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Copepod distribution and biodiversity patterns from the surface to the deep sea along a latitudinal transect in the eastern Atlantic Ocean (24°N to 21°S)

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ABSTRACT

Vertical distribution, community structure and diversity of calanoid copepods were studied at six stations along a latitudinal transect from 24°N to 21°S in the eastern Atlantic Ocean, resolving nine discrete depth layers to 2000 m. Total copepod abundances integrated from 0 to 2000 m ranged from 148,000 to 197,000 ind m^{-2}. Usually, abundance and biomass were highest in the upper 100 m, exponentially decreasing with increasing depth. Only at the northern- and southernmost stations, a deeper biomass maximum was observed at 100–200 m and 200–400 m, respectively. In total, 26 families, 79 genera and at least 172 species were identified among calanoid copepods. Although there were certain regional differences in species composition between tropical and subtropical stations from north to south, depth had the strongest impact on the community structure of calanoids, resulting in statistically distinct communities in different depth zones. Maximum diversity of calanoids was observed between 100–200 m in the tropical zone and between 400–700 m in subtropical regions. Various interacting mechanisms such as vast spatial extent of the ecosystem, physical stability, avoidance from predators under dim light, small population sizes and high biologically generated heterogeneity possibly contribute to the biodiversity maxima in the twilight zone.

1. Introduction

Copepods dominate mesozooplankton communities in all oceans (Longhurst, 1985; Gallienne et al., 2001; Champalbert et al., 2005). They play a key role in marine food webs and elemental cycles (Longhurst and Harrison, 1989). Copepod communities are usually characterized by strong latitudinal and bathymetric gradients. Their biodiversity is regulated by environmental parameters, biological interactions and species-specific ecophysiological performances. However, major driving mechanisms generating high biodiversity are still poorly understood, especially in the pelagic deep sea.

Tropical zooplankton communities are characterized by high species richness, complex trophic networks and small changes of biomass throughout the year (Longhurst, 1993; Woodd-Walker, 2001; Woodd-Walker et al., 2002; Finenko et al., 2003; Piontkovski et al., 2003; Rombouts et al., 2009; Schnack-Schiel et al., 2010). Horizontal distribution in tropical oceans is more or less unrestricted, due to the absence of physical barriers allowing co-occurrence and wide latitudinal ranges of many oceanic species (Woodd-Walker et al., 2002; Piontkovski et al., 2003; Rombouts et al., 2009; Schnack-Schiel et al., 2010). In contrast, strong vertical stratification, i.e. a pronounced thermocline and oxycline, effectively separates the mixed, well oxygenated, warm surface layer from cooler, less oxygenated waters below. Hence, zooplankton communities may be structured vertically according to species-specific ecophysiological performances (Ekau et al., 2010; Stramma et al., 2008; Wishner et al., 2008, 2013; Teuber et al., 2013).

While the mesopelagic or so-called “twilight zone” (200–1000 m) is still influenced by strong gradients of environmental factors, chemical and physical parameters are rather stable in the bathypelagic zone below 1000 m (Koppelmann and Frost, 2008; Robinson et al., 2010). In general, zooplankton abundance exponentially decreases with depth, while species diversity increases with increasing depth with maxima in meso- to bathypelagic zones (Ward and Shreeve, 2001; Ramirez-Llorda et al., 2010; Kosobokova et al., 2011; Laakmann et al., 2012). Yet, seasonal and regional differences of mesozooplankton community structure also exist in the deep sea (Wishner, 1980; Koppelmann and Weikert, 1999, 2007; Sasaki et al., 1988; Yamaguchi et al., 2002; Koppelmann et al., 2004; Homma et al., 2011). Mechanisms driving high biodiversity in the deep sea are not well understood, as data are especially poor for the deep pelagic realm (Angel, 1993, 1997; Robison 2004; Duffy and Stachowicz, 2006; Webb et al., 2010; Laakmann et al.,

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2012). Various competition-reducing mechanisms like fine-scale vertical partitioning of the water column (spatial niches) and the evolution of different trophic niches or other life-history traits are likely to interact (Laakmann et al., 2012). Furthermore, physical-biological interactions such as advection processes and continuous re-colonization of water masses may be equally important (Ambler and Miller, 1987; Weikert and Koppelmann, 1993; Auel, 1999; Matsuura et al., 2010; Laakmann et al., 2009a, 2009b, 2012).

Due to the high biodiversity in tropical oceans, species identification and community analyses with high taxonomic resolution are extremely challenging and time-consuming. Most previous studies in tropical regions were restricted to the upper 200 or 300 m and/or concentrated on higher taxonomic groups or prevailing species. Other studies separated size classes instead of species (e.g. Huskin et al., 2001; Isla et al., 2004; San Martin et al., 2006; Calbet et al., 2009). However, low abundances are not equivalent to low ecological importance (Kosobokova et al., 2011). A high biodiversity may strongly contribute to an ecosystem's resistance to environmental perturbations (Duffy and Stachowicz, 2006), while the presence or absence of certain species will affect ecosystem functioning (e.g. diel migrants) (Ducklow et al., 2001; Steinberg et al., 2012). Changing distribution patterns of indicator species may reveal changes in marine habitats (Beaugrand, 2004, 2005). Thus, studying biodiversity and observing transitions in copepod communities can help to relate fluctuations in marine ecosystems to potential environmental changes (Beaugrand et al., 2002; Hays et al., 2005; Hooff and Peterson, 2006). Detailed studies with high resolution at all scales will be necessary, if we want to model zooplankton dynamics and impacts of changes in zooplankton composition to ecosystem functioning realistically one day. Resolving nine depth strata from the upper 2000 m, we investigated horizontal and vertical distribution, community structure and diversity of calanoid copepods at six stations along a latitudinal transect in the eastern Atlantic Ocean (24°N to 21°S), identifying which mechanisms may be driving these patterns. Our study covers the Canary Basin in the subtropical North Atlantic, the Cape Verde, Sierra Leone, and Guinea basins in the tropical North Atlantic, the Angola abyssal plains of the subtropical South Atlantic and the beginning of the Walvis Bay ridge in a region influenced by the Benguela Current.

