcar*, and *Enallopsammia rostrata*. It is worth noting that Laborel (1970) was the first to mention the occurrence of deep-water coral reefs off Santos Basin (SE Brazil), and together with Tommasi (1970) and Leite and Tommasi (1976), were the only studies at that time that did not rely solely on the sampling efforts of foreign vessels/expeditions (see Pires 2007).

The next pulse of studies that included Brazilian deep-water Scleractinia started with the revision of the Caribbean and Antarctic and Sub-Antarctic corals (Cairns 1977a, b, 1978, 1979, 1982, 2000). Totalling the first report of 27 species, in addition to descriptions and comparisons of further 18 previously recorded species from Brazilian waters, these series continues to serve as the basis for the taxonomy of the Southwestern Atlantic deep-water corals (see Table 4.1). During the time span of these studies, other contributions to the distributional knowledge of the Brazilian azooxanthellate coral fauna have been published (Fernandes and Young 1986; Zibrowius 1988; Pires 1997; Sumida and Pires-Vanin 1997). In addition, although no station numbers were provided, Zibrowius (1988) listed the occurrence of 34 species based on the material collected by the R/V Marion Dufresne (Campagne MD55) including the first report of *Caryophyllia barbadensis*, *Concentrotheca laevigata*, *Deltocyathus agassizi*, and *D. moseleyi*.

The last additions to the azooxanthellate coral fauna from Brazil started on the onset of the twenty-first century, with efforts of Kitahara and Cairns (2005), Castro et al. (2006), Kitahara (2007), Pires et al. (2007), Cordeiro et al. (2012), Pires et al. (2016), and Cavalcanti et al. (2017). Together, these publications added the occurrence of 11 species not previously known to the region, bringing the number of azooxanthellate scleractinians with occurrence in depths greater than 150 m in Brazilian waters to 54 (Fig. 4.3, Table 4.1).

Table 4.1 Deep-water (>150 m) *Scleractinia* and *Octocorallia* and their latitudinal and depth range in Brazil

Species	Latitudinal range	Depth range (m)	Source (first species report)
<i>Scleractinia</i>			
<i>Madracis asperula</i>	1°54'S-22°40'S	45–166	de Pourtalès (1874)
<i>Fungiacyathus symmetricus</i>	09°01'S-27°38'S	46–250	Laborel (1970)
<i>Fungiacyathus crispus</i>	0°18'S-24°20'S	274	Cairns (1979)
<i>Bathelia candida</i>	32°S	500	Cairns (1982)
<i>Madrepora oculata</i>	09°01'S-30°03'S	287–800	Cairns (1979)
<i>Madrepora carolina</i>	ASPSP	100–300	Cairns (1979)
<i>Caryophyllia berteriana</i>	20°40'S-31°20'S	250–800	Kitahara (2007)
<i>Caryophyllia crypta</i>	ASPSP	291	Kitahara (2007)
<i>Caryophyllia barbadensis</i>	Southeastern	5–249	Zibrowius (1988)
<i>Caryophyllia antillarum</i>	24°54'S	141–1000	Cairns (1979)
<i>Caryophyllia paucipalata</i>	19°17'S-19°17'S	500	Pires et al. (2007)
<i>Caryophyllia scobinosa</i>	Southern	–	Kitahara (2007)
<i>Caryophyllia ambrosia</i>	0°18'S-32°50'S	274–1326	Cairns (1979)
<i>Premocyathus cornuformis</i>	0°18'N-31°14'S	46–600	Cairns (1979)
<i>Coenocyathus parvulus</i>	21°48'S-31°17'S	50–300	Cairns (1979)
<i>Concentrotheca laevigata</i>	–	–	Zibrowius (1988)
<i>Trochocyathus rawsonii</i>	0°18'N-31°05'S	274–300	Cairns (1979)
<i>Trochocyathus laboreli</i>	15°54'S-33°45'S	125–390	Cairns (2000)
<i>Paracyathus pulchellus</i>	0°18'N-33°37'S	6*-310	Cairns (1979)
<i>Cladocora debilis</i>	19°43'S-34°29'S	46–438	de Pourtalès (1874)
<i>Stephanocyathus diadema</i>	8°37'S-25°53'S	1234–2212	Laborel (1970)
<i>Stephanocyathus coronatus</i>	–	900	Cordeiro et al. (2015b)
<i>Stephanocyathus laevifundus</i>	–	900	Cordeiro et al. (2015b)
<i>Stephanocyathus paliferus</i>	0°18'N-22°24'S	274–1649	Cairns (1977b)
<i>Deltocyathus italicus</i>	03°20'S-29°29'S	46–2150	Laborel (1970)
<i>Deltocyathus agassizi</i>	–	–	Zibrowius (1988)
<i>Deltocyathus calcar</i>	09°01'S-32°40'S	91–560	Cairns (1979)
<i>Deltocyathus eccentricus</i>	0°18'S-29°29'S	240–700	Cairns (1979)
<i>Deltocyathus moseleyi</i>	20°40'S	120–520	Zibrowius (1988)
<i>Deltocyathus pourtalesi</i>	24°09'S	600	Pires et al. (2007)
<i>Desmophyllum dianthus</i>	22°13'S-34°12'S	768–1127	Laborel (1970)
<i>Desmophyllum pertusum</i> (former <i>Lophelia pertusa</i>)	17°25'S-34°50'S	272–1152	Laborel (1970)
<i>Monohedotrochus capitollii</i>	28°43'S-35°00'S	150–460	Kitahara and Cairns (2005)
<i>Anomocora fecunda</i>	0°55'N-0°18'S	182	Cairns (1979)
<i>Pourtalesmilium conferta</i>	0°55'N-33°41'S	55–220	Cairns (1978)
<i>Phacelocyathus flos</i>	09°01'S	560	Cairns (1979)

(continued)

Table 4.1 (continued)

Species	Latitudinal range	Depth range (m)	Source (first species report)
<i>Solenosmilia variabilis</i>	03°20'S-34°33'S	46–1350	Laborel (1970)
<i>Dasmosmilia lymani</i>	03°20'S-31°23'S	86–320	Laborel (1970)
<i>Dasmosmilia variegata</i>	0°18'S-24°25'S	180–320	Cairns (1979)
<i>Deltocyathoides simpsonii</i>	0°18'N	274	Cairns (1979)
<i>Sphenotrochus auritus</i>	1°12'S-34°35'S	15–171	de Pourtalès (1874)
<i>Flabellum</i> cf. <i>alabastrum</i>	19°50'S-20°04'S	666–686	Pires et al. (2007)
<i>Flabellum apertum</i>	5°S-34°36'S	400–900	Cairns (1982)
<i>Flabellum floridanum</i>	Off São Paulo	–	Pires et al. (2007)
<i>Placotrochides frustum</i>	3°22'S	763	Cairns (1979)
<i>Javania cailleti</i>	17°04'S-33°42'S	107–250	Cairns (1979)
<i>Polymyces fragilis</i>	0°18'S-32°24'S	130–650	Cairns (1979)
<i>Schizocyathus fissilis</i>	24°42'S-25°16'S	258–320	Pires et al. (2004)
<i>Stenocyathus vermiformis</i>	0°18'S-24°36'S	128–650	Laborel (1970)
<i>Eguchipsammia gaditana</i>	0°55'S	110–291	Cairns (1979)
<i>Eguchipsammia cornucopia</i>	03°54.9'S	380	Cordeiro et al. (2012)
<i>Cladopsammia manuelensis</i>	27°51'S-33°42'S	78–320	Cairns (1979)
<i>Dendrophyllia alternata</i>	23°49'S-31°03'S	277–530	Le Goff-Vitry et al. (2004)
<i>Enallopsammia rostrata</i>	20°28'S-30°03'S	270–1332	Laborel (1970)
Octocorallia			
<i>Acanthogorgia aspera</i>	04°N-18°S	60–417	Castro et al. (2006)
<i>Acanthogorgia schrammi</i>	04°N-20°S	60–360	Bayer (1959)
<i>Anthoptilum murrayi</i>	13°S-22°S	600–1799	Castro et al. (2006)
<i>Anthomastus grandiflorus</i>	19°S-22°S	808–1664	Castro et al. (2006)
<i>Anthothela grandiflora</i>	22°S-34°S	882–1059	Arantes and Medeiros (2006)
<i>Caliacis nutans</i>	22°S	240–300	Castro et al. (2006)
<i>Corallium medea</i>	22°S	552	Castro et al. (2003)
<i>Corallium niobe</i>	22°S	1150–1152	Pires and Castro et al. (2010)
<i>Iciligorgia schrammi</i>	04°N-01°S	1110–1130	Bayer (1959)
<i>Chrysogorgia elegans</i>	08°S	128–1.716	Deichmann (1936)
<i>Chrysogorgia fewkesi</i>	04°S	430–1200	Cordeiro et al. (2015a)
<i>Chrysogorgia multiflora</i>	04°N-22°S	320–1280	Deichmann (1936)
<i>Chrysogorgia tuberculata</i>	04°N	914–2.265	Cordeiro et al. (2015a)
<i>Radicipes kopelatos</i>	13°S-21°S	592–750	Castro et al. (2006)
<i>Telestula kuekenhali</i>	19°S	1059–1732	Pires and Castro et al. (2010)
<i>Ellisella elongata</i>	04°N-27°S	3–706	Bayer (1959)
<i>Nicella americana</i>	02°S	62–237	Cairns (2007b)

(continued)

Table 4.1 (continued)

Species	Latitudinal range	Depth range (m)	Source (first species report)
<i>Nicella guadalupensis</i>	01°S-22°S	27–395	Castro et al. (2006)
<i>Nicella toepflitzae</i>	18°S	55–329	Viada and Cairns (2007)
<i>Leptogorgia pseudogracilis</i>	19°S-21°S	66–180	Castro et al. (2010)
<i>Acanella arbuscula</i>	19°S-21°S	425–2875	Pires et al. (2004)
<i>Isidella longiflora</i>	15°S-21°S	1130	Castro et al. (2006)
<i>Paragorgia johnsoni</i>	13°S-21°S	513–4152	Grasshoff (1980)
<i>Bebryce cinerea</i>	19°S-22°S	60–619	Medeiros and Castro (1999)
<i>Bebryce parastellata</i>	04°N	104–497	Medeiros and Castro (1999)
<i>Heterogorgia uatumani</i>	04°N-SC	52–200	Medeiros and Castro (1999)
<i>Muricea midas</i>	01°S	?–324	Bayer (1959)
<i>Muriceides hirtus</i>	01°S	234	Medeiros and Castro (1999)
<i>Paramuricea placomus</i>	13°S-24°S	665–1000	Castro et al. (2006)
<i>Placogorgia atlantica</i>	ASPS, 04°N-18°S	1700(?)	Medeiros and Castro (1999)
<i>Scleracis guadalupensis</i>	04°N-18°S	60–390	Medeiros and Castro (1999)
<i>Thesea antiopae</i>	01°S	315–324	Bayer (1959)
<i>Thesea bicolor</i>	04°N-21°S	60–180	Deichmann (1936)
<i>Villogorgia nigrescens</i>	19°S-20°S	100–520	Medeiros and Castro (1999)
<i>Calyptrophora microdentata</i>	21°S	1059–1152	Arantes and Loiola (2014)
<i>Candidella imbricata</i>	21°S	1059–1605	Arantes and Loiola (2014)
<i>Callogorgia americana</i>	04°S	183–965	Bayer et al. (2015)
<i>Callogorgia arawak</i>	04°S	137–365	Bayer et al. (2015)
<i>Dasysystenella acanthina</i>	34°S	810	Arantes and Loiola (2014)
<i>Plumarella diadema</i>	22°S-24°S	640–659	Arantes and Loiola (2014)
<i>Primnoella delicatissima</i>	04°N-34°S	10–160	Cairns (2006)
<i>Primnoella polita</i>	08°S-22°S	36–154	Cairns (2006)
<i>Thouarella koellikeri</i>	22°S-24°S	609–659	Arantes and Loiola (2014)
<i>Pennatula bayeri</i>	13°S-19°S	727–1318	Castro and Medeiros (2001)
<i>Umbellula thomsonii</i>	04°S-21°S	557–6200	Castro and Medeiros (2001)

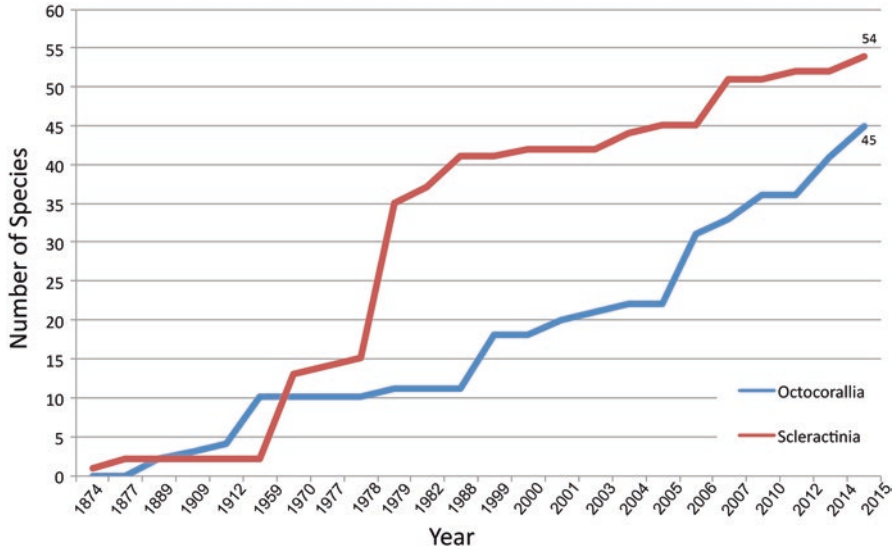


Fig. 4.3 Cumulative number of deep-water (>150 m deep) *Scleractinia* and *Octocorallia* species recorded in Brazil from 1874 through 2015

4.2.2 History of the Study of the Deep-Water Octocorallians from Brazil

Considering the reports of deep-water octocorals from Brazil, we propose two periods of research and discovery: the first, resulting from international surveys (1872 to the early 1980s), and the second, led by Brazilian national endeavors (from 1990s to present days). It is worth to mention that we arbitrarily accounted records below 150 m herein, which unfortunately may ignore some continental shelf/upper-slope species, even when they are expected to occur in such depths (e.g., *Nicella goreau*, 45 to 146 m, and *Swiftia exserta*, 34 to 93 m).

The first period started with surveys of the USCSS *Hassler* (1872) (see Deichmann 1936) and the HMS *Challenger* (1873) expeditions. The latter took almost 20 years to have its results published (Wright and Studer 1889), including the report of two species from the St. Peter and Paul's archipelago: *Paramuricea aequatorialis* and *Placogorgia atlantica*. The first period has also the contributions from expeditions of the RV *Valdivia* (1898) (Kükenthal 1919), RV *Oregon* (Bayer 1959), and RV *Calypso* (Tixier-Durivault 1970). Some of the *Oregons'* material has been published only recently (Cairns 2001, 2007b). By the end of this period (1960–1970), some Brazilian deep-sea oceanographic expeditions were performed, but their results, especially those focusing on Octocorallia, have been only recently published (Cairns 2006; Cordeiro et al. 2015a).

The examination of the REVIZEE materials and samples from other sources resulted in the description of several species and the first summarization of the

knowledge of the Brazilian Octocorallia (Marques and Castro 1995; Castro and Medeiros 2001; Arantes and Medeiros 2006; Castro et al. 2006; Pires et al. 2007). In addition, results from other deep-water surveys mostly from the southern Brazilian slope (Arantes et al. 2009; Pires and Castro 2010; Arantes and Loiola 2014) have quadruplicated the number of deep-water octocorals recorded from Brazil (Fig. 4.3, Table 4.1). More recently, preliminary and/or partial results of the BPot (Environmental Characterization of the Continental Slope from the Potiguar Basin – Brazilian northern slope), Rio Grande Rise Iatá-Piúna Brazil/Japan Cooperation (Fig. 4.4), and of the South Atlantic MAR-ECO (SA MAR-ECO) projects suggest a higher Octocorallia diversity in the Southwestern Atlantic (Perez et al. 2011; Bayer et al. 2015; Cordeiro et al. 2015a).

Indeed, several factors suggest that the Octocorallia species richness in Brazil is underestimated. Rarefaction curve (not shown) of the best-known region for this fauna in Brazil (southeastern region) shows that the area is still insufficiently sampled, as also indicated by species accumulation curve (Fig. 4.3). Furthermore, there are at least 30 morphotypes/undescribed species known from unpublished work during the last decade, and about half of the specimens collected in Brazil by the RV *Oregon* are not identified to species level yet (S. D. Cairns, pers. comm.). Thus, revisionary studies are also needed. For example, the identification of the 31 species

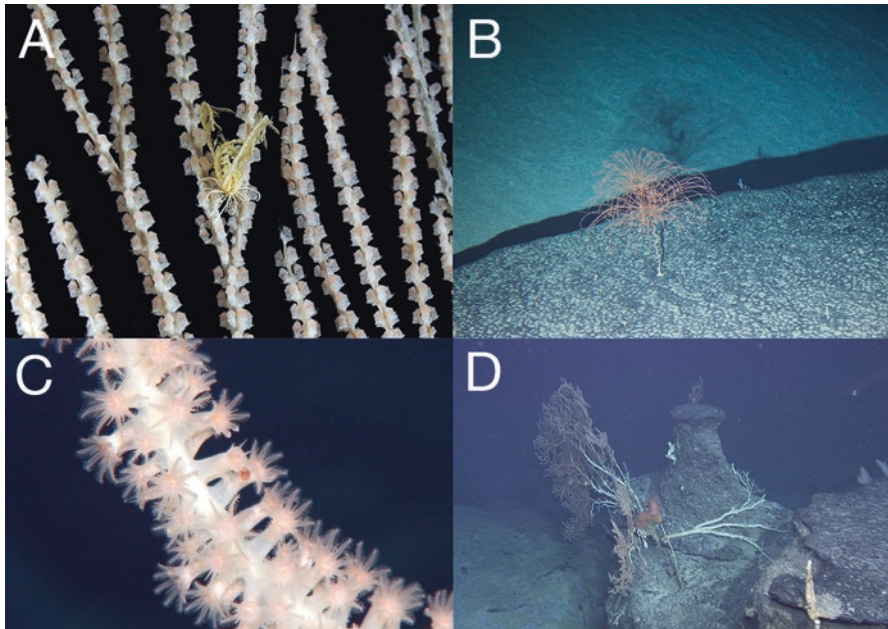


Fig. 4.4 Octocorals from the Rio Grande Rise (SW Atlantic) at ca. 900 m depth. A. Primnoid specimen with a crinoid attached. B. The spiral octocoral *Iridogorgia*. C. Detail of the polyps of an isidid octocoral. D. General view of octocorals attached to basalts. Images: Iatá-Piúna Consortium – JAMSTEC/IOUSP

sampled by the RV *Calypso* (Tixier-Durivault 1970) remains uncertain (Castro et al. 2006; Ofwegen 2007), and the Brazilian records of *Nicella guadalupensis* (Castro et al. 2006; Cordeiro et al. 2015b) also need confirmation in light of a recent revision of the genus, once Cairns (2007b) did not consider the occurrence of this species in Brazil.

4.3 Modeling the Distribution of Deep-Sea Corals from Brazil

Deep-water coral habitats, considered Vulnerable Marine Habitats (VMEs; see Fuller et al. 2008), are widespread along continental margins around the world (Roberts et al. 2009). These habitats are important targets for conservation given the biodiversity they sustain and also their susceptibility to anthropogenic impact (Rogers et al. 2008). Since these environments occur over large ocean areas and costs associated to their exploration are high, Habitat Suitability Models (HSM) may offer important insights on where to implement protection areas. HSM, also called Ecological Niche Models (ENMs), determine the associations between species and environmental conditions where they occur (Soberón and Peterson 2005; Peterson 2006). From these results it is possible to identify the suitability of different habitats for each species along a grid in the geographic space, which are defined by real or modelled conditions (Soberón 2007).

HSM for Octocorallia and Scleractinia run for the Brazilian margin between 200 and 2,500 m depth show that, in general, particulate organic carbon (POC), dissolved oxygen, water current velocity, carbonate saturation state, temperature, and bathymetry characterize the potential distribution areas of corals (Barbosa et al. 2020). Octocorallia and Scleractinia models suggest that carbonate saturation state (i.e., calcite and aragonite for Octocorallia and Scleractinia, respectively), temperature, and bathymetry are the main factors structuring habitat suitability distributions along the Brazilian slope (Barbosa et al. 2020). Similar results have been also observed from global HSM studies (Davies et al. 2008; Tittensor et al. 2009; Davies and Guinotte 2011; Yesson et al. 2012). Nevertheless, models indicate that dissolved oxygen and POC are also important factors for scleractinian and octocoral distributions, respectively.

HSM for Octocorallia show a large latitudinal habitat suitable distribution covering all continental slope (Fig. 4.5a). However, the Southern Brazilian slope is characterized by a low suitability, being considered unsuitable (suitability index-SI < 0.41) in the major part of their slope (based in the 10% training presence logistic threshold) (Fig. 4.6). On the contrary, Central and North Brazilian continental slope are highly suitable (SI > 0.41). In concordance with these results, recent studies have reported that octocorals, in association with sponges, are important framework builders in the Northern Brazilian mesophotic and shallow waters (Cordeiro et al. 2015b; Moura et al. 2016) (see also Sect. 4.2). The suitable habitat

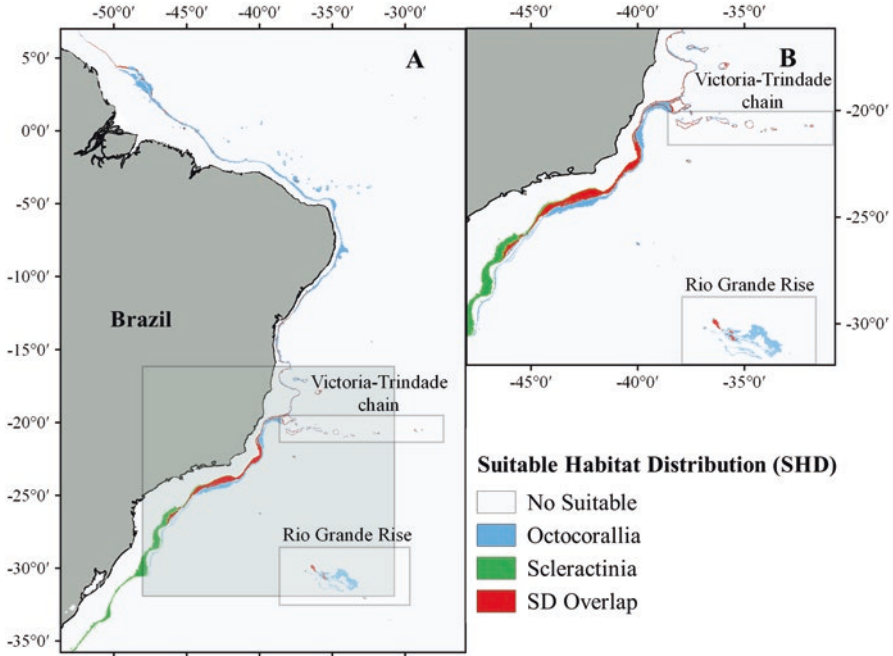


Fig. 4.6 Suitable habitat distribution (SHD) for Octocorallia (light blue) and Scleractinia (green) on the Brazilian continental slope (a), with the main overlap area between Octocorallia and Scleractinia suitable habitat (red) (b). The SHD was generated from binary maps of MaxEnt models, based in the threshold of 10 percentile training presence

predicted at the Rio Grande Rise is also in concordance with unpublished data from recent expeditions (Fig. 4.4) (Barbosa et al. 2020).

Conversely, models suggest that the Central and Southern Brazilian slope provides highly suitable habitat for scleractinians (Fig. 4.5b), whereas the Northern and Northeastern slopes are considered as a not suitable habitat (SI < 0.38) (based on the 10% training presences logistic threshold) (Fig. 4.6a). Such predictions in the Central and Southern slopes are supported by observation in the Campos (Arantes and Loiola 2014), Santos (Sumida et al. 2004), and Pelotas Basins (Kitahara 2007) (see Sect. 4.2.1). In the Northern slope, dissolved oxygen decreases to $\leq 3.5 \text{ ml.l}^{-1}$ near the bottom in the shelf break (Moura et al. 2016) and could be a limiting factor for scleractinians since it is considered an important factor for its survival. For example, *Desmophyllum pertusum* cannot maintain respiration rates if subjugated to dissolved oxygen concentrations lower than 3.3 ml.l^{-1} (Dodds et al. 2007; Brooke et al. 2013; Lunden et al. 2014). Scleractinia HSM suggest that most suitable habitats present between 4 and 5 ml.l^{-1} dissolved oxygen concentrations. Similarly, in the Northeast Atlantic, *D. pertusum* records were from sites with oxygen concentration from 4.3 to 7.2 ml.l^{-1} (Davies et al. 2008). Bottom oxygen concentrations from the Central and South Brazilian slope (bathed by Antarctic Intermediate Water

mass – AIW) are favorable for deep-water corals and necessary for Scleractinia (Viana et al. 1998; Arantes et al. 2009; Sumida et al. 2004).

The wide suitable area for octocorals reflects the high number of species of the group (see Sect. 4.1.2), indicating that they likely have higher tolerance and adaptations to variable environmental conditions as a group. For instance, Octocorallia suitable habitat distribution also included areas with low values of dissolved oxygen concentrations (2 ml.l^{-1}), which are unsuitable for Scleractinia.

Both, Scleractinia and Octocorallia have overlapping of habitat suitable distribution at the Central and South slope, on the Vitória-Trindade seamount chain, and on the Rio Grande Rise (Fig. 4.6b). These overlapping areas may be hotspots of deep-water corals and should be of priority for conservation. Particularly, Campos and Santos basins are especially important for management and conservation efforts, since there is a high economic interest for fisheries, oil and gas, and other natural resources (Almada and Bernardino 2017, Bernardino and Sumida 2017; see Sect. 4.5).

4.4 Reproduction in the Deep-Sea Coral Habitats

Coral reefs are hotspots of biodiversity, providing a rich habitat and plentiful food supply for assemblages of invertebrates and fishes. The diversity of organisms associated with deep-sea coral habitats, including several commercially valuable species, is high, and may be even higher than that found in tropical shallow reefs. Reproduction is the key process for the maintenance and renewal of coral populations. Data on biology and reproductive strategies are crucial for conservation, improvement of management practices, and design of marine protected areas.

Until recently, there was only sporadic and sparse information about aspects of reproduction from reef corals around the world. Approximately four decades ago, the spectacular phenomenon of coral mass spawning was discovered on the Great Barrier Reef of Australia (Harrison et al. 1984).

After that, reproductive data of corals from the North Atlantic, Caribbean, Red-Sea, and Indo-Pacific became available. In the Southwestern Atlantic (Brazil), the reef coral reproduction research began 20 years ago, and the first information were obtained through the study of three species of the endemic genus *Mussismilia* (Pires et al. 1999). This knowledge on the Brazilian coral fauna has advanced through dissertations, thesis, and scientific articles, and, nowadays, reproduction data are available from the ten major shallow coral reef building species, as well as for the endemic gorgonian *Phyllogorgia dilatata*, and two invasive sun-coral species (*Tubastraea*) (Pires et al. 2016). Nonetheless, the reproductive aspects of deep-sea corals are more restricted and sparse. Among the approximately 700 known azooxanthellate scleractinians, of which the majority inhabits the deep sea, information on sexual reproduction is available for approximately 20 species.

Studies in the deep-sea impose logistical and economical challenges, limiting investigations that require chronological long-term sampling, such as those for

reproduction studies, which include timing and periodicity aspects. Data are usually based on incomplete sampling, using specimens collected for general fauna surveys and not specifically for research on their reproductive strategies (Pires et al. 2014).

The first reproduction study of a deep-sea coral species from Brazil was performed in the Octocorallia – pennatulacean *Anthoptilum murrayi* (see Pires et al. 2009). Results indicated that *A. murrayi* is gonochoric, following the same general pattern of sexual development as seen in pennatulaceans and some other octocorals. It displays a 1:1 sex ratio, and a continuous and long breeding activity (Fig. 4.7), differing from most pennatulaceans, which rather present seasonal cycles. Male and female gametes are visible to naked eye, reaching up to 1250 μm , indicating the production of lecithotrophic larvae. Most oocytes were observed in the earliest stages of development and basal polyps present the highest frequency of small eggs. Females have up to 90 oocytes per polyp and 25,713 to 35,918 oocytes per colony. Male colonies of similar size to female samples were shown to have 6 to 76 cysts per polyp and 14,014 to 27,019 cysts per colony.

High fecundity, the presence of primitive “spermatophores” (sensu Eckelbarger et al. 1998), a large number of polyps per colony, and a patchy distribution would enhance the chance of fertilization for *A. murrayi* and may guarantee a successful reproductive strategy for this gonochoric sessile species (Pires et al. 2009).

Data on the reproductive biology of deep-sea reef-building corals from Campos Basin (CB), off Rio de Janeiro State, were obtained from 2008/2009 collections (Pires et al. 2014). These five selected framework-forming species *Madrepora oculata*, *Desmophyllum pertusum*, *Solenosmilia variabilis*, *Enallopsammia rostrata*

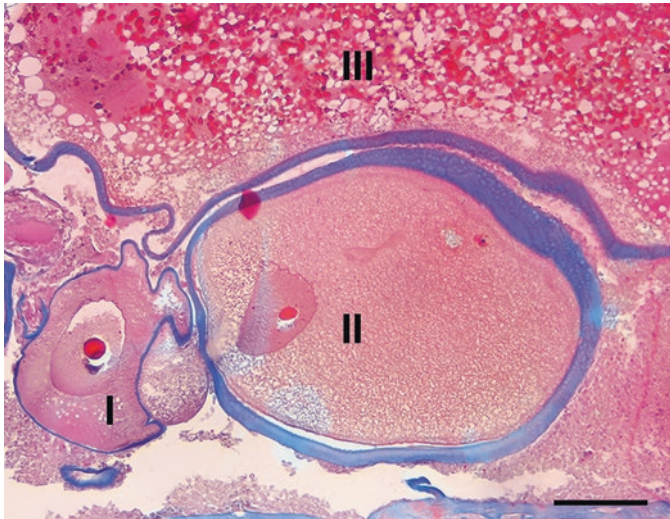


Fig. 4.7 *Anthoptilum murrayi*. Oocytes in three different stages of development occurring together, indicating a continuous reproduction. Stage I oocyte (1), Stage II oocyte (2), and part of a Stage III oocyte (3). Scale bar: 100 μm

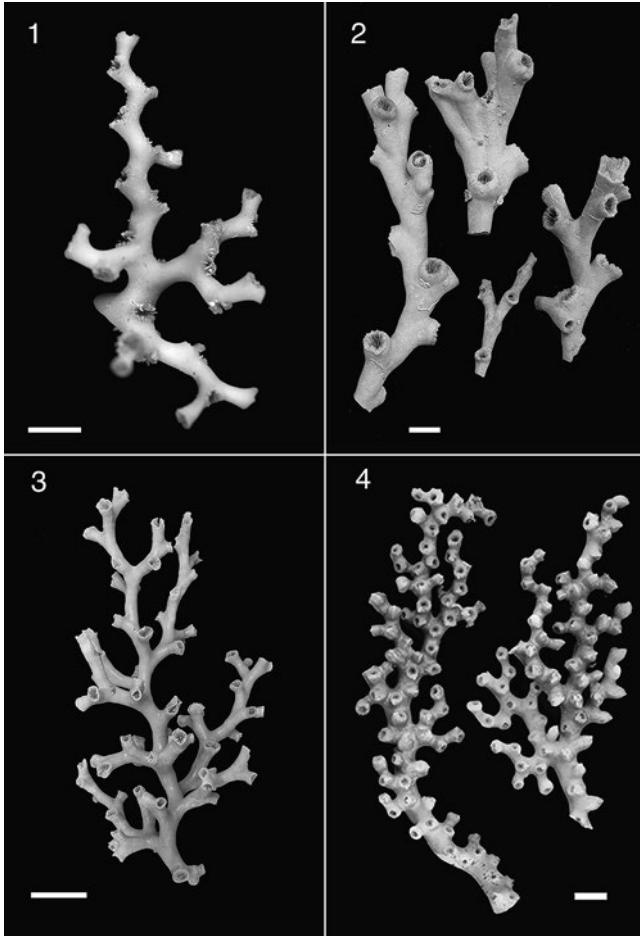


Fig. 4.8 Deep-sea coral reef builders from Campos Basin, Brazil. 1. *Madrepora oculata*, 2. *Desmophyllum pertusum* (former *Lophelia pertusa*), 3. *Solenosmilia variabilis*, 4. *Enallopsammia rostrata* (Anthozoa, Scleractinia). Scale bars: (1) = 5 mm, (2)–(4) = 1 cm

(Anthozoa, Scleractinia) (Fig. 4.8), and *Errina* sp. (Hydrozoa, Anthoathecata) (Fig. 4.9) occur along the Brazilian continental margin (Pires and Castro 2010).

The hydrocoral *Errina* sp. is a gonochoric brooder species, as the vast majority of Stylasteridae (Silva 2013). Although considered gonochoric, among 56 examined specimens, one colony was hermaphroditic, and the observed sex ratio was 1:1. *Errina* sp. has a continuous gametogenesis, with no reproductive peak. Embryos and planulae were observed throughout the year (Fig. 4.9). The presence of large mature oocytes, with maximum diameter of 790 μm , indicates the production of lecithotrophic larvae (Silva 2013).

Colonies of the deep-sea scleractinians of both sexes were also observed, indicating that all five coral species are gonochoric. This appears to be the predominant

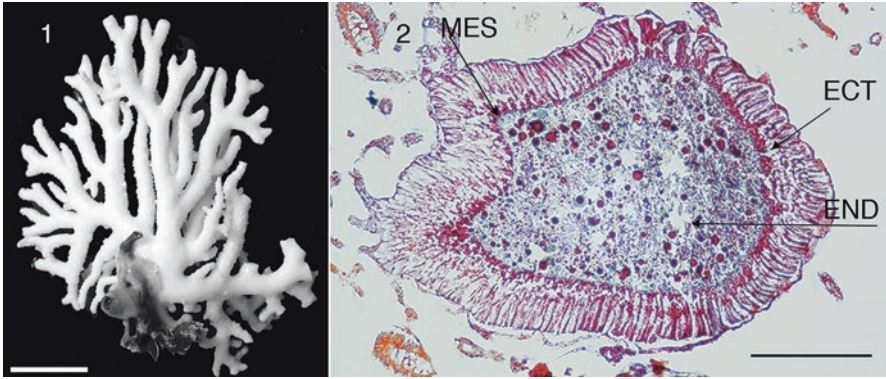


Fig. 4.9 *Errina* sp. (Hydrozoa, Anthoathecata). 1. Colony fragment. 2. Planulae. Ect, ectoderm; end, endoderm; mes, mesoglea. Scale bars: (1) = 2 cm, (2) = 200 μ m. (Adapted from Silva 2013) (See descriptions of gametogenesis and embryogenic processes in Silva 2013)

reproductive pattern observed in the studied area, as well as in deep-sea corals in general. Although also considered functionally gonochoric as *Errina* sp., *M. oculata* and *D. pertusum* presented a few colonies showing different hermaphroditism patterns. In one colony of *M. oculata*, oocyte and spermatocysts were observed in the same polyp, and in other specimens oocytes and spermatocysts occurred in different polyps (60 examined colonies). Surprisingly, these hermaphroditic colonies presented oocytes in only one stage of development, differing from all other examined female colonies, which had a high frequency of oocytes at stage I, as well as the occurrence of oocytes in different maturation phases. Among the 59 examined specimens of *D. pertusum*, only one was hermaphroditic.

The timing of reproduction varied among the different scleractinian species. *Enallopsammia rostrata* and *M. oculata* presented continuous reproduction (as *Errina* sp.) (Fig. 4.10). Based in female colonies from four different months and years, the former species was considered as having a periodical reproduction in the Northeastern Atlantic (see Waller and Tyler 2005). Colonies of *S. variabilis* were fertile year-round, but the timing of reproduction was not so obvious (Fig. 4.11). It seems that they have a reproductive peak between April and September (Autumn–Spring), contrasting with the seasonal reproduction recorded in the Southwestern Pacific, based in an April sample only (Burgess and Babcock 2005). The possible spawning season of *D. pertusum* from CB concentrates between May and July and was indicated by the high frequency of mature gametes during these months (Fig. 4.11) (Pires et al. 2014). Spawning of *D. pertusum* occurs between January and March in the North Atlantic and between September and November in the Gulf of Mexico (Brooke and Järnegren 2013).

According to Pires et al. (2014), these deep-sea corals are broadcast spawners, which is the dominant pattern of reproduction in CB (four deep-sea reef coral builder spp. and *A. murrayi*). These corals produce large oocytes (*M. oculata* – up to 650 μ m, *S. variabilis* – up to 337 μ m, and *E. rostrata* – up to 1095 μ m), which

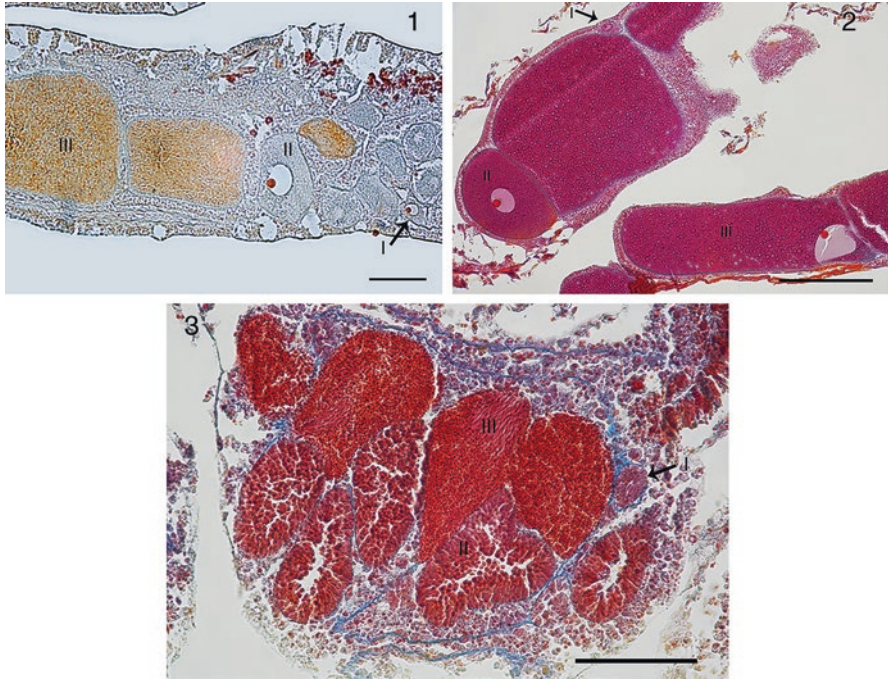


Fig. 4.10 Different stages of development of oocytes and spermatic cysts occurring together in the same mesentery, indicating a continuous reproduction. 1. *Madrepora oculata*, stages I–III oocytes, (2) and (3) *Enallopsammia rostrata*, stages I–III oocytes and stages I–III spermatic cysts, respectively. Scale bars: (1)–(2) = 100 μm , (3) – 200 μm (See descriptions of gametogenesis processes of *M. oculata* and *E. rostrata* in Pires et al. 2014)

may give rise to lecithotrophic larvae. However, the maximum oocyte diameter observed in *D. pertusum* was 242 μm . The presence of both sexes and fertile colonies suggest that potentially cross-fertilization and larval production may occur in CB.

Fragmentation is very common in branching coral colonies. This mode of asexual reproduction may also be occurring in these key deep-sea coral reef builder species (Pires et al. 2014).

4.5 Anthropogenic Impacts on Brazilian Deep-Water Coral Ecosystems

Deep-water coral ecosystems are primarily structured by slow growing, long-lived scleractinians, which sometimes take several thousands of years to flourish (Risk et al. 2002; Roark et al. 2006, 2009; Orejas et al. 2008). In general, if impacted, deep-water reefs take longer to recover if compared to their shallow-water

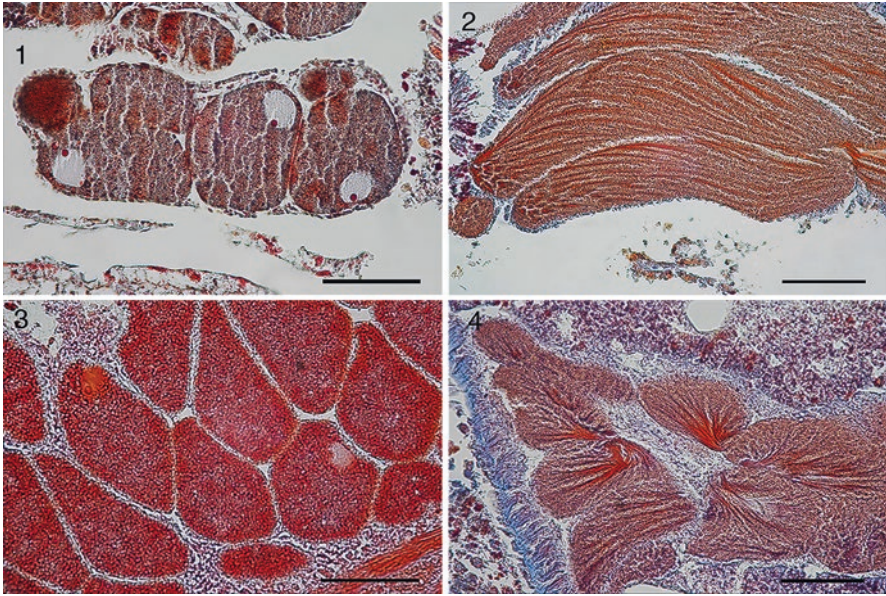


Fig. 4.11 Presence of only mature gametes, indicating a close possible spawning event. (1, 2) *Solenosmilia variabilis*. (3, 4) *Desmophyllum pertusum* (former *Lophelia pertusa*). (1, 3) Stage III oocytes, (2, 4) Stage III spermatid cysts. N, nucleus; n, nucleolus; St, sperm tail. Scale bars: (1)–(2) = 100 μ m (See descriptions of gametogenesis processes of *S. variabilis* and *D. pertusum* in Pires et al. 2014)

counterparts. Several human activities exert direct and indirect impacts on these ecosystems, being deep-water trawling the most damaging (e.g., Hall-Spencer et al. 2002; Watling 2014). This fishery uses nets that bear several meters of chains that are dragged across the ocean floor, breaking the corals and disturbing the sediments (re-suspending them) around it. In addition to industrial fisheries, mining and oil and gas exploration are also harmful to deep-water reefs (Roberts et al. 2009). The impacts of oil and gas activities are related to chronic/acute spills and the deployment of pipes and other equipment (see Etnoyer et al. 2016). In terms of mining, especially focused in polymetallic nodules, sulfide deposits and cobalt-rich ferromanganese crusts, deep-water reefs risks include habitat degradation and reduced complexity, increase of suspended sediments, and potential release of toxic waste (e.g., Ahnert and Borowski 2000). According to Jones et al. (2017), impacts from polymetallic nodules mining are severe, including major negative changes in density and diversity of deep-water species.

