

Climate-induced hydrography change favors small-bodied zooplankton in a coastal ecosystem

by

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ABSTRACT

In the Baltic Sea, the climate change is expected to reduce salinity and increase temperature, and shift mesozooplankton communities towards dominance of small-bodied brackish-water taxa and cause a decline in large-bodied marine taxa. Here, we analyse environmental monitoring data, collected in a coastal area in the northern Baltic Archipelago Sea during May–September, 1967—2013, for trends and relationship between mesozooplankton biomass anomalies, salinity and temperature. During the study period, the surface water temperature increased and salinity decreased. Since the mid-1980s, the community was dominated by small-bodied brackish-water taxa whereas large-bodied calanoid copepods and marine taxa were mostly scarce or absent from the samples. The observed decline of marine taxa was related to the decline in salinity and, to some extent, to the increase of temperature. The brackish-water taxa were, for the most part, positively influenced by the temperature increase, although possibly other direct or indirect factors, not considered in this study, were also influencing the dynamics. This study adds to the knowledge of a possible on-going shift in the food web structure towards smaller-sized species and emphasizes the significance of long-term environmental monitoring in understanding the dynamics in plankton communities.

Keywords: Zooplankton, Salinity, Temperature, Baltic Sea, Time series

INTRODUCTION

The Baltic Sea and its climate have been under a constant change over the last 10 000 years (BACC, 2008). However, environmental monitoring only covers the last 50 years with biological oceanographic data (e.g. [Segerstråle, 1969](#)), and time series have been only collected on a regular basis since the 1970s by the Baltic Marine Environment Protection Commission (Helsinki Commission or HELCOM). In the existing hydrographic time series, sea water salinity changes show a clear signal with subsequent consequences in biological time series. For example, during the 1970s increased rainfall led to a decrease in salinity (Hänninen et al., 2000) that consequently caused changes in the abundance and biomass of zooplankton taxa (Vuorinen et al., 1998), herring prey composition, and herring growth (Flinkman et al., 1992; Hänninen et al., 2000, 2003; Vuorinen et al., 2003). These changes were most pronounced in the northern Baltic Sea as the impact of runoff is not as strong in the southern Baltic Sea (Rajasilta et al., 2006). In addition, the effect of global warming has already been observed as a slight increase in water temperature at sea surface (Leppäranta & Myrberg, 2009; BACC II, 2015). However, in coastal areas, so far no trend in temperature has been observed that could explain the changes in zooplankton species diversity (Vuorinen et al., 1998; Dippner et al., 2001), although such results have been reported for offshore areas (e.g. Suikkanen et al., 2013).

Here, we study the state and dynamics of mesozooplankton community composition, the biomass of individual taxa, salinity and temperature in the Archipelago Sea during a 46-year time interval. The current study is a continuation of previous studies focusing on different periods of the time series over the years 1967–1996 (Vuorinen & Ranta, 1987; Ranta & Vuorinen, 1990; Vuorinen et al., 1998). As little attention has been given to the monitoring series since the study by Vuorinen et al. (1998), this study provides a long-needed update on

the long-term dynamics of mesozooplankton taxonomic composition. In this study, we combined monitoring data, used in the previous studies, with new monitoring data. Our working hypothesis is based on the expected outcome of the global climate change in the Baltic Sea (BACC, 2008; BACC II, 2015) that predicts a decrease in salinity (due to increased runoff) and an increase in temperature. As the salinity and temperature tolerances of zooplankton taxa largely depend on their origin (e.g. marine, brackish-water and freshwater), spatial distribution and stratification patterns, causing the taxa to react differently to short- and long-term fluctuations in salinity and temperature (Flinkman et al., 1998; Ojaveer et al., 1998), these changes are expected to favour small-bodied brackish-water taxa, inhabiting the surface layer and, conversely, be unfavourable to large-bodied marine taxa, inhabiting the deep water layers (see e.g. Viitasalo et al., 1995). Therefore, we studied whether the community composition and the biomasses of dominant taxa have (1) changed between 1967–1984 and 1991–2013 and (2) whether they are connected to long-term and/or short-term fluctuations in salinity and temperature. The purpose of the present study was also to (3) study the dynamics of the small-bodied brackish-water and large-bodied marine taxa between 1967–1984 and 1991–2013, periods before and after the last ecosystem regime shift in the Baltic Sea in 1989/1990 (Möllmann et al., 2009).

MATERIAL AND METHODS

Study area

The study area is an extensive archipelago of the southwest coast of Finland, in the northern Baltic Sea (59°45'N – 60°45'N and 21°–23°E). (Fig. 1). The sampling site lies in a relatively open middle region of the Archipelago Sea (HELCOM, 2013). Zooplankton and water samples were collected from a monitoring station (60°15.315' N, 21°57.174' E) by the Archipelago Research Institute of the University of Turku. The station is located in the

vicinity of the Island of Päiväluoto, which lies between two stretches of open water, Airisto and Omenaistenaukko (Fig. 1). The study site is characterized by long, continuous, 50 m deep channels, enabling saline water flow to the inner archipelago region (Virtaustutkimuksen neuvottelukunta, 1979), and pronounced freshwater impact from rivers. The halocline is also weak and stratification is mainly controlled by temperature (Leppäranta & Myrberg, 2009).

