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COMPARISON BETWEEN THE SHRIMP SPECIES RICHNESS (CARIDEA AND DENDROBRANCHIATA, DECAPODA, CRUSTACEA) OF THE SOUTH AND NORTH MID ATLANTIC RIDGE

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ABSTRACT

The Mid Atlantic Ridge (MAR) is a seamount chain extending for 60.000 km, divided into south and north regions by the Equatorial Fracture which cuts across it. This latter has a maximum depth of 7,760 m and an average width of 19 km. In this study we include data from the two cruises of the international project MAR-ECO, undertaken, respectively, one on the north and the other on the south MAR. Our main objective is to compare the species richness and species composition of pelagic and benthic decapod shrimps of these two areas to observe the patterns of their latitudinal distribution along the MAR. Using rarefaction methods, we obtained interesting results: the pelagic samples curve of the northern MAR is almost an asymptote, so we concluded that we are close to the true number of pelagic shrimp species for this region. The pelagic samples curve of the southern MAR had the greatest slope, so our conclusion is that we are still far from the true number of species for this region. A comparison of species richness at 12 samples (the smallest number of samples shared by both the surveys) revealed that the pelagic species richness was greater than the demersal, and that the northern MAR contained a larger number of species than the southern.

RESUMO

A Cordilheira Meso Atlântica (CMA) é uma cadeia de montes submersos com 60.000 km, dividida em região norte e sul, separadas pela Fratura Equatorial, que corta transversalmente a CMA. A Fratura Equatorial possui profundidade máxima de 7.760 m e largura média de 19 km. Incluímos aqui dados de dois cruzeiros do projeto internacional MAR-ECO, um no norte e um no sul da CMA. Nosso principal objetivo é comparar a riqueza de espécies e a composição específica de camarões decápodes, pelágicos e bentônicos, dessas duas áreas para observar padrões de distribuição latitudinal ao longo da CMA. Usando métodos de rarefação, obtivemos resultados interessantes: a curva de amostras pelágicas da CMA norte encontra-se perto de uma assíntota, o que nos levou a concluir estarmos próximos ao número verdadeiro de espécies de camarões pelágicos nesta região. Por sua vez, a curva de amostras pelágicas da CMA sul possui uma inclinação muito forte, o que nos permitiu concluir que nessa região ainda estamos longe do número verdadeiro de espécies. Uma comparação da riqueza de espécies em 12 amostras (menor número de amostras compartilhado pelos dois cruzeiros) revelou que a riqueza de espécies pelágicas é maior do que a demersal, e que a CMA norte contém uma riqueza maior que a região ao sul.

Descriptors: Mid Atlantic Ridge, Decapoda, Caridea, Dendrobranchiata, Species richness, Specific composition, Distributional patterns.
Descritores: Cordilheira Meso-Atlântica, Decapoda, Caridea, Dendrobranchiata, Riqueza de espécies, Composição específica, Padrões de distribuição.

INTRODUCTION

The Mid Atlantic Ridge (MAR) is a topographically complex seamount chain that rises from 4000 m depth to peaks of just 500 m below the sea's surface. The ridge is 100-200 km wide and 60,000 km long. Seamounts are considered biologically distinctive habitats, mainly due to the formation of eddies of water associated with the upwelling of nutrient rich waters, leading to increased productivity. Food supplies in the open-ocean are restricted, so seamounts and mid-ocean ridges may serve as important habitats, feeding grounds and sites of reproduction for many deep-sea species (ROGERS, 1994).

Especially complex is the Equatorial Fracture (or Romanche Fracture) that extends transversally to the Mid Atlantic Ridge, from 2°N to 2°S and from 16°W to 20°W. The fracture has a maximum depth of 7,760 m, is 400 km long and has an average width of 19 km (DEMIDOV et al., 2006). It is a pathway for the Atlantic deep water masses that flow from west to east (FERRON et al., 1998). The Equatorial Fracture Zone is deep enough to allow significant eastward flows of Antarctic Bottom Water (ABW) from the Brazil Basin to the Sierra Leone and Guinea Abyssal Plains. After passing through the Equatorial Fracture Zone, the Antarctic Bottom Water spreads only to the southeastern and equatorial parts of the Atlantic. While flowing through the Equatorial Fracture Zone, the bottom-water properties are strongly modified due to intense vertical mixing (FERRON et al., 1998; DEMIDOV et al., 2006).