In addition to these direct impacts, the increase of atmospheric carbon dioxide from human activities is warming up the oceans and decreasing its pH. Consequences of such changes include the Aragonite Saturation Horizon (ASH) depth decrease (see Guinotte et al. 2006), which means that deep-water corals may decalcify, erode, or stop/slow down their growth.

4.5.1 Fisheries

The escalating demand for marine related protein associated to the collapse of fisheries on continental shelves and the high commercial value of demersal fishes and crustaceans, resulted in a substantial fishery effort increment for deep-sea species. In Brazil, several deep-sea fisheries have rapidly depleted or severely decreased the stock of long-lived, slow-growing deep-sea fishes (e.g., *Lophius gastrophisus*, *Urophycis brasiliensis*, and *Genipterus brasiliensis*) and crustaceans (e.g., *Chaceon* spp., *Aristaeopsis edwardsiana*, *Aristaeomorpha foliacea*, *Aristeus antillensis*) along the upper slope (e.g., Perez and Wahrlich 2005). Within these and other species, numerous have been shown to live adjacent to or in deep-water coral ecosystems (e.g., Auster 2005; Pezzuto et al. 2006; D’Onghia et al. 2012) or even have part of its life cycle associated to these biogenic bottoms (Costello et al. 2005).

Several studies have shown that large concentrations of deep-water corals provide several biological/ecological functions that are scarce in deep ocean (Fosså et al. 2002; Hosebø et al. 2002; Krieger and Wing 2002; Costello et al. 2005; Roos and Quattrini 2007). Indeed, highly valuable commercial deep-water fishes, crustaceans, and cephalopods are usually associated with deep-water reefs (Roos and Quattrini 2007; Foley et al. 2010), resulting in a fishery activity trend that imposes several impacts to azooxanthellate coral habitats (Roberts et al. 2009).

Among the common deep-water demersal fisheries (bottom-trawl, bottom-gillnet, bottom-longline, and trap), trawling is the one causing the most threat/damage to sessile invertebrate communities such as those formed by corals and sponges (Roberts et al. 2000, 2003; Rogers 2004; Freiwald et al. 2004, reviewed in Clark et al. 2016). Indeed, it was not uncommon the report of large trawlers deploying nets over large deep-water reefs. Such impact has been extensively documented in areas previously known as *D. pertusum* habitats, which later displayed only scarred or crushed coral skeleton fragments (Fosså et al. 2002). Apart from North Atlantic, several other deep-water coral ecosystems have been severely impacted by fisheries, including those in the continental shelf/slope from Australia (Koslow et al. 2001; Althaus et al. 2009), New Zealand (Clark and Rowden 2009), Canada (Gass and Willison 2005), Ireland (Hall-Spencer et al. 2002), United Kingdom (Wheeler et al. 2005), United States (Reed 2002), and Brazil (Kitahara 2009) (Fig. 4.12).

In Brazilian waters, Kitahara (2009) showed that not only bottom-trawlers but also other demersal fisheries such as bottom-gillnet, bottom-longline, and trap were seriously damaging unidentified deep-water coral reefs. In the same study, the main areas used by demersal fisheries were indicated to overlap the known Southern Brazilian continental slope coral distribution (Fig. 4.13). In addition to the severe impact on the main framework builders (e.g., *D. pertusum*, *S. variabilis*, *M. oculata*) (Fig. 4.8), small solitary scleractinian species, large octocorallians (e.g., *Paragorgia* spp.), and antipatharians have also been reported as by-catch (Kitahara 2009). According to Freiwald et al. (2004), due to their (i) very low growth rate (mature deep-sea coral reefs take thousands of years to accumulate), (ii) unknown resilience (recovery from trawling impacts, if it occurs, is likely to be slow, and where corals



Fig. 4.12 By-catch of corals in southern Brazilian waters: (a) bottom-gillnet (FV Sufolck chief-tain, photo: Jackson Z. Krauspenhar/PROA/UNIVALI/SEAP), (b) bottom-trawl (photo: Leandro Desso/PROA/UNIVALI/SEAP), (c) bottom-trawl (FV Insung 207, photo: Anderson R. Voos/PROA/UNIVALI/SEAP), and (d) trap (FV Eder Sands, photo: G.S. Soares/PROA/UNIVALI/SEAP). Image modified from Kitahara (2009)

were completely destroyed recovery is unlikely (Gianni 2004; Althaus et al. 2009; Williams et al. 2010)), and (iii) ecological importance (once destroyed, all associated animal community will be lost), it is considered that deep-water corals are “extremely vulnerable” to fishing gear in both, direct and indirect ways.

4.5.2 Mining and Oil and Gas Exploration

Mirroring the offshore trend in fisheries, the mining and hydrocarbon industry are exploiting resources in progressively deeper waters (Roberts et al. 2009; Cordes et al. 2016). To date, the risks imposed by such industries are still poorly understood. However, it may be affecting the nearby deep-water corals with increasingly turbidity, leaking of fluids and waste, and also equipment deployments. Cordes et al. (2016) thoroughly reviewed the environmental impacts of the deep-water oil and gas industry, relating the impacts to routine operations or accidental oil and gas

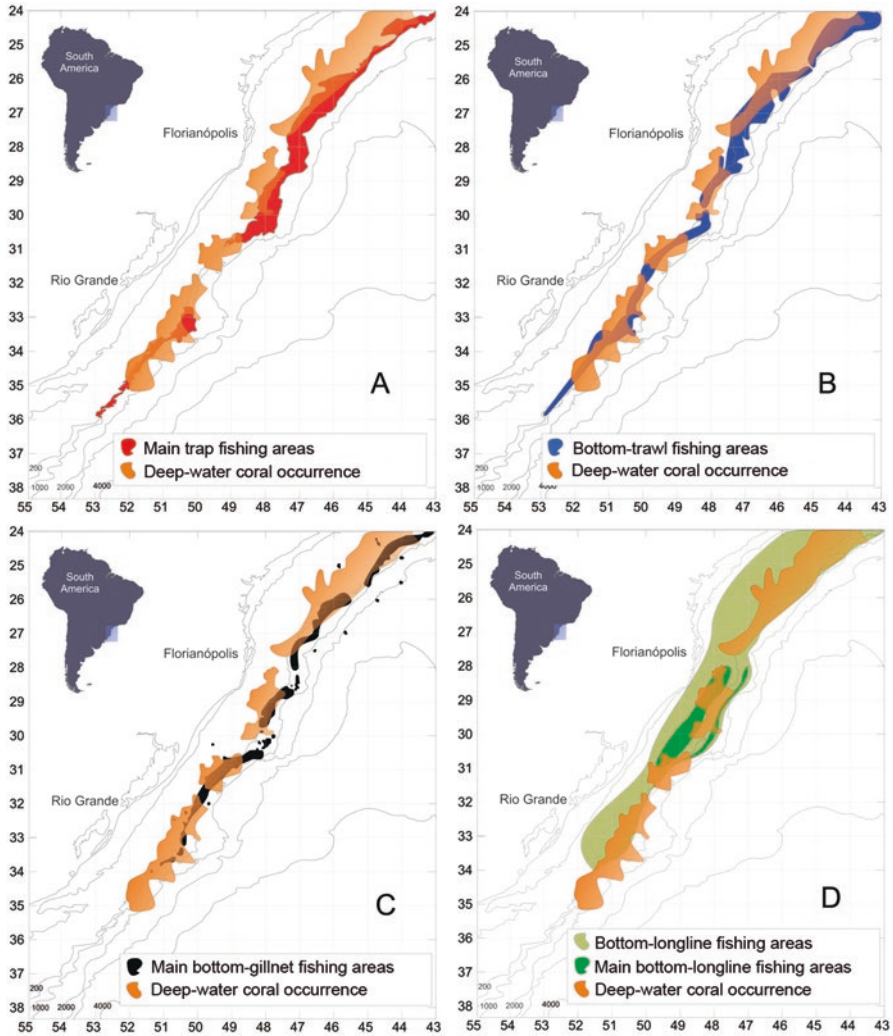


Fig. 4.13 Map covering the main regions used by demersal fisheries: (a) trap, (b) trawl, (c) bottom-gillnet, and (d) bottom-longline, overlapped with the distribution of southern Brazilian deep-sea corals (Image modified from Kitahara 2009)

releases to the environment. According to the same authors, the main routine concerns are (i) drilling discharges, (ii) waste toxicity, and (iii) physical damage caused by anchors, cables, pipelines, umbilicals, and risers. The environmental issues on deep-water coral ecosystems arising from these concerns are distributed from direct physical impact at emplacement of equipment to mortality related to toxicity and sediment burial/smothering effect of drill cuttings (see also Pivel et al. 2009; Bakke et al. 2013; Larsson et al. 2013; Ulfnes et al. 2013). It is important to note that these routine operations can display localized (dozens of meters) or in some cases a more

widespread impact (kilometers), in both mining and oil and gas deep-water exploration.

Although much of the risks are related to the routine operation, the accidental hydrocarbon release (chronic or acute quantities) has been shown to severely impact deep-water corals (Etnoyer et al. 2016). For example, Etnoyer et al. (2016) detected a significant increase of injury on gorgonian populations in the Northern Gulf of Mexico after the Deepwater Horizon oil spill. According to Cordes et al. (2016), such impacts can persist for several years, especially in ecosystems that have low resilience, as deep-water coral reefs. In the same way, Roberts et al. (2009) stated that seabed disturbance from mining operations (sediment plumes) and the release of toxic material (see also Jones et al. 2017) could irreparably damage benthic ecosystems.

4.5.3 Climate Change

Previous periods of global environmental changes have resulted in mass extinctions events (MEE) affecting all or most marine phyla (e.g., Alvarez et al. 1980; Jablonski 1986; Stanley 1988, 2001; McLaren and Goodfellow 1990; Hallam and Wignall 1997; Erwin 2006), with the synergistic and global impacts of atmospheric CO₂ concentration, and sea level and temperature fluctuations particularly influencing (Hallam 1989; Yasuhara et al. 2008). In a foreseeable future, the major threat to calcifying organisms such as scleractinian corals are the increasing seawater temperatures, progressive ocean acidification, and the rise of the Aragonite Saturation Horizon (ASH) (see Guinotte et al. 2006; Kiessling and Simpson 2010).

The reaction of atmosphere CO₂ with seawater forms carbonic acid (H₂CO₃) that dissolves forming H⁺ ions and bicarbonate. The natural buffering capacity of seawater neutralizes the H⁺ ions forming more bicarbonate. However, as the buffering capacity (carbonate ions) gets depleted, seawater becomes undersaturated to aragonite and calcite, which are essential to calcification for several organisms, including scleractinian and octocorals. Associated to ocean warming, such changes will have devastating implications not only for deep-water corals but also for all calcareous organisms and species that rely on the habitats formed by them (see Hall-Spencer et al. 2015). In general, more acidic waters promote skeletal dissolution, which will ultimately change the balance between reef accretion/erosion to a more erosive state. It is worth to note, however, that several deep-water scleractinian corals have distribution in CaCO₃ undersaturated waters (e.g., *Leptopenus discus*, *Fungiacyathus marenzelleri*). Although most of these species have tissue completely encapsulating their skeleton, the main deep-water scleractinian framework builders have not. Consequently, the water exposed skeleton tends to dissolve at a faster rate.

In a correlation between the Brazilian deep-water reefs and climate change (i.e., warming, altered food inputs, ocean acidification, ASH depth change, and their synergistic aspects), although no direct study has been undertaken, the ASH change might have the most profound negative effect. According to Orr et al. (2005) and

Guinotte et al. (2006), ASH is moving progressively to shallower depths, and by 2099 all waters deeper than 800 m in the Brazilian coast will be under the ASH. Once below the ASH, calcification for some coral species might be impaired or so energy consuming that other physiological aspects would be compromised, and the balance between accretion and erosion will tend to the latter. As detailed in Table 4.1, the knowledge on the distribution of deep-water reefs in Brazil is still scarce, but for those places that have been mapped (part of Campos Basin – see Cavalcanti et al. 2017), the ASH depth change will impact some of the main framework builders (e.g., *Solenosmilia variabilis*, *Desmophyllum pertusum*, *Enallopsammia rostrata*) and consequently all other organisms associated with them. It is worth to note that the ASH change could alter the habitat suitability not only for scleractinian corals (Fig. 4.5) but also for those octocoral species that display their axes composed of aragonite. In addition, as the calcite (another form of CaCO_3) used by octocorals (at least for their sclerites) saturation horizon is also getting shallower, exclusively calcite octocorals will also be impacted.

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Chapter 5

Chemosynthetic Ecosystems on the Brazilian Deep-Sea Margin



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Abstract Chemosynthetic ecosystems are fueled by reduced compounds (CH_4 and/or H_2S), which are important for the chemosynthetic production by microbiota. They comprise hydrothermal vents, cold seeps, and large organic “islands” or patches, such as whale skeletons and wood falls. Despite common along a large range of geological settings around the world, chemosynthetic ecosystems have only been recently found in the Southwestern Atlantic Ocean. This knowledge gap hinders the understanding of the distribution, biogeography, and evolution of chemosynthetic-related fauna. Only one active seep is known in the SW Atlantic at the Rio Grande Cone where anaerobic methanotrophic archaea sustain typical chemosynthetic fauna hosting symbiotic chemoautotrophic bacteria, such as vestimentiferan annelids and solemyid bivalves. However, abundant geological and biological evidence point out that seeps could be frequent along the Brazilian margin. The degradation of the massive organic matter input from a whale carcass and/or large amount of wood increases the concentration of reduced compounds, such as sulfide, which allows chemosynthetic production. As a result, the community established in whale falls or sunken wood resembles those of vents and seeps with part of the fauna relying on the chemosynthetic production. These communities can be common around the world mainly along migratory routes of whales. The Amazon and La Plata rivers are likely to contribute with an abundant quantity of dead wood remains in the SW Atlantic. Despite that, the potential amount of wood was probably negatively affected by the heavy deforestation of the Atlantic rain forest in the

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last century, reducing the habitat available to wood specialists. The intense exploitation of oil and gas industry along the Brazilian margin as well as the deforestation of Brazilian forests and the pressure on the whale populations could impact indirectly the chemosynthetic communities of this region. Therefore, studies on the chemosynthetic communities of the SW Atlantic as well as the connectivity with other ocean basins are important for conservation efforts in the deep areas off Brazil.

Keywords Seeps · Pockmark field · Diapirism · Whale fall · Wood fall · Species overlap

5.1 Introduction

Most of the deep sea (>200 m depth) is dependent on photosynthetic-derived detritus originated in the sea surface, and, for this reason, the deep sea is considered a food-deprived heterotrophic ecosystem (Dayton and Hessler 1972; Thiel 1979; Gooday and Turley 1990; Smith et al. 1996; Gooday 2002; Ramirez-Llodra et al. 2010). However, some deep-sea ecosystems are rich in reduced-chemical compounds, such as methane or sulfide, which can sustain in situ microbial primary production. In these ecosystems, free-living microorganisms and those in symbiosis with metazoans can obtain their energy through the oxidation of such compounds, a process known as chemosynthesis (Jannasch and Wirsen 1979; Karl et al. 1980; Jannasch and Mottl 1985). As a result, chemosynthetic production in the deep sea sustains ecosystems that are oases of life, being hotspots of abundance and refuges for unique metazoan lineages (Van Dover et al. 2002). Indeed, chemosynthetic ecosystems completely challenged the paradigm that the deep sea only relies on allochthonous and pelagic organic matter (Lonsdale 1977; Paull et al. 1984).

The first chemosynthetic ecosystem discovered were the hydrothermal vents from the Galapagos Spreading Center in 1977 (Lonsdale 1977; Corliss et al. 1979). After 40 years of their discovery, deep-sea chemosynthetic ecosystems are nowadays recognized to be widespread, diverse, and ecologically and evolutionarily related forming a continuum of reducing habitats (Van Dover 2000; Levin et al. 2012; Portail et al. 2016; Kiel 2016, 2017). The knowledge of these communities has dramatically increased in last decades mainly due to technological advances and international research programs such as the Census of Marine Life (German et al. 2011; Danovaro et al. 2014). In this scenario, the Southwest Atlantic Ocean, and thus the Brazilian margin, remains one of the least studied areas of the world's ocean (German et al. 2011).

Deep-sea chemosynthetic communities have only recently been found in the Brazilian margin, although their presence has been hypothesized for years (Sumida et al. 2004). During a long time, the South Atlantic was not considered in vents studies owing to the slow spreading rate of the ridge in this area. However, recent

investigations report hydrothermal activity and vent fauna in both slow and ultra-slow spreading centers in the North Atlantic and the Indian Ocean (German et al. 1996, 1998). Up to date, vents sites from South Mid-Atlantic Ridge (SMAR) are known between 2° and 15° S (Haase et al. 2007, 2009; German et al. 2008; Ta et al. 2017). There are no active ridges or spreading centers along the Brazilian margin. However, Saint Peter and Saint Paul rocks is thought to be a potential place for vents similar to those found in the Lost City (Kelley et al. 2005). A recent research in the Brazilian margin has resulted in the discoveries of other chemosynthetic communities including methane and asphalt seeps and natural organic falls (Fig. 5.1) (Sumida et al. 2016; Giongo et al. 2016; Mahiques et al. 2017; Fujikura et al. 2017). This chapter reviews the importance of deep-sea chemosynthetic environments along the SW Atlantic. Here, we compile the geological and biological evidence of seeps along this ocean basin and the knowledge of fauna associated with whale falls and sunken woods comparing with other ocean basins.

5.2 Seeps on the Brazilian Margin

Cold seeps are ecosystems energetically sustained by hydrogen sulfide and methane seepage, distributed around the world along passive and active margins (Paull et al. 1984; Sibuet and Olu 1998; Tunnicliffe et al. 2003; Levin 2005). In active margins, cold seeps occur in the tectonic subduction zone of accretionary prisms or erosive margins (Sibuet and Olu 1998; Tunnicliffe et al. 2003). Accretionary prism seeps are usually methane rich and the anaerobic oxidation of methane (AOM) is a key process (Sibuet and Olu 1998). AOM is carried out by a consortium of sulfate-reducing bacteria and methanotrophic archaea. Its main by-product is sulfide, which is used as energy source for chemosynthesis (Boetius 2002; Boetius et al. 2000; Orphan et al. 2002). This microbial consortium also produces bicarbonate that reacts and precipitates creating areas of carbonate rocks, pavements, and slabs around seeps (Stakes et al. 1999).

The extrusion of reduced compounds to surface sediments can also be related to gas hydrates dissociation and diapirism (Sibuet and Olu 1998; Levin 2005). The latter is a process that deforms overlying sedimentary strata by the intrusion of sub-surface low-density sedimentary rocks (diapir), such as salt or mudstone (Chapman 1983). The shape of diapirs ranges according to the tectonic activity, with a mushroom shape in regions of low activity and as narrow dikes along fractures zones. The upward migration of diapirs promotes fractures and permeability, enabling the seepage of gas and/or fluids to surface layers (Taylor et al. 2000; Hovland 2002). This process can contribute to pockmark formation and are frequently associated with gas hydrate accumulations (Hovland and Judd 1988; MacDonald et al. 1990), which is an important process for gas escape in the Southwest Atlantic (Sumida et al. 2004; Schattner et al. 2016; Mahiques et al. 2017).

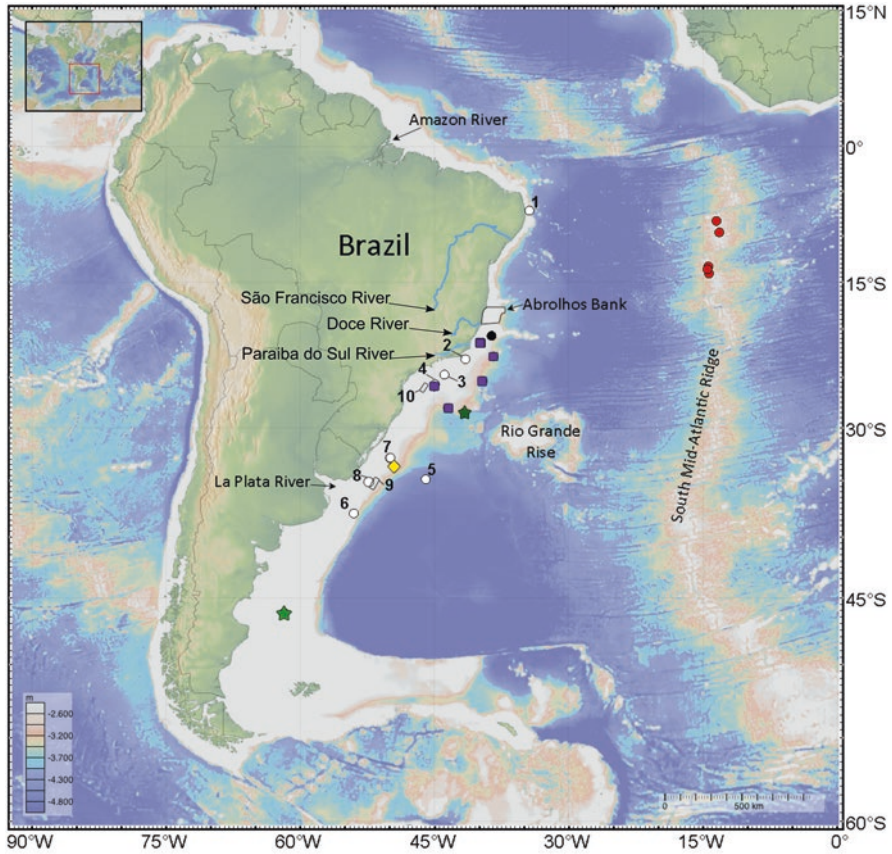


Fig. 5.1 Chemosynthetic ecosystems and geological and biological evidence of such ecosystems in the Southwest Atlantic and South Mid-Atlantic Ridge (S-MAR). Red circles, hydrothermal vents from S-MAR; yellow diamond, cold seep; black circle, asphalt seep; green star, natural whale falls (the southernmost light green star is a skull of Sei whale trawled and densely colonized by *Adipicola*; see Signorelli and Crespo 2017); purple squares, implanted organic substrates (wood, *Pinus elliottii*, and humpback vertebrae, *Megaptera novaeangliae*); white circles, biological evidence ((1) *Crassibrachia brasiliensis* (Southward 1968), (2) *Vesicomya albida* (Dall 1890), (3) *Siboglinum besnardi* and *S. nonatoi* (Tommasi 1970), (4) *Calyptogena birmani* (Domanechi and Lopes 1990), (5) empty siboglinid tubes, (6) *Laubiericoncha puertodeseadoi* (Signorelli and Pastorino 2015), (7 and 8) *Lamellibrachia* cf. *luymesii* (7, Shimabukuro, pers. comm.; 8, Mané-Garzon and Montero, 1985); rectangle shapes, areas with geological evidence of pockmarks ((9) (Mahiques, pers. comm.), (10) (Mahiques et al. 2017)). Source: Map created in GeoMapApp 3.6.6, using GEBCO 2014 and GMRT 3.4 datasets

5.2.1 Known Brazilian Seeps

Geological and biological evidence of seeps are relatively common on the Brazilian and adjacent margins. For example, high-resolution seismic analyses have revealed pockmark fields associated with salt diapirism in Santos Basin (Fig. 5.2), which is indicative of gas or fluid seepage (Sumida et al. 2004; Mahiques et al. 2017). Diapirism is also important in Campos and Espírito Santo Basins (Kowsmann and

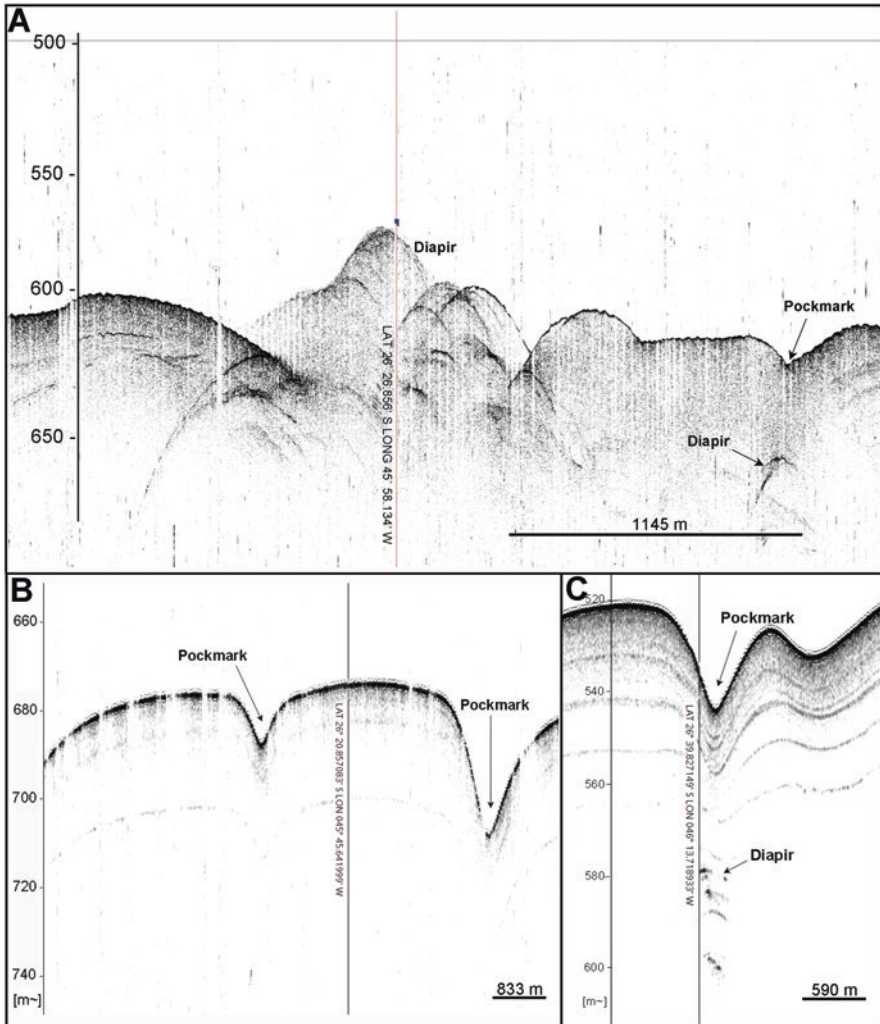


Fig. 5.2 Seismic profile with evidence of salt diapirism (a) and pockmark formation (b and c) in Santos Basin. The seismic profiles were obtained through a Knudsen 3260 (3.5 kHz) sub-bottom profiler

Carvalho 2002; Contreras et al. 2010; Freire et al. 2017; Mahiques et al. 2017), where Kowsmann and Carvalho (2002) found authigenic carbonates possibly resulting from AOM. Moreover, the upper slope of Santos Basin seems to bear active pockmarks with geophysical evidence of gas seepage (Dias 2015; Mahiques et al. 2017). Biological assemblages typical of cold seep ecosystems were also sampled in Santos and Campos Basins, including chemosynthetic symbiont-bearing organisms (see distribution in Fig. 5.1), such as *Siboglinum besnardi* and *S. nonatoi* (Tommasi 1970) and the vesicomyid clams *Calyptogena birmani* and *Vesicomya albida* (Dall 1890; Domaneschi and Lopes 1990). On the Northeastern Brazilian margin (Paraíba Basin), Southward (1968) described the siboglinid tubeworm *Crassibrachia brasiliensis* between 768 and 805 m depth. Further south, empty tubes of siboglinid tubeworms were found in the abyssal province off Argentina (Southward and Southward 1967). Also, the vesicomyid clam *Laubiericoncha puer-todeseadoi* was found between 870 and 2200 m in the Argentina Basin (Signorelli and Pastorino 2015).

The seepage of heavy hydrocarbon compounds, such as asphalt or oil, can also fuel chemosynthetic communities similar to those of sulfide and/or methane-rich seeps (Kennicutt et al. 1985; Hovland and Thomsen 1989; Jones et al. 2014; MacDonald et al. 2004). Along the outer escarpment of the São Paulo Plateau and Espírito Santo Basin, an active fault system related to salt diapirism revealed extensive (ca. 5.6 km) and disconnected asphalt seeps (Freire et al. 2017; Fujikura et al. 2017). The absence of typical symbiont-bearing fauna and authigenic carbonates indicated that this asphalt seep was not supporting a chemosynthetic-based community at the time of sampling (Freire et al. 2017; Fujikura et al. 2017). Moreover, isotopic signatures of fauna relied mostly on particulate organic matter and detritus from sediments (Fujikura et al. 2017). Despite the lack of a chemosynthetic community, a rich faunal assemblage, mainly composed of sponges, gorgonians, sea stars, squat lobsters, and tunicates, thrived in that area (Fujikura et al. 2017).

The first and only known active seep on the Brazilian margin was found in the Rio Grande Cone in Pelotas Basin (Southern of Brazil) at 1200 m depth (Giongo et al. 2016). This seep is associated with a giant pockmark and gas hydrates deposits (Miller et al. 2015). Different from Santos and Campos Basins, pockmarks from Pelotas Basin are not result of salt tectonism (Contreras et al. 2010). The Rio Grande Cone, which is located south of the Pelotas Basin, was considered as the palaeodelta of the La Plata River and, for this reason, a region of high accumulation of riverine deposits (Martins et al. 2003). This large deposit layer makes compressional force and can enhance faults and fractures, which can conduct reduced compounds to the sediment surface. The AOM consortium is likely to be important in Pelotas basin owing to the presence of anaerobic methanotrophic archaea and sulfate-reducing bacteria (Deltaproteobacteria) in this seep (Giongo et al. 2016). Furthermore, the Pelotas seep is home to two typical symbiont-bearing invertebrates: the tubeworm *Escarpi* sp. and the solemyid bivalve *Acharax* sp. (Giongo et al. 2016; Medina-Silva et al. 2018).

In Pelotas Basin, bottom-trawling fishermen have frequently reported the presence of “bushes” of strange organisms in their fishing nets (Kitahara, person.

comm.). Analyses of these bushes were determined as *Lamellibrachia* tubeworms (Shimabukuro, person. observ.). This species has 7-sheath lamellae resembling *Lamellibrachia victori* collected off Uruguay (Mané-Garzon and Montero 1985). However, Southward (1991) and Gardiner and Hourdez (2003) demonstrated that *L. victori* is actually *L. luymesii*, which seems to bear large morphological variation but small genetic divergence (McMullin et al. 2003; Miglietta et al. 2010). Even though its geographic range has significantly expanded, Gulf of Mexico populations seem to be interestingly isolated by distance with low capacity to dispersion (McMullin et al. 2010). Future research on *Lamellibrachia* cf. *luymesii* populations from Brazil may have dramatic implications to resolve the biogeography and taxonomy of this tubeworm.

5.3 Organic Falls

Large organic remains, such as wood logs, kelps, gelatinous organisms, and carcasses of big animals, can sink rapidly to the deep sea (Turner 1973; Wolff 1979; Smith 1985; Smith et al. 1989; Smith and Baco 2003; Billett et al. 2006; Bernardino et al. 2010, 2012; Higgs et al. 2014). Because of their size, these large parcels reach the seabed nearly intact, representing an intense enrichment to the ocean bottom. These oases of food are known as organic falls. At the deep seafloor, wood and whale carcasses create remarkable communities of opportunists and specialists and can sustain chemosynthesis for years or even decades (Turner 1973; Wolff 1979; Smith 1985; Smith et al. 1989; Smith and Baco 2003; Billett et al. 2006; Bernardino et al. 2012; Higgs et al. 2014). The decay of organic compounds released during degradation of wood and whale carcasses can lead to sediment anoxia in the vicinity of carcasses, resulting in the availability of free hydrogen sulfide at concentrations similar to seep and vent ecosystems (Treude et al. 2009; Bienhold et al. 2013). The sulfide becomes available to microbes and symbiont-bearing fauna, resulting in faunal overlaps of organic falls with other chemosynthetic ecosystems (Bernardino et al. 2012).

5.3.1 Whale Falls

Whale carcasses have been considered as important food sources to deep-sea organisms for a long time (Krogh 1934; Stockton and DeLaca 1982). A recently arrived 40-ton gray whale carcass in the seabed is equivalent to more than 2000 years of background carbon flux to the sediment below it (Smith 2006). The intense organic enrichment caused by the arrival of a whale carcass creates specific faunal communities that pass at least through three overlapping successional stages (Bennett et al. 1994; Smith et al. 2002; Smith and Baco 2003; Braby et al. 2007; Lundsten et al. 2010a): (1) the mobile scavenger, (2) enrichment opportunist, and (3) sulfophilic

stage. A fourth and last stage has been hypothesized, the reef stage, which occurs after the consumption of all organic content of the skeleton with only the mineral matrix remaining (Smith and Baco 2003). However, this stage may happen only in particular circumstances, such as when manganese minerals encrust the bones or in the absence of bone-eating worms *Osedax*, which degrade the mineral matrix (Lundsten et al. 2010a; Higgs et al. 2011; Smith et al. 2015).

In the first stage, the mobile scavenger, the main nutritional resource is the flesh, which is consumed by scavengers (Smith and Baco 2003). The duration of this stage lasts from few months to some years depending on necrophage abundance, scavenging rate, and carcass size (Smith and Baco 2003). The mobile scavenger stage itself undergoes a temporal succession with the arrival of megafaunal necrophages first, such as sleeper sharks, hagfishes, macrourids, and lithodid and galatheid crabs, gradually changing to a dominance of macrofaunal necrophages such as lysianassid amphipods, some isopods and echinoderms (Hessler et al. 1978; Smith et al. 2002; Smith and Baco 2003). In general, however, generalist fauna that are usually found in background ecosystems dominates this stage (Goffredi et al. 2004; Glover et al. 2010; Lundsten et al. 2010a, b; Smith et al. 2014b).

The sloppy consumption of soft tissue by scavengers expands the enrichment to sediments around the carcass and exposes the bones. A dense assemblage of heterotrophic invertebrates colonizes sediments and bones characterizing the enrichment opportunist stage (Smith and Baco 2003). Here, the density of macroinvertebrates can increase 10–25 times reaching 50,000 ind.m⁻² in sediments surrounding the carcass (Smith et al. 2014a). Annelids are one of the most important fauna, and their density may be high, such as that of the chrysopetalid annelid *Boudemos flokati*, which can reach up to 40,000 ind.m⁻² (Smith and Baco 2003). In contrast, species richness is dramatically reduced (Smith and Baco 2003; Smith et al. 2014a). Despite the dominance of a few species, many annelids are only known from whale falls as *B. flokati* and *B. ardabilia* (Dahlgren et al. 2004; Wiklund et al. 2009a), as well as some dorvilleids (Wiklund et al. 2009b, 2012), polynoids (Pettibone 1993; Glover et al. 2005) and hesionids (Pleijel et al. 2008; Summers et al. 2015; Shimabukuro et al. 2019).

The microbial decomposition of organic matter from the carcass, mainly lipids from bones, is extremely important. In the beginning, decomposition occurs aerobically, but the intense bacterial activity rapidly decreases oxygen content. Assemblages of sulfur-reducing bacteria and methane-oxidizing archaea are the main taxa that anaerobically decompose organic matter (Deming et al. 1997; Goffredi et al. 2008; Treude et al. 2009). This degradation causes the increase in sulfide and methane effluxes, characterizing the sulfophilic stage (Smith et al. 1989; Naganuma et al. 1996; Deming et al. 1997; Smith and Baco 2003).

During the sulfophilic stage, dense microbial mats of free-living chemoautotrophic microorganisms are found in bones and sediments as a result of the high flux of reduced compounds (Smith et al. 1989; Smith and Baco 2003; Lundsten et al. 2010a; Amon et al. 2013; Sumida et al. 2016; Alfaro-Lucas et al. 2017). The chemosynthetically derived carbon is fundamental to some heterotrophic fauna at this

stage (Smith and Baco 2003; Glover et al. 2005; Alfaro-Lucas et al. 2018). Moreover, invertebrates bearing chemosynthetic symbionts are also found in the sulfophilic stage, e.g., the siboglinids *Escarpia spicata*, *Lamellibrachia satsuma*, *L. barhami*, and many bathymodioline and vesicomid bivalves (Smith et al. 1989, 2002; Feldman et al. 1998; Baco et al. 1999; Distel et al. 2000; Smith and Baco 2003; Fujiwara et al. 2007; Lundsten et al. 2010b).

Smith et al. (1989) show affinities in the faunal composition between whale falls and vents/seeps. Because of that, whale falls were considered important stepping stones for the dispersal of chemosynthesis-dependent deep-sea fauna (Smith et al. 1989, 2002; Smith and Baco 2003). This idea was controversial at the beginning since most affinities were based on higher taxonomic levels (Tunnicliffe and Juniper 1990). However, there is now substantial evidence that whale falls provide intermediate steps for some species to disperse between and among vents, seeps, and wood falls, such as the siboglinid annelids *Escarpia spicata*, *Lamellibrachia satsuma*, and *L. barhami* and the alvinocaridid shrimp *Alvinocaris muricola* (Naganuma et al. 1996; Baco et al. 1999; Fujiwara et al. 2007; Lundsten et al. 2010b; Amon et al. 2013; Teixeira et al. 2013; Glover et al. 2005; Hilário et al. 2015; Ravara et al. 2015; Smith et al. 2015, 2017; Sumida et al. 2016; Pereira et al. 2020).

The importance of whale falls facilitating the dispersion among chemosynthetic ecosystems has potential implication for the evolution of some lineages inhabiting vents and seeps. The molecular phylogeny of deep-sea bathymodioline mussels shows that species occurring in whale and wood falls, usually with extracellular symbionts, are basal lineages for vents and seeps species with intracellular symbionts (Distel et al. 2000; Lorion et al. 2009, 2013; Fujiwara et al. 2010; Miyazaki et al. 2010). Moreover, the molecular phylogeny of deep-sea chrysopetalid annelids shows that bacterivorous species living in whale falls are basal to parasitic lineages inhabiting vents and seeps (Watson et al. 2016). All these studies suggest that organic falls were used as stepping stones, serving as intermediate habitats where several adaptations were acquired before the colonization of more extreme reducing ecosystems, such as vents and seeps (e.g., physiological tolerance to reduced compounds, symbiont acquisition, or exploitation of new niches).

On the opposite direction, a biogeographic network data using a reduced dataset (without some whale-fall sites and only for some specific mollusks clades), shows that whale sites have low connection with vents and seeps (Kiel 2016). However, reanalyzing the network only including chemosynthetic ecosystems from the Pacific Basin (where more whale falls have been studied), Kiel (2017) found higher connectivity between whale falls and other chemosynthetic ecosystems. This highlights the importance to increase the knowledge of deep-sea whale falls by sampling more sites, especially in different ocean basins. Moreover, a global connectivity pattern among deep-sea reducing communities needs the inclusion of all taxa, since most of shared species among these ecosystems are annelids (Smith et al. 2017). It is likely that whale falls may be important stepping stones for some groups, especially annelid and some mollusk lineages, and not for others (Kiel 2017; Smith et al. 2017).

5.3.1.1 Whale Falls in the Brazilian Margin

Whale carcasses in Brazilian deep-sea waters are probably abundant. Whale falls are more likely to occur along continental margins matching migratory routes from high-latitude high-productivity feeding areas to low-latitude low-productivity breeding areas of large whales (Smith and Baco 2003; Smith et al. 2015).

In the South Atlantic Ocean, the sub-Antarctic population of humpback whale migrates from South Georgia Islands through Rio Grande Rise and northwards to the Abrolhos Bank (see regions in Fig. 5.1), which is a nursery area for this population (Zerbini et al. 2006). Assuming that the population of humpback whales, which breeds on the Brazilian margin, was about 20,300 individuals in 2012 (Bortolotto et al. 2017) and using the same natural mortality rate and percentage of sink carcasses from Smith and Baco (2003) ($0.05 \text{ ind. year}^{-1}$ and 50%, respectively), we estimate ca. 507 humpback carcasses on the seafloor at the mobile scavenger stage along this migratory route. Moreover, assuming equal durations for each successional stage (*sensu* Smith and Baco 2003), we estimate 760 and 5019 carcasses at the enrichment opportunist and sulfophilic stages, respectively. If we include the South Atlantic population of Antarctic minke whales with a population of about 58,400 individuals (IWC 2013), we have a combined total of ca. 1967 carcasses in mobile scavenger, 2950 in enrichment opportunist and 19,473 in the sulfophilic stage in the South Atlantic region, only considering these two great whale species. In fact, eight baleen whales are found in Brazil, six of which undertake migrations to the Southern Ocean and one migrates from coastal to oceanic waters (Table 5.1) (Santos et al. 2010). Moreover, the SW Atlantic margin is a residence region and/or migratory route for at least 22 toothed whales (Santos et al. 2010). The cosmopolitan distribution of some whales, such as sperm whales, may probably supply Brazilian equatorial waters too (Smith and Baco 2003; Smith et al. 2015). The Bryde's whale also permanently inhabits Brazilian waters from equatorial latitudes to southern Brazil, together with the false killer, killer, and short- and long-finned pilot whales (Table 5.1). In addition, Brazilian islands, seamounts, and oceanic mountain chains are also frequently visited by cetaceans and thus potentially enhance carcass sink around these areas (Lodi et al. 1996; Silva and Godoy 2010; Wedekin et al. 2014).

