Marine Biology (2024) 171:116
https://doi.org/10.1007/s00227-024-04435-0

ORIGINAL PAPER

Warming drives phenological changes in coastal zooplankton

Louise Forsblom[1] · Tjardo Stoffers[2] · Andreas Lindén[3] · Maiju Lehtiniemi[1] · Jonna Engström-Öst[2,4]

Received: 14 December 2023 / Accepted: 8 April 2024 / Published online: 23 April 2024

Abstract

Climate warming has led to phenological changes over time, typically displayed as earlier emergence of various organisms in spring or summer in temperate terrestrial and marine systems alike. Similarly, warm conditions can extend seasonal occurrence. Using a time series of zooplankton data from a coastal area in the Gulf of Finland, we calculated the start, end and the length of the season for the occurrence in rotifers and for adult and juvenile stages of three calanoid copepods. We investigated whether the start and end of the season of these taxa have shifted earlier and later, respectively, and whether the season length has increased. We further investigated if potential changes are driven by climate warming. We show that both copepods and rotifers do indeed emerge earlier, but that the pattern in recent years was not conclusive, and that both temperature and ice conditions influenced the seasonal abundance patterns of some taxa. Warmer years led to earlier occurrence of *Temora longicornis* copepodites. Earlier ice break-up coincided with longer seasons for *Acartia* and earlier emergence of *Eurytemora affinis*. The phenological changes in zooplankton demonstrated here may have cascading effects on other trophic levels in the food web. We also demonstrate how decreased sample number influences the ability to capture intra-annual abundance patterns and discuss the implications for monitoring.

Keywords Phenology · Climate change · Zooplankton · Monitoring

Introduction

Studies in phenology investigate annually repeated biological seasonal patterns. Many populations in marine temperate regions, including zooplankton, initiate a rapid increase in abundance after the winter, coupled with an increase in primary production (Richardson et al. 2000). Climate warming has led to shifts in the seasonal patterns of occurrence with earlier emergence of various organisms in terrestrial and marine systems alike (Parmesan and Yohe 2003; Edwards and Richardson 2004; Durant et al. 2007; Thackeray et al. 2016). Similarly, an extended period with warm conditions toward autumn can extend the season by postponing its end, by affecting the timing of resting egg production (Chen and Folt 1996; Tachibana et al. 2019), or leading to enhanced overwintering survival (Schlüter et al. 2010). Changes in the timing of occurrence can modify trophic interactions by inducing or lessening trophic mismatches between interacting species (Cushing 1990; Mackas et al. 2012; Sommer et al. 2012), which can cause cascading effects by influencing trophic interactions and the cycling of energy in the food web (Aberle et al. 2012; Thackeray et al. 2016; Hedberg et al. 2024).

Extrinsic conditions that affect organism population growth are likely to alter both the total annual abundance and important cardinal dates, such as the timing of spring emergence, peak abundance and autumn decline (Scharfe and Wiltshire 2019). Temperature can influence timing of occurrence in different ways (Chmura et al. 2019), and affect zooplankton abundance by influencing individual growth, and hence population turnover time and individual body size (Daufresne et al. 2009; Winder et al. 2009). Especially with smaller sized organisms with fast turnover time, the timing

Responsible Editor: E. Kozak.

✉ Louise Forsblom
louise.forsblom@syke.fi

1 Finnish Environment Institute, Latokartanonkaari 11, Helsinki, Finland

2 Tvärminne Zoological Station, University of Helsinki, J.A. Palménin tie 260, Hanko, Finland

3 Natural Resources Institute Finland, Latokartanonkaari 9, Helsinki, Finland

4 Novia University of Applied Sciences, Raseborgsvägen 9, Ekenäs, Finland

and frequency of monitoring are crucial to capture intra-annual dynamics (Klais et al. 2016; Lehtiniemi et al. 2022; Ratnarajah et al. 2023).

The present study was conducted in the Gulf of Finland, which is a brackish-water estuary in the northern Baltic Sea, where the total abundance of pelagic mesozooplankton, in particular large copepods, have decreased since the 1970s (Flinkman et al. 1998; Suikkanen et al. 2013; Jansson et al. 2020). The post-winter zooplankton emergence in coastal regions of the area is typically induced by reproduction of overwintering individuals, and by hatching of resting eggs from the sediment that occurs when the environmental conditions become favourable in spring (Viitasalo 1992; Katajisto et al. 1998). The taxa can have multiple reproductive cycles over the summer depending on species and prevailing environmental conditions. The duration of ice cover in the area has shortened by almost 1 month during the last century and the sea surface temperature has increased by almost 1 °C during the past 85 years (Merkouriadi and Leppäranta 2014), with a projected continued increase until 2100 (Meier et al. 2022). Due to its unique combination of characteristics and good data availability, the Baltic Sea is suitable to work as a time machine to study changes that might happen in other oceans in the future (Reusch et al. 2018).

In this study, we examined the phenological patterns of zooplankton, explicitly modelling changes in the timing of their seasonal occurrence. We analysed potential phenological changes in calanoid copepods *Acartia* spp., *Eurytemora affinis* and *Temora longicornis*, as well as in rotifers *Keratella* spp. and *Synchaeta* spp. over a period spanning 55 years. We expected earlier occurrence of zooplankton in spring and due to the milder winters, we hypothesised that the length of the seasonal occurrence of zooplankton is increasing due to earlier start of the season linked to temperature. Longer periods of warm conditions in autumn were also expected to extend the end of the season, enabling an increased number of annual generations. We further discuss the implications of zooplankton monitoring on assessing phenological change.

Material and methods

Time-series data

The zooplankton data were collected at Storfjärden in Hanko (59°51.35′N 23°15.93′E) by Tvärminne Zoological Station, University of Helsinki (TZS) and the Finnish Institute of Marine Research (now Finnish Environment Institute) (Fig. 1). The monitoring was conducted in two periods: the first in 1967–1984 and the second in 1993–2020. Years 2008 and 2017 had too few analysed samples and were dropped from the analysis. In the first period, the sampling was done on average three times monthly, usually day 1, 11 and 21, and during the second period once a month (Fig. 1). There was also a slight shift in the timing of the monthly sampling in 2017 when it was shifted to mid-month. The sampling procedure has remained consistent, except for a change of sampling net diameter. The diameter of the 150 µm Hensen net decreased from 0.72 m in the first period to 0.35 m in the second period. The samples were taken from 25 m to the surface (station depth 35 m) and preserved in a 4% buffered formaldehyde solution. Prior to analysis, the samples were divided using a Folsom splitter a maximum of ten times (corresponding to a subsample of 1/1024) due to differing zooplankton densities. The groups considered in the present study are adults and copepodites from stage I to IV of *Acartia* spp., *Eurytemora affinis* and *Temora longicornis*, as well as the rotifers *Synchaeta* spp. and *Keratella* spp.

