Journal of Marine Systems 140 (2014) 130–137

Contents lists available at ScienceDirect

Journal of Marine Systems

journal homepage: www.elsevier.com/locate/jmarsys

Succession of micro- and nanoplankton groups in ageing upwelled waters off Namibia

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ARTICLE INFO

Article history:
Received 29 August 2013
Received in revised form 29 April 2014
Accepted 5 May 2014
Available online 15 May 2014

Keywords:
Northern Benguela
Phytoplankton succession
Species composition
Upwelling
Remote sensing
Diatoms to dinoflagellates ratio

ABSTRACT

The phytoplankton composition was investigated on a cross-shore transect in the Northern Benguela upwelling system in August and September 2011. Micro- and nanorganisms were microscopically analysed and assigned to appropriate phytoplankton groups. The distribution of diatoms, dinoflagellates, coccolithophores and nanoflagellates along the transect was studied in order to reflect the phytoplankton succession. Typical phytoplankton communities indicating different stages of succession were found in relation to the distance to the coast and in relation to the aged upwelled water. Three succession stages could be well defined and verified by satellite data in the newly upwelled water, matured water and aged offshore water. The different stages were distinguished not only by the significant differences in the nutrient concentrations but also by the dominating species and phytoplankton life forms.

A mixed population of dinoflagellates, coccolithophores and microflagellates was observed in the newly upwelled water. Small diatom cells (*Cylindrotheca closterium*) marked the transition to the matured water at about 40 km from the shore. A diatoms to dinoflagellates ratio up to 33 and biomasses up to 250 μgC l^{-1} were characteristic for the matured stage, between 40 km and 250 km from the coast. As observed by satellite data, highly productive water bands intrude the water masses which also represent this stage. They were characterized by accumulated biomasses dominated by diatoms (*Pseudo-nitzschia seriata* group). Diatoms to dinoflagellates ratios less than 1 and maximum biomasses of 15 μgC l^{-1} characterized the aged water at the later stage of succession. Abundances of dinoflagellates smaller than 10 μm increased just after the decline of the diatoms.

1. Introduction

The Benguela region in front of southwest Africa is one of the most intensive upwelling systems of the world (Bakun et al., 2010; Boyer et al., 2000; Nelson and Hutchings, 1983). It is separated into the Southern and the Northern Benguela system by the powerful Lüderitz upwelling cell (Hart and Currie, 1960; Hutchings et al., 2009). The Northern Benguela upwelling system is influenced by southward currents from the Angolan Dome in austral summer, while in late winter nutrient rich water is intruded to the north, owing to most intense winds and upwelling during this season (Boyer et al., 2000; Hutchings et al., 2009; Shannon, 1985). Under normal upwelling conditions as during this cruise, nutrient rich South Atlantic Central Water reaches the upper water layer (Bakun et al., 2010; Stramma and England, 1999) and resting phytoplankton cells contained in the water start to germinate as they are transported to the well lit surface. At the beginning of the phytoplankton succession nutrients are highly available and, depending on the quality of the starting populations, an early bloom may develop (Barlow, 1982b; Mitchell-Innes et al., 1999; Pitcher et al., 1991; Smayda, 1980, 1997). In general diatoms are associated with recently upwelled, nutrient rich water, but red tides caused by dinoflagellates were also detected in the inshore regions of the Northern Benguela (Boyer et al., 2000; Pitcher et al., 1998; Shannon and Pillar, 1986). The conditions for the occurrence of the so called harmful algal blooms have been studied by Smayda and Reynolds (2001, 2003) and Pitcher et al. (2010) but the relationship between the spatial variability and succession of the phytoplankton in the research area is only poorly investigated. As the highly available nutrients in the upwelling water are consumed, phytoplankton groups which are adapted to these nutrient levels may be replaced by those aligned to the altered nutrient conditions. For the Southern Benguela such successions are already described. Barlow (1982a,b) as well as Brown and Hutchings (1987) suggest three stages in the upwelling region: newly upwelled water, matured water and aged water. In the newly upwelled water the production and biomass are found to be low. In the matured water increased production and biomass are considered to be consequences of stabilization and warming. Low production and biomass in the aged water is owed to minimum nutrient concentrations. Different phytoplankton groups have been linked to these stages (Margalef, 1978; Pitcher et al., 1998; Smayda and Reynolds, 2001, 2003). Small cells, preliminary diatoms which are adapted to turbulences and high nutrient concentrations

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http://dx.doi.org/10.1016/j.jmarsys.2014.05.003
0924-7963/

are associated with the freshly upwelled water while larger cells and a significant reduction of nutrients are characteristical for the matured water (Walker and Peterson, 1991). Dinoflagellates, adapted to stratified and nutrient poor waters, are associated to the offshore regions (Hart and Currie, 1960; Margalef, 1978; Shannon and Pillar, 1986). Pitcher et al. (1998) differentiate two dinoflagellate populations: a frontal population resistant to physical disturbation and an offshore population which is subject to nutrient limitation. Smayda and Reynolds (2001, 2003) distinguish three life strategies within nine different types of dinoflagellate populations, of which at least three occur nearshore. In summary, the succession process was well studied in the Southern Benguela, but the Northern Benguela system which has to be separated, is poorly investigated. Biomass values based on cell countings and on the specific biovolumes of the organisms are lacking in the recent literature.

