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# First insights into genus level diversity and biogeography of deep sea benthopelagic calanoid copepods in the South Atlantic and Southern Ocean



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## ABSTRACT

Calanoid copepods constitute the most numerous organisms not only in the pelagic realm, but also in the benthic boundary layer, which gives them an important role in the turnover of organic matter in the benthopelagic habitat. During seven expeditions to the South Atlantic and Southern Ocean, the diversity and biogeography of deep-sea benthopelagic calanoid copepods were studied. The communities of calanoids living in the vicinity of the seabed were characterized by high diversity comparable to many pelagic habitats, but low abundance of individuals. Members of the taxon Clausocalanoidea dominated the communities, and within this taxon most individuals belonged to detritivore calanoids characterized by sensory setae on the second maxillae or aetideid copepods. 73% of all genera classified as obligate or predominantly benthopelagic copepods detected during these expeditions were new to science and a vast number of genera and species have been described since then. Comparing the communities of calanoid genera between different regions, the assemblages in the Southern Ocean differed significantly from the Southeast and Southwest Atlantic. A latitudinal diversity gradient could be observed, with highest numbers of genera in the Southwest Atlantic and low numbers at stations in the Southern Ocean. Reviewing the literature, endemism for benthopelagic calanoids appeared to be low on a latitudinal range caused by connectivity in benthopelagic habitats through spreading water masses. However, considering the habitats structuring the water column vertically, a high number of genera are endemic in the benthopelagic and specialized to living within the vicinity of the seabed.

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## 1. Introduction

The deep sea benthic boundary layer (BBL), the dynamic interface between the seafloor and the ocean, is a region of elevated chemical and biological activity (Boudreau and Jorgensen, 2001) with high concentrations of particulate matter and elevated zooplankton biomass (e.g., Wishner 1980a, Wishner and Meise-Munn 1984; Angel, 1990). As a potential sinking or transition zone for carbon from shallower regions of the ocean, it has an important role in the carbon cycling within the water column (Etiope et al., 2006). Organisms inhabiting this region have access to a potentially rich food source of large particles that can sink rapidly to the seafloor, like planktonic cells, marine snow and associated organisms or fecal pellets as well as to suspended and resuspended material from the bottom (e.g., Gowing and Silver, 1985; Gowing

and Wishner, 1986).

Associations living in the region of the BBL in the deep sea are often referred to as benthopelagic fauna (Marshall and Merrett, 1977). They contain endemic species from the near bottom environment, planktonic species migrating (seasonally) downward, or with habitats reaching downward to the bottom, as well as infaunal species emerging into the water column (Mauchline and Gordon, 1991). The most numerous members of this community are copepods (Wishner, 1980a, 1980b), and some of them seem to have specialized to this habitat (e.g. Bradford, 1969; Grice and Hulsemann, 1970; Grice, 1972).

The deep sea harbors a rich fauna, varying in diversity on local, regional and global scales (Vinogradova, 1997; Rex and Etter, 2010). While some taxa, like polychaetes, are thought to be more widespread (e.g. Kirkegaard, 1995, in Watling et al. (2013)), others are found to have a large number of endemic species (e.g., Rex and Etter, 2010 and references therein) and species assemblages are considered to show faunal boundaries connected to sharp changes in bottom and water column conditions (e.g., Carney, 2005). However, only the recent invention of modern devices in the last

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century, designed specifically for sampling in the vicinity of the seabed, made it possible to get insights into the diversity of the benthic and benthopelagic fauna of the deep sea. Still, most of the benthopelagic fauna is still poorly known and knowledge on the distribution and ecology of benthopelagic calanoids is rare. Among the first to describe the occurrence of a specialized benthopelagic copepod fauna was the work by Sars (1902), followed by e.g., Bradford (1969), Grice and Hulsemann (1970) and Grice (1972) and first attempts to study the ecology of deep sea benthopelagic calanoids were made by Wishner (1980a, 1980b).

The highly diverse copepod fauna associated with the sea floor is often characterized by a specific morphotype, e.g., compactly built individuals, possessing heavy and enlarged outer exopodal spines on the swimming legs (Bowman and Gonzalez, 1961; Bradford-Grieve, 2004) and sometimes short and partly asymmetrically developed antennules (Ohtsuka et al., 1993a). However, the habitus of many near bottom taxa also resembles that of their pelagic relatives, and identification of individual calanoids within the BBL is significantly impeded by the striking morphological similarity between different species of some taxonomic groups.

In general, the calanoid fauna within the region of the BBL is characterized by low abundance, but high diversity of species (Bradford-Grieve, 2004). On the background of calanoid copepod evolution over geological time, Bradford-Grieve (2004) hypothesized the deep sea benthopelagic calanoid copepods to represent invasions of the benthopelagic environment from the water column. Within those taxa abundant in the BBL, the superfamily Clausocalanoidea was also discussed to be of benthopelagic origin (Markhaseva and Schulz, 2006; Markhaseva et al., 2008).