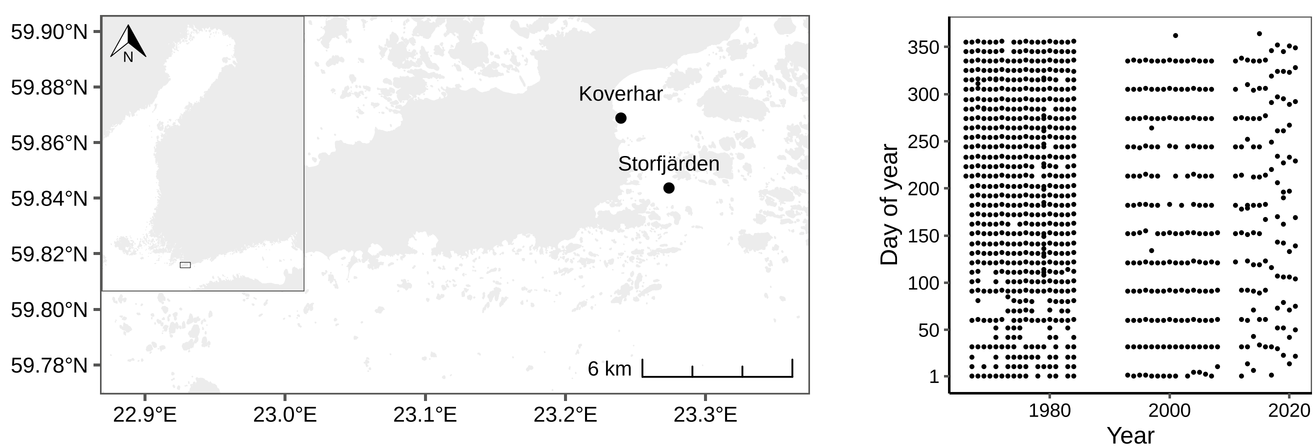

Fig. 1 Map of the study area indicating the zooplankton sampling (Storfjärden) and ice break-up sites (Koverhar), as well as a figure of the timing of all the zooplankton sampling events at Storfjärden

The most common copepod taxa in the study area are the calanoid copepods *Acartia* spp., (*A. bifilosa*, *A. longicornis* and *A. tonsa*). *A. bifilosa* occurs throughout the year, whilst *A. longiremis* mostly occurs during spring, and appears at the end of summer, after having assumedly spent the rest of the year as resting eggs (Katajisto et al. 1998). *A. tonsa* has mainly been frequently observed after 1990 (Fig. S1). *Acartia* have not been consistently identified to species level and were, thus, grouped in this study. *E. affinis* is recognised in the data set, but also *E. carolleeae* inhabits the Gulf of Finland nowadays (Sukhikh et al. 2019).

The environmental drivers of interest are water temperature, and day of ice break-up. Temperature data were provided by Tvärminne Zoological Station and were measured from discrete depths (0, 20 and 30 m), or continuously with a CTD and were used to calculate the mean temperature. The timing of ice break-up was measured at Koverhar (59°52.8′N, 23°13.7′E) close to the zooplankton sampling station by the Finnish Meteorological Institute. The variable indicates the day when < 10% of the ice cover remains (Kalliosaari 1978, 1982; Kalliosaari and Seinä 1987; Seinä and Kalliosaari 1991; Seinä et al. 1996, 2001, 2006).

Seasonal abundance patterns

We investigated the intra-annual seasonal patterns for both periods of the time-series by fitting generalised additive models (GAM), using the mgcv package in R (Wood 2017, 2020). As the second period has less frequent sampling, we also investigated how this influenced the seasonal abundance patterns. We modelled the abundance using a log link function and a Tweedie error distribution with estimated power parameter (determining the level of dispersion). We modelled the average seasonal patterns by including day of year in a cyclic smoothing function. We analysed the two periods of the time-series separately (i.e. 1967–1984 and 1993–2020). To investigate the possible effects of differing sampling frequency between the two periods, we mimicked the effects of sparser sampling by separately modelling the data gathered on day 1, 11 and 21 of the months using data from the first period.

Estimating the start, end and length of the season

There exist several approaches for comparing phenological patterns between years based on abundance and biomass measures (reviewed by Ji et al. 2010). We calculated the start and the end of the season using annual cumulative abundances (Greve et al. 2005). The start and end of the season were defined according to the day the cumulative annual abundance exceeded 15% and 85% of the annual abundance, respectively. We calculated the annual abundance estimated for each species by calculating the cumulative sum for each year, filling in the gaps by interpolating (Fig. 2). As the increase and decrease in abundance do not necessarily conform to our idea of a calendar year, we defined the start of the season for each species to correspond to the day of the year when the species was at its abundance minimum. The abundance minimum for each species was estimated using the same GAM approach described in the section on seasonal patterns but using the full zooplankton time series. The annual mean estimates together with the starting point are shown in the electronic supplementary material (Fig. S2).

Trends and drivers of phenological change

The between-year patterns in the derived annual phenology-related variables, i.e. timing of the start, end and length of the season, were investigated as response variables using linear regression. The continuous variable year was centred to mean zero, by subtracting the mean of year, for each period separately. As the time series has a gap from 1985–1992, we added the period of the time series as a binary factor variable to the model. This accounts for a possible difference in the average level between the two time periods, and the interaction between this variable and (period-wise centred) year describes the difference in trends compared to the reference period. We fitted each model twice—with the first and the second period as the reference factor level—to

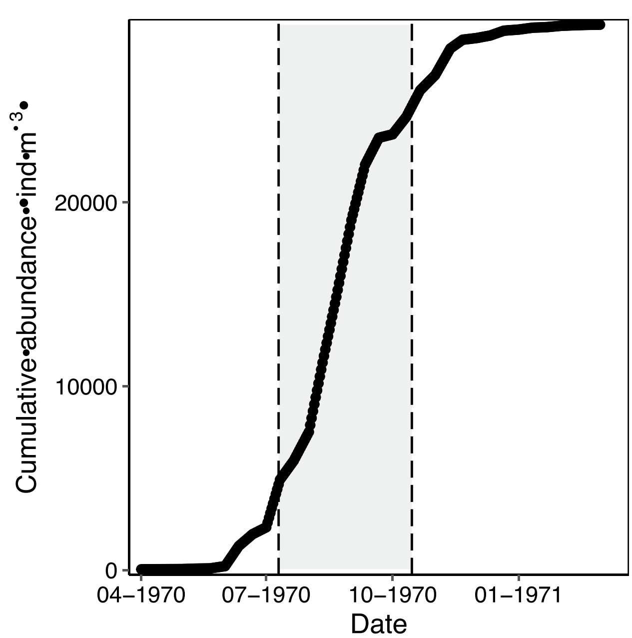

Fig. 2 The cumulative abundance for adult *Acartia* spp. in 1970 (bold line). From left to right, the vertical lines indicate when 15 and 85%, respectively, of the cumulative abundance is reached. These are considered to mark the start and end of the season in the present study, and to correspond to the length of the season (grey area)

obtain straightforward estimates for the temporal trends of both periods.