Along the Brazilian margin, smaller carcasses may also potentially contribute to the development of small chemosynthetic ecosystems and the dispersion of both whale-fall and sulfophilic fauna. The reduced organic input of smaller animal carcasses, such as juvenile whales and sharks, creates lesser sulfophilic habitats but potentially colonizable by common whale-fall specialists and sulfophilic fauna, respectively (Smith and Baco 2003; Lundsten et al. 2010a; Cunha et al. 2013; Higgs et al. 2014; Hilário et al. 2015; Alfaro-Lucas et al. 2017, 2018). For instance, *Osedax* has been found on implanted bones and carcasses of cows and fishes (Jones et al. 2008; Rouse et al. 2011; Hilário et al. 2015), and evidence of fossil carcasses suggests that it may also colonized ancient marine reptile and bird carcasses (Kiel et al. 2011; Danise and Higgs 2015). The description of a chemosynthetic community associated with marine fossil reptiles, such as plesiosaurs and sea turtles, suggests

Table 5.1 Main great baleen and toothed whales found in Brazilian waters

Common name	Scientific name	Distribution along Brazil	Migration	Season inhabiting Brazilian waters	References
Southern right whale	<i>Eubalaena australis</i>	NE, C, S	SW-OO	Winter and spring	Câmara and Palazzo (1986), Lodi et al. (1996)
Humpback whale	<i>Megaptera novaeangliae</i>	N*, NE, C, S	SO-Brz	Winter and spring	Siciliano (1997)
Common minke whale	<i>Balaenoptera acutorostrata</i>	NE, C, S	SO-Brz	Winter and spring	Zerbini et al. (1996, 1997)
Antarctic minke whale	<i>Balaenoptera bonaerensis</i>	NE, C, S	SO-Brz	Winter and spring	Williamson (1975), Zerbini et al. (1997)
Bryde's whale	<i>Balaenoptera edeni</i>	N, NE, C, S	No	All year	Zerbini et al. (1997)
Sei whale	<i>Balaenoptera borealis</i>	NE, C, S	SO-Brz	Winter and spring	Williamson (1975), Pinedo et al. (1992)
Fin whale	<i>Balaenoptera physalus</i>	NE, C, S	SO-Brz	Winter and spring	Williamson (1975), Pinedo et al. (1992)
Blue whale	<i>Balaenoptera musculus</i>	NE, C, S	SO-Brz	Winter and spring	Williamson (1975), Dalla Rosa and Secchi (1997)
Sperm whale	<i>Physeter macrocephalus</i>	N*, NE, C, S	No	All year	Pinedo et al. (1992)
False killer whale	<i>Pseudorca crassidens</i>	N*, NE, C, S	–	–	Pinedo et al. (1992), Di Benedetto et al. (1998)
Killer whales	<i>Orcinus orca</i>	N*, NE, C, S	–	–	Pinedo et al. (1992), Dalla Rosa (1995)
Long-finned pilot whale	<i>Globicephala melas</i>	C, S	–	–	Secchi et al. (1991), Pinedo et al. (1992), Zerbini and Kotas (1998)
Short-finned pilot whale	<i>Globicephala macrorhynchus</i>	N*, NE, C, S	–	–	Zerbini et al. (1999), Schmiegelow and Paiva-Filho (1989)

N north, NE northeast, C central, S south. (*) Very probably area of occurrence but not demonstrated yet. SW shallow waters, OO oceanic waters, SO southern ocean, Brz Brazil

that extant marine reptiles may be playing a similar role nowadays (Jenkins et al. 2017). Indeed, five out of seven worldwide extant species of sea turtles inhabit Brazilian open-ocean waters and are also frequently found around deep-sea mountain chains and seamounts, such as the Vitória-Trindade Seamount chain and Rio Grande Rise (reviewed in Sales et al. 2008). Furthermore, several species of sea lions and seals present seasonal migratory movements from higher latitudes to south Brazil with some individuals registered as far the Central and Northeast coast (Campos et al. 2011 and references therein). Magellanic penguins (*Spheniscus*

magellanicus) may also sporadically arrive in large numbers off the Brazilian coast (Mäder et al. 2010).

The only natural whale fall studied thus far in Brazilian waters was found at the base of São Paulo Ridge, and it is the world's ocean deepest whale-fall community studied (4204 m depth). This whale carcass belonged to a partial carcass of a juvenile Antarctic minke whale formed by nine caudal vertebrae and was determined to be a 5–10-year-old community (Sumida et al. 2016). The study of this carcass led to several discoveries with implications for the biogeography, ecology, and biodiversity of these communities hitherto only detailed studied in the north Pacific (Smith and Baco 2003; Smith et al. 2015).

One of the most important findings of this discovery was the affinity of this community with those from the Pacific Basin, highlighted by the presence of the annelids *Sirsoe sirikos*, *Bathykurila* cf. *guaymasensis*, *Vrijenhoekia* sp. and the new bone-eating gastropod *Rubyspira brasiliensis* (Sumida et al. 2016; Alfaro-Lucas et al. 2017; Hasegawa et al. 2019; Shimabukuro et al. 2019). At the genus taxonomic level, the fauna described in this Atlantic whale fall by Sumida et al. (2016) and Alfaro-Lucas et al. (2017) had ca. 26% of its fauna shared with the Pacific Basin. The bone-eating worm *Osedax frankpressi* is also shared between Atlantic and Pacific whale falls (Shimabukuro and Sumida 2019). Moreover, it also showed substantial genera overlapping with other vents, seeps, and wood falls, such as the annelids *Grassleia* sp. (Fig. 5.3a), *Bathykurila* cf. *guaymasensis*, and *Lindaspio* sp. (Fig. 5.3b), genera thus far known in vents and seeps and also *Pleijelius* sp., a genus only known in North Atlantic wood falls (Fig. 5.3c), (Sumida et al. 2016). A recent experimental deployment of humpback whale vertebrae in the vicinity area has increased species overlap among cognate ecosystems with the presence of *Alvinocaris muricola* (Fig. 5.3e), *Sirsoe maximiano*, and *Hyalogyrina rissoella* (Pereira et al. 2020; Souza 2018; Shimabukuro et al. 2019).

Contrasting patterns of skeleton epi- and infaunal assemblages show that the whale skeleton provided a very heterogeneous ecosystem with different bone microhabitats (Alfaro-Lucas et al. 2017). This mosaic of microhabitats is formed due to the distinct environmental conditions found in different parts of the skeleton, as well as the engineering activities of the bone-eating worms of the genus *Osedax* (Alfaro-Lucas et al. 2017, 2018). Environmental conditions and *Osedax* species not only regulate the biodiversity in distinct microhabitats but also drive the establishment of different food webs helping to explain the high species richness of these restricted deep-sea ecosystems (Alfaro-Lucas et al. 2018). One of the main differences found in this Brazilian whale fall from others described elsewhere was the dominance of the annelid *Capitella* (Silva et al. 2016; Alfaro-Lucas et al. 2017), instead of the more common presence of dorvilleids in other whale falls (Smith and Baco 2003; Amon et al. 2013; Ravara et al. 2015).

This abyssal Atlantic whale-fall community had faunal overlaps with cognate ecosystems and other whale falls around the world, but many new species were also found (Sumida et al. 2016). One remarkable finding was the discovery of the deepest *Osedax* species hitherto recorded, *O. brasiliensis* (Sumida et al. 2016; Fujiwara et al. 2019). Newly described species include the annelids *Capitella iatapiuna*

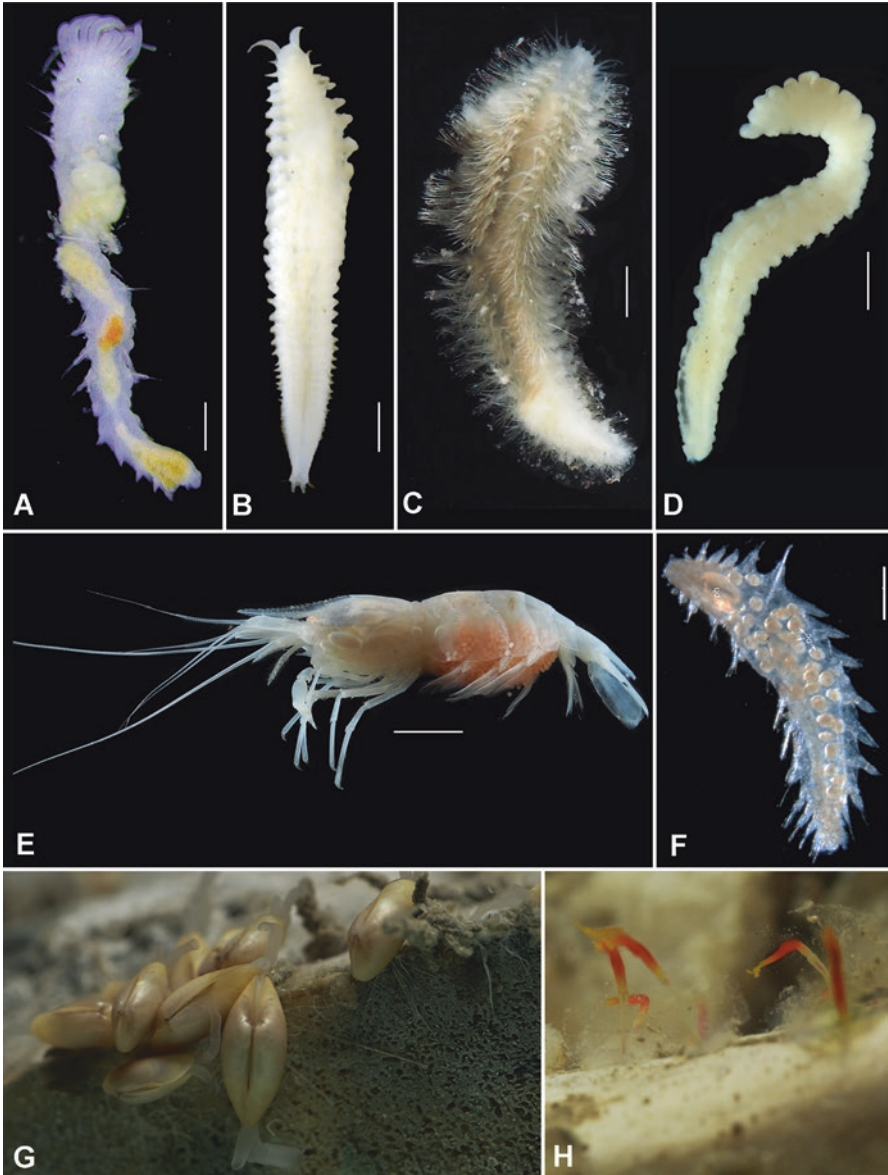


Fig. 5.3 Fauna discovered in whale falls at the SW Atlantic Ocean and known in other chemosynthetic ecosystems around the world. (a) *Grassleia* sp. (scale, 0.3 mm), (b) *Lindaspio* sp. (0.3 mm), (c) *Pleijelius* sp. (0.1 mm), (d) *Capitella iatapiuna* (0.3 mm), (e) *Alvinocaris muricola* (10 mm), (f) *Sphaerodoropsis kitazatoi* (0.5 mm), (g) Bathymodilinae (0.5 mm), (h) *Osedax* sp. (0.5 mm)

(Fig. 5.3d), *Sphaerodoropsis kitazatoi* (Fig. 5.3f), *Neanthes shinkai* (Silva et al. 2016; Shimabukuro et al. 2017a, b) and three new gastropods (Souza et al. 2020). Moreover, at least eight different species of *Ophryotrocha* (Alfaro-Lucas et al. 2017) and three new hesionid species were also described for the abyssal SW Atlantic natural whale fall (Shimabukuro et al. 2019). These findings highlight the role of whale falls as hotspots of biodiversity in the world deep ocean (Smith et al. 2015).

5.3.2 Wood Falls

Plant remains are widespread in the deep sea (Turner 1973, 1977; Wolff 1979) and are presumably more common along forested continental margins (Bernardino et al. 2010). The transport of wood remains to the deep sea depends on the type of wood, its size, and the hydrological regime (Maser and Sedell 1994). Rivers may be the best conduit to introduce wood blocks to the sea (Maser and Sedell 1994). Besides, active canyons may be important to channel wood into the deep, as they are known to trap and transport organic debris (Vetter and Dayton 1998). In the Brazilian margin, two main regions can especially concentrate deep-sea wood falls: (a) the North margin close to the Amazon and Tocantins River mouths and (b) the South close to the La Plata River (Fig. 5.1). Even though these are the main fluvial outflows in the West Atlantic Ocean, other rivers are important contributors, such as the São Francisco, Doce, and Paraíba do Sul (Fig. 5.1). The presence of the Atlantic rainforest may also provide significant inputs of wood to the deep SW Atlantic.

After the arrival at the seafloor, the wood suffers an initial degradation of cellulose by microbial aerobic and anaerobic processes (Palacios et al. 2006; Bienhold et al. 2013; Kalenitchenko et al. 2018). Complex fungal and bacterial communities are present including cellulolytic bacteria, fermenters, sulfate reducers, methanogens, and sulfide oxidizers (Palacios et al. 2006; Fagervold et al. 2012; Bienhold et al. 2013; Ristova et al. 2017). The anaerobic breakdown of wood by sulfate-reducing bacteria produces sulfide, which is in turn oxidized by chemolithoautotrophic bacteria forming the base of a chemosynthetic food web (Bienhold et al. 2013; McClain and Barry 2014).

Sunken woods create specific faunal communities that also undergo a series of successional stages (Bienhold et al. 2013). Specialized wood-fall organisms, such as xylophagid bivalves, accelerate the degradation process promoting the growth of bacteria (Bienhold et al. 2013, Kalenitchenko et al. 2018). Following initial degradation by woodborers and microbes, a diverse fauna exploits the available food and microhabitats (Bienhold et al. 2013; McClain and Barry 2014).

No natural wood falls have been found in the Brazilian margin; however, recent experimental deployments indicated chemosynthesis (Peres 2016) and colonization by specialized fauna (Fig. 5.4; Saeedi et al. 2019). First insights suggest that at least three xylophagid bivalve species occur in the bathyal and abyssal region of Brazil. The rich taxa diversity included many new species such as the amphinomid *Cryptonome barbada*, which was dominant in the sunken woods (Barroso et al.

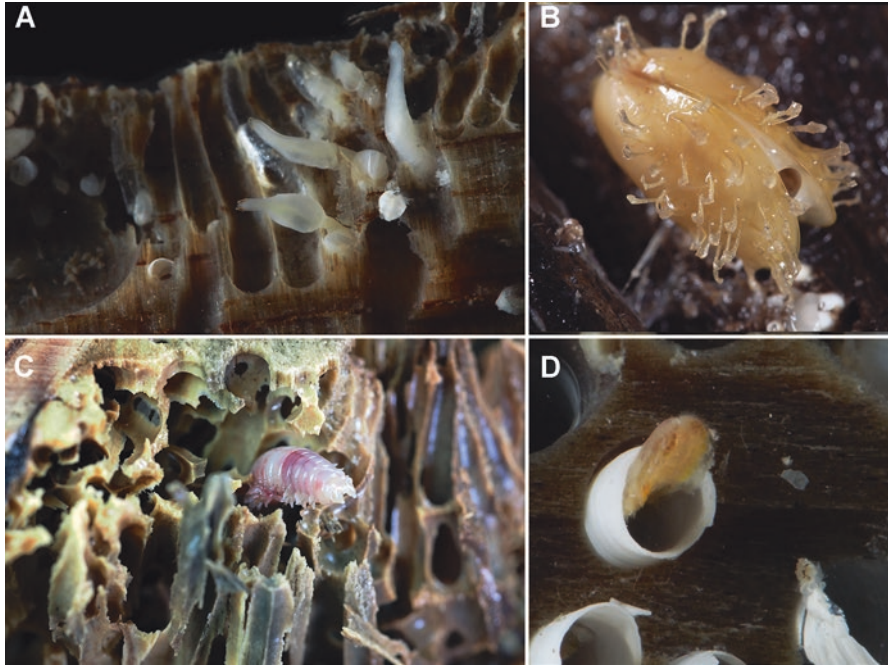


Fig. 5.4 Wood-fall fauna in implanted woods (*Pinus elliottii*) at the SW Atlantic Ocean. (a) xylophagid bivalves (0.5 mm), (b) bathymodioline bivalve (0.1 mm), (c) nereidid annelid (10 mm), (d) *Strepteros didymopton* in a xylophagid bivalve calcareous tube (0.3 mm)

2018). In addition, chemosymbiont-bearing bathymodioline bivalves were also present. High-level taxonomic comparisons of benthic organisms associated with implanted wood revealed similarities with other wood falls sampled in the Pacific and North Atlantic. However, differences included the dominance of ampharetids in the Pacific and capitellids in the Atlantic (Bernardino et al. 2017).

5.4 Future Perspectives

Only two chemosynthetic ecosystems have been hitherto described in the Brazilian margin (Fig. 5.1). However, this chapter provided abundant geological and biological evidence that they are probably common along the Brazilian margin (Fig. 5.1). On the upper and middle slope along Santos, Campos, and Espírito Santo Basins, the salt diapirism is the main process generating pockmarks and producing seepage of reduced compounds or heavy hydrocarbons (Kowsmann and Carvalho 2002; Contreras et al. 2010; Mahiques et al. 2017; Freire et al. 2017). Further south, the presence of large gas hydrate deposits in the Pelotas Basin and Uruguayan margin is probably associated with the input of organic matter from the La Plata River

(Tomasini et al. 2011; Miller et al. 2015). The wealth of geological and biological evidence, together with the potential abundance of whale carcasses and wood, makes the Brazilian margin a key area for future studies on the biogeography and ecology of seeps and organic falls. In addition, the Brazilian margin is under strong anthropogenic pressure mainly from oil and gas prospection (Bernardino and Sumida 2017) and trawl fisheries rendering the urgent conservation of these ecosystems.

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Chapter 6

Deep-Sea Microbes in the Southwestern Atlantic



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Abstract Microbes possess a great genetic repertoire and metabolic versatility that allow them to face the extreme conditions of the deep sea, drive the biogeochemical cycles, and feed chemosynthetic web chains. These microbes respond to historical, global, regional, and local processes in deep-sea habitats and are influenced by microenvironmental variations and the availability of nutrients and electron acceptors to move and survive. By the use of a suite of different methods, as omics techniques and in situ measurements, buoyant particles and the light-independent chemoautotrophic microbes are increasingly being considered as important carbon sources to heterotrophic biota below the euphotic zone. Studies conducted in asphalt seeps, gas hydrates, sunken organic substrates, natural whale carcasses, and seamounts in the Southwestern Atlantic Ocean have revealed a largely unknown diversity of microbes and their high potential for biotechnology. Further promising discoveries are about to come with increasing efforts to determine the microbial community composition, their metabolic diversity, and ecological role in the deep ocean across oceanographic features.

Keywords Deep-sea microbiome · Bacteria and Archaea · Microbial diversity and processes · Biogeochemical cycles · Southwestern Atlantic Ocean · Microbial Oceanography

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6.1 Microbial Habitats in the Dark Ocean

6.1.1 General Physical and Chemical Characteristics

Microbes in the deep sea encounter a vast world of diverse habitats in the Southwestern Atlantic. From the aphotic water column to abyssal plains, and below to the subsurface crusts, they occupy niches where no other organism can thrive, providing food or developing symbiotic associations that enhance adaptability of animals to the harsh environmental conditions.

The deep-sea floor covers more than 60% of the Earth's surface and is an extreme environment characterized by water pressure ranging from 20 to over than 1000 atm, an overall low food input (1–10 mmol C m⁻² year⁻¹), and low temperatures from below zero up to 10 °C, sometimes showing steep gradients over relatively short distances (Tyler 2003; Smith et al. 2008; Bienhold et al. 2016). Isolated seamount chains, oceanic island slopes, and the mid-Atlantic ridge break the monotony of the landscape, providing heterogeneous substrata at lower bathyal depths and interrupting currents and creating hydrographic eddies and flows that enhance production by concentrating larvae and other plankton (Clark et al. 2010; Watling et al. 2013). At abyssal depths (3501 to 6000 m), we find the bulk of the deep-sea floor, the mid-ocean ridge system and ridges associated with island arcs and seamount chains. The hadal zone (> 6000 m) is restricted to plate boundaries bearing deep ocean trenches, mostly formed by subduction of lithospheric plates (Jamieson et al. 2010).

Large-scale oceanographic processes shape deep-sea sediments, which can be uniform in areas over hundreds of square kilometers, while local heterogeneity leading to patchiness of diversity, food content, and sediment texture can occur as a consequence of animal activity and small-scale disturbances, such as whale and wood falls (Tyler 2003; Shimabukuro et al. [this volume](#), Chap. 5). Sediments in the deep-sea floor are formed by (1) the runoff or wind deposition of terrigenous particles derived by rock weathering on land; (2) biological oozes, originated from the deposition of coccoliths or diatom shells; and (3) polymetallic nodules, generated by the accretion of metals (mostly iron and manganese) (Tyler 2003; Orcutt et al. 2011). Sediment thickness varies from near absence at the mid-ocean ridges and low productivity zones under ocean gyres to 10-km thick deposits at trenches and some highly productive continental margins (Orcutt et al. 2011). Particle sizes vary greatly, from small-scale clay particles to macroscopic sands and pebbles, impacting on sediment porosity and transport of chemicals and fluids (Orcutt et al. 2011).

The near-bottom currents are constant but slower than in shallow waters, reaching speeds of less than 10 and 4 cm.s⁻¹ in the bathyal and abyssal zones, respectively, which is sufficient to bring food and remove waste, but causing less turbulence and little erosion (Tyler 2003; Orcutt et al. 2011). Such vertical differences in hydrodynamics and in sediment characteristics are factors that contribute to an observed distinction between microbial communities (at class taxonomic level) of pelagic zones and surface and subsurface sediments at global scale (Orcutt et al. 2011; Bienhold et al. 2016).

6.1.2 *Benthic Habitats*

Despite the extreme conditions, more than half of all microbial cells in the oceans live in the deep seabed. Microorganisms in sediments feed mainly from organic matter above, using electron donors according to a redox potential gradient (oxygen, nitrate, metal oxides sulfate, bicarbonate) made available through reactions derived from seawater, cold seep plumes and hydrothermal fluids circulation through oceanic crusts (Orcutt et al. 2011). Transport of nutrients and substrates is mainly driven by molecular diffusion against chemical gradients, which can limit nutrients supply to microbial cells. In addition, advective transport, where fluids are actively moved, and bioturbation and bioirrigation activities of animals can also contribute to increase substrate availability, generating hotspots of microbial activity (Orcutt et al. 2011). In shallow or surface sediment layers, ranging from centimeters to some meters, more pronounced geochemical gradients are established, resulting in higher local rates of microbial activity, in contrast to deep layers (sub-surface), where gradients are more stable, and relatively lower microbial activity takes place (Orcutt et al. 2011; Bienhold et al. 2016).

In reducing environments, such as cold seeps, microbial activity can sustain complex food chains, and sophisticated symbiotic relationships are developed between microbes and animals, allowing life oases to grow in the desert landscape of the deep realm (Jørgensen and Boetius 2007; Smith 2012; Shimabukuro et al. [this volume](#), Chap. 5). Cold seeps can be found on both active subduction margins and passive continental margins and are related to tectonically induced high-pore-fluid processes (as in mud volcanoes), petroleum or natural gas escape, artesian flow or erosion, and submarine slides (Tyler 2003). Cold seeps fluids enrichment with hydrogen sulfide can occur near the surface where microbial sulfate reduction is coupled with methane oxidation (Joye et al. 2004). The carbon sources are methane, petroleum, other hydrocarbon gases, and methane hydrates, or ice-bound methane, which can release enough gas to support a dependent community (Tyler 2003). Similar to the vents, the presence of high concentration of reduced energy sources (sulfide, methane) in close proximity to oxidants (oxygen, nitrate, sulfate) in cold seeps make available many types of energetically favorable redox reactions (Orcutt et al. 2011). This “chemical soup” harbors abundant populations of chemosynthetic microorganisms, responsible for the primary production that supports large and highly productive metazoan communities (Levin 2005; Smith 2012). Most metazoan biomass in seeps and vents is associated with microbial symbionts, the dominant species being the vestimentiferan tube worms, bathymodiolin mussels, vesicomyid clams, and shrimp, which developed different behavioral and physiological strategies to deliver the oxidants (mostly from the surrounding waters) and reductants (from the sediment) to the symbionts (Dubilier et al. 2008; Shimabukuro et al. [this volume](#); Chap. 5). In cold seeps, anaerobic oxidation of methane (AOM) is a dominant process carried out by Archaea (ANME) associated with deltaproteobacterial sulfate-reducing bacteria (SRB) (Jørgensen and Boetius 2007; Case et al. 2015). AOM in seeps causes an increase in alkalinity, leading to the formation of

authigenic carbonates, presenting as blocks with centimeters to tens of meters or as continuous pavements spreading both laterally and vertically from the site of methane seepage (Case et al. 2015). These carbonates are pervasive substrate and can host distinctive, diverse, and dynamic microbial assemblages, including, but not exclusively, viable autoendolithic methane-oxidizing Bacteria and Archaea, as well as metazoan communities (Case et al. 2015).

Representing the largest organic input to the deep sea, whale and wood falls change the local biological density and diversity (Smith and Baco 2003; Shimabukuro et al. [this volume](#), Chap. 5). They go through decay processes that are initiated by the heterotrophic degradation of organic matter, with subsequent chemosynthetic stages involving reactions from carbon and sulfur cycles that are very similar to those observed at vents and seeps (Smith and Baco 2003; Treude et al. 2009; Bernardino et al. 2010, 2012). The successional process is composed of four stages and initiates with a carcass settling on the seafloor. During the first stage (mobile scavenger), the carcass's soft tissue is consumed by active necrophage species. This is followed by the enrichment opportunist stage, when heterotrophic macrofauna colonize the bones, and organically supplemented sediments surround the whale fall. At the third phase (sulfophilic), the anaerobic microbial community decomposes the organic-enriched sediments and the lipid-rich skeleton, creating high fluxes of reduced compounds and allowing the establishment of the sulfur-based chemoautotrophic ecosystem (Treude et al. 2009) that supports fauna, including mollusks, crustaceans, and polychaetes (Smith and Baco 2003; Smith et al. 2014). Additionally, methane may be released by bacterial anaerobic activity, which favors the colonization of methanotrophic microorganisms. Finally, at the reef stage, after full depletion of the organic material, the remaining bone minerals are colonized by suspension feeders, which use the seawater flux crossing the skeletons to access greater nutrient content. As an ecological succession, the changes on community structure are continuous, and those stages are overlapped by each other, being dependent upon carcass size and surrounding community composition (Smith et al. 2014, 2015). At each phase, the microbial community becomes more diverse, as macrofauna bring to the ecosystem their associated microbiomes. In addition, microorganisms from sediment, water column, and whale microbiome also contribute to amplify the species number. The chemosynthetic community shares its structure with other deep-sea communities, such as hydrothermal vents, cold seeps, and wood falls (Bernardino et al. 2012). Thus, it is proposed that whale and wood falls may act as stepping stones for faunal dispersal among those ecosystems, facilitating their dispersal along the ocean floor (Smith et al. 1989; Distel et al. 2000; Sumida et al. 2016).

Microbial colonization goes beyond the deep-sea floor surface. Active bacterial and archaeal cells, as well as a sparse community of eukaryotic microorganisms, inhabit hundreds of meters down the seabed surface. This microbial community, whose size drops with depth and age, turns over very slowly, with mean generation times reaching thousands of years (Jørgensen and Marshall 2016). The deep biosphere harbors cells adapted to an extreme energy limitation, feeding on complex organic matter and featuring enhanced nutrient uptake, facilitated ATP synthesis,

reduced energy loss, and ability to counteract biomolecule decay. Viruses are also abundant in deep subsurface and may be the cause of mortality of microbial cells in the deep biosphere (Jørgensen and Marshall 2016).

6.1.3 *Pelagic Habitats*

Overlying all ecosystems in the deep seafloor is the dark ocean. It is the largest habitat in the biosphere, rich in inorganic nutrients, such as nitrate, phosphate, silica, and metals, and sharing the extreme conditions of pressure and temperature with most deep-sea habitats. The water column at depths higher than 200 m harbors the largest pool of microorganisms in aquatic systems (Aristegui et al. 2009; Orcutt et al. 2011).

Since dissolved organic matter available in the dark ocean is quite refractory to degradation, heterotrophic activity in this large microbial community is mostly supported by sinking organic carbon (Nagata et al. 2010; Herndl and Reinthaler 2013). The size and velocity of sinking particles will depend on the composition of the particles, and the distribution of the particles ranging between 250 μm and 1.5 mm depends on the combination of the phytoplankton community structure in the euphotic zone, the size of exported particles, and the extent of the vertical attenuation of particle flux to the dark ocean (Herndl and Reinthaler 2013). Part of the carbon exported consists of buoyant, slow-sinking particles, which also contributes significantly for the metabolic activity in the dark ocean. Their stable concentration in the dark ocean is contrasting with the rapid attenuation observed for fast-sinking particles, suggesting autochthonous production at depth, possibly related to chemolithoautotrophy (Herndl and Reinthaler 2013). The topic on the microbial view of chemosynthesis is further discussed in this chapter.

Microorganisms living in the pelagic environment face different challenges in comparison to the microbiota associated with sediments or other hard surfaces. Due to their size, seawater becomes a viscous medium, where gravity plays a negligible force. Free-living motile cells can swim relatively fast in this environment, but when they stop, they do not sink. In addition, if we consider the microscale of the microbial microenvironment, bacterial and archaeal cells find a great number of gradients, either associated to other organisms (such as the phycosphere, surrounding a phytoplankton cell with gradients of DOM and oxygen) or derived from the presence of particles and other substances (oil droplets, gas bubbles, marine snow). Physical gradients also include viscosity changes in and around particles, and in the medium, where colloids and mucus sheets can form polymer webs, as well as salinity gradients in interstitial fluid carried by porous particles travelling through the water column. Consequently, microbial cells are heterogeneously distributed, with cell concentrations varying up to 20-fold over a 10–30-mm distance. In this particular world, differentiated patterns of motility and chemotaxis play an important role in helping microbial cells increase the nutrient uptake by placing themselves in high-concentration microenvironments (Longhurst 2007; Stocker 2012).

Microbial biogeographical patterns are shaped by selection, drift (changes in genotypes and species frequencies due to chance demographic events), dispersal, and mutation (Hanson et al. 2012). Selection and drift contribute by increasing differences in microbial composition with spatial distance, dispersal reduces these differences, and mutation increases local genetic diversity, adding variance to microbial composition between locations. Relative importance of each of these processes define microbial diversity, and in most habitats variation in microbial composition can be better explained by local environmental variables than to geographical distances, following similar trends as observed for larger organisms (Hanson et al. 2012; Fuhrman et al. 2015).

When compared to surface waters, the microbial abundance in aphotic pelagic ocean decreases one to two orders of magnitude (Orcutt et al. 2011). A remarkable increase in density occurs a few hundred meters from the seabed, due to fluxes of nutrients coming up from the benthos. On the other hand, microbial diversity follows a different trend, showing an increase with depth (Orcutt et al. 2011). Biogeographic patterns can be identified, for both dominant groups and the rare biosphere, in general with a stratification with depth (and water masses) and in response to environmental variables. There is also an increase in the proportion of Archaea to Bacteria in deeper layers of the dark ocean. The phylum Thaumarchaeota, especially ammonia-oxidizing Archaea and sponge symbiotic mixotrophs, may represent up to 40% of microbial diversity in the deep ocean (Orcutt et al. 2011 and references therein, Sjöstedt et al. 2014; Nunoura et al. 2015; Santoro et al. 2019 and references therein).

In summary, the deep sea is a collection of the largest ecosystems in the planet, which is shaped by a unique combination of historical, global, regional, and local processes. Microorganisms not only respond to these processes but also face micro-environmental variations, as well as the availability of nutrients and electron acceptors, which influence their ability to move and survive. They can create a great number of niches, resulting in a deep realm teeming with microbial taxonomical and ecological diversity. We still have more questions than answers and many kilometers of deep sea yet to explore. But it is already evident, from what has been discovered so far, that the deep-sea habitats host high microbial taxonomic and functional diversity, with many microbial processes still to be unveiled, in particular in the underexplored Southwestern Atlantic.

6.2 Microbial Role in the Dark Ocean

Bacteria and Archaea host a wide range of metabolic capabilities that include different pathways related to biogeochemical cycles, such as ammonia and methane oxidation, sulfate reduction, and carbon and nitrogen fixation. Revealing their metabolic plasticity and pathways, as well as measuring their *in situ* activities, are key steps to better understand their specific adaptations, their contribution to organisms at higher trophic levels, and their ecological role in marine ecosystems. Recent advances in

molecular analytical techniques have helped to provide more information about these issues along with providing support to improved strategies for cultivation (Overmann and Lepleux 2016).

Functional analyses of the global ocean microbiome obtained from Tara Oceans expedition have revealed that genes related to transport mechanisms in general (such as coenzyme, lipid, nucleotide, amino acids, secondary metabolites) and energy production (including photosynthesis) are abundant, estimated at 67% of the total genes (Sunagawa et al. 2015). The non-core orthologous groups, although less abundant (only 4% of the total genes) and encoding mostly unknown functions, display a great variability across samples worldwide and are relevant for environment-specific adaptations, such as increased lipid metabolism in the oxygen minimum zones (Sunagawa et al. 2015).

Some studies using metagenomics combined with environmental data show the influence of environmental conditions on the functional composition of microbial communities (e.g., Tringe et al. 2005; DeLong et al. 2006; Dinsdale et al. 2008; Gianoulis et al. 2009; Raes et al. 2011), which are structured not only across latitudinal and longitudinal gradients but also along depth (Alves Junior et al. 2015; Acinas et al. 2019). In the ventilated mesopelagic waters, some particularities were found, such as aerobic respiration genes, important for remineralization of exported production, as well as flagellar assembly and chemotaxis, associated with reduction of grazing mortality of bacterioplankton, and colonization of sinking particles or marine snow aggregates by Bacteria (Matz and Jürgens 2005; Aristegui et al. 2009; Sunagawa et al. 2015). The occurrence of photosynthesis genes in the mesopelagic zone suggests the microbial sedimentation from the epipelagic layer onto the ocean floor (Sunagawa et al. 2015). In fact, even the photosynthetic microbes, such as the most abundant marine cyanobacteria *Prochlorococcus* and *Synechococcus* spp., may contribute to the food web in the deep ocean, playing an indirect role, when photosynthetically derived organic matter is transported from the euphotic realm to the deeper layers in the form of sinking particles such as fecal pellets, phytodetritus, and marine snow (Turner 2015). The vertical community connectivity was further noted by the presence of the most abundant deep-water prokaryotes in the surface waters, occurring mainly through the largest particles (Mestre et al. 2018).

Deep-water prokaryotes present a high abundance of genes responsible for glyoxylate and dicarboxylate metabolisms, corresponding to relatively greater oxidized and degraded dissolved organic matter (DOM) when compared to surface-water DOM (Benner 2002). These prokaryotes also have genes for protein export and urea metabolism (DeLong et al. 2006). They are additionally more enriched in genes for transposases and the synthesis of polysaccharides and antibiotics, which might indicate a mechanism to maintain genetic flexibility under slow growth conditions and their role for a particle-attached lifestyle in the deep (DeLong et al. 2006).

More recently, a global metagenomics evaluation of the tropical and subtropical bathypelagic microbiome under the Malaspina circumnavigation initiative resulted in 71% of new genes, 11 potential novel phyla, and revealed contrasted functional gene repertoires between the particle-attached and the free-living microbial assemblages. An irregular microbial distribution and the prevalence of mixotrophy with

the ability to alternate between autotrophic and heterotrophic metabolisms provide support for microbial metabolic versatility in the deep sea (Acinas et al. 2019).

A vertical pattern of genes distribution in the water column was also reported for samples in the Southwestern Atlantic along the Brazilian coast (Alves Junior et al. 2015). The pattern was similar to previously observed in the Pacific Ocean (DeLong et al. 2006), and indicated several ecological roles of Bacteria and Archaea in marine ecosystems. When comparing to the global core microbiome, approximately 150,000 genes were exclusively found in the Southwestern Atlantic. Genes involved in metabolic processes, such as acetyl-CoA acetyltransferase, enoyl-CoA hydratase, cysteine desulfurase, tRNA modification and processing, ABC transport system, ATP-binding proteins, and ATPases, were very common (Alves Junior et al. 2015). Genes related to the regulation and cell signaling, cell division and cell cycle, photosynthesis, protein metabolism, and phage-related sequences were more abundant in surface layers, whereas genes associated with respiration, iron acquisition, stress response, membrane transport, virulence, disease, and defense were more abundant in deep waters (Alves Junior et al. 2015).

Not only the use of metagenomics/transcriptomics have revealed the potential role of microbes in the deep ocean, but also the measurements of chemosynthetic rates (by the dark carbon fixation of radioactive ^{14}C or stable isotope ^{13}C labelling) have confirmed that microbial metabolism below the euphotic zone is dominated by chemoautotrophy and is fueled light independently by the oxidation of reduced inorganic compounds. More recently, it was discovered that autotrophic dark carbon assimilation may be significant not only in oxygen minimum zones, anoxic basins, and hot springs (e.g., Taylor et al. 2001; Walsh et al. 2009; Canfield et al. 2010; Hügler and Sievert 2011; Ulloa et al. 2012; Wright et al. 2012; McNichol et al. 2018) but also throughout the oxygenated water column (Herndl et al. 2005; Baltar et al. 2010; Reinthaler et al. 2010; Swan et al. 2011; Herndl and Reinthaler 2013), being of the same order of magnitude as the dark ocean's heterotrophic production (Manganelli et al. 2009; Reinthaler et al. 2010; Signori 2014). The use of such a wide range of energy sources by Bacteria and Archaea points to a substantial niche differentiation in the dark ocean. For instance, it was found that Deltaproteobacteria/SAR 324, Gammaproteobacteria clusters ARCTIC96BD-19 and Agg47, and some representatives of Oceanospirillales possess genes for both carbon fixation and sulfur oxidation. In addition, several Proteobacteria lineages are likely mixotrophs and methylotrophs (Swan et al. 2011; Sheik et al. 2014). The non-thermophilic pelagic Archaea were shown to be involved in autotrophic processes in the nitrogen cycle, using ammonia oxidation as an energy source, and in heterotrophic processes, using an organic substrate barely used by other groups (Ingalls et al. 2006; Arístegui et al. 2009).

Some estimates of global rates of oceanic dark carbon fixation (ca. $0.77 \text{ PgC} \cdot \text{year}^{-1}$) showed that chemosynthetic microbes represent a major source of newly synthesized organic carbon to the dark pelagic realm, which is comparable to the organic carbon supplied by the world's rivers and buried in oceanic sediments (Ingalls et al. 2006; Middelburg 2011). Chemosynthesis was shown to correspond to 15–53% of the phytoplankton export production in the dark ocean (Reinthaler

et al. 2010), being potentially a significant source (12–72%) of organic carbon required by heterotrophs in the mesopelagic and bathypelagic zones (Baltar et al. 2010; Signori 2014). Additionally, not only autotrophic microbes, but also heterotrophic bacteria, may contribute to bulk inorganic carbon fixation via anaplerotic reactions under sporadic inputs of organic matter to the oligotrophic deep ocean (Baltar et al. 2016) to replenish TCA cycle intermediates, synthesis of amino acids or nucleic acids precursors, and biosynthesis of fatty acids (Dijkhuizen and Harder 1984; Erb 2011). Therefore, chemosynthesis should be taken into consideration for ocean carbon budgets and cycling models (Middelburg 2011; Herndl and Reinthaler 2013).

Chemoautotrophic processes, such as nitrification, denitrification, and anammox in nitrogen cycling, and sulfide oxidation and sulfate reduction in sulfur cycling, are also relevant at or near the seafloor, particularly in the first centimeters of the marine sediments, where a wide variety of microbes coexist and interact at the oxic-anoxic transition zone between seawater and seafloor (e.g., Orcutt et al. 2011; Parkes et al. 2014; Bolhuis and Cretoiu 2016). The microbial community composition and the prevailing metabolism can vary depending on the different types of sediments (shelf, seeps, hydrate associated, turbidities, etc.). For instance, organic-rich subsurface sediments, as well as gas hydrates, are dominated by the candidate phylum JS1 and members of Thaumarchaeota, whereas oligotrophic oceanic provinces host mostly members of Chloroflexi and Planctomycetes. Reducing cold seeps, which are characterized by sulfur and methane cycling, harbor sulfate reducers from Epsilonproteobacteria (including lithotrophic sulfur oxidizers) and Archaea belonging to the anaerobic methanotrophic (ANME) group and methanogenic Methanosarcinales (Orcutt et al. 2011; Parkes et al. 2014). Heterotrophic microbes also play an important role in the water-sediment interfaces, where they transform organic matter and use up the available oxygen resulting in anoxic conditions at the first millimeters in the sediment, where anaerobic metabolism will prevail (Orcutt et al. 2011).

For whale biomass degradation, sulfate reduction and methanogenesis are important processes performed by the microbial community (Goffredi et al. 2007; Treude et al. 2009). Consequently, high concentrations of sulfide (> 11 mM) and methane (> 4.2 mM) can be detected at the whale fall system (Treude et al. 2009; Smith et al. 2014). This is in part processed by the Epsilonproteobacteria, a class that may grow chemoautotrophically with H_2 and reduced sulfur compounds as electron donors. They include cultivable genera (e.g., *Sulfurovum*, *Nitratiruptor*, and *Sulfurimonas*) and noncultivated groups, which are recognized in a variety of marine chemosynthetic ecosystems, as hydrothermal vents (Nakagawa et al. 2005), cold seeps (Pop Ristova et al. 2014), and whale falls (Goffredi and Orphan 2010; Cavalett et al. 2017). They participate in reduced sulfur oxidation by using the sox system, as reported for *Sulfurovum* sp. NBC37-1 (Yamamoto et al. 2010) and other genera (Akerman et al. 2013). It has been proposed that the sox system or thiosulfate oxidation system, which was studied in the alphaproteobacterial *Paracoccus pantotrophus*, requires at least four soluble proteins, soxAX, soxYZ, soxB, and sox(CD)2, for the total oxidation of thiosulfate (Friedrich et al. 2001, 2005, 2007).

In oxygenated deep-sea sediments, where ammonia is the dominant reduced inorganic compound produced by organic matter mineralization processes (Schulz and Zabel 2006), it is expected that chemoautotrophy is mainly sustained by ammonia oxidation instead of the reoxidation of other reduced compounds (such as sulfides) (Middelburg 2011; Molari et al. 2013). In these areas, archaeal assemblages are responsible for the high rates of inorganic carbon incorporation and contribute to organic matter consumption, playing an important role in carbon cycling and sustaining food web functions of benthic deep-sea ecosystems (Molari et al. 2013). In the pelagic system, the existence of two ecotypes of ammonia-oxidizing Archaea was confirmed at nucleotide and amino acid levels in the Atlantic Ocean, reflecting the ammonia availability and the environmental conditions (Sintes et al. 2016).

