Spatial and temporal variability of mesozooplankton in the Baltic Sea

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Summary
Spatiotemporal patchiness of plankton, and the adequate sampling strategy to capture the short-scale heterogeneity of the plankton, are crucial for the climate change research of lower trophic levels of marine food webs: they determine the confidence with which statistically significant (spatial differences in) ecological changes can be related to specific causes. Detecting and describing the spatiotemporal heterogeneity is the starting point for discovering the mechanisms that generate and maintain the patchy distribution of plankton. We analyze the spatiotemporal variability of the zooplankton abundance in the Baltic Sea using available monitoring data collected independently by different institutions. We sought dominant patterns in the variability emerging at scales between 1-100 km and 1-90 days, in different hydrological regions of the Baltic Sea (small lagoons, larger gulfs, open Baltic Proper) and by differently sized zooplankton groups – large and small copepods and cladocerans. We show that for most groups and regions, temporal variability dominates over the spatial variability, and that smaller organisms with faster reproduction (cladocerans) vary more in abundance than larger and slow reproducing organisms (copepods). No clear common patterns could be found that would characterize one group in all regions, or all groups in one region. Most often, the highest difference in the abundance is found in samples that are collected about 1 month apart.

Introduction
The plankton of oceans and lakes is distributed patchily. Between the scales 1mm-10m, biological processes dominate, at scales between 10m-1km, biological and physical processes combine and interact, whereas >1 km, physical processes, including wind driven advection, eddies and currents, dominate (Folt and Burns, 1999). Most zooplankton species vary seasonally in abundance and biomass due to their life history strategies and environmental preferences. Cladocerans can increase their numbers in a matter of days to weeks (Egloff et al. 1997), small copepods in weeks to months, large copepods have only one generation per growth season (Hansen et al. 2006). This study quantifies the spatial and temporal variability of zooplankton in different regions of the Baltic Sea within these zooplankton groups. We use the zooplankton monitoring data compiled and harmonized from six institutional monitoring programs, covering small lagoons and bays (Vistula Lagoon, Curonian Lagoon, Pärnu Bay), one larger gulf (Gulf of Riga) and the northern, central and southern Baltic Proper, to answer following questions: Q1: Does zooplankton abundance vary more in space or time, and at which temporal and spatial scales the differences are largest; Q2: do the smaller organisms vary more than larger organisms, and Q3: do the patterns depend more on the region (from small lagoons to the open sea), or the group that is studied (from small cladocerans to large copepods).

Methods
From the data collected by six institutions (see author affiliations, and the website of the dataset: http://kodu.ut.ee/~riina82) we harmonized a dataset consisting of 23000 samples, from 1957-2013. We extracted from that dataset all unique sample pair combinations that were collected within the 100 km distance and 3 months time difference of each other with the same net type. Next, we calculated the
abundance differences of selected zooplankton groups between the samples in each pair, to be used as dependent variable in the later modeling, as
\[ D = \text{abs}[\log(x_1+1)-\log(x_2+1)] \]
where \(x_1\) and \(x_2\) are the abundance in the first and the second sample of the sample pair, respectively. We then fitted the generalized additive model smoothers (GAM) to the abundance differences, using the time (days) and distance (km) between samples as explanatory variables. We used three different GAMs: i) smoothing function of \(D\) against the distance from samples < 5 days apart; or ii) against the time from samples <5 km apart; and iii) two-dimensional smoothing function against the interaction of time and distance using all data. We also used balanced resampling (n=1000) for models i) and ii) to account for the non-uniform distribution of data.

**Results and discussion**

Fig. 1 shows the three types of GAM fits for large copepods in the open Baltic Sea. Similar figures were produced for all groups and regions. From these figures, we collected information regarding the time and distance, at which the maximum difference of abundance is found. These figures revealed variable patterns, and the answers to the three key questions raised in the beginning: Q1: Zooplankton is more variable in time than in space, highest variation was found between the samples 1 month to 40 days apart. Q2: smaller and fast reproducing organisms (cladocerans) vary relatively more in time (up to 30 times), than small or large copepods (up to 8 and 6 times). Q3: Apart from the very high temporal variation of cladocerans, we found yet no clear region- or group specific spatiotemporal patterns. In the current study, scales most relevant for the ecosystem survey design, i.e. up to 100 km and up to 3 months, were addressed, and at these scales, temporal variability of abundance and biomass almost always exceeded the spatial variability. The time between samples being a better predictor of biomass difference at these scales can be explained with strong seasonality in all zooplankton groups in the region (Viitasalo et al. 1992; Hansen et al. 2006), and considering that fluctuations in the drivers of zooplankton seasonal variability (temperature, phytoplankton biomass) are more pronounced at coastal areas (and seas) than open ocean. Baltic Sea, especially the coastal areas, exhibits spatial variability in productivity and zooplankton biomass, as well as in salinity gradients (Viitasalo et al. 1992; Ojaveer et al. 1998). However, this spatial variability was not pronounced at the scales studied here (< 100 km), and also not as consistent as the temporal effect.