Hydrographic data

Since 1967, hydrographic parameters (salinity and temperature) have been measured all year round at ca 10-day intervals as a part of the long-term monitoring of the Archipelago Sea water quality by the former Finnish Institute of Marine Research (FIMR) and the Finnish Meteorological Institute (FMI). Since the beginning of the time series, temperature (°C) and salinity (PSU) data have been collected with a Limnos-sampler (capacity of 3.6 L) (0 m, 5 m, 10 m, and 20 m water depths considered in this study). Prior to statistical analyses, we calculated monthly arithmetic means for each water depth in order to stabilize the measurement intervals. Also, the temperature and salinity data during 1967–2013 were depth-averaged over the sampled water column 0–20 m.

Mesozooplankton data

Since 1967, vertical zooplankton samples have been collected once a month all year round. From 1967 to 1984, the samples were collected with a Hensen net (mesh size 150, μm , mouth diameter 70 cm). Since 1991, samples have been collected with a standard plankton net (mesh size 150 μm , mouth diameter 33 cm). Throughout the data set, the samples were collected in a single haul from the depth of 25 m to the sea surface. The contents of the net were emptied to a 250-mL plastic bottle and stored in buffered formalin (4%). The samples were analyzed

according to standard methods (HELCOM, 1988) first, during 1967–1984, by the former Finnish Marine Research Institute (FIMR) and later, during 1991–2013, by a Company Zwerver. Throughout the data set, the samples were identified to either species or genus level, whenever possible. Copepods were identified into copepodite stages CI–CIII, copepodite stages CIV–CV, females, and males. Cladocerans and rotifers were identified as juvenile, and/or adult stages. Prior to statistical analyses, we pooled the developmental stages of each copepod taxa into copepodite (inc. CI–CV) and adult stages (inc. females and males). Altogether 56 different taxa were identified from the samples. Zooplankton data, considered in this study, were sampled from May to September, 1967–1984 and 1991–2013, consisting of 205 samples in total. No zooplankton data were collected during 1985–1990.

In order to obtain biomass values (wet weight mg/m^3), we multiplied abundance (individuals/ m^3) with taxon-specific body wet weight values for all taxa and development stage that wet weight values were available in the literature (Flinkman et al., 1998; [Hernroth, 1985](#)): *Acartia* spp. adults and copepodites (including mainly *A. bifilosa*, *A. longiremis*, and *A. tonsa*), *Eurytemora affinis* adults and copepodites, *Centropages hamatus* adults and copepodites, *Temora longicornis* adults and copepodites, *Limnocalanus macrurus* adults and copepodites, *Pseudocalanus elongatus* adults and copepodites, *Bosmina longispina* adults and juveniles, *Evadne nordmanni* adults and juveniles, *Podon polyphemoides* adults and juveniles, *Podon intermedius* adults and juveniles, and *Synchaeta baltica*. These taxa represent >50% of the total abundance of zooplankton in the time series.

From the taxon-specific biomass values, we calculated a value for total zooplankton biomass. Pooled biomasses were also calculated for small cladocerans (inc. *E. nordmanni*, *P. polyphemoides*, *P. intermedius*, and *B. longispina*) and Copepoda (*Acartia* spp., *E. affinis*, *C. hamatus*, *T. longicornis*, *L. macrurus*, and *P. elongatus*). In order to study whether salinity

and temperature variation had influenced the zooplankton community as expected, pooled biomasses were also calculated for small-bodied copepods, having an affinity for warm and low-saline waters (*Acartia* spp., and *E. affinis*) and for large-bodied copepods, having an affinity for either cold and high-salinity waters (*C. hamatus*, *T. longicornis*, *P. elongatus*) or cold and low-salinity waters (*L. macrurus*). Pooled biomasses were also calculated for all brackish-water taxa (*Acartia* spp., *E.affinis*, *B.longispina*, *P.polyphemoides* and *S. baltica*) and marine taxa (*C.hamatus*, *T.longicornis*, *P.elongatus*, *P. intermedius* and *E.nordmanni*).

Annual anomalies

To visualize, study and facilitate comparisons of the inherently highly variable temperature, salinity, and mesozooplankton biomass data in the study period, we converted the raw biomass data to annual anomalies according to a method, described by Mackas & Beaugrand (2010) and O'Brien et al. (2013). Annual anomalies were calculated for the following groups and taxa present in both time series: total zooplankton biomass, Copepoda, small copepods, large copepods, small cladoceras, brackish-water taxa, marine taxa, *Acartia* spp. adults and copepodites, *E. affinis* adults and copepodites, *C. hamatus*, *P. elongatus*, *L.macrurus*, *T. longicornis*, *B.longispina*, *P. polyphemoides*, *E.nordmanni*, *P. intermedius* and *S.baltica*.

Then, each zooplankton time series ($B(t)$) was \log_{10} -transformed, while temperature and salinity were not. After that, we calculated a long-term seasonal average (\bar{B}) for each month. Due to differences in the sampling methods during 1967–1984 and 1991–2013, the long-term seasonal average was calculated separately for the two time periods. After calculating the long-term average, we subtracted each month's long-term average from each month-by-year value in order to calculate the monthly anomaly values. Then, we calculated annual anomalies ($b'(t)$) for all of the study years as the average of all the monthly anomalies present in that

year. In summary, the unitless annual anomalies ($b'(t)$) were calculated in the following manner:

$$b'(t) = \log_{10}[B(t)] - \log_{10}[\bar{B}] = \log_{10}[B(t)/\bar{B}]$$

Finally, linear regression lines between the annual anomalies and year were drawn for each anomaly figure. The anomaly calculations and visualizations were done using COPEPOD's Interactive Time-series Explorer (COPEPODITE) toolkit (O'Brien et al., 2013).

