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Patterns of Life on the Southern Mid-Atlantic Ridge

Compiling What is Known and Addressing Future Research

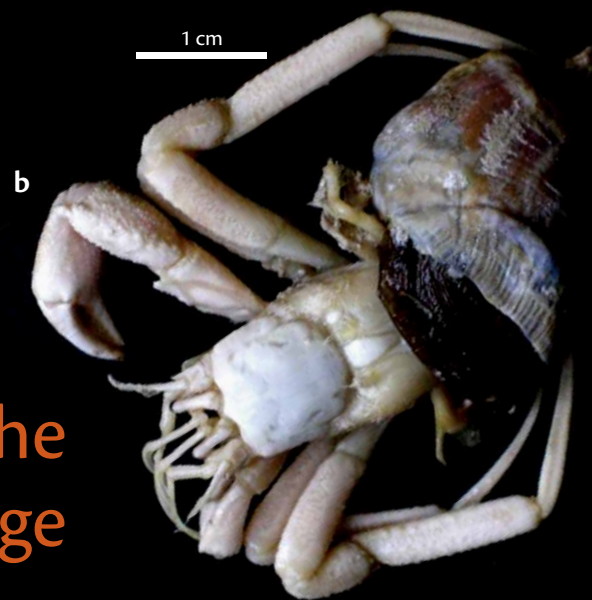
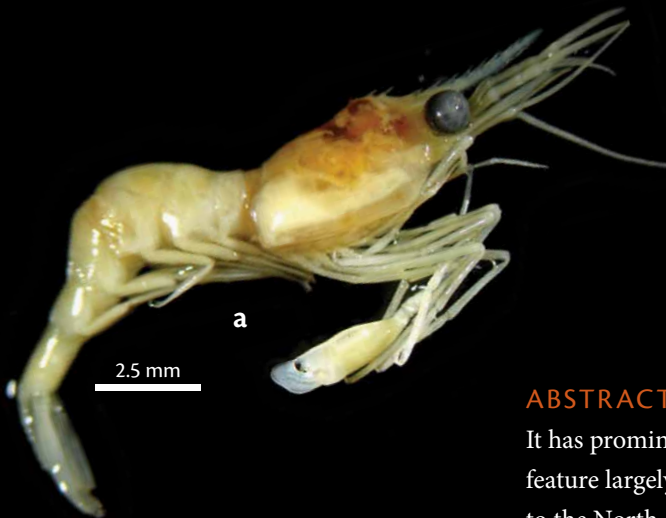
BY JOSÉ ANGEL A. PEREZ,

ELIANA DOS SANTOS ALVES, MALCOLM R. CLARK,

ODD AKSEL BERGSTAD,

ANDREY GEBRUK, IRENE AZEVEDO CARDOSO,

AND ANTONINA ROGACHEVA



Fauna collected during the South Atlantic MAR-ECO cruise, October–November 2009. (a) *Leontocaris smarensis* new sp. (b) *Parapagurus abyssorum*. (c) *Parapagurus pilosimanus* in symbiosis with zoanthid *Epizoanthus* sp. Photos: a–b, Irene Cardoso; c, André Barreto

ABSTRACT. The South Atlantic is one of the youngest of all the major oceans. It has prominent topographic features, in particular, the Mid-Atlantic Ridge. This feature largely determines deepwater circulation patterns that connect this ocean to the North Atlantic, Southern, Indian, and Pacific Oceans. Yet very little is known about biodiversity patterns in the South Atlantic or its connectivity with other deep areas of the world ocean. The South Atlantic MAR-ECO (SA MAR-ECO) project was developed as part of the Census of Marine Life to fill such knowledge gaps, particularly focusing on the southern Mid-Atlantic Ridge. This article summarizes and reviews published information on the deep South Atlantic as background knowledge for the concepts, principal questions, and goals of SA MAR-ECO. It also describes the strategies and methodological approaches adopted for a southern Mid-Atlantic Ridge sampling program and the limitations and achievements of the first field survey in November 2009.



INTRODUCTION

Mid-ocean ridges and seamount chains are prominent structures of the deep seafloor that have attracted considerable attention for their biodiversity, fisheries, and mineral resources (Clark et al., 2010). The potential for sustainable exploration of these ecosystems and the need for their conservation have been issues of increasing concern worldwide and have motivated modern scientific initiatives such as those within the scope of the global Census of Marine Life (CoML) (McIntyre, 2010). One of these initiatives, MAR-ECO: Patterns and Processes of the Ecosystems of the Northern Mid-Atlantic, was proposed in 2001 as a CoML field project to study the diversity and ecology of the northern Mid-Atlantic Ridge (MAR; Bergstad and Godø, 2003). Historically, this extensive and topographically rough seafloor spreading area has been poorly sampled, except for the chemosynthetic ecosystems that lie along small portions of the ridge. Consequently, there were many unanswered questions regarding the origin and dispersion of the MAR's deep-sea fauna and the significance of its "comparatively shallow structures in the middle of the deep oligotrophic ocean, for the distribution and production of biota" (Bergstad et al., 2008). MAR-ECO addressed this knowledge gap by combining modern technology, an intensive and well-planned sampling strategy, and the collaborative work of international scientific experts (Bergstad and Godø, 2003). Pelagic and benthic habitats were sampled to a maximum depth of 4,500 m over the North Atlantic mid-ocean ridge, providing well-documented new information on previously described and undescribed species and models

indicating how mid-ocean ridge communities are structured (Vecchione et al., 2010). As with all CoML projects, MAR-ECO necessarily began with a data-mining effort to determine what was known about the area.

In 2006, an initiative to expand sampling activities and studies to the South Atlantic mid-ocean ridge spun off the MAR-ECO project, supported by the CenSeam (Census of Marine Life on Seamounts) project (Consalvey et al., 2010). This initiative was particularly concerned with addressing biological questions considering (a) complex patterns of geological morphology and deepwater circulation of the ridge, (b) its connections with the North Atlantic, Pacific, Indian, and Southern Oceans, and (c) its recent origin, as it is virtually "the youngest of the major world oceans" (Levin and Gooday, 2003). A first field expedition conducted in 2009 to sample pelagic and benthic biota of the southern Mid-Atlantic Ridge effectively initiated the "South Atlantic MAR-ECO" (SA MAR-ECO) project focused on improving knowledge about the biodiversity patterns of this vast and little known area of the world ocean.

This article reviews published

information on the South Atlantic as background knowledge for the concepts, major questions, and goals of SA MAR-ECO. It also describes the strategies and methodological approaches to be adopted by the proposed southern Mid-Atlantic Ridge sampling program and the limitations and achievements of the first field experience in 2009.

WHAT DO WE KNOW ABOUT THE DEEP SOUTH ATLANTIC OCEAN?

Geological Origins

The South Atlantic Ocean was formed by the separation of the South American and African Plates 175–90 million years ago. Its configuration and size are outcomes of two independent spreading processes: one that formed the North Atlantic in the early Mesozoic nearly 200 million years ago and another that formed the South Atlantic 100 million years later. This latter spreading process resulted in connections with three other oceans—the Southern, Pacific, and Indian. Also, it included a north-south as well as an east-west component, which shaped the sinuous seafloor and defined most of its features (Figure 1; Fairhead and Wilson, 2004). Because it is relatively

José Angel A. Perez (angel.perez@univali.br) is Professor, Centro de Ciências Tecnológicas da Terra e do Mar, Universidade do Vale do Itajaí, Santa Catarina, Brazil.

