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The deep-sea zooplankton of the North, Central, and South Atlantic: Biomass, abundance, diversity

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ABSTRACT

Ocean-scale surveys of vertical distribution of the zooplankton from the surface to the bathypelagic zone along transects are quite rare in the North Atlantic and absent in the Equatorial and South Atlantic. We present the first deep-sea quantitative survey of the zooplankton in the Equatorial and South Atlantic, analyze the interaction between environment (depth, water masses, surface productivity) and zooplankton abundance and biomass, and assess the biodiversity and role of copepods in various deep strata. Samples were taken at 20 sites along a submeridional transect between 40°N and 30°S at four discrete depth strata: epi- meso-, upper- and lower- bathypelagic. A closing Bogorov–Rass plankton net (1 m^2 opening, 500 μm mesh size, towed at a speed of 1 m s^{-1}) was used and three major plankton groups were defined: non-gelatinous mesozooplankton (mainly copepods and chaetognaths; 1–30 mm length), gelatinous mesozooplankton (mainly siphonophorans, medudae and salps; individual or zooid; 1–30 mm length) and macroplankton (mainly shrimps; over 30 mm length). Over 300 plankton taxa were identified, among which 243 belonged to Copepoda. Two-dimensional distribution (latitude versus depth zone) of major group biomass, total copepod abundance, and abundance of dominant species is presented as well as distribution of biodiversity parameters (number of species, Shannon and 'dominance' indices). Biomass and abundance of all major groups were depth-dependent. The number of taxa (*N*) was depended on surface productivity, diversity of the communities was strongly linked to depth, whilst 'evenness' was independant upon both variables. Each of depth strata was inhabited by distinct copepod assemblages, which significantly differed from each other. The paper is concluded with brief descriptions of the deep Atlantic plankton communities from studied strata.

1. Introduction

The vertical distribution of the deep plankton is correlated with the flux of organic matter from the euphotic surface layer, which is a function of the surface production and consumption of organic particles in deep waters; the zooplankton abundance and biomass in the deep sea decrease with depth and the rate of this decrease varies in different geographical areas (e.g., Vinogradov, 1970; Wishner, 1980; Angel and Baker, 1982; Scotto di Carlo et al., 1984; Roe, 1988; Weikert and Koppelmann, 1996). The vertical distribution of the open ocean plankton in the Atlantic remains insufficiently explored, especially in the Southern Anticyclonic gyre. Distribution and diversity of the zooplankton in the upper water layers of the Atlantic Ocean has been intensively studied during last two decades (Hays et al., 2001; Gallienne et al., 2001; Beaugrand et al., 2001, 2002; Beaugrand and Ibañez, 2002). Studies of the deep-sea plankton are much rarer and are usually local (Gislason, 2003; Vinogradov et al., 1997, 1999, 2000, 1995; Vereshchaka and Vinogradov, 1999). Surveys of large-scale vertical distribution of the zooplankton from the surface to the bathypelagic zone along transects are rare and cover manly the North Atlantic (e.g., Longhurst and Williams, 1979; Gallienne et al., 2001; Gaard et al., 2008). Vertical distribution of the Mediterranean zooplankton, which is of Atlantic origin, has also been analyzed, also reaching the bathypelagic zone (e.g., Pérès, 1958; Scotto di Carlo et al.,1984; Siokou-Frangou et al., 1997; Siokou et al., 2013). Large-scale quantitative deep-sea zooplankton surveys in vast areas of the Equatorial and South Atlantic are absent.

In the open ocean, zooplankton distribution is strongly affected by the presence of land (islands, continents, seamounts) and the sea-floor (Vereshchaka, 1995). The presence of islands and seamounts is responsible for modifications in the hydrodynamics of the environments where these features occur, generating a diversity of physical and ecological processes, influencing the structure of local communities (Boehlert and Genin, 1987). These processes are resulted in the formation of the benthopelagic

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contact zone dominated by the specific benthopelagic fauna and recorded at a distance of hundreds of meter above the continental slopes (e.g., in the Mediterranean: Cartes et al., 2010), and seamounts of the Atlantic and Indian Oceans (Vereshchaka, 1995; Vereshchaka and Vinogradov, 1999). In the vicinities of land, around seamounts and islands, we observe both the increase of the benthopelagic biomass and the decrease of the proper pelagic biomass in the Pacific (Vereshchaka, 1990a), in the Indian (Vereshchaka, 1990b, 1994), and in the Atlantic Oceans (Melo et al., 2014). In order to minimize the land and sea-floor effects, any survey of the pelagic zooplankton in the open ocean should be made some distance away from the bottom in the vertical direction (at least hundreds of meter) and from the land in the horizontal direction (at least tens of kilometer).

A large-scale effect of the Mid-Atlantic Ridge, which is major subsurface mountain-chain bisecting the ocean latitudinally, remains unclear. The recent ECOMAR project was addressed to the null hypothesis that the presence of the Mid-Atlantic Ridge had no impact on overlying biology (Priede et al., 2013). Detailed studies at the Mid-Atlantic Ridge and Charlie–Gibbs Fracture Zone have shown that zooplankton and micronekton biovolume differed longitudinally, not latitudinally (Cox et al., 2013) and the copepod community structure depended rather on water masses than on the position relative to the Ridge (Gaard et al., 2008). These data, however, were obtained in the frontal areas where latitudinal gradients are more prominent than in the zones with lower north-south hydrological gradients. The effect of the Mid-Atlantic Ridge may be more prominent between the North and the South Subpolar fronts and needs a future research.

