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Zooplankton dynamics on the northern Benguela suboxic shelf

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The Benguela Current Large Marine Ecosystem off southwestern Africa is dominated by strong wind-driven coastal upwelling, which sustains high rates of primary production. The productivity has a high temporal and spatial variability caused by aperiodic upwelling of nutrient rich water and the development of mesoscale patterns. On the northern Benguela shelf, a combination of oxygen consumption during mineralisation of sinking detritus and upwelling of oxygen poor tropical South Atlantic central water (SACW) results in oxygen-depleted bottom waters over large areas of the Benguela shelf. We evaluated in this study the long-term and diurnal zooplankton variability of a 2.5 years long, depth-resolved time series recorded at an oceanographic mooring on the northern Benguela shelf.

An oceanographic mooring was continuously operated on the northern Benguela shelf with a bottom depth of 128 m (Fig. x1). A self-contained, upward looking 300 kHz Workhorse Acoustic Doppler Current Profiler (ADCP) was moored at 8 m above the sea bed. The acoustic backscatter target strength was recorded for 2.5 years: 6-Dec-2002 until 1-Apr-2003 and 7-Jan-2004 until 5-Sept-2005, with otherwise only short interruptions of maximal four days. The ADCP sampled the water column at a temporal and spatial resolution of 1 h and 4 m, respectively. Accordingly, three (partial) summer periods (2002/03, 2003/04, 2004/05) and two winter periods (2004, 2005) were studied. Complementary data sets of temperature and salinity were recorded. Dissolved oxygen (DO) concentration was only measured for two partial periods: 12-Dec-2002 until 11-Feb-2003 and 02-Sep-2004 until 04-Sep-2005.

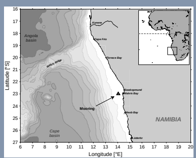

Fig. x1. The location of the mooring at (23°00'S, 14°03'E).

We used the long-term time series of the Acoustic Backscatter Cross Section (ABCS) as an estimate of the total zooplankton dry biomass. A 24 h series of MultiNet hauls was taken on 26/27-Jan-2004. A MultiNet was deployed approximately every 4 h and seven profiles were obtained. We applied the linear regression model without an intercept to obtain a factor to convert the ABCS signal into zooplankton dry biomass (Fig. x2). The coefficient of determination r^2 was 0.73, i.e. 73% of the total variance between of the data was explained by this model.

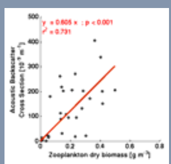

Fig. x2. Linear regression model to convert the Acoustic Backscatter Cross Section into zooplankton dry biomass.

We adopted a Nutrient-Phytoplankton-Zooplankton-Detritus (NPZD)-ecosystem model for the Benguela upwelling system (Fig. 3x). The physical model component is derived from MOM-4. The state variables are three phytoplankton functional groups, one bulk zooplankton, detritus that sinks through the water column, and sedimented detritus on the seafloor. The model explicitly represents several nutrients: nitrate, ammonium, phosphate, but also dinitrogen, elements of the sulfur cycle and oxygen. Prokaryotes are no explicit model variables, but all relevant metabolic processes mediated by them are implemented and the environmental conditions define their metabolic rate.

Fig. x3. Conceptual diagram of the nitrogen-based ecosystem model. State variables are denoted by ellipses (organisms) and circles (nutrients), processes by rectangular boxes, flows with arrows. For the sake of simplicity, not all nutrient fluxes are shown.

Following rules are used to force diel vertical migration (DVM) of bulk zooplankton: It sinks passively with ω_{sink} = -300 m d^{-1} and swims upward with ω_{rise} = -600 m d^{-1}. It avoids light (I > 0.1 W m^{-2}) and hypoxic conditions ([DO] < 5 µmol kg^{-1}). This behaviour is described by two smooth cost functions (Θ_I, Θ_O). Zooplankton follows the food gradient at small food concentrations, but moves randomly otherwise (evaluation function Θ_F). The resulting vertical zooplankton migration velocity ω_Z is:

$$\omega_Z = \min[(\Theta_O + \Theta_I), 1]\,(\omega_{rise}\,(1 + \Theta_F)) + \omega_{sink}$$

Acknowledgements

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High long-term zooplankton variability and the impact of suboxic conditions

A high variability of zooplankton biomass was detected with the 2.5 years long, high resolution time series. Daily-averaged zooplankton dry biomass varied by a factor of one hundred with concentrations of 0.1 - 10 g m^{-3} in the surface water (Fig. 1A) and 1 - 100 g m^{-2} when integrated over the water column (Fig. 1B). A conspicuous period of persistent low concentrations (< 0.01 g m^{-3}) even at 40 m depth was found between January and May 2005. This period coincided with a thick suboxic bottom layer, which was predominantly caused by a high proportion of oxygen poor SACW-water masses (> 55%, Fig. 1).