Eliana dos Santos Alves is Research Associate, Centro de Ciências Tecnológicas da Terra e do Mar, Universidade do Vale do Itajaí, Santa Catarina, Brazil. **Malcolm R. Clark**

is Principal Scientist, National Institute for Water and Atmospheric Research, Wellington, New Zealand. **Odd Aksel Bergstad** is Principal Scientist, Institute of Marine Research, Bergen, Norway. **Andrey Gebruk** is Head of Laboratory, P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences (IORAS), Moscow, Russia.

Irene Azevedo Cardoso is a researcher in the Setor de Carcinologia, Departamento de Invertebrados, Museu Nacional/Universidade Federal do Rio de Janeiro, São Cristóvão, Rio de Janeiro, Brazil. **Antonina Rogacheva** is PhD Candidate, P.P. Shirshov Institute of Oceanology, IORAS, Moscow, Russia.

young, the South Atlantic is narrow and has a high ratio of margin to deep water (Levin and Gooday, 2003).

The most prominent ocean floor feature is the Mid-Atlantic Ridge, which extends 14,000 km continuously from Iceland in the north (87°N) to Bouvet Island (54°S) in the south, and rises 2,000–3,000 m above the seafloor (Figure 1). The joining of the north-south spreading centers in the early mid-Cretaceous resulted in development of a shear zone between West Africa and the northeastern margin of Brazil. It produced the Equatorial Fracture Zone, a large geological feature about 60 million years old, that affects both the

linearity of the ridge system and large-scale ocean circulation (Huang and Jin, 2002; Fairhead and Wilson, 2004). At the southern extreme, two seamount chains, Walvis Ridge and Rio Grande Rise, form bridges that run from the central ridge to the African and South American continental margins, respectively. Kumar (1979) called them “paired aseismic rises” of the South Atlantic and proposed a common geological origin between 100 and 80 million years ago. During this early phase of the South Atlantic opening, “abnormally intense” volcanism along the axis of a MAR segment created a volcanic pile that was subsequently separated by east-west movement of

transform faults as the ridge axis subsided. Seamounts on both rises were also formed by intermittent volcanic activity that followed this separation (< 80 million years ago); they include the islands of the Tristan da Cunha group and Gough (Fodor et al., 1977; Kumar, 1979; Camboia and Rabinowitz, 1984). The MAR, the Equatorial Fracture Zone, and the seamount ridges surround five basins: Brazil, Argentine, Guinea, Angola, and Cape (Figure 1). These basins are connected by deep channels that include the Vema Sill and Hunter Channel on either side of the Rio Grande Rise, and Kane Gap on the eastern side of the Equatorial Fracture Zone (Murray and Reason, 1999).

Oceanography

The counterclockwise “Subtropical Gyre” formed by the interconnected Brazil, Antarctic Circumpolar, Benguela, and South Equatorial Currents dominates the surface circulation of the southern Atlantic Ocean. Wind-effect and thermohaline processes determine this circulation pattern, which affects subsurface waters as deep as 1,500 m (Schmid et al., 2000). Below 2,000 m, the interactions between North Atlantic Deep Water (NADW) and Antarctic Bottom Water (AABW), induced by their thermohaline properties and the seafloor topography (Figure 2), drive the main flow path of deep water. In the western basin, NADW flows southward between 1,500 and 4,000 m depth. Below this layer, AABW flows in the opposite direction, penetrating the South Atlantic through the Vema Sill and the Hunter Channel and into the North Atlantic (Murray and Reason, 1999). At the equator, this water mass also branches eastward, flowing through the Kane Gap back into the Southeast Atlantic below

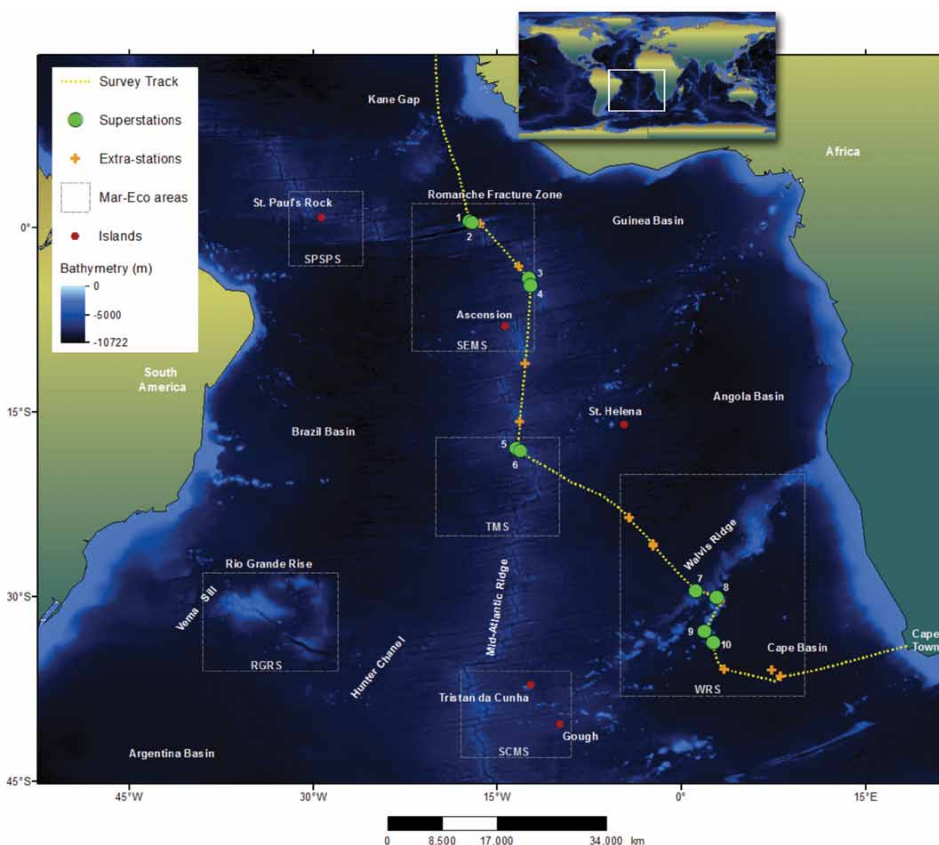


Figure 1. South Atlantic Ocean seafloor and its main topographic features as extracted from ETOPO (<http://www.earthmodels.org>). Boxes represent target sectors defined for the South Atlantic MAR-ECO project. SPSPS = St. Peter and St. Paul’s Sector. SEMS = South Equatorial Mid-Atlantic Ridge Sector. TMS = Tropical Mid-Atlantic Ridge Sector. SCMS = Subtropical Convergence Mid-Atlantic Ridge Sector. WRS = Walvis Ridge Sector. RGRS = Rio Grande Rise Sector. The yellow dotted line depicts the track of the twenty-ninth voyage of R/V *Akademik Ioffe* (Shirshov Institute, Academy of Sciences, Russia) in November 2009, including South Atlantic MAR-ECO predefined “superstations” and extra stations.