In the Southwestern Atlantic, more efforts are needed to quantify and address the importance of microbial processes in deep seabed. Current and future research initiatives are pointing into this direction.

6.3 Microbial Communities in the Southwestern Atlantic

Research on microbial communities in deep-sea ecosystems off Brazil has been intensified since 2015, revealing a largely unknown diversity and high potential for biotechnology. Although most microbial studies were carried in the Pacific or in the North Atlantic Ocean, a few studies have investigated the diversity and community structure of microorganisms in the deep Southwestern Atlantic (Fig. 6.1). Here, we present some findings about microbial composition and function from asphalt seeps, gas hydrates, sunken organic substrates, natural whale carcasses, seamounts, and pelagic realm.

The North São Paulo Plateau was sampled during the Iatá-Piúna Expedition using the submersible Shinkai 6500 and Yokosuka Vessel. The main interest of the cruise was to discover and study in detail chemosynthetic ecosystems in the Southwestern Atlantic. An asphalt seep ecosystem was discovered during the cruise but with no evidence of active seepage supporting chemosynthetic communities (Fujikura et al. 2017). The 16S rRNA sequencing of sediment samples of ca. 2500 m depth revealed that the most abundant bacterial classes were Alphaproteobacteria, Acidimicrobiia, Gammaproteobacteria, and Deltaproteobacteria. Compared to other studies conducted in the deep sea, it was found an unexpected high abundance of some hydrocarbon degrading groups of Alphaproteobacteria and Acidimicrobiia, which may be related to the presence of asphalt seeps in the North São Paulo Plateau (Jiang et al. 2018; Queiroz et al. 2020). Fungal diversity was also studied in the same sediment samples and analyzed by Ion Torrent PGM targeting ITS region of rRNA (Nagano et al. 2017). The results on fungal taxonomic composition described the dominance of *Penicillium* sp., *Cadophora malorum*, and *Rhodosporidium diobovatum*.

A chemosynthetic-based community was previously discovered at Rio Grande Cone Gas Hydrate Province (Miller et al. 2015). In sediment samples with high

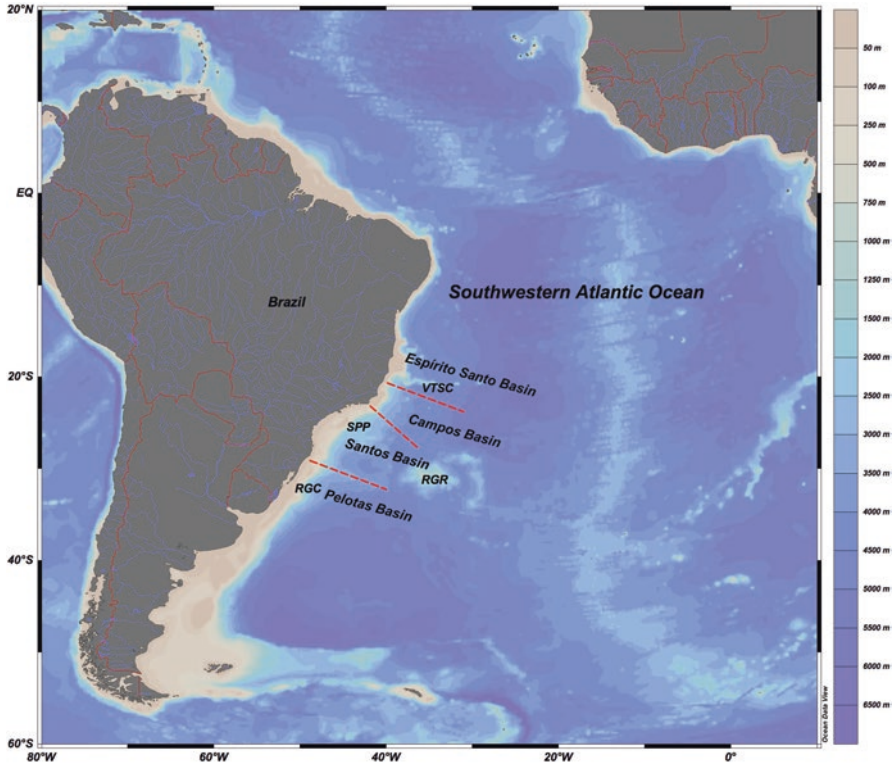


Fig. 6.1 Main physiographic features of the Southwestern Atlantic Ocean mentioned in this chapter. *VTSC* Vitória-Trindade seamount chain, *SPP* São Paulo Plateau, *RGR* Rio Grande Rise, *RGC* Rio Grande Cone

levels of methane and the presence of gas hydrates, a high abundance of Archaea related to ANME groups were detected, besides multiple bacterial lineages that were closely related to microbes found worldwide at methane seeps with similar geochemical settings (Giongo et al. 2016). A study carried out in the same sampling region, but in the pelagic realm, found the family Pelagibacteraceae (Alphaproteobacteria) as the most frequent taxa at chlorophyll maximum and oxygen minimum depths and the ammonia oxidizers *Nitrosopumilus* (Thaumarchaeota) as the most relatively abundant near the bottom (around 1300 m deep) (Medina-Silva et al. 2018). A high number of unassigned groups along the water column reinforced the need for further studies on microbial diversity.

In comparison to the sediment and water samples, a very distinct microbial community dominated by Pirellulaceae (Planctomycetes) was found attached to wall of the cold-seep polychaete *Escarpiia* sp. (Medina-Silva et al. 2017).

Another example of chemosynthetic-based microbial habitats are the sunken organic substrates (wooden blocks and whale bones) that simulate phenomena that reach the ocean floor and are remarkable reservoirs of energy and carbon,

constituting habitats with potential to harbor high microbial diversity. Bacterial diversity and community structure associated with synthetic (rubber carpet) and organic substrates (whale bone, wooden blocks) were assessed at 3300 m depth after 22 months in the Southwestern Atlantic. The results of 16S rRNA sequencing showed the dominance of the classes Alphaproteobacteria and Flavobacteria in the synthetic and wood substrates, whereas the classes Deltaproteobacteria and Epsilonproteobacteria were dominant in the whale vertebra (Peres 2016). The same study showed significant differences between the substrates and within the geographical sites, being only 3 OTUs (Alphaproteobacteria, Rhodobacteraceae_unclassified; Epsilonproteobacteria, *Sulfurovum*; and Alphaproteobacteria, Sedimentitalea) shared among all the samples. The identified genera *Sulfurovum*, *Desulforhopalus*, *Desulfuromusa*, *Sulfurospirillum*, *Desulfobacter*, *Desulfotalea*, and *Sulfurimonas* are likely to contribute to chemosynthesis, in particular in the deep-sea organic substrates. There is evidence that the chemosynthetic microbes can rapidly colonize the vertebra substrates, taking advantage of the labile organic matter (Peres 2016). This study provided new insights about how substrates and geographic locations may influence microbial community structure in the deep Southwestern Atlantic.

Recently, the first natural sunken whale carcass was discovered in the Southwestern Atlantic (Sumida et al. 2016), and the metagenome of the bacterial community in sediments associated with decomposing whale bone was analyzed. Gene sequences from the sox system (soxA, soxB, soxD, soxH, soxX, soxY, soxW e soxZ) were detected, part of it organized in a cluster (soxX-Y-Z-A-B) mostly from Epsilonproteobacteria (Cavalett et al. 2017). For the sulfur cycle, enzymes involved in both sulfur reduction and oxidation were identified, including the sulfate adenylyltransferase, sulfite oxidase, adenylyl-sulfate reductase, sulfite reductase (NADPH and ferredoxin), and adenylyl-sulfate kinase. The microbial community associated with the whale fall ecosystem reserves a still underexplored variety of genes codifying for biotechnological relevance, as well as enzymes and secondary metabolites with potentially relevant properties. This potential for industrial enzymes was assessed through metagenomics, revealing many proteases and lipases (de Freitas et al. 2017), and reflecting how the microbes adapt to consume the rich food source of whale tissues and bones (Lundsten et al. 2010). In addition, proteins were found to have low identity percentage (under 50%) when compared to the UniProt database (~600,000 reviewed protein sequences), suggesting that these proteins are potentially novel and may contain unique molecular characteristics, as a result of adaptations to the extreme deep-sea whale fall environment. This may be evidenced by residue preferences among the protein domains evolving specific structural and functional constraints during evolution (Moses and Durbin 2009). In this context, amino acid preferences (polar, aromatic, and acidic) are recognized as characteristic of extremophile microorganisms. For example, characteristics of psychrophilic proteins, such as reduced proline and arginine residues, were detected along with less nonpolar residues, such as those noted by Reed et al. (2013). Additionally, preference for aspartic acid and glutamic acid, acidic and negatively charged amino acids, agrees with halophilic proteins (Ebrahimie et al. 2011; Reed et al. 2013). Amino

acids (arginine, serine, glycine, valine, and aspartic acid), previously associated with barophilic proteins (Di Giulio 2005), were also detected by de Freitas et al. (2017). This ecosystem will be further explored by metagenomic analysis and enzymatic characterization to discover new molecules of potential interest.

Although still underinvestigated, seamounts represent hot spots of microbial diversity and productivity along with being potential repositories for investigation of the biogeography of microbial populations, as they tend to be geographically isolated from one another (Emerson and Moyer 2010). In the Southwestern Atlantic, rates of chemosynthesis and heterotrophic bacterial production were assessed by dark incubations of ^{14}C -bicarbonate and ^3H -leucine, respectively, within the pelagic zones across the Vitória-Trindade Seamount Chain (Signori 2014). Although no direct association was found between these topographic features and the enhancements of chemolithoautotrophic rates, it was found that these rates were at the same order of magnitude as heterotrophic bacterial production in bathypelagic and abyssopelagic zones, showing the importance of chemoautotrophic metabolism even in well-oxygenated areas of the deep Southwestern Atlantic Ocean (Signori 2014). This contribution is partially explained by the outstanding metabolic plasticity of Bacteria and Archaea that can use a variety of reduced inorganic compounds, such as hydrogen, sulfide, and ammonia, as energy sources in oxygenated waters (Gasol et al. 2008; Swan et al. 2011; Anantharaman et al. 2013).

In the deep waters, the microbial composition belonging to the Brazil basin collected during the Malaspina circumnavigation expedition was characterized by the overrepresentations of the *Acinetobacter* genus and two OTUs assigned to the *Marinobacter* and *Psychrobacter* genus, all belonging to Gammaproteobacteria. From a global perspective, microbial samples from the Brazil basin were more similar to samples from the Canary basin, in contrast to samples from the North Atlantic that were clustered with the Pacific group (Salazar et al. 2016).

6.4 Future Challenges

Studying microbes in the deep ocean includes difficulties and limitations in logistics and technology that are inherent to these ecosystems. Some examples include the need of good and expensive research vessels normally equipped with ROVs or AUVs to explore the deep-sea habitats, appropriate equipment for sampling and laboratory analyses, the hard task of simulating in situ conditions for incubations, proper methods for molecular biology (e.g., getting enough DNA/RNA from oceanic crusts and nodules is not usually simple, transcriptomics is an interesting tool to evaluate functionality, but still expensive), well-trained human resources, and enough funding to cover all the high expenses.

In the Southwestern Atlantic, increasing efforts are made to discover the microbial community composition and their metabolic diversity and ecological role in the deep ocean across oceanographic features. Promising discoveries are about to come in sites related to whale falls, cold seeps and pockmarks (São Paulo Plateau and

Pelotas Basin), seamounts (Vitória-Trindade Seamount Chain), polymetallic crusts and nodules (Rio Grande Rise – see Montserrat et al. 2019; Jovane et al. 2019), deep-sea corals and endosymbionts, and pre-salt basins (Campos and Santos Basins), which may contribute to a better understanding of the microbial role in the deep ocean, as well as their potentialities for biotechnological applications. Upcoming results will certainly help to build the current scenario of the microbial community structure and further improve our knowledge on the ecological importance of Bacteria and Archaea in the deep ecosystems of the Southwestern Atlantic Ocean, covering some gaps and giving space for potential connections to worldwide initiatives.

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Chapter 7

The Scientific Explorations for Deep-Sea Fishes in Brazil: The Known Knowns, the Known Unknowns, and the Unknown Unknowns



Marcelo Roberto Souto de Melo, Rodrigo Antunes Caires,
and Tracey T. Sutton

Abstract The deep sea is the largest and one of the most extreme environments on Earth. It is estimated that 10–15% of all fish species are dwelling in the deep sea, most of which have unique morphological and physiological adaptations. Biological expeditions to sample the deep ocean off Brazil started with the British HMS Challenger Expedition (1872–1876), followed by a few fishery stations made by the German RV *Ernst Haeckel* (1966) and the North-American MIV *Oregon II* (1957–1975), the cruises of the French RVs *Marion Dufresne* (1987) and *Thalassa* (1999, 2000), the Brazilian RV *Atlântico Sul* (1996–1999), the FV *Diadorim* and FV *Soloncy Moura* (1996–2002), OSB *Astro Garoupa* (2003), and, more recently, the American RV *Luke Thomas* and *Seward Johnson* (2009, 2011), the French RV *Antea* (2015, 2017), and the Brazilian RV *Alpha Crucis*. A total of 712 species of deep-sea fishes were recorded, including five species of Myxini, six species of Holocephali, 81 species of Elasmobranchii, and 620 species of Actinopteri. As in other parts of the world, the Brazilian deep-sea ichthyofauna struggles under severe anthropogenic impacts caused by the commercial fishing, and the extraction of oil and gas. The deep ocean is a delicate environment and its recovery is considerably slower than an equivalent in shallow water habitat. Therefore, increasing the research efforts is needed to avoid that part of its diversity disappear without our accurate knowledge.

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Western South Atlantic

7.1 Introduction

The oceans cover 70% of the Earth's surface, which represents 97% of the water available as fish habitats. The average depth of the oceans is 3800 m and more 50% of their volume below is 3000 m, and 95% is below 200 m, making the deep sea the largest environment available on Earth (Horn 1972; Angel 1997). Even though the oceans are continuous and interconnected, there are well-defined basins limited by the continents, water masses, currents, and a great variety of habitats that range from continental slopes and rises, abyssal plains, trenches, canyons, zones of oxygen depletion, and hydrothermal vents (Tyler 2003).

The deep sea is characterized by extreme conditions of pressure, temperature, and light penetration (Angel 1997; Thistle 2003) that influence fish assemblages. The pressure increases one atmosphere for every 10 m of water depth and can reach up to 1100 atmospheres in the deepest parts of the world's oceans. The sunlight intensity decreases exponentially with depths, while the long wavelengths of the light spectrum – red, yellow, and orange – only penetrate to approximately 15, 30, and 50 m, respectively, making photosynthesis impossible below depths greater than 250 m. However, the short wavelengths of the light spectrum – violet, blue and green – can penetrate in depths of up to 1000 m, creating the twilight zone. Below 1000 m depth, the sunlight is completely absent and the only light available is produced by bioluminescent organisms, such as cnidarians, fishes, cephalopods, and crustaceans. In the deepest regions, the water temperature is constant between 2 and 3 °C, but it is extremely variable from 200 to 400 m, with the formation of thermoclines. Gases such as oxygen and carbon dioxide have a higher solubility at greater pressure, making the levels of oxygen similar to the surface waters, with the exception of the zones with oxygen depletion (Brinton 1979; Rogers 2000; Tunnicliffe et al. 2003).

It is estimated that 10–15% of the known diversity of fishes and over 160 families occur in depths greater than 500 m (Weitzman 1997; Priede and Froese 2013). Among the hagfishes (Myxini), more than 50% of the species are from deep waters, 800 m on average. Two myxinid species, *Eptatretus deani* (Evermann and Goldsborough 1907) and *E. fritzi* Wisner and McMillan 1990, were reported at 2743 m (Fernholm 1998). More than 50% of chimaeras, sharks, and rays (Chondrichthyes) occur in depths greater than 500 m; however, they become extremely rare at depths over 3000 m. The deepest records for a chimaera belong to the chimaerid *Hydrolagus affinis* (De Brito Capello 1868) at 3000 m, for the sharks, to the dalatiid *Isistius brasiliensis* (Quoy and Gaimard 1824) and the somniosid *Centroscymnus coelolepis* Barbosa du Bocage and de Brito Capello, 1864 at 3700 m, and for a skate, to the rajid *Rajella bigelowi* (Stehmann 1978) at 4156 m (Priede et al. 2006, Musick and Cotton 2015). The bony fishes (Actinopterygii) comprise the majority of the biodiversity, and the deepest records belonging to the

liparid *Pseudoliparis amblystomopsis* (Andriashev 1955) at 7703 m, and the ophiidiid *Abyssobrotula galathea* Nielsen 1977, known as the deepest-living known vertebrate, living at 8370 m (Nielsen 1977; Smith Fujii et al. 2010). The two extant species of coelacanth (Sarcopterygii), the latimerids *Latimeria chalumnae* Smith 1939 and *Latimeria menadoensis* Pouyaud et al. 1999, are also from deep waters, occurring in depths from 150 to 700 m (Fricke et al. 1991; Pouyaud et al. 1999; Jewett 2001).

7.1.1 Early Discoveries of Deep-Sea Organisms

Historically, the first reports of deep-sea organisms collected with precise depths were the polychaete *Lumbriclymene cylindricauda* Sars 1872, and an ophiuroid, probably *Gorgonocephalus arcticus* Leach 1819. Both were brought to the surface from off the northeast coast of Canada on a sounding line deployed at 1095 m, by the British HMS *Isabella* under the command of Captain Sir John Ross RN (Ross 1819; Anderson and Rice 2006).

The first reports of deep-sea fishes were made even before their formal description by Linnaeus (1758) – for instance, the velvet belly lanternshark *Etmopterus spinax* (Linnaeus 1758) (Etmopteridae) appeared in Willughby (1686), Ray (1713), and Artedi (1738), however, without a precise depth record. By 1775, 26 species of deep-demersal fishes were known from the Atlantic (Haedrich 1996) and, in the early nineteenth century, Risso (1810, 1820a, b) compiled a primary summary of the bathymetric distributions of fishes in the Mediterranean, including myctophids [e.g., *Gasteropelecus humboldti* Risso 1810 (now valid as *Myctophum punctatum* Rafinesque, 1810) and *Lampanyctus crocodilus* (Risso 1810)] and alepocephalids [e.g., *Alepocephalus rostratus* Risso 1820)].

“The shape of these fish [*Alepocephalus rostratus* Risso 1820a, b], their extraordinarily large eyes, the dark hues, and little variations which cover them, reveal that they are from the deep abyssal pelagic, which make their home, and their habits and habitats will remain, for the naturalists, long buried in these profound regions.” [Translated from Risso 1820b].

Ignoring these data, Forbes (1844) reportedly proposed the azoic hypothesis, which predicted a decrease of abundance and diversity of marine animals with depth, which would cease to exist at a depth of 300 fathoms, about 550 m. Surprisingly, the azoic theory became widely accepted among the scientific community (Anderson and Rice 2006). A few years later, James Clark Ross (1847) and Michael Sars (1872, 1875) obtained several specimens of deep-sea invertebrates at depths of up to 700 m from the Antarctic, and between 360 and 500 m from deep areas off Norway, respectively. Nevertheless, it was only after the expeditions coordinated by the Scottish naturalist Charles W. Thomson onboard of the British HMS *Lightning* (1868) and HMS *Porcupine* (1869, 1870) that the azoic theory was finally dismissed (Thomson 1873; Levin and Gooday 2003; Anderson and Rice 2006).

Thomson used the results of those expeditions to convince the British Royal Navy to allow the use of the HMS *Challenger* in a worldwide expedition to explore

the deep sea. The Challenger Expedition took place between December 7th, 1872 and May 24th, 1876, traveling 68,890 nautical miles (=127,584 km) across the Atlantic, Pacific, and Indian Oceans. It was the first oceanographic expedition to obtain biological, chemical, and physical samples from around the world, collecting data from 362 stations, in depths of up to 8183 m – the majority between 1800 and 5400 m (Thomson 1880). The outcome of the Challenger Expedition was published in a series of reports between 1885 and 1895, that includes four volumes on botany, one volume on deep-sea deposits, and an introduction plus 83 volumes on zoology, with the descriptions of astonishing 715 genera and 4417 species of marine organisms, most of which are still valid nowadays (Murray 1895). The fishes were studied by the German ichthyologists Albert Günther (1877, 1878a, b, 1880, 1887), which recognized 385 species living below 180 m and 230 species below 550 m.

The western South Atlantic deep-sea ichthyofauna remained unstudied until the two passages of the *Challenger* Expedition off Northeastern Brazil (1873) and off Uruguay and Argentina (1976). In Brazil, the deep sea had not been further explored for almost a century, until the passages of the German RVs *Ernst Haeckel* (1966) between Southern Brazil and Argentina and the American MIV *Oregon II* (1957–1976) in northern South America. The first expedition focused exclusively on Brazilian waters was carried out much later, onboard the French RV *Marion Dufresne* (1987), and the most important contributions were made during the REVIZEE years (1996–2002), especially with the cruises of the French RV *Thalassa* (1999, 2000), the Brazilian RV *Atlântico Sul* (1996–1999), and the Brazilian FVs *Diadorim* and *Soloncy Moura* (1996–2002). The Brazilian oil company Petróleo Brasileiro S.A. – Petrobras hired the Brazilian OSB *Astro Garoupa* (2001, 2007) and the American RVs *Luke Thomas* and *Seward Johnson* (2009, 2011) to evaluate the deep-sea biodiversity on the oil basins. The most recent expeditions were made onboard the French RV *Antea* (2015, 2017) and the Brazilian RV *Alpha Crucis* (2019), as part of the ABRACOS (Acoustics along the BRAzilian COaSt) and the DEEP-OCEAN (Diversidade E Evolução de Peixes de Oceano Profundo) projects, respectively. In this chapter, we provide a historical overview about the discoveries of deep-sea fishes in the Brazilian Economic Exclusive Zone (EEZ), including a summary of the results obtained by either the major scientific expeditions or the additional fisheries exploratory surveys of interest (Table 7.1, Fig. 7.1).

The search for the taxonomic records was initially made in Catalog of Marine Fishes of Brazilian Coast (Menezes et al. 2003) and the Catálogo Taxonômico da Fauna do Brasil (Boeger et al. 2015) and restricted to those species that occur in depths greater than 200 m. To minimize the chance of error and update taxonomic status, each record was double-checked in the Eschmeyer's Catalogue of Fishes (Fricke et al. 2020), literature reviews, and the original descriptions, and only those records with a voucher specimen obtained in the Brazilian EEZ were considered. Reports of species that had been substantiated by material deposited in museums were confirmed or excluded from the account by accessing the online databases of the Museum of Comparative Zoology of Harvard University, the National Museum of Natural History of the Smithsonian Institution, and the Zoologisches Institut und Zoologisches Museum der Humboldt Universität, and also examining material in the Museu de Zoologia da Universidade de São Paulo, and the Museu Nacional da Universidade Federal do Rio de Janeiro.

Table 7.1 List of deep-sea expeditions in the Brazilian Economic Exclusive Zone that contributed to knowledge of the ichthyofauna

Year	Vessel	Country	Cruise	Gear	Depth (m)	Area explored
1873, 1976	HMS <i>Challenger</i>	British	Challenger Expedition	Dredge (4.15 m) and trawl nets (4 and 6 m)	32–2350	Pernambuco, Alagoas, Sergipe, and Bahia
1966	RV <i>Ernst Haeckel</i>	Germany		Bottom trawl (not specified)	54–500	Brazil and Argentina
1957–1976	MIV <i>Oregon II</i>	USA	# 47, 58, 66, 84	Shrimp trawl (12 m)	0–411	Amapá, Maranhão, and Pará, off mouth of Rio Amazonas
1987	RV <i>Marion Dufresne</i>	France	MD-55	Chalut à Pache beam trawl (4.5 m); Blake trawl (4 m); Sanders dredge	20–5092	Rio de Janeiro, Espírito Santo, and Victoria-Trindade seamount
1999	RV <i>Thalassa</i>	France	Bahia-1	Midwater net (56 × 25 m)	30–2000	Bahia to Rio de Janeiro
2000	RV <i>Thalassa</i>	France	Bahia-2	ARROW trawl (47.4 × 26.8 m); GOV trawl (36 × 47 m)	195–2137	Bahia to Rio de Janeiro
1996–1999	RV <i>Atlântico Sul</i>	Brazil	REVIZEE I–VI	Pelagic trawl (268 m circumference)	100–1500	Rio de Janeiro to Rio Grande do Sul
1996–2002	FV <i>Diadorim</i> and FV <i>Soloncy Moura</i>	Brazil		Longline and traps; Engel star balloon trawl (40.4 m)	100–1200	Rio de Janeiro to Rio Grande do Sul
2003	OSV Astro Garoupa	Brazil	OCEANPROF I, II	Semi-balloon otter trawl (5.5 m)	1059–1640	Rio de Janeiro
2009	RV <i>Luke Thomas</i>	USA		Semi-balloon otter trawl (8 m)	150–2000	Rio Grande do Norte
2011	RV <i>Seward Johnson</i>	USA		Semi-balloon otter trawl (15 m)	150–2068	Rio Grande do Norte
2012–present	MS <i>Teahupoo</i>	Brazil	TAMAR	Longline and fish traps	250–900	Bahia
2012–2014	FV <i>Transmar I</i>	Brazil		Longline and fish traps	170–700	Saint Peter and Saint Paul Archipelago
2015, 2017	RV <i>Antea</i>	France	ABRACOS I, II	Micronekton and mesopelagic nets	0–1113	Seamounts off Northeastern Brazil and Fernando de Noronha
2019–present	RV <i>Alpha Crucis</i>	Brazil	DEEP-OCEAN	Shrimp trawl (19 m)	400–1500	Southern Brazil

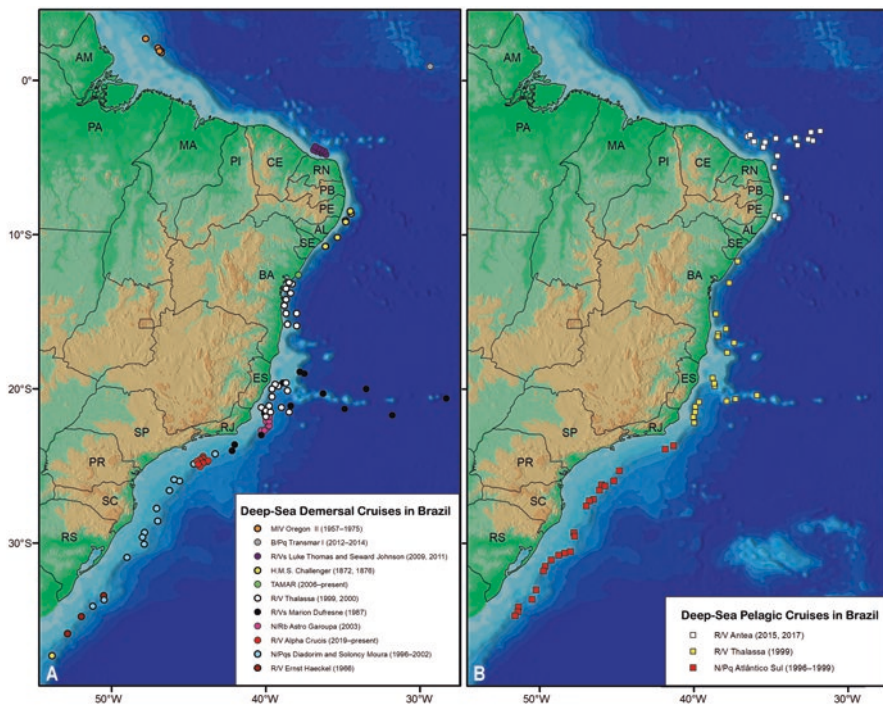


Fig. 7.1 Cruises to the Brazilian Economic Exclusive Zone that produced information about the deep-sea ichthyofauna using (a) demersal gear such as bottom trawl, longline, and fish traps (circles) or (b) pelagic net (square). To avoid excessive overlapping, each point may represent more than one station

The arrangement of Classes, Orders, and Families follows Fricke et al. (2020) for Myxini and Chondrichthyes, which are divided into the Classes Elasmobranchii and Holocephali; Betancur-R et al. (2017) was used for the ranks within the Class Actinopteri. Prefixes of vessels used along text are as follows: FV, fishery vessel; MV or MIV, motor vessel; RV research vessel; HMS, His/Her Majesty's Ship; OSV, offshore supply vessel.

The habitat definition adopted herein is adapted from Briggs (1960) and Gaither et al. (2016): (A) shallow benthopelagic, species that live on or near to the bottom and are typically found on the continental shelf in shallower waters and mesophotic reefs, which were also reported in depths greater than 200 m (e.g., muraenids, seranids); (B) epipelagic, species that generally inhabit the upper 200 m of the water column, but also visit deeper waters (e.g., lamnids and scombrids); (C) deep benthopelagic, species that live on or near to the bottom at depths greater than 200 m (e.g., chimaerids and synphobranchid eels); (D) mesopelagic, species that are encountered in the water column at depths between 200 and 1000 m (e.g., etmopterids, myctophiforms, and stomiiformes), and (E) bathypelagic, species that occur in the water column in depths great than 1000 m (e.g., dalatiids, ceratioids, and

eurypharyngids). All the records were organized considering the cruise and presented along with the existing information on habitat occupation.

7.2 Records of Deep-Sea Fishes in Brazilian EEZ

7.2.1 *HMS Challenger Expedition (1872–1876)*

In Brazil, the Challenger Expedition passed through the Saint Paul Rocks (August 28–29th, 1873) and the Fernando de Noronha Archipelago (September 1^s–8th, 1873), but only obtained biological collections between Pernambuco and Bahia States (September 9–14th, 1873) (Thomson 1880). Those specimens were used by Günther (1877, 1878a, b, 1880, 1887) for the descriptions of the first Brazilian deep-sea fishes, including the grenadier *Coryphaenoides leptolepis* Günther 1877 (Macrouridae), the tripod fish *Bathypterois quadrifilis* Günther 1878, the grideye *Ipnops murrayi* Günther 1878 (Ipnopidae), the serranid *Bathyanthias roseus* Günther 1880 (Serranidae), the flatfish *Citharichthys cornutus* (Günther 1880) (Paralichthyidae), the armored-searobin *Peristedion truncatum* (Günther 1880) (Peristediidae), the viviparous brotula *Diplacanthopoma brachysoma* Günther 1887 (Bythitidae), the clusk eel *Neobythites ocellatus* Günther 1887 (Ophidiidae), and the bigscale *Poromitra crassiceps* (Günther 1878a, b) (Melamphaidae).

The Challenger Expedition also visited other parts of South America, obtaining samples from Punta Arenas, Chile to the Falkland Islands (January 20th–February 3rd, 1976), from the Falkland Islands to off the Rio de la Plata mouth, at the border between Argentina and Uruguay (February 8–26th, 1876), and from the Rio de la Plata mouth to the Tristan da Cunha Islands (February 28th–March 14th, 1876) (Thomson 1880). Those stations in adjacent waters resulted in the descriptions of additional five species that also occur in the Brazilian EEZ: the gadiforms *Coryphaenoides affinis* Günther, 1878, *Laemonema longifilis* Günther 1880 [valid as *Urophycis brasiliensis* (Kaup 1858) (Lemes et al. 2016)] (Phycidae), and *Antimora rostrata*; the tripodfish *Bathypterois longipes* Günther 1878 (Ipnopidae); and the viviparous brotula *Cataetx messieri* (Bythitidae).

7.2.2 *Fishery Surveys in the Nineteenth Century (1950–1970)*

In 1966, the western German RV *Ernst Haeckel* made a cruise to the southern part of South America between Brazil and Argentina (32°–51° S), resulting in records of 85 species of Actinopterygii, nine from deeper waters, and the description of the flathead *Cottunculus granulatus* Karrer 1968 (Psychrolutidae) (Krefft 1968a, Lima and Mincarone 2004).

Between 1957 and 1975, the United States National Oceanic and Atmospheric Administration MIV *Oregon II* conducted several expeditions to Northern Brazil, off the mouth of the Rio Amazonas. Most part of the samples was taken from up to 80 m, on the continental shelf; however, a few stations were made on the continental slope, in depths of up to 411 m (Cohen 1958, Collette and Rützler 1977). Those stations resulted in the discovery of a deep-reef of sponges and rhodoliths, and the descriptions of the slender catshark *Schroederichthys tenuis* Springer 1966 (Scyliorhinidae), the shortspine boarfish *Antigonia combatia* Berry and Rathjein 1958, a slope dragonet *Centrodraco oregonus* (Briggs and Berry 1959) (Draconettidae), the Atlantic green eye *Chlorophthalmus brasiliensis* Mead 1958 (Chlorophthalmidae), a grenadier *Malacocephalus okamurai* Iwamoto and Arai 1987 (Macrouridae), an argentine *Glossanodon pygmaeus* Cohen 1958 (Argentinidae), a clusk eel *Neobythites brasiliensis* Nielsen 1999 (Ophidiidae), the anguilliforms *Bathycongrus bullisi* (Smith and Kanazawa 1977) (Congridae) and *Chlorophthalmus brasiliensis* Mead 1958 (Chlorophthalmidae), and the western luminous roughy *Aulotrachichthys argyrophanus* (Woods 1961) (Trachichthyidae) (Mead 1958; Briggs and Berry 1959; Woods 1961; Springer 1965; Smith and Kanazawa 1977; Iwamoto and Arai 1987; Gadig et al. 1996; Nielsen 1999).

7.2.3 *RV Marion Dufresne (1987)*

In 1987, the expedition MD-55 was conducted onboard of the French RV *Marion Dufresne*, as part of a collaboration between the Universidade Santa Úrsula, Brazil, and the Muséum National d'Histoire Naturelle, France (Guille and Ramos 1988; Tavares 1999). A total of 33 stations using bottom trawls were made on the continental shelf and slope between northern Rio de Janeiro and Espírito Santo States, and on the Vitória-Trindade Seamount Chain (23°36'40"–18°49'00" S and 42°10'–28°20' W), in depths of 200 to 5092 m. The MD-55 expedition produced 500 specimens, comprising 81 species and 39 families of Osteichthyes and four Elasmobranchii (Séret and Andreata 1992). The specimens were split between the two leading institutions, but more recently the fish specimens deposited at the Universidade Santa Úrsula were transferred to the Museu Nacional/UFRJ.

7.2.4 *The REVIZEE Years (1994–2004)*

In 1994, the Brazilian Government launched the Program Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone (REVIZEE), a 10 years long project which objective was to evaluate the marine resources in the Brazilian Exclusive Economic Zone. The Brazilian EEZ was divided into four scores, according to their oceanographic and biological

characteristics, and dominant seabed type: North, Northeast, Central, and Southeast-South (Ministério do Meio Ambiente 2006; Serafim 2007).

During the REVIZEE program, the French RV *Thalassa* of the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER) was hired to explore the continental slope. Two cruises were conducted in 1999 and 2000, between Bahia and Rio de Janeiro States (11°–22° S and 34°40'–40°30' W), formerly named as Bahia-1 and Bahia-2, respectively. The goal of the Bahia-1 cruise was to explore the epipelagic (0–200 m) and mesopelagic (200–1000 m) resources. The samples were obtained from 51 stations, from depths between 14 and 910 m and resulted in the capture of 96 species of Osteichthyes from 38 families (Madureira et al. 2004, Braga et al. 2007). During the Bahia-2 cruise, focused on the demersal and benthopelagic organisms, samples were obtained from 58 stations between 195 and 2137 m and resulted in the capture of 208 species from 61 families of Actinopteri, and 14 species sharks from eight families (Costa et al. 2000, 2007; Nunan et al. 2007). The collections made by the RV *Thalassa* served as base for descriptions of nine new species: the angelshark *Squatina varii* Vaz and Carvalho 2018 (Squatinaidae); the catsharks *Scyliorhinus cabofriensis* Soares et al. 2016 and *S. ugoi* Soares et al. 2015 (Scyliorhinidae); the dogsharks *Squalus bahiensis* Viana et al. 2016 and *S. albicaudus* Viana et al. 2016 (Squalidae); the skates *Dipturus mennii* Gomes and Paragó 2001 and *Malacoraja obscura* Carvalho et al. 2005 (Rajidae); the swallower *Kali colubrina* Melo 2008 (Chiasmodontidae); the clusk eel *Neobythites monocellatus* Nielsen 1999 (Ophidiidae); the eelpout *Pachycara alepidotum* Anderson and Mincarone 2006 (Zoarcidae); and, in part, the bald cutthroat eel *Synphobranchus calvus* Melo 2007 (Synphobranchidae) (Anderson and Mincarone 2006; Carvalho et al. 2005; Melo 2007, 2008; Melo et al. 2009; Nielsen et al. 2009; Soares et al. 2015, 2016; Soares and Carvalho 2016; Viana et al. 2016; Vaz and Carvalho 2018).

For the Southeast-South score, three cruises were made onboard of the RV *Atlântico Sul* from the Fundação Universidade Rio Grande, between Rio de Janeiro and Rio Grande do Sul States (22°–34° S and 40°–53° W), formerly named as REVIZEE I, II, and III. Most samples were obtained using pelagic nets mainly from 100 to 500 m, but a single station at 675 m during the cruise REVIZEE I, eight stations from 500 to 1480 m during REVIZEE II, and 12 stations from 500 to 1457 m, during REVIZEE III. Those materials collected during those cruises resulted in records of 171 species from 71 families of Actinopterygii and the description of the chimaera *Hydrolagus matallanasi* Soto and Vooren 2004 (Chimaeridae) (De Figueiredo et al. 2002; Soto and Vooren 2004; Bernardes et al. 2007 and Rossi-Wongtschowski 2007).

For the demersal fauna, the samples were obtained onboard of the Brazilian FVs *Diadorim* and *Soloncy Moura*, both from the Centro de Pesquisa e Extensão Pesqueira das Regiões Sudeste e Sul (CEPSUL/IBAMA). Different types of fishing gear were used, including fish traps launched to depths of up to 500 m, long lines to depths between 100 and 1200 m, and bottom trawls made between 100 and 600 m. From these samplings, two species of Myxini, 37 species of Elasmobranchii, and 184 species of Actinopteri were collected (Bernardes et al. 2005a, b; Haimovici et al. 2008). The hagfish *Eptatretus menezes* Mincarone 2000 (Myxinidae) and the

catshark *Schroederichthys saurissqualus* Soto 2001 (Scyliorhinidae) were described based on specimens collected by the RV *Diadorim* (Mincarone 2000; Soto 2001).

7.2.5 *The Petrobras Expeditions (2000–2011)*

Since 2000, the Brazilian oil company Petróleo Brasileiro S.A. – Petrobras started to invest in projects to increase the knowledge of the deep-water fauna (Morais 2013). During the projects OCEANPROF – Oceano Profundo (2001–2007) and HABITATS – Heterogeneidade Ambiental da Bacia de Campos (2008–2015), two expeditions were conducted onboard the Brazilian OSV *Astro Garoupa* to the continental slope off northern Rio de Janeiro State. Using a bottom trawl, the OSV *Astro Garoupa* obtained samples from 40 stations on the continental slope, between 1059 and 1640 m. Two species of Elasmobranchii and 80 species of Actinopteri were reported; including part of the specimens used in the description of the cut-throat eel *Synaphobranchus calvus* (Synaphobranchidae) (Melo 2008; Lavrado and Brasil 2010).

During the Projeto de Monitoramento Ambiental Marinho da Bacia Potiguar (2009–2011), two expeditions were made onboard of the North American RVs *Luke Thomas* and *Seward Johnson* off the Rio Grande do Norte State. The samples were obtained using bottom trawl, from depths between 150 and 2000 m, and resulted in the capture of five species of Elasmobranchii and one Holocephali and 159 species of Actinopteri (Oliveira et al. 2015), and was used for the description of *Barathronus linsi* (Nielsen et al. 2015).

7.2.6 *FRV Antea (2015, 2017)*

The Acoustics along the BRAZILIAN COaSt (ABRACOS) is an integrated program between the French Institut de Recherche pour le Développement and the Brazilian institutions Universidade Federal do Rio de Janeiro, Universidade Federal de Pernambuco, and Universidade Federal Rural de Pernambuco, with the goal to monitor the tropical marine ecosystems between oceanic islands and the continental margin in Northeastern Brazil. Two cruises were carried out onboard the French RV *Antea* (2015, 2017) using micronekton and mesopelagic nets for deep-pelagic organisms in depths of up to 1113 m (Bertrand 2015, 2017; Eduardo et al. 2018a, b). A bottom trawl was also used in 2017, but focused on the continental shelf, therefore not included in this account (Melo et al. 2020). So far, the results of the two expeditions resulted in new records in the Brazilian EEZ of a trichiurid, two howelliids and four caristiids, and regional accounts for 11 mesopelagic species (Eduardo et al. 2018a, c, 2019, Mincarone et al. 2019).

7.2.7 *RV Alpha Crucis (2019–Present)*

The Projeto Diversidade E Evolução de Peixes de Oceano Profundo – DEEP-OCEAN, hosted at the Instituto Oceanográfico da Universidade de São Paulo, has the goal to study the diversity and evolution of deep-sea fishes in the western South Atlantic. The first cruise to the Brazilian EEZ was conducted onboard the Brazilian RV *Alpha Crucis* in September 2019 using a bottom trawl between 400 and 1500 m. Preliminary, unpublished data indicates the capture of 88 species of Elasmobranchii (11), Holocephali (1), and Actinopteri (76). Two additional cruises are planned for 2020/2021.

7.2.8 *Additional Contributions*

Since 2006, the Projeto TAMAR systematically carry out deep-sea fishing off Praia do Forte, Bahia, using the MV *Teahupoo* adapted to deploy longline and traps. The specimens collected are regularly destined to scientific collections and served for the new records of nine species of Actinopterygii in the Brazilian EEZ (Carvalho-Filho et al. 2009, 2010a, b, 2011a, 2011b, 2012, 2020).

Several projects developed at the Universidade Federal Rural de Pernambuco obtained samples from the Saint Peter and Saint Paul Archipelago (ASPSP) and the continental slope off Pernambuco. According to Nunes (2016), the fishing boat FV *Transmar I* was used between 2012 and 2014 to deploy longlines and fish traps at depths from 200 to 700 m in the ASPSP, resulting on records of 11 species of Actinopterygii, one of which was recently described by Pires et al. (2019) as *Physiculus cirm* Carvalho-Filho and Pires 2019 (Moridae).

