Relationship between Dissolved Oxygen and the Vertical and Longitudinal Distribution of Zooplankton off the Namibian coast

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Abstract

Zooplankton play an important role in the marine food web and are abundant on the Namibian coast, which is part of the highly productive Benguela upwelling system. In the Benguela system zooplankton populations are dominated by copepods and euphausiids. The abundance and distribution of zooplankton are affected by various environmental factors such as temperature, light intensity and dissolved oxygen (DO). This study investigated the relationship between DO and the diversity of zooplankton at different depths in the water column on the continental shelf off the Namibian coast. There was a positive correlation between DO and diversity of zooplankton offshore (Pearson's r =0.83), while there exists a very weak positive correlation between DO and zooplankton diversity onshore (r= 0.196). Diversity of zooplankton does not differ significantly with depth at both onshore and offshore stations (Shannon's Index $H' < 1$). However, Divesity of zooplankton between offshore (H'=2.8 to 3.6) and onshore (H'=0.8 to 0.9) stations differs significanty ($p = 0.0271, df = 4$) in the top 90m, but is not significantly different below 90m ($p = 0.406, df = 4$). Nevertheless, the onshore stations had higher species richness compared to the offshore stations. Dissolved oxygen does not have a direct effect on the diversity of zooplankton, but an indirect effect and it is the interplay and interaction between several biological and environmental factors that affects zooplankton assemblage composition.

Keywords: zooplankton, dissolved oxygen, Namibian coast.

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1 Introduction

Zooplankton are free floating and drifting animals with limited power of locomotion (Goswami 2004) and they range from microscopic to unicellular or multicellular forms with size ranging from a few microns to a millimetre or more (Gibbons 2007). Some zooplankton settle on the bottom of the sea, while some of the motile benthic animals may still move up into the plankton at different depths where abiotic factors characteristics favour them (Boyer and Hampton 2001) or where they can find food (Hutching 1988) or avoid predation (Horgher 2011). The continental shelf of Namibia is under the influence of the cold Benguela current upwelling system that introduces a large amount of nutrients into the water column, supporting high primary productivity and those communities that feed on the phytoplankton. On the continental shelf along the Namibian coast, the average number of zooplankton per 1m^2 of the sea surface can range from 15 000 to 40 000 and from 4000 to 10 000 offshore (Taivo 1996). In the Benguela system zooplankton populations are dominated by copepods and euphausiids (Shannon and O'Toole 1999).

Zooplankton feed on phytoplankton and are in turn fed on by invertebrates and fish. Adults of most small pelagic fishes such as anchovy, sardine, club mackerel and round-herring prey on zooplankton. Zooplankton is also food for large pelagic (tuna) and ichthyoplankton and play a key role in the pelagic food web as they transfer organic energy produced by phytoplankton to higher trophic levels (Gibbons et al. 1992). Therefore, they form an important link in the marine food web, which supports the productive fishing industry of Namibia and their occurrence and distribution indirectly influence pelagic fishery potential. Studies of zooplankton abundance are important because they give an indication of the potential feeding conditions available to pelagic species that prey on zooplankton.

Species composition, abundance and diversity of zooplankton change as you go deeper in the ocean due to the vertical characteristics of the ocean (Boyer and Hampton 2001). The factors that affect the distribution of zooplankton include both abiotis factors such as temperature (Gillooly 1999), dissolved oxygen (DO) and turbidity (Lebourges-Dhaussy et al. 2009) as well as biotic factors such as predation (Gibbons et al. 1992) and food availability (Lebourges-Dhaussy et al. 2009; Barange et al. 1991).

The concentration of DO is a reflection of the production and consumption processes of organic matter. Primary production exceeds consumption by respiration and decomposition in the surface water and therefore higher DO concentrations are measured in the photic zone. Below the photic zone DO concentrations decrease rapidly, because the rate of consumption processes exceeds primary production (Martin and Peter 2010). In addition concentration of DO decreases as you move from inshore toward the offshore area (Goswami 2004; Kristmannsson 1999).