In addition to the trend, we investigated whether variation in the start and length of the season could be explained by day of ice break-up or anomaly in water temperature at the start of the season, and if the end of the season could be explained by the anomaly in water temperature during June, July and August. Effects of ice break-up were only analysed using data until 2006. The anomalies at the start of the season were tailored to each species specifically so that they included the 2 months prior to the abundance minimum. February–March anomalies were used for *Acartia* copepodites, March–April anomalies for adult *Acartia, Keratella, Synchaeta*, and *E. affinis* and *T. longicornis* copepodites, and finally April–May anomalies for adult *E. affinis* and *T. longicornis* copepodites. The summer anomalies included July, August and September for all taxa. The temperature anomaly time series was derived using a GAM with a cyclic smoothing function of month to each of the covariates and extracting the relevant anomalies from the model residuals.

Results

The comparison between the modelled mean abundances of the two periods, 1967–1984 and 1993–2020, shows changes in overall seasonal patterns and abundances. The mean annual abundance decreased for *Temora longicornis*, adult *Acartia* spp. and *Eurytemora affinis* (Fig. 3). However, as the diameter of the sampling equipment has changed preceding a gap of 9 years in the time series, abundance comparisons between the periods should be done with some caution.

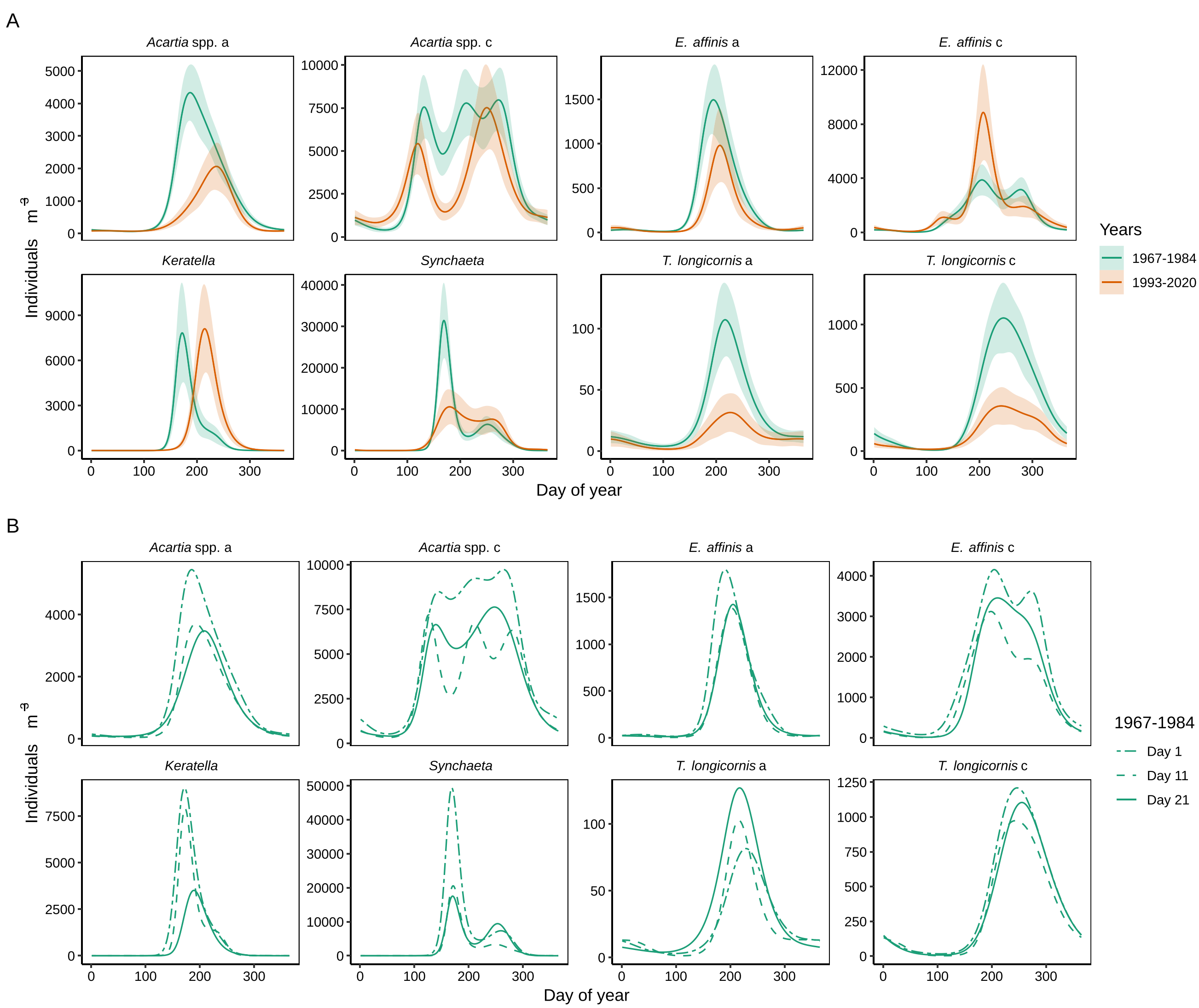

Fig. 3 Predicted mean seasonal abundance patterns for 1967–1984 and 1993–2020 (**A**), and for 1967–1984 using data from day 1, 11 and 21 only (**B**) indicated by line type. Letters a and c in titles indicate adults and copepodites, respectively

When thinning the data of the first period to mimic the lower sampling frequency (one sample per month) of the second period, the estimated peak can vary strongly as seen in both rotifers and adult *Acartia* with only one monthly estimate. More complex seasonal patterns were also lost for *Acartia* spp. copepodites using only the observations from day 21. However, rough patterns of e.g. emergence and season length were retained, of course, with increased uncertainty compared to the full data set.

The start of the seasonal occurrence, i.e. the date when 15% of the maximum abundance of that year was achieved, became statistically significantly earlier for *Acartia* spp. copepodites, *E. affinis* adults and copepodites, as well as for *Keratella* spp. until 1984, but after the break in the time series, the change levelled out or reversed (Fig. 4, Table 1). Trends towards earlier emergence in the second period were only significant for *Synchaeta* and *T. longicornis* copepodites and adults. The timing of the end of the season occurred statistically significantly earlier for *Acartia* spp. copepodites during the earlier time period, but not so for the latter time period (Fig. S5). There were no significant trends or patterns in the length of the season in the first period, as many of the changes in the start and end of the season point in the same direction, with approximately similar magnitude. During the second period, the length of the season increased only for *E. affinis* adults and decreased for *Acartia* spp. Models that yielded statistically significant parameters are shown in Table 1 and all models are shown in Table S1.

The mean water temperature (at 0–30 m) increased over the investigated period, and some of the earliest ice break-up days were observed in the 1990s (Figs. S3 and S4). There was a weak trend in the ice break-up of −0.64 ($p=0.06$, F-statistic: 3.65 on 1 and 36 DF). For *T. longicornis* copepodites, the start of the season occurred earlier during warm years. The length of the season increased during warm years for adult *Acartia* spp. and *T. longicornis* copepodites. Earlier ice break-up lengthened the season for adult *Acartia* spp., whereas later ice break-up coincides with the later emergence of *E. affinis* copepodites.