Partnership with commercial fishing boats also are a good source of scientific material, serving the base for new records of nine species of Actinopterygii in Northeastern Brazil and the description of a new genus and species, *Leucogrammolycus brychios* Anderson and Mincarone 2008 (Zoarcidae) (Anderson and Mincarone 2008; Caires et al. 2008; de Paiva et al. 2011).

7.3 Important Expeditions to Other Parts of the Western South Atlantic

After the scientific achievements of the Challenger Expedition, there was a considerable increase in oceanographic expeditions across the world to obtain physical, chemical, and biological samples (Wust 1964; Hopper 1995). Several fisheries expeditions were conducted off South America that improved the taxonomic knowledge of the deep-sea ichthyofauna in the western South Atlantic, thus providing additional records for several species that occur in the Brazilian EEZ.

Beginning in the 1960s, the German Institute of Sea Fisheries (Institut für Seefischerei, Hamburg, Germany) conducted several expeditions across the Atlantic Ocean, and off Argentina and Uruguay, using the FRV *Walther Herwig* (1960–1971) and FRV *Walther Herwig II* (1973–1985). The results included descriptions of several deep-sea species and extensive taxonomic reviews (Krefft 1968a, b, 1974, 1976; Stehmann and Hulley 1994; Stein 2010).

From the 1970s to the early 2000s, the Japanese Marine Fisheries Research and Development Center (JAMARC) and the Japan Deep-Sea Trawlers Association (JDSTA) performed several fisheries surveys in South America to evaluate the fishery stocks along the coasts of Patagonia (1976–1979), French Guiana and Suriname (1979–1983), and Peru (Uyeno et al. 1983; Nakamura et al. 1986; Nakaya et al. 2009). Off French Guiana and Suriname, bottom trawling was conducted onboard by the whaler MV *Nisshin-Maru No. 201* to explore the resources on the continental shelf and slope, between 90 and 1000 m. A total of 453 species were recorded, including two species of Myxini, 45 Chondrichthyes and 406 Actinopteri (Uyeno et al. 1983). Off Patagonia, the Japanese expeditions were conducted by the MVs *Akebono Maru No. 72* and *Shinkai Maru* focused on the continental shelf and slope off Argentina and the Atlantic Chilean coast, between 20 and 1200 m. The results include a single species of Chondrichthyes and 130 species of Actinopteri (Nakamura et al. 1986).

Between 1970s and 1980s, the Ministry of Fishing Industry of the then Soviet Union promoted an expansion of the deep-sea fisheries in the Southern Atlantic, as a part of a global program. Scientific and commercial explorations were conducted on the Victoria-Trindade Seamount Chain (1982) and on the Rio Grande Rise (1982–1984, 2000) using several fisheries vessels equipped with different types of gear. Those expeditions resulted in reports and species descriptions of about 70 species of fish, including the rare goblin shark *Mitsukurina owstoni* Jordan 1898 (Parin et al. 1995; Shcherbachev 1995; Clark et al. 2007; Prokofiev and Kukuev 2009).

7.4 The Diversity of Deep-Sea Fishes in the Brazilian EEZ

Hitherto, 712 species from 145 families and 37 orders of deep-sea fishes had been recorded in the Brazilian EEZ (Table 7.2). Those records include five species from a single family of Myxiniformes (Table 7.3), six species from three families of Holocephali, 81 species from 23 families and eight orders of Elasmobranchii, and (Table 7.4), and 620 species from 118 families and 27 orders of Actinopteri (Table 7.5). Additionally, 51 species previously mentioned in the area did not have their occurrence confirmed and, therefore, were excluded from this account (Table 7.6).

Among the Brazilian deep-sea ichthyofauna, 40.4% are deep-benthopelagic (e.g., *Bathyroconger vicinus*, *Coelorinchus caribbaeus*, and *Bathyraja schroederi*), 20.2% are mesopelagic (e.g., *Isistius brasiliensis*, *Argyropelecus aculeatus*, and *Diaphus adenomus*), and 21.6% are bathypelagic (e.g., *Barbourisia rufa*,

Table 7.2 Summary of the deep-sea fishes occurring in the Brazilian Economic Exclusive Zone

Class	Order	#Families	#Species	Habitat	
Myxini	Myxiniiformes	1	5	DB	
Holocephali	Chimaeriformes	3	6	SB, DB	
Elasmobranchii	Carcharhiniiformes	3	16	SB, DB	
	Hexanchiformes	1	3	SB, DB	
	Lamniiformes	7	9	EP, BP, SB	
	Myliobatiformes	1	1	EP	
	Rajiformes	2	23	SB, DB	
	Squaliformes	6	23	MP, BP, SB, DB	
	Squatiniiformes	1	3	SB, DB	
	Torpediniiformes	2	3	SB, DB	
	Actinopteri	Acanthuriformes	1	1	EP
Alepocephaliformes		2	21	DB	
Anguilliformes		15	59	BP, SB, DB	
Argentiniiformes		4	11	BP	
Ateleopodiformes		1	1	DB	
Aulopiformes		10	53	BP, DB, SB	
Beryciformes		9	20	BP, DB, SB	
Caproiformes		1	2	DB	
Gadiformes		6	52	MP, DB, SB	
Malacanthidae		2	3	SB	
Opistognathidae		1	1	SB	
Istiophoriformes		1	1	EP	
Lampridiformes		4	8	BP	
Lophiiformes		11	27	BP, SB, DB	
Lutjaniformes		1	2	SB	
Myctophiformes		2	79	MP	
Notacanthiformes		2	10	DB	
Ophidiiformes		4	39	SB, DB	
Pempheriformes		4	15	BP, SB, DB	
Perciformes		9	46	BP, SB, DB	
Pleuronectiformes		4	16	SB, DB	
Polymixiiformes		1	2	DB	
Scobriformes		10	59	EP, MP, BP, DB	
Stomiiformes		4	77	MP, BP	
Syngnathiformes		3	6	DB	
Tetraodontiformes		2	4	EP, DB	
Zeiformes		4	5	BP, DB	
Total		37	145	712	

Abbreviations: *DB* deep benthopelagic, *BP* bathypelagic, *EP* epipelagic, *MP* mesopelagic, and *SB* shallow benthopelagic

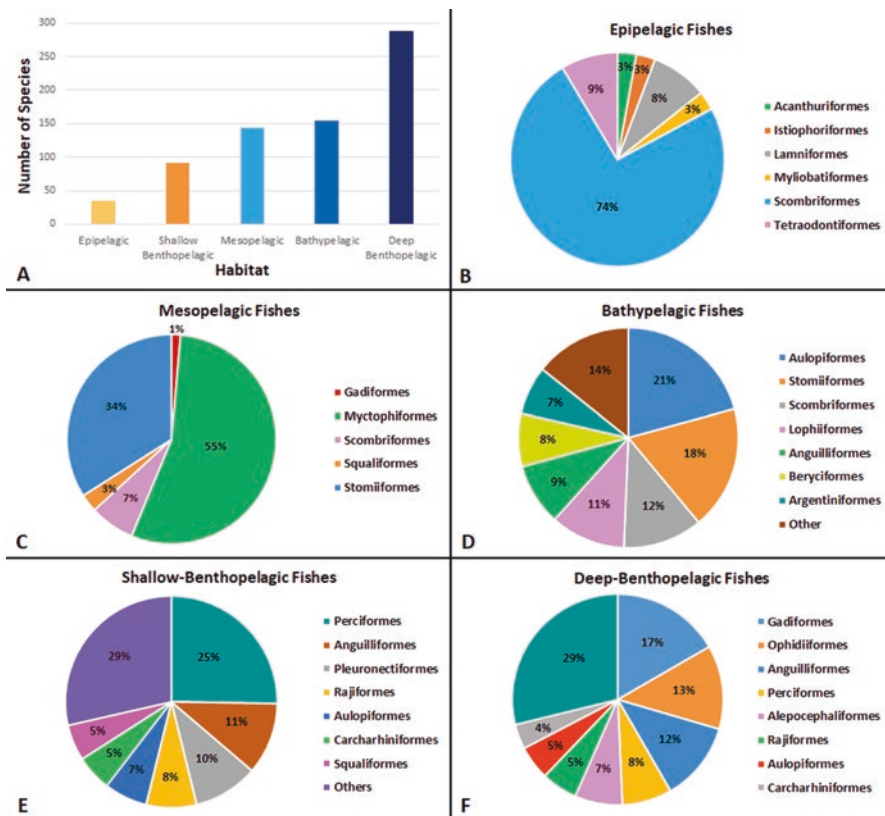


Fig. 7.2 In (a), the composition of the deep-sea fishes in the Brazilian Economic Exclusive Zone per habitat. The proportions of the most diversified groups in each habitat are as follows: (b) epipelagic; (c) shallow benthopelagic; (d) mesopelagic; (e) bathypelagic; and (f) deep-benthopelagic fishes

Gigantactis verhoeffeni, and *Kali indica*) (Fig. 7.2). Noteworthy, several species classified herein as bathypelagic are not restricted to greater depths and frequently occur in the mesopelagic zone (Rofen 1966; Melo 2008; Pietsch 2009).

The shallow benthopelagic species represent 12.8% (e.g., *Callorhynchus callosyrinchus*, *Merluccius hubbsi*, and *Polyprion americanus*), and only 4.9% are epipelagic (e.g., *Characarodon carcharias*, *Mola mola*, and *Xiphias gladius*).

The deep-benthopelagic fishes are the most diversified, including 288 species (Fig. 7.3). All five species of hagfishes (Myxinidae) are benthopelagic. The Elasmobranchii are represented by 41 species from 11 families and six orders: Rajiformes, with 16 species from the families Rajidae (15) and Arhynchobatidae (1); Carcharhiniformes, with 11 species from the families Pseudotriakidae (1) and Scyliorhinidae (11); Squaliformes, with ten species from the families Somniosidae (4), Centrophoridae (2), Dalatiidae (2), Echinorhinidae (1), and Squalidae (1); Hexanchiformes, with two species from the family Hexanchidae (2);

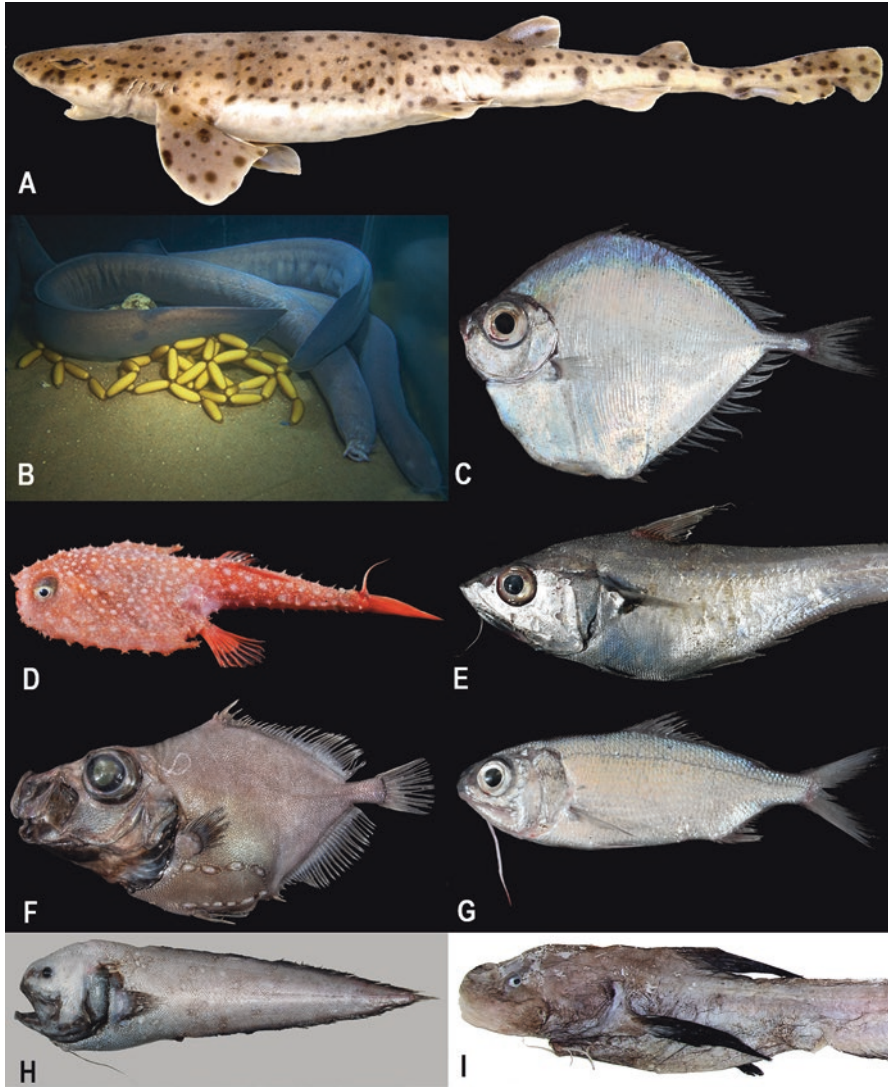


Fig. 7.3 Diversity of the Brazilian deep-benthopelagic fishes: (a) freckled catshark *Scyliorhinus haeckelii*; (b) hagfish *Eptatretus multidens* (Myxinidae); (c) spotted tinseltfish *Xenolepidichthys dalgleishi* (Grammicolepididae); (d) Atlantic batfish *Dibranchius atlanticus* (Ogcocephalidae); (e) western softhead grenadier *Malacocephalus occidentalis*; (f) warty oreo *Alloctytus verrucosus* (Oreosomatidae), (g) beardfish *Polymixia lowei* (Polymixiidae), (h) cargoyle cusk *Xyelacyba myersi*, and (i) Lope's tadpole fish *Ijimaia cf. loppei* (Ateleopodidae)

Squatiniiformes, with a single species in the family Squatinidae; and Torpediniiformes, with a single species in the family Narcinidae. The Holocephali is represented by three species from the two families of Chimaeriformes, Chimaeridae (2) and Rhinochimaeridae (1).

Most deep-benthopelagic fishes are actinopterygians, with 237 species from 51 families from 18 orders. Gadiformes is the most diversified order, with 48 species from the families Macrouridae (32), Moridae (12), Merlucciidae (2), Gadidae (1), and Melanonidae (1); followed by Ophidiiformes, with 37 species from the families Ophidiidae (26), Bythitidae (4), Carapidae (4), and Aphyonidae (3); Anguilliformes, with 35 species from the families Congridae (15), Synphobranchidae (14), Nettastomatidae (5), and Colocongridae (1); Perciformes, with 22 species from the families Bembropidae (5), Scorpaenidae (6), Zoarcidae (4), Serranidae (3), Peristediidae (2), Psychrolutidae (1), and Setarchidae (1); and Alepocephaliformes, with 21 species from the families Alepocephalidae (18) and Platytrociidae (3).

Other deep-benthopelagic fishes includes the Aulopiformes (15), Notacanthiformes (10), Pempheriformes (10), Lophiiformes (7), Pleuronectiformes (7), Syngnathiformes (6), Beryciformes (6), Scombriformes (5), Caproiformes (2), Polymixiiformes (2), Zeiformes (2), Atelepodiformes (1), and Tetraodontiformes (1).

The 144 species of mesopelagic fishes are included in only a single order of Elasmobranchii and four orders of Actinopteri (Fig. 7.4). The elasmobranchs are represented by four species of Squaliformes from the families Etmopteridae (3) and Dalatiidae (1). The actinopterygians are represented by 79 species of Myctophiiformes from the families Myctophidae (77) and Neoscopelidae (2), followed by 49 species of Stomiiformes from the families Gonostomatidae (16), Sternoptychidae (14), Stomiidae (10), and Phosichthyidae (9). Other mesopelagic fishes are the scombriform families Chiasmodontidae (6) and Caristiidae (4), and the gadiform family Bregmacerotidae (2).

The bathypelagic fishes include 147 species (Fig. 7.4). The Elasmobranchii are represented by only seven species of deep-sea sharks from the orders Laminiformes, families Cetorhinidae (1), Megachasmidae (1) and Mitsukurinidae (1), and Squaliformes, families Dalatiidae (2) and Etmopteridae (2). Among the Actinopteri, the most diversified groups are the Aulopiformes, with 32 species from the families Paralepididae (14), Scopelarchidae (6), Notosudidae (5), Evermannellidae (4), and Alepisauridae (3); followed by Stomiiformes, with 28 species from the family Stomiidae, Scombriformes, with 18 species from the families Chiasmodontidae (6), Trichiuridae (5), Gempylidae (4), Caristiidae (1), Centrolophidae (1), and Nomeidae (1); Lophiiformes with 17 species from the families Oneirodidae (4), Ceratiidae (3), Himantolophidae (3), Gigantactinidae (2), Melanocetidae (2), Chaunacidae (1), Diceratiidae (1), and Neoceratiidae (1); and Anguilliformes, with 14 species from the families Nemichthyidae (5), Serrivomeridae (3), Nettastomatidae (2), Cyematidae (1), Derichthyidae (1), Eurypharyngidae (1), and Saccopharyngidae (1). Other bathypelagic fishes belong to the orders Beryciformes (12), Argentiniiformes (11), Lampridiformes (8), Pempheriformes (3), Zeiformes (3), and Perciformes (1).

Within the two groups of shallow water fishes that can be occasionally be found in the deep sea, the epipelagic fishes are represented by two species of the lamniform sharks families Lamnidae (2) and Alopiidae (1); and 31 species of the orders Scombriformes families Bramidae (10), Scombridae (6), Nomeidae (4),

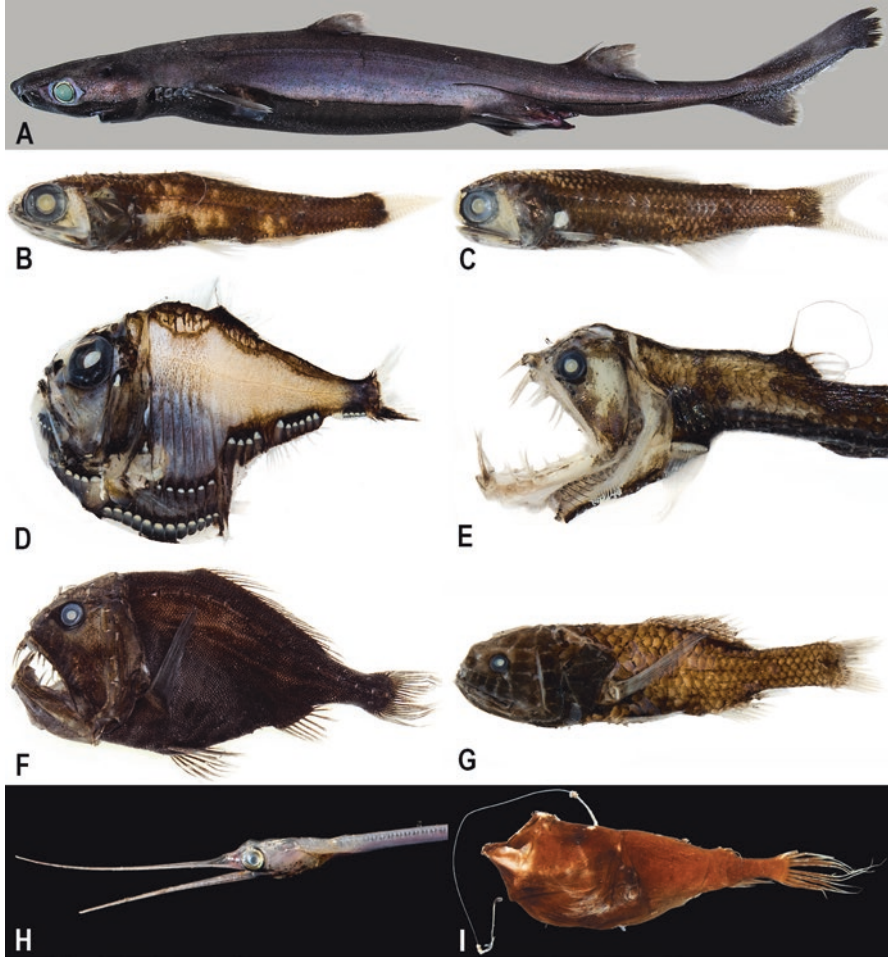


Fig. 7.4 Diversity of the Brazilian mesopelagic (a–d) and bathypelagic fishes (e–i): (a) blackbelly lanternshark *Etmopterus lucifer* (Etmopteridae), (b) Madeira lanternfish *Ceratoscopelus maderensis* (Myctophidae), (c) Soft lanternfish *Diaphus* cf. *mollis*, (d) silver hatchetfish *Argyropelecus aculeatus* (Sternoptychidae), (e) Sloane's viperfish *Chauliodus sloani* (Stomiidae) (f) ogresfish *Anoplogaster cornuta*, (g) ridge head *Poromitra* sp. (Melamphaidae), (h) slender snipe eel *Nemichthys scolopaceus* (Nemichthyidae), (i) Kroyer's deep-sea anglerfish *Ceratiidae holboelli* (Ceratiidae)

Ariommatidae (2), Gempylidae (2), Centrolophidae (1), and Trichiuridae (1), followed by the orders Tetraodontiformes (3), Acanthuriformes (1), and Istiophoriformes (1).

The shallow benthopelagic fishes are composed by 91 species from 36 families. Holocephali is represented by a single species of Callorhynchidae, and the Elasmobranchii by 25 species, including seven species of Rajiformes from the families Arhynchobatidae (4) and Rajidae (3); five species of Carcharhiniformes,

families Triakidae (4) and Scyliorhinidae (1); and five species of Squaliformes, family Squalidae (5). The additional species belong to the orders Lamniformes (3), Squatiniformes (2), Torpediniformes (2), and Hexanchiformes (1).

Among the Actinopteri, Perciformes is the most diverse group, with 23 species from the families Serranidae (12), Peristediidae (4), Priacanthidae (3), Triglidae (3), and Scorpaenidae (1), followed by the Anguilliformes, with ten species from families Muraenidae (3), Ophichthidae (3), Chlopsidae (2), Congridae (1), and Muraenesocidae (1); Pleuronectiformes, with nine species from the families Cynoglossidae (4), Bothidae (3), and Paralichthyidae (1); and Aulopiformes, with six species from the families Synodontidae (5) and Aulopidae (1). Other shallow benthopelagic fish groups include the Lutjaniformes (2), Beryciformes (2), Gadiformes (2), Pempheriformes (2), Lophiiformes (3), the families Malacanthidae (2) and Emmelichthyidae (1), which are *incertae sedis* in Eupercaria, and Opistognathidae (1), *incertae sedis* in Ovolentaria.

7.5 Anthropogenic Impacts and Major Treats

Recent accounts of the Brazilian fauna at risk of extinction include 16 species of deep-sea fishes (ICMBIO/MMA 2018a, b). Five species were categorized as vulnerable, including the Soto's hagfish (*Myxine sotoi*), the great white shark (*Carcharodon carcharias*), the argentine torpedo (*Tetronarce puelcha*), the snowy grouper (*Hyporthodus niveatus*), and the tile fish (*Lopholatilus villarii*). Three species are categorized as endangered, the dusky smooth-hound (*Mustelus canis*), the spotback skate (*Atlantoraja castelnaui*), and the warsaw grouper (*Hyporthodus nigritus*). Seven species are categorized as critically endangered, the picked dogfish (*Squalus acanthias*), two angelsharks (*Squatina argentina* and *S. occulta*), two houndsharks (*Galeorhinus galeus* and *Mustelus fasciatus*), the broadnose-sevengill shark (*Notorynchus cepedianus*), and the Atlantic wreckfish (*Polyprion americanus*). Major treats for those species are related to overfishing causing considerable populational decline in the past 20 years.

Fishing operations targeting deep-sea species on the Brazilian EEZ have been conducted by international vessels since the late 1990s, focusing on both fishes and crustaceans from the continental slopes off Northern and Southern Brazil, the Ceará Plateau, and the Fernando de Noronha Chain (Athiê and Rossi-Wongtschowski 2005; Alvarez Perez et al. 2009; Kitahara 2009). Targeted stocks of several deep-sea species such as the blackfin goosefish (*Lophius gastrophysus*), Argentine hake (*Merluccius hubbsi*), and Atlantic wreckfish (*Polyprion americanus*) are currently depleted (Perez and Haimovici 1998; Perez and Wahrlich 2005; Pezzuto et al. 2006). The ecological impacts of deep-sea fisheries are similar to the impacts in shallow systems and may result on the removal of habitat-formers, decline in diversity, changes in abundance and biomass, reduction in distribution, and changes in the community structure; however, the rates of recovery are much slower and difficult to estimate (Clark et al. 2016).

Additionally, the deep-sea species have been consistently affected by human activities as disposal of litter and waste in sea beds, residuals from sewage, discards from fishing activities and transport of livestock, chemical contamination such as oil spills and pharmaceuticals, mining, ocean acidification, and fisheries (Koslow et al. 2000; van den Hove and Moreau 2007; Ramirez-Llodra et al. 2011; White et al. 2012).

The exploration oil and gas obtained from deep waters in Brazil started back in 1979, and, nowadays, Brazil is one of the world leaders in the exploration of oil and gas in deep (500–1500 m) and ultra-deep (>1500 m) waters. Major fields of explorations include the pre-salt layers of the Bacia de Campos and Bacia de Santos, which extends for about 800 km from the Espírito Santo and Santa Catarina States, and the Bacia Potiguar, located off the Rio Grande do Norte and Ceará States (Trindade et al. 1992; van den Hove and Moreau 2007; Morais 2013). There are substantial risks associated with this kind of activity, including light and acoustic disturbance, disposal of wastes produced during the drilling process, produced water, mechanical impacts caused by anchors, control cables, pipelines and risers, change of habitats by seabed infrastructures, mass hydrocarbon release caused by oil and gas spill, and mass dispersant and chemical amplificant release applied to oil spills (White et al. 2012; Cordes et al. 2016).

7.6 Challenges and Perspectives

The Brazilian deep-sea known unknowns include large areas of the continental slope in Northern and Northeastern Brazil and, in South and Southern Brazil, depths below 500 m, specially from the southern part of Rio de Janeiro to Rio Grande do Sul.

Besides the continental slope, key areas for further exploration are seamounts and oceanic islands, such as the North Brazilian ridge, the Fernando de Noronha ridge, including the oceanic islands of the Fernando de Noronha Archipelago and Atol das Rocas, the Victoria-Trindade Seamount Chain with the Trindade and Martin Vaz archipelago, and the isolated Saint Peter and Saint Paul archipelago, and Rio Grande Rise. Those remote areas are particularly challenging to sample, because of the difficult access and adverse oceanographic conditions of the strong currents, the steep and rocky bottom, and frequent inclement weather in the Rio Grande rise area.

The many efforts to obtain samples from greater marine depths since the beginning of the twenty-first century are contributing to cover such gaps and boosting significant gains to better understand the biodiversity of deep-sea fishes in the western South Atlantic. In the past years, a number of scientific contributions were published focusing on the deep-sea fish fauna, including general inventories and books

(De Figueiredo et al. 2002; Madureira et al. 2004; Bernardes et al. 2005b; Costa et al. 2007; Lavrado and Brasil 2010; Oliveira et al. 2015), ecological data on distribution and abundance (Bernardes and Rossi-Wongtschowski 2007; Braga et al. 2014), comprehensive taxonomic reviews (Mincarone et al. 2008; Santos and Figueiredo 2008; Melo 2009, 2010; Lima et al. 2011), and descriptions of sixteen new taxa (see above).

Indeed, only with the development of long-term projects to sample the deep ocean, the deposit of specimens in well-established natural history collections, and extensive public outreach will ensure fantastic discoveries, the appropriate monitoring of anthropogenic impacts on deep-sea communities, and inspire new generations of scientists.

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Appendix (Tables 7.3, 7.4, 7.5 and 7.6)

Table 7.3 Checklist of the deep-sea species of Myxini recorded in the Brazilian Economic Exclusive Zone

Class	Order	Family	Species	Habitat
Myxini	Myxiniformes	Myxinidae	<i>Eptatretus menezesi</i> Mincarone, 2000	DB
			<i>Eptatretus multidentis</i> Fernholm & Hubbs, 1981	DB
			<i>Myxine australis</i> Jenyns, 1842	DB
			<i>Myxine sotoi</i> Mincarone, 2001	DB
			<i>Nemamyxine krefftii</i> McMillan & Wisner 1982	DB

Abbreviations: *DB* deep benthopelagic, *BP* bathypelagic, *EP* epipelagic, *MP* mesopelagic, and *SB* shallow benthopelagic

Table 7.4 Checklist of the deep-sea species of Chondrichthyes (Holocephali and Elasmobranchii) recorded in the Brazilian Economic Exclusive Zone

Class	Order	Family	Species	Habitat		
Holocephali	Chimaeriformes	Callorhynchidae	<i>Callorhynchus callorynchus</i> Linnaeus, 1758	SB		
		Chimaeridae	<i>Hydrolagus affinis</i> de Brito Capello, 1868	DB		
			<i>Hydrolagus alberti</i> Bigelow & Schroeder, 1951	DB		
			<i>Hydrolagus matallanasi</i> Soto & Vooren, 2004	DB		
		Rhinochimaeridae	<i>Harriotta raleighana</i> Goode & Bean, 1895	DB		
			<i>Rhinochimaera atlantica</i> Holt & Byrne, 1909	DB		
		Elasmobranchii	Carcharhiniformes	Pseudotriakidae	<i>Pseudotriakis microdon</i> de Brito Capello, 1868	DB
				Scyliorhinidae	<i>Apristurus parvipinnis</i> Springer & Heemstra, 1979	DB
					<i>Apristurus profundorum</i> Goode & Bean, 1896	DB
					<i>Galeus mincaronei</i> Soto, 2001	DB
<i>Parmaturus angelae</i> Soares, Carvalho, Schwingel & Gadig, 2019	DB					
<i>Schroederichthys bivius</i> Müller & Henle, 1838	SB					
<i>Schroederichthys saurisqualus</i> Soto, 2001	DB					
<i>Schroederichthys tenuis</i> Springer, 1966	DB					
<i>Scyliorhinus boa</i> Goode & Bean, 1896	DB					
<i>Scyliorhinus cabofriensis</i> Soares, Gomes & Carvalho, 2016	DB					
<i>Scyliorhinus haeckelii</i> Miranda-Ribeiro, 1907	DB					
<i>Scyliorhinus ugoi</i> Soares Gadig & Gomes, 2015	DB					
Triakidae	<i>Galeorhinus galeus</i> Linnaeus, 1758				SB	
<i>Mustelus canis</i> Mitchell, 1815	SB					

(continued)

Table 7.4 (continued)

Class	Order	Family	Species	Habitat
			<i>Mustelus fasciatus</i> Garman, 1913	SB
			<i>Mustelus higmani</i> Springer & Lowe, 1963	SB
	Hexanchiformes	Hexanchidae	<i>Hepranchias perlo</i> Bonnaterre, 1788	DB
			<i>Hexanchus griseus</i> Bonnaterre, 1788	DB
			<i>Notorynchus cepedianus</i> Péron, 1807	SB
	Lamniformes	Lamnidae	<i>Lamna nasus</i> Bonnaterre, 1788	EP
			<i>Carcharodon carcharias</i> Linnaeus, 1758	EP
		Alopiidae	<i>Alopias superciliosus</i> Lowe 1841	EP
		Megachasmidae	<i>Megachasma pelagios</i> Taylor, Compagno & Struhsaker, 1983	BP
		Cetorhinidae	<i>Cetorhinus maximus</i> Gunnerus, 1765	BP
		Mitsukurinidae	<i>Mitsukurina owstoni</i> Jordan, 1898	BP
		Odontaspidae	<i>Odontaspis ferox</i> Risso, 1810	SB
			<i>Odontaspis noronhai</i> Maul, 1955	SB
		Pseudocarchariidae	<i>Pseudocarcharias</i> <i>kamoharai</i> Matsubara, 1936	SB
	Myliobatiformes	Dasyatidae	<i>Pteroplatytrygon</i> <i>violacea</i> Bonaparte, 1832	EP
	Rajiformes	Arhynchobatidae	<i>Atlantoraja castelnaui</i> Miranda-Ribeiro, 1907	SB
			<i>Atlantoraja cyclophora</i> Regan, 1903	SB
			<i>Atlantoraja platana</i> Günther, 1880	SB
			<i>Bathyraja brachyurops</i> Fowler, 1910	SB
			<i>Bathyraja schroederi</i> Kreffft, 1968	DB
		Rajidae	<i>Amblyraja frerichsi</i> Kreffft, 1968	DB
			<i>Breviraja nigriventralis</i> McEachran & Matheson, 1985	DB

(continued)

Table 7.4 (continued)

Class	Order	Family	Species	Habitat
			<i>Breviraja spinosa</i> Bigelow & Schroeder, 1950	DB
			<i>Cruriraja rugosa</i> Bigelow & Schroeder, 1958	DB
			<i>Dactylobatus clarkii</i> Bigelow & Schroeder, 1958	DB
			<i>Dipturus chilensis</i> Guichenot, 1848	SB
			<i>Dipturus garricki</i> Bigelow & Schroeder, 1958	SB
			<i>Dipturus leptocaudus</i> Krefft & Stehmann, 1975	DB
			<i>Dipturus mennii</i> Gomes & Paragó, 2001	SB
			<i>Dipturus teevani</i> Bigelow & Schroeder, 1951	DB
			<i>Gurgesiella atlantica</i> Bigelow & Schroeder, 1962	DB
			<i>Gurgesiella dorsalis</i> McEachran & Compagno, 1980	DB
			<i>Malacoraja obscura</i> Carvalho, Gomes & Gadig, 2005	DB
			<i>Malacoraja</i> <i>spinacidervis</i> Barnard, 1923	DB
			<i>Rajella bigelowi</i> Stehmann, 1978	DB
			<i>Rajella fuliginea</i> Bigelow & Schroeder, 1954	DB
			<i>Rajella purpuriventralis</i> Bigelow & Schroeder, 1962	DB
			<i>Rajella sadowskii</i> Krefft & Stehmann, 1974	DB
	Squaliformes	Centrophoridae	<i>Centrophorus</i> <i>granulosus</i> Bloch & Schneider, 1801	DB
		Centrophoridae	<i>Deania profundorum</i> Smith & Radcliffe, 1912	DB

(continued)

Table 7.4 (continued)

Class	Order	Family	Species	Habitat
		Dalatiidae	<i>Dalatias licha</i> Bonnaterre, 1788	DB
			<i>Euprotomicroides zantedeschia</i> Hulley & Penrith, 1966	DB
			<i>Isistius brasiliensis</i> Quoy & Gaimard, 1824	BP
			<i>Isistius plutodus</i> Garrick & Springer, 1964	BP
			<i>Squaliolus laticaudus</i> Smith & Radcliffe, 1912	MP
		Echinorhinidae	<i>Echinorhinus brucus</i> Bonnaterre, 1788	DB
		Etmopteridae	<i>Etmopterus bigelowi</i> Shirai & Tachikawa, 1993	MP
			<i>Etmopterus gracilispinis</i> Krefft, 1968	BP
			<i>Etmopterus granulosus</i> Günther, 1880	MP
			<i>Etmopterus hillianus</i> Poey, 1861	MP
			<i>Etmopterus lucifer</i> Jordan & Snyder, 1902	BP
		Somniosidae	<i>Centroscymnus coelolepis</i> Barbosa du Bocage & de Brito Capello, 1864	DB
			<i>Centroscymnus owstonii</i> Garman, 1906	DB
			<i>Somniosus antarcticus</i> Whitley, 1939	DB
			<i>Zameus squamulosus</i> Günther, 1877	DB
		Squalidae	<i>Cirrhigaleus asper</i> Merrett, 1973	DB
			<i>Squalus acanthias</i> Linnaeus, 1758	SB
			<i>Squalus albicaudus</i> Viana, Carvalho & Gomes, 2016	SB
			<i>Squalus bahiensis</i> Viana, Carvalho & Gomes, 2016	SB
			<i>Squalus lobularis</i> Viana, Carvalho & Gomes, 2016	SB
			<i>Squalus quasimodo</i> Viana, Carvalho & Gomes, 2016	SB

(continued)

Table 7.4 (continued)

Class	Order	Family	Species	Habitat
	Squatiniformes	Squatinaidae	<i>Squatina argentina</i> Marini, 1930	SB
			<i>Squatina varii</i> Vaz & Carvalho, 2018	DB
			<i>Squatina occulta</i> Vooren & Silva, 1991	SB
	Torpediniformes	Narcinidae	<i>Benthobatis krefftii</i> Rincón, Stehmann & Vooren, 2001	DB
			<i>Tetronarce nobiliana</i> Bonaparte, 1835	SB
			<i>Tetronarce puelcha</i> Lahille, 1928	SB

Abbreviations: *DB* deep benthopelagic, *BP* bathypelagic, *EP* epipelagic, *MP* mesopelagic, and *SB* shallow benthopelagic

Table 7.5 Checklist of the deep-sea species of Actinopterygii recorded in the Brazilian Economic Exclusive Zone

Class	Order	Family	Species	Habitat
Actinopteri	Acanthuriformes	Luvaridae	<i>Luvarus imperialis</i> Rafinesque, 1810	EP
	Alepocephaliformes	Alepocephalidae	<i>Alepocephalus australis</i> Barnard, 1923	DB
			<i>Asquamiceps caeruleus</i> Markle, 1980	DB
			<i>Bajacalifornia calcarata</i> Weber, 1913	DB
			<i>Bathytroctes michaelisarsis</i> Koefoed, 1927	DB
			<i>Bathytroctes microlepis</i> Günther, 1878	DB
			<i>Bathytroctes oligolepis</i> Krefft, 1970	DB
			<i>Bathytroctes squamosus</i> Alcock, 1890	DB
			<i>Conocara macropterum</i> Vaillant, 1888	DB
			<i>Conocara microlepis</i> Lloyd, 1909	DB
			<i>Conocara murrayi</i> Koefoed, 1927	DB
			<i>Einara macrolepis</i> Koefoed, 1927	DB
			<i>Leptoderma macrops</i> Vaillant, 1886	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Mirognathus normani</i> Parr, 1951	DB
			<i>Narcetes erimelas</i> Alcock, 1890	DB
			<i>Narcetes stomias</i> Gilbert, 1890	DB
			<i>Rouleina attrita</i> Vaillant, 1888	DB
			<i>Talismania homoptera</i> Vaillant, 1888	DB
			<i>Xenodermichthys copei</i> Gill, 1884	DB
		Platyroctidae	<i>Maulisia microlepis</i> Sazonov & Golovan, 1976	DB
			<i>Mentodus rostratus</i> Günther, 1878	DB
			<i>Normichthys yahganorum</i> Levenberg, 1965	DB
	Anguilliformes	Chlopsidae	<i>Chlopsis bicolor</i> Rafinesque, 1810	SB
			<i>Chlopsis dentatus</i> Seale, 1917	SB
		Colocongridae	<i>Coloconger meadi</i> Kanazawa, 1957	DB
		Congridae	<i>Acromycter atlanticus</i> Smith, 1989	DB
			<i>Acromycter perturbator</i> Parr, 1932	DB
			<i>Ariosoma balearicum</i> Delaroche, 1809	DB
			<i>Ariosoma</i> <i>opisththalmus</i> Ranzani, 1839	DB
			<i>Ariosoma selenops</i> Reid, 1934	DB
			<i>Bassanago albescens</i> Barnard, 1923	DB
			<i>Bathycongrus bullisi</i> Smith & Kanazawa, 1977	DB
			<i>Bathycongrus dubius</i> Breder, 1927	DB
			<i>Bathycongrus vicinalis</i> Garman, 1899	DB
			<i>Bathyuroconger vicinus</i> Vaillant, 1888	DB
			<i>Conger esculentus</i> Poey, 1861	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Conger orbignyanus</i> Valenciennes, 1837	SB
			<i>Pseudophichthys splendens</i> Lea, 1913	DB
			<i>Rhynchoconger flavus</i> Goode & Bean, 1896	DB
			<i>Xenomystax congroides</i> Smith & Kanazawa, 1989	DB
		Cyematidae	<i>Cyema atrum</i> Günther, 1878	BP
		Derichthyidae	<i>Derichthys serpentinus</i> Gill, 1884	BP
		Eurypharyngidae	<i>Eurypharynx pelecanooides</i> Vaillant, 1882	BP
		Muraenesocidae	<i>Cynoponticus savanna</i> Bancroft, 1831	SB
		Muraenidae	<i>Gymnothorax conspersus</i> Poey, 1867	SB
			<i>Gymnothorax ocellatus</i> Agassiz, 1831	SB
			<i>Gymnothorax polygonius</i> Poey, 1875	SB
		Myrocongridae	<i>Myroconger compressus</i> Günther, 1870	DB
		Nemichthyidae	<i>Avocettina acuticeps</i> Regan, 1916	BP
			<i>Avocettina infans</i> Günther, 1878	BP
			<i>Labichthys carinatus</i> Gill & Ryder, 1883	BP
			<i>Nemichthys curvirostris</i> Strömman, 1896	BP
			<i>Nemichthys scolopaceus</i> Richardson, 1848	BP
		Nettastomatidae	<i>Hoplunnis macrura</i> Ginsburg, 1951	DB
			<i>Hoplunnis similis</i> Smith, 1989	DB
			<i>Hoplunnis tenuis</i> Ginsburg, 1951	DB
			<i>Nettastoma melanura</i> Rafinesque, 1810	BP
			<i>Saurenhelys cancrivora</i> Peters, 1865	DB
			<i>Saurenhelys stylura</i> Lea, 1913	DB
			<i>Venefica procera</i> Goode & Bean, 1883	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Ophichthidae	<i>Echiophis intertinctus</i> Richardson, 1848	SB
			<i>Myrophis punctatus</i> Lütken, 1852	SB
			<i>Pseudomyrophis frio</i> Jordan & Davis, 1891	SB
		Saccopharyngidae	<i>Saccopharynx harrisoni</i> Beebe, 1932	BP
		Serrivomeridae	<i>Serrivomer</i> <i>lanceolatooides</i> Schmidt, 1916	BP
			<i>Serrivomer schmidtii</i> Bauchot-Boutin, 1953	BP
			<i>Stemonidium hypomelas</i> Gilbert, 1905	BP
		Synaphobranchidae	<i>Atractodenchelys phrix</i> Robins & Robins, 1970	DB
			<i>Diastobranchus capensis</i> Barnard, 1923	DB
			<i>Dysommia rugosa</i> Ginsburg, 1951	DB
			<i>Haptenchelys texis</i> Robins & Martin, 1976	DB
			<i>Histiobranchus australis</i> Regan, 1913	DB
			<i>Histiobranchus bathybius</i> Günther, 1887	DB
			<i>Ilyophis blachei</i> Saldanha & Merrett, 1982	DB
			<i>Ilyophis brunneus</i> Gilbert, 1892	DB
			<i>Meadia abyssalis</i> Kamorrara, 1938	DB
			<i>Simenchelys parasitica</i> Gill, 1879	DB
			<i>Synaphobranchus affinis</i> Günther, 1877	DB
			<i>Synaphobranchus</i> <i>brevadorsalis</i> Günther, 1887	DB
			<i>Synaphobranchus calvus</i> Melo, 2007	DB
			<i>Synaphobranchus oregoni</i> Castle, 1960	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat	
	Argentiniformes	Argentinidae	<i>Argentina brasiliensis</i> Kobyliansky, 2004	BP	
			<i>Argentina georgei</i> Cohen & Atsrides, 1969	BP	
			<i>Glossanodon pygmaeus</i> Cohen, 1958	BP	
		Bathylagidae	<i>Dolicholagus longirostris</i> Maul, 1948	BP	
			<i>Melanolagus bericoides</i> Borodin, 1929	BP	
		Microstomatidae	<i>Nansenia atlantica</i> Blache & Rossignol, 1962	BP	
			Opisthoproctidae	<i>Dolichopteryx</i> <i>binocularis</i> Beebe, 1932	BP
		<i>Dolichopteryx longipes</i> Vaillant, 1888		BP	
		<i>Monacoa grimaldii</i> Zugmayer, 1911		BP	
		<i>Opisthoproctus soleatus</i> Vaillant, 1888		BP	
		<i>Winteria telescopa</i> Brauer, 1901		BP	
		Ateleopodiformes	Ateleopodidae	<i>Ijimaia loppei</i> Roule, 1922	DB
		Aulopiformes	Alepisauridae	<i>Alepisaurus brevirostris</i> Gibbs, 1960	BP
				<i>Alepisaurus ferox</i> Lowe, 1833	BP
				<i>Anotopterus pharao</i> Zugmayer, 1911	BP
	Aulopidae		<i>Aulopus filamentosus</i> Bloch, 1792	SB	
	Bathysauridae		<i>Bathysaurus ferox</i> Günther, 1878	DB	
	Bathysauridae		<i>Bathysaurus mollis</i> Günther, 1878	DB	
	Chlorophthalmidae		<i>Chlorophthalmus agassizi</i> Bonaparte, 1840	DB	
			<i>Chlorophthalmus</i> <i>brasiliensis</i> Mead, 1958	DB	
			<i>Parasudis truculenta</i> Goode & Bean, 1896	DB	

