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# Spatial and temporal variability of zooplankton in a temperate semi-enclosed sea: implications for monitoring design and long-term studies

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Spatiotemporal patchiness of plankton and appropriate sampling strategy are crucial considerations for long-term studies of plankton dynamics, determining the confidence with which statistically significant ecological changes will be detected and attributed to the drivers. We analyze the spatiotemporal variability of Baltic Sea zooplankton using historical data from various monitoring programs. We determined the scales of highest temporal and spatial variability, focusing on distances and time periods shorter than 100 km and 90 days. Analyses were made for different hydrological regions (small lagoons, larger gulfs, Baltic Proper), and with differently sized zooplankton groups (large and small copepods and cladocerans). Temporal variability in one place usually exceeded the synoptic spatial variability. Smaller, faster reproducing cladocerans varied more in abundance than larger, slower reproducing copepods. The variability increased with time and distance between samples. For copepods, a temporal cycle of 60–70 days emerged, implying the need for sampling after every 20–23 days. For cladocerans, we propose 14 days as a sampling interval, the time during which the average abundance differences between samples doubled. In the future, these guidelines should be used in conjunction or as an addendum to HELCOM (Helsinki Commission) guidelines, to optimize the zooplankton sampling effort in the Baltic Sea.

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KEYWORDS: zooplankton; spatiotemporal variability; sampling frequency; coastal sea

# INTRODUCTION

The plankton of oceans and lakes is patchily distributed, and the importance of spatial and temporal heterogeneity for plankton ecology is well recognized (Folt and Burns, 1999). Before the biological drivers of patchiness were acknowledged, and based on the then accepted notion that plankton were unable to swim against water currents, zooplankton were considered passive members of patches that were the product of large-scale physical processes (Mackas *et al.*, 1985; Pinel-Alloul, 1995). However, the mechanisms are now recognized to be more complex. Currently, physical and biological drivers are considered to operate at different spatial scales. At under 10 m, biological processes dominate, including predator avoidance, diel vertical migration, searching for food patches and swarming (Kerfoot and Sih, 1987). At scales between 10 m and 1 km, biological and physical processes combine and interact. At scales >1 km, eddies, currents and wind-driven advection dominate (Folt and Burns, 1999). In coastal and shelf environments with strong salinity and temperature gradients, spatial distribution may also be limited by environmental preferences; for example, reduced salinity or higher temperatures can limit the distribution of large marine copepods that prefer cold and saline water (Pershing *et al.*, 2010; Otto *et al.*, 2014).

Temporal variation in the distribution of zooplankton is usually expressed on seasonal time scales and is the product of biological factors, including reproduction, predation and other forms of mortality and wind-induced mixing and eddies (Wiafe and Frid, 1996). Most zooplankton vary seasonally in abundance due to their life history strategies and environmental preferences. Abundance of cladocerans can increase in a matter of days to weeks (Egloff *et al.*, 1997; Park and Marshall, 2000), small copepods in weeks to months, and large copepods often have only one generation per year (Hansen *et al.*, 2006). In open systems with strong currents, temporal dynamics of zooplankton communities take place while drifting along with water masses. In those systems, the spatial and temporal variability needs to be considered interactively, whether when merely describing and explaining zooplankton patterns and their control mechanisms (Ji *et al.*, 2010; Pershing *et al.*, 2010), or when modeling predator-prey interactions and fish recruitment (Hansen *et al.*, 2006). The EU Marine Strategy Framework Directive (MSFD) and the associated Commission Decision (European Commission, 2008, 2010) require advanced understanding of the variability of plankton communities along spatial and temporal scales, not only to define target levels of indicators, but also to develop appropriate ecosystem survey designs.

In the Baltic Sea, zooplankton time-series data have been collected since the 1950s (Viitasalo, 1992; Ojaveer *et al.*, 1998). The basin-wide coordination of zooplankton monitoring was started by the Helsinki Commission (HELCOM) in 1979, which aims to harmonize sampling and analysis methods to obtain comparable data covering the whole Baltic Sea area (HELCOM, 2014). Although the guidelines provide detailed suggestions on the sampling procedures and sample counting, no guidelines about spatial or temporal sampling frequency have been given so far, and each institute, depending on its aims, still has its own sampling strategy.