4,000 m depth (Stephens and Marshall, 2000). That is the main source of AABW in the eastern basins because the Walvis Ridge blocks northward flow of this water mass from the Southern Ocean. As a result, the Southeast Atlantic basin, above 4,000 m, is almost exclusively NADW that flows in through the fracture zones (e.g., Romanche and Chain) at the equator (Huang and Jin, 2002; Bickert and Mackensen, 2003).

Except for limited areas of hydrothermal vents and seeps, life patterns along the Mid-Atlantic Ridge depend on biological production exported from the sunlit epipelagic layers (Vecchione et al., 2010). In the South Atlantic, spatial and temporal patterns of production are associated with large-scale pelagic systems, defined by Longhurst (1995) as “biogeochemical provinces,” each having specific “currents, fronts, topography and recurrent features in the sea surface chlorophyll field” (Figure 2).

The equatorial sector of the MAR, including the Equatorial Fracture Zone, lies under the South Equatorial Current System where two provinces are defined as the East Tropical Atlantic and the West Tropical Atlantic (ETRA and WTRA). Phytoplankton blooms in eastern equatorial waters, which may represent important sources of energy input into the MAR region, seasonally influence these oligotrophic waters (Longhurst, 1993). During the boreal summer, the northern displacement of the Intertropical Convergence Zone (ITCZ) tends to intensify the southeast trade winds that, in turn, cause deepening of the thermocline in the WTRA and shoaling in the ETRA. Both the thermocline and the upper mixed layer become shallower in the east equatorial Atlantic where primary production is enhanced (Figure 2). In this area, Pérez et al. (2005) reported chlorophyll *a* concentrations varying between 0.66 and 1.28 mg m⁻³

(10°W) between June and December. These authors pointed out that the coastal upwelling system off Namibia and the plume produced by the Congo River runoff also contributed to such concentrations. Because all these processes principally influence areas of the Southeast Atlantic, energy input to the deep seafloor, and consequently benthic biomass distribution, may be higher toward the east (Wei et al., 2010).

The South Atlantic Gyral Province is delimited by the extension of the South Atlantic subtropical gyre and may influence a significant portion of the southern MAR that extends between latitudes 10° and 37°S. These are stable oligotrophic waters where mean productivity is less than 35 g C m⁻² yr⁻¹ (Berger, 1989). Between 30° and 60°S, however, the ridge axis crosses beneath the Subtropical and Sub-Antarctic Frontal Zones (Stramma and Peterson, 1990) as well as two productive biogeochemical provinces,

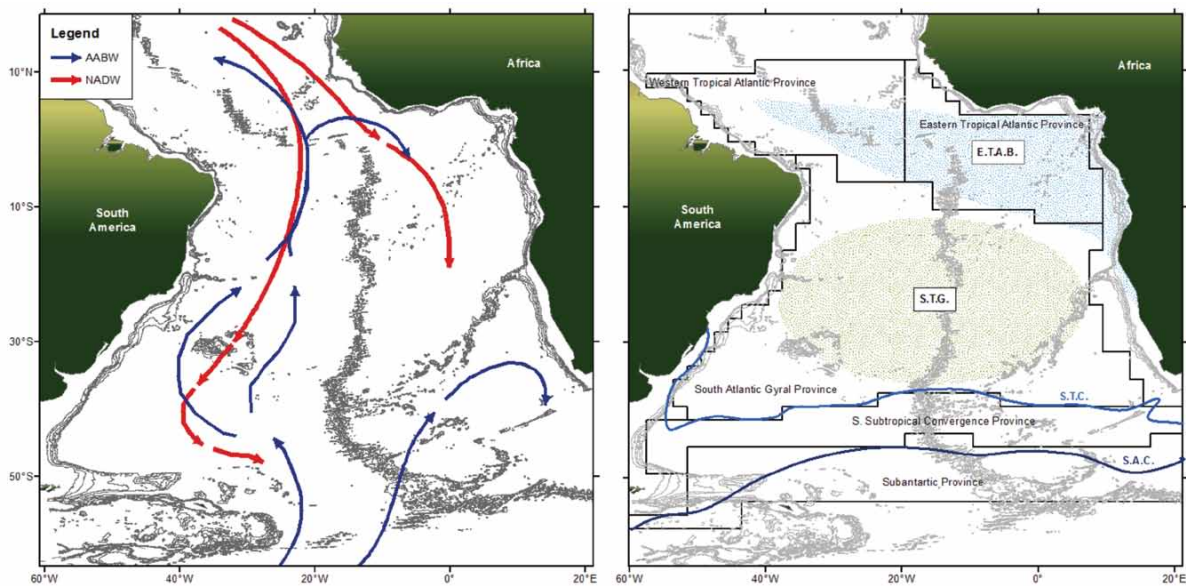


Figure 2. Schematic representation of South Atlantic Ocean patterns of deepwater circulation (left panel) and pelagic productivity and biogeochemical provinces (right panel) based on Stramma and Peterson (1990), Longhurst (1993, 1995), Murray and Reason (1999), Stephens and Marshall (2000), and Pérez et al. (2005). Red and blue arrows represent the circulation of North Atlantic Deep Water (NADW, 1,500–4,000 m deep) and Antarctic Bottom Water (AABW, > 4,000 m deep), respectively. ETAB = East Tropical Atlantic Bloom. STG = Subtropical Gyre. STC = Subtropical Convergence. SAC = Sub-Antarctic Convergence. The 1,000 and 2,000 m isobaths are displayed in the background.

the South Subtropical Convergence Province and the Sub-Antarctic Province (Longhurst, 1995). Mean surface productivity nearly doubles ($71.4 \text{ g C m}^{-2} \text{ yr}^{-1}$) and also exhibits a moderate seasonal fluctuation pattern (Moore and Abbot, 2000), the implication being that deep-water habitats (benthic and pelagic) of the southern MAR to the north and to the south of $\sim 30^\circ\text{S}$ may obtain surface food supply at low/constant and high/seasonally varying rates, respectively. Such a latitudinal pattern parallels that described in the North Atlantic (Gordon et al., 2008), although both primary production rates and seasonal fluctuations seem more important in the Northern Hemisphere (Moore and Abbot, 2000; Levin and Gooday, 2003).

Biological Information

Biological information available for South Atlantic oceanic areas compiled as background for the SA MAR-ECO project includes more than 720 records to date (for a complete reference list, see <http://www.mar-eco.no>; Table 1). Biological studies have generally focused on (a) the epipelagic environment around oceanic islands such as St. Peter and St. Paul's Rocks, Ascension, St. Helena, Tristan da Cunha group, Gough, and Bouvet (e.g., Duhamel et al., 1983; Edwards and Glass, 1987; Andrew et al., 1995; Floeter and Gasparini, 2000; Trunov, 2006), and (b) the epipelagic and mesopelagic environments over seamount chains associated with the central ridge. They were focused primarily on species occurrence and/or description, taxonomic reviews, and biogeography. Data on vertical distribution patterns, population dynamics, and ecological processes of macrofauna are scarce or absent. Pelagic and demersal fishes were

the faunal groups most widely studied, principally from collections obtained by large-scale expeditions and fishery surveys around oceanic islands and seamounts (e.g., Krefft, 1976; Pakhorukov, 1976, 1980; Shcherbachev et al., 1985, 1995; Trunov, 1981; Parin et al., 1995). Air-breathing vertebrates, such as turtles, seabirds, and mammals, have been studied by regional surveys around oceanic islands (e.g., St. Peter and St. Paul's Rocks and Ascension) and in some fishing grounds, where these animals interact with commercial fishing activities.