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Evermannellidae	<i>Coccorella atlantica</i> Parr, 1928	BP
			<i>Evermannella balbo</i> Risso, 1820	BP
			<i>Evermannella melanoderma</i> Parr, 1928	BP
			<i>Odontostomops normalops</i> Parr, 1928	BP
		Ipnopidae	<i>Bathypterois bigelowi</i> Mead, 1958	DB
			<i>Bathypterois grallator</i> Goode & Bean, 1886	DB
			<i>Bathypterois longipes</i> Günther, 1878	DB
			<i>Bathypterois perceptor</i> Sulak, 1977	DB
			<i>Bathypterois phenax</i> Parr, 1928	DB
			<i>Bathypterois quadrifilis</i> Günther, 1878	DB
			<i>Bathypterois viridensis</i> Roule, 1919	DB
			<i>Bathytyphlops marionae</i> Mead, 1958	DB
			<i>Bathytyphlops sewelli</i> Norman, 1939	DB
			<i>Ipnops murrayi</i> Günther, 1878	DB
		Notosudidae	<i>Ahliesaurus berryi</i> Bertelsen, Krefft & Marshall, 1976	BP
			<i>Luciosudis normani</i> Fraser-Brunner, 1931	BP
			<i>Scopelosaurus argenteus</i> Maul, 1954	BP
			<i>Scopelosaurus herwigi</i> Bertelsen, Krefft & Marshall, 1976	BP
			<i>Scopelosaurus smithii</i> Bean, 1925	BP
		Paralepididae	<i>Dolichosudis fuliginosa</i> Post, 1969	BP
			<i>Lestidiops affinis</i> Ege, 1930	BP
			<i>Lestidiops jayakari</i> Boulenger, 1889	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Lestidiops mirabilis</i> Ege, 1933	BP
			<i>Lestidium atlanticum</i> Borodin, 1928	BP
			<i>Lestrolepis intermedia</i> Poey, 1868	BP
			<i>Macroparalepis affinis</i> Ege, 1933	BP
			<i>Macroparalepis brevis</i> Ege, 1933	BP
			<i>Magnisudis atlantica</i> Krøyer, 1868	BP
			<i>Stemonosudis intermedia</i> Ege, 1933	BP
			<i>Stemonosudis siliquiventer</i> Post, 1970	BP
			<i>Sudis atrox</i> Rofen, 1963	BP
			<i>Sudis hyalina</i> Rafinesque, 1810	BP
			<i>Uncisudis advena</i> Rofen, 1963	BP
		Scopelarchidae	<i>Benthalbella infans</i> Zugmayer, 1911	BP
			<i>Rosenblattichthys hubbsi</i> Johnson, 1974	BP
			<i>Scopelarchoides danae</i> Johnson, 1974	BP
			<i>Scopelarchus analis</i> Brauer, 1902	BP
			<i>Scopelarchus guentheri</i> Alcock, 1896	BP
			<i>Scopelarchus michaelsarsi</i> Koefoed, 1955	BP
		Synodontidae	<i>Saurida brasiliensis</i> Norman, 1935	SB
			<i>Saurida caribbaea</i> Breder, 1927	SB
			<i>Saurida normani</i> Longley, 1935	SB
			<i>Synodus intermedius</i> Spix & Agassiz, 1829	SB
			<i>Trachinocephalus myops</i> Forster, 1801	SB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Beryciformes	Anoplogasteridae	<i>Anoplogaster cornuta</i> Valenciennes, 1833	BP
		Barbourisiidae	<i>Barbourisia rufa</i> Parr, 1945	BP
		Berycidae	<i>Beryx decadactylus</i> Cuvier, 1829	DB
			<i>Beryx splendens</i> Lowe, 1834	DB
		Diretmidae	<i>Diretmichthys parini</i> Post & Quéro, 1989	DB
		Gibberichthyidae	<i>Gibberichthys pumilus</i> Parr, 1933	BP
		Melamphaidae	<i>Melamphaes polylepis</i> Ebeling, 1962	BP
			<i>Melamphaes typhlops</i> Lowe, 1843	BP
			<i>Poromitra crassiceps</i> Günther, 1878	BP
			<i>Scopeloberyx robustus</i> Günther, 1887	BP
			<i>Scopelogadus mizolepis</i> Günther, 1878	BP
			Rondeletiidae	<i>Rondeletia bicolor</i> Goode & Bean, 1895
			<i>Rondeletia loricata</i> Abe & Hotta, 1963	BP
		Stephanoberycidae	<i>Acanthochaenus luetkenii</i> Gill, 1884	BP
			<i>Stephanoberyx monae</i> Gill, 1883	BP
		Trachichthyidae	<i>Aulotrachichthys</i> <i>atlanticus</i> Menezes, 1971	SB
			<i>Aulotrachichthys</i> <i>argyrophanus</i> Woods, 1961	SB
			<i>Gephyroberyx darwinii</i> Johnson, 1866	DB
			<i>Hoplostethus</i> <i>mediterraneus</i> Cuvier, 1829	DB
			<i>Hoplostethus occidentalis</i> Woods, 1973	DB
	Caproiformes	Caproidae	<i>Antigonia capros</i> Lowe, 1843	DB
			<i>Antigonia combatia</i> Berry & Rathjein, 1959	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Gadiformes	Bregmacerotidae	<i>Bregmaceros atlanticus</i> Goode & Bean, 1886	MP
			<i>Bregmaceros cantori</i> Milliken & Houde, 1984	MP
		Macrouridae	<i>Cetonurus globiceps</i> Vaillant, 1884	DB
			<i>Coelorinchus caribbaeus</i> Goode & Bean, 1885	DB
			<i>Coelorinchus carminatus</i> Goode, 1880	DB
			<i>Coelorinchus marinii</i> Hubbs, 1934	DB
			<i>Coelorinchus occa</i> Goode & Bean, 1885	DB
			<i>Coryphaenoides affinis</i> Günther, 1878	DB
			<i>Coryphaenoides asper</i> Günther, 1877	DB
			<i>Coryphaenoides leptolepis</i> Günther, 1877	DB
			<i>Coryphaenoides mediterraneus</i> Giglioli, 1893	DB
			<i>Coryphaenoides rudis</i> Günther, 1878	DB
			<i>Coryphaenoides thelestomus</i> Maul, 1951	DB
			<i>Gadomus arcuatus</i> Goode & Bean, 1886	DB
			<i>Gadomus capensis</i> Gilchrist & von Bonde, 1924	DB
			<i>Haplomacrourus nudirostris</i> Trunov, 1980	DB
			<i>Hymenocephalus aterrimus</i> Gilbert, 1905	DB
			<i>Hymenocephalus billsam</i> Marshall & Iwamoto, 1973	DB
			<i>Hymenocephalus gracilis</i> Gilbert & Hubbs, 1920	DB
			<i>Hymenocephalus italicus</i> Giglioli, 1884	DB
			<i>Lucigadus ori</i> Smith, 1968	DB
			<i>Macrosmia phalacra</i> Merrett, Sazonov & Shcherbachev, 1983	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Macrouroides inflaticeps</i> Smith & Radcliffe, 1912	DB
			<i>Macrourus holotrachys</i> Günther, 1878	DB
			<i>Malacocephalus laevis</i> Lowe, 1843	DB
			<i>Malacocephalus</i> <i>occidentalis</i> Goode & Bean, 1885	DB
			<i>Malacocephalus</i> <i>okamurai</i> Iwamoto & Arai, 1987	DB
			<i>Nezumia atlantica</i> Parr, 1946	DB
			<i>Nezumia suilla</i> Marshall & Iwamoto, 1973	DB
			<i>Sphagemacrurus</i> <i>grenadae</i> Parr, 1946	DB
			<i>Squalogadus modificatus</i> Gilbert & Hubbs, 1916	DB
			<i>Trachonurus sulcatus</i> Goode & Bean, 1885	DB
			<i>Ventrifossa macropogon</i> Marshall, 1973	DB
			<i>Ventrifossa mucocephalus</i> Marshall, 1973	DB
		Melanonidae	<i>Melanonus zugmayeri</i> Norman, 1930	DB
		Merlucciidae	<i>Macruronus</i> <i>magellanicus</i> Lönnberg, 1907	DB
			<i>Merluccius hubbsi</i> Marini, 1933	SB
			<i>Steindachneria argentea</i> Goode & Bean, 1896	DB
		Moridae	<i>Antimora rostrata</i> Günther, 1878	DB
			<i>Gadella imberbis</i> Vaillant, 1888	DB
			<i>Halargyreus johnsonii</i> Günther, 1862	DB
			<i>Laemonema barbatulum</i> Goode & Bean, 1883	DB
			<i>Laemonema</i> <i>goodebeanorum</i> Meléndez & Markle, 1997	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Laemonema robustum</i> Johnson, 1862	DB
			<i>Notophycis marginata</i> Günther, 1878	DB
			<i>Physiculus fulvus</i> Bean, 1884	DB
			<i>Physiculus karrerae</i> Paulin, 1989	DB
			<i>Physiculus kaupi</i> Poey, 1865	DB
			<i>Physiculus cirm</i> Carvalho-Filho & Pires, 2019	DB
			<i>Tripterophycis gilchristi</i> Boulenger, 1902	DB
		Gadidae	<i>Urophycis brasiliensis</i> Kaup, 1858	SB
			<i>Urophycis cirrata</i> Goode & Bean, 1896	DB
	Istiophoriformes	Xiphiidae	<i>Xiphias gladius</i> Linnaeus, 1758	EP
	Lampridiformes	Lamprididae	<i>Lampris guttatus</i> Brünnich, 1788	BP
		Lophotidae	<i>Eumecichthys fiski</i> Günther, 1890	BP
			<i>Lophotus lacepede</i> Giorna, 1809	BP
			<i>Lophotus machadoi</i> Miranda Ribeiro, 1927	BP
		Regalecidae	<i>Regalecus glesne</i> Ascanius, 1772	BP
		Trachipteridae	<i>Desmodema polystictum</i> Ogilby, 1897	BP
			<i>Trachipterus jacksonensis</i> Ramsay, 1881	BP
			<i>Zu cristatus</i> Bonelli, 1819	BP
	Lophiiformes	Ceratiidae	<i>Ceratias holboelli</i> Krøyer, 1845	BP
			<i>Ceratias uranoscopus</i> Murray, 1877	BP
			<i>Cryptopsaras couesii</i> Gill, 1883	BP
		Chaunacidae	<i>Chaunax suttkusi</i> Caruso, 1989	BP
		Diceratiidae	<i>Bufoceratias wedli</i> Pietschmann, 1926	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Gigantactinidae	<i>Gigantactis longicirra</i> Waterman, 1939	BP
			<i>Gigantactis verhoeffeni</i> Brauer, 1902	BP
		Himantolophidae	<i>Himantolophus groenlandicus</i> Reinhardt, 1837	BP
			<i>Himantolophus macroceras</i> Bertelsen & Krefft, 1988	BP
			<i>Himantolophus paucifilosus</i> Bertelsen & Krefft, 1988	BP
		Lophiidae	<i>Lophiodes beroe</i> Caruso, 1981	DB
			<i>Lophius gastrophysus</i> Miranda-Ribeiro, 1915	DB
			<i>Sladenia shaeferi</i> Caruso & Bullis, 1976	DB
		Melanocetidae	<i>Melanocetus johnsonii</i> Günther, 1864	BP
			<i>Melanocetus murrayi</i> Günther, 1887	BP
		Neoceratiidae	<i>Neoceratias spinifer</i> Pappenheim, 1914	BP
		Ogcocephalidae	<i>Dibranchus atlanticus</i> Peters, 1876	DB
			<i>Dibranchus tremendus</i> Bradbury, 1999	DB
			<i>Halieutichthys aculeatus</i> Mitchill, 1818	DB
			<i>Ogcocephalus declivirostris</i> Bradbury, 1980	SB
			<i>Ogcocephalus nasutus</i> Cuvier, 1829	SB
			<i>Ogcocephalus vespertilio</i> Linnaeus, 1758	SB
		Oneirodidae	<i>Chaenophryne draco</i> Beebe, 1932	BP
			<i>Microlophichthys microlophus</i> Regan, 1925	BP
			<i>Oneirodes notius</i> Pietsch, 1974	BP
			<i>Pentherichthys atratus</i> Regan & Trewavas, 1932	BP
		Thaumatichthyidae	<i>Thaumatichthys binghami</i> Parr, 1927	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Myctophiformes	Myctophidae	<i>Benthoosema suborbitale</i> Gilbert, 1913	MP
			<i>Bolinichthys distofax</i> Johnson, 1975	MP
			<i>Bolinichthys indicus</i> Nafpaktitis & Nafpaktitis, 1969	MP
			<i>Bolinichthys photothorax</i> Parr, 1928	MP
			<i>Bolinichthys supralateralis</i> Parr, 1928	MP
			<i>Centrobranchus nigroocellatus</i> Günther, 1873	MP
			<i>Ceratoscopelus warmingii</i> Lütken, 1892	MP
			<i>Dasyscopelus asperum</i> Richardson, 1845	MP
			<i>Diaphus adenomus</i> Gilbert, 1905	MP
			<i>Diaphus anderseni</i> Tåning, 1932	MP
			<i>Diaphus bertelseni</i> Nafpaktitis, 1966	MP
			<i>Diaphus brachycephalus</i> Tåning, 1928	MP
			<i>Diaphus dumerilii</i> Bleeker, 1856	MP
			<i>Diaphus effulgens</i> Goode & Bean, 1896	MP
			<i>Diaphus fragilis</i> Tåning, 1928	MP
			<i>Diaphus garmani</i> Gilbert, 1906	MP
			<i>Diaphus hudsoni</i> Zurbrigg & Scott, 1976	MP
			<i>Diaphus lucidus</i> Goode & Bean, 1896	MP
			<i>Diaphus luetkeni</i> Brauer, 1904	MP
			<i>Diaphus meadi</i> Nafpaktitis, 1978	MP
			<i>Diaphus metopoclampus</i> Cocco, 1829	MP
			<i>Diaphus mollis</i> Tåning, 1928	MP
			<i>Diaphus ostenfeldi</i> Tåning, 1932	MP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Diaphus perspicillatus</i> Ogilby, 1898	MP
			<i>Diaphus problematicus</i> Parr, 1928	MP
			<i>Diaphus splendidus</i> Brauer, 1904	MP
			<i>Diaphus subtilis</i> Nafpaktitis, 1968	MP
			<i>Diogenichthys atlanticus</i> Tåning, 1928	MP
			<i>Electrona risso</i> Cocco, 1829	MP
			<i>Electrona paucirastra</i> Bolin, 1962	MP
			<i>Gonichthys barnesi</i> Whitley, 1943	MP
			<i>Gonichthys cocco</i> Cocco, 1829	MP
			<i>Gymnoscopelus bolini</i> Andriashev, 1962	MP
			<i>Gymnoscopelus braueri</i> Lönnerberg, 1905	MP
			<i>Gymnoscopelus nicholsi</i> Gilbert, 1911	MP
			<i>Gymnoscopelus piabilis</i> Whitley, 1931	MP
			<i>Hygophum hanseni</i> Tåning, 1932	MP
			<i>Hygophum hygomii</i> Lütken, 1892	MP
			<i>Hygophum macrochir</i> Günther, 1864	MP
			<i>Hygophum reinhardtii</i> Lütken, 1892	MP
			<i>Hygophum taaningi</i> Bekker, 1965	MP
			<i>Lampadena anomala</i> Parr, 1928	MP
			<i>Lampadena chavesi</i> Collett, 1905	MP
			<i>Lampadena luminosa</i> Garman, 1899	MP
			<i>Lampadena notialis</i> Nafpaktitis & Paxton, 1968	MP
			<i>Lampanyctus alatus</i> Goode & Bean, 1896	MP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Lampanyctus ater</i> Tåning, 1928	MP
			<i>Lampanyctus australis</i> Tåning, 1932	MP
			<i>Lampanyctus cuprarium</i> Tåning, 1928	MP
			<i>Lampanyctus festivus</i> Tåning, 1928	MP
			<i>Lampanyctus lepidolychnus</i> Bekker, 1967	MP
			<i>Lampanyctus isaacsi</i> Wisner, 1974	MP
			<i>Lampanyctodes lineatus</i> Tåning, 1928	MP
			<i>Lampanyctus nobilis</i> Tåning, 1928	MP
			<i>Lampanyctus photonotos</i> Parr, 1928	MP
			<i>Lampanyctus pusillus</i> Johnson, 1890	MP
			<i>Lampanyctus tenuiformis</i> Brauer, 1906	MP
			<i>Lampanyctus vadulus</i> Hulley, 1981	MP
			<i>Lampichthys procerus</i> Brauer, 1904	MP
			<i>Lepidophanes gaussi</i> Brauer, 1906	MP
			<i>Lepidophanes guentheri</i> Goode & Bean, 1896	MP
			<i>Lobianchia dofleini</i> Zugmayer, 1911	MP
			<i>Lobianchia gemellarii</i> Cocco, 1838	MP
			<i>Loweina rara</i> Lütken, 1892	MP
			<i>Myctophum affine</i> Lütken, 1892	MP
			<i>Myctophum nitidulum</i> Garman, 1899	MP
			<i>Myctophum obtusirostre</i> Tåning, 1928	MP
			<i>Myctophum phengodes</i> Lütken, 1892	MP
			<i>Myctophum selenops</i> Tåning, 1928	MP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Notolychnus valdiviae</i> Brauer, 1904	MP
			<i>Notoscopelus</i> <i>caudispinosus</i> Johnson, 1863	MP
			<i>Notoscopelus resplendens</i> Richardson, 1845	MP
			<i>Scopelopsis</i> <i>multipunctatus</i> Brauer, 1906	MP
			<i>Symbolophorus barnardi</i> Tåning, 1932	MP
			<i>Symbolophorus rufinus</i> Tåning, 1928	MP
			<i>Taaningichthys</i> <i>bathyphilus</i> Tåning, 1928	MP
			<i>Taaningichthys minimus</i> Tåning, 1928	MP
		Neoscopelidae	<i>Neoscopelus</i> <i>macrolepidotus</i> Johnson, 1863	MP
			<i>Neoscopelus microchir</i> Matsubara, 1943	MP
	Notacanthiformes	Halosauridae	<i>Aldrovandia affinis</i> Günther, 1877	DB
			<i>Aldrovandia gracilis</i> Goode & Bean, 1886	DB
			<i>Aldrovandia oleosa</i> Sulak, 1977	DB
			<i>Aldrovandia phalacra</i> Vaillant, 1888	DB
			<i>Halosauropsis macrochir</i> Günther, 1878	DB
			<i>Halosaurus attenuatus</i> Garman, 1899	DB
			<i>Halosaurus guentheri</i> Goode & Bean, 1896	DB
		Notacanthidae	<i>Lipogenys gillii</i> Goode & Bean, 1895	DB
			<i>Notacanthus sexspinis</i> Richardson, 1846	DB
			<i>Polyacanthonotus</i> <i>africanus</i> MacGilchrist & Von Bonde, 1924	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Ophidiiformes	Aphyonidae	<i>Aphyonus gelatinosus</i> Günther, 1878	DB
			<i>Barathronus bicolor</i> Goode & Bean, 1886	DB
			<i>Barathronus linsi</i> Nielsen, Mincarone & Di Dario, 2015	DB
		Bythitidae	<i>Cataetyx messieri</i> Günther, 1878	DB
			<i>Diplacanthopoma brachysoma</i> Günther, 1887	DB
			<i>Saccogaster parva</i> Cohen & Nielsen, 1972	DB
			<i>Saccogaster staigeri</i> Cohen & Nielsen, 1972	DB
			<i>Stygnobrotula latebricola</i> Böhlke, 1957	SB
			Carapidae	<i>Echiodon cryomargarites</i> Markle, Williams & Olney, 1983
	<i>Echiodon dawsoni</i> Williams & Shipp, 1982	DB		
	<i>Echiodon drummondi</i> Thompson, 1873	DB		
	<i>Snyderidia canina</i> Gilbert, 1905	DB		
	Ophidiidae	<i>Acanthonus armatus</i> Günther, 1878		DB
		<i>Barathrites parri</i> Nybelin, 1957	DB	
		<i>Barathrodemus manatinus</i> Goode & Bean, 1883	DB	
		<i>Bassogigas gillii</i> Goode & Bean, 1896	DB	
		<i>Bassozetus compressus</i> Günther, 1878	DB	
		<i>Bassozetus normalis</i> Gill, 1883	DB	
		<i>Bassozetus robustus</i> Smith & Radcliffe, 1913	DB	
		<i>Bathyonus laticeps</i> Günther, 1878	DB	
		<i>Benthocometes robustus</i> Goode & Bean, 1886	DB	
		<i>Brotula barbata</i> Bloch & Schneider, 1801	DB	

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Dicrolene introniger</i> Goode & Bean, 1883	DB
			<i>Dicrolene kanazawai</i> Grey, 1958	DB
			<i>Eremichthys pinnatus</i> Garman, 1899	DB
			<i>Genypterus brasiliensis</i> Regan, 1903	SB
			<i>Holcomycteronus squamosus</i> Roule, 1916	DB
			<i>Lamprogrammus brunswigi</i> Brauer, 1906	DB
			<i>Leucicorus atlanticus</i> Nielsen, 1975	DB
			<i>Luciobrotula brasiliensis</i> Nielsen, 2009	DB
			<i>Monomitopus agassizii</i> Goode & Bean, 1896	DB
			<i>Monomitopus americanus</i> Nielsen, 1971	DB
			<i>Neobythites brasiliensis</i> Nielsen, 1999	DB
			<i>Neobythites monocellatus</i> Nielsen, 1999	DB
			<i>Neobythites ocellatus</i> Günther, 1887	DB
			<i>Penopus microphthalmus</i> Vaillant, 1888	DB
			<i>Porogadus catena</i> Goode & Bean, 1885	DB
			<i>Porogadus miles</i> Goode & Bean, 1885	DB
			<i>Xyelacyba myersi</i> Cohen, 1961	DB
	Pempheriformes	Acropomatidae	<i>Parascombrops spinosus</i> Schultz, 1940	DB
			<i>Synagrops bellus</i> Goode & Bean, 1896	DB
			<i>Synagrops pseudomicrolepis</i> Schultz, 1940	DB
			<i>Synagrops trispinosus</i> Mochizuki & Sano, 1984	DB
			<i>Verilus costai</i> Schwarzjans et al., 2020	DB
			<i>Verilus sordidus</i> Poey, 1860	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Epigonidae	<i>Epigonus occidentalis</i> Goode & Bean, 1896	DB
			<i>Epigonus oligolepis</i> Mayer, 1974	DB
			<i>Epigonus robustus</i> Barnard, 1927	DB
			<i>Epigonus telescopus</i> Risso, 1810	DB
		Howellidae	<i>Bathysphyaenops simplex</i> Parr, 1933	BP
			<i>Howella atlantica</i> Post & Quéro, 1991	BP
			<i>Howella sherborni</i> Norman, 1930	BP
		Polyprionidae	<i>Polyprion americanus</i> Bloch & Schneider, 1801	SB
			<i>Polyprion oxygeneios</i> Schneider & Forster, 1801	SB
	Perciformes	Bembropidae	<i>Bembrops anatirostris</i> Ginsburg, 1955	DB
			<i>Bembrops gobioides</i> Goode, 1880	DB
			<i>Bembrops greyi</i> Poll, 1959	DB
			<i>Bembrops heterurus</i> Miranda-Ribeiro, 1903	DB
			<i>Bembrops ocellatus</i> Thompson & Suttkus, 1998	DB
		Peristediidae	<i>Peristedion altipinne</i> Regan, 1903	SB
			<i>Peristedion antillarum</i> Regan, 1914	DB
			<i>Peristedion ecuadorensis</i> Teague, 1961	DB
			<i>Peristedion gracile</i> Goode & Bean, 1896	SB
			<i>Peristedion thompsoni</i> Fowler, 1952	SB
			<i>Peristedion truncatum</i> Günther, 1880	SB
		Priacanthidae	<i>Cookeolus japonicus</i> Cuvier, 1829	SB
			<i>Heteropriacanthus cruentatus</i> Lacepède, 1801	SB
			<i>Pristigenys alta</i> Gill, 1862	SB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Psychrolutidae	<i>Cottunculus granulosis</i> Karrer, 1968	DB
		Scorpaenidae	<i>Helicolenus lahillei</i> Norman, 1937	SB
			<i>Idiastion kyphos</i> Eschmeyer, 1964	DB
			<i>Phenacoscorpius nebris</i> Eschmeyer, 1965	DB
			<i>Pontinus corallinus</i> Miranda-Ribeiro, 1903	DB
			<i>Pontinus longispinis</i> Goode & Bean, 1897	DB
			<i>Pontinus</i> <i>nematophthalmus</i> Günther, 1860	DB
			<i>Pontinus nigropunctatus</i> Günther, 1868	DB
		Serranidae	<i>Anthias asperilinguis</i> Günther, 1859	SB
			<i>Anthias menezesi</i> Anderson & Heemstra, 1980	DB
			<i>Anthias nicholsi</i> Firth, 1933	SB
			<i>Baldwinella vivanus</i> Jordan & Swain, 1885	DB
			<i>Bathyanthias roseus</i> Günther 1880	DB
			<i>Epinephelus morio</i> Valenciennes, 1828	SB
			<i>Epinephelus nigritus</i> Holbrook, 1855	SB
			<i>Gonioplectrus hispanus</i> Cuvier, 1828	SB
			<i>Hemanthias vivanus</i> Jordan & Swain, 1885	SB
			<i>Hyporthodus</i> <i>flavolimbatus</i> Poey, 1865	SB
			<i>Hyporthodus nigritus</i> Holbrook, 1855	SB
			<i>Hyporthodus niveatus</i> Valenciennes, 1828	SB
			<i>Plectranthias garrupellus</i> Robins & Starck, 1960	SB
			<i>Pronotogrammus</i> <i>martinicensis</i> Guichenot, 1864	SB
			<i>Serranus atrobranchus</i> Cuvier, 1829	SB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Setarchidae	<i>Ectreposebastes imus</i> Garman, 1899	BP
			<i>Setarches guentheri</i> Johnson, 1862	DB
		Triglidae	<i>Bellator brachychir</i> Regan, 1914	SB
			<i>Bellator egretta</i> Goode & Bean, 1896	SB
			<i>Prionotus nudigula</i> Ginsburg, 1950	SB
		Zoarcidae	<i>Iluocoetes fimbriatus</i> Jenyns, 1842	DB
			<i>Leucogrammolycus</i> <i>brychios</i> Mincarone & Anderson, 2008	DB
			<i>Notolycodes schmidti</i> Gosztanyi, 1977	DB
			<i>Pachycara alepidotum</i> Anderson & Mincarone, 2006	DB
		Bothidae	<i>Ancylopsetta kumperae</i> Tyler, 1959	SB
			<i>Chascanopsetta danae</i> Bruun, 1937	DB
			<i>Monolene antillarum</i> Norman, 1933	SB
			<i>Monolene atrimana</i> Goode & Bean, 1886	DB
			<i>Monolene megalepis</i> Woods, 1961	DB
			<i>Monolene sessilicauda</i> Goode, 1880	DB
			<i>Trichopsetta caribbaea</i> Anderson & Gutherz, 1967	SB
		Cynoglossidae	<i>Symphurus ginsburgi</i> Menezes & Benvegnú, 1976	SB
			<i>Symphurus marginatus</i> Goode & Bean, 1886	SB
			<i>Symphurus plagiusa</i> Linnaeus, 1766	SB
			<i>Symphurus plagusia</i> Bloch & Schneider, 1801	SB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
		Paralichthyidae	<i>Citharichthys cornutus</i> Günther, 1880	DB
			<i>Citharichthys dinoceros</i> Goode & Bean, 1886	DB
			<i>Syacium papillosum</i> Linnaeus, 1758	SB
			<i>Paralichthys brasiliensis</i> Ranzani, 1842	SB
		Pleuronectidae	<i>Poecilopsetta inermis</i> Breder, 1927	DB
	Polymixiiformes	Polymixiidae	<i>Polymixia lowei</i> Günther, 1859	DB
			<i>Polymixia nobilis</i> Lowe, 1838	DB
	Scombriformes	Ariommatidae	<i>Ariomma bondi</i> Fowler, 1930	EP
			<i>Ariomma melanum</i> Ginsburg, 1954	EP
	Scombriformes	Bramidae	<i>Brama brama</i> Bonnaterre, 1788	EP
		Bramidae	<i>Brama caribbea</i> Mead, 1972	EP
			<i>Brama dussumieri</i> Cuvier, 1831	EP
			<i>Eumegistus brevorti</i> Poey, 1860	EP
			<i>Pteraclis aesticola</i> Jordan & Snyder, 1901	EP
			<i>Pteraclis carolinus</i> Valenciennes, 1833	EP
			<i>Pterycombus brama</i> Fries, 1837	EP
			<i>Pterycombus petersii</i> Hilgendorf, 1878	EP
			<i>Taractes rubescens</i> Jordan & Evermann, 1887	EP
			<i>Taractichthys longipinnis</i> Lowe, 1842	EP
		Caristiidae	<i>Caristius macropus</i> Bellotti, 1903	BP
			<i>Paracaristius nudarcus</i> Stevenson & Kenaley, 2011	MP
			<i>Platyberyx andriashevi</i> Kukuev, Parin & Trunov, 2012	MP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Platyberyx paucus</i> Stevenson & Kenaley, 2013	MP
			<i>Platyberyx pietschi</i> Stevenson & Kenaley, 2013	MP
		Centrolophidae	<i>Centrolophus niger</i> Gmelin, 1789	BP
		Centrolophidae	<i>Hyperoglyphe macrophthalma</i> Miranda-Ribeiro, 1915	EP
		Chiasmodontidae	<i>Chiasmodon microcephalus</i> Norman, 1929	MP
			<i>Dysalotus alcocki</i> MacGilchrist, 1905	BP
			<i>Kali colubrina</i> Melo, 2008	BP
			<i>Kali indica</i> Lloyd, 1909	BP
			<i>Kali kerberti</i> Weber, 1913	BP
			<i>Kali normani</i> Parr, 1931	BP
			<i>Kali parri</i> Johnson & Cohen, 1974	BP
			<i>Pseudoscopelus altipinnis</i> Parr, 1933	MP
			<i>Pseudoscopelus australis</i> Prokofiev & Kukuev, 2006	MP
			<i>Pseudoscopelus pierbartus</i> Spitz, Quéro & Vayna, 2007	MP
			<i>Pseudoscopelus scriptus</i> Lütken, 1892	MP
			<i>Pseudoscopelus scutatus</i> Krefft, 1971	MP
		Gempylidae	<i>Diplospinus multistriatus</i> Maul, 1948	BP
			<i>Gempylus serpens</i> Cuvier, 1829	EP
			<i>Lepidocybium flavobrunneum</i> Smith, 1843	BP
			<i>Nealotus tripes</i> Johnson, 1865	BP
			<i>Neopinnula americana</i> Grey, 1953	DB
			<i>Nesiarchus nasutus</i> Johnson, 1862	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Promethichthys prometheus</i> Cuvier, 1832	DB
			<i>Ruvettus pretiosus</i> Cocco, 1833	DB
			<i>Thyrstitops lepidopoides</i> Cuvier, 1832	EP
		Nomeidae	<i>Cubiceps caeruleus</i> Regan, 1914	EP
			<i>Cubiceps capensis</i> Smith, 1845	EP
			<i>Cubiceps pauciradiatus</i> Günther, 1872	BP
			<i>Psenes arafurensis</i> Günther, 1889	EP
			<i>Psenes cyanophrys</i> Valenciennes, 1833	EP
		Scombridae	<i>Auxis rochei</i> Risso, 1810	EP
			<i>Auxis thazard</i> Lacepede, 1800	EP
			<i>Euthynnus alletteratus</i> Rafinesque, 1810	EP
			<i>Thunnus albacares</i> Bonnaterre, 1788	EP
			<i>Sarda sarda</i> Bloch, 1793	EP
			<i>Scomber japonicus</i> Houttuyn, 1782	EP
		Scombrolabracidae	<i>Scombrolabrax heterolepis</i> Roule, 1921	DB
		Trichiuridae	<i>Aphanopus intermedius</i> Parin, 1983	DB
			<i>Assurger anzac</i> Alexander, 1917	BP
			<i>Benthodesmus elongatus</i> Clarke, 1879	BP
			<i>Benthodesmus tenuis</i> Günther, 1877	BP
			<i>Evoxymetopon taeniatus</i> Gill, 1863	BP
			<i>Lepidopus altifrons</i> Parin & Collette, 1993	BP
			<i>Trichiurus lepturus</i> Linnaeus, 1758	EP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Stomiiformes	Gonostomatidae	<i>Bonapartia pedaliota</i> Goode & Bean, 1896	MP
			<i>Cyclothone acclinidens</i> Garman, 1899	MP
			<i>Cyclothone alba</i> Brauer, 1906	MP
			<i>Cyclothone braueri</i> Jespersen & Tåning, 1926	MP
			<i>Cyclothone microdon</i> Günther, 1878	MP
			<i>Cyclothone pallida</i> Brauer, 1902	MP
			<i>Cyclothone pseudopallida</i> Mukhacheva, 1964	MP
			<i>Cyclothone parapallida</i> Badcock, 1982	MP
			<i>Cyclothone signata</i> Garman, 1899	MP
			<i>Diplophos australis</i> Ozawa, Oda & Ida, 1990	MP
			<i>Diplophos taenia</i> Matsubara, 1940	MP
			<i>Gonostoma atlanticum</i> Norman, 1930	MP
			<i>Gonostoma elongatum</i> Günther, 1878	MP
			<i>Manducus maderensis</i> Johnson, 1890	MP
			<i>Margrethia obtusirostra</i> Jespersen & Tåning, 1919	MP
			<i>Sigmops bathyphilus</i> Vaillant, 1884	MP
		Phosichthyidae	<i>Ichthyococcus australis</i> Mukhacheva, 1980	MP
			<i>Ichthyococcus ovatus</i> Cocco, 1838	MP
			<i>Ichthyococcus polli</i> Blache, 1964	MP
			<i>Phosichthys argenteus</i> Hutton, 1872	MP
			<i>Pollichthys maui</i> Poll, 1953	MP
			<i>Polymetme corythaeola</i> Alcock, 1898	MP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Polymetme thaeocoryla</i> Parin & Borodulina, 1990	MP
			<i>Vinciguerria nimbaria</i> Jordan & Williams, 1896	MP
			<i>Vinciguerria poweriae</i> Cocco, 1838	MP
		Sternoptychidae	<i>Argyripnus atlanticus</i> Maul, 1952	MP
			<i>Argyropelecus aculeatus</i> Valenciennes, 1850	MP
			<i>Argyropelecus affinis</i> Garman, 1899	MP
			<i>Argyropelecus gigas</i> Norman, 1930	MP
			<i>Argyropelecus hemigymnus</i> Cocco, 1829	MP
			<i>Argyropelecus sladeni</i> Regan, 1908	MP
			<i>Maurolicus muelleri</i> Gmelin, 1788	MP
			<i>Maurolicus stehmanni</i> Parin & Kobylansky, 1993	MP
			<i>Polyipnus clarus</i> Harold, 1994	MP
			<i>Polyipnus laternatus</i> Garman, 1899	MP
			<i>Sternoptyx diaphana</i> Hermann, 1781	MP
			<i>Sternoptyx pseudobscura</i> Baird, 1971	MP
			<i>Sternoptyx pseudodiaphana</i> Borodulina, 1977	MP
			<i>Valenciennellus tripunctulatus</i> Esmark, 1871	MP
		Stomiidae	<i>Astronesthes barbatus</i> Kner, 1860	BP
			<i>Astronesthes gemmifer</i> Goode & Bean, 1896	BP
			<i>Astronesthes haplophos</i> Parin & Borodulina, 2002	BP
			<i>Astronesthes macropogon</i> Goodyear & Gibbs, 1970	BP
			<i>Astronesthes similus</i> Parr, 1927	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Chauliodus danae</i> Regan & Trewavas, 1930	BP
			<i>Chauliodus minimus</i> Parin & Novikova, 1974	BP
			<i>Chauliodus sloani</i> Bloch & Schneider, 1801	BP
			<i>Echiostoma barbatum</i> Lowe, 1843	BP
			<i>Eustomias arborifer</i> Parr, 1927	BP
			<i>Eustomias braueri</i> Zugmayer, 1911	BP
			<i>Eustomias brevibarbus</i> Parr, 1927	BP
			<i>Eustomias curtifilis</i> Clarke, 2000	BP
			<i>Eustomias filifer</i> Gilchrist, 1906	BP
			<i>Eustomias ignotus</i> Gomon & Lubbock, 1985	BP
			<i>Eustomias krefftii</i> Gibbs, Clarke & Gomon, 1983	MP
			<i>Eustomias longibarba</i> Parr, 1927	BP
			<i>Eustomias posti</i> Gibbs, Clarke & Gomon, 1983	MP
			<i>Eustomias schmidti</i> Regan & Trewavas, 1930	MP
			<i>Eustomias spherulifer</i> Gibbs, Clarke & Gomon, 1983	BP
			<i>Eustomias tetranema</i> Zugmayer, 1913	BP
			<i>Flagellostomias boureei</i> Zugmayer, 1913	BP
			<i>Grammatostomias dentatus</i> Goode & Bean, 1896	BP
			<i>Idiacanthus atlanticus</i> Brauer, 1906	BP
			<i>Leptostomias longibarba</i> Regan & Trewavas, 1930	BP
			<i>Malacosteus niger</i> Ayres, 1848	BP
			<i>Melanostomias bartonbeani</i> Parr, 1927	BP

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
			<i>Melanostomias niger</i> Gilchrist & von Bonde, 1924	BP
			<i>Melanostomias</i> <i>tentaculatus</i> Regan & Trewavas, 1930	MP
			<i>Melanostomias valdiviae</i> Brauer, 1902	MP
			<i>Photonectes mirabilis</i> Parr, 1927	BP
			<i>Photostomias atrox</i> Alcock, 1890	MP
			<i>Photostomias goodyeari</i> Kenaley & Hartel, 2005	BP
			<i>Photostomias guernei</i> Collett, 1889	BP
			<i>Stomias affinis</i> Günther, 1887	MP
			<i>Stomias boa</i> Risso, 1810	MP
			<i>Stomias colubrinus</i> Garman, 1889	MP
			<i>Stomias danae</i> Ege, 1933	MP
	Syngnathiformes	Callionymidae	<i>Foetorepus agassizii</i> Goode & Bean, 1888	DB
			<i>Foetorepus dagmarae</i> Fricke, 1985	DB
		Centriscidae	<i>Centriscops humerosus</i> Richardson, 1846	DB
			<i>Macroramphosus</i> <i>scolopax</i> Linnaeus, 1758	DB
			<i>Notopogon</i> <i>fernandezianus</i> Delfin, 1899	DB
		Draconettidae	<i>Centrodraco oregonus</i> Briggs & Berry, 1959	DB
	Tetraodontiformes	Molidae	<i>Masturus lanceolatus</i> Liénard, 1840	EP
			<i>Mola mola</i> Linnaeus, 1758	EP
			<i>Ranzania laevis</i> Pennant, 1776	EP
		Triacanthodidae	<i>Hollardia hollardi</i> Poey, 1861	DB

(continued)

Table 7.5 (continued)

Class	Order	Family	Species	Habitat
	Zeiformes	Grammicolepididae	<i>Grammicolepis brachiusculus</i> Poey, 1873	BP
			<i>Xenolepidichthys dalgleishi</i> Gilchrist, 1922	BP
			Oreosomatidae	<i>Allocyttus verrucosus</i> Gilchrist, 1906
		Zeidae	<i>Zenopsis conchifer</i> Lowe, 1852	DB
		Zeniontidae	<i>Zenion hololepis</i> Goode & Bean, 1896	DB
	Lutjaniformes	Lutjanidae	<i>Pristipomoides aquilonaris</i> Goode & Bean, 1896	SB
	Lutjaniformes		<i>Pristipomoides freemani</i> Anderson, 1966	SB
	<i>incertae sedis</i> in Eupercaria	Emmelichthyidae	<i>Erythrocles monodi</i> Poll & Cadenat, 1954	SB
		Malacanthidae	<i>Caulolatilus chrysops</i> Valenciennes, 1833	SB
			<i>Lopholatilus villarii</i> Ribeiro, 1915	SB
	<i>incertae sedis</i> in Ovolentaria	Opisthognathidae	<i>Lonchopisthus meadi</i> Menezes & Figueiredo, 1971	SB