Given the region's great complexity, it may be expected to shelter a diverse deep-sea fauna. This expectation has prompted recent biological investigations on the southern Mid Atlantic Ridge, including the Equatorial Fracture area, within the framework of the international South Atlantic MAR-ECO (SA MAR-ECO) project. This project is a spin-off of the MAR-ECO project (Patterns and Processes of the Ecosystems of the Northern Mid Atlantic Ridge), an element of the Census of Marine Life. The aim of MAR-ECO and SA MAR-ECO is to enhance our understanding of the occurrence, distribution and ecology of animals and animal communities along the MAR.

The aim of this study is to compare the shrimp fauna of the Northern and Southern MAR, and evaluate the effect of the Equatorial Fracture as a barrier.

The shrimp species analyzed herein are included in two crustacean groups: Suborder Dendrobranchiata, that is a relatively small and uniform decapod group with about 533 species (DE GRAVE; FRANSEN, 2011), all shrimp-like; and the Infraorder Caridea that is a highly diversified group among Decapoda, with about 3,438 species (DE GRAVE; FRANSEN, 2011). Many of its members are shrimp-like, but many variations of this basic shape can be observed to occupy a wide range of aquatic niches. In both groups most of the species are marine, pelagic or benthic, occurring from the coastal shore to the deep sea (BAUER, 2004; FARFANTE; KENSLEY, 1997).

The species richness and species composition of pelagic and benthic decapod shrimps from the northern and southern MAR are compared in order to observe the patterns existing in the latitudinal distribution of decapod shrimps along the MAR.

Material and Methods

We include here data from two cruises. The material from the Northern MAR was collected during the 2004 MAR-ECO expedition (from June 5 to August 5) on the R/V G.O. Sars, between the Azores and Iceland (59º-41ºN). A total of 17 locations were sampled with bottom trawls (980 – 3460 m depth) and 39 locations with pelagic trawls (0-2800 m depth) (Fig. 1). The bottom shrimp trawl was a Campelen 1800. Three different mid-water trawls were used for the pelagic sampling: a large “Egersund trawl”, the “Åkra trawl” and the Macrozooplankton trawl. The study area on the northern MAR included three main domains defined by the distribution of water masses: the northern domain infuenced by the subpolar gyre; the SubPolar front, crossing the ridge at the Charlie Gibbs Fracture Zone; and the southern domain influenced by the subtropical gyre. See Wenneck et al. (2008) for additional sampling details, and Søiland et al. (2008) for hydrographic description.

In 2009 (from October 25 to November 29) the first oceanographic cruise of SA MAR-ECO was undertaken on the R/V Akademik Ioffe, between the latitudes 00º34´S and 33º40´S. Ten Superstations were defined, distributed in three main domains stated in terms of the occurrence of the water masses: four in the South Equatorial MAR Sector (SEMS), influenced by the eastward inflow of the North Atlantic deep Water through the Equatorial Fracture (at depths of 1500-4000 m) and by the Antarctic Bottom Water's eastward inflow (at depths of more than 4000 m). Two Superstations in the Tropical MAR Sector (TMS) influenced mainly by the North Atlantic deep Water's southward inflow, that is restricted by the Walvis Ridge and fills the Angola Basin almost exclusively. Finally, four Superstations in the Walvis Ridge Sector (WRS) influenced by the North Atlantic deep Water's southward inflow in the north (Angola Basin) and by the Antarctic Bottom Water's northward inflow in the south (Fig. 2). See Huang and Jin (2002) for hydrographic description. A total of 12 benthic sampling events, using a Sigsbee trawl, were conducted, five in the SEMS, two in the TMS and five in the WRS. During the same cruise 26 pelagic sampling events, using a Isaac-Kidd Midwater Trawl (IKMT) were undertaken, nine in the SEMS, five in the TMS and 12 in the WRS. The sampling events occurred at depths of from 902 to 4715 m.