Zooplankton has evolved adaptations that enable them to cope with physical characteristics (such as cold temperature, high salinity and turbidity) of the continental shelf off the Namibian coast (Hutchings 1988). Coastal waters in upwelling areas are characterized by variability and thus, zooplankton have to cope with extreme variability in food supply, temperature and DO (Hutchings 1988). This study aims to investigate what effects the concentration of DO may have on the vertical distribution of zooplankton along the continental shelf off the Namibian coast, specifically by looking at how the distribution differs in terms of diversity as well as species composition.

The management of Fisheries globally is increasingly taking an ecosystem approach whereby environmental factors and food web effects are incorporated in models that are used to predict sustainable harvesting quotas for various stocks. Therefore the study of possible correlations of DO with zooplankton diversity and abundance is very important since it puts the zooplankton in context of their environment. Although limited studies attempted to investigate the relationship between DO and zooplankton abundance (Lebourges-Dhaussy et al. 2009; Postel et al. 2007), thus far a comparison between offshore (deep) and onshore (shallow) water has not been conducted. The specific questions addressed in the study were firstly, if there exists a significant relationship between DO and vertical distribution of zooplankton and secondly, if there exists a significant difference on the species composition and diversity of zooplankton with depth onshore and offshore?

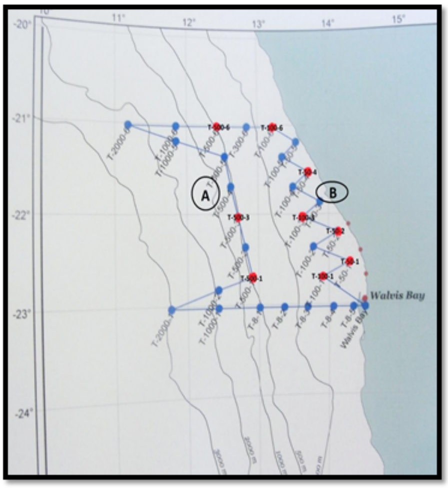

Figure 1: Sampling stations and transects sampled during the research cruise. A indicates offshore stations, while B indicate the onshore transect and stations.

2 Methodology

2.1 Sampling site

Sampling took place on the continental shelf off the Namibian coast from Walvis Bay to the northern part of Angola (Fig. 1). Sampling took place in October 2011 during the research cruise on the RV Maria S Merian. Zooplankton samples were taken along two transects: Transect A was between 22° 59.99S, 12° 45.00E and 23° 59.97S, 12° 30.00E, with a depth of 500 m and is referred to as the offshore station, while Transect B was between 22° 59.97S, 13° 44.97E and 23° 59.99S, 13° 30.00E, was shallower than 100 m and is referred to as the onshore station (Fig. 1). This area is under the influence of south western winds, which create an upwelling system that result in cold nutrient-rich bottom water being introduced into the surface water. The high primary productivity on the shelf of 175-240 mmol C/m^2/d (Summerhayes et al. 1995) results in a high amount of dead organic matter decomposition in the water column. This leads to periodic low oxygen events in this area (Julies et al. 2010; Naqvi et al. 2010).

2.2 Sampling procedure

Samples of zooplankton were collected using a Multi-net that consists of five nets (made of nylon) of the same mesh size (335μm). The nets had a conical shape, consisting of a filtering cone and collecting bucket for collecting organisms at the bottom. The lowering velocity and heave velocity was 0.3 m/s, while the towing speed was 2 knots. Five samples were taken at each station. The concentration of DO at each depth where the samples collected was measured with a CTD. Samples collected were filtered with a mesh size of 300μm and then preserved in a solution of 4% formaldehyde.