Statistical analyses

Trends in hydrography and mesozooplankton

As COPEPODITE calculates the trend from annual anomalies with linear regression and, thereby, is dependent on sample size and cannot include information on seasonal variation, we also used a nonparametric seasonal Kendall test to analyse the environmental variables and the \log_{10} -scale monthly anomaly mesozooplankton data for monotonic trends during May–September, 1967–2013. The test was done for the same taxa and developmental stages that annual anomalies had been calculated. The test was chosen because it combines the seasonal Kendall's test for trend (Hirsch et al., 1982), the Belle-Hughes heterogeneity test (van Belle & Hughes, 1984) and the Hirsch & Slack's (1984) extension allowing for serial dependence in the observations. The test was performed using the “KendallSeasonalTrendTest” function of the “EnvStats” package 1.0.2 in R version 3.2.0 (R Development Core Team, 2015).

Relationships between mesozooplankton and environmental variables

We studied the long-term effect of the salinity and temperature on mesozooplankton biomass anomalies with Generalized Linear Mixed Models (GLMM) with the procedure GLIMMIX in SAS® v. 9.4 (SAS Institute Inc., 2009). We fitted the models to monthly log-scale anomaly

data of 7 groups (total zooplankton biomass, brackish-water taxa, marine taxa, Copepoda, small copepods, large copepods and small cladocerans) and 7 taxa (*Acartia* spp. adults and copepodites, *E. affinis* adults and copepodites, *B. longispina*, *E. nordmanni* and *S. baltica*) that were present frequently and abundantly enough to fit the models. The monthly anomaly of each group or taxon was the dependent variable, i.e., altogether 14 separate models were formed. The depth-averaged anomalies of salinity and temperature (0–20 m) were used as fixed explanatory variables. Before GLIMMIX, the distributions and covariance structures of each variable were examined with SAS Enterprise Guide® 4.3.-software (SAS Institute Inc., 2009) in order to choose a correct link function and covariance matrix. Based on this analysis, we applied a normal distribution with the link function “IDENTITY” in each model. The covariance matrix structure had, without exception, a first order autoregressive structure $AR_{(1)}$, which is typical in time series. For this reason, we controlled the autocorrelation of the time series by a first-order autoregressive structure (a random-statement with ARH(1) as a covariance structure in GLIMMIX). The denominator degrees of freedom were calculated with Satterthwaite approximation in order to adjust the degrees of freedom for the unequal variances (SAS Institute Inc., 2009). Residual pseudo-likelihood was used as the default estimation technique. Overdispersion was controlled by modeling the residuals as residual-type random components (“random_residual_” statement in GLIMMIX) with observations as a subject-effect. The assumption of homoscedasticity of variances was tested with a “COVTEST”-statement in GLIMMIX that analyses whether varying the covariance parameter between years shows an increased fit in the model.

We studied the effect of high- and low-salinity and temperature periods (i.e. short-term periods) on the zooplankton anomalies with post-hoc comparisons whenever a significant relationship was observed between the response and explanatory variables. The differences were studied between a) periods of high- and low-salinity/temperature and other years and b)

between the high- and low-salinity/temperature periods. We modeled the comparisons using “ESTIMATE”-statements in the models (SAS Institute Inc., 2009). The maximum and minimum salinity/temperature values used in the analyses were selected on the basis of annual averages shown in Table 1. For more details, see Table 3.

RESULTS

Trends in hydrography

During May–September, 1967–2013, the sea water salinity decreased from ca. 6.4 to 5.9 (Fig. 2) in all studied water depths (0 m, 5 m, 10 m and 20 m) (Table 2). Simultaneously, the temperature increased from ca. 11.0 to 12.5 °C (Fig. 2) in all studied water depths (Table 2). During the study period, thermocline developed annually approximately at 17 m depth, the sampling point at 20 m water depth being just below the bottom edge of the thermocline.

Changes in mesozooplankton

The decline of salinity and increase of temperature was reflected in the mesozooplankton community composition, most obvious of which was the decreasing abundance of marine taxa (Seasonal Kendall, $\tau = -3.17$, $p = 0.002$) and large copepods ($\tau = -4.91$, $p < .001$) (Fig. 3). On the contrary, no significant patterns were found in the total zooplankton biomass, brackish-water taxa, Copepoda, small copepods and small cladocerans (Fig. 3).

The small-bodied brackish-water taxa *Acartia* spp. or *E. affinis* showed mostly negative anomalies at the beginning of the time series and mostly positive anomalies from 1991 to 2005. Nevertheless, no monotonic abundance trends were observed for either taxon. The large-bodied marine copepods (*C.hamatus*, *T. longicornis*, and *P.elongatus*) were mostly