Abbreviations: *DB* deep benthopelagic, *BP* bathypelagic, *EP* epipelagic, *MP* mesopelagic, and *SB* shallow benthopelagic

Table 7.6 List of species previously reported from the Brazilian Economic Exclusive Zone, excluded from the current account

Class	Order	Family	Species	Reason
Elasmobranchii	Carcharhiniformes	Scyliorhinidae	<i>Scyliorhinus hesperius</i> Springer, 1966	Occurrence not confirmed
			<i>Apristurus manis</i> Springer, 1979	Occurrence not confirmed
			<i>Parmaturus</i> cf. <i>campechiensis</i> Springer, 1979	Occurrence not confirmed
	Rajiformes	Arhynchobatidae	<i>Bathyraja multispinis</i> Norman, 1937	Occurrence not confirmed
			<i>Bathyraja scaphiops</i> Norman, 1937	Occurrence not confirmed
		Rajidae	<i>Dipturus bullisi</i> Bigelow & Schroeder, 1962	Occurrence not confirmed

(continued)

Table 7.6 (continued)

Class	Order	Family	Species	Reason
	Squaliformes	Dalatiidae	<i>Euprotomicroides zantedeschia</i> Hulley & Penrith, 1966	Occurrence not confirmed
			<i>Euprotomicrus bispinatus</i> Quoy & Garman, 1824	Occurrence not confirmed
	Squaliformes	Etmopteridae	<i>Etmopterus pusillus</i> Lowe, 1839	Occurrence not confirmed
		Somniosidae	<i>Centroscyrnus cryptacanthus</i> Regan, 1906	Confirmed as <i>Centroscyrnus owstonii</i> Garman, 1906
			<i>Somniosus pacificus</i> Bigelow & Schroeder, 1944	Occurrence not confirmed
		Squalidae	<i>Squalus cubensis</i> Howell Rivero, 1936	Current status: <i>Squalus bahiensis</i> Viana, Carvalho & Gomes, 2016
			<i>Squalus megalops</i> Macleay, 1881	Current status: <i>Squalus albicaudus</i> Viana, Carvalho & Gomes, 2016
			<i>Squalus mitsukurii</i> Jordan & Snyder, 1903	Current status: <i>Squalus lobularis</i> Viana, Carvalho & Gomes, 2016 or <i>Squalus quasimodo</i> Viana, Carvalho & Gomes, 2016
Actinopteri	Alepocephaliformes	Alepocephalidae	<i>Talismania antillarum</i> Goode & Bean, 1896	Occurrence not confirmed
			<i>Talismania homoptera</i> Vaillant, 1888	Occurrence not confirmed

(continued)

Table 7.6 (continued)

Class	Order	Family	Species	Reason
	Anguilliformes	Congridae	<i>Parabathymyrus oregoni</i> Smith & Kanazawa, 1977	Occurrence not confirmed
			<i>Rhynchoconger guppyi</i> Norman, 1925	Occurrence not confirmed
	Argentiniformes	Argentinidae	<i>Argentina striata</i> Goode & Bean, 1896	Occurrence not confirmed
		Opisthoproctidae	<i>Dolichopteryx anascopa</i> Brauer, 1901	Occurrence not confirmed
	Aulopiformes	Evermannellidae	<i>Evermannella indica</i> Brauer, 1906	Occurrence not confirmed
		Paralepididae	<i>Arctozenus risso</i> Bonaparte, 1840	Occurrence not confirmed
			<i>Paralepis elongata</i> Brauer, 1906	Occurrence not confirmed
			<i>Uncisudis advena</i> Rofen, 1963	Occurrence not confirmed
			<i>Uncisudis quadrimaculata</i> Post, 1969	Occurrence not confirmed
	Gadiformes	Bregmacerotidae	<i>Bregmaceros maclellandi</i> Thompson, 1840	Occurrence not confirmed
		Macrouridae	<i>Bathygadus melanobranchus</i> Vaillant, 1888	Occurrence not confirmed
			<i>Nezumia aequalis</i> Günther, 1978	Occurrence not confirmed
			<i>Odontomacrus murrayi</i> Norman, 1939	Occurrence not confirmed
			Merlucciidae	<i>Macruronus magellanicus</i> Lonnberg, 1907
		Moridae	<i>Salilota australis</i> Günther, 1878	Occurrence not confirmed
		Lophiiformes	Oneirodidae	<i>Oneirodes notius</i> Pietsch, 1974

(continued)

Table 7.6 (continued)

Class	Order	Family	Species	Reason
	Myctophiformes	Myctophidae	<i>Ceratoscopelus maderensis</i> Lowe, 1839	Occurrence not confirmed
			<i>Lampadena speculigera</i> Goode & Bean, 1896	Occurrence not confirmed
			<i>Loweina rara</i> Lütken, 1892	Occurrence not confirmed
			<i>Symbolophorus veranyi</i> Moreau, 1888	Occurrence not confirmed
	Notacanthiformes	Halosauridae	<i>Aldrovandia gracilis</i> Goode & Bean, 1896	Occurrence not confirmed
	Pempheriformes	Howellidae	<i>Howella brodiei</i> Ogilby, 1899	Confirmed as <i>Howella atlantica</i> Post & Quéro, 1991
	Scombriformes	Nomeidae	<i>Psenes maculatus</i> Lütken, 1880	Occurrence not confirmed
	Stomiiformes	Astronesthidae	<i>Astronesthes leucopogon</i> Regan & Trewavas, 1929	Occurrence not confirmed
			<i>Astronesthes niger</i> Richardson 1845	Occurrence not confirmed
		Phosichthyidae	<i>Vinciguerria attenuata</i> Cocco, 1838	Occurrence not confirmed
		Stomiidae	<i>Eustomias braueri</i> Zugmayer, 1911	Occurrence not confirmed
			<i>Eustomias krefftii</i> Gibbs, Clarke & Gomon, 1983	Occurrence not confirmed
			<i>Grammatostomias circularis</i> Morrow, 1959	Occurrence not confirmed
			<i>Leptostomias gladiator</i> Zugmayer, 1911	Occurrence not confirmed
	<i>Melanostomias macrophotus</i> Regan & Trewavas, 1930		Occurrence not confirmed	
	<i>Melanostomias melanops</i> Brauer, 1902	Occurrence not confirmed		

(continued)

Table 7.6 (continued)

Class	Order	Family	Species	Reason
			<i>Photonectes braueri</i> Zugmayer, 1913	Occurrence not confirmed
			<i>Stomias brevibarbatulus</i> Ege, 1918	Occurrence not confirmed
			<i>Stomias longibarbatulus</i> Brauer, 1902	Occurrence not confirmed

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Chapter 8

Living and Non-living Resources in Brazilian Deep Waters



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Abstract In Brazil, deep-sea marine environments extend over 3.5 million km², covering nearly 80% of Brazil's Economic Exclusive Zone (EEZ) in the southern tropical and subtropical Atlantic Ocean. Over this area, the exploitation of both living and non-living resources have gradually increased and supported by natural geological resources, scientific knowledge, geopolitics, economic interests, and technological development. Deep-sea fisheries developed between 2000 and 2008 in the slope areas off southeastern and southern Brazil, declining afterwards mostly because fish and shellfish stocks were shown to be little productive and little resilient. In contrast, large deep (200–2000 m) and ultra-deep (> 2000 m) oil and gas reservoirs were discovered off southeastern Brazil (Campos and Santos Basins) and were increasingly exploited by the national industry. In recent years, over 80% of Brazil's annual oil and gas production is extracted from these reservoirs, particularly from the so-called pre-salt layers. Deep-sea minerals off Brazil have long been mapped but the exploration and exploitation initiatives were incipient and focused on cobalt-rich ferromanganese crust deposits distributed in a large topographic feature known as Rio Grande Rise. Studies of the biotechnological potential of marine bacteria from the deep South Atlantic Ocean have focused mainly on hydrolytic enzymes and bioremediation. Their use in technological products in the next decade, however, still demands considerable technological development. A major concern, common to all deep-sea resources off Brazil, includes the effectiveness of the

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regulatory and management processes. Deficiencies, particularly regarding governance issues, have greatly hampered deep-sea fishing and may affect other activities as well. International management regimes, as required outside areas of national jurisdiction, are sometimes absent or need improvement to allow for the environmentally sustainable use of living and non-living deep-sea resources.

Keywords Brazilian EEZ · Fishing resources · Marine biotechnology · Pre-salt oil reservoirs · Deep sea mineral deposits · South Atlantic

8.1 Introduction

Deep-sea resources comprise mineral deposits, oil, gas, and biodiversity, either used as food or as biotechnological products, which can be extracted from deep marine environments beyond the continental shelf. In Brazil, these environments extend for over 3.5 million km², nearly 80% of the Economic Exclusive Zone (EEZ) surface area¹ (IBGE 2011). In the EEZ, the rights and obligations to study, exploit, and preserve have been secured since 1982 by the United Nations Convention of the Law of the Sea (UNCLOS, UNGA 1982). Most of this area is a seaward extension of the 8500-km-long continental margin bathed by the southern tropical and subtropical Atlantic Ocean (Fig. 8.1). In addition, areas surrounding oceanic islands (e.g. St. Peter's and Sr. Paul's Archipelago, Fernando de Noronha, Trindade) and, more recently, the Rio Grande Rise area are legal extensions to Brazil's EEZ.

This geographical situation has historically granted Brazil a wide access to deep-sea areas and its resources in the Southwest Atlantic. Nonetheless, the development of exploitation systems for both living and non-living resources has been gradual and determined by rich natural resources, increasing scientific knowledge, geopolitics, economic interests, and technological development. In the 1980s these elements converged in the development of the first oil extraction operations in the Campos Basin, 500–1600 m below the sea surface (Morais 2013). During the following decades, national research programs and commercial enterprises assessed further opportunities to exploit a number of deep-sea resources, also promoting studies to investigate the structure and functioning of ecosystems directly affected by deep ocean activities.

This chapter reviews the current knowledge on living and non-living deep-sea resources off the Brazilian coast, their exploration activities, and regulation or conservation initiatives. For convenience, we limit this analysis shoreward to the shelf break (200 m depth) and extend it offshore to areas 'beyond national jurisdiction', where the country has expressed interest in exploiting natural resources under UNCLOS regulations and other international agreements.

¹ These figures are estimates including the areas claimed in 2018 by Brazil to the UN Commission on the Limits of the Continental Shelf (e.g., the Rio Grande Rise area).

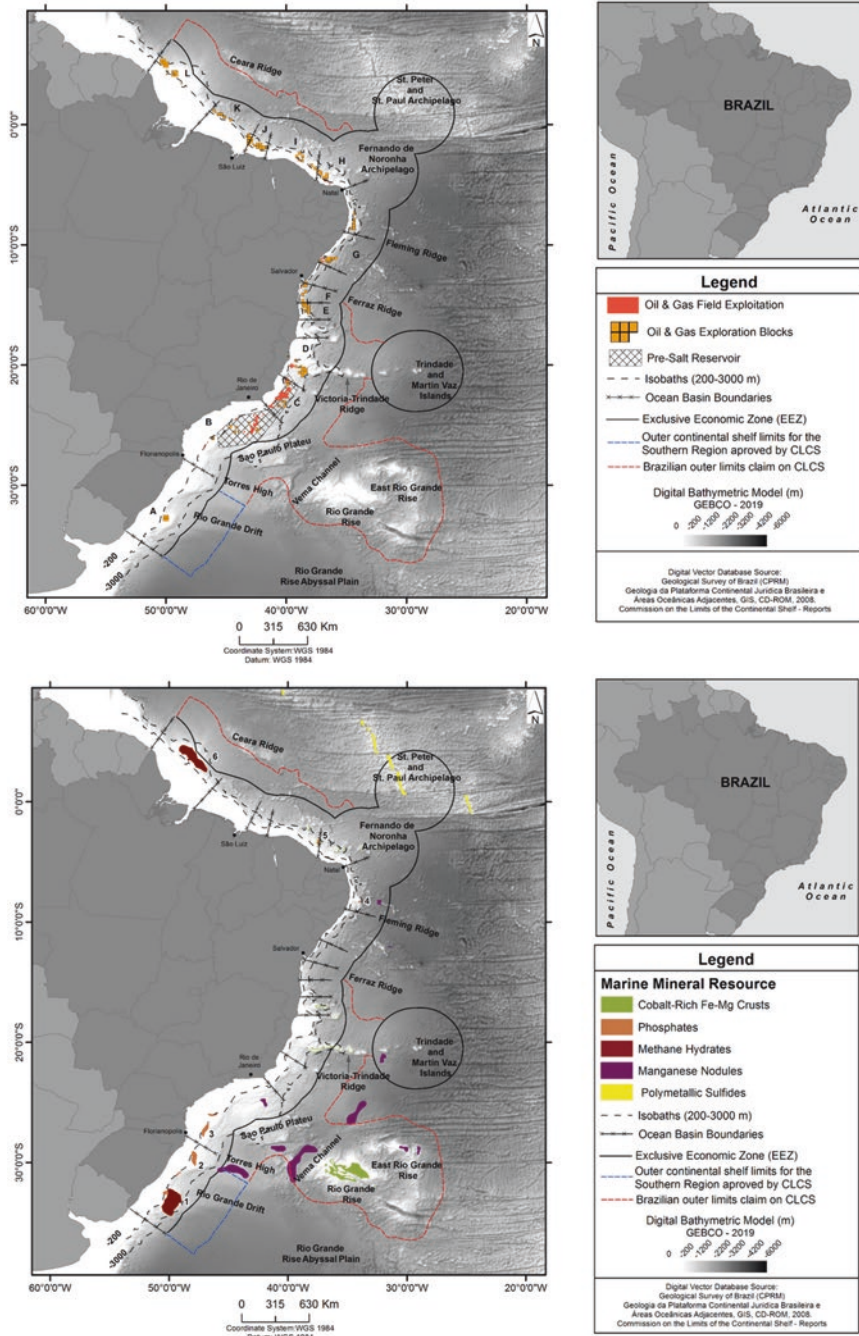


Fig. 8.1 Bathymetric charts of Brazil's continental margin and adjacent Southwest Atlantic basin depicting the distribution of oil and gas fields (upper map) and marine mineral deposits (lower map) within the Brazilian Exclusive Economic Zone and International Waters. Sedimentary basins and geomorphological features are indicated: A. Pelotas, B. Santos, C. Campos, D. Espírito Santo, E. Jequitinhonha, F. Camamu-Almada, G. Sergipe-Alagoas, H. Potiguar, I. Ceará, J. Barreirinhas, K. Pará-Maranhão, L. Foz do Amazonas. 1. Rio Grande Cone, 2. Rio Grande Terrace, 3. Florianópolis Terrace, 4. Pernambuco Plateau, 5. Ceará Plateau, 6. Amazon submarine fan

8.1.1 Motivations to Exploit Deep-Sea Resources Off Brazil

The deep sea is generally remote and most unreceptive to human activities. It is also vast and poorly studied (Ramirez-Llodra et al. 2010 and chapters of this book). Valuable resources have been mapped and assessed in deep marine areas, but their economic exploitation tends to face large operational costs, which may reduce profitability. In general, these resources would necessarily be more productive and more valuable than those found in shallow waters or in terrestrial areas to be economically attractive.

Notwithstanding, deep-sea activities have been established worldwide driven by motivations other than those purely economical, including (a) the need to secure access to potential deposits of raw materials, ever so demanded by new technological development (Hein et al. 2013), (b) the need to find alternatives to compensate for the depletion of continental and shallow water resources, and (c) strategic political interests. A combination of these motivations has historically driven the development of exploitation systems for deep-sea resources off Brazil.

In the 1960s, the Brazilian oil and gas company Petrobras started to focus its exploration activities on the deep seafloor, following experiences of other countries that have access to extensive sedimentary basins. Such a strategic decision followed a governmental policy towards attaining self-sufficiency in oil production and the expectations of finding oil reservoirs on the deep continental margin large enough to compensate for the general shortage of oil deposits on land (Milani et al. 2000; Morais 2013). These expectations were initially attained in the shallow water marine oil fields found in Campos Basin, which sustained increasing oil productions from 1973 to 1985, and stimulated, during the 1990s, new prospections and discoveries of even larger and deeper reservoirs.

In the same decade, the Brazilian ‘industrial fishing’ developed and expanded to exploit fish and shellfish stocks in the most productive continental shelf areas of northern, southeastern, and southern Brazilian coasts down to 100 m depths. In the following 20 years, fishing fleets increased and overcapitalized leading to important biomass reductions of their main pelagic and demersal resources, which provoked a process of diversification of fishing activities, targets, and areas (Perez et al. 2001). Among these activities, a substantial expansion of demersal fishing fleets towards the upper slope (200–500 m) took place from the late 1990s onwards, initially searching for profitable concentrations of traditional targets, but soon identifying new fishing resources (Perez et al. 2009). Technological limitations for deep-sea fishing operations were critical at this point and motivated the implementation of a governmental program based on chartering foreign fishing vessels to operate deeper and over valuable deep-sea resources (see below). While productivity was generally low, the high quality of the flesh of targeted fish species tended to raise their economic value, compensating for the higher costs of deep operations (Martínez-Musoles et al. 2016).

Substantial efforts have been exerted worldwide to map deep marine deposits, measure their mineral contents, develop extraction methods, and assess their

ecological impacts (Hein et al. 2013). In Brazil, research initiatives have also been implemented since the 1960s (see below) to (a) map the EEZ seafloor and identify deposits with potential economic interest for the country including those occurring outside the Brazilian EEZ and, in this case, (b) to prepare for submission of exploration plans to the International Seabed Authority (ISA), an organization under UNCLOS created to regulate the access and rights to explore and exploit mineral resources in areas beyond national jurisdictions (or just the ‘Area’). Motivations for these efforts have not been only economic or driven by the need for raw materials but also to ensure and expand the country’s presence in the South Atlantic, particularly in those areas directly connected to the EEZ limits and those surrounding Brazil’s oceanic islands (CGEE 2007).

8.1.2 Surveying for Deep-Sea Resources Off Brazil

Prospecting for living and non-living marine resources off the Brazilian coast date back to the late 1960s and 1970s, when the Brazilian Navy, universities, and research institutes collaborated in the development of early exploratory marine studies. During this period, several fishing surveys were conducted, most of them as part of the ‘Brazilian Program for Fisheries Research and Development (PDP)’, which resulted from a bilateral agreement between the Brazilian Government and the United Nations Food and Agriculture Organization (FAO) in 1967 (see review in Haimovici et al., 2007). Another important initiative was the ‘Exploration of Brazilian Continental Shelf Project (REMAC)’, led by the Navy, Petrobras, and the Mineral Resources Research Company (later named Geological Survey of Brazil – CPRM). This initiative mapped the entire continental margin off Brazil between 1972 and 1978 collecting information on seafloor topography, sediments, and the location of potential mineral deposits, including oil (Zembruscki 1979). Efforts were mainly focused on continental shelf resources, but many initiatives conducted during this early period produced primary information on the environments and resources of deeper areas beyond the shelf break.

After the findings produced by the REMAC project, and stimulated by the discovery of the ‘Garoupa’ shallow water oil field in 1974, Petrobras continued its independent oil and gas survey program, reaching deep (500–2000 m) and ultra-deep areas (> 2000 m) in the 1990s and 2000s. Other living and non-living marine resources were studied mostly under the so-called National Policy for Marine Resources (PNRM), first established in 1980, and overseen by the newly created (1974) Interministerial Commission for Sea Resources (CIRM). Since 1982, CIRM has implemented the PNMR through 4-year ‘Sectorial Plans for the Sea Resources’ (PSRM).

In 1995–1997, during the implementation of the fourth PSRM, two programs were created with the objectives of describing and assessing the potential for

exploitation of non-living² and living³ resources within the Brazilian EEZ. Both programs were a response to the 1994 UNCLOS deliberations, which granted coastal states rights and responsibilities regarding the use of marine resources within their EEZ, and were intended to improve scientific knowledge particularly in the poorly described external limits of the continental margin. After nearly 10 years, REVIZEE came to an end having produced assessments of fishing resources down to 2000 m (Olavo et al. 2005, MMA 2006, Costa et al. 2007, Olavo et al. 2011 and others). REMPLAC is still active and has made efforts to assess phosphates, massive sulphide deposits, and cobalt-rich ferromanganese crusts and nodules along Brazil's continental margin and around oceanic islands (Martins 2009).

In 2009, CIRM created a new research program named PROAREA (Program for Prospection and Exploration of Mineral Resources of the International Seabed Area in the South and Equatorial Atlantic Ocean), following novel principles highlighted in the seventh PSRM, which demanded information to secure strategic political interests in both national waters and the high seas (CIRM 2009). PROAREA was objectively designed to increase scientific knowledge on deep South Atlantic geology and ecosystems, to a level that would permit Brazil (a) to elaborate and submit to the ISA proposals for deep-sea mineral exploration and, by doing so, (b) to increase the country's presence in the South Atlantic. From 2009 to 2013, a number of research cruises under PROAREA were carried out to prospect mineral deposits in the Rio Grande Rise area and the Mid-Atlantic Ridge. As a practical result, in 2015, the Geological Survey of Brazil (CPRM) signed with the ISA a contract for exploration of cobalt-rich ferromanganese crusts in the Rio Grande Rise, the first of this nature to be signed in the Atlantic Ocean.

Outside the umbrella of the PNRM, research initiatives contributed significantly to the understanding of deep-sea marine resources and ecosystems both within and outside Brazilian EEZ. Between 1999 and 2008, Brazilian fisheries authorities stimulated the development of deep-sea fishing by authorizing foreign vessels to operate off Brazil under chartering contracts with Brazilian companies. As part of the fishing companies' obligations, observers were kept on board during 100% of the operations and reported a variety of detailed fishing data (Perez et al. 2009). These data formed a robust empirical basis on fishing resources available on the slope and seamounts off Brazil, which sustained biomass assessments and further biological studies that are critical for establishing management plans (e.g. Perez et al. 2005; Dallagnolo et al. 2009; Sant'Ana and Perez 2016).

Furthermore, the environmental licensing process of offshore oil operations within Brazil's EEZ led to several regional assessments of deep-sea ecosystems. In the Campos Basin, Petrobras and an extensive collaboration of the scientific community carried out projects that described deep-sea habitats and continental margin biodiversity of an area encompassing the five largest oil fields (Lavrado and Brasil

²Evaluation of the Mineral Potential of the Brazilian Legal Continental Shelf – REMPLAC.

³Evaluation of the Sustainable Potential of Living Resources in the Exclusive Economic Zone – REVIZEE.

2010a, b; Costa et al. 2015; Cavalcanti et al. 2017; Martins et al. 2017; Lavrado et al. 2017a, b). Similar efforts have been taken on eastern and northeastern Brazil in areas targeted for offshore development (Marchioro et al. 2005; Bernardino et al. 2016, 2019). Considering that these fields have been responsible for nearly 80% of Brazil's oil and gas production, the referred research projects made a significant contribution to the construction of an environmental baseline in such a critical area.

Finally, it is worth mentioning international scientific initiatives focusing on the understanding of the South Atlantic deep ecosystems and biodiversity, with participation of Brazilian scientists. Under the 'Census of Marine Life' (CoML) initiative, projects like MAR ECO,⁴ COMARGE,⁵ and ChEss⁶ produced valuable data for assessing perspectives of use and conservation of marine resources and ecosystems in the South Atlantic (Baker et al. 2010; Menot et al. 2010; Vecchione et al. 2010). The South Atlantic MAR ECO was led by Brazil and further produced information on deep biota including microbiological communities in the Rio Grande Rise, Mid-Atlantic Ridge and Walvis Ridge, and their potential for technological products (Perez et al. 2012). Similar studies were conducted in 2013, by a Brazil-Japan bilateral scientific agreement, which promoted the exploration of Brazil's continental margin (São Paulo Ridge and São Paulo Plateau) and oceanic areas including the Rio Grande Rise (Sumida et al. 2016; Fujikura et al. 2017; Montserrat et al. 2019). The latter area was also the target of a more recent Brazil-UK joint project called Marine E-tech⁷ that promoted two oceanographic cruises (2018–2019) focused on understanding Fe-Mn deposit formation and environmental assessments for possible future mining activities on the RGR (Jovane et al. 2019).

8.1.3 Geological and Oceanographic Origin of Deep-Sea Resources Within Brazil's EEZ

The geological expansion of the South Atlantic Ocean, as part of the continuous separation of the South American and African plates, provided some key elements to the understanding of the availability and potentialities of deep-sea resources off Brazil (Pérez-Díaz and Eagles 2017). During the Aptian period (~120 myr) the South Atlantic expansion was initiating with oceanic environments progressively expanding equatorward (Fig. 8.2). In this period, however, a topographic feature associated to the Rio Grande Fracture Zone elevated perpendicularly to the Mid-Atlantic Ridge, acting as a barrier to the northward marine circulation. In the Neo-Aptian (~112 myr), such a restriction contributed to the formation, to the north of this barrier, of a shallow water marine environment subject to dry climate conditions

⁴Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic.

⁵Continental Margin Ecosystems.

⁶Biogeography of Deep-Water Chemosynthetic Ecosystems Project.

⁷Marine ferromanganese deposits: a major resource of E-tech elements.

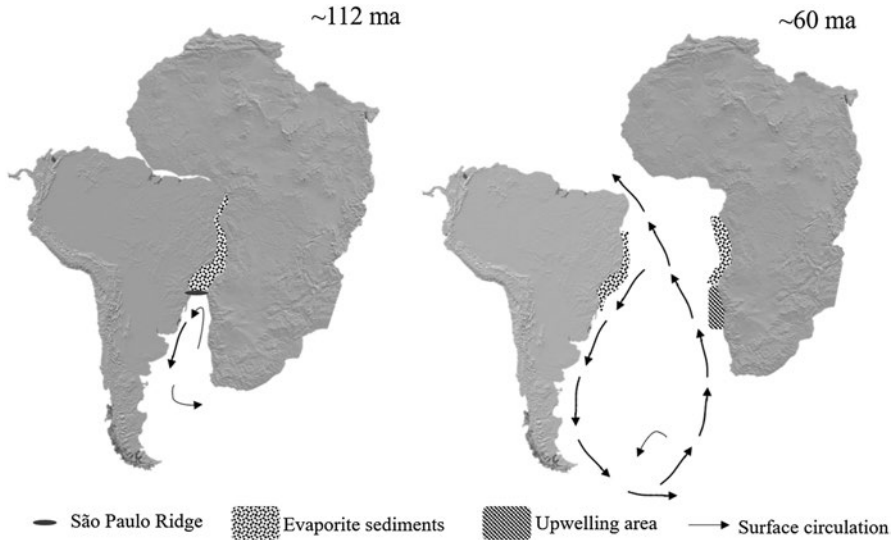


Fig. 8.2 Schematic view of the South Atlantic expansion in the Neo-Aptian (~112 myr) and Maastrichtian periods (~60 myr), indicating the evaporitic deposition period and the likely reconstruction of surface circulation patterns and the SE Atlantic upwelling area (after Parrish and Curtis 1982; Angel 2003; Dias 2005; Pérez-Díaz and Eagles 2017)

that allowed the deposition of a thick layer of evaporite deposits (Mohriak 2003; Bizzi et al. 2003; Pérez-Díaz and Eagles 2017). As the distance between African and South American plates increased, marine circulation was established allowing for the enhanced deposition of deep marine sediments on both East and West continental margins. In the South American margin, this linear topographic feature is known as the São Paulo Ridge, and the evaporite and deep-sea sediments compose the São Paulo Plateau (Dias 2005; Alberoni et al. 2019). The evaporite layers, up to 2000 m thick in the São Paulo Plateau, have been associated with the formation of important pre-salt oil and gas deposits that today sustain the bulk of the offshore oil and gas industry in Brazil (Mohriak 2003; Bizzi et al. 2003).

Current patterns of oceanic wind-driven circulation and associated biophysical processes were also progressively established during the expansion of the South Atlantic (Pérez-Díaz and Eagles 2017). According to Parrish and Curtis (1982), the South Atlantic subtropical gyre and upwelling zones off the coast of West Africa appeared 70–60 million years ago, as a result of processes associated with climate-related wind fields and constraints of the basin morphology (Fig. 8.2). In that sense, the oceanic oligotrophic conditions that predominate in today's subtropical gyre could have been established back in the late Cretaceous, long influencing POC (particulate organic Carbon) flux and deep-sea life in the Brazilian continental margin and adjacent Southwest Atlantic basin. Primary productivity levels in surface waters overlaying the slope areas off Brazil have been historically limited, which also explains the generally low benthic biomass (Brandini 1990; Capítoli and Bemvenuti

2006; Smith et al. 2008a). In fact, using POC flux models, Wei et al. (2010) have predicted that such biomass should be significantly lower than that observed in the Southeast Atlantic margin, where the seafloor is under the influence of major coastal upwelling systems (Fig. 8.2).

Notwithstanding the apparent energy limitation, general descriptions of oceanographic conditions at the shelf-break and slope off southeastern and southern Brazil suggest a highly dynamic environment, which derives from the southward geostrophic flow of the Brazil current and its interactions with the continental margin topography. The Brazil current originates at approximately 10°S, as a southward flowing branch of the South Equatorial Current. Initially a shallow current formed by tropical waters, it flows southward over the shelf break and becomes faster, thicker, and deeper (0–750 m) at approximately 20°S, where it incorporates contributions of the South Atlantic Central Waters. South of 25°S the Brazil current overlies deep water currents (Antarctic Intermediate Water and North Atlantic Deep Water) that also flow southwards, influencing the slope region down to 3000 m (Castro et al. 2006). Along this path, meanders and eddies are frequently produced in association with along-shelf topography, which are known to induce shelf break upwellings (Campos et al. 2000; Palma et al. 2008). These tend to enhance subsurface primary productivity that locally exceeds levels recorded over shelf and coastal areas (Brandini 1990; Acha et al. 2004). Such biophysical processes may be relevant to sustain concentrations of slope predator fish and shellfish off southeastern and southern Brazil, which have been elemental to the development of deep-sea fishing activities (see below).

8.2 Living Resources

8.2.1 Fish and Shellfish

The development of the deep-sea fisheries in Brazil started in 2000, driven by the offshore expansion of the national trawl fleet and operations of foreign fishing vessels authorized to fish in Brazilian waters under chartering contracts. In this process, upper bathyal depths (200–1000 m) were explored and profitable finfish and shellfish resources were identified and commercially exploited. Foreign fishing vessel activities introduced the use of deep-sea fishing methods in Brazil's EEZ, as well as international market opportunities. Their fishing operations, along with those of the national fleet, also led to an unprecedented impact on previously undisturbed areas of the Brazilian continental margin (see review in Perez et al. 2009).

Fishing activities of the foreign fleet extended widely along the Brazilian continental margin, from areas off the northern border with French Guiana (4–5° N) to the southern border with Uruguay (34°S), including seamount fishing off northeastern (Ceará Plateau and Fernando de Noronha Chain, 3–5°S) and southeastern (Vitória-Trindade Chain, 20°S) Brazil. However, 96% of over 32,000 fishing hauls conducted by the various fleets between 2000 and 2007 concentrated south of 18°S,

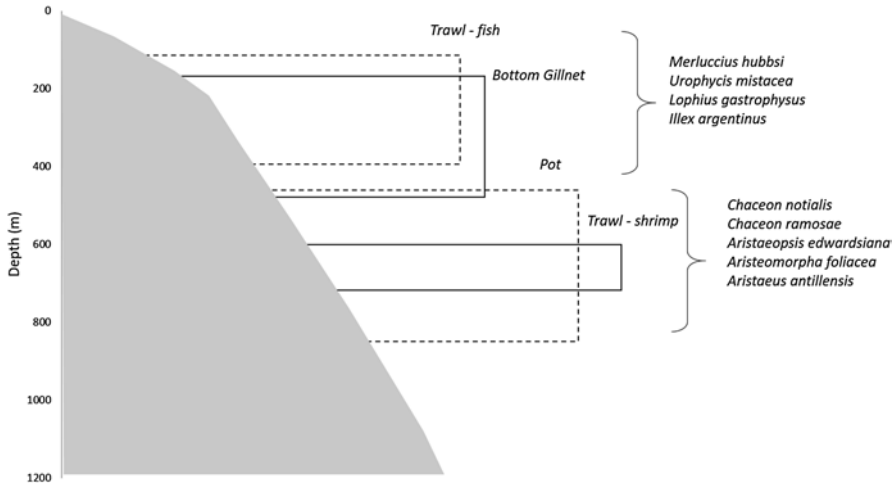
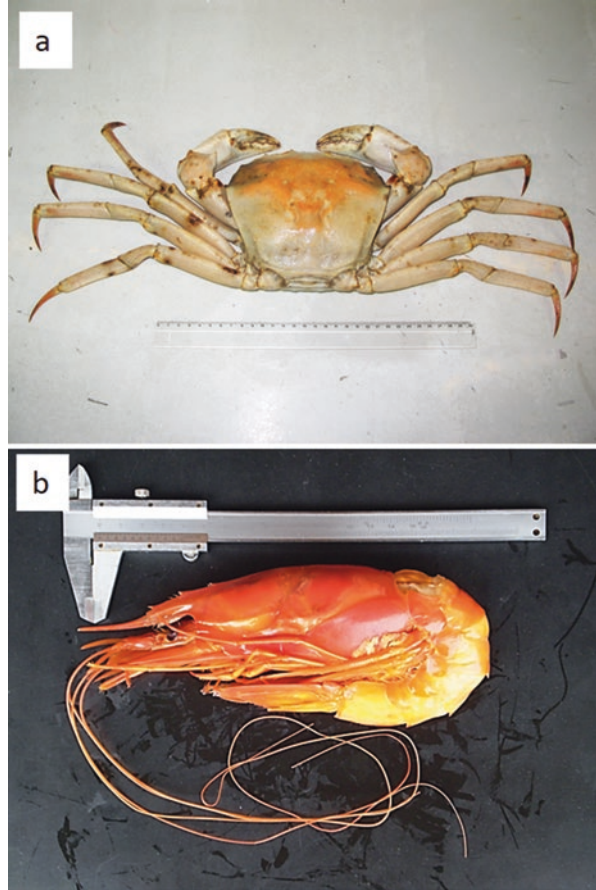


Fig. 8.3 Schematic view of the bathymetric distribution of fishing resources and methods in the continental margin off Southeastern and Southern Brazil

and particularly in the southeastern sector of Brazilian coast (23–30°S) (Perez et al. 2009). Fishing operations, using different methods and targeting different species, were distributed in distinctive bathymetric zones along the slope (Fig. 8.3).

In 2000–2002, bottom gillnet fishing operations concentrated on the upper bathyal depths (250–500 m) in search for profitable catches of the monkfish (*Lophius gastrophysus*). This species was also a component of the catches of foreign trawlers that operated in the same depth strata, but whose main targets were the argentine-hake (*Merluccius hubbsi*) and other slope species, including the argentine short-fin squid (*Illex argentinus*) and the codling (*Urophycis mystacea*). Pot fishing for deep-sea crabs (family *Geryonidae*) was carried out between 1999 and 2005 in two distinct areas off southern Brazil. The southernmost one (south of 33°S) explored concentrations of the red crab *Chaceon notialis* between 200 to 900 m depths. This stock straddles the border with Uruguay, where it was also exploited by Uruguayan vessels. To the north, between 27° and 30°S, pot fishing operations aimed at the royal crab *Chaceon ramosae* (Fig. 8.4a) between 500 and 900 m depths. By the end of 2002, a new foreign trawl fleet entered the southeastern areas, this time targeting extremely valuable concentrations of three deep-sea shrimp species: *Aristaeopsis edwardsiana* (scarlet shrimp, Fig. 8.4b), *Aristaeomorpha foliacea* (giant red shrimp), and *Aristeus antillensis* (alistado shrimp). These trawlers operated down to 1100 m, but commercial catches were limited to a narrow bathymetric band between 700 to 750 m depths. They concentrated between 24 and 26°S, but after 2005, there were expansions to southern (south of 26°S) and northern (19–20°S) areas, the latter also including fishing operations at the Besnard seamount, a component of the Vitória-Trindade Chain (Dallagnolo et al. 2009). By 2008 this fishery also came to an end, terminating the foreign deep-sea fishing episode in Brazil (see review in Perez et al. 2009).

Fig. 8.4 Deep-sea resources exploited off Brazilian coast. (a) Royal crab (*Chaceon ramosae*), (b) scarlet shrimp (*Aristaeopsis edwardsiana*). (Photos by Jose Angel A. Perez)



Deep-sea fishing, after the exit of the international fleet, continued through the operations of technologically adapted national bottom gillnet and pot vessels (e.g. Pio et al. 2016) but, most importantly, by national trawlers that increased their operations in the upper slope off southeastern and southern Brazil. Dias and Perez (2016) investigated the process of formation of this fleet that gradually adapted, both operationally and economically, to thrive year-round exclusively on catches of slope concentrations of the argentine hake, codling, and monkfish. Between 2007 and 2009, this fleet included 37 trawlers of slope ‘specialist’ skippers (sensu Branch et al. 2006). These, however, shared slope fishing areas with over 180 trawlers of ‘generalist’ skippers that operated opportunistically over the entire continental shelf and slope for a variety of resources.

Most slope fishing resources identified off Brazil underwent a ‘boom and bust’ exploitation pattern, commonly reported in deep-sea fishing developments worldwide (Norse et al. 2012). The period between 2000 and 2006 concentrated the bulk of catches reported along nearly 12 years of slope fishing development (total

landings ~87,655 t, Fig. 8.5). Peaks were recorded in 2001 (monkfish, 7064 t), 2002 (argentine hake, 3709 t, codling, 7847 t, royal crab, 1252 t, argentine shortfin squid, 2600 t), 2003 (red crab, 1378 t), and 2005 (scarlet shrimp, 183 t, giant red shrimp, 43 t, alistado shrimp, 16 t). Trawling by national vessels continued the exploitation of the main slope fish targets from 2005 onwards landing, until 2011, relatively stable annual catches of monkfish and argentine hake (mean landings 2573 t and 1893 t, respectively). In the case of codling, annual catches exhibited an increasing trend until 2009, stabilizing thereafter (Fig. 8.5). Over 80% of the total royal and red crabs reported catches were landed between 2001 and 2006. The latter has been exploited by a single national pot vessel since 2010. Deep-sea shrimps sustained very limited but valuable catches which extended until 2008.

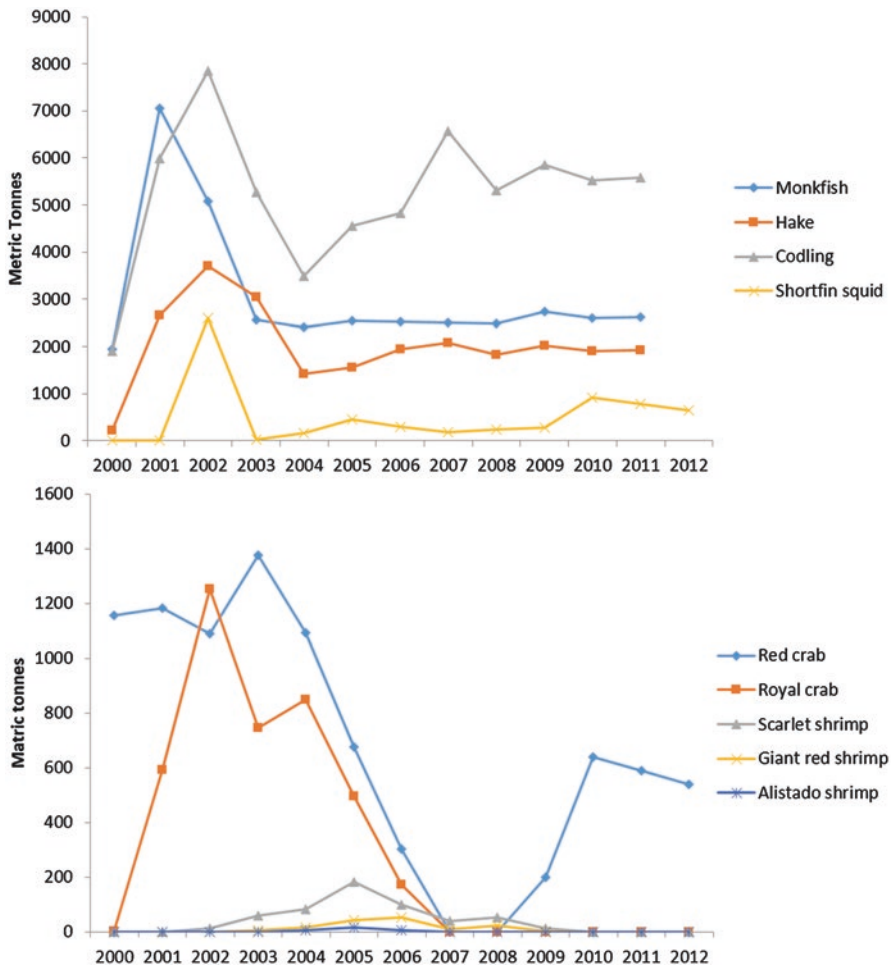


Fig. 8.5 Landings of demersal fish and shellfish species caught in slope areas off Brazil from 2000 to 2012

Biomass dynamics assessments and maximum sustainable yield (MSY) estimates were available during the main exploitation period for most slope stocks targeted off Brazil (Table 8.1) (Perez et al. 2009). Important biomass reductions and overfishing scenarios were characterized for monkfish, argentine hake, codling, scarlet shrimp, and royal crab. By 2009 these stocks were regarded as fully exploited or overexploited (Table 8.1). These scenarios, in association with fluctuations in the international markets and changes in the national fishing policies, provoked the termination of the deep-sea fishing development program around 2008. Deep-sea crustaceans have been scarcely exploited or not exploited ever since. Slope fish exploitation, however, has persisted through a process adaptation of traditional demersal fishing methods (trawls and gillnets). Their catches have been relatively stable under or near MSY levels, except for the codling whose catches have greatly exceeded the estimated MSY.

The development of deep-sea fishing activities has produced an increasing spatial footprint whose effects may have extended beyond the overfishing scenarios. Slope trawlers, for example, have extended their operations over nearly 11% of the available and previously untouched slope area off southern and southeastern Brazil between 2003 and 2011. Within this footprint, trawling tended to concentrate in limited areas that were 'swept' 1 to 6 times during this period, burning 46.4 million litres of diesel and releasing to the atmosphere 125.2 thousand tons of CO₂ (Port et al. 2016a, b).