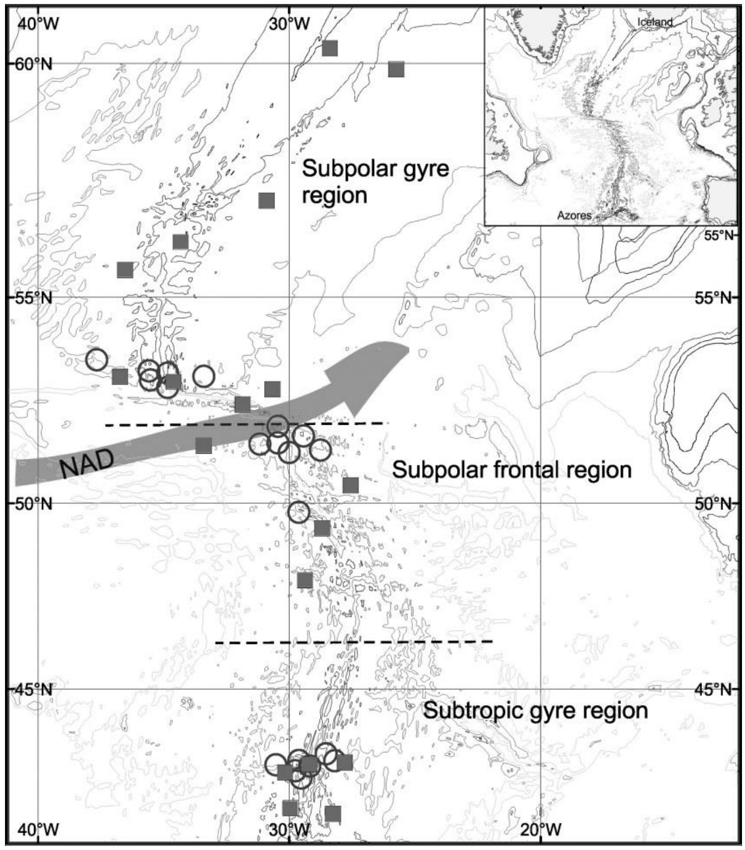

Fig. 1. Sample areas of North MAR. Pelagic (squares) and benthic (circles) samples.

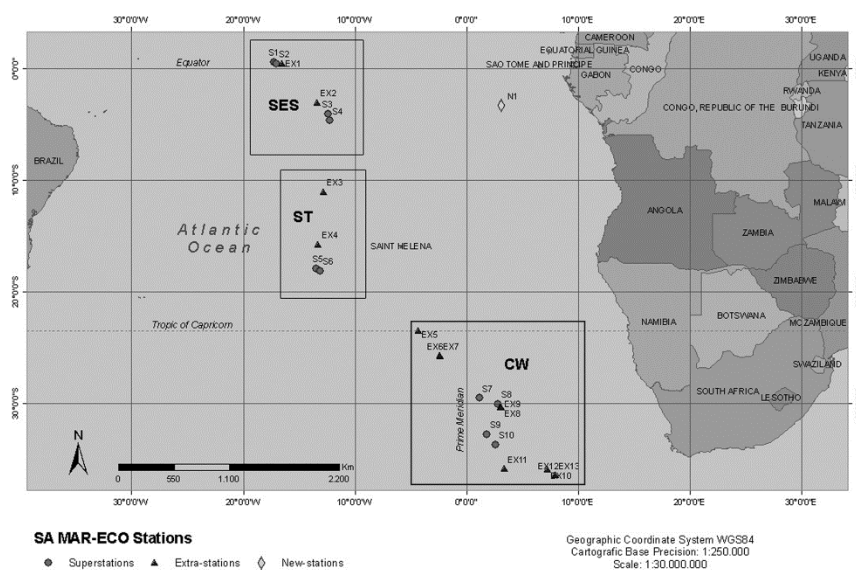

Fig. 2. Sample areas of South MAR. Only superstations (circles) were used herein.