present and fairly abundant in 1967–1984. Also, the large-bodied glacial-relict species *L.macrurus* was, for the most part, present during the first years of the time series. However, after 1991, the negative annual anomalies of most of the large-bodied copepods either increased or the species appeared in the samples sporadically or were almost totally absent from the samples (Fig. 3). However, over the whole data set a significant decreasing trend was observed for only *C.hamatus* adults ($\tau = -3.19$, $p = 0.002$) and copepodites ($\tau = -5.41$, $p < .001$) and *T.longicornis* copepodites ($\tau = -6.34$, $p < .001$). For the others, no trend could be either found (*T.longicornis* adults) or determined due to zero-inflated data (*P.elongatus* and *L.macrurus*). On the contrary to large-bodied copepods, small cladocerans were abundantly present throughout the study period. The most pronounced change was observed for *B.longispina* that showed only positive anomalies from 1991 to 2000 and mostly negative anomalies from 2000 to 2013 (Fig. 3). Nevertheless of these changes, no significant trend was found for *B. longispina*, whereas the brackish-water cladoceran species *P. polyphemoides* clearly decreased in abundance ($\tau = -2.97$, $p = 0.003$). Similarly, the marine cladocerans *E.nordmanni* and *P. intermedius* also decreased ($\tau = -2.40$, $p = 0.02$; $\tau = -4.80$, $p < .001$, respectively). No trend was observed for the brackish-water rotifer species *S. baltica*, which was relatively abundant throughout the study period.

Relationships between the mesozooplankton taxa and environmental factors

The relationship between salinity, temperature and mesozooplankton anomalies varied considerably between each studied taxa and group. The most evident result was the negative influence of the salinity decrease on the total zooplankton biomass, Copepoda, marine taxa and large copepods (Table 3). On the other hand, the temperature increase seemed to have a negative influence on Copepoda and marine taxa, but the results did not give very strong evidence on this (Table 3). Conversely, the brackish-water taxa showed a positive relationship

with temperature, but the results did not give very strong evidence on this either as no significant relationships were observed with the high- and low-temperature periods (Table 3; Fig. 4). No significant relationships were either observed for the small-bodied copepods as *Acartia* spp. and *E. affinis* showed somewhat mixed responses to the environmental variables: salinity and temperature had a positive influence on *Acartia* spp. adults whereas no significant relationships were found for *Acartia* spp. copepodites and *E. affinis* (Table 3). The high-salinity periods had a positive influence on both *Acartia* spp. adults and *E. affinis* copepodites whereas no significant relationships were observed with the low-salinity periods (Table 3). Conversely, small cladocerans showed no significant relationships with either salinity or temperature, although the increased temperature seemed to have a positive influence on both *B. longispina* and *E. nordmanni* (Table 3; Fig. 4). The rotifer *S. baltica*, on the contrary, showed a strong negative relationship with salinity. The high-salinity years seemed to have had a negative effect on the *S. baltica* biomass whereas the low-salinity years had had a positive effect (Table 3; Fig 4). In addition to the salinity decrease, the results also indicated that the temperature increase had a favourable influence on *S. baltica* (Table 3; Fig. 4).

DISCUSSION

The global climate change scenarios for the Baltic Sea, such as the projection presented by the BALTEX Assessment of Climate Change (BACC, 2008; BACC II, 2015), predict a 2 to 4 °C increase in the annual sea water surface temperature towards the end of this century, whereas the sea water salinity predictions are ambiguous and range between -45% and +4% (BACC, 2008; BACC II, 2015). So far, the coastal and pelagic ecosystems of the Baltic Sea have undergone major environmental changes both due to climate-driven changes in hydrography and to anthropogenic influence (e.g. Hänninen et al., 2000; Möllmann et al., 2009). The present study also confirms that, in the northern Baltic Archipelago Sea, a major transition in

environmental conditions occurred in 1967–2013, from more saline summer conditions, towards higher summer temperatures and lower salinity levels. The observed changes in hydrography are in consent with trends found in other areas of the Baltic Sea (e.g. Möllmann et al., 2009; Suikkanen et al., 2013) and are connected to a period of mostly positive anomalies of the North Atlantic Oscillation (NAO) index in the last 20–30 years (e.g. Hänninen et al., 2000; Visbeck et al., 2001).

Our working hypothesis is based on the expectation that species of different origin (mainly marine and brackish-water) would react differently to short- and long-term fluctuations in salinity and temperature. In general, the warming and freshening of the water column is expected to favor small-bodied brackish-water species (rotifers, small cladocerans and small copepods) and be unfavourable to marine species (mainly large-bodied copepods). In consent with this hypothesis, our results indicated that the summer mesozooplankton community composition has changed during 1967–2013, most obvious of which was the declining of large-bodied copepods and marine taxa. The abundance of the small-bodied copepods and brackish-water taxa remained relatively stable throughout the study period, reflecting their wide tolerance for salinity and temperature. We did not find any abundance trends in the total biomass of zooplankton, Copepoda or small cladocerans, most likely because they incorporate both marine and brackish-water taxa, showing contrasting dynamics.

Thus far, salinity has been considered to be the most important environmental factor influencing the mesozooplankton in the study area (Vuorinen & Ranta, 1987; Ranta & Vuorinen, 1990; Viitasalo et al., 1990; Vuorinen et al., 1998). In the present study, salinity was the major influencing factor for the large-bodied copepods and marine taxa, whereas the small-bodied copepods and brackish-water taxa mainly responded to changes in temperature or showed no significant results. Nevertheless the total biomass of zooplankton, Copepoda