Records of deepwater macrofauna diversity largely concentrate on the South American and African continental margins and the Southern Ocean. The deep central South Atlantic is one of the least-studied areas of the world ocean (OBIS, 2011). Much of the data available from the South Atlantic MAR derive from large-scale expeditions conducted by North Atlantic countries since the late nineteenth century (Wüst, 1964). The first and highly significant contribution was the HMS *Challenger* Expedition between 1873 and 1876, the first worldwide effort to describe deep-sea macrofauna biodiversity (Murray, 1895). In particular, during the ship's return trip to England, in March 1876, this vessel set a straight track along the top of the ridge, from Tristan da Cunha to Ascension Island, conducting benthic dredge tows at 2,200–3,600 m depths and recording over 80 taxa (e.g., Agassiz, 1881; McIntosh, 1885; Busk, 1886). Other historical contributions were provided by the former USSR's expeditions in the second half of the twentieth century, although most published data refer to trenches and oceanic basins, and only a few samples were obtained from ridge habitats such as the Romanche Fracture

Zone (e.g., Pasternak, 1968; Parin and Andriyashev, 1972; Andriyashev et al., 1974; Malyutina, 1999, 2004).

Novel biological data have been produced from the recently discovered MAR hydrothermal vent sites $3\text{--}7^\circ$ south of the equator, the hottest reported to date, with temperatures up to 407°C (Devey et al., 2005; Koschinsky et al., 2006; German et al., 2008). A detailed taxonomic description of most groups is still unavailable in the literature, but visual assessments indicate that the southern fauna may be similar to northern MAR vent fauna; for example, the mussel *Bathymodiolus puteoserpentis*, the vesicomys clam *Abyssogena southwardae*, and the alvinocarid shrimp *Rimicaris exoculata* (German et al., 2011) are dominant in both habitats. *A. southwardae* inhabits both hydrothermal vents and cold seeps in the Atlantic, including those on the eastern and western continental margins and in the mid-ocean system (Krylova et al., 2010). *R. exoculata* is endemic to the MAR, and no genetic differences were found between individuals sampled to the north and to the south of the equator (Teixeira et al., 2012). The *Rimicaris*-associated copepod *Stygiopontius cladarus* was also observed at southern MAR vent sites (Ivanenko et al., 2007). These faunal similarities are inconsistent with the hypothesized role of equatorial fracture zones and the MAR as barriers for the dispersal of vent fauna north-south and east-west, respectively (German et al., 2011).

Further knowledge is derived from benthic diversity studies on non-chemosynthetic ecosystems off Bouvet Island and Spiess Seamount (100–600 m depths) at the southernmost end of the South Atlantic MAR system (see *Polar*

Table 1. Themes and marine environments examined by studies conducted in SA MAR-ECO target areas and other deep areas of South Atlantic.

Sunlit Levels: Studies on epipelagic or intertidal/infratidal environments.

Deep Sea: Studies on meso/bathypelagic or abyssal/bathyal environments.

All Depths: Studies on a wide range of depths or where it was not possible to identify the depth range.

Target Area/Theme	Depth Range			Totals
	Sunlit Levels	Deep Sea	All Depths	
Southern Mid-Atlantic Ridge				
Plankton	1	1	-	2
Benthos	28	21	-	49
Nekton	50	2	-	52
Various Zoological Groups	9	-	-	9
Environmental Setting				84
St. Peter and St. Paul's Rocks				
Plankton	5	-	-	5
Benthos	20	1	-	21
Nekton	42	-	-	42
Various Zoological Groups	8	-	-	8
Environmental Setting				28
Rio Grande Rise				
Nekton	4	5	2	11
Various Zoological Groups		1		1
Environmental Setting				19
Walvis Ridge				
Benthos	1	5	2	8
Nekton	5	4	2	11
Microbiology	-	1	-	1
Various Zoological Groups	-	1	-	1
Environmental Setting				14
Totals	173	42	6	366
South Atlantic				
Plankton	36	-	-	36
Benthos	4	35	1	40
Nekton	29	3	5	37
Microbiology	-	2	-	2
Various Zoological Groups	9	3	-	12
Environmental Setting				117
Totals	78	43	6	244
OTHER SOUTH ATLANTIC DEEP WATER				111
TOTAL				721

Biology, 2006:29, special issue). These studies show that the megabenthic fauna of these relatively “young” (~ 1 million years old), small (~ 800 km² above the 500 m isobath), and isolated environments can be remarkably diverse and are probably influenced by their exposure to the Antarctic Circumpolar Current, which connects them with other bathyal habitats in the Patagonian and Antarctic continental margins, sub-Antarctic islands, and the South Pacific Ocean (Arntz, 2006). A total of 217 taxa were identified by video transects, Agassiz trawls, and baited traps around Bouvet Island and on the summit of Spiess Seamount (Arntz et al., 2006; Gutt et al., 2006). Echinoderms, in particular ophiuroids (e.g., *Ophionotus victoriae* and *Ophiurolepis* sp.), were the most frequently recorded taxon around Bouvet Island. Diversity was found to be much higher than previously reported, with dramatic increases in species records of molluscs (16 to 45 species), cheilostome bryozoans (20 to 34 species), and especially amphipods (5 to 62 species) (Arntz et al., 2006; Barnes, 2006; Linse, 2006). Many of these records were new to science, including the Opisthobranchia *Tritonia dantari* (Ballesteros and Avila, 2006), the amphipod *Atyloella tribinicuspidata* (Rauschert, 2006), and the crab *Paralomis elongata* (Spiridonov et al., 2006). An analysis combining stable isotopes and feeding relationships showed that the benthic ecosystem around Bouvet Island is dominated by a variety of suspension feeders and mobile benthic predators and scavengers, particularly peracarid crustaceans (but not fishes, which were rare in the samples; Jacob et al., 2006).