The specimens were fixed in 70% ethanol and identified to species level in the laboratory. The decapod material from the SA MAR-ECO expedition was deposited at the Crustacea collection of the Museu Nacional/Universidade Federal do Rio de Janeiro (MNRJ), Brazil; and the material from the R/V G.O. Sars expedition on the northern MAR was deposited at the Natural History Collections, University of Bergen, Norway.

In order to compare species richness between surveys, to estimate the total richness, and to evaluate the success of the sampling, the software EstimateS 8.0 (COLWELL, 2009) was used. The data analyzed were the total number of species found per trawl haul. The pattern of species accumulation (rarefaction) was examined using 500 randomizations to generate sample-based rarefaction curves (using the Mau Tao estimates of Sobs; COLWELL, 2009). Rarefaction requires some assumptions such as sufficient sampling and comparative sampling methods. As sampling methods and sampling effort differed between surveys, four separate curves were made, one for each sampling mode (pelagic or demersal) and region (northern or southern MAR).

Rarefaction curves allow comparison of species richness among surveys with different sampling efforts. To compare species richness, we truncated sampling effort to the smallest number of samples shared by all surveys. Estimates of the total species richness were calculated using the classic Chao 2 estimator. Chao 2 was chosen as nonparametric estimator as it performs well on small samples (COLWELL, 2009; COLWELL; CODDINGTON, 1994) and has been considered the least biased estimator dealing with total species richness (WALTHER; MOORE, 2005). The data sets were randomized 1000 times for estimation of log-linear 95% confidence intervals.

Results

A total of 65 shrimp species (Table 1), 38 being Caridea and 27 Dendrobranchiata, were observed in the North MAR, while 50 species, 25 Caridea and 25 Dendrobranchiata, were observed in the South (Fig. 3).

Of the 12 Caridean and Dendrobranchiata families sampled, 10 were common to the two hemispheres. Despite this high level of homogeneity between South and North MAR at family level, in terms of species composition the two MAR hemispheres seem to be distinct, only 28 (32 %) of the 87 species sampled being shared (Table 1).

Only two new species were described for the MAR, one on the Northern MAR, the benthesicymid *Altelatipes falkenhaugae* Crosnier and Vereshchaka, 2008 and one on the southern MAR, the hippolytid *Leontocaris smarensis* Cardoso and Fransen, 2012 (CROSNIER; VERESCHAKA, 2008; CARDOSO; FRANSEN, 2012). As these two species have only recently been described, it is not possible to affirm that they are endemic to the MAR, thus sustaining the idea of a low level of endemism for this region.

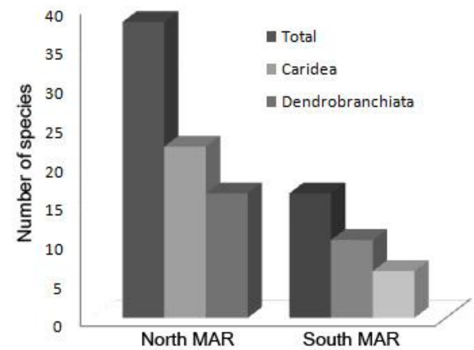

Fig. 3. Number of decapods shrimps species.

More than half of the species sampled (48 spp.; 57.8%) (considering here only identifications at species level = 83 spp.) present widespread distribution, occurring in more than one ocean; 22 of them in the Atlantic and Indian Oceans (including the Indo-Pacific region) and 26 reaching also the Pacific Ocean (thus being considered cosmopolitan) (Table 1). In contrast, 35 spp. (42.1%) presented a restricted distribution, occurring only in the Atlantic Ocean (Table 1).

Interestingly, in both regions of the MAR, the deep sea pelagic family Oplophoridae was the most sampled group (Table 1, Figure 4). A total of 32 oplophorid species were sampled, 12 of which were shared between the two MAR hemispheres (Table 1). The greater part of the oplophorid species dealt with here were sampled only during pelagic trawls (88% of the species sampled on the southern MAR and 80% on the northern MAR).

As regards the family Pasiphaeidae, a small number of species was sampled (Table 1, Fig. 4), but mainly in pelagic trawls (Table 1), thus confirming its pelagic habit. Six Pasiphaeidae species were sampled, all occurring on the northern MAR, only one being shared with the southern MAR (Table 1).

