Available online at www.sciencedirect.com
ScienceDirect
Journal of Marine Systems 67 (2007) 47–58
JOURNAL OF MARINE SYSTEMS
www.elsevier.com/locate/jmarsys

Vertical zonation of the zooplankton community in the Central Baltic Sea in relation to hydrographic stratification as revealed by multivariate discriminant function and canonical analysis

Jan Schulz [a,*], Christian Möllmann [b], Hans-Jürgen Hirche [a]

[a] *Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Germany*
[b] *Institute for Hydrobiology and Fisheries Science, University of Hamburg, Germany*

Received 29 May 2006; received in revised form 1 September 2006; accepted 4 September 2006
Available online 15 November 2006

Abstract

The vertical zonation of zooplankton in a deep central Baltic Sea basin was studied in relation to hydrography based on vertically resolved sampling. The study period covered different seasonal hydrographic conditions as well as inflow events of water masses from the North Sea, important for the physical condition of this marginal sea. By means of multivariate discriminant function and canonical analysis, we show a distinct vertical zonation of the zooplankton community in the water column. Three main habitats, which reflect the hydrographic situation, were identified with distinct differences in zooplankton composition: (1) the summer surface layer, bound by the thermocline at its lower rim; species inhabiting this layer are only seasonally abundant or forced to adjust to the cooler winter water; (2) the intermediate winter water, bound by the halocline from below and the thermocline or surface as the upper boundary; species dwelling in this layer face a reduced volume and are cut off from the high primary production when their habitat is limited from above by the summer thermocline; (3) the layer between the permanent halocline and the seafloor; the taxonomic composition in this layer shows no significant effect in relation to the observed inflows. The consequences of this zonation for trophodynamic interrelationships and advection processes are discussed.

Keywords: Baltic Sea; Stratification; Vertical zonation; Zooplankton; Multivariate discriminant function analysis; Canonical analysis; Community analysis

1. Introduction

In stratified waters, different water masses are intercepted along their contact surfaces by changes in physical parameters (clines). These clines are often characterised by steep gradients of temperature (thermocline) and salinity (halocline) and can put strong constraints on the distribution and dispersal of zooplankton species (e.g., Fager and McGowan, 1963; Banse, 1964; Ackefors, 1969; Hernroth and Ackefors, 1979; Owen, 1989; Yamazaki et al., 2002; Gallager et al., 2004). Hence, they may cause an inhomogeneous biomass distribution in the water column and affect the energy transfer within the food web (Roemmich and McGowan, 1995; Viitasalo et al., 1995; Vuorinen et al., 1998; Ojaveer et al., 1998; Dippner et al., 2000; Möllmann et al., 2000).

* Corresponding author. Alfred-Wegener-Institute, Am alten Hafen 26, 27568 Bremerhaven. Tel.: +49 471 4831 1313.
E-mail address: jan.schulz@awi.de (J. Schulz).

0924-7963/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.jmarsys.2006.09.004

Steep vertical gradients make the deep basins of the Central Baltic Sea a unique study site to investigate the relationship between hydrographic structures and the zonation of zooplankton in the water column. A permanent halocline is present in approximately 60 m depth and separates deep waters with a salinity of often more than 12 from less saline waters of approximately 7, while the upper layer is brackish, freshened by riverine input and precipitation (Fonselius, 1970). The deep saline waters are replaced during inflow events from the North Sea with highly saline and oxygenised waters (Matthäus and Schinke, 1994). During stagnation, e.g., longer times without inflows, the conditions below the halocline deteriorate due to decomposition processes of organic matter resulting in hypoxic or anoxic conditions in the deep and only a narrow zone of oxygenated water remains below the halocline (Fonselius, 1970). In addition to the halocline, the annual thermocline is established in spring, separating the warm surface layer from an intermediate winter-water layer. The zooplankton community in the Baltic Sea consists of freshwater, brackish and marine species which consequently use different parts of this highly stratified habitat (e.g., Ackefors, 1969; Remane and Schlieper, 1971; Hernroth and Ackefors, 1979; Ojaveer et al., 1998). While stenoecious species are expected to inhabit a distinct layer with certain hydrographic characteristics, euryoecious species may use several strata. Consequently, the vertical distribution of the zooplankton species depends on their ecophysiological tolerances and the availability of food resources.

As trophodynamic relationships in pelagic systems depend on spatial overlap of predators and prey, understanding the mechanisms that lead to different vertical distributions is essential (Banse, 1964). Investigation of the physical processes that influence trophic interactions between zooplankton and higher trophic levels in the central Baltic Sea is one of the aims of the GLOBEC-Germany Project (www.globec-germany.de). The present study contributes to this goal by assessing species-specific vertical distribution patterns in the zooplankton and to relate them to the physical environment.

Most methods focus on the distribution pattern of single species (Fager and McGowan, 1963) and it is thus difficult to identify the influence of physical parameters on community assemblages. As the vertical distribution is often a result of more than one parameter, it requires mathematical approaches to extract meaningful results about zooplankton composition from highly variable data. Towards this goal, we applied multivariate disriminant function analysis (MDFA) combined with a canonical analysis (CA) on a data set with a high spatio-temporal resolution. The MDFA addresses the problem how well it is possible to separate two or more groups of samples, given measurements for these on several variables, by a discriminant function calculated from the weighted variables (Manley, 1994). The advantage of this approach in relation to similarity-matrix-based community analysis is further the possibility of the a posteriori analysis of the separating parameters with CA and the quality of the classification. To our knowledge, this work is the first application of a MDFA in the field of zooplankton ecology. Our results show that the thermo- and halocline in the Baltic Sea constrain the vertical distribution of zooplankton species and result in characteristic vertical assemblage patterns in the different layers.

2. Materials and methods

2.1. Sampling

Data were based on the analysis of samples collected on 15 cruises between March 2002 and May 2003 with an almost monthly coverage. Samples were taken at a station located in the deepest part of the Bornholm Basin (95 m depth; 55.292°N, 15.750°E; Fig. 1). Zooplankton was collected using a multinet (Hydrobios, Kiel, 0.25 m^2 mouth opening, 50 μm mesh size) in stacked, 10-m intervals from bottom to surface. As diel vertical migration is not pronounced in the Central Baltic Sea (e.g., Hansen et al., 2004, 2006; Renz and Hirche, 2006) samples were taken regardless of the time of day. A total of 146 samples was preserved immediately after collection in borax-buffered 4% formalin–seawater solution.

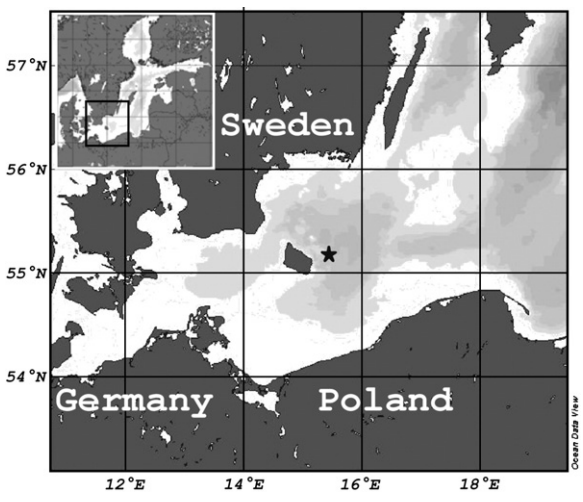

Fig. 1. Sampling site in the Bornholm Basin (Central Baltic Sea).