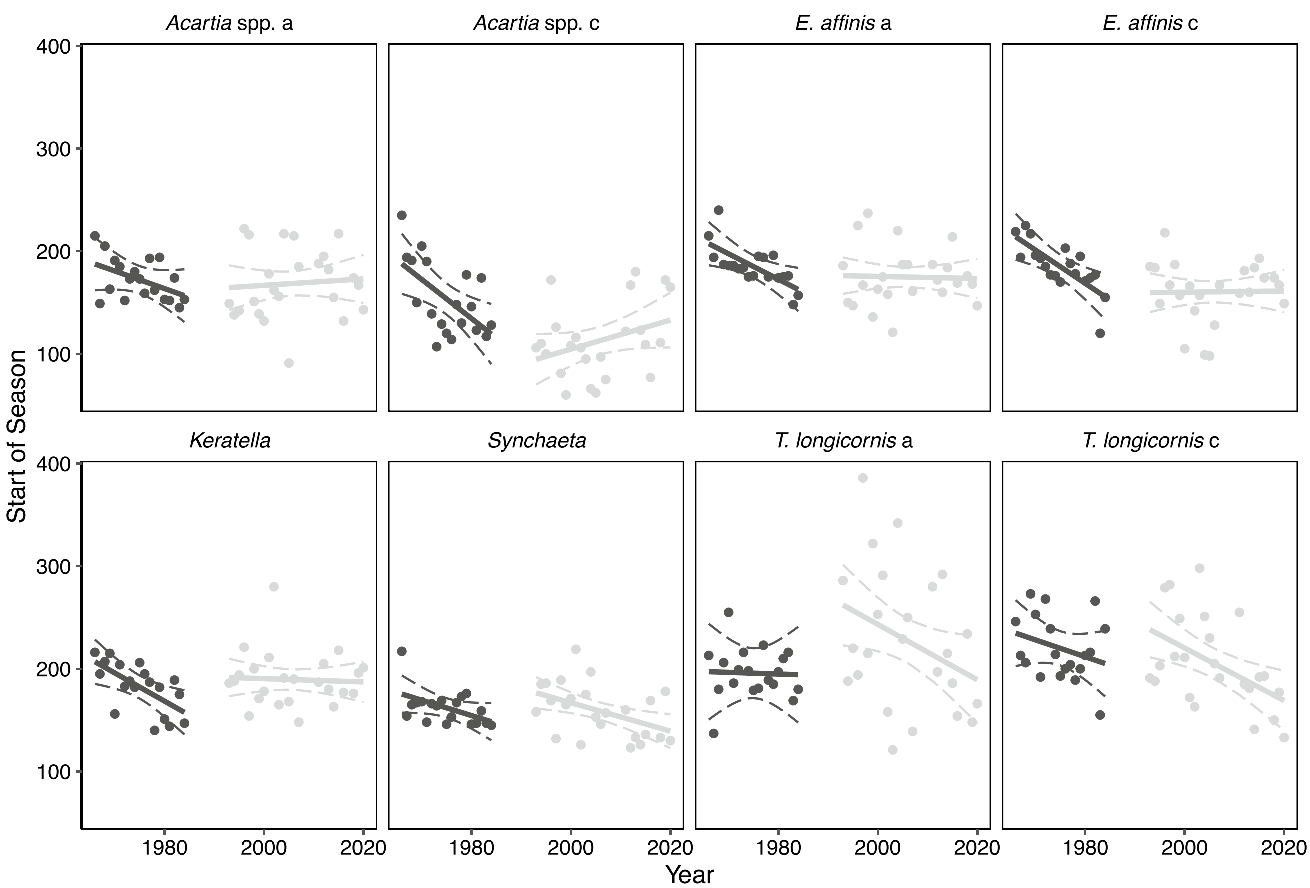

Fig. 4 The temporal change in start of the season. Points indicate the time when cumulative abundance exceeds 15% of the annual abundance and lines are the model fit from the regression. Black dots indicate the first period (1967–1984) and grey dots the later period (1993–2020). Letters a and c in titles indicate adults and copepodites, respectively

Table 1 Temporal patterns of the studied phenological variables (y; start, end and length of the season) in the light of linear model effects. The table shows the estimates, SE and p values for the trend for the first and second period, the change in mean level of the estimate between periods, the change in trend between the periods, and the effects of an additionally included environmental covariate