In this study, we analyzed zooplankton spatiotemporal variability from the data that have been collected between 1957 and 2012 within the auspices of nine institutional monitoring programs. Institutes usually sample at standard stations within their respective national waters. The data covered three small lagoons or bays (Vistula Lagoon, Curonian Lagoon, Pärnu Bay), one larger gulf (Gulf of Riga), and the northern, central and southern Baltic Proper (Fig. 1). We compared spatial and temporal variability, not only to compare their relative importance, but also to develop optimal sampling strategies for the future. We expected to see higher temporal variability of smaller and faster reproducing organisms than of larger and slower reproducing organisms. We tested this prediction by comparing the patterns of four

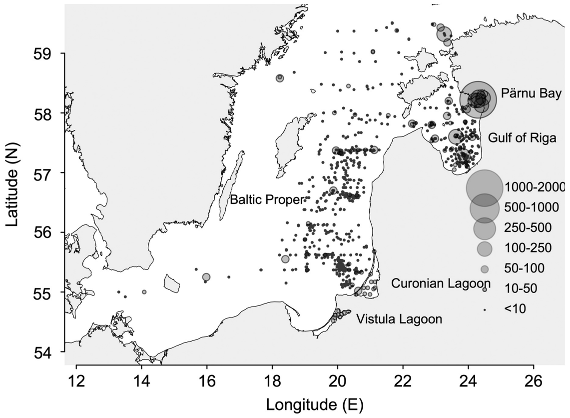

**Fig. 1.** Map of the samples used in the analysis (8760 samples). Size of the circle indicates the number of samples collected from each site.

functional groups of crustacean mesozooplankton: small and large cladocerans and copepods. We also tested whether the dynamics within these functional groups differed among regions. Although zooplankton is patchy at all scales, from millimeters to kilometers, and from hours to months, the data used here cannot resolve patterns shorter than 1 day, and smaller than 1 km. Therefore, we focus on the patterns at intermediate scales, during one season and at distances between 1 and 100 km. Patterns emerging at these scales are the most useful for designing monitoring sampling strategies.

## METHOD

### Data harmonization

Raw data were usually stored in Excel worksheets and organized in the wide format, with one column per variable, and included metadata (sample time, location, and depth), as well as the abundances of organisms in the samples. This format is wasteful, as the tables consist mostly of zeros, especially if the list of organisms is long. Therefore, the raw data were re-organized into two tables: a "count" table and "sample" table. The count table contains the species counts in a long format, where one column specifies the sample from which the measurement is made, the second column a variable and third column the value of the variable. The sample table contains the metadata of the samples in a wide format, including also the details of data providers, sampling gear and any other sample-specific variables. An identifier (sampling ID) is cross-indexed between sample and count tables. In most cases, the sampling represented the whole water column, by means of a vertical tow from bottom to the surface. In the deeper regions, the vertical tows were performed in 2 or 3 sections, data that were also kept. The most time-consuming part of the harmonization process was addressing differences in taxonomy and nomenclature in the original data sets. These included different taxonomic resolution (especially for rotifers and small cladocerans), number of copepodite stages that were counted separately (either all of I-V, or in groups I−III and IV−V), and numerous typos and misspellings of species names. In some cases, the organism was given as the abbreviation (e.g. "EaI" for *Eurytemora affinis* copepodite stage I), that had to be corrected manually and checked and confirmed individually. The original name of the organism was kept as a reference, just in case. These names often also specified the stage and gender. In such cases, the information was re-organized into separate columns with the currently used name, the stage, and gender. Harmonization of all the raw data yielded a dataset of 16 800 vertical profiles (hereinafter referred to as "samples") and 25 000 vertically separated subsamples (http://kodu.ut.ee/~riina82/).

Before 1979, samples were collected and processed according to UNESCO (UNESCO, 1968) guidelines, and since 1979, according to HELCOM guidelines (Manual for Marine Monitoring in the COMBINE Programme of HELCOM, Annex C-7). Different sampling gears have been used: 100 µm WP-2 net, and Juday nets with 90 µm, and 160 µm mesh size. Such small mesh sizes were used to include rotifers, small cladocerans, and naupliar stages of copepods in the samples. The sampling intervals and locations were determined by the aims of the original sampling, which were either environmental monitoring, or the assessment of fish stocks and their food sources. The longest running sampling has been in the Pärnu Bay (Gulf of Riga, since 1957), and the Baltic Sea wide sampling frequency increased markedly after 1979.

### Statistical analysis

All sample pairs that were collected both within a 100 km distance and 3 months time of each other were identified. Each such sample pair was combined with the following additional information: sample IDs of both samples, distance between them (km), time difference (days), respective depths (m) and the gear that was used. Pairs were discarded if the samples were not collected with the same sampling gear, had a depth difference of $>30$ m or were from separate lagoons. The resulting data set consisted of 4700 and 9700 sample pairs from Vistula and Curonian Lagoons, respectively (based on 270 and 491 samples), 122 000 from Pärnu Bay (3894 samples), 14 400 from the Gulf of Riga (1937 samples) and 13 400 from the Baltic Proper (2168 samples).