Embedded in the upwelling ecosystem study of this special issue of the Journal of Marine Systems, where hydrographical, chemical and biological analyses concerning the succession have been linked together, the biomass and species composition of the micro- and nanoplankton community is investigated. The aim of this study is to identify the different succession stages and to characterize the water bodies representing these stages, with focus on the phytoplankton as primary producers in a complex system. In this context the different water bodies will be related to satellite data and an age using the concept of pseudo-age (Mohrholz et al., 2014). Differences in the aged and freshly upwelled populations will be pointed out. The development in an isolated- and in a natural waterbody will be compared, using results of mesocosm experiments undertaken on the same cruise (Wasmund et al., 2014). At the end of this study the relationship between temporal and spatial aspects of the succession process will be clarified with regard to the micro- and nanoplankton species composition in the Northern Benguela upwelling region.

2. Methods

The samples were taken during the cruise MSM18/5 of R.V. 'Maria S. Merian' from 23 August to 19 September 2011. To achieve a temporal as well as a spatial resolution of the system the same transect was sampled three times successively between 13°E 20°S and 11°E 21°S which corresponds to a track from 10 km to 250 km from the coast (Fig. 1; T1–T3). All 9 to 12 stations of T1 to T3 were located on the shelf. An elongated fourth transect (T4) reached a distance of 480 km from the coast at 9°E 22.5°S. The additional 6 stations of T4 were supposed to be located in offshore waters. As to be seen from the satellite images, three of the additional six stations were placed in blue green offshore waters (see Fig. 2B).

Remote sensing level-2 products of MODIS sensor (Moderate Resolution Imaging Spectroradiometer) of Aqua satellite were available for the transects T2 and T4 (http://oceancolor.gsfc.nasa.gov/). The surface remote sensing reflectances at 412 nm, 554 nm and 665 nm in a spatial resolution of 1 km were used for the derivation of false colour RGB-images (RGB: red–green–blue) on the basis of VISAT-software (http://www.brockmann-consult.de/). The different colours in the RGB-images represent different waters with different optical water properties. For instance, bluish colours characterize waters with high surface remote sensing reflectances in the blue wavelength range and low concentrations of optical active water constituents. In combination with data like the sea surface temperature, the chlorophyll-*a* (chl*a*) concentration, the biomass, the nutrient composition and other ones, the different false colours can be assigned to different water masses with clearly specified properties. In this study the RGB-images were used for the characterization of Namibian waters, especially in relation to the micro- and nanoplankton community.

Water samples from 0 m and 10 m water depths were taken by means of a rosette sampler and pooled before preservation, in order to get one representative sample of the upper mixed layer. The samples were preserved with neutral Lugol iodine solution to a 0.5% final concentration. Nano- (2–20 μm) and microplankton taxa (20–200 μm) were identified to the species level if possible, under the light- and scanning electron microscope. The numbers of cells were counted according to the method of Utermöhl (1958) by the use of an inverted microscope after sedimentation in 50 ml sedimentation chambers (Hasle, 1978). The counting software "Orgacount" (AquaEcology Oldenburg, Germany) provided an automatic conversion from abundances [cells l^{-1}] into biovolumes [mm^3 l^{-1}] by means of the geometric shapes of the cells (Hillebrand et al., 1999) and a further conversion

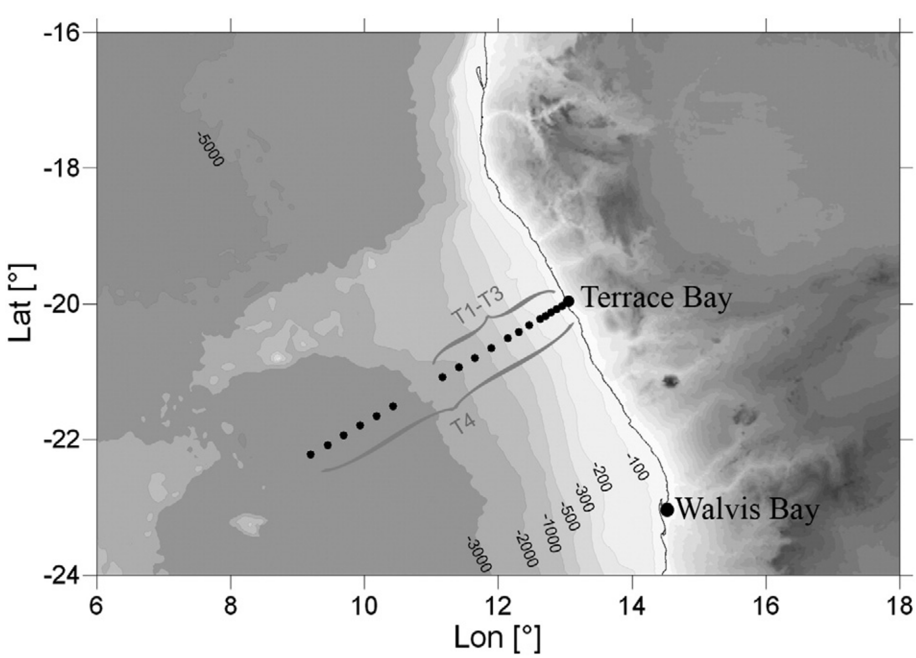

Fig. 1. The investigation area off the Namibian coast is shown. The transect was sampled four times during the cruise MSM18/5 of R.V. 'Maria S. Merian' from 23 August to 19 September 2011.