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Distribution of zooplankton biomass and potential metabolic activities across the northern Benguela upwelling system

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A B S T R A C T

The distribution of zooplankton biomass and potential metabolic rates, in terms of electron transport system (ETS) and glutamate dehydrogenase (GDH), were analyzed along a cross-shelf transect in waters off Namibia. The highly variable dynamics of upwelling filaments promoted short-term fluctuations in the zooplankton biomass and metabolism. Maximum values were characteristically found over the shelf-break, where zooplankton biomass as dry mass (DM) reached peaks of 64.5 mg m^{-3} within the upper 200 m in late August. Two weeks later, the zooplankton-DM decreased by more than a third (19 mg DM m^{-3}). Zooplankton potential respiration and NH_4^+ excretion averaged 234 μmol O_2 m^{-3} d^{-1} and 169 μmol NH_4^+ m^{-3} d^{-1} in the Namibian shelf, respectively. High protein-specific ETS activities even in the low-chlorophyll waters outside the filament suggested a shift into greater omnivory seaward. In this light, zooplankton elemental and isotopic compositions were used to investigate the pelagic food web interactions. They evidenced spatial changes in the carbon resource for zooplankton as well as changes in the form of nitrogen that fueled the biological production in aging advected waters. Overall, both aspects of zooplankton metabolism impacted the primary productivity at a level less than 10% under all the different oceanographic conditions.

1. Introduction

Upwelling ecosystems are among the most productive areas in the ocean. They mainly occur along the eastern boundaries of an ocean where the wind-driven divergence forces deep cold waters, rich in nutrients, into the sunlit layer. Both nutrient enrichment and light availability together, provide a suitable environment for sustaining high biological productivity. One of the major eastern boundary current systems of the world is the Benguela, which is divided in two sub-systems by a permanent upwelling cell located around 27–28°S (Boyer et al., 2000). Here, the northern part is the focus of investigation. It is limited by the warm water of the Angola–Benguela Front (Shannon, 2001) and exhibits important instabilities at short temporal and spatial scales in addition to the well-documented interannual fluctuations (Hutchings et al., 2009; Shannon and Nelson, 1996). Both oceanographic and atmospheric forces intensify the upwelling pulses during the austral winter and spring, and relax them in autumn (Boyd et al., 1987). Other processes such as jets and filaments emerging from the perennial cell also promote the variability in the northern Benguela ecosystem. These mesoscale structures will ultimately impact the plankton populations dynamics.

In this and in all upwelling systems, mesozooplankton play a key role in the mass and energy flows through the food web (Moloney, 1992). They are the primary food resource for fish larvae and consequently, the main trophic link to the top predators. In recognizing the importance of zooplankton in the Benguela system, several studies have paid attention to its spatial distribution (Hansen et al., 2005; Olivar and Barangé, 1990; Postel et al., 2007; Verheye and Hutchings, 1988, among others), as well as to the long-term trends in the zooplankton abundance (Verheye et al., 1998) and biomass (Huggett et al., 2009). Changes in the community composition (Gibbons and Hutchings, 1996; Verheye et al., 2001), ecology (Gibbons et al., 1992; Verheye et al., 1992) and secondary production (Hutchings et al., 1991; Richardson and Verheye, 1999) in relation to physical and biological forcings have also been described in the last decades. However, these studies have not considered the short-term zooplankton structural dynamics caused by successive upwelling-relaxation events, filaments or eddies which take place in a particular region. Wind-driven offshore advection, for instance, causes the stratified plankton-rich waters to be rapidly replaced by deeper waters, which introduce a new batch of nutrients into the photic layer, but little plankton. Accordingly, the inherent variability of these chemical and physical phenomena constrains the integrity of biological communities on the order of days.

Furthermore, the instability of the oceanographic setting also affects the physiological dynamics of zooplankton (Gaudy and Youssara, 2003). Respiration and NH_4^+ excretion are important processes in marine

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ecology, as the balance between synthesis and demand of both carbon and nitrogen controls the efficiency of the net production (Margalef, 1982). In this context, Chapman et al. (1994) measured electron transport system (ETS) activities in microplankton to broadly estimate the carbon requirements and the nutrient regeneration in the waters south of Walvis Bay. Few studies have directly dealt, however, with mesozooplankton metabolism in this upwelling ecosystem. Recently, Huenerlage and Buchholz (2013) demonstrated variations in the physiological behavior of *Euphausia hanseni* under changeable trophic conditions in the Angola–Benguela frontal waters. The respiration in terms of ETS activity was also determined, but only on the dominant copepod species from Benguela (Bode et al., 2013; Timonin et al., 1992). Indeed, from respiration measurements, Schukat et al. (2013) assessed an important daily phytoplankton removal by copepods. Here we elucidate the magnitude of the respiration and NH_4^+ excretion rates by the total mesozooplankton community in a cross-shelf transect off Namibia. We used the enzymatic approach because direct measurements of physiology such as the water-bottle procedures give low spatial resolution and are additionally complicated by artifacts derived from organism manipulation, overcrowding and even starvation when long incubation times are needed (Bidigare, 1983). Enzymatic assays in turn, require the addition of saturating levels of substrates to ensure the specificity of the reaction (Maldonado et al., 2012; Segel, 1993), resulting in a potential measurement which gives the maximum rate (V_{max}) instead of the actual one. Nevertheless, studies have demonstrated the utility of enzymes as an accurate index of metabolic rates, specially when they are previously calibrated for the surveyed system (e.g., Bode et al., 2013; Hernández-León et al., 1999; Packard, 1985).