and small cladocerans showed no abundance trends, their dynamics seemed to be negatively connected to the salinity decline and also, partly, to the temperature increase. Despite of the observed group-level trends and relationships, the results were not clear for all individual taxa as in some species and developmental stages, no trend was either observed (e.g. *T.longicornis* copepodites, *Acartia* spp. and *E.affinis*) or could be determined due to zero-inflated data (*P.elongatus* and *L.macrurus*). The almost total absences of *P.elongatus* and *L.macrurus* were not surprising as *P.elongatus* requires high salinities for reproduction (Möllmann et al., 2002) and *L.macrurus* requires low salinities and cold temperatures (Ackefors, 1969; Hernroth & Ackefors, 1979). It is unclear to which extent the results of these large-bodied species were influenced by vertical migration behavior as the species are able to migrate below 25 m depth. Therefore, during sampling, the taxa could have been either genuinely absent or located below our sampling depth. As our focus was not on the vertical distribution and migration of the species, further studies, collecting samples below 25 m depth, are required to verify this. Conversely to the large-bodied copepods, both the daily and ontogenetic migration of rotifers, small cladocerans and small copepods in the northern Baltic Sea takes place in the 0–25 m depth range (Burris, 1980; Holliland, 2012), exposing the taxa to a constant variety of environmental factors. Therefore, the non-significant and variable results of rotifers, small cladocerans and small copepods are most likely linked to the species' wide tolerance zones.

However, as we found some relationships between the brackish-water species' biomasses and the environmental parameters, it is possible that the freshening and warming of sea water could have influenced the species' dynamics through other, environmental or indirect, factors, not considered in this study. For example, the brackish-water taxa, located above the thermocline, could have been affected by environmental factors that are directly or indirectly coupled to solar radiation (Viitasalo et al., 1990), for example, a shift in phyto- and/or microplankton (Otto et al., 2014) or an increase in visual predation (Ljunggren et al., 2010;

Suikkanen et al., 2013). In comparison, the large-bodied marine species, located below the thermocline, are suggested to be most affected by changes in salinity (Viitasalo et al., 1990). The dynamics could have also been influenced by several factors acting concurrently. For example, increased predation pressure together with changes in the hydrography could force the species migrate deeper in the water column and, thereby, imply several costs to the taxa, such as longer generation development times (due to low temperature), decreased fecundity and poor food, that could be detrimental to the species population growth (as discussed for *E. affinis* by [Vuorinen, 1978](#); [Lehtiniemi & Gorokhova, 2008](#)).

The sampling frequency could have also affected the detection probability of fast-reproducing taxa, such as parthenogenetically reproducing small cladocerans. According to [Klais et al. \(2016\)](#), an optimal sampling frequency for copepods is 20–30 days, whereas for cladocerans it is 14 days. Therefore, the monthly sampling interval of our data (mean sample size of 5 per year) might explain some of the observed inconsistent long-term trends and relationships. The different size of sampling equipment in 1967–1984 and 1991–2013 could have also influenced the sampling efficiency to some extent, although we took the difference into account in the statistical analyses.

To conclude, our study describes the long-term changes in the mesozooplankton community in the northern Baltic Archipelago Sea in response to the freshening and warming of surface water. Despite of the limitations in sampling frequency, the present study clearly shows that since the mid-1980s, the mesozooplankton community in the studied coastal area has been dominated by small-bodied brackish-water taxa, large-bodied calanoid copepods and marine cladocerans being scarce or even totally absent from the samples. The decline of large calanoid copepods and marine taxa were connected to the salinity decrease and also, to some extent, to the warming of sea water. On the contrary, the brackish-water taxa showed only few

abundance trends, but their dynamics were mainly connected to the increase in surface water temperature, albeit the connections were not totally clear and likely involve other factors, such as changes in visual predation and phytoplankton abundance, not considered in this study. Together with studies from other areas of the Baltic Sea (e.g. Berglund et al., 2007; Suikkanen et al., 2013), our study adds to the knowledge of a possible ongoing shift in the food web structure towards smaller-sized species and emphasizes the significance of long-term environmental monitoring in understanding the plankton dynamics.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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FIGURE LEGENDS

Fig. 1 Study area and location of the sampling site (red point) in the northern Baltic Archipelago Sea.

Fig. 2 Annual positive (red) and negative (blue) anomalies (May–September, 1967–2013) of a) salinity (PSU) and b) temperature (°C) at 0–20 m water depth in the northern Baltic Archipelago Sea. Lines are linear regressions of the annual anomalies vs. year (solid black line = $p \leq 0.01$). Note the difference between Y-axes.

Fig. 3 Annual positive (red) and negative (blue) biomass (wet weight mg/m^3) anomalies (May–September, 1967–2013) of mesozooplankton taxa in the northern Baltic Archipelago Sea. No data during 1985–1990 (black points). Blank circles indicate that the number of individuals of the taxon in question was below the detection limit in the sample. The lines represent linear regressions of the annual anomalies vs. year (solid black line = $p \leq 0.01$; dashed black line = $p \leq 0.05$; grey line = non-significant). Note the difference between Y-axes. Ad = adults; cop = copepodites.

Fig. 4 Box-and-whisker plots of annual mesozooplankton biomass anomalies during selected high- and low-salinity (S) and temperature (T) years. a) High S years: 1973–1976, 1978, 1980; (b) Low S years: 1994, 2001–2002, 2007, 2010, 2013; c) High T years: 1992, 2002, 2007–2009, 2011; d) Low T years: 1977–1979, 1982, 1996, 1998). Note the difference between Y-axes. Ad= adults; cop= copepodites.

Table 1 Selected maximum and minimum values of salinity and temperature. The values in the table show annual averages of May–September salinity (S; PSU) and temperature (T; °C) at 0–20 m water depth.