Commercial and exploratory fishing have also been sources of data

on megafauna diversity and ecology on the Walvis Ridge and Rio Grande Rise seamount chains adjacent to the MAR. Catches and biological data are available from these areas for alfonso (*Berix splendens*), orange roughy (*Hoplostethus atlanticus*), southern boarfish (*Pseudopentaceros richardsoni*), cardinalfishes (*Epigonus* spp.), bluenose (*Hyperoglyphe antarctica*), Patagonian toothfish (*Dissostichus eleginoides*), and red crab (*Chaceon* spp.) (see Clark et al., 2007, and Rogers and Gianni, 2010, for reviews). Russian and Spanish fishing surveys undertaken in the Valdivia Bank (Walvis Ridge) have also provided benthic and benthopelagic diversity inventories and community structure data (McPherson, 1987; Fedorov, 1991; Fedorov and Karamyshev, 1991). Decapod crustacean fauna was studied by McPherson (1984), who described 28 species (20 benthic, eight pelagic, seven new to science), extending the geographic distribution of most of them to the Southeast Atlantic. On the same seamount, Zibrowius and Gili (1990) reported nine species of scleractinian cold-water corals, two of them (*Lophelia pertusa* and *Caryophyllia profunda*) occurring on the summit (230–250 m), one (*Enallopsammia rostrata*) on the upper flanks (511–586 m), and the remaining species (*Fungyaciathus hydra*, *Caryophyllia balaenacea*, *C. valdiviae*, *Stephanocyathus campaniformes*, *Deltocyathus conicus* and *Truncatoflabellum* sp.) on the lower flanks (882–1,230 m). The geographic distribution of most species is probably limited to the Southeast Atlantic, but two species (*L. pertusa* and *E. rostrata*) were found to be widely distributed in the North Atlantic, Indian, and Pacific Oceans, and two species (*D. conicus* and

C. profunda) were at the likely southern and northern limits of their distribution ranges, respectively. The Valdivia Bank was also shown to be a potential stepping-stone for west-east dispersion of the benthic octopod *Scaevargus unicolorrhus* (Sánchez and Alvarez, 1988) in the South Atlantic and to provide unique Atlantic outposts for fish (*Parapercis roseoviridis*, *Chironema chlorotaenia*) and crustacean (*Benthescimus investigatoris*, *Projasus parkeri*) species only known to occur in the Indian and Pacific Oceans (McPherson, 1983; Melville-Smith, 1990; Bañon et al., 2000, 2001). Investigations on diversity and benthic ecology of the Walvis Ridge seamounts have recently resumed through initiatives of countries such as Spain and Namibia, motivated by the need to identify vulnerable marine ecosystems and support the ecosystem-based fishing management measures adopted by the South Atlantic Fisheries Organization (SEAFO) (Durán Muñoz et al., 2012).

Much less information is available from the Rio Grande Rise, except for fish fauna records produced by Russian exploratory fishing. Parin et al. (1995), examining bottom-trawl collections from 1974 and 1988–1989, reported 65 species of benthic, benthopelagic, and bathypelagic fish, nearly half of them (34) belonging to the families Macrouridae, Alepocephalidae, Synphobranchidae, and Chlorophthalmidae. One species, *Gaidropsarus pakhorukovi* (Family Gadidae), was described as new to science, and nine species were reported for the first time in the Southwest Atlantic. The reported ichthyofauna was basically composed of equal shares of subtropical-temperate water species, mostly of the Southern Hemisphere, and tropical species distributed in the Atlantic and

other oceans. A high level of similarity was found between this fauna and that reported for similar depths around the Walvis and Madagascar Ridges in the Indian Ocean. The Rio Grande Rise has also been subject to current biodiversity investigation, particularly due to its potential for cobalt-rich ferromanganese crust exploration and the need to produce comprehensive “environmental baseline” studies as recommended by the International Seabed Authority (ISA, 2007; recent work of author Perez).

It is clear from the examples outlined above that existing knowledge on biodiversity of the southern MAR is fragmented and concentrated on its northern and southern extremes as well as the adjacent seamount chains. An extensive area between 10° and 50°S still remains undersampled and much less understood than the northern MAR.

Biogeography

Combining the available information on biodiversity with bathymetry and the geographical distribution of bottom temperature, salinity, oxygen, and organic matter flux, a set of benthic biogeographical provinces has been proposed (through an expert workshop) for different depth zones in the deep South Atlantic Ocean (UNESCO, 2009). The lower bathyal depth zone (800–3,500 m) includes a wide “South Atlantic” province that extends from the equator to the Antarctic Convergence and encompasses the lower continental margins of Africa and South America, isolated seamounts, and seamount chains (e.g., Rio Grande Rise, Walvis Ridge), oceanic island slopes, and the southern Mid-Atlantic Ridge. Also a “sub-Antarctic” province delimited by Antarctic and Subtropical Convergences encircles the globe and

includes the southern extreme of the South Atlantic mid-ocean ridge and seamount chains mostly south of 30°S. In the abyssal depth zone (3,500–6,500 m), four provinces are proposed in the South Atlantic, as delimited by the extent of major deep basins: Brazil, Angola-Sierra Leone, Argentine, and East Antarctic-Indian. In the hadal depth zone (> 6,500 m), a “Romanche” province is defined at the Romanche trench (a component of the Romanche Fracture Zone) in the Equatorial Atlantic. This study also includes an independent province classification for hydrothermal vent environments. A “Mid-Atlantic Ridge South” province was hypothesized, although recent biological data from vent fields south of the equator have generally supported a connection with North Atlantic vent sites (see above).

DEFINING PRIORITIES FOR UNDERSTANDING DIVERSITY PATTERNS OF THE SOUTHERN MAR

Sampling efforts within the umbrella of the CoML significantly enhanced diversity inventories in the world ocean in general (Snelgrove, 2010). Yet, they also revealed how incomplete our knowledge is on what lives in the deep environments that are particularly critical in some areas, such as the Southeast Pacific and the South Atlantic. Hence, determining faunal composition of deep-sea benthic and pelagic fauna associated with the southern MAR constitutes a major goal to be addressed by any ridge-oriented sampling program.

CoML studies also emphasize that deep-sea habitats are not isolated, but rather are both connected in horizontal space and dynamically linked to the water column (McIntyre, 2010;

Schlacher et al., 2010). For example, seamounts, ridges, canyons, and slope areas on continental margins may share similar patterns of faunal composition (e.g., Rowden et al., 2010; Menot et al., 2010), but can differ in structure and relative abundance (e.g., McClain et al., 2009). Along the North Atlantic mid-ocean ridge, there are notable latitudinal discontinuities in deep fauna composition in association with productivity gradients in the epipelagic layers (Vecchione et al., 2010). These findings highlight the importance of understanding biogeographic patterns as well as mechanisms of dispersal and connectivity whereby faunal communities in such habitats are linked across a range of spatial scales (Clark et al., 2012). Therefore, as the geological history of the South Atlantic basin and its complex interactions with deepwater circulation patterns are taken into consideration, a number of scientific questions about deep-sea biodiversity patterns of the South Atlantic arise:

- Are the faunal communities of the Mid-Atlantic Ridge and seamounts related to and part of broader deep South Atlantic environments?
- Is the southern Mid-Atlantic Ridge fauna different from that of the bathyal sectors of the South American and African continental margins?
- What are the environmental drivers of faunal composition and abundance? (e.g., is there a relationship between surface production and abundance? Do the physical ridges in the South Atlantic such as the Romanche Fracture Zone, Rio Grande Rise, and Walvis Ridge provide linkages or obstacles to faunal communities?)
- Are the MAR diversity patterns different from other ridge systems in the Southern Hemisphere?