Species	*y*	Trend 1967–1984	Trend 1993–2020	Period level change	Change in trend	Environmental covariate	R^2	*p*	*n*
Acartia spp. a	Length	−0.86 ± 1.36 SE (*P* = 0.54)	−0.51 ± 2.45 SE (*P* = 0.84)	12.10 ± 21.77 SE (*P* = 0.58)	0.34 ± 2.80 SE (*P* = 0.90)	**Ice −1.09 ± 0.37 SE (P = 0.01)**	0.40	**0.01**	31
Acartia spp. a	Length	−0.01 ± 1.75 SE (*P* = 1.00)	**−2.25 ± 0.99 SE (P = 0.03)**	18.43 ± 13.00 SE (*P* = 0.16)	−2.24 ± 2.03 SE (*P* = 0.28)	**temp_ma 23.09 ± 10.91 SE (P = 0.04)**	0.21	0.06	43
Acartia spp. a	End	−2.46 ± 1.50 SE (*P* = 0.11)	**−1.81 ± 0.87 SE (P = 0.04)**	10.20 ± 11.14 SE (*P* = 0.37)	0.66 ± 1.74 SE (*P* = 0.71)	temp_s -4.66 ± 4.70 SE (*P* = 0.33)	0.19	0.09	43
Acartia spp. c	Start	**−3.80 ± 1.37 SE (P = 0.01)**	1.42 ± 0.80 SE (*P* = 0.08)	**−37.81 ± 10.11 SE (P = 0.00)**	**5.22 ± 1.59 SE (P = 0.00)**		0.41	**< 0.01**	43
Acartia spp. c	End	**−3.69 ± 1.23 SE (P = 0.00)**	−0.76 ± 0.72 SE (*P* = 0.29)	−1.11 ± 9.07 SE (*P* = 0.90)	**2.92 ± 1.43 SE (P = 0.05)**		0.21	**0.03**	43
Acartia spp. c	Length	0.12 ± 1.67 SE (P = 0.94)	**−2.18 ± 0.97 SE (P = 0.03)**	**36.70 ± 12.26 SE (P = 0.00)**	−2.30 ± 1.93 SE (*P* = 0.24)		0.28	**0.01**	43
Acartia spp. c	Start	**−3.83 ± 1.20 SE (P = 0.00)**	−4.33 ± 2.16 SE (*P* = 0.06)	**−78.69 ± 19.18 SE (P = 0.00)**	−0.50 ± 2.47 SE (*P* = 0.84)	Ice 0.42 ± 0.33 SE (*P* = 0.21)	0.62	**< 0.01**	31
Acartia spp. c	Start	**−3.52 ± 1.43 SE (P = 0.02)**	1.42 ± 0.80 SE (*P* = 0.08)	**−33.41 ± 11.61 SE (P = 0.01)**	**4.94 ± 1.64 SE (P = 0.00)**	temp_fm 7.97 ± 10.15 SE (*P* = 0.44)	0.42	**< 0.01**	43
Acartia spp. c	Length	0.46 ± 1.73 SE (*P* = 0.79)	**−2.17 ± 0.97 SE (P = 0.03)**	**42.07 ± 14.07 SE (P = 0.00)**	−2.63 ± 1.98 SE (*P* = 0.19)	temp_fm 9.72 ± 12.30 SE (*P* = 0.43)	0.29	**0.01**	43
Acartia spp. c	End	**−3.57 ± 1.25 SE (P = 0.01)**	−0.81 ± 0.72 SE (*P* = 0.27)	0.34 ± 9.26 SE (*P* = 0.97)	2.75 ± 1.45 SE (*P* = 0.06)	temp_s −3.31 ± 3.91 SE (*P* = 0.40)	0.22	**0.05**	43
E. affinis a	Start	**−2.48 ± 0.99 SE (P = 0.02)**	−0.10 ± 0.58 SE (*P* = 0.86)	−9.01 ± 7.27 SE (*P* = 0.22)	**2.38 ± 1.14 SE (P = 0.04)**		0.18	**0.05**	43
E. affinis a	Length	−0.54 ± 2.06 SE (*P* = 0.80)	1.92 ± 3.71 SE (*P* = 0.61)	**68.97 ± 32.96 SE (P = 0.05)**	2.46 ± 4.24 SE (*P* = 0.57)	Ice −0.40 ± 0.57 SE (*P* = 0.49)	0.32	**0.04**	31
E. affinis a	Start	**−2.40 ± 0.98 SE (P = 0.02)**	0.10 ± 0.59 SE (*P* = 0.86)	−7.16 ± 7.34 SE (*P* = 0.34)	2.50 ± 1.14 SE (*P* = 0.03)	temp_am −5.78 ± 4.36 SE (P = 0.19)	0.21	**0.05**	43
E. affinis c	Start	**−3.25 ± 1.05 SE (P = 0.00)**	0.06 ± 0.61 SE (*P* = 0.92)	**−22.81 ± 7.74 SE (P = 0.00)**	**3.31 ± 1.22 SE (P = 0.01)**		0.34	**< 0.01**	43
E. affinis c	Start	**−3.28 ± 0.78 SE (P = 0.00)**	**−7.50 ± 1.40 SE (P = 0.00)**	**−75.56 ± 12.46 SE (P = 0.00)**	−4.21 ± 1.60 SE (*P* = 0.01)	**Ice 0.63 ± 0.21 SE (P = 0.01)**	0.73	**< 0.01**	31
E. affinis c	Length	0.12 ± 1.40 SE (*P* = 0.93)	**7.04 ± 2.51 SE (P = 0.01)**	**88.04 ± 22.30 SE (P = 0.00)**	**6.91 ± 2.87 SE (P = 0.02)**	Ice −0.22 ± 0.38 SE (*P* = 0.58)	0.41	**0.01**	31
E. affinis c	Start	**−3.35 ± 1.10 SE (P = 0.00)**	0.08 ± 0.62 SE (*P* = 0.90)	**−23.66 ± 8.16 SE (P = 0.01)**	**3.43 ± 1.27 SE (P = 0.01)**	temp_ma −2.51 ± 6.85 SE (*P* = 0.72)	0.34	**< 0.01**	43
Keratella	Start	**−2.74 ± 1.01 SE (P = 0.01)**	−0.16 ± 0.59 SE (*P* = 0.79)	8.54 ± 7.46 SE (*P* = 0.26)	**2.58 ± 1.17 SE (P = 0.03)**		0.18	**0.05**	43
Keratella	Start	**−2.28 ± 1.01 SE (P = 0.03)**	−0.26 ± 0.58 SE (*P* = 0.65)	12.54 ± 7.54 SE (*P* = 0.10)	2.02 ± 1.18 SE (*P* = 0.09)	temp_ma 11.83 ± 6.33 SE (*P* = 0.07)	0.25	**0.03**	43

Table 1 (Continued)

Species	y	Trend 1967–1984	Trend 1993–2020	Period level change	Change in trend	Environmental covariate	R^2	p	n
Synchaeta	Start	−1.50 ± 0.85 SE (P = 0.09)	**−1.39 ± 0.50 SE (P = 0.01)**	−3.24 ± 6.26 SE (P = 0.61)	0.11 ± 0.98 SE (P = 0.91)		0.22	**0.02**	43
Synchaeta	Start	−1.69 ± 0.88 SE (P = 0.06)	**−1.34 ± 0.50 SE (P = 0.01)**	−4.87 ± 6.55 SE (P = 0.46)	0.34 ± 1.02 SE (P = 0.74)	temp_ma − 4.84 ± 5.50 SE (P = 0.38)	0.24	**0.03**	43
T. longicornis a	Start	−0.16 ± 2.19 SE (P = 0.94)	**−2.70 ± 1.28 SE (P = 0.04)**	30.07 ± 16.13 SE (P = 0.07)	−2.54 ± 2.54 SE (P = 0.32)		0.18	**0.05**	43
T. longicornis c	Start	−1.65 ± 1.51 SE (P = 0.28)	**−2.57 ± 0.88 SE (P = 0.01)**	−15.55 ± 11.09 SE (P = 0.17)	−0.92 ± 1.74 SE (P = 0.60)		0.23	**0.02**	43
T. longicornis c	Start	−1.34 ± 1.31 SE (P = 0.31)	**−1.80 ± 0.79 SE (P = 0.03)**	−8.69 ± 9.84 SE (P = 0.38)	−0.46 ± 1.52 SE (P = 0.76)	**temp_am -21.38 ± 5.84 SE (P = 0.00)**	0.43	**<0.01**	43
T. longicornis c	Length	0.82 ± 2.05 SE (P = 0.69)	0.84 ± 1.24 SE (P = 0.50)	22.90 ± 15.35 SE (P = 0.14)	0.03 ± 2.38 SE (P = 0.99)	**temp_am 19.27 ± 9.12 SE (P = 0.04)**	0.21	0.06	43

Candidate covariates include mean temperature anomaly for February–March (temp_fm), March–April (temp_ma), April–May (temp_am), July–September (temp_s) and ice break-up day (Ice). Additional statistics shown are the coefficient of determination (R^2), the full model statistical significance (p), as well as the number of data points, i.e. years included (n). The trend for the second period was derived from refitting the linear model with the factor variable period in different order. Ice effects were only modelled using data until 2006. Estimates with p value less than 0.05 are bolded

Discussion

Climate change affects the timing of zooplankton occurrence in many ways, with temperature rise being the most studied and most often suggested cardinal driver of change. Our study shows that five of the studied zooplankton taxa emerged earlier in spring, at least for part of the investigated time and for some life stages. Previous studies have reported that zooplankton emerged earlier in spring in some but not all temperate regions (Mackas et al. 2012; Uriarte et al. 2021), which we also observed in *Acartia* spp. copepodites, *E. affinis* and *Temora* as well as in rotifers *Synchaeta* spp. and *Keratella* spp. for either the first or second half of the studied time period. The exact mechanism that triggered these shifts is unclear, but water temperatures have increased in the area and induced changes in ice break-up, and both variables are known to affect spring and early summer abundances of copepods (Klais et al. 2017; Viitasalo et al. 1994). Light is unlikely important for hatching of resting eggs as it does not penetrate to the bottom in the investigated area (Almén et al. 2014). Hedberg et al. (2024) recently showed that egg hatching from the sediment does not seem to be directly influenced by temperature or light conditions, and suggested that conditions in the water column are more important in shaping the annual dynamics.