2.3 Identification of zooplankton and data analysis

Identification of zooplankton was done under a compound microscope following Todd et al. (1996), Botolvskoy (1999) as well as online keys http://www.crustacea.net/intro.htm and http://www.nmnh.si.edu/iz/copepod/. Identification was done as far as possible to genus or species level and larvae that are part of the zooplankton were also identified according to their stage of development. Counting was done by taking a sample volume of 100 ml from the whole sample at that depth into a petri dishes divided into grids to avoid repetitions of counting individuals. The number of individuals from each taxonomic group in each sample was counted. Diversity of zooplankton was calculated using the Shannon Wiener Index (H') defined as $H' = -\sum p_i \ln p_i$, where H' is diversity index, p_i (Magurran 1998), where H'= Diversity index; S = number of taxonomic groups in zooplankton community and p_i = proportion of total sample belonging to ith taxon. A Kolmogorov-Smirnov test was used to test for normality of the data. Data were not normally distributed with $p = 0.026$ and $\alpha = 0.05$. Therefore, the Spearman non-parametric correlation was used to find the relationship between zooplankton diversity and DO concentrations. The Kruskal-Wallis test was used to test for a difference in diversity of zooplankton between different depths onshore and offshore, respectively.

3 Results

Temperature and DO concentrations measured at various depths on transect B (shallower than 100 m) are indicated in Figure 2. Oxygen concentrations varied from 5-6 ml/L in the top 40m of the water column and were about 4 ml/L at depths between 30-70m. At depths below 70 m DO concentrations was less than 3ml/L. Furthermore, DO concentrations were lower onshore than offshore (Fig. 2 and 3). Higher sea surface temperatures were measured offshore (approximately 16°C) and in the top 50 m, while lower temperatures (13-14°C) were measured onshore and at depths greater than 50 m (Fig. 2).

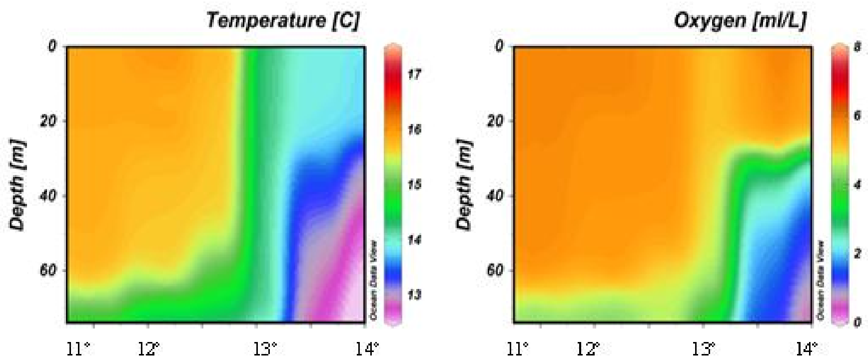

Figure 2: Temperature and DO concentrations throughout the water column on the shelf. The image depicts average concentrations measured throughout the duration of the cruise.

Oxygen concentrations decreased with depth at the offshore station from 5.6 ml/L at a depth of 20m to 1.4 ml/L at a depth of 400m (Fig. 3). At the onshore stations oxygen concentrations decreased from 5.3 ml/L at 20 m depth to 0.9 ml/L at a depth of 400 m (Fig. 3).

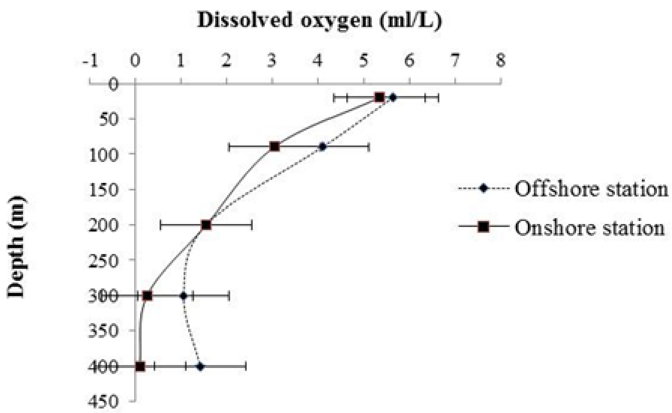

Figure 3: Mean DO concentrations ($n = 5$) with depth at the onshore and offshore stations.