High S years	High S	Low S years	Low S	High T years	High T	Low T years	Low T
1975	6.44	2013	5.74	1992	13.12	1977	10.32
1973	6.46	2001	5.76	2009	13.14	1979	10.38
1980	6.55	2007	5.80	2011	13.28	1996	10.45
1976	6.56	1994	5.82	2008	13.69	1998	10.47
1974	6.56	2010	5.84	2002	13.87	1982	10.51
1978	6.7	2002	5.87	2007	14.13	1978	10.56

Table 2 Mean and standard deviations and Seasonal Kendall test results for monotonic trends in temperature and salinity at 0 m, 5 m, 10 m, 20 m water depths. The overall number of observations was 235.

Depth (m)	Temperature (°C)						Salinity (PSU)					
	Mean±SD	n	Z	tau	Slope	p	Mean±SD	n	Z	tau	slope	p
0	13.90 ± 4.51	232	3.31	0.15	0.03	<.001	6.07 ± 0.28	229	-9.36	-0.43	-0.01	<.001
5	13.34 ± 4.66	232	4.72	0.21	0.03	<.001	6.10 ± 0.27	229	-10.08	-0.46	-0.01	<.001
10	12.32 ± 4.73	232	6.00	0.27	0.04	<.001	6.13 ± 0.26	229	-10.27	-0.47	-0.01	<.001
20	8.80 ± 3.93	232	4.10	0.19	0.04	<.001	6.24 ± 0.26	234	-11.28	-0.51	-0.01	<.001

Table 3 Fixed effect solutions for mesozooplankton monthly anomalies, showing the effect of surface layer (0–20 m) salinity (S; PSU) and temperature (T; °C) during May–September, 1967–2013. Dashed line separates the fixed effect solutions from the post-hoc comparisons between high-low temperature and salinity years calculated with “*ESTIMATE*” statements (High S years: 1973–1976, 1978, 1980; Low S years: 1994, 2001–2002, 2007, 2010, 2013; High T years: 1992, 2002, 2007–2009, 2011; Low T years: 1977–1979, 1982, 1996, 1998). See text for details. Emboldened p-values are those judged to be significant ($p \leq 0.05$). Ad = adults; cop = copepodites; n = observations used by the model. The overall number of observations was 205.

Total zooplankton biomass n=196						Marine taxa n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	8.29	4.47	153	1.85	0.06	Intercept	3.00	2.30	153	1.30	0.20
S	17.70	7.98	153	2.22	0.03	S	9.80	4.10	153	2.40	0.02
T	0.29	0.47	153	0.63	0.53	T	-0.40	0.20	153	-1.50	0.10
High S vs. other years	2390.52	829.11	153	2.88	0.005	High S vs. other years	1037.30	429.50	153	2.40	0.02
Low S vs. other years	-789.67	707.88	153	-1.12	0.27	Low S vs. other years	-466.20	366.70	153	-1.30	0.20
High S vs. low S years	-232.70	109.97	153	-2.12	0.04	High S vs. low S years	-110.00	56.90	153	-1.90	0.05
High T vs. other years	-33.68	343.78	153	-0.10	0.92	High T vs. other years	-373.90	178.10	153	-2.10	0.04
Low T vs. other years	1010.69	405.16	153	2.49	0.01	Low T vs. other years	816.00	209.90	153	3.90	<.001
High T vs. low T years	-76.42	49.01	153	-1.56	0.12	High T vs. low T years	-87.10	25.40	153	-3.40	<.001
Brackish-water taxa n=196						Copepoda n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	4.90	3.20	153	1.50	0.10	Intercept	7.30	3.20	153	2.30	0.02
S	6.01	5.80	153	1.00	0.30	S	15.40	5.70	153	2.70	0.008
T	0.70	0.30	153	2.00	0.05	T	-0.10	0.30	153	-0.40	0.70
High S vs. other years	1087.00	602.20	153	1.80	0.07	High S vs. other years	1912.48	596.0	153	3.21	0.002
Low S vs. other years	-89.40	514.10	153	-0.20	0.90	Low S vs. other years	-1065.24	508.8	153	-2.09	0.04
High S vs. low S years	-86.10	79.90	153	-1.10	0.30	High S vs. low S years	-217.88	79.10	153	-2.76	0.007
High T vs. other years	441.70	249.70	153	1.80	0.08	High T vs. other years	-289.87	247.10	153	-1.17	0.20
Low T vs. other years	97.10	294.30	153	0.30	0.70	Low T vs. other years	998.22	291.20	153	3.43	<.001
High T vs. low T years	25.20	35.60	153	0.70	0.50	High T vs. low T years	-94.25	35.20	153	-2.68	0.008

Large copepods						Small copepods					
n=196						n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	0.22	0.93	153	0.24	0.81	Intercept	0.33	0.44	153	0.76	0.45
S	3.81	5.80	153	2.29	0.02	S	0.64	0.79	153	0.82	0.41
T	-0.08	0.09	153	-0.77	0.44	T	-0.06	0.05	153	-0.12	0.90

High S vs. other years	244.11	172.76	153	1.41	0.16						
Low S vs. other years	-97.64	146.63	153	-0.67	0.51						
High S vs. low S years	-25.00	22.85	153	-1.09	0.28						
High T vs. other years	2.38	71.35	153	0.03	0.97						
Low T vs. other years	31.39	84.43	153	0.37	0.71						
High T vs. low T years	-2.12	10.18	153	-0.21	0.84						