Annual fluctuations in population abundance and timing of occurrence are also expected to be influenced by food availability, and e.g. Uriarte et al. (2021) found that chlorophyll-*a* influenced phenological patterns at Stonehaven in the North Sea. Due to lack of consistent phytoplankton time-series, we were not able to account for that in the present study. However, Almén and Tamelander (2020) indicate a shift in phytoplankton spring bloom to earlier timing and that zooplankton peak biomasses are more tightly coupled to the phytoplankton peaks during warmer years. The timing and the magnitude of the spring phytoplankton bloom are likely of more importance for herbivorous taxa such as the rotifers compared to generalist copepods (Hansson et al. 1990).

The rising temperatures in the study area can lead to faster development time of resting eggs from sediment (Katajisto 2003), and potentially extend the seasonal occurrence (Borkman et al. 2018). Our expectation was that this would lead to an extended season of occurrence as observed in other estuarine areas (Borkman et al. 2018), and whilst there was no trend in the length of the season, indicating season becoming longer, we show that years with higher-than-average temperatures were linked to longer seasonal occurrence for *Acartia* adults and *T. longicornis* copepodites. It is possible that the warmer temperature enables hatching from the sediment to occur for longer for *Acartia*, and especially in late summer, it is likely that at least part of the population consists of the non-native *Acartia tonsa,* which prefers high temperatures (Katajisto et al. 1998; Diekmann et al. 2012). The majority of the annual abundance consists of *Acartia bifilosa*, but as the other two species occur mainly at the start and end of the season, there could still be an impact on the estimated timing of occurrence. The reversal of the trend in emergence of *Acartia* spp. copepodites seems to coincide with the introduction of *Acartia tonsa*; however, it is hard to estimate the potential impact as the identification to species level has not been consistent, especially since 2006 onwards. In addition, the species-level identification has almost exclusively been applied to adult stages. *A. longiremis* only occurs during colder periods of the year.

We saw no indications of extension in total length of season and the timing of the end of the season occurred earlier for *Acartia* copepodites in the earlier time period. One possible explanation is that even with the higher temperature, the food quality might not be ideal in late summer. The phytoplankton community in late summer partly consists of cyanobacteria that are known to be poor-quality food for zooplankton (Engström-Öst et al. 2015) and their abundance has been increasing and is projected to increase due to elevating temperatures in the Gulf of Finland (Olofsson et al. 2020); there is also some indication of summer blooms becoming more frequent at the study site in recent years (Almén and Tamelander 2020).

Changes in phenological patterns can be hard to detect when monitoring variation in annual abundances, in particular, if the timing of the annual peak abundance varies and monitoring data cover only a narrow time window, the resulting measure could reflect a change in peak or average abundance, a change in the timing of occurrence or both. This is particularly relevant when studying rotifers and other taxa that have shorter generation times compared with copepods (Lehtiniemi et al. 2022). Klais et al. (2016) has recommended that the sampling frequency for these groups should be every fortnight to capture patterns in abundance with high accuracy. When subsampling the older more frequently sampled data to have monthly interval, we did indeed see that the mean intra-annual pattern varied substantially in timing (Fig. 3). Not only species with the fastest turn over times were affected, *Acartia bifilosa* is known to have two or more generations per season in the area (Viitasalo and Katajisto 1994), but when sampling frequency was decreased from three samples per month to one, this pattern disappears in favour of two peaks (Fig. 3). We also noted that the later and more sparsely sampled part of the time series seemed to estimate patterns in the timing of occurrence with higher variability (see Fig. 4 and Fig. S5). Thus, it is difficult to say if the disappearances of the observed trends in phenological patterns from the first to the second part of the time series are due to actual change, or due to increased noise as a result of the decline in sampling frequency. This situation was likely not improved by the shift in timing of the sampling in 2017 (Fig. 1). The mean annual estimates shown, based on the different fractions of the first time period, would similarly suggest that less frequent sampling influences the annual timing of cardinal events (e.g. *Keratella* and *E. affinis* copepodites Fig. 3B).

Globally, temperature has been shown to shift community composition of zooplankton (Jonkers et al. 2019), and additionally, local studies indicate ongoing shifts in community composition, such as decline in marine taxa (Mäkinen et al. 2017) and increase in smaller sized organisms like cladocerans and rotifers (Suikkanen et al. 2013; Hall and Lewandowska 2022). Comparing the mean abundance patterns of the taxa between 1967–1984 and 1993–2020 (Fig. 3), the annual mean abundances show a decrease. It is difficult to be sure of the magnitude of the decrease as the diameter of the net decreased between the sampling periods; however, other studies in the Gulf of Finland indicate a decline in overall zooplankton abundance, also in copepods (Suikkanen et al. 2013). In addition, looking at the variability in the abundance estimates of Fig. 3B infrequent sampling also influences our ability to estimate annual average peak abundances as well.

The present study shows that the emergence of some zooplankton have become earlier and that the mean annual abundance of many taxa has decreased in the area compared to the situation prior to 1980s. Changes in the timing of occurrence zooplankton abundance and timing can have cascading effects on higher trophic levels. Changes in the timing of occurrence and in particular, earlier emergence of zooplankton in spring can lead to a trophic mismatch (in the timing of occurrence) with higher trophic levels such as fish for which phenological changes are slower compared with zooplankton, leading to potential consequences in ecosystem functioning (Ratnarajah et al. 2023). A decrease in the abundance of large copepods has been shown to detrimentally affect the Baltic herring in the open Gulf of Finland (Flinkman et al. 1998). Zooplankton have also previously been shown to mature at smaller size with warming (Daufresne et al. 2009), and further studies into how changes in abundance are reflected in changes in biomass are needed to properly understand ramifications for the whole food web and carbon cycling.

Our study highlights potential issues faced by annual monitoring carried out in a narrow temporal window, as a directional shift in the timing of occurrence can look like an increase or decrease in abundance depending on the direction of the shift. In addition, we show that decreasing the sampling frequency influences both our ability to estimate the annual timing and the abundance of zooplankton.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-024-04435-0.