Considering the benthic family Nematocarcinidae, two species were sampled in each MAR hemisphere, but none was shared between them (Table 1). Two nematocarcinid species were sampled in demersal trawls on the southern MAR, and two species were also found by pelagic trawls on the northern MAR (Table 1).

Table 1. Number of species by family sampled with the distinct sampling methods (DT - demersal trawls; PT - pelagic trawls; DPT - demersal and pelagic trawls).

Classification	Occurrence at MAR	Distribution	Sampling method
Suborder Dendrobranchiata			
Family Aristeidae			
Aristeus antennatus	North MAR	widespread	DT
Austropenaeus nitidus	South MAR	restricted	DT
Hepomadus tener	North MAR	widespread	DT
Plesiopenaeus armatus	North MAR	widespread	DT
Family Benthesicymidae			
Altelatipes falkenhaugae	North MAR	restricted	PT
Bentheogennema intermedia	North and South MAR	widespread	PT
Bentheogennema sp.	South MAR	-	PT
Benthesicymus brasiliensis	North MAR	restricted	DT
Benthesicymus hjorti	North MAR	restricted	DT
Gennadas brevirostris	South MAR	widespread	PT
Gennadas capensis	South MAR	widespread	PT
Gennadas elegans	North MAR	restricted	DPT
Gennadas gilchristi	South MAR	restricted	DPT
Gennadas parvus	South MAR	widespread	PT
Gennadas scutatus	South MAR	widespread	DPT
Gennadas talismani	South MAR	restricted	DPT
Gennadas tinayrei	North and South MAR	widespread	PT
Gennadas valens	North and South MAR	restricted	DPT
Family Penaeidae			
Funchalia villosa	North and South MAR	widespread	PT
Funchalia woodwardi	North and South MAR	widespread	PT
Family Sergestidae			
Deosergestes corniculum	North and South MAR	restricted	DPT
Deosergestes henseni	North and South MAR	restricted	DPT
Parasergestes armatus	North and South MAR	widespread	PT
Petalidium sp.	South MAR	-	PT
Sergestes arcticus	North MAR	widespread	DPT
Sergestes atlanticus	North and South MAR	widespread	DPT
Sergestes pectinatus	North MAR	widespread	PT
Sergestes sargassi	North MAR	widespread	PT
Sergestes vigilax	North MAR	widespread	PT
Sergia creber	South MAR	widespread	PT
Sergia grandis	North and South MAR	restricted	DPT
Sergia japonica	North MAR	widespread	DPT
Sergia laminatus	South MAR	restricted	PT
Sergia robusta	North and South MAR	restricted	DPT
Sergia splendens	North and South MAR	widespread	PT
Sergia tenuiremis	North and South MAR	restricted	DPT
Family Solenoceridae			
Hymenopenaeus chacei	North MAR	restricted	DT
Hymenopenaeus laevis	North and South MAR	widespread	DT
Suborder Pleocyemata			
Infraorder caridea			
Family Crangonidae			
Sabinea sp.	North MAR	-	DT
Parapontophilus abyssi	South MAR	widespread	DT
Parapontophilus longirostris	South MAR	widespread	DT
Family Hippolytidae			
Leontocaris smarensis	South MAR	restricted	DT

Table 1. Continuation.

