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Diversity of the benthic macrofauna off northern Namibia from the shelf to the deep sea



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ABSTRACT

In late summer 2011, shortly after an upwelling event, 17 stations ranging from 30 to 2513 m water depth have been sampled at 20° south in the northern part of the Benguela Current Large Marine Ecosystem (BCLME) for the investigation of the benthic macrofauna. Sediments of this area are dominated by silt. At the time of sampling, oxygen conditions on the shelf were poor (between 0.42 and 0.68 ml l^{-1}) but not hypoxic. Below 400 m, however, concentrations rose steadily up to 5.28 ml l^{-1} . Macrozoobenthic communities along this depth gradient are described, revealing among others the community structure for the continental margin area and the deep sea off northern Namibia for the first time. Cluster analysis revealed 5 different communities along the depth gradient with three shelf communities, one continental margin community and one deep-sea community. All in all, 314 different taxa were found with polychaetes being the most abundant group. Diversity index (Shannon) was lowest for the shallow water community with 2.21 and highest for the deep-sea community with 4.79, showing a clear trend with increasing water depth. Species richness, however, reached its maximum with 187 taxa along the continental margin between 400 and 1300 m water depth. Dominant species for each community are named with the two Cumacea, Iphinoe africana and Upselaspis caparti, being characteristic for the shallow water community. On the shelf, we found surprisingly high biomass values $(23-123 \text{ g m}^{-2})$, mainly caused by polychaetes, the bivalve Sinupharus galatheae and the gastropod Nassarius vinctus. In terms of composition, the remaining communities were dominated by polychaetes with members of the Paraonidae dominating along the continental margin where we also found surprisingly high abundances of the bivalves Pecten sp. and Dosinia sp. Spionid polychaetes and some representatives of the genus Paraonis were the most common organisms for the deep-sea community.

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1. Introduction

Diversity is a key aspect of benthic community structure and seems to be closely connected with ecosystem functions (Danovaro et al., 2008). Environmental factors driving the distribution and diversity of species along environmental gradients are topics of a number of studies in aquatic systems. In general, diversity and faunal zonation have early been found to be influenced as well by physical factors such as hydrographical conditions (temperature or pressure) and topography of the continental slope as by geochemical factors such as sediment grain size and sedimentation rates (Carney, 2005; Haedrich et al., 1975; Lampitt et al., 1995; Rex, 1976; Rice et al., 1990; Rowe and Menzies, 1969; Tyler et al., 2001; Young et al., 1996). In particular, low oxygen concentrations have been identified to have a major impact on benthic zonation and diversity (Rosenberg and Loo, 1988; Wishner et al., 1990). Also, biological parameters such as resource availability, predation, trophic level, larval dispersal and interspecific competition (Billett, 1991;

* Corresponding author. *E-mail address:* michael.zettler@io-warnemuende.de (M.L. Zettler). Cartes and Sardà, 1993; Rex, 1976, 1981; Rowe and Menzies, 1969; Young et al., 1997) have been identified.

Some areas are still not yet sufficiently explored in terms of biodiversity as shown by Konar et al. (2010). Among others, they rated Namibia's marine environment as one of eight regions of the world with "major biodiversity gaps", which they defined as missing information for most taxonomic groups.

The marine environment off Namibia belongs to the Benguela Current Large Marine Ecosystem (BCLME), which is one of the world's largest coastal upwelling areas. Nutrient-rich deep water comes to the surface and promotes the growth of phytoplankton, which results in a high productivity of the system (Mohrholz et al., 2014 and references therein).

In general, the marine species richness off Namibia has however been rated as relatively poor (Sakko, 1998). There are several studies on macrozoobenthic communities from intertidal waters of southwest Africa (e.g., Kensley and Penrith, 1980; McLachlan, 1985; Penrith and Kensley, 1970a,b; Tarr et al., 1985), and a more recent study by Scott et al. (2012) summarises the state of knowledge on macrozoobenthic diversity in water depths <15 m. The first review of the Namibian margin benthos has been made by Sanders (1969) off Walvis Bay. However, little attention has been paid to the benthic communities in sublittoral regions ever since. Most previous studies merely refer to selected benthic species (Bochert and Zettler, 2011; Glück et al., 2012; Thandar et al., 2010) and research on commercially important benthic organisms covers only a few species such as lobster and demersal fish (Bianchi et al., 1999; Boyer and Hampton, 2001; Pulfrich et al., 2003).

Some more comprehensive studies, however, have been made by Zettler et al. (2009, 2013), who attempted to assess and describe benthic communities off Namibia down to 300 m water depth with a special focus on the oxygen minimum zones (OMZ) that stretch along the whole Benguela upwelling area.

The present study gives an overview of benthic diversity in the northern part of the Benguela upwelling region shortly after an upwelling event and presents benthic communities along a depth gradient at 20°S. Our goal is to give an idea of what is there and thus help to extend the knowledge about macrozoobenthic diversity in Namibian sublittoral and deep waters in the first place, including for the first time data on benthic fauna beyond the Namibian shelf.

2. Materials and methods

2.1. Study area

The marine environment off Namibia belongs to the Benguela Current Large Marine Ecosystem (BCLME), which is one of the world's largest coastal upwelling areas. Nutrient-rich deep water comes to the surface and promotes the growth of phytoplankton, which results in a high productivity of the system (Mohrholz et al., 2014 and references therein).