Based on their size and life cycle, organisms were divided into four functional groups: large copepods (e.g. *Pseudocalanus* sp., *Limnocalanus macrurus*, *Centropages hamatus*), small copepods (e.g. *Eurytemora* spp., *Acartia* spp.), large cladocerans (e.g. *Daphnia* spp., *Leptodora kindtii*, *Cercopagis pengoi*) and small cladocerans (e.g. *Bosmina* spp., *Evadne* spp., *Pleopis*/*Podon* sp.). Sample pairs were discarded if a particular functional group was absent in one of the samples in a pair. Copepod abundances included adults and copepodite stages IV and V. All abundances were converted from individuals $m^{-3}$ to individuals $m^{-2}$, thus integrating the counts of the entire water column. When the profile consisted of more than one vertical subsampling, the value used in the analysis refers to the whole water column abundance, integrated over all vertical sub-samplings. The dependent variables in the modeling were the abundance differences

($D$) of different zooplankton groups, calculated for each sample pair as:

$$D = |\log(x_1) - \log(x_2)|$$

where $x_1$ and $x_2$ are the abundance of the particular zooplankton group in the first and the second sample of the sample pair, respectively.

## Pattern detection

It was assumed that with increasing distance and/or time, the differences between the sample pairs would increase up to a certain point that marks the scale of dominant patterns. The Baltic Sea is strongly seasonal, with a rapid increase of water temperature in the late spring, and cooling in autumn. Species with narrower temperature optima should go through distinctive peak abundance periods during the year. When analyzing the total abundances within any given functional group, not individual species, the resulting patterns will depend on whether the species' abundance peaks coincide with each other.

The abundance differences of sample pairs were modeled as a non-parametric generalized additive model (GAM) smoothing function of the time (days) and/or distance (km) between samples. Three types of GAMs were fitted for every functional group and region: (i) a smoothing function of $D$ against time, using only the sample pairs where the distance between samples was $<5$ km, (ii) a smoothing function of $D$ against the distance, using only the sample pairs where the time between samples was $<5$ days apart and (iii) a two-dimensional smoothing function of $D$ against the time and distance. For the first two models, the selection criteria of $<5$ km and $<5$ days were chosen as a compromise to assure a reasonable number of sample pairs in each model while keeping the variability minimal. Different hydrological regions were represented by Pärnu Bay, Vistula Lagoon and Curonian Lagoon (shallow and coastal), the Gulf of Riga (large gulf, intermediate depth) and Baltic Proper (open sea). In the first two models, the thin plate regression spline was used, setting "4" as the maximum dimension of the basis when constructing the smooth term, and using a Gaussian error distribution (function *gam* in R library *mgcv*). In third model, the tensor product smooth function (smooth term "*te*") was used to fit the $D$ on two-dimensional surface of time and space.

To ensure that the emerging patterns were not significantly affected by the uneven distribution of data points over the time difference or spatial distance axis, the first two models were fitted 1000 times with resampled data. In resampling with replacement (function *sample* in R *base* library), each sample pair was weighed with 1/frequency of the sample pairs within a particular time or distance class, so that in the resampled dataset, each time and distance class was represented by a similar number of sample pairs. The 1000 refitted models yielded fitted values and adjusted $R^2$, which were used as a proxy for the ecological significance of patterns.

To compare the temporal and spatial variability of functional groups in different regions, mean curves derived from 1000 fitted lines are shown. The first turning point of $D$ along the mean curve is identified, in case it emerges, and the value of $D$ at the beginning of the curve, and the time or distance to the point where the $D$ reaches twice the starting value. The mean $R^2$ of 1000 models is reported to compare the strength of the patterns between groups and regions. Fitted values were back-transformed from log to linear scale, so that the $y$-axis values correspond to the multiplicative difference of abundance between the samples (exponent of the subtraction of log-transformed values corresponds to division of non-transformed values). The two-dimensional GAM fitted $D$ to time and distance simultaneously, using all possible combinations of time and distance between the samples, without resampling. The temporal models were also fitted to the most frequently observed taxa that were listed above as examples of the members of four functional groups, extracting the doubling times of starting values to test the expectation that smaller and faster reproducing organisms show higher temporal variability, not only for the functional groups, but also for each individual taxon.

The analytical approach used here is in principle similar to the variogram analysis, which quantifies the variation as a function of distance between the individual measurements with a parametric function. However, variogram analysis assumes that the spatial pattern does not change in time, or at least did not while the measurements were done, and that variation in values only depends on the distance between the points. This is not the case here, since the patchiness of plankton results from interaction of spatial and temporal dynamics. All conventional variogram fitting functions use the spatial coordinates to cluster the measurements into distance classes. To be done properly, only data that were collected simultaneously could have been used, or averages of repeated samples from the same location. The latter would be again problematic, as it integrates the spatial and temporal dynamics; the same location after 1 week time is not truly the same anymore as far as drifting organisms are concerned. The solution of using sample pairs that are disconnected from exact dates and locations, looking only at the pairwise distance and time difference of samples, is a powerful solution in the current case, as it allows the direct effect of space and time between the samples to be studied using all the data points with another data point collected in suitable proximity.