Zooplankton biomass was always extraordinary low at suboxic conditions. As DO was only measured for half of the sample period, we inspected the frequency distribution of the zooplankton biomass at [DO] < 4 µmol l^{-1} and derived a zooplankton threshold of < 0.001 g m^{-3} indicating suboxic conditions (data not shown). We applied this value to estimate the thickness of the suboxic bottom layer for the entire sampling period (black line in Fig. 1A). ■

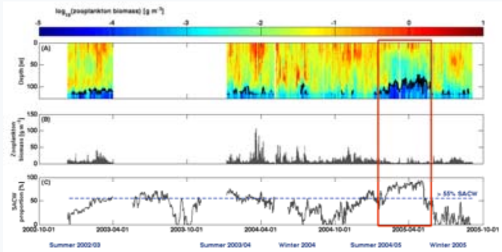

Fig. 1: (A) Daily averaged, depth-resolved zooplankton biomass [g m^{-3}] estimated from the acoustic backscatter cross section. The thickness of the suboxic bottom layer, defined as the water layer with zooplankton biomass < 1 mg m^{-3}, is also drawn (black line). (B) Daily averaged, depth-integrated zooplankton biomass [g m^{-2}]. (C) Fraction of nutrient rich, oxygen poor South Atlantic central water (SACW) as calculated from temperature and salinity data (Mohrholz et al. 2008). The red box marks the persistent suboxic period.

High diurnal zooplankton variability and diel vertical migration (DVM)

The 24 h series of MultiNet hauls showed DVM behaviour of zooplankton (Fig. 2). At nighttime, highest biomass was found at 0-20 m depth and biomass peaks at 30-50 m at daytime. However, we did not regularly detect DVM in the zooplankton time series (Fig. 3). DVM had a strong seasonal signal, occurring maximal half of the days in summer and being very rare in winter. No DVM was detected during the suboxic period between January and May 2005. This supports the ecological hypothesis that (most) zooplankton organisms rather be preyed upon than poisened. The exemplary period with 'DVM-events' lasting seven days (10-Dec-2002 until 17-Dec-2002) suggests that solar radiation is the synchronizer (Fig. 4). While in most cases a large portion of the biomass moves up and down, a substantial part of the biomass (~ 1 g m^{-3}) did not migrate. ■

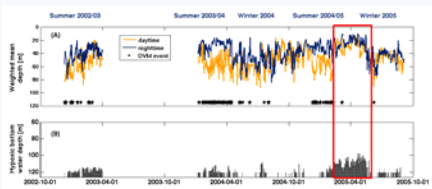

Fig. 3: Weighted mean depth (WMD) of zooplankton biomass during daytime (orange line) and nighttime (blue line). Crosses mark DVM events which were defined as minimal differences between daytime and nighttime WMD of 20 m during at least two consecutive days. The red box marks the persistent suboxic period.

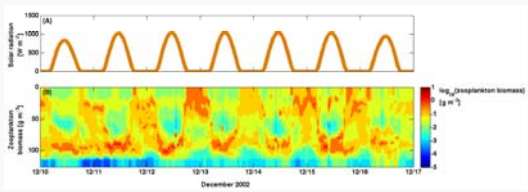

Fig. 4: (A) Diel solar cycle. (B) Hourly, depth-resolved zooplankton biomass of an exemplary period with 'DVM-events' lasting seven days (10-Dec-2002 until 17-Dec-2002).

Implementation of zooplankton in a regional ecosystem model

Bulk zooplankton is implemented in our regional 3D ecosystem model of the Benguela Current System. Depth-integrated zooplankton biomass shows mesoscale features with highest biomass (25-30 mmol N m^{-2}, integrated over 0-40 m) is found along the upwelling filaments (Fig. 5). These concentrations are very similar to field measurements (45 mmol m^{-2}, Heymans 1996). As DVM is assumed to play an important role in the downward flux of particulate organic matter, we implemented this behavior in our ecosystem model. Forced by light, food and oxygen concentration, zooplankton descents at dawn down to ~ 40 m and swims to the surface at dusk (Fig. 6A). The migration depth coincides with the subsurface chlorophyll maximum (Fig. 6B). ■

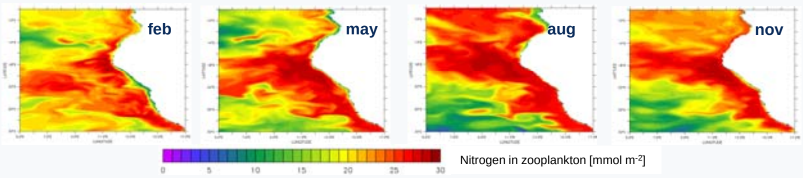

Fig. 5: Monthly averages of zooplankton concentration integrated over 0-40 m water depth for February, May, August and November 2010. The model run from Jun-1999 through Feb-2011 and 5 day averages were written. region

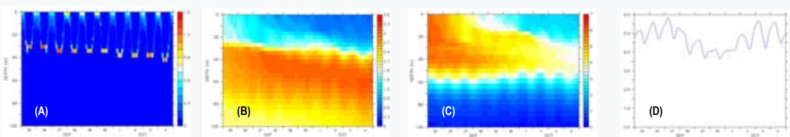

Fig. 6: Results of a temporal high resolution model at 23°S, 14°E. The model run from Aug-1999 through Oct-2001. 3-hour means of model results were written. (A) Depth-resolved zooplankton concentration. (B) Depth-resolved phytoplankton concentration. (C) Depth-resolved detritus concentration. (D) Depth-integrated zooplankton concentration.