Family Glyphocrangonidae			
Glyphocrangon longirostris	North MAR	restricted	DT
Glyphocrangon sculpta	North MAR	restricted	DT
Family Nematocarcinidae			
Nematocarcinus agassizii	South MAR	restricted	DT
Nematocarcinus ensifer	North MAR	widespread	PT
Nematocarcinus exilis	North MAR	restricted	DPT
Nematocarcinus faxoni	South MAR	restricted	DT
Family Oplophoridae			
Acanthephyra acanthitelsonis	South MAR	restricted	DPT
Acanthephyra acutifrons	North MAR	widespread	DT
Acanthephyra brevirostris	North MAR	widespread	DPT
Acanthephyra eximia	North MAR	widespread	DT
Acanthephyra curtirostris	North and South MAR	widespread	PT
Acanthephyra gracilipes	North MAR	restricted	DPT
Acanthephyra microphthalma	North MAR	restricted	DT
Acanthephyra pelagica	North and South MAR	widespread	DPT
Acanthephyra purpurea	North MAR	restricted	DPT
Acanthephyra quadrispinosa	South MAR	restricted	DPT
Acanthephyra stylorostratis	South MAR	widespread	PT
Ephyrina benedicti	North and South MAR	widespread	PT
Ephyrina bifida	North MAR	restricted	DPT
Ephyrina figueirai	North MAR	restricted	PT
Ephyrina ombango	North MAR	widespread	PT
Heterogenys monnioti	South MAR	restricted	DT
Hymenodora sp.	North MAR	-	DT
Hymenodora gracilis	South MAR	widespread	DPT
Kemphyra corallina	North and South MAR	restricted	DT
Meningodora compsa	North MAR	restricted	PT
Meningodora miccyla	North MAR	widespread	PT
Meningodora mollis	North MAR	widespread	DPT
Meningodora vesca	North and South MAR	widespread	DPT
Notostomus elegans	North and South MAR	widespread	PT
Notostomus gibbosus	North and South MAR	widespread	DPT
Notostomus robustus	North and South MAR	restricted	PT
Oplophorus novazeelandiae	South MAR	widespread	PT
Oplophorus spinosus	North and South MAR	widespread	DPT
Systellaspis braueri	North MAR	restricted	DPT
Systellaspis cristata	North and South MAR	widespread	PT
Systellaspis debilis	North and South MAR	widespread	DPT
Systellaspis pellucida	North and South MAR	widespread	DPT
Family Pandalidae			
Stylopandalus richardii	North and South MAR	widespread	PT
Family Pasiphaeidae			
Eupasiphae gilesi	North MAR	widespread	PT
Parapasiphae sulcatifrons	North and South MAR	widespread	DPT
Pasiphaea ecarina	North MAR	restricted	DT
Pasiphaea hoplocera	North MAR	widespread	PT
Pasiphaea multidentata	North MAR	restricted	DPT
Pasiphaea tarda	North MAR	widespread	PT

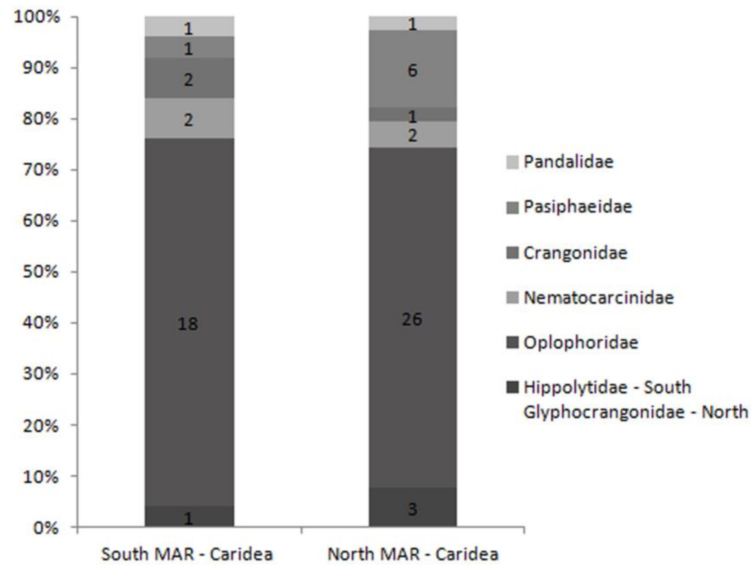

Fig. 4. Caridean families composition (number of species are inside the graph).

Only one species of Pandalidae was sampled in the present study, occurring on both the southern and northern MAR (Table 1): *Stylopandalus richardii* (Coutiére, 1905) that was only sampled during pelagic trawls (Table 1).