## RESULTS

The temporal variation usually exceeded the spatial variability (left and middle panels in Figs 2–5), except for the large copepods (Fig. 5). Variability of small and large cladocerans (Figs 2 and 3) increased either nearly monotonously with increasing time between samples, without an intermediate maximum, or that maximum appeared quite late (after 65 days for large cladocerans in Vistula Lagoon, Fig. 3). For copepods, highest differences were found between samples 20 and 30 days apart (Figs 4 and 5). Spatial patterns (middle panels) were diverse, without noticeable common patterns across groups or regions. Values of *D* at the beginning of curves (starting values) indicate the potential variability of samples collected within 5 km radius from each other the same day (left panels), or of the samples collected up to 5 days apart

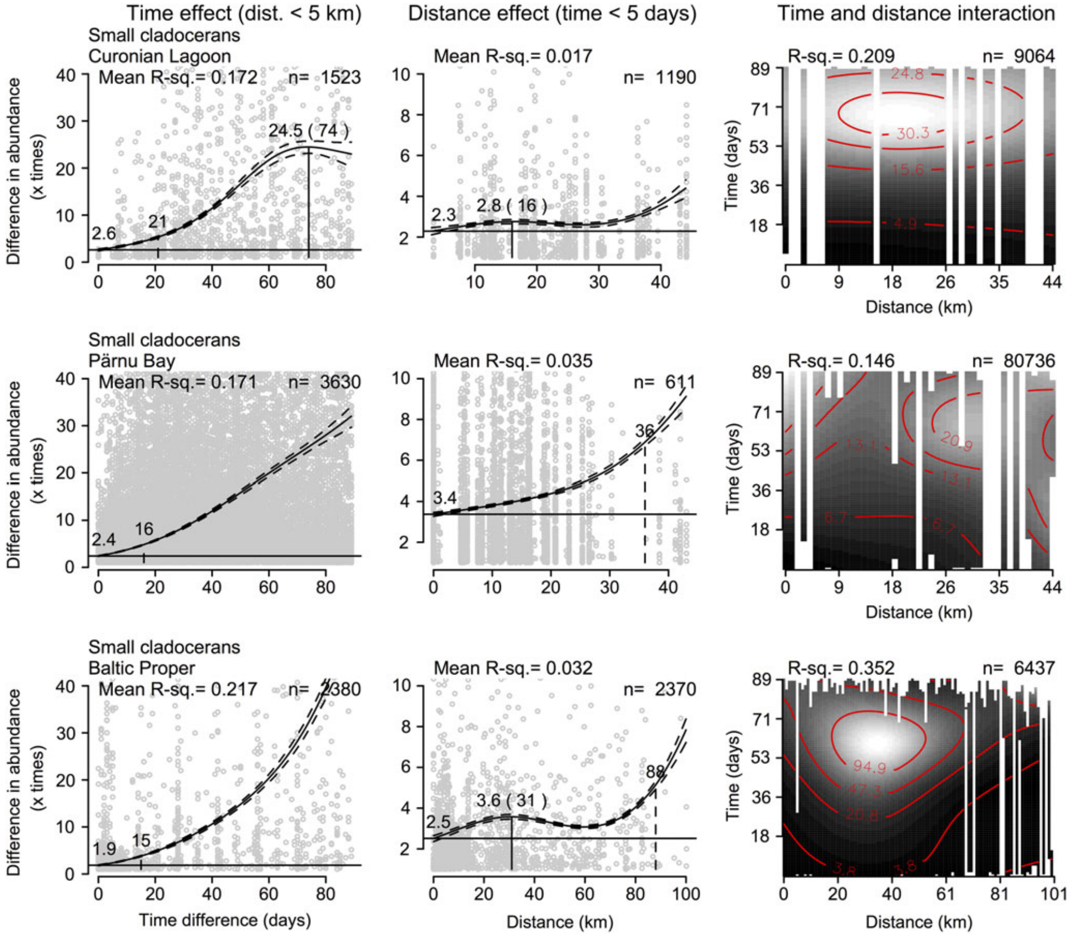

**Fig. 2.** Temporal (left panel), spatial (middle panel) and spatiotemporal (right panel) variability of small cladocerans in Curonian Lagoon, Pärnu Bay and open Baltic Proper. Grey points are the observed differences, but figures do not include all values, the upper range of *y*-axis was accommodated to the fitted values, so that the shapes of the curve would still be discernible. Curves and $R^2$ values on left and middle panels are averaged from 1000 GAM fits of resampled data, confidence intervals show the 25th and 75th percentiles of 1000 fitted values. The first value at the beginning of each curve is the starting value of the curve. In case a local maximum occurs on the curve (such as in middle panel of Curonian Lagoon), it is marked with two values: the fitted value, and the *x*-axis position of maximum (in parentheses). The point where the curve approaches double the starting value is marked with an *x*-axis value (for example the left panel of Curonian Lagoon, "16" days). *n* is the number of sample pairs in each analysis. The right panel shows the trend of *D* simultaneously in time and space. When either spatial or temporal variability dominates, the resulting surface is vertical or horizontal gradient, respectively. When temporal and spatial dynamics are interacting, due to displacement of water masses hosting the communities, the pattern is either a diagonal gradient (increasing *D* from lower left corner to higher right corner), or regions of higher values somewhere along the diagonal. To save space, only the results from these regions are shown for each group where there was enough data for consistent and discernible patterns to arise.