2. Materials and methods

2.1. Sampling

Zooplankton was collected during the research cruise ANT-XXIX/1 on board of RV *Polarstern* along a transect in the eastern Atlantic Ocean from 23° 41′N to 20° 59′S in November 2012. Sampling was carried out during daylight between 8:00 and 12:00 a.m. local time by vertical hauls with a HydroBios Multinet Maxi (0.5 m^2 mouth opening) equipped with nine nets of 150 µm mesh size. The volume of filtered seawater was measured with a flowmeter attached to the net frame (hauling speed 0.5 m s^{-1}). Mesozooplankton was sampled at six stations from discrete depth layers (Fig. 1 2000–1500–1000–700–400–300–200–100–50–0 m). The depth layers at stn. 17 deviated from the general scheme (2000–1500–1000–700–500–400–200–100–50–0 m). Due to technical problems net samples are missing from 50 to 100 m at stn. 8 and from 300 to 400 m at stn. 14. The samples were preserved in a 4% borax-buffered formaldehyde in seawater solution. Profiles of temperature, salinity, oxygen concentration and fluorescence were obtained at each station from surface to maximum sampling depth (800 or 2000 m) with a conductivity temperature depth (CTD) sensor attached to a rosette water sampler (Fig. 2, Rohardt and Wisotzki, 2013; see also Fig. 2 in Bode et al., 2015). Fluorescence provided a proxy for chlorophyll *a* content in the upper 200 m. Surface primary production (PP) was measured at each station (see details in Fonseca-Batista et al., 2017).

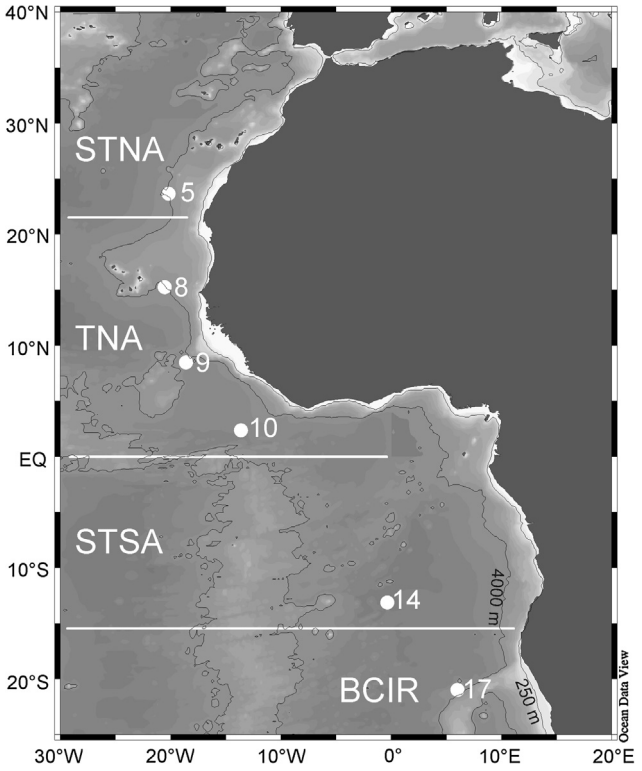

Fig. 1. Station map showing all deep stations (0–2000 m) during ANT-XXIX/1 of RV *Polarstern* in November 2012. The 250 m and 4000 m bathymetry lines are indicated as black lines. Hydrographic provinces were identified based on oceanographic data (Fig. 2). STNA = Subtropical North Atlantic, TNA = Tropical North Atlantic, STSA = Subtropical South Atlantic, BCIR = Benguela Current Influenced Region.

2.2. Abundance analysis

Mesozooplankton samples were transferred to a sorting fluid consisting of 0.5% propylene-phenoxetol, 5% propylene glycol and 94.5% fresh water (Steedman, 1976) and split into subsamples (1/2 to 1/32) using a Motoda plankton splitter (Motoda, 1959) and then analyzed. Abundant species were enumerated until at least 80 individuals within a subsample were counted. Rare species were counted from the entire sample. Calanoid copepods were identified to genus level or, if possible, to species level under a dissecting microscope. The animals were separated into adult females, adult males and copepodids (CI-CV). Cyclopoid copepods were separated into Oncaeidae and Oithonidae (*Oithona* spp.). Abundance data for all species are available from the data publisher PANGAEA via the persistent identifier https://doi.org/10.1594/PANGAEA.884570.

Species diversity H′ was calculated according to Shannon (1948):

$$H' = -\Sigma p_i \ln(p_i)$$

where p_i is the proportion of the *i*th ranked species in the calanoid community in each sampling layer. A multidimensional scaling (MDS) plot was created using the Primer software based on the Bray-Curtis similarity matrix of the log(x + 1) transformed abundance data (Primer v6; Clarke and Gorley, 2006). A log(x + 1) transformation was necessary due to high variations in abundance data. Hierarchical agglomerative clustering was performed on this similarity matrix combined with a similarity profile analysis (SIMPROF) to identify significant groups. Similarities among depth layers were statistically tested for significance using a one-way analysis of similarities (ANOSIM).

To assess biomass, species- and/or genera-specific dry mass (DM) data were calculated from median total length (TL) for adult females, adult males and copepodids (Chisholm and Roff, 1990; Homma et al., 2011):