These descriptive aspects of benthic and pelagic faunal composition denote priorities toward understanding the patterns of life in the southern MAR and define a knowledge basis with which more complex questions about deep ecosystem processes can be addressed in the future. They also define major goals for the development of a field project to: (a) describe and understand the patterns of diversity, distribution, and abundance of the organisms inhabiting the southern MAR and adjacent seamounts, and (b) explore the role of these deep-ocean features in faunal dispersal processes between the coasts of Africa and South America and among the North Atlantic, Pacific, Indian, and Southern Oceans. They would also contribute to the sustainable use of natural resources (e.g., mining, fishing, biotechnology) and conservation of unique deep-sea ecosystems, as required by both governmental and nongovernmental agencies in the South Atlantic. These include regional fisheries management organizations, principally SEAFO (Southeast Atlantic Fisheries Organization) and ICCAT (International Commission for the Conservation of Atlantic Tuna) as well as other international forums such as CBD (Convention on Biological Diversity), ISA (International Seabed Authority), and FAO (United Nations Food and Agriculture Organization).

SAMPLING SOUTHERN MAR HABITATS

In order to address the goals outlined above, a sampling strategy needs to incorporate spatial and operational concepts and technology developed for the North Atlantic MAR-ECO (Bergstad et al., 2008; Wenneck et al., 2008) while considering the area and the geological

and ecological complexities of the deep South Atlantic. Relevant to such sampling are (a) target areas for concentration of sampling activity, (b) the range of biota and ridge habitats to be sampled, (c) spatial strategy and technology to be adopted in sampling plans, and (d) sampling platforms.

Target Areas

Practical limitations of time and effort mean that sampling efforts should focus on a few representative sectors of the ridge system. Six target sectors were initially defined (Figure 1, Table 2). Two of them, St. Peter and St. Paul's Sector (SPSPS) and South Equatorial MAR (SEMS), are located on equatorial fracture zones and include an array of benthic habitats mostly formed by ridge crests and trenches. At the surface, these habitats are under the influence of the seasonal eastern equatorial Atlantic primary production blooms (Longhurst, 1993), which may be a critical source of energy to the deep habitats.

Two sectors were identified at the central axis of the MAR: (1) the Tropical MAR Sector (TMS) located beneath the core of the South Atlantic Subtropical Gyre and under the influence of an oligotrophic and stable water column, and (2) the Subtropical Convergence MAR Sector (SCMS) that crosses underneath the Subtropical Convergence and extends into the sub-Antarctic zone (Figure 1). Surface waters are highly productive in the latter sector (Moore and Abbot, 2000), and geologically, it includes an area where the MAR, Walvis Ridge, and Rio Grande Rise converge. The remaining sectors are located to the west and the east of the MAR and enclose the Rio Grande Rise (RGRS) and Walvis Ridge Sectors (WRS) (Figure 1).

The former comprises a massive flat-topped structure that rises approximately 3,000 m from the ocean basin and is bordered on the eastern side by ridges and seamounts. The Walvis Ridge is a seamount chain that extends obliquely from the Namibia-Angola continental margin to the Tristan da Cunha island group, at the MAR (Figure 1). Seamount fisheries surveys have been conducted on Walvis Ridge seamounts (Clark et al., 2007), an area managed by SEAFO (Rogers and Gianni, 2010).

Targeted Fractions of Marine Biota and Ridge Habitats

A comprehensive study on biodiversity patterns and processes of the MAR ecosystems, as proposed by the MAR-ECO project, involves macrofauna sampling in benthopelagic and benthic habitats on the flanks and summits of the ridge, as well as in the overlying pelagic zone (Bergstad and Godø, 2003). The South Atlantic MAR-ECO initiative incorporates the same focus with microbial sampling in both the water column and sediments added, not only to address a major component of deepwater communities (Snelgrove, 2010) but also to include bioprospecting as a potential economic by-product of the project. Sampling is structured as follows:

- **Microbiology:** Focused on prokaryotic (e.g., bacteria and Archaea) and eukaryotic (e.g., phytoplankton, protozooplankton, and benthic protists) microbial diversity. Capacity for producing certain enzymes such as lipases and cellulases is also included in this theme as preliminary steps toward further bioprospecting.
- **Zooplankton:** Including meso-, macro-, and megaplankton inhabiting meso- and bathypelagic layers associated

with the southern MAR summits.

- **Pelagic Nekton:** Including micronekton forming the deep sound scattering layer (e.g., larval, juvenile, and small pelagic crustaceans, fishes, and cephalopods) as well as meso- and bathypelagic fishes and cephalopods occurring over the ridge and seamount summits. It also includes large predators such as tuna, elasmobranchs, seabirds, and marine mammals that may visit the epipelagic layers in the vicinity of the MAR and seamount ridges.
- **Demersal Nekton:** Defined by the mobile megafauna, mostly benthopelagic fishes and cephalopods, that inhabit the Benthic Boundary Layer.

- **Macrobenthos:** Including large-sized epibenthic organisms inhabiting both hard and soft substrates of the ridge and seamounts. Also, sediment layers sampled over the MAR for microbiology screening will allow meiofauna to be opportunistically addressed.

Sampling Strategy and Technology

Sampling was planned with two kinds of surveys. First, large-scale surveys were conducted along the ridge axis and adjacent structures following the model used by the MAR-ECO project in the North Atlantic (Wenneck et al., 2008). In these surveys, previously defined “superstations” were placed within the target

sectors, aligned across the ridge axis, to address bathymetric gradients of benthic and benthopelagic fauna and the effects of summit vs. slope areas on the pelagic communities. Each superstation consists of several stations where different sampling gear is operated to record the range of biota and environments. Second, surveys targeted particular sectors of St. Peter and St. Paul’s Rocks, Rio Grande Rise, and Walvis Ridge. These surveys address seamount biodiversity as well as current resource management questions. For example, benthic community structure in relation to seafloor morphology and mineral composition is a specific issue in the Rio Grande Rise sector due

Table 2. Summary of the South Atlantic MAR-ECO target areas

Target Area	Lat/Long	Geological Features	Surface Oceanographic Regime	Biodiversity Knowledge	Human Threats
St. Peter and St. Paul’s Sector (SPSPS)	3°N–3°S 26°–32°W	Ridge crests and trenches; St. Peter and St. Paul’s islets	South Equatorial Current pelagic system and seasonal primary production cycles of the eastern equatorial Atlantic Ocean	Mostly epipelagic and associated with the islet coasts; Deep benthic areas unsampled	Mining interest (polymetallic sulfides and cobalt crusts)
South Equatorial MAR Sector (SEMS)	2°N–10°S 12°–22°W	Ridge; Ascension Island	South Equatorial Current pelagic system and seasonal primary production cycles of the eastern equatorial Atlantic Ocean	Mostly epipelagic and associated with the coast of Ascension Island; Some deep benthic sampling	Mining interest (polymetallic sulfides and cobalt crusts)
Tropical MAR Sector (TMS)	17°–25°S 10°–20°W	Ridge	South Atlantic Subtropical Gyre; Oligotrophic waters	Some deep benthic sampling	Mining interest (cobalt crusts)
Subtropical Convergence MAR Sector (SCMS)	36°–43°S 9°–18°W	Ridge; Point of convergence with Walvis Ridge and Rio Grande Rise; Tristan da Cunha group, and Gough Islands	Subtropical Convergence system extending into sub-Antarctic zone; Highly productive waters	Mostly epipelagic and associated with the coast of Tristan da Cunha group and Gough Islands; Some deep benthic sampling	Fished area (mostly spiny lobster)
Rio Grande Rise Sector (RGRS)	28°–36°S 28°–39°W	Seamounts (guyots)	South Atlantic Subtropical Gyre	Some benthic and benthopelagic sampling	Fished area (mostly alfonsinos); Mining interest (cobalt crusts)
Walvis Ridge Sector (WRS)	20°–33°S 5°W–10°E	Seamount chain (some are guyots)	South Atlantic Subtropical Gyre; Bounded by productive waters of the Benguela Current System and the Subtropical Convergence	Some benthic and benthopelagic sampling	Fished area (mostly orange roughy, toothfish, deepwater crabs)