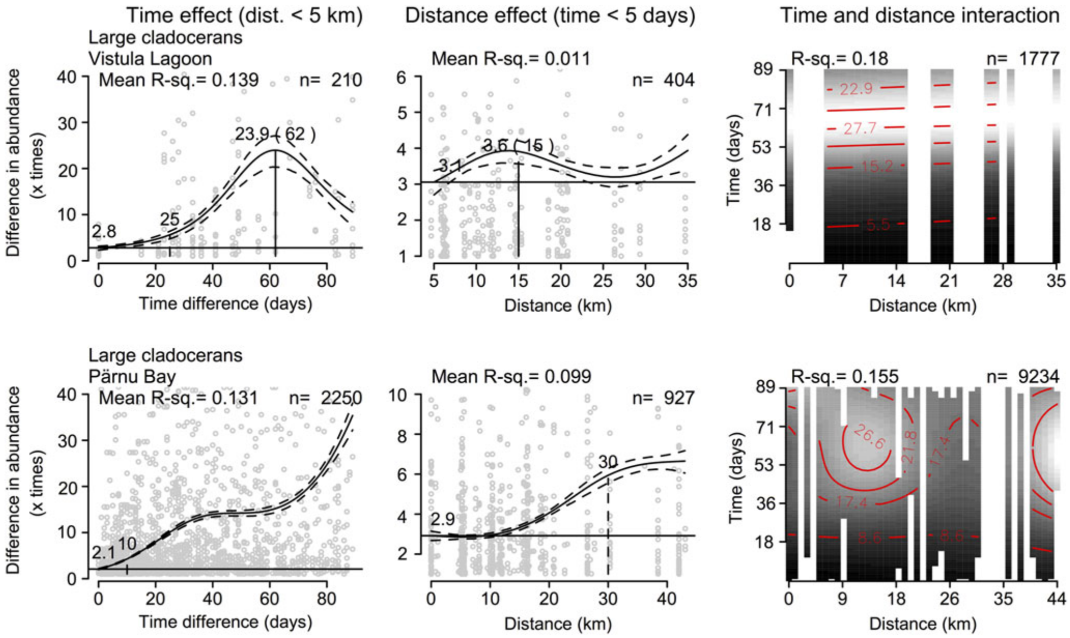

**Fig. 3.** Temporal, spatial and spatiotemporal variability of large cladocerans in Vistula Lagoon and Pärnu Bay. For details, see the legend of Fig. 2.

in exactly the same location (middle panels), and these values usually ranged from 2 to 3.

Spatiotemporal models (right panels) resulted in vertical or diagonal gradients over the surface of time *versus* space. Vertical gradient indicates strong effect of temporal dynamics, the diagonal gradient is expected when the temporal and spatial dynamics of communities are interacting, for example due to currents and spatial displacement of water masses hosting the communities. Clear vertical patterning can be seen in Vistula and Curonian Lagoons (Figs 2–4). In all other regions, irrespective of the group, the fitted values increase along the diagonal gradient.

Faster reproducing cladocerans, small and large, were temporally more variable than slower reproducing copepods (40 times *versus* 10 times, Figs 2–4). Small copepods were more variable in time (up to 10 times) than large copepods (up to 6 times) (Figs 4 and 5). The same pattern holds for individual taxa (Fig. 6), although the variability within the functional groups was notable.

The average $R^2$ values of models ranged from 0.01 to 0.35. Temporal and spatiotemporal GAMs of cladocerans had close to an order of magnitude higher explanatory power (0.13–0.35) than the respective spatial GAMs (0.01–0.04). With copepods, the $R^2$ were similar between the temporal and spatial models, but also much lower than of the models of cladocerans (0.008–0.066). Only the $R^2$ values of spatiotemporal models of small copepods in Vistula Lagoon and the Gulf of Riga were notably higher (0.1 and 0.18).

# DISCUSSION

We quantified the temporal and spatial variability in the abundance of four zooplankton functional groups in the different hydrological regions of the Baltic Sea. As expected, in most cases, temporal variability exceeded spatial variability. The temporal variability decreased as the size of organisms increased, and reproduction rate decreased. Spatial patterns were less important in small closed lagoons, where the abundance patterns showed temporal synchrony. The role of currents was more apparent in the open sea.