The Walvis Shelf off Northern Namibia is one of the deepest and broadest shelf areas in the world (Bremner, 1981; Shannon, 1985). Muddy sediments on the shelf show a high organic content and contain a high amount of biogenic components (calciferous remains of diatoms, foraminifers and molluscs), whereas in shallow water, sandy sediments of terrigenous origin occur and display the impact of the Namib Desert (Bremner, 1981; Rogers and Bremner, 1991).

According to Emanuel et al. (1992), who divided the South African Coastline into four different zoogeographical regions, the Northern Namibia region is referred to as "Cool-temperate North West Coast" and ranges from the Kunene River (17°S) to Lüderitz (26°S). The marine region along and off this coastline is of special interest as several water masses of different temperatures interfere and create a highly unstable environment, which is bordered in the North by the Angola-Benguela frontal zone (ABFZ) (Mohrholz et al., 2008; Veitch et al., 2006; von Bodungen et al., 2008). The seasonal variability of upwelling events gives rise to warm water masses flowing into the Northern Benguela System in austral summer (Meeuwis and Lutjeharms, 1990). These water masses have the potential to triple nutrient concentrations. Oxygen concentration, however, can decrease by 70% to 90% (Mohrholz et al., 2008). In austral winter, upwelling intensifies again and cold water masses dominate the shelf region (Boyer et al., 2000). Upwelling further stimulates primary and secondary production in the euphotic zone. The decomposition of the sinking detritus by bacteria results in hypoxic (<0.5 ml l⁻¹) and periodically anoxic (complete absence of dissolved oxygen) areas on the seafloor. In times of oxygen deficiency, hydrogen sulphide can be produced in the sediments and accumulate in the bottom water of the shelf regions (Mohrholz et al., 2008; Ohde et al., 2007; van der Plas et al., 2007). Local oxygen consumption during remineralisation of sinking detritus and also the southward advection of oxygen-poor tropical water both contribute to the poor oxygen budget on the shelf (Mohrholz et al., 2008; Monteiro et al., 2006; von Bodungen et al., 2008).

For further information on hydrographical conditions during the expedition and successive ecosystem response take a look at Journal of Marine Systems, Vol. 140, Part B.

2.2. Sampling

During the 18th research cruise of the German research vessel Maria S. Merian (MSM 18/5) conducted by the Leibniz Institute for Baltic Sea Research in 2011 from 23rd of August to 20th of September, 17 stations ranging from 30 to 2513 m water depth (Fig. 1) have been sampled using Van Veen grab and box corer, both covering 0.1 m². The usage of two different sampling devices is due to the wide range of different water depths that was sampled. We found the Van Veen grab is not particularly suitable for water depths deeper than 300 m. However, as both appliances cover the same surface and this study aims to give merely a faunal overview, there is no difference being made in the result section. Table 1 gives an overview of all stations including sampling effort. Additional dredge samples have been taken where possible to collect epibenthic and mobile fauna. However, they are not part of further community analysis such as abundance or biomass as they cover different surface dimensions. All samples have been sieved through a 1 mm² screen, and animals were preserved in 4% buffered formaldehyde. Abiotic parameters such as temperature, oxygen and salinity were measured approximately 1 m above ground using a profiling CTD-system (Seabird, USA) with an oxygen sensor attached (Seabird, USA). Median grain size was determined using laser particle sizer Cilas 1180L and organic matter estimation have been made by weight loss upon ignition for 12 h at 500 °C. Sorting procedures of the faunal samples took place in the lab using a stereomicroscope with up to $80 \times$ magnification. All animals were identified to the lowest taxonomic level possible. Nomenclature was checked using the World Register of Marine Species (WoRMS: www.marinespecies.org).

Biomass was measured on micro scales (excluding dredge samples) and is given in wet mass [g m⁻¹]. All biological data from this study have been transferred to AfrOBIS—a marine biogeographic information system for sub-Saharan Africa and one of 11 global nodes of the Ocean Biogeographic Information System (OBIS). Preserved organisms are stored at the Leibniz Institute for Baltic Sea Research, Warnemünde, in the benthic ecology lab for further study.

2.3. Statistical analysis

Considering only grab samples, abundance (individuals m^{-2}) and biomass (g wet mass m^{-2}) were calculated for each taxon and station. Median values were favoured over mean values. Dredge samples were analysed separately and have not been included in this study.

In order to compare diversity, the Shannon index *H*['] was calculated for each station (Shannon, 1948).

A cluster analysis based on species abundance was conducted using Bray–Curtis similarity (Bray and Curtis, 1957) after square root transformation of data in order to define communities along the depth gradient using PRIMER v6 (Clarke and Warwick, 2001). Living conditions are not integrated, so the result of the analysis is not to be seen as absolute as conditions can change drastically over this wide range of water depths.

3. Results

3.1. Environmental conditions

Table 2 summarises bottom water conditions along the depth gradient with minor salinity changes between 34.5 and 35.2 psu along the transect where values lower than 35 psu occurred only below 400 m. On the shelf and down to 400 m, oxygen concentrations varied between 0.42 and 0.68 ml l⁻¹. Deep water stations, however, showed an increase in oxygen concentrations up to 5.3 ml l⁻¹ at the deepest station (2513 m). Temperature decreases with increasing water depth reaching a 12.7°C maximum at 56 m water depth and a temperature minimum of 2.8°C again at the deepest station. Sediments were dominated by silt, and there were only 3 stations (NAM-BE04, NAM 004 and NAM009) where fine sand was found. In general, median grain size tended to

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