to Brazil's interest in mineral exploration and the environmental assessments recommended by the ISA. Similarly, the description of benthic and benthopelagic community structure is a requirement for the definition of vulnerable marine ecosystems (e.g., FAO, 2009), critical for the development of environmentally sound fisheries management by the SEAFO convention on the Walvis Ridge seamounts. By designing sampling strategies to combine fundamental scientific objectives with those of resource use and conservation initiatives, a wider funding base might become available to enable greater sampling opportunities.

The use of modern tools to observe life in the ocean has been central to MAR-ECO, CenSeam, and other field projects within the umbrella of the CoML (Boyle, 2009; Snelgrove, 2010). In particular, the combination of acoustic and optical instruments with capture gear has increased the range of information extracted from deepwater organisms and their dynamic distribution and habitats, and allowed researchers to reach, in a noninvasive way, areas formerly inaccessible to conventional samplers (e.g., nets). Table S1 presents the array of available technology used for measuring physical, chemical, and biological properties of deep-sea habitats as well as for sampling deep pelagic, benthopelagic, and benthic biota. These technologies have permitted comprehensive analyses of diversity patterns associated with ridge habitats in the North Atlantic Ocean (see Bergstad et al., 2008, and Vecchione et al., 2010, for reviews). Together with similar and complementary approaches developed for seamount ecological studies by CenSeam (Consalvey et al., 2010; Clark et al. 2012), they define survey parameters to be replicated in the southern MAR.

Sampling Platforms

A detailed and comprehensive survey of a wide range of biota in such a complex and remote environment necessarily requires sophisticated, multitask research vessels capable of enduring long journeys in the open sea and preferably with advanced technology to operate precise and safe sampling procedures (e.g., dynamic positioning, multibeam sonars). Research vessels operating under the flag of South Atlantic coastal countries seldom have these features and are mostly designed or equipped to operate near continental margins. Therefore, important options for the SA MAR-ECO initiative include: (a) research vessels from non-South Atlantic countries that can operate in the region, and (b) research vessels that operate in other oceans but could provide sampling time along their routes (vessels of opportunity). Because the Southern Ocean is the target of concentrated research activity by several countries during the austral summer months, a range of research vessels transit through the central South Atlantic. The first field expedition in 2009 arose from such an opportunity.

THE R/V AKADEMIK IOFFE EXPEDITION TO THE SOUTHERN MAR

The first opportunity to sample the southern MAR under the framework of the SA MAR-ECO project came about through a consortium established between MAR-ECO and the P.P. Shirshov Institute of Oceanology (Russian Academy of Sciences). A multihabitat sampling plan was adapted to the twenty-ninth annual voyage of R/V *Akademik Ioffe* to the Antarctic Continent. MAR-ECO scientists from Russia, Brazil, Uruguay,

and New Zealand embarked in Gran Canaria Island (Spain) and ended field work in Cape Town (South Africa) after 34 days at sea (from October 25 to November 29, 2009).

Methods

Sampling was planned along the vessel's original route through the South Atlantic Ocean during a nine-day work period. Sampling design was based on the overall plan described above. Ten "superstations" combining sampling procedures for microbiology, zooplankton, pelagic nekton, and macrobenthos were distributed along the ship's track in order to cover the largest number of defined target sectors (Figure 1). Four superstations were located within SEMS, two at the northern and two at the southern extremes. Two superstations were placed at the TMS and four over the WRS. In each sector, superstations were organized to cover 1,000–2,000 m and 2,000–3,000 m depth strata (Table S2). There were also extra stations in intermediate areas and continuous observations of marine mammal and Sound Scattering Layer (SSL) acoustic records.

Because this was an opportunistic survey, sampling was determined by the gear and methodology adopted by the Shirshov Institute science team, the operational capabilities of the vessel, and logistic limitations of the non-Russian science team. Micronekton was sampled with a 6 m² opening and 25 m long Isaacs-Kidd Midwater Trawl (IKMT), as modified by Samyshev-Aseev (Figure 3). Planktonic and micronektonic organisms were collected in stepped oblique tows. Trawl duration at each step was 5–10 minutes, while the vertical distance between neighboring steps was 25–200 m. At each superstation, two

IKMT tows were conducted consecutively, one at depths as close as possible to the ridge and another down to the lower depth of the SSL (Kobylianski et al., 2010). The same procedure was repeated at six extra stations placed in intermediate areas along the ship's track.

Macrobenthos was sampled with 2.5 m and 1.5 m wide Sigsbee Trawls (Figure 3). Bottom contact was determined with the winch tension meter, or, in some cases, with a Benthos acoustic pinger attached to the wire ~ 300 m from the trawl. Trawls were conducted in a drifting regime; the Aquamaster 360° thruster was used when needed. Tow distance varied depending on depth and trawling conditions from 0.5 to 2 nm (0.92 to 3.7 km). All trawls were conducted after an initial acoustic survey of the topography with a single-beam echosounder. Microbiology samples were collected from the water column in Niskin bottles set on a rosette array and also from the sediment collected by benthic trawls and piston corers. Conductivity-temperature-depth (CTD) data were obtained in four 0–2,000 m casts in the vicinity of the superstations. Surface temperature and chlorophyll distribution during the survey were extracted from the SeaWiFS Satellite database (available at <http://oceancolor.gsfc.nasa.gov>; Figure 4).

Preliminary Results

The cruise track was mostly between the ITCZ and the subtropical highs (~ 30°S). Permanent thermoclines were 700–1,000 m deep, and surface thermoclines (~ 30–40 m deep) were present in the profiles from the equatorial area. SEMS, TMS, and WRS superstations were influenced by different oceanographic regimes: the seasonal eastern equatorial bloom (ETRA), the



Figure 3. South Atlantic MAR-ECO cruise, October–November 2009. (a) Isaac-Kidd Midwater Trawl. (b) Sigsbee Trawl. (c) Benthic catch at the Romanche Fracture Zone. Photos: André Barreto

oligotrophic subtropical gyre, and the border of the subtropical convergence, respectively (Figure 4). The seafloor was typically gently sloping and sediment covered on the summit (893 m) and northern slope (1,360 m) regions of the Romanche Fracture Zone where the first two benthic trawls were conducted. Two subsequent trawls were made on the ridge south of the Romanche Fracture Zone (~ 3,080 m and ~ 1,875 m), where the seafloor was rough and covered with volcanic fragments, including ferromanganese crusts. The same seafloor composition characterized the TMS ridge area sampled, where a 3,800 m deep trawl was conducted south of a transform fault. Walvis Ridge sampling was conducted on a large guyot rising ~ 4,000 m from the seafloor and oriented in a north–south direction. Three trawls were conducted on the flat summit (997–1,401 m deep), and two trawls were

made on the northern and southern base of the seamount between 4,120 and 4,703 m depths. The latter, particularly, included part of the Cape Abyssal Plain, which is covered by high concentrations of ferromanganese nodules—over a metric ton of these nodules were caught in one trawl.