## Scales of temporal and spatial variation in abundance and biomass of zooplankton

Large spatial and temporal scales have been simultaneously considered in many zooplankton investigations in marine ecosystems. Gislason *et al.* (Gislason *et al.*, 2009) compared zooplankton between the south and north of Iceland and found marked differences in the abundance and species composition, driven mainly by hydrography. Pershing *et al.* (Pershing *et al.*, 2010) analyzed long-term zooplankton patterns from Continuous Plankton Recorder data along the shelf seas off the northeast coast of USA, and found that temporal variability in dominant copepods was driven by spatial displacement of oceanic waters and changes in salinity. Harris *et al.* (Harris *et al.*, 2013) demonstrated spatial variability in the effects that large-scale atmospheric patterns (North Atlantic Oscillation) place on

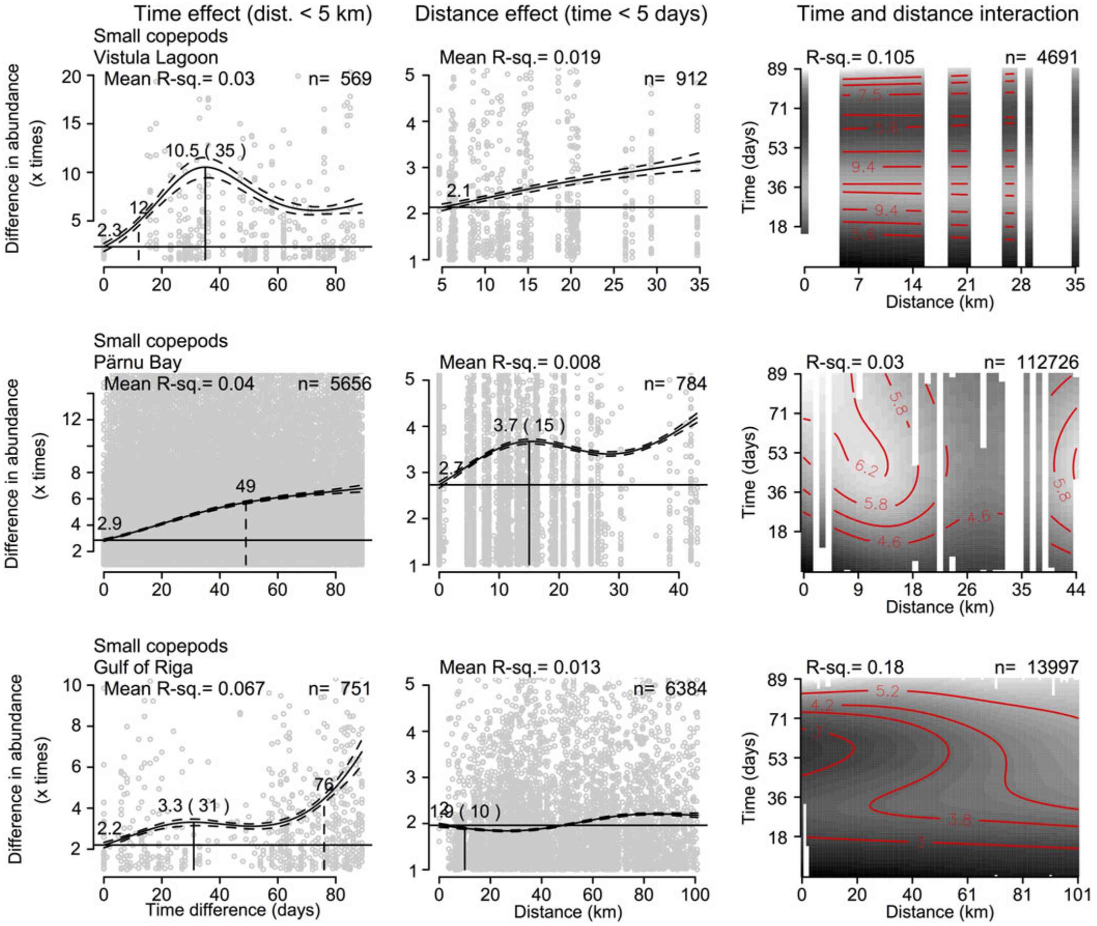

**Fig. 4.** Temporal, spatial and spatiotemporal variability of small copepods in Vistula Lagoon, Pärnu Bay and Gulf of Riga. For details, see the legend of Fig. 2.

plankton dynamics. In the Baltic Sea, Otto *et al.* (Otto *et al.*, 2014) showed that the climate variability affects different zooplankton groups differently, and that the effect is spatially variable and linked to the water column structure in different sub-basins. In all these studies, spatial variability played an important role in zooplankton variability, comparable with temporal variability. However, the spatial and temporal scales of these comparisons always exceeded the scales that were considered in present study.

Other studies show that spatial heterogeneity is a significant component of zooplankton variability at small (1 mm−10 m) and mesoscales (10 m−1 km) (Folt and Burns, 1999). For routine monitoring, sampling within the scales below 1 km is not cost-efficient, neither is it likely that daily variability in abundance will be assessed. Therefore, we focused on the scales that are most relevant for the optimization of ecosystem survey design, up to 100 km and up to 3 months. At these scales, temporal variability of abundance and biomass generally exceeded spatial variability, except for the large copepods (mostly *Pseudocalanus* spp. and *Limnocalanus macrurus*). The time between samples being a better predictor of abundance difference can be explained with strong seasonality in all zooplankton groups in the region (Hansen *et al.*, 2006; Lennuk *et al.*, 2016), considering that fluctuations in the drivers of zooplankton seasonal variability (temperature, phytoplankton biomass) are more pronounced in coastal areas (and seas) than the open ocean.