This field study is embedded in an interdisciplinary research of the aging process of a coastal upwelling system. We aimed to characterize how the physical structuring processes affect the biomass of zooplankton, as well as to describe the impact that zooplankton metabolism has on the primary productivity from the northern Namibian cell. Elemental composition and stable isotopes of zooplankton were additionally used to infer spatial changes in the pelagic food web of this ecosystem. Since continuous monitoring is required to understand the structure and functioning of the plankton community, we applied a Eulerian approach by sampling a cross-shelf transect four times during a month of intense wind-forcing. The irruption of eddies and filaments will affect the maturation pattern of the fresh upwelled waters along its pathway seaward. This influences the successional developments in these aging advected waters, promoting the heterogeneity in zooplankton populations towards the open ocean. In this scenario, our research illustrates the dynamics of zooplankton biomass and potential metabolism in face of the different oceanographic situations recorded in the northern Benguela.

2. Material and methods

Four consecutive transects were made to collect zooplankton samples and hydrographic data at 20°S off Namibia during the SUCCESSION cruise onboard RV Maria S. Merian from August 27th to September 15th, 2011. Three of the transects sampled 12 stations to a distance of 230 km from the coast, while the fourth one was extended seaward by 9 stations to 500 km (Fig. 1). Stations from NAM001 to NAM018 were sampled during both day and night in order to minimize the effect of the vertical migrations by the large zooplankton. Salinity, temperature, chlorophyll-a fluorescence and dissolved oxygen profiles were obtained at each station by deployment of a CTD SBE 911+, equipped with a WETlab FLRT-1754 fluorometer, and mounted on a rosette sampler with twenty-four 10 L Niskin bottles. Nutrients (NO_2^-, NO_3^-, PO_4^-, NH_4^+ and SiO_4^{4-}) as well as chlorophyll-a concentrations were also measured at different depths (Mohrholz et al., this volume; Nausch and Nausch, this volume).

2.1. Zooplankton sampling

Zooplankton was collected by Multinet vertical hauls (Hydrobios GmbH, Kiel, Germany). The equipment consisted of a net frame with an opening of 0.25 m², fitted alternatively with 100 and 500 μm meshed nets (L = 2.5 m, diameter at the end = 0.11 m) and stabilized by V-fin depressor. Each net ended in a cod-end consisting of a plastic bucket with side windows covered by gauze. The two flowmeters, mounted inside and outside of the frame, measured the amount of water filtered by

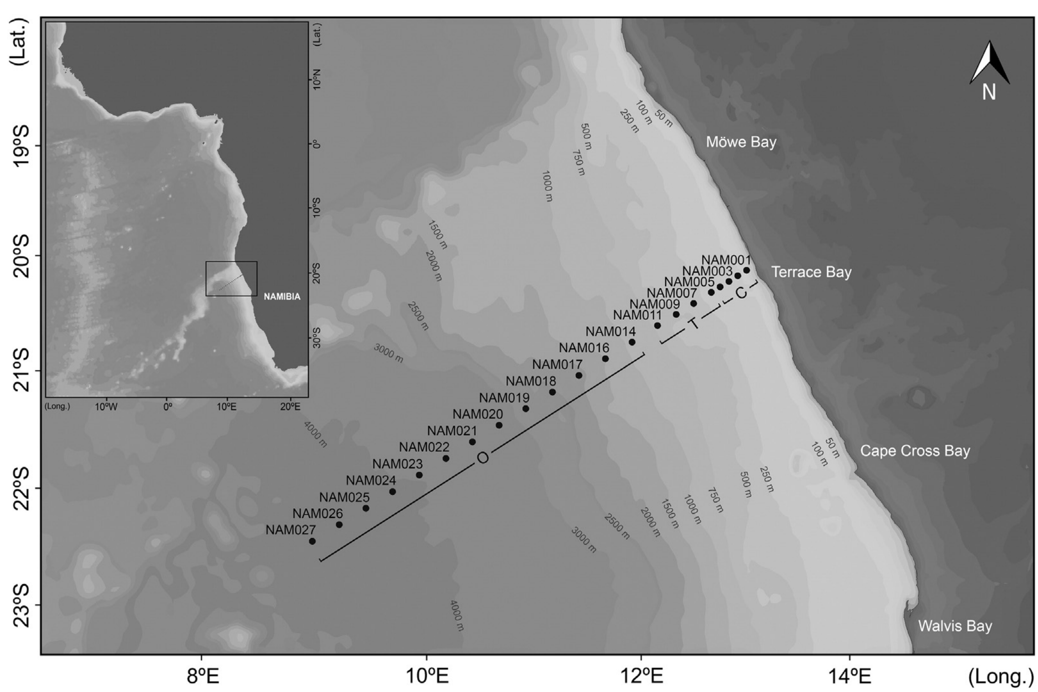

Fig. 1. Map of the study area showing the cross-shelf transect of the Namibian upwelling where zooplankton samples were collected during the SUCCESSION cruise. Stations from NAM001 to NAM018 were sampled four times, while samples from NAM019 to NAM027 were collected only once. The transect was divided into coastal (C), transition (T) and offshore (O) areas according to the geological and oceanographical properties of the stations.

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