Crangonidae and Glyphocrangonidae are benthic and all the species sampled on the southern and northern MAR were caught by demersal trawls (Table 1). No crangonid species were shared between South and North MAR (Table 1) and the family Glyphocrangonidae was sampled only on the northern MAR (Table 1). The only Caridean family sampled exclusively on the South MAR was Hippolytidae (Table 1) - a highly diverse group with pelagic and benthic members occurring in shallow and deep waters. The hippolytid species sampled on the South MAR is benthic (sampled during demersal trawls), typical of deep sea coralline habitats.

Regarding the Dendrobranchiata fauna, five families were sampled in both MAR hemispheres (Fig. 5). On the southern MAR most benthesicymid species are members of the pelagic genus *Gennadas* (8 species), all of them sampled during pelagic trawls (Table 1). On the northern MAR, members of the benthic genus *Benthesicymus* were sampled in demersal trawls while species of the *Gennadas* and other genera were sampled in pelagic trawls (Table 1). Of the 14 benthesicymid species sampled during this study, only three were shared between the two hemispheres (Table 1).

The Sergestidae, represented here by the deep sea, pelagic genera *Deosergestes*, *Parasergestes*, *Sergestes* and *Sergia*, occurred in both MAR hemispheres, but were more diverse on the northern MAR (Table 1, Figure 5). On the southern MAR all but one species were sampled in pelagic trawls, thus confirming its habit. The exception was one juvenile specimen of *Sergestes atlanticus* sampled by demersal trawl. On the northern MAR about half of the species were sampled only by pelagic trawls and the others by both pelagic and demersal trawls (Table 1). Of the 16 species sampled, 8 were shared between the two MAR hemispheres (Table, 1).

Members of Aristeidae were only caught in demersal trawls in this study (Table 1) and no species was shared between the southern and northern MAR. In this study two species of the solenocerid genus *Hymenopenaeus* were sampled during demersal trawls, one of them was shared between the two MAR hemispheres, the cosmopolitan *Hymenopenaeus laevis* (Bate, 1881) (Table 1).

It is interesting to observe that only two species sampled during this study with demersal trawls were shared between the southern and northern MAR (Table 1). The great majority of species shared between the two MAR hemispheres were sampled during pelagic trawls (26 spp. / 92.8%) and present widespread distribution (20 spp. / 71.4%) (Table 1). Species sampled only with demersal trawls (23 spp.), that probably present a predominantly benthic habit, are usually of restricted distribution (13 spp. / 56.5%) (Table 1), while species sampled during pelagic trawls (64 spp.) usually present widespread distribution (42 spp. / 65.6%) (Table 1).

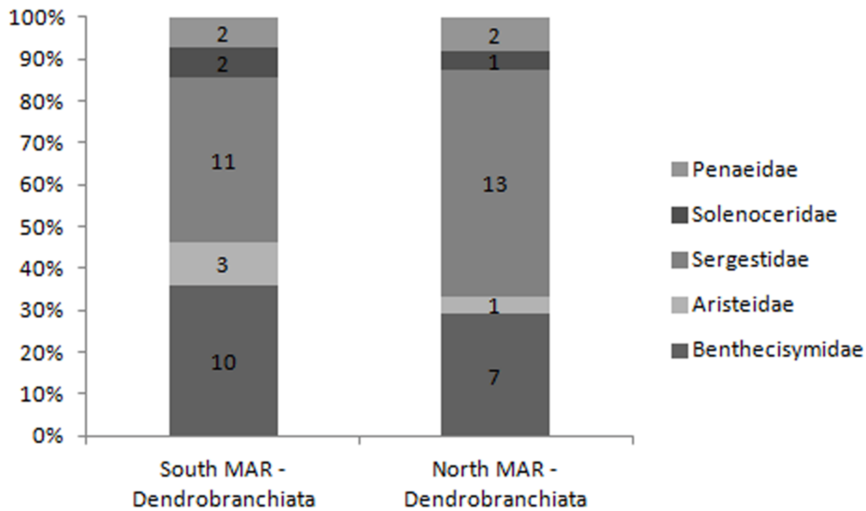

Fig. 5. Dendrobranchiata families composition (number of species are inside the graph).