The Baltic Sea, especially the coastal areas, exhibits spatial variability in productivity, zooplankton abundance and salinity, all of which affect the dominant species composition (Viitasalo, 1992; Ojaveer *et al.*, 1998). However, this spatial variability was not pronounced at the scales studied here (<100 km), nor was it as consistent as the temporal effect. Most often, the highest variability of copepod abundances emerged between samples 30 and 35 days

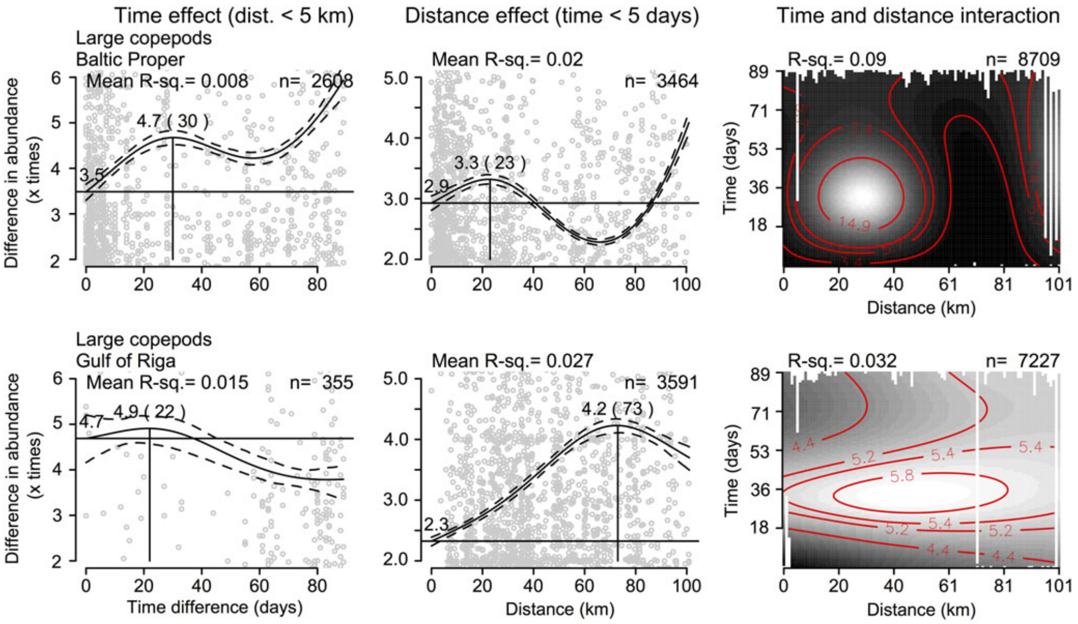

**Fig. 5.** Temporal, spatial and spatiotemporal variability of large copepods in open Baltic Proper and Gulf of Riga. For details, see the legend of Fig. 2.

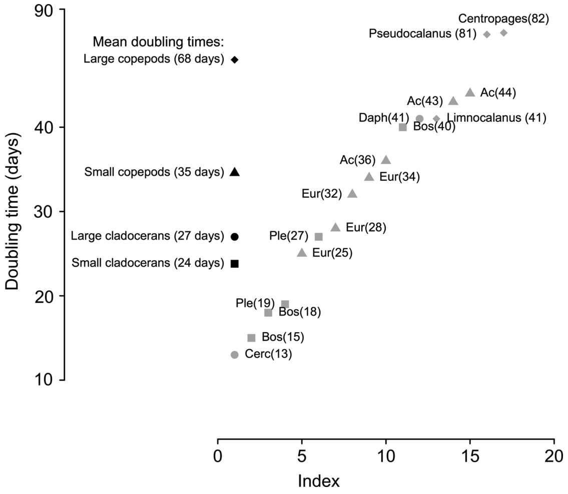

**Fig. 6.** Temporal variability of individual taxa. The taxon-specific doubling times from these regions where taxa were abundant are plotted in increasing order along the *x*-axis, symbols distinguish the functional group that each taxa belongs to. Next to each point, the name of a taxon and the doubling time in days are provided: Ac, *Acartia* sp.; Bos, *Bosmina* sp.; Cerc, *Cercopagis pengoi*; Daph, *Daphnia* sp.; Eur, *Eurytemora affinis*; Lim, *Limnocalanus* sp.; Ple, *Pleopis* sp. or *Podon* sp. Means of doubling times per functional group are shown with black symbols. Note that *y*-axis is no longer linear above the value 45.

apart, while variability in the cladoceran abundance increased nearly monotonously with the time between samples.

