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 (subsurface), 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 (Arístegui 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 teaming 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; Arístegui 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 repertories 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 PgC. 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

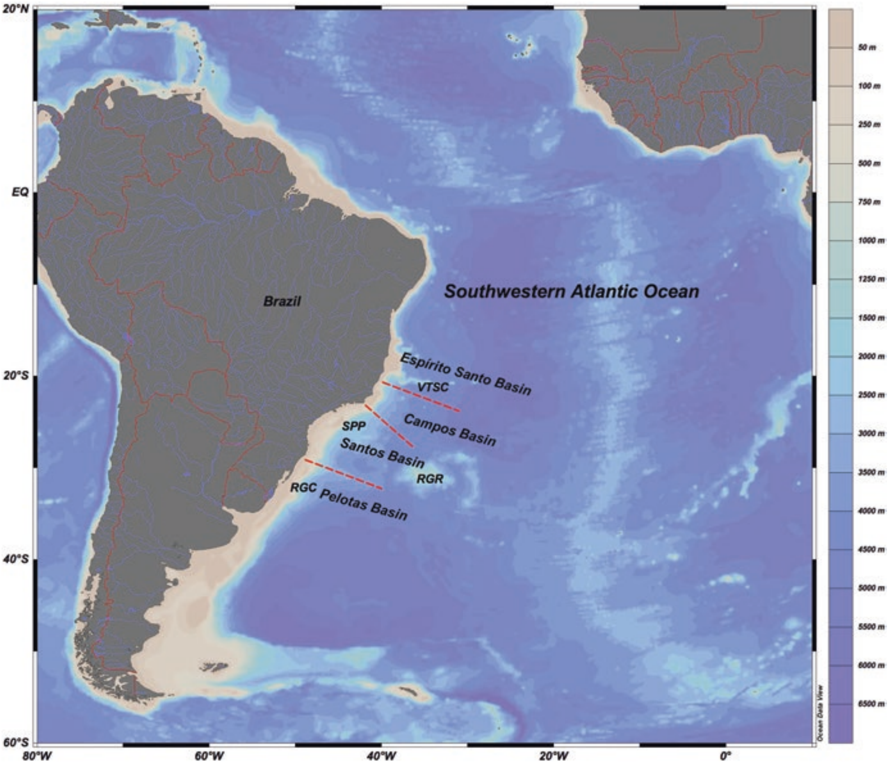

Fig. 6.1 Main physiographic features of the Southwestern Atlantic Ocean mentioned in this chapter. *VTSC* Vitória-Trindade seamount chain, *SPP* São Paulo Plateau, *RGR* Rio Grande Rise, *RGC* Rio Grande Cone

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 *Escarpia* 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 ^{3}H-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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