The rate of species accumulation differed between sampling modes and regions (Fig. 6). Pelagic samples from the northern MAR were close to an asymptote (Fig. 6), indicating that we are close to the true number of pelagic shrimp species for this region. Pelagic samples from the southern MAR presented the greatest slope, suggesting that in this region we are still far from the true number of species (Fig. 6).

Estimated species richness (Chao-2 estimator) in the pelagic trawls on the northern MAR is 53 (mean of 1,000 resampling runs, 95% C.I. 51 – 68; Figure 7, Table 2), which is very close to the observed number of species (50).

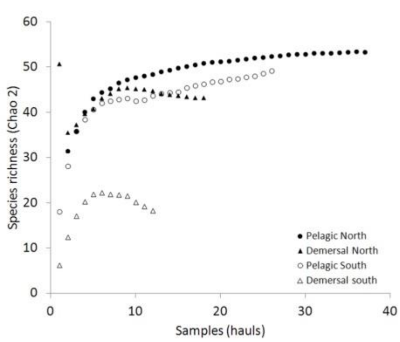

Fig. 6. Species rarefaction curves (Mau Tao) for pelagic trawls and demersal trawls in northern and southern MAR, based on 500 replicate randomizations.

Neither the estimated total species richness in pelagic trawls on the southern MAR, nor the demersal trawls in either region reached an asymptote (Fig. 6) and they demonstrated a wide 95% CI (Table 2), suggesting that the estimates of total community diversity would likely be higher with greater sampling (Fig. 7).

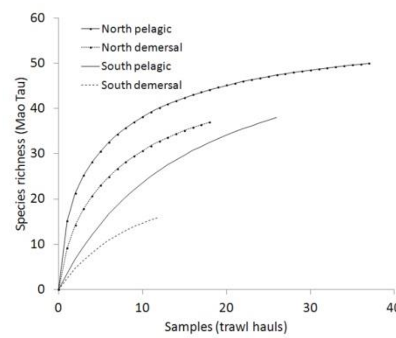

Fig. 7. Classic Chao-2 estimates of total species richness (1000 randomizations).

Table 2. Decapods species richness on northern and southern MAR, determined by pelagic and demersal sampling.

	Observed species richness (S_{obs})	Estimated total species richness (Classic Chao 2)	95 % CI (1000 replicates)
Pelagic North	50	53	51-68
Demersal North	37	43	39-93
Pelagic South	38	49	41-76
Demersal South	16	18	16-30

Summing up the estimates for both the pelagic and demersal trawls within each region, we arrived at a greater total Chao-2 estimate of diversity than with the total data set, reflecting an overlap in pelagic and demersal species associations (Table 2).

A comparison of species richness at 12 samples (smallest number of samples shared by all surveys) revealed that the pelagic species richness was greater than the demersal, and that the northern MAR contained a larger number of species than the southern.

Discussion

Considering that only 32 % of the species sampled were shared by both MAR hemispheres we consider that the Equatorial Fracture zone may be acting as a biogeographical barrier for benthic decapod shrimps on the MAR. For pelagic shrimps the eastward flow of ABW through the EF strongly modifies water properties due to intense vertical mixing (FERRON et al., 1998; DEMIDOV et al., 2006) and also may be acting as a biogeographical barrier.

The high level of endemism attributed by Rogers (2004) to seamounts in general, and also expected for the MAR, has not here been confirmed, as only two new species were described for the region.

For the great majority of species the sample method used in this survey confirmed the life habit predominantly benthic or pelagic known to the literature (CROSNIER, 1978; CROSNIER; FOREST, 1973; CHACE, 1986; BAUER, 2004). Some cases, where the sample method used here reveals a different life habit for a family from that already known (Sergestidae may be taken as an example), can be explained by a behavior pattern relatively common to many deep sea shrimps, i.e., vertical migration: many of them live in the mud or soft sand during the daytime and perform vertical migrations up into the water column during the night to feed.

It is important to note that the data analyzed here are but a small piece in the huge puzzle of the distributional patterns existing on the MAR. The results may, even so, be used as a starting point for thinking about the biogeographical barriers and connections between the Southern and Northern MAR.

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