The composition of zooplankton at the offshore and onshore stations is shown in Figure 4 and is a representation of the taxonomic groups found at all stations throughout the water column. The onshore stations had a higher amount of taxonomic groups compared to the offshore stations. *Calanoides carinatus* and *Metridia lucens* dominated at both onshore and offshore stations. *Chaetognaths* and *Rhincalanus nasutus* were also abundant both onshore and offshore stations.

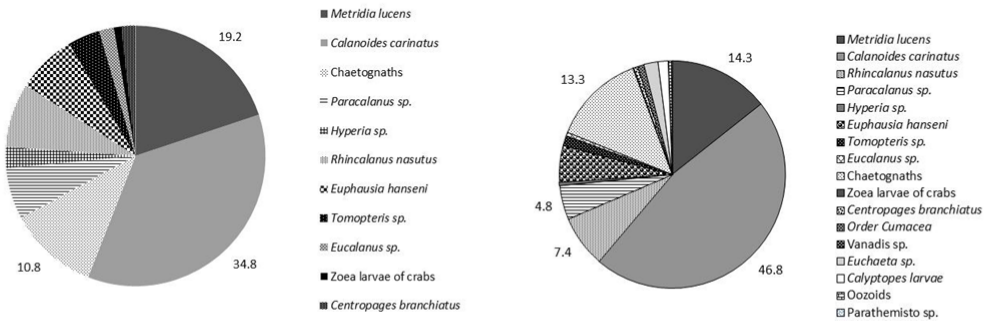

Figure 4: Composition of zooplankton (a) offshore and (b) onshore.

At the offshore stations diversity of zooplankton decreased with depth (Fig.5), however no significant difference in zooplankton diversity with depth was found offshore ($p = 0.406, df = 4$) where diversity decreased from H' = 3.6 at 20 m to H' = 0.8 at 400 m depth. At the onshore stations diversity of zooplankton was low ($H' < 1$) in the top 100m and higher ($H' = 2$) at depths between 200m and 300m (Fig. 5), but no significant difference was found in the diversity with depth at the onshore stations either ($p = 0.406, df = 4$). Furthermore, diversity was higher in the top 100m at the offshore station compared to that of the onshore station (Fig. 5). Diversity of zooplankton between offshore and onshore differs significantly ($p = 0.0271, df = 4$) and the offshore stations had a higher diversity throughout the sampled water column compared to the onshore stations.

There was a positive correlation between DO and diversity of zooplankton offshore (Pearson's r =0.83) (Fig. 6), while there exists a very weak positive correlation between DO and zooplankton diversity onshore (r= 0.196) (Fig. 7).

At the offshore stations diversity was not significantly higher in the top 100 m where higher DO concentrations were measured compared to lower DO concentrations measured at greater depths, exceeding 200 m water depth (Fig. 6). Similarly, at the onshore station a low diversity was measured, even though DO concentrations were similar to that of the offshore stations in the surface 100 m. However, at depths exceeding 200 m water depth diversity was not significantly changing, although DO concentrations were less than 2 ml/L.

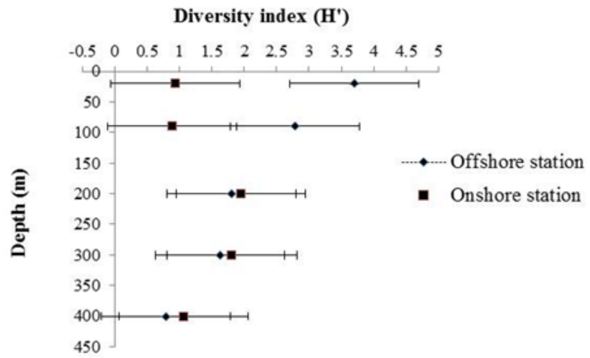

Figure 5: Mean diversity of zooplankton with depth at the onshore and offshore stations. The diversity index at each depth is an average of the stations sampled along each transect and the error bars indicate the standard deviations ($n = 5$).