Acknowledgements We thank the numerous colleagues that have taken and analysed the monitoring samples over the decades. We would also like to thank Siru Tasala for help with the time-series data. We thank the Reviewers, whose thoughtful and detailed comments improved the manuscript. The study utilized Tvärminne Zoological Station's and Finnish Environment Institute's (Syke) marine research infrastructures as a part of the national FINMARI consortium.

Author contributions Louise Forsblom, Andreas Lindén, Jonna Engström-Öst and Maiju Lehtiniemi contributed to the study conception and design. Material preparation, data collection and analysis were performed by Louise Forsblom, with contributions from Andreas Lindén, Tjardo Stoffers and Maiju Lehtiniemi. The first draft of the manuscript was written by Louise Forsblom and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Finnish Environment Institute.

Data availability The zooplankton data and the derived phenological variables are available from Zenodo https://zenodo.org/records/10900172.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

References

Aberle N, Bauer B, Lewandowska A, Gaedke U, Sommer U (2012) Warming induces shifts in microzooplankton phenology and reduces time-lags between phytoplankton and protozoan production. Mar Biol 159:2441–2453. https://doi.org/10.1007/s00227-012-1947-0

Almén A-K, Tamelander T (2020) Temperature-related timing of the spring bloom and match between phytoplankton and zooplankton. Mar Biol Res 16:674–682. https://doi.org/10.1080/17451000.2020.1846201

Almén A-K, Vehmaa A, Brutemark A, Engström-Öst J (2014) Coping with climate change? Copepods experience drastic variations in their physicochemical environment on a diurnal basis. J Exp Mar Biol 460:120–128. https://doi.org/10.1016/j.jembe.2014.07.001

Borkman DG, Fofonoff P, Smayda TJ, Turner JT (2018) Changing Acartia spp. phenology and abundance during a warming period in Narragansett Bay, Rhode Island, USA. J Plankton Res 40:580–594. https://doi.org/10.1093/plankt/fby029

Chen CY, Folt CL (1996) Consequences of fall warming for zooplankton over wintering success. Limnol Oceanogr 41:1077–1086. https://doi.org/10.4319/lo.1996.41.5.1077

Chmura HE, Kharouba HM, Ashander J, Ehlman SM, Rivest EB, Yang LH (2019) The mechanisms of phenology: the patterns and processes of phenological shifts. Ecol Monogr 89:1–22

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. In: Advances in marine biology. Elsevier, Amsterdam, pp 249–293

Daufresne M, Lengfellner K, Sommer U (2009) Global warming benefits the small in aquatic ecosystems. Proc Natl Acad Sci 106:12788–12793. https://doi.org/10.1073/pnas.0902080106

Diekmann ABS, Clemmesen C, St. John MA, Paulsen M, Peck MA (2012) Environmental cues and constraints affecting the seasonality of dominant calanoid copepods in brackish, coastal waters: a case study of *Acartia*, *Temora* and *Eurytemora* species in the south-west Baltic. Mar Biol 159:2399–2414. https://doi.org/10.1007/s00227-012-1955-0

Durant J, Hjermann D, Ottersen G, Stenseth N (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33:271–283. https://doi.org/10.3354/cr033271

Edwards M, Richardson AJ (2004) Impact of climate change on marine pelagic phenology and trophic mismatch. Nature 430:881–884. https://doi.org/10.1038/nature02808

Engström-Öst J, Brutemark A, Vehmaa A, Motwani NH, Katajisto T (2015) Consequences of a cyanobacteria bloom for copepod reproduction, mortality and sex ratio. J Plankton Res 37:388–398. https://doi.org/10.1093/plankt/fbv004

Flinkman J, Aro E, Vuorinen I, Viitasalo M (1998) Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. Mar Ecol Prog Ser 165:127–136. https://doi.org/10.3354/meps165127

Greve W, Prinage S, Zidowitz H, Nast J, Reiners F (2005) On the phenology of North Sea ichthyoplankton. ICES J Mar Sci 62:1216–1223. https://doi.org/10.1016/j.icesjms.2005.03.011

Hall CAM, Lewandowska AM (2022) Zooplankton dominance shift in response to climate-driven salinity change: a mesocosm study. Front Mar Sci 9:1–10. https://doi.org/10.3389/fmars.2022.861297

Hansson S, Larsson U, Johansson S (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J Plankton Res 12:1099–1116. https://doi.org/10.1093/plankt/12.5.1099

Hedberg P, Olsson M, Höglander H, Brüchert V, Winder M (2024) Climate change effects on plankton recruitment from coastal sediments. J Plankton Res 46:117–125. https://doi.org/10.1093/plankt/fbad060

Jansson A, Klais-Peets R, Grinienė E, Rubene G, Semenova A, Lewandowska A, Engström-Öst J (2020) Functional shifts in estuarine zooplankton in response to climate variability. Ecol Evol 10:11591–11606. https://doi.org/10.1002/ece3.6793

Ji R, Edwards M, Mackas DL, Runge JA, Thomas AC (2010) Marine plankton phenology and life history in a changing climate: current research and future directions. J Plankton Res 32:1355–1368. https://doi.org/10.1093/plankt/fbq062

Jonkers L, Hillebrand H, Kucera M (2019) Global change drives modern plankton communities away from the pre-industrial state. Nature 570:372–375. https://doi.org/10.1038/s41586-019-1230-3

Kalliosaari S (1978) Ice winters 1971–1975 along the Finnish coast. Merentutkimuslaitoksen julkaisu, Helsinki, p 245

Kalliosaari S (1982) Ice winters 1976–1980 along the Finnish coast. Merentutkimuslaitoksen julkaisu, Helsinki, p 249

Kalliosaari S, Seinä A (1987) Ice winters 1981–1985 along the Finnish coast. Merentutkimuslaitoksen julkaisu, Helsinki, p 254

Katajisto T, Viitasalo M, Koski M (1998) Seasonal occurrence and hatching of calanoid eggs in sediments of the northern Baltic Sea. Mar Ecol Prog Ser 163:133–143

Katajisto T (2003) Development of *Acartia bifilosa* (Copepoda: Calanoida) eggs in the northern Baltic Sea with special reference to dormancy. J Plankton Res 25:357–364. https://doi.org/10.1093/plankt/25.4.357

Klais R, Lehtiniemi M, Rubene G, Semenova A, Margonski P, Ikauniece A, Simm M, Põllumäe A, Grinienė E, Mäkinen K, Ojaveer H (2016) Spatial and temporal variability of zooplankton in a temperate semi-enclosed sea: implications for monitoring design and long-term studies. J Plankton Res 38:652–661. https://doi.org/10.1093/plankt/fbw022

Klais R, Otto SA, Teder M, Simm M, Ojaveer H (2017) Winter–spring climate effects on small-sized copepods in the coastal Baltic Sea. ICES J Mar Sci 74:1855–1864. https://doi.org/10.1093/icesjms/fsx036

Lehtiniemi M, Fileman E, Hällfors H, Kuosa H, Lehtinen S, Lips I, Setälä O, Suikkanen S, Tuimala J, Widdicombe C (2022) Optimising sampling frequency for monitoring heterotrophic protists in a marine ecosystem. ICES J Mar Sci 79:925–936. https://doi.org/10.1093/icesjms/fsab132