## Faster reproducing organisms have higher temporal variability

The expectation that fast reproducing organisms vary temporally more than slow reproducing organisms was supported. The temporal variability in cladocerans exceeded the variability of the copepods. Within the two groups, small copepods varied more than large copepods, and small cladocerans more than large cladocerans. This result is not surprising, but still relevant, since finding predictable patterns supports the robustness of the methods and the data. The $R^2$ values, despite of being relatively low in all models, demonstrated the relatively stronger role of temporal dynamics in the cladoceran communities.

## Are the patterns linked to the region or the organism group?

Spatiotemporal patterns had some region-specific properties. In the small and closed Vistula and Curonian lagoons, zooplankton dynamics were more in synchrony. In all other regions, highest differences in abundance were found when the sample pairs were separated both by time and distance. In coastal areas (Vistula and Curonian Lagoons and Pärnu Bay), the variability maximum was sometimes found at distances below 100 km. That can be due to the geography of the coastline and hydrography of the lagoons, or to the sampling scheme, which was in some cases limited to only few stations. Hydrological conditions, such as inflow regimes of large rivers, timing of ice break-off during spring, depth, and bottom vegetation, can cause differences in seasonality of abundance at very small spatial scales, leading to more pronounced spatial differences in abundance (Lesutiene *et al.*, 2012).

Relatively higher spatial variability was characteristic of large copepods. Large copepods mostly consist of *Pseudocalanus* spp. and *Limnocalanus macrurus*. Both of them are under stress in the Baltic Sea due to fish predation (Sandström, 1980; Kornilovs *et al.*, 2001), but *Pseudocalanus* spp. also due to low salinity, and *L. macrurus* due to high temperature and low oxygen. These species usually have one generation per year, in contrast to cladocerans and small copepods that can produce multiple generations per year. The reproductive differences and tolerance limits could explain the relatively stronger spatial variability of large copepods. With only a few generations per season, temporal variability in abundance is weaker, whereas small changes in environmental constraints (temperature, salinity) can cause peaks in mortality.

### Implications for monitoring designs and long-term assessments

The relative higher temporal variability of most zooplankton groups indicates a need for higher temporal sampling frequency at the expense of spatial frequency, especially in the small lagoons and gulfs. This advice is timely as the EU member states are revising their monitoring programs to meet the requirements of the MSFD (European Commission, 2008, 2010). These aim to obtain reliable data for ecosystem assessments, including zooplankton, for indicators of biodiversity, non-indigenous species and food web dynamics.

The patterns for different groups were diverse at first sight. Nevertheless, some guidelines can be envisaged. Sampling interval needs to be three times shorter than the pattern one desires to capture, or at least four samplings per full cycle (Platt and Denman, 1975). The highest variability of copepods that was mostly found at 30–35 days between samples, implies a dominant cycle of 60–70 days and 20–23 days for the sampling interval. This is the least conservative estimate, because with better data coverage, we might have detected even shorter cycle. For cladocerans, we did not detect a cycle within the 90 days. We propose to use the time step at which the difference in abundance is twice the difference at the beginning of the curve (i.e. between the simultaneously collected samples) as a desired sampling interval. In most cases, this would be around 14 days. These results call for caution when using data collected once per season to interpret long-term trends. Zooplankton definitely follow a recurrent seasonal cycle, and seasonal peaks for all groups can be identified from already existing long-term datasets. However, interannual variation in the timing of these cycles can vary by as much as couple of weeks. Mistiming the sampling relative to the seasonal cycle may bias the annual and long-term trend estimates, especially when climate warming might shift phenological events over the years. For short-term variation that cannot be captured with the sampling frequency used, such as that caused by diurnal vertical migration of zooplankton, Platt and Denman (Platt and Denman, 1975) suggest an integrated sampling that would average these variations out, which is currently done by taking the vertically integrated samples that cover the entire water column.

## CONCLUSIONS

Sampling zooplankton is necessary to keep track on what's happening with the sea, and every country that borders Baltic Sea shares that obligation. However, it is not clear how often one should sample, in time and space, to assess the inter-annual variability and trends. Sampling zooplankton is expensive and labor-extensive. Samples are analyzed microscopically, and each sample takes a (highly qualified) person about 3–4 h of microscope work. In this study we used the existing and sub-optimally sampled data to determine the optimal sampling strategy. Because the dataset was compiled from independently collected datasets from nine institutions, each of them sampling for their own purposes, we obtained reasonably good data coverage, even if no extra sampling was done for this analysis. Pooling all available data resulted in about 25 000 samples, theoretically representing about 12 500 working days. We analyzed differently sized organism groups, small and large copepods and cladocerans, in different hydrological regions. In most cases, temporal variability in one place exceeded the synoptic spatial variability, and smaller, faster reproducing cladocerans varied more in abundance than larger, slower reproducing copepods. The average abundance differences systematically increased with increasing time and space between samplings. The desirable sampling intervals detected were 20–23 days for copepods, and 2 weeks for cladocerans. In the future, these guidelines should be used in conjunction with, or as an addendum to, HELCOM guidelines, to optimize the sampling effort of zooplankton in the Baltic Sea.

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