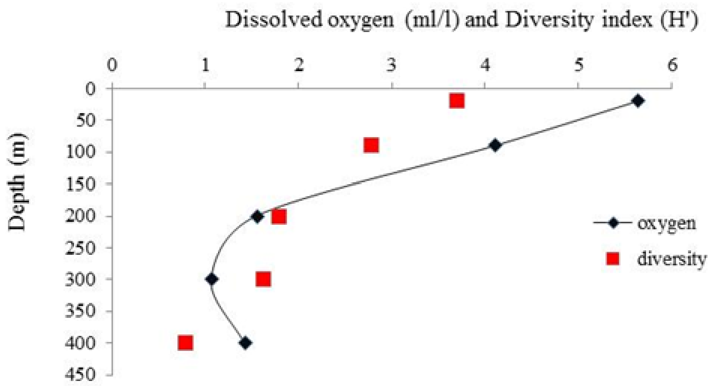

Figure 6: Relationship between DO (ml/L) and the diversity of Zooplankton offshore.

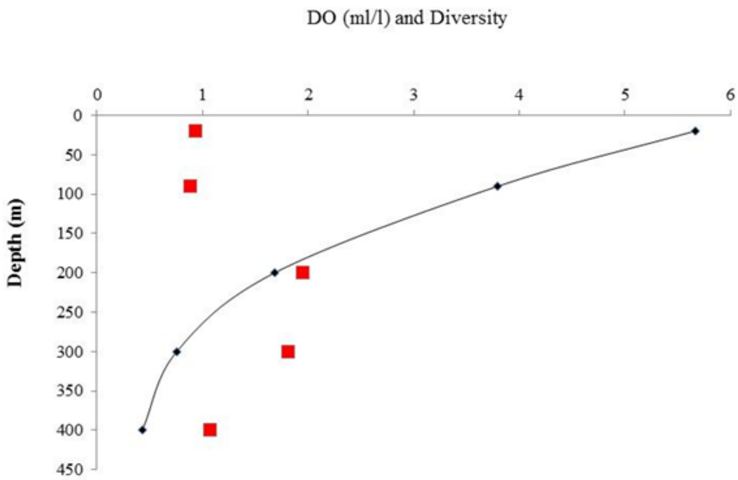

Figure 7: Relationship between DO (ml/L) and the diversity of Zooplankton onshore.

4 Discussion

This study provided a snapshot of the diversity of zooplankton onshore and offshore where oxygen concentrations at a depth of 400 m was twice as high at the offshore stations compared to the onshore stations. The lower oxygen concentrations in the bottom water onshore can be explained by higher amounts of productivity, organic matter and consequently oxygen consumption in the water column onshore (Shannon & O'Toole 1999; Julies et al. 2010). In contrast the surface water (top 20 m) at the onshore stations was saturated above 80% with dissolved oxygen due to the production of oxygen by photosynthesis in the photic zone (Shannon & O'Toole 1999). Water offshore consists of Thermocline Water (Central Water from the South-east Atlantic Ocean) and is the upwelling source water that contains 4.8-5.2 ml/L dissolved oxygen (Shannon & O'Toole 1999), which is similar to oxygen concentrations measured in the present study in the top 20m of the water column.

4.1 The effect of oxygen on the diversity of zooplankton

Low oxygen concentrations in the bottom water of the onshore environment i.e. on the shelf affect the distribution of several marine species (Rabalais et al. 2010; Shannon & O'Toole 1999). However results from the present study indicated that other environmental factors and biotic factors are more important in determining the diversity of zooplankton, since this study revealed only a positive correlation between oxygen and diversity of zooplankton at the offshore stations, but a very weak correlation at the onshore stations. Furthermore, there was no significant change in the diversity of zooplankton with depth at both onshore and offshore stations, although dissolved oxygen concentrations changes significantly.