<i>Acartia spp. ad</i>						<i>Eurytemora affinis ad</i>					
n=196						n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	1.60	0.60	153	2.70	0.008	Intercept	0.80	0.80	153	1.04	0.30
S	2.10	1.05	153	2.00	0.05	S	0.40	1.40	153	0.30	0.70
T	0.10	0.06	153	2.10	0.04	T	0.10	0.080	153	1.60	0.10

High S vs. other years	265.00	109.10	153	2.40	0.020						
Low S vs. other years	-163.40	93.10	153	-1.80	0.08						
High S vs. low S years	-31.30	14.50	153	-2.20	0.03						
High T vs. other years	42.10	45.20	153	0.90	0.40						
Low T vs. other years	69.00	53.30	153	1.30	0.20						
High T vs. low T years	-2.00	6.50	153	-0.30	0.80						

<i>Eurytemora affinis cop</i>						<i>Bosmina longispina</i>					
n=196						n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	1.20	0.50	153	2.20	0.03	Intercept	0.90	0.80	153	1.20	0.20
S	1.70	1.00	153	1.80	0.07	S	1.04	1.40	153	0.80	0.50
T	0.03	0.06	153	0.50	0.60	T	0.20	0.08	153	2.04	0.04

High S vs. other years	220.10	98.80	153	2.20	0.03	High S vs. other years	259.57	143.61	153	1.81	0.07
Low S vs. other years	-148.70	84.40	153	-1.80	0.08	Low S vs. other years	-48.89	122.61	153	-0.40	0.69
High S vs. low S years	-27.00	13.10	153	-2.10	0.04	High S vs. low S years	-22.57	19.04	153	-1.18	0.23
High T vs. other years	47.00	41.00	153	1.20	0.30	High T vs. other years	66.36	59.54	153	1.11	0.27
Low T vs. other years	69.40	48.30	153	1.40	0.20	Low T vs. other years	-30.27	70.18	153	-0.43	0.67
High T vs. low T years	-1.64	5.84	153	-0.28	0.78	High T vs. low T years	7.07	8.49	153	0.83	0.41

<i>Evadne nordmanni</i>						<i>S.baltica</i>					
n=196						n=196					
Effect	Estimate	SE	DF	t	p	Effect	Estimate	SE	DF	t	p
Intercept	1.20	0.50	153	2.20	0.03	Intercept	-2.53	0.82	153	-3.09	0.002
S	1.70	0.90	153	1.80	0.07	S	-4.28	1.46	153	-2.93	0.004
T	0.20	0.09	153	2.30	0.03	T	-0.08	0.086	153	-0.94	0.35
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High S vs. other years	-75.01	153.40	153	-0.50	0.60	High S vs. other years	-484.03	151.78	153	-3.19	0.002
Low S vs. other years	236.40	131.00	153	1.80	0.07	Low S vs. other years	487.88	129.26	153	3.77	<.001
High S vs. low S years	22.80	20.30	153	1.10	0.30	High S vs. low S years	71.12	20.12	153	3.54	<.001
High T vs. other years	187.10	63.60	153	2.90	0.004	High T vs. other years	171.87	62.63	153	2.74	0.007
Low T vs. other years	-122.60	75.00	153	-1.60	0.10	Low T vs. other years	-159.63	73.89	153	-2.16	0.03
High T vs. low T years	22.70	9.10	153	2.50	0.01	High T vs. low T years	24.26	8.93	153	2.72	0.007