The pelagic area between the North and South Subpolar fronts includes oligotrophic North and South Anticyclonic Gyres and the more productive Equatorial area. (Fig. 1). Fine vertical hydrological structure is variable but four principal layers may be defined within the upper 3000 m, including the upper mixed, the main thermocline, the Antarctic Intermediate Waters, and the North Atlantic Deep Waters (Fig. 2).

In this paper, we explore the biodiversity and vertical distribution of the net zooplankton, with an emphasis on copepods, along a submeridional transect between 30°S and 42°N (Fig. 1). The objectives of our studies are: (1) deep-sea quantitative survey of the zooplankton in the Equatorial and South Atlantic, (2) understanding the interaction between environment (depth/water masses, surface productivity) and zooplankton abundance and biomass, and (3) assess the biodiversity and role of copepods in various deep strata. We analyze the role of such composite environmental factors as water masses, which occupy different depth strata. In fact, each of depth ranges / water masses is characterized by a complex of abiotic variables (e.g., temperature, salinity, oxygen concentration, pressure, etc.), which may be masked by the dominating depth gradient. Here we describe distribution of the deep sea plankton as a function of surface production and depth/water mass factor and do not pretend to evaluate contribution of partitioned abiotic variables.

2. Methods

Samples were taken in October–November 2012 (36th cruise of the R/V 'Akademik Sergey Vavilov') and in September–October 2013 (37th cruise of the R/V 'Akademik Sergey Vavilov') (Fig. 1, Table 1). The sampling periods were 24 October–10 November 2012 (36th cruise) and 23 September–21 October 2012 (37th cruise). The transect crossed two zones of increased productivity: the Equatorial Divergence (ED) between 5°S and 5°N and the vicinity of the Canary Upwelling (CU) between 15°N and 25°N. Samples were taken between one hour after sunset and one hour before sunrise in order to make a unified nighttime picture of the vertical distribution of animals. This method was adopted to minimize the effects of diel vertical migrations. We sampled four discrete depth strata: the epipelagic zone (0–200 m), the main pycnocline within the mesopelagic zone (from 200 m to the depth of the 7 °C isotherm, within 550–800 m), the upper bathypelagic zone (from the lower boundary of the mesopelagic zone to 1500 m, Antarctic Intermediate Waters), and the lower bathypelagic zone (1500–3000 m, North Atlantic Deep Waters) (Fig. 2). We used a closing BR plankton net (1 m^2 opening, 500 μm mesh size, towed at a speed of 1 m s^{-1}), which was proven to successfully sample deep-sea plankton (Vinogradov et al., 1996, 2000). The net was deployed at the maximal depth of haul, then opened and towed vertically upwards, and finally closed at the minimal depth of haul with a mechanical device (activated by a messenger).

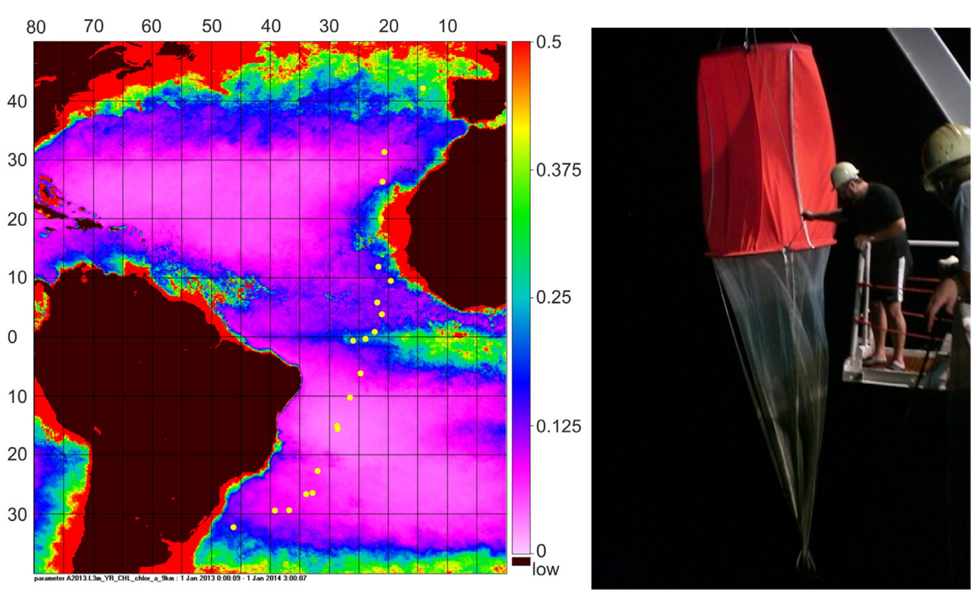

Fig. 1. Deep-sea plankton stations (yellow circles) in the Atlantic Ocean (left) and the BR plankton net in action (right). Background of the map: surface chlorophyll-a concentration averaged over 2013, scale (mg m^{-2}) on right. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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