Gowing and Wishner (1986) predicted that detritivore copepods most likely form the major component of the BBL. This view has been supported in recent years by the description of a large number of new species, possessing a set of sensory setae on the second maxillae (e.g., Schulz and Beckmann, 1995; Schulz, 1998, 2005, 2006; Ferrari and Markhaseva, 2000; Ohtsuka et al., 2003; Bradford-Grieve, 2004, 2005; Markhaseva and Ferrari, 2005; Markhaseva and Schulz, 2007, 2009, 2010; Markhaseva and Renz, 2011; Markhaseva et al., 2014). These sensory setae are thought to function as chemoreceptors (Nishida and Ohtsuka, 1997) and appear to be important in the detection of food in oligotrophic environments (Ohtsuka et al., 1993b).

The Census of Diversity of Abyssal Marine Life within the Census of Marine Life aimed to document the diversity of marine organisms of abyssal plains to increase the understanding of the ecological factors regulating biodiversity. Within this framework, a range of cruises to the South Atlantic and Southern Ocean was performed. Here, we present a unique dataset from 7 expeditions aimed at describing the biodiversity and large scale biogeography of calanoid copepod genera occurring in the BBL.

The objectives of this study were: (1) to make an interim report on the diversity of deep sea benthopelagic calanoid copepod genera in the South Atlantic and Southern Ocean and summarize the taxonomic composition; (2) to determine if there are significant differences in communities at the generic level that vary with a priori defined regions, discuss the potential factors that might govern the distribution of benthopelagic calanoid copepod assemblages and investigate whether their distribution corresponds to abyssal provinces established by Watling et al. (2013); and (3) to give a worldwide biogeographic overview of genera detected in the benthopelagic during the expeditions, including data presented here and reviewing the existing literature.

## 2. Material and methods

### 2.1. Sampling

Calanoid copepods were collected from 68 stations, at depths between 774 and 6348 m from the benthic boundary layer (BBL) in the South Atlantic and Southern Ocean (Table 1) during RV Polarstern and Meteor cruises (Table 1, Fig. 1).

All stations were sampled with an epibenthic sledge (EBS; Brenke, 2005) that consists of a closable 500  $\mu\text{m}$  epi- and supranet, each with an opening of 1 m width and 0.35 m height. Both nets end up in a cod end with a mesh size of 300  $\mu\text{m}$ . The net openings are positioned 0.2–0.6 m (epinet) and 0.77–1.12 m above the seabed (supranet). The EBS was hauled over the seabed at 1 knot for 10 min. Nets were opened before starting the trawl and closed before starting to haul the sledge from the seabed. On board, the samples were immediately fixed in either a 4% buffered formalin/seawater solution or in 96% pure undenaturated ethanol.

### 2.2. Sorting and identification

Calanoid copepods were sorted in the laboratory and, whenever possible, identified to genus level using a stereomicroscope and a microscope. In most cases it was necessary to stain individuals in a solution of 1% Chlorazol black E dissolved in 70% ethanol to check setation on oral limbs and swimming legs and facilitate identification.

Identifications were based on the taxonomic literature on calanoids, e.g., Damkaer (1975), Park (1978, 1980, 1982, 1983a, b), Brodsky et al. (1983), Schulz (1989, 1998), Ohtsuka et al. (1993a), Bradford-Grieve (1994, 1999a,b), Markhaseva (1996), Bradford-Grieve et al. (1999) and Andronov (2002).

All individuals were further classified into adult females, adult males and copepodites. Individuals, that were either broken or disintegrated could not be identified and were classified into juveniles and adults but not further identified to genus level.

All genera were classified according to their known habitat preferences from the literature and placed into 3 categories: group I. Obligate benthopelagic calanoids; group II. Predominantly benthopelagic calanoid genera, which have a few pelagic species; group III. Pelagic calanoids, damaged individuals and copepodites that could not be identified to genus level since the identification literature for copepodites of non-epipelagic species is nearly always lacking. Several genera were classified as pelagic taxa, which are only reported from the pelagic environment in the existing literature so far. Some genera have to be considered to be truly pelagic (e.g., Grice and Hulsemann, 1967, 1970; Wishner, 1980b; Gowing and Wishner, 1992; Schulz and Markhaseva, 2000), since they usually only occur in the epipelagic, e.g. *Acartia*, *Clausocalanus* or *Temora* and most likely represent contaminations from upper water layers and occurred only with few individuals. Others, however, might perform active vertical migrations into the region of the benthopelagic to benefit from enhanced food supply in the BBL, migrate actively for predator avoidance or they are passively drifted by advection (Vereshchaka, 1995). Pelagic individuals were identified and enumerated (Appendix 1).

Genera and species new to science were identified as undescribed genera and species. While the analysis of this deep-sea material has already resulted in the descriptions of 29 new species, 13 new genera and 2 new calanoid families (Table 2), some genera new to science still await description. These undescribed 102 individuals were marked as undescribed genera 1–34 and belong to at least 6 families.

The material is archived in the collection of the German Center for Marine Biodiversity Research (DZMB), Senckenberg Research Institute, Hamburg.

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