Fig 1

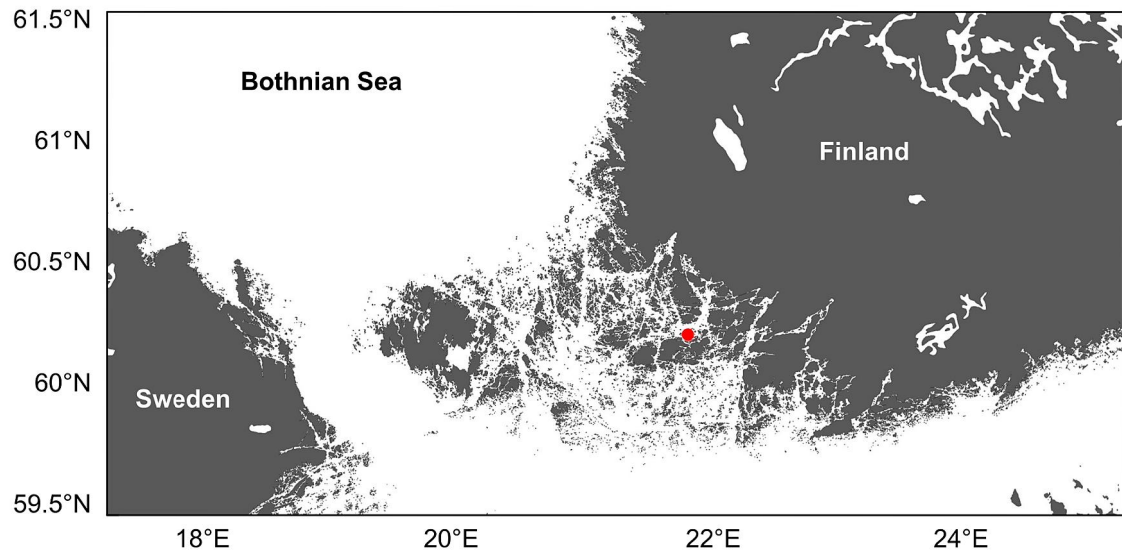


Fig 2

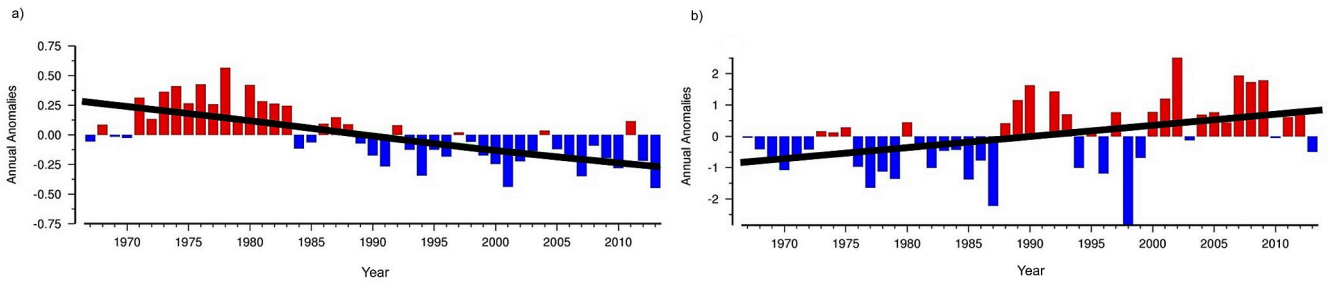


Fig 3

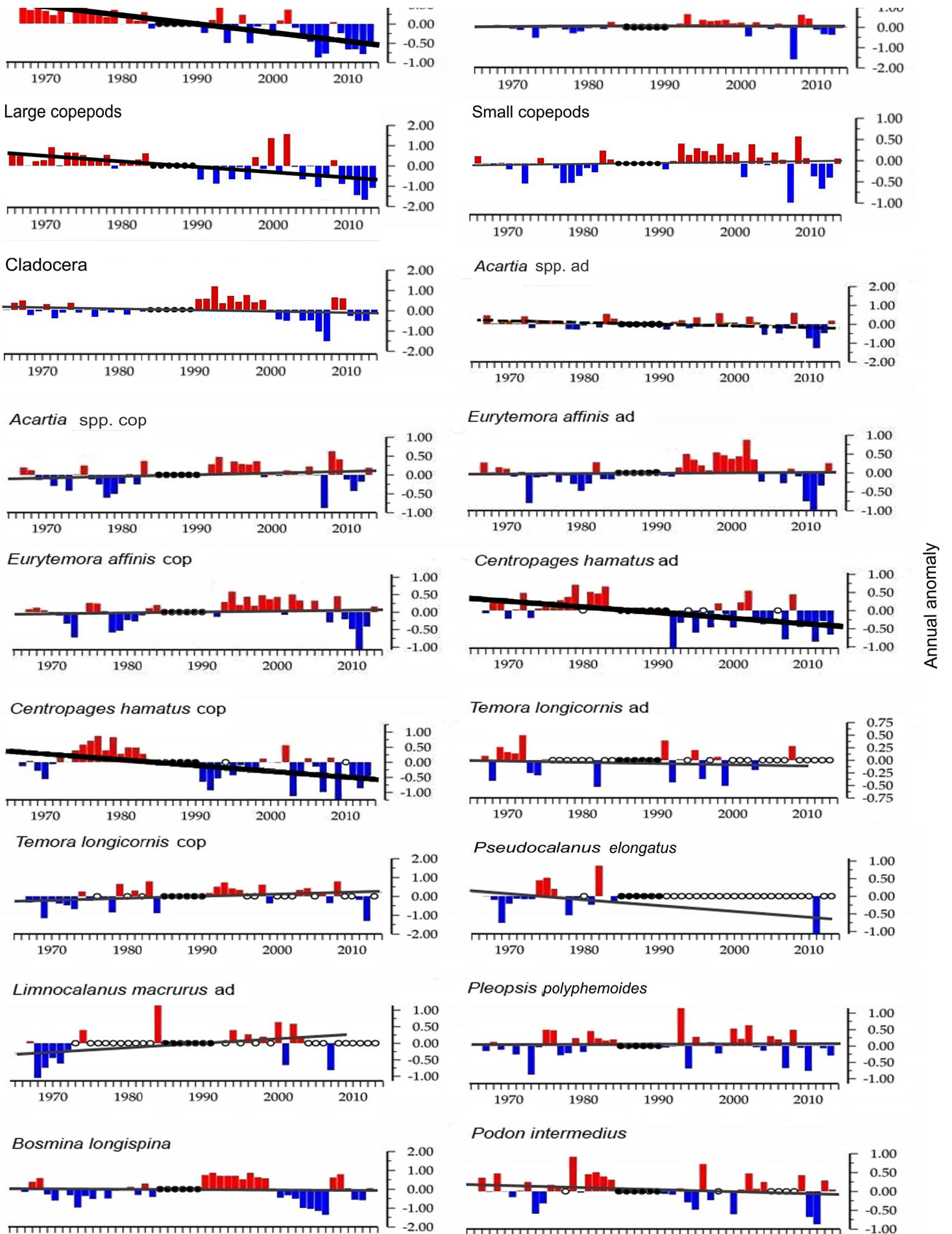


Fig 4