Similar results were found by Gibbons et al. (1999) who studied the distribution of non-copepod zooplankton off St Helena Bay and suggested that low oxygen in the bottom water may on its own not lead to the accumulation of zoobenthos in the water column, but rather that there exists an interplay between biological and environmental factors which affect changes in zooplankton assemblage composition. Postel et al. (2007) also found that the oxygen minimum zone (OMZ) in bottom water where oxygen concentrations are lower than 0.2 ml/L does not prevent migrating organisms from undergoing vertical migrations. Studies performed by Longhurst (1992), revealed contrasting results to the present study. They collected zooplankton samples at discrete depths off the coast of central Peru and a high abundance and diversity were found at the shelf break, slope and offshore stations (Longhurst 1992). The concentration of oxygen in this area was very high within 5065 m at the slope station and it continued to decrease gradually at a depth of 2035 m at the shelf break station (Longhurst 1992). Offshore oxygen concentration exceeded 1.0 ml/L throughout the upper 85 m and most zooplankton species were limited in vertical distribution by the oxygen concentration of 0.1 ml/L (Longhurst 1992). Clarke and Peck (1991) studied the oxygen consumption of several zooplankton groups in Arctic and Anarctic water and found that the oxygen consumption of zooplankton is directly related to temperature. They also found that different taxonomic groups have different Q10 values, which affect the growth rates and distribution of the organisms. Sea surface temperatures were lower onshore (13-14°C) and at depths exceeding 50m and therefore, oxygen consumption of zooplankton in these areas will be lower as well, due to lower $Q10$. They are therefore able to survive at the low oxygen concentrations measured in these areas. In contrast, oxygen consumption at the higher sea surface temperatures offshore and at the surface will be higher due to higher temperatures (16°C). The effect of dissolved oxygen on the distribution and diversity of zooplankton is therefore an indirect effect that is reflected through their oxygen demand as a result of temperature or other environmental stress factors.

In the north east Atlantic, a close association between zooplankton numerical abundance and concentration of oxygen with depth exists (Boyer and Hampton 2001). Research showed that such vertical distribution resulted from behaviour mechanisms that the species have developed to avoid predation (McManus & Woodson 2012) or to search for food (phytoplankton) (Gibbons et al. 1999) independent of the concentration of oxygen.

4.2 Diversity and composition of zooplankton between offshore and onshore stations

The taxonomic groups found in this study are common members of the zooplankton that were also identified from many previous studies (Postel et al. 2007; Huggett 2009). The most abundant member of the zooplankton both onshore and offshore was *Calanoides carinatus*, which was also encountered in an in-depth study by Gibbons and Hutchings (1996) who studied in particular the development and physiology of *C. carinatus*. According to them their vertical migration and population maintenance strategies allow them to exploit cross-shelf water movements, which explain their dominance both onshore and offshore. The different larval stages of *C. carinatus* are moved onshore and offshore by lateral water movements (Gibbons and Hutchings 1996). The other abundant zooplankton at both onshore and offshore stations was *Rhincalanus nasutus*, which is widespread through most ocean basins and has been reported from shelf and slope areas (Hansen et al. 2005; Irigoien et al. 2005). Both *Calanoides* and *Rhincalanus* are herbivorous. *M. lucens* was also abundant in the samples from both offshore and onshore stations. However, Gibbons (1994) found *M. lucens* to be more common in deep than in shallow water layers.

Diversity of zooplankton in offshore differs significantly from onshore diversity where offshore water has a higher diversity with depth. Similar findings were reported by Shannon and O'Toole (1999). However, oxygen concentration does not have a strong effect on the diversity between offshore and onshore in the Benguela region. In contrast, studies in the southern part of the California Current showed that species composition of zooplankton in the oxygen minimum zone of this area was very low in comparison to the areas that were very rich in oxygen (David 1980).

This study provided a snapshot on the relationship between dissolved oxygen concentrations and diversity of zooplankton with depth and along a longitudinal gradient. Dissolved oxygen does not have a direct effect on the diversity of zooplankton, but an indirect effect and it is the interplay and interaction between several biological and environmental factors that affects zooplankton assemblage composition.

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