In total, 63 samples were obtained during the trip: 12 macrobenthos, 26 micronekton, 19 plankton, and 15 microbiology (Table S2). Preliminary identification was conducted onboard and included 175 species of fish (~ 5,700 specimens), 50 species of cephalopods (~ 262 specimens), and at least 192 benthic invertebrate species (~ 1,980 specimens). Kobylianski et al. (2010) presented a complete list of fish species, and Table S3 provides a provisional list of the remaining taxa. The latter was summarized from a total of 1,120 records submitted to

the Ocean Biogeographic Information System (OBIS; <http://www.iobis.org>) in 2011. Species numbers will certainly increase, as a large number of specimens, particularly of the macrozooplankton, are yet to be examined by taxonomic specialists. There were 23 sightings of cetaceans along the MAR and Walvis Ridge, with seven species positively identified. Nearly 300 bacteria were isolated from deep sediment and water samples, 50 of them showing potential for biotechnological use (Odisi et al., 2012).

The first published study derived from the cruise addressed meso- and bathypelagic fish collected by the IKMT trawls. Kobylansky et al. (2010) showed that mesopelagic fish assemblages differed geographically in accordance with oceanographic regimes of the South Atlantic. However, in the lower mesopelagic and bathypelagic layers, assemblages were more geographically homogeneous. Highest and lowest diversity (and abundance) occurred in the south equatorial MAR and tropical

MAR sectors, respectively, suggesting potential influence of surface biological productivity in meso- and bathypelagic communities over the ridge (Figure 4). This influence seems to have also affected cephalopod and benthic invertebrate catches (recent work of author Perez and colleagues). Gordeeva (2011) found intraspecific genetic structure in four species of mesopelagic lanternfish (Myctophidae) and suggested that some widely distributed species may be locally isolated. This could result from circulation patterns locally induced by seamounts and ridges.

Studies conducted on the benthic crustaceans revealed one new species of caridean shrimp *Leontocaris smarensis* (Cardoso and Fransen, 2012; see photo a on page 16) collected on the Romanche Fracture Zone (902 m depth) in association with live stony (*Enallopsammia rostrata* and *Corallium cf. bayeri*) and soft (*Narella alvinae*) corals (Débora Pires, National Museum, Federal University of Rio de Janeiro, pers. comm., July 2010).

Eight species of this genus are described worldwide, all of them living on deep coralline habitats of the Southern Hemisphere (Cardoso and Fransen, 2012). In addition, three deep-sea hermit crabs of the genus *Parapagurus* were reported (Cardoso and Lemaitre, 2012): *P. abyssorum* and *P. pilosimanus* were caught at the base (3721 m) and summit (997 m) of a seamount on the Walvis Ridge (Figure 4), and *P. nudus* was caught south of the Romanche Fracture Zone (2,014–3,342 m). Known from North Atlantic deep areas, *P. abyssorum* and *P. nudus* were reported from this cruise for the first time on the South Atlantic MAR; *P. pilosimanus* was previously reported for both the North and South Atlantic. These three species were found living with anthozoans (Actiniaria) in gastropod shells and in large colonies of *Epizoanthus* sp. (see photo c on page 16).

CONCLUDING REMARKS

The Census of Marine Life program attempted to describe the known and unknown biodiversity and life patterns in the deep ocean. A large (and difficult to predict) number of species remain to be found and described, especially in poorly sampled parts of the world ocean (McIntyre, 2010). It is clear that deep-sea communities are neither isolated nor static, but dynamically connected over a range of spatial scales through dispersal processes and dynamic interactions with the pelagic ecosystem (Snelgrove, 2010).

The rough morphological and topographic features in the South Atlantic Ocean determine deepwater circulation patterns that connect it to the North Atlantic, Southern, Indian, and Pacific Oceans. We know that surface biological production patterns differ on both

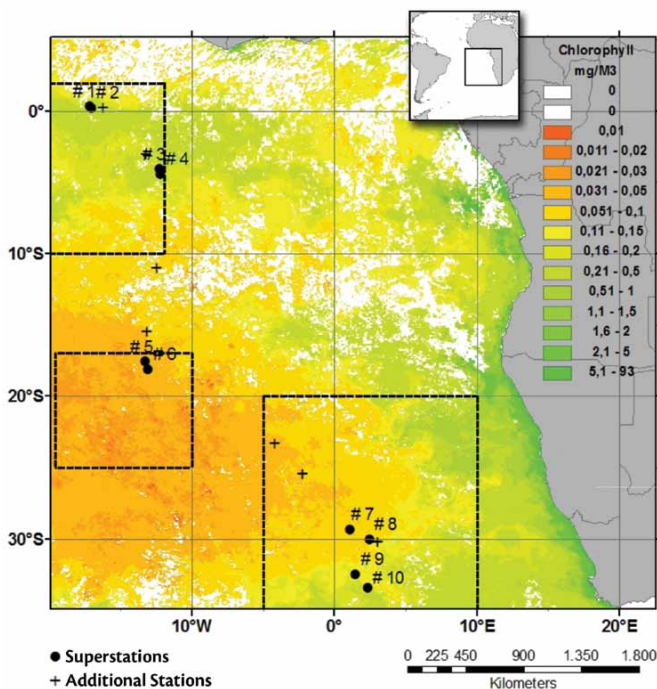


Figure 4. Chlorophyll a concentration (mg m^{-3}) during South Atlantic MAR-ECO Cruise #1_2009 (November 26–20, 2009). Numbers represent superstation positions. Crosses represent extra-station positions. Images from SeaWiFS Satellite database available at <http://oceancolor.gsfc.nasa.gov>


north-south and east-west sides of the southern MAR, but abundance and distribution patterns of the deep-sea fauna are largely unknown. The South Atlantic MAR-ECO project has been conceived to address these important unknowns. The CoML MAR-ECO and CenSeam projects have posed a set of principal questions and set high standards for optimal sampling strategies and technologies to be used for investigating seamounts and ridges. Preliminary sampling by R/V *Akademik Ioffe* (P.P. Shirshov Institute of Oceanology, Russian Academy of Sciences) in November 2009 highlighted constraints, including long distances, deep and rough topography, time, and technology, that limit sampling the southern Mid-Atlantic Ridge. However, the overwhelming number of diversity records as well as the geographic patterns of deepwater faunal distribution emerging from this first experience have increased the general motivation to continue the MAR-ECO project legacy beyond CoML and to better sample the overlooked depths of the South Atlantic Ocean.

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SUPPLEMENTAL TABLES

The supplemental tables for this article (Tables S1–S3) are available at http://www.tos.org/oceanography/archive/25-4_perez_supp.pdf. 

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