Bottom gillnets set to catch monkfish in 2001–2002 produced the unwanted mortality of 101 species of elasmobranchs, teleosts, crustaceans, marine birds, marine turtles, and cetaceans, most of them discarded at sea (Perez and Wahrlich 2005). The royal crab and a group of spider crabs (family Majidae) were also abundant in

Table 8.1 Main finfish and shellfish species exploited in deep areas of the Brazilian continental margin. Biomass estimates refer to the period 2002–2006. Ov, over exploited; Fe, fully exploited; Un, unknown; MSY, maximum sustainable yield. After Perez et al. (2009)

Species	Estimated biomass (t)	MSY (t/year)	Stock status 2009	Mean catch (t) (after 2008)
Teleosts				
<i>Lophius gastrophysus</i>	62,776	2500–2000	Ov	2600
<i>Merluccius hubbsi</i>	21,934	2100–2200	Fe/Ov	1915
<i>Urophycis mystacea</i>	12,446	1182	Fe/Ov	5572
Crustaceans				
<i>Chaceon notialis</i>	17,118	1027	Fe	0
<i>Chaceon ramosae</i>	11,634	593	Fe/Ov	357
<i>Aristaeopsis edwardsiana</i>	865	60	Ov	17
<i>Aristaeomorpha foliacea</i>	87	13–17	Un	6
<i>Aristeus antillensis</i>	50	9–11	Un	<1
Mollusks				
<i>Illex argentinus</i>	Un	Un	Un	552

the catches as well as the argentine hake, the codling, the beard fish (*Polimixia lowei*), the angel shark (*Squatina argentina*), and various skates. Visintin and Perez (2016), using a productivity–susceptibility risk analysis (PSA), estimated that over 80% of individuals captured non-intentionally by this fishery belonged to biologically vulnerable species, including four skates (genera *Dipturus*, *Atlantoraja*, and *Torpedo*) and five sharks (genera *Squalus*, *Squatina*, *Hexanchias*, *Echinorhinus*, and *Sphyrna*). A similar analysis assessed the retained catch of national slope trawlers revealing that 70% of individuals landed by this fishery were highly vulnerable to fishing mortality (Visintin 2015). These organisms belonged to eight species including some of those previously mentioned and the extremely vulnerable pink cusk-eel (*Genypterus brasiliensis*). Trawlers fishing for the deep-sea shrimps produced relatively abundant discards containing 108 species that included 72 fish, 19 crustaceans, and 10 cephalopod species (Perez et al. 2013). Because these were the deepest trawl fishing operations off Brazil, the affected megafauna included deep pelagic (e.g. family Neoscopelidae) and benthopelagic (e.g. families Macrouridae, Acropomatidae, Ophidiidae, Moridae, Ogcocephalidae, Etmopteridae) species also likely vulnerable to fishing mortality.

8.2.2 *Biotechnological Products*

Biotechnology can be defined as the use of living beings or their products in commercial and industrial processes (Evans and Furlong 2003). Among the different types of living creatures that may be employed in biotechnology, microorganisms and bacteria in particular are key components of deep-sea ecosystems (Fang and Kato 2010; Gao et al. 2015; Zhang et al. 2016). In Brazil the prospection of biotechnological products from marine organisms, including those from the deep sea, has been another strategic initiative promoted by de PSRM under the BIOMAR⁸ program since 2005 (CIRM 2009).

The diversity and prospection of deep-sea bacteria have been carried out by two approaches. The first one is based on the cultivation of microorganisms from the samples studied (culture-dependent approach); the second is based on the study of DNA and other molecules obtained directly from the samples (culture-independent approach) (Tringe and Rubin 2005). It is accepted that the latter is the best approach to access the majority of the components of the microbial communities, since most of the bacteria in marine samples are non-cultivable by traditional microbiology methods (Fuhrman and Hagström 2008). Nevertheless, the microbial cultures provide a more efficient way to study the physiology and may be essential to describe new bacteria species (Krieg 2001) and identify biotechnological uses of these organisms (Bhatnagara and Kim 2012). Finally, both approaches should be used in

⁸Marine Biotechnology.

accessing the microbial diversity of a particular environment, since they may be complementary to each other in both the ecological and biotechnological contexts.

Culturable bacteria reported from culture-dependent studies in the deep South Atlantic are similar to those reported in other oceanic regions and belong to the phyla Proteobacteria, Bacteroidetes, Rhodothermaeota, Cyanobacteria, Firmicutes, and Actinobacteria (Schon et al. 2002; Berkenheger et al. 2003; Berkenheger and Fischer 2004; Wang et al. 2010; Odisi et al. 2012; da Silva et al. 2013; Li et al. 2014; Gao et al. 2015; Xu et al. 2016; Rigonato et al. 2016). These microorganisms were detected in samples of sediment (Odisi et al. 2012; da Silva et al. 2013; Gao et al. 2015; Xu et al. 2016), seawater (Schon et al. 2002; Wang et al. 2010; Rigonato et al. 2016), suspended organic aggregates (Berkenheger et al. 2003; Berkenheger and Fischer 2004), hydrothermal vents (Xu et al. 2016), and deep-sea animals (Deming et al. 1984), collected from the distinct regions of the South Atlantic including the Rio Grande Rise, the Equatorial, the mid-ocean ridge, and the Walvis Ridge regions.

In studies employing culture-independent techniques, the dominance of Proteobacteria in seawater of the deep Southeast Atlantic was also reported, which was represented mainly by Alphaproteobacteria, being *Alteromonas* as one of the most abundant genera. Other phyla included Cyanobacteria, Bacteroidetes, Verrucomicrobia, Acidobacteria, Actinobacteria, and Firmicutes (Friedline et al. 2012). In sediments collected from the Angola, Cape, and Guinea basins, Schauer et al. (2010) reported the dominance of the phylum Proteobacteria, including the classes Gammaproteobacteria and Deltaproteobacteria, and prominence of Acidobacteria. Other phyla detected include Chloroflexi, Bacteroidetes, and Planctomycetes.

The studies of the biotechnological potential of marine bacteria from the deep South Atlantic Ocean have focused mainly on hydrolytic enzymes and bioremediation. Enzymes are among the most prospected biomolecules from marine organism in general. Its application includes detergent supplementation (Nerurkar et al. 2013) and fuel production (Tan et al. 2010), for instance, and the interest in marine enzymes arises from their unusual properties including salinity, thermostability, and activity in high pressures (Debashish et al. 2005).

Lipases, i.e. enzymes that act on lipids, are the best studied enzymes in deep South Atlantic bacteria; these enzymes are produced by a wide range of marine bacteria, in agreement with its biological importance in the nutrition and the normal function of cells. Most of the marine bacteria with lipolytic activity were reported among the phyla Proteobacteria (class Gammaproteobacteria) and Firmicutes (class Bacilli) (Berkenheger et al. 2003; de Beer et al. 2006; Odisi et al. 2012). Important genera producing these enzymes include *Bacillus* and *Marinobacter*. Bacteria from sediments and suspended organic matter seems to be more lipolytic than those living free in the water (Berkenheger et al. 2003; Odisi et al. 2012), which may indicate the presence of polymeric and particulate organic matter in these microhabitats (Fenchel et al. 2012).

Other enzymes, such as cellulase, i.e. enzymes that act on cellulose, and amylase, i.e. those that act on starch, were also reported from bacteria isolated from the deep South Atlantic (Smith 1970; Berkenheger et al. 2003; Odisi et al. 2012; Lima

et al. 2013). These bacteria were obtained from sediment samples of the Rio Grande Rise region (Odisi et al. 2012, Lima et al. 2013) and off the northeast coast of Brazil (Smith 1970), and from suspended organic matter of seawater collected at the South Equatorial region (Berkenheger et al. 2003).

Bioremediation is the use of organisms, mainly microorganisms, in the recovery of environments contaminated with oil, metals, and other toxic substances. Oil-degrading bacteria, with potential of bioremediation, have been isolated from deep waters of the equatorial and mid-ocean regions (Wang et al. 2010) and from the mid-ocean ridge sediments of the South Atlantic Ocean (Gao et al. 2015). Most of the isolated bacteria belong to the phylum Proteobacteria, with *Alcanivorax* and *Dietzia* being the most commonly reported genera from seawater and sediments, respectively.

Culture-independent approaches have also been used for the discovery of novel molecules with biotechnological potential (Fang et al. 2010; Leis et al. 2015; Ferrer et al. 2016). This is a promising approach for the biotechnological prospection of South Atlantic deep-sea microorganisms.

In general, recent initiatives to explore the deep sea off Brazil and in the South Atlantic, as previously mentioned, have provided opportunities for the prospection of microorganisms and molecules and their potential application in technological products and processes. Yet the country has benefitted little from these potentialities as the development of mechanisms of transformation, particularly in association with the industry, is still limited.

8.3 Non-living Resources

8.3.1 Oil and Gas

The Brazilian continental margin has experienced a significant development of deep-sea oil exploration activities that were comparable to other productive areas such as the Gulf of Mexico and the North Sea. Petrobras has explored deep oil reservoirs for nearly 30 years, becoming a global player in offshore hydrocarbon production (Milani et al. 2000). A milestone in this exploration and exploitation process was the discovery of the giant ‘Albacora’ and ‘Marlim’ offshore oil fields, between 1984 and 1987, which represented not only an evidence of new frontiers for the oil industry but also a motivation for a subsequent technological leap, as required to improve oil extraction in deep and remote oceanic areas (Morais 2013). This leap involved significant investment in research programs designed to develop technological solutions for submarine systems including production outflow, production units, and their anchoring systems (Morais 2013).

Deep-sea post-salt deposits, found in areas deeper than 2000 m, are associated with ancient shales covered by deltaic progradations. In Campos Basin (Fig. 8.1), these turbiditic deposits contain oil reserves estimated in 12 billion barrels (Milani

et al. 2000), being comparable to reserves found in other important deep-sea oil provinces of the world, such as those found off Congo, Niger, and Nile river deltas. The pre-salt oil fields are located along the Campos and Santos Basin (between 20° and 27°S), distributed within a marine area 800 km long, 200 km wide, and 5000–7000 m below the sea surface (Fig. 8.1). In this area, low-density oil reservoirs are found in a sequence of over 100 million years old sedimentary rocks, 3000–5000 m below the seafloor surface. These rocks are compressed below an extensive salt layer and are rich in organic matter originated in the continent and transported by river systems to troughs formed by the rifting process during the breakup of Gondwana (Morais 2013). Pre-salt oil and gas reservoirs comprise 30% of all Brazilian reserves, estimated (in 2014) in 16,183 billion barrels.

In recent years, over 80% of Brazil’s annual oil and gas production has been extracted from deep (200–2000 m) and ultra-deep (> 2000 m) oil fields (Fig. 8.6). These areas comprise nearly 10% of all Brazilian oil fields in a production phase and are located in Campos and Santos basins, where extraction of oil and gas is mostly from pre-salt reservoirs. In 2017, the most productive fields included ‘Lula’ (2200 m depth, 73,4500 barrels per day), ‘Sapinhoá’ (2140 m depth, 25,2200 barrels per day), and ‘Jubarte’ (1355 m depth, 12,1700 barrels per day). The offshore oil and gas production in Brazil’s EEZ has expanded towards deeper sedimentary

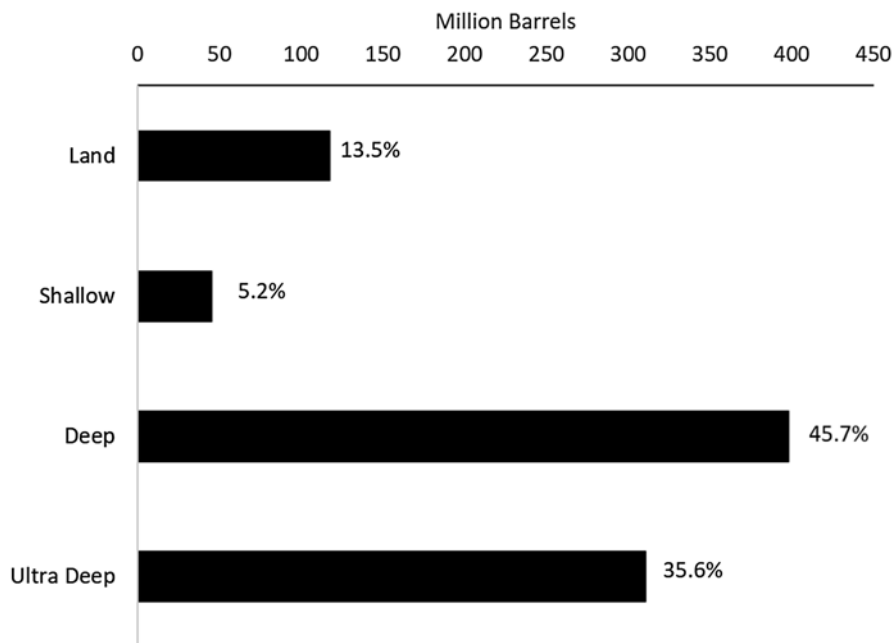


Fig. 8.6 Total amount of oil extracted in Brazil between January and November of 2017 (million barrels) in land, shallow (0–200 m), deep (200–2000 m), and ultra-deep (> 2000 m) waters. Percentages indicate the relative contribution of each category to the total production. Data from the ‘Brazilian National Agency of Petroleum, Natural Gas and Biofuels’ – ANP (www.anp.gov.br)

basins in the equatorial and subtropical areas. New bidding rounds starting in 2017 are leasing hundreds of deep-sea offshore areas in the Amazon Basin, on the north-eastern and southeastern margins (ANP 2017; Bernardino and Sumida 2017).

8.3.2 *Phosphates*

Marine phosphate deposits tend to occur in authigenic sedimentary rocks (Notholt 1980; Slansky 1992) as a result of diagenetic processes (phosphogenesis) that take place in the sedimentary layers rich in organic matter mostly between 200 and 1500 m depth, under the effect of minimum oxygen zones, and low terrigenous sedimentation (Baturin 1982; Filippelli 2011). In addition, these deposits must have been reworked during the eustatic sea level oscillation, which occurred between the Triassic and the Quaternary periods, concentrating phosphorus in the seabed sediments (Glenn et al. 1994).

In general, phosphoric pentoxide (P_2O_5) is a minor component of marine authigenic sedimentary rocks. However, their concentration may raise above 18% in some rocks, which are known as ‘phosphorites’ (Trappe 1998, 2001). These deposits are often found in oceanic areas under the influence of permanent upwelling systems, which tend to occur in the western margin of most continents (Baturin and Bezrukov 1979; Baturin 1982) and on top of rises and seamounts in the deep sea (Glenn et al. 1994).

The Brazilian coast is located in the eastern side of the South American continent deprived of major permanent upwelling zones (Fig. 8.2). However, according to the global model of phosphogenesis proposed by Riggs and Sheldon (1990), natural conditions at the shelf break and on top of seamounts off Brazilian continental shelf tended to favour phosphogenesis and the formation of phosphorites during the transgression and regression of Lower to Middle Miocene (~25 to 10 MaBP), known as Episode II of phosphogenesis (Riggs and Sheldon 1990). In addition, along the Brazilian margin, there are small and seasonal upwelling events, from São Tomé Cape (20°S) to Santa Marta Grande Cape (28°S), determined by local wind-circulation patterns, which allow for moderate primary productivity enhancement (Acha et al. 2004) and which may have favoured modern phosphogenesis.

In the Brazilian EEZ, deposits of phosphorites have been recorded in the summit of Ceará Plateau (400 m depth, 3°S) and upper level of Pernambuco Plateau (700–1250 m, 8°S) (Millimann and Amaral 1974; Melo et al. 1978; Guazelli and Costa 1978; Menor et al. 1979; Schobbenhaus 1984; Lenoble et al. 1995; Santana 1999), in the Florianópolis Terrace (200–600 m, 28°S), and the Rio Grande Terrace (200–800 m, 30°S) (Abreu et al. 2014) (Fig. 8.1). Furthermore, backscattering and bathymetric data were used to map potential deposits in an extensive area between 200 and 1000 m depth from São Tomé Cape (20°S) to Chuí (34°S) (Pinho et al. 2011).

Phosphorites off Brazil were found to occur in different forms, including nodules with few centimetres in diameter, to plate-like crusts paving the seafloor (Fig. 8.7). They contain 0.2–27% of phosphoric pentoxide (P_2O_5), and in some rocks there are

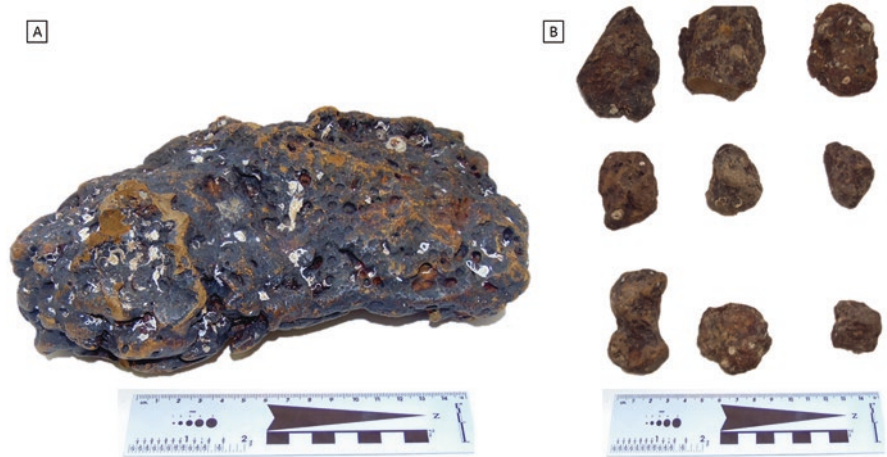


Fig. 8.7 Phosphate rocks dredged at the shelf-break off southern Brazil. (a) plate-like crusts, (b) nodules with few centimetres in diameter. (Photos by Luis H. P. de Souza. Scale = 15 cm)

significant contents of Fe_2O_3 (14%) and TiO_2 (1.7%) as well rare earth elements (REE) (Rocha et al. 1975; Lenoble et al. 1995). Recently, phosphate rocks were dredged by CPRM at depths between 700 and 1500 m on the Rio Grande Rise with high content of P_2O_5 (16.0 wt.%) and REE. These deposits represent the main substrate of Co-rich iron-manganese crusts (Cavalcanti et al. 2015).

Deposits found at the shelf break and upper slope, where P_2O_5 contents exceed 15%, can be regarded as potential mineral resources of the deep Brazilian continental margin, which are greatly demanded by the national agro-industry. In addition, phosphate rocks with a moderate to high contents of REE can be a likely source of raw materials needed for high-tech and green-tech development in the nearest future (Hein et al. 2016). Because available geochemical data is highly variable, a more precise delimitation of areas where phosphate mining can be economically viable is needed. CPRM has promoted and strongly supported these studies among the national scientific community in the context of the REMPLAC project.

8.3.3 Gas Hydrates

Gas hydrates are methane molecules trapped inside ice crystalline structures. The combination of methane gas and frozen water is known as clathrate or methane hydrates. The origin of methane gas contained in hydrates is related to hydrocarbon reserves and the activity of bacteria on organic matter within the ocean floor, under high pressure and low temperature ($<5^\circ\text{C}$) (Clennell 2000; Grauls 2001). Gas hydrates are abundantly present in the frozen soil of polar and subpolar regions (e.g. permafrost), where they are formed a few metres below the soil surface, and in the

deep ocean floor inside chilled layers of sediment that cover the lower slope and continental rise areas. Sediment layers that contain gas hydrates are generally found more than 500 m below the ocean surface and within the upper 100 m of the sedimentary package. In sedimentary areas of the Gulf of Mexico and the Niger River delta, they have been found in structures associated with gas escapement (Hovland et al. 1997). The so-called pockmarks are seafloor depressions formed by the dissolution of gas hydrate and its escape during glacial-interglacial cycles (Judd and Hovland 2007; Davy et al. 2010).

Gas hydrates are found in deep marine sediments of all continental margins and may comprise twice the volume of all known marine resources, including oil and gas (Clennell 2000). For that reason, they have been regarded as a future source of energy. Storing and using gas hydrates for that purpose, however, is still technologically difficult; one cubic metre of methane trapped in the clathrate structure will expand to 164 m³ of gas when exposed to normal levels of pressure and temperature and can combust spontaneously. Moreover, methane is an important greenhouse gas and its usage may imply important environmental consequences related to global warming.

Gas hydrates have been reported off Brazil on the Amazon submarine fan and in the Rio Grande Cone on the Southwest Atlantic (Fig. 8.1, Maslin et al. 1998, Sad et al. 1998, Fontana and Mussumeci 1994, Giongo et al. 2016). Pockmarks with diameters as large as 230 m were also reported in association with salt diapirism and extensional faults that likely promote gas hydrate seepage in Santos Basin between 300 and 800 m (Sumida et al. 2004; Sharp and Badalini 2013; Schattner et al. 2016; Mahiques et al. 2017). Evidence of methane gas seepage were also recorded in sediment cores obtained inside a pockmark in the Pelotas Basin (Miller et al. 2015). Using seismic data, these authors also proposed the likely presence of gas hydrates in the Rio Grande Cone. In addition, chemosynthesis-based communities were found in the same area (Giongo et al. 2016).

These indications are little comprehensive and insufficient for any projection about the future use of these hydrates as sources of energy in Brazil. However, ongoing research projects are directing efforts and resources to understand the existence of large pockmark fields and their association with methane seepage off the coasts of São Paulo, Paraná, and Santa Catarina States (Schattner et al. 2016, Mahiques et al. 2017).

8.3.4 *Metal-Rich Mineral Deposits*

Cobalt-rich ferromanganese crusts, polymetallic nodules, and seafloor massive sulphides are metallic mineral deposits found on deep oceanic basins and topographic features (e.g. seamounts and ridges) with potential for commercial exploitation in the future (Hein and Koschinsky 2013; Boschen et al. 2013). Seafloor massive sulphides (SMS) are formed by precipitation of sulfides and metals dissolved in 200–400 °C seawater expelled from hydrothermal vent systems (Boschen et al. 2013). The full process involves (a) percolation of deep seawater into the seafloor

leading to (b) subsequent heating by geothermal activity with dissolution of metals and sulfides from surrounding rocks and (c) their precipitation when such fluids mix again with cold seawater. This precipitation can take place below or above the seafloor, in the latter case forming chimneys around the point of hydrothermal fluid flow (vent), which will eventually collapse and form mounds. SMS deposits have been found in areas of volcanic activity, particularly near the central axis of mid-ocean ridges and back-arc spreading systems, and can contain varying proportions of Cu, Zn, Al, as well as gold and silver (Boschen et al. 2013). These deposits have been little explored in the South Atlantic Ocean, yet they are likely to occur along the mid-Atlantic ridge including areas within Brazil's EEZ in the vicinity of St. Peter's and St. Paul's Archipelago (Fig. 8.1, CGEE 2007).

Polymetallic nodules typically occur between 3500 and 6500 m depth and over sediment-covered basins. They grow around a nucleus by precipitation of Fe and Mn oxides that originate from seawater, pore water, and a mixture of both (Hein et al. 2013). Seawater (hydrogenetic process) is the main source of Co that concentrates in deposition areas defined by specific geomorphology and deep-water flux regimes (Palma and Pessanha 2000). Pore water (diagenetic process) is a source of other metals such as Ni and Cu. Nodule fields are extensive below areas of moderate to high primary productivity, high oxygen concentration, low sedimentation rate, high availability of nuclei, and usually below the calcite compensation depth (Hein et al. 2013). The most prominent known nodule field is located in central Pacific Ocean, an area known as Clarion Clipperton Zone (CCZ) where nearly 34 billion tons of nodules have been estimated, containing large amounts of Mn (7.5 billion tons), Ni (340 million tons), Cu (265 million tons), and Co (78 million tons) (Morgan 2000; Martins et al. 2006; Cavalcanti 2011). Other known fields are in central Indian Ocean, Peru basin (SE Pacific), and the Blake Plateau, (NE Atlantic) (Manhein 1972; Palma and Pessanha 2000; Cavalcanti 2011).

Polymetallic nodules were first recorded off Brazil in 1974, during the geological surveys conducted under the REMAC project. Nearly 150 kg of polymetallic nodules were sampled in the Pernambuco Plateau, northeastern Brazil, between 1750 and 2200 m depths (Fig. 8.1, Souza et al. 2009). The nuclei of these nodules were formed by phosphorites containing 28% of phosphorus, and the periphery contained Mn (20–30%), Fe (30%), Ni (0.2–1.4%), Co (0.6–1.55%), Cu (0.04–0.26%), Pb (0.08–0.53%) and Zn (0.12%) (Melo et al. 1978). Other areas of nodule occurrence near the Brazilian continental margin include the Vema Channel and the flanks of Vitória-Trindade Chain (Fig. 8.1, CGEE 2007).

Cobalt-rich ferromanganese crusts normally occur between 400 and 4000 m depth as pavements or as coatings on hard rock surfaces. Deposits are found on flanks and summits of isolated seamounts, oceanic rises and ridges, plateaus, and abyssal hills where the rocks have been swept clean of sediments for millions of years (Hein et al. 2000). Crusts may form from diagenetic, hydrogenetic, or hydrothermal processes (Roy 1992; Usui and Someya 1997). Crusts of higher economic interests are formed over the seafloor by precipitation and accretion of Fe and Mn oxides from cold seawater (hydrogenetic) and are probably influenced by bacterial biomineralization that increases trace metal concentrations including Co, Ni, Cu, Zn, Pt, Te, Ce, and Tl (Hein et al. 2000; Liao et al. 2011; Hein et al. 2013).

Hydrogenetic cobalt-rich ferromanganese crusts grow at rates of approximately 1 to 5 mm.My⁻¹. Crust growth is more effective in areas below the minimum oxygen zone where concentrations of dissolved Mn and associated metals are highest (Hein et al. 2013). The thickness of the crusts can vary from a few centimetres to 25 cm. Deposits may cover approximately 1.7% of ocean seafloor surface (6.3 million km²) and are thickest between 800 and 2200 m depths in the Northwest Pacific, where seamounts date back to the Jurassic Period, the oldest recorded in the world ocean (Hein 2006; Cavalcanti 2011). In the Brazilian EEZ, cobalt-rich ferromanganese crusts were reported in the Pernambuco Plateau, northeastern Brazil, but the most significant deposits were found in the Rio Grande Rise (Fig. 8.1, Martins et al. 2006). Such a finding motivated the implementation of the PROAREA program (see above), which promoted prospecting operations of CPRM in the area, between 2009 and 2011, using both national and foreign research vessels. Seafloor mapping and geological sampling during these surveys allowed the description of areas of crust distribution and characterized plate-like and film-like crust pavements (Fig. 8.7) that frequently covered phosphate rocks as nuclei (Cavalcanti et al. 2015). Mean crust geochemical composition indicated the presence of MnO (26.7%), Fe₂O₃ (27.7%), Co (0.81%), Ni (0.37%), and other trace metals (Ba, Cu, Ce, TiO₂) (Cavalcanti et al. 2015).

Because the Rio Grande Rise was originally located in areas beyond national jurisdiction, these prospective studies were used for the elaboration of a ‘Plan of Work’ for crust exploration, submitted in 2013 to the ISA. In 2015, a fifteen-year contract was signed between Brazil’s CPRM and the ISA, whereby new surveys were carried out in the Rio Grande Rise, improving knowledge on these deposits and their potential for exploitation, as well as on the associated benthic ecosystem, as required by the ISA regulations (see below). Substantial contributions to such knowledge have also derived from scientific surveys conducted under the E-tech project in 2018–2019 (Jovane et al. 2019).

After the development of the offshore oil and gas production, the exploration of cobalt-rich ferromanganese crusts in the Rio Grande Rise area represented a new milestone in the national process of developing means for exploitation of deep-sea non-living resources. The scientific results attained during exploration activities, combined with political interests, further motivated the Brazilian Government to include the Rio Grande Rise area in a proposal for extension of the limits of Brazilian EEZ submitted in 2018 to the UN Commission on the Limits of the Continental Shelf (Alberoni et al. 2019).

8.4 Sustainable Use and Conservation Issues

8.4.1 Fisheries Management

In 1999, the management of underexploited or unexploited fisheries resources in Brazil was attributed to a specific management authority, outside the regular fishery administration regime established by the Ministry of the Environment. When the

deep-sea fishery development initiated in 2000, most resources fell within this definition, being, since then, submitted to a less restrictive management regime. This management regime included an advisory committee composed of representatives of government authorities, fishers, and scientists, with the mandate to propose management measures for deep-sea fisheries and resources. A parallel scientific committee was also created to promote deep-sea fisheries data collection by observers on board fishing vessels, logbooks, and landings monitoring systems. Based on available data, this scientific committee assessed commercial stocks and proposed management options.

Between 2001 and 2008, the advisory committee effectively proposed timely management plans for the monkfish fishery, multi-species slope trawl, and red and royal crab fisheries (Perez et al. 2009). Their implementation, however, was generally slow, obstructed by ineffective governance, and therefore unable to prevent overfishing of most resources. After 2008, the advisory committee structure was deactivated and management of deep-sea resources was reincorporated into a regime common to all fishing resources, which involved a top-down decision process shared by fishing authorities of the Ministry of Environment and the recently created Ministry of Fisheries and Aquaculture. This ministry was extinct in 2015 leading to a period of uncertainty in the country's fishing management process. In 2019 this process concentrated again in a single agency linked to the Ministry of Agriculture and Livestock.

After nearly 10 years of the termination of the foreign fleet activity in slope areas, and in the absence of any new significant fishing activity in the area, recovery of deep-sea stocks such as deep-sea crabs and deep-sea shrimp is uncertain. Stocks of monkfish and other slope fishes however have remained under considerable fishing pressure exerted by trawlers and their management regime is currently unclear (Dias and Perez 2016).

Another legacy of the 2000–2008 deep-sea fishery management regime was the adoption of two 'no take' areas as spatial management measures in the monkfish and slope trawl fisheries management plans (Perez 2007). These zones were placed across the slope topographic profile, between 100 and 1000 m depth, off the states of Santa Catarina and Rio Grande do Sul (28° and 30°S) and off the state of São Paulo (23° and 25°S). Their design aimed at protecting the monkfish stock integrity and reducing the unintentional mortality of megafaunal species including sharks, cetaceans, wreckfish, and royal and spider crabs (Perez and Wahrlich 2005). Their adoption extended to other management plans in the area, but their enforcement has been inefficient due to the generally unstable governance of the fishing management regimes in Brazil (Perez et al. 2009).

8.4.2 Leasing of Offshore Oil and Gas Fields

Activities involving exploration, development, and exploitation of oil and gas in the marine environment are conducted in Brazil through concession contracts obtained after a bidding process (Mariano and La Rovere 2007). Because such activities are

capable of potentially causing pollution and habitat degradation (Cordes et al. 2016), contractors must submit their projects to an environmental licensing process carried out by the Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA). Most activities related to drilling of wells for prospection of oil and gas reservoirs and production, either for research or commercial purposes, are regulated by specific legal instruments, whereas marine seismic surveys follow Brazil's general regulations for environmental licensing. Each of these activities requires environmental impact assessments (EIA) and specific licenses from IBAMA (Porto et al. 2007). These assessments must follow project-based guidelines issued by IBAMA after the project submission by the contractors. Licenses for installation of offshore structures are valid for up to 10 years, and all other activities, including seismic surveys, are licensed by IBAMA for periods compatible with the schedule of approved activities.

In general terms, IBAMA has demanded Petrobras and other oil companies operating in Campos and Santos Basin to conduct environmental studies that allow assessing the effects of seismic and other activities of the oil industry on vulnerable fauna and coastal fishing activities. Baseline studies on the deep-sea basins where oil and gas offshore activities take place have included extensive chemical, physical, biological, and ecological assessments (Lavrado and Brasil 2010b; Bernardino et al. 2016; Almeida and Kowsmann 2017; Lavrado et al. 2017a, b; Silveira et al. 2017). However, whereas these broad baseline studies have provided important environmental characterization of slope and abyssal areas within offshore oilfields, the occurrence of deep-sea vulnerable ecosystems, including cold-water coral reefs and cold seeps, has still been largely overlooked (Bernardino and Sumida 2017). For example, there is large evidence for the presence of deep-sea seeps (Sumida et al. 2004; Giongo et al. 2016; Fujikura et al. 2017; Mahiques et al. 2017), cold-water coral reefs and submarine canyons within offshore fields (Almada and Bernardino 2017; Bernardino et al. 2019). Yet areas offered on bidding rounds by the Brazilian Government (ANP) broadly overlap areas where these vulnerable ecosystems occur, a sign that existing baseline environmental assessments may have been completely disregarded (Almada and Bernardino 2017). In Campos Basin, for example, the offshore oil and gas leased blocks significantly overlap (>80% of ecosystem area) with cold-water coral reefs and submarine canyons. Furthermore, the expansion of the offshore industry in the 14th ANP bidding rounds (2017–2019) have the potential to expand the overlap of leased areas with vulnerable deep-sea ecosystems to other basins in the northern, northeastern, and southern margins of Brazil's EEZ (Bernardino and Sumida 2017).

8.4.3 Licensing Mineral Exploration

The use of mineral deposits, either terrestrial or marine within Brazil's EEZ, require a two-stage authorization process that will result in research and mining permits, both issued by the Ministry of Mines and Energy (MME). This permit determines a

period whereby applicants will assess the deposit qualitatively and quantitatively as well as the feasibility of its economical use. Results of these studies are then submitted in the form of a report to the National Mining Agency (ANM) who will decide on its approval and determine if the project can proceed to the second stage. The concession for mining permits will require a submission to ANM of a plan of economical use that will delimit precisely the exploitation area and the mining activities. If approved, DNMP will grant a mining concession for an undetermined period of time (Cavalcanti 2011).

Because mining activities potentially degrade the environment, deep-sea mining within the EEZ also requires an Environmental Impact Assessment (EIA), environmental licensing, and, eventually, a plan for recuperation of a degraded area. All permits are issued by IBAMA, but they are mandatory for mining concessions only, and not research activities. The EIA must be contained in an Environmental Impact Report whose approval by IBAMA determines whether the mining project can be granted an environmental license or not. Also, a plan for recuperation of degraded areas should be submitted and approved by IBAMA, whereby it is indicated how natural conditions will be restored once mining is ceased in the licensed area. Because deep-sea mining has not been attempted in the Brazilian jurisdictional waters, these are all regulations prescribed by law, but never put in practice in Brazil.

Outside the EEZ limits, Brazil's initiatives to explore deep-sea minerals are submitted to UNCLOS and regulations established by the ISA. Mining companies, sponsored by an UNCLOS member State, can apply for prospection, exploration, and exploitation permits in the area. Exploration permits have been requested in international areas and follow 'mining codes' developed for polymetallic nodules (ISBA 2013), Cobalt-rich ferromanganese crusts (ISBA 2012), and SMS (ISBA 2010). These regulations require applications to inform the size of exploration area, in the case of ferromanganese crusts formed by no more than 150 rectangular blocks with 20 km² surface (total of 3000 km²). They must also contain a 'Plan of Work' for the first 5 years of activities describing an exploration program, with detailed oceanographic and environmental baseline studies that would enable an assessment of the potential environmental impacts of exploration activities. The plan must also provide a preliminary assessment of the possible impact of the proposed exploration activities on the marine environment and detail proposed actions for the prevention, reduction, and control of pollution and other hazards (ISBA 2012). The Plan of Work is reviewed by ISA's Legal and Technical Commission (LTC) who has the mandate to recommend its approval to ISA's Council and Assembly. After the contract is signed between the applicant and the ISA, the contractors must deliver annual reports and environmental data collected in the claim area to the ISA secretariat who will submit to the LTC for approval.

CPRM's Plan of Work for cobalt-rich ferromanganese crusts was recommended for approval by the LTC in February 2014 and approved by the Council and Assembly in July 2014. It includes the development of environmental baseline studies in the claim area on the Rio Grande Rise during the first 3 years (2016–2018) and geological exploration studies in the following 2-year period (2019–2020). In 2017–2018, CPRM submitted annual reports, informing results of exploration

activities in claim area. In the context of the inclusion of this area in the extension of the Brazilian EEZ, the development of the referred ‘Plan of Work’ is currently uncertain. As part of Brazilian extended EEZ, any cobalt crust exploration/exploitation initiative in the Rio Grande Rise would normally follow national regulations, as previously described.

8.4.4 Ecosystem Conservation

In 2007 the Brazilian Ministry of the Environment defined priority areas for conservation in the national territory and marine areas within national jurisdiction (MMA 2007). Extensive deep-sea areas were classified as ‘insufficiently known’, yet some deep regions were considered of ‘extreme biological importance’ both in the continental margin (e.g. Rio Grande Terrace and Rio Grande Cone) and the adjacent oceanic basin mostly around oceanic islands (e.g. St. Peter’s and St. Paul’s Archipelago, Fernando de Noronha, Trindade, Rocas Atoll) and seamounts (e.g. Vitória-Trindade Chain, Almirante Saldanha bank, Sirius, and others).

Beyond areas of national jurisdiction, a number of governmental initiatives have established procedures regarding conservation of deep-sea ecosystems all of them applicable to the Southwest Atlantic. Deep-sea fisheries in the high seas, for example, have been submitted to management recommendations that include criteria for identifying and protecting ‘Vulnerable Marine Ecosystems (VMEs)’, i.e. communities and organisms that when submitted to ‘adverse impacts’ would hardly recover (FAO 2016). These recommendations however have been mostly applied in regional fisheries organizations, non-existing in the SW Atlantic (Rogers and Gianni 2010). A similar concept was defined by the Convention on Biological Diversity (CBD) as ‘Ecologically and Biologically Significant Areas’ (EBSAs) to be used as starting points to the definition of marine protected areas in the high seas (Smith et al. 2008b; Wedding et al. 2013; Dunn et al. 2014). Four EBSAs proposed in the ‘Wider Caribbean and Western Mid-Atlantic Region’ encompass deep-sea areas off Brazil: (a) Banks Chain of Northern Brazil and Fernando de Noronha, (b) Abrolhos Bank and Vitória-Trindade Chain, (c) Southern Brazilian Sea, and (d) Atlantic Equatorial Fracture Zone and high productivity system (CBD 2014). The latter covers a large extension across the equatorial Atlantic including crests and trenches of the Romanche Fracture Zone and Saint Peter’s and Saint Paul’s Archipelago and its surrounding EEZ. This area was also considered an ‘Area of Particular Environmental Interest - APEI’ (sensu Lodge et al. 2014) in the process for designing a Strategic Environmental Management Plan (SEMP) for the northern Mid-Atlantic Ridge (Dunn et al. 2018). In 2018 a large marine-protected area was created around the Saint Peter’s and Saint Paul’s Archipelago aimed at preservation of ‘... the marine environment, water column and seamounts ...’ (Brasil 2018).

Finally, in 2015 the United Nations General Assembly proposed the ongoing development of an international legally binding instrument under UNCLOS on the conservation and sustainable use of marine biological diversity in areas beyond

national jurisdiction (ABNJ) (UNGA 2015). Focal points of this instrument include regulations regarding the access to marine genetic resources in the high seas (Druel et al. 2013), which will be applicable in the South Atlantic basin, where bioprospection initiatives have been carried out by Brazil (e.g. Odisi et al. 2012; Lima et al. 2013) and other countries.

8.5 Conclusions

The use of living and non-living resources of Brazilian deep waters and adjacent Southwest Atlantic basin has been guided by different motivations and subject to different levels of scientific knowledge on their occurrence, value, availability, and productivity potential (Table 8.2). It has also been limited by the existence and availability of technologies suitable for extraction and transformation into products, and a regulatory process that ensure sustainability, in a broad ecological sense.

Fisheries resources and oil and gas have been explored with extant technologies during the past decade or more. Deep-sea fishing requires a costly transformation of traditional fishing fleets, but stocks were shown to be little productive and little

Table 8.2 Qualitative assessment of the use of deep-sea living resources in Brazil

	Living		Non-living	
	Fish and shellfish	Biotech products	Oil and gas	Mineral deposits
Main motivations to exploit	Economic	Economic	Economic	Economic
	Compensation for productivity loss of shallow water stocks	Scientific and technological development	Self-sufficiency in oil production	Geopolitical strategy
Knowledge on natural occurrence and availability	Mostly known	Insufficiently known	Mostly known	Insufficiently known
Known potential productivity	Low	Uncertain	High	Uncertain
Availability of technologies for exploitation and use	Available	Partially available	Mostly available	Mostly unavailable
Availability of regulations for sustainable use or to minimize environmental impacts	Mostly available (but little effective)	Unavailable	Available (but likely insufficient)	Mostly available (but effectiveness is uncertain)
Perspectives of use in the future	Unpromising (but possible in very small scale)	Uncertain but promising	Promising	Uncertain but promising

resilient, sustaining only very small fisheries. Deep-sea oil and gas reserves, on the contrary, are estimated to be large and suitable for extraction. In part, such a contrast is historically associated with the genesis of the South Atlantic Ocean that favoured the formation of extensive oil deposits along sedimentary margins off Brazil, but also led to the formation of a nutrient-poor subtropical gyre that influences most of Brazil's continental margin and consequently sustains limited fish exploitable biomass, especially in deep areas. Both activities, however, leave clear footprints in the deep-sea environments, with impacts not fully dimensioned or prevented by environmental regulations.

On the other hand, biotechnological products and deep-sea minerals have been preliminarily prospected and their potential use in the next decade is uncertain. The former depends on microorganisms (or their DNA) extracted from the deep-sea environments at the cost of little (or none) environmental impacts. Yet the transformation of potentially useful molecules and genes into technological products still needs considerable development, although with promising results. Mining deep-sea minerals is still largely dependent on the availability of suitable technologies, and most of the countries' efforts have been focused on acquiring knowledge not only on the potential of deposits but also on environmental impacts by exploitation activities.

A major concern, common to all deep-sea resources off Brazil, includes the effectiveness of the regulatory and management processes. Deficiencies, particularly regarding governance issues, have greatly hampered deep-sea fishing and may affect other activities as well. International management regimes, as required outside areas of national jurisdiction, are sometimes absent, for example, in the case of demersal fisheries in the SW Atlantic that, unlike other regions, lack a regional management body. In other cases, regulations have been in place (e.g. ISA's mining codes), but probably need improvement to effectively protect sensible areas and their fragile biodiversity (Wedding et al. 2013).

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