Mackas DL, Greve W, Edwards M, Chiba S, Tadokoro K, Eloire D, Mazzocchi MG, Batten S, Richardson AJ, Johnson C, Head E, Conversi A, Peluso T (2012) Changing zooplankton seasonality in a changing ocean: Comparing time series of zooplankton phenology. Prog Oceanogr 97–100:31–62. https://doi.org/10.1016/j.pocean.2011.11.005

Mäkinen K, Vuorinen I, Hänninen J (2017) Climate-induced hydrography change favours small-bodied zooplankton in a coastal ecosystem. Hydrobiologia 792:83–96. https://doi.org/10.1007/s10750-016-3046-6

Meier HEM, Dieterich C, Gröger M, Dutheil C, Börgel F, Safonova K, Christensen OB, Kjellström E (2022) Oceanographic regional climate projections for the Baltic Sea until 2100. Earth Syst Dynam 13:159–199. https://doi.org/10.5194/esd-13-159-2022

Merkouriadi I, Leppäranta M (2014) Long-term analysis of hydrography and sea-ice data in Tvärminne, Gulf of Finland, Baltic Sea. Clim Change 124:849–859. https://doi.org/10.1007/s10584-014-1130-3

Olofsson M, Suikkanen S, Kobos J, Wasmund N, Karlson B (2020) Basin-specific changes in filamentous cyanobacteria community composition across four decades in the Baltic Sea. Harmful Algae. https://doi.org/10.1016/j.hal.2019.101685

Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42

Ratnarajah L, Abu-Alhaija R, Atkinson A, Batten S, Bax NJ, Bernard KS, Canonico G, Cornils A, Everettason D, Grigoratou M, Ishak NHA, Johns D, Lombard F, Muxagata E, Ostle C, Pitois S, Richardson AJ, Schmidt K, Stemmann L, Swadling KM, Yang G, Yebra L (2023) Monitoring and modelling marine zooplankton in a changing climate. Nat Commun 14:1–17. https://doi.org/10.1038/s41467-023-36241-5

Reusch TBH, Dierking J, Andersson HC, Bonsdorff E, Carstensen J, Casini M, Czajkowski M, Hasler B, Hinsby K, Hyytiäinen K, Johannesson K, Jomaa S, Jormalainen V, Kuosa H, Kurland S, Laikre L, MacKenzie BR, Margonski P, Melzner F, Oesterwind D, Ojaveer H, Refsgaard JC, Sandström A, Schwarz G, Tonderski K, Winder M, Zandersen M (2018) The Baltic Sea as a time machine for the future coastal ocean. Sci Adv 4:eaar8195

Richardson K, Visser A, Pedersen F (2000) Subsurface phytoplankton blooms fuel pelagic production in the North Sea. J Plankton Res 22:1663–1671. https://doi.org/10.1093/plankt/22.9.1663

Scharfe M, Wiltshire KH (2019) Modeling of intra-annual abundance distributions: constancy and variation in the phenology of marine phytoplankton species over five decades at Helgoland Roads (North Sea). Ecol Modell 404:46–60. https://doi.org/10.1016/j.ecolmodel.2019.01.001

Schlüter MH, Merico A, Reginatto M, Boersma M, Wiltshire KH, Greve W (2010) Phenological shifts of three interacting zooplankton groups in relation to climate change. Glob Change Biol 16:3144–3153. https://doi.org/10.1111/j.1365-2486.2010.02246.x

Seinä A, Kalliosaari S (1991) Ice winters 1986–1990 along the Finnish coast. Merentutkimuslaitoksen julkaisu, Helsinki, p 259

Seinä A et al (1996) Ice seasons 1991–1995 along the Finnish coast. Meri—Report Series of the Finnish Institute of Marine Research, p 27

Seinä A et al (2001) Ice seasons 1996–2000 along the Finnish coast. Meri—Report Series of the Finnish Institute of Marine Research, p 43

Seinä A et al (2006) Ice seasons 2001–2005 along the Finnish coast. Meri—Report Series of the Finnish Institute of Marine Research, p 57

Sommer U, Aberle N, Lengfellner K, Lewandowska A (2012) The Baltic Sea spring phytoplankton bloom in a changing climate: an experimental approach. Mar Biol 159:2479–2490. https://doi.org/10.1007/s00227-012-1897-6

Suikkanen S, Pulina S, Engström-Öst J, Lehtiniemi M, Lehtinen S, Brutemark A (2013) Climate change and eutrophication induced shifts in northern summer plankton communities. PLoS ONE 8:e66475. https://doi.org/10.1371/journal.pone.0066475

Sukhikh N, Souissi A, Souissi S, Holl A-C, Schizas NV, Alekseev V (2019) Life in sympatry: coexistence of native *Eurytemora affinis* and invasive *Eurytemora carolleeae* in the Gulf of Finland (Baltic Sea). Oceanologia 61:227–238. https://doi.org/10.1016/j.oceano.2018.11.002

Tachibana A, Nomura H, Ishimaru T (2019) Impacts of long-term environmental variability on diapause phenology of coastal copepods in Tokyo Bay, Japan: long-term valiability of coastal copepods. Limnol Oceanogr 64:S273–S283. https://doi.org/10.1002/lno.11030

Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, Burthe S, Helaouet P, Johns DG, Jones ID, Leech DI, Mackay EB, Massimino D, Atkinson S, Bacon PJ, Brereton TM, Carvalho L, Clutton-Brock TH, Duck C, Edwards M, Elliott JM, Hall SJG, Harrington R, Pearce-Higgins JW, Høye TT, Kruuk LEB, Pemberton JM, Sparks TH, Thompson PM, White I, Winfield IJ, Wanless S (2016) Phenological sensitivity to climate across taxa and trophic levels. Nature 535:241–245. https://doi.org/10.1038/nature18608

Uriarte I, Villate F, Iriarte A, Cook K (2021) Opposite phenological responses of zooplankton to climate along a latitudinal gradient through the European Shelf. ICES J Mar Sci 78:1090–1107

Viitasalo M (1992) Calanoid resting eggs in the Baltic Sea: implications for the population dynamics of *Acartia bifilosa* (Copepoda). Mar Biol 114:397–405. https://doi.org/10.1007/BF00350030

Viitasalo M, Katajisto T (1994) Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. Mar Biol 120:455–466. https://doi.org/10.1007/BF00680221

Viitasalo M, Katajisto T, Vuorinen I (1994) Seasonal dynamics of *Acartia bifilosa* and Eurytemora affinis (Copepoda: Calanoida) in relation to abiotic factors in the northern Baltic Sea. Hydrobiologia 292(293):415–422

Winder M, Schindler DE, Essington TE, Litt AH (2009) Disrupted seasonal clockwork in the population dynamics of a freshwater copepod by climate warming. Limnol Oceanogr 54:2493–2505. https://doi.org/10.4319/lo.2009.54.6_part_2.2493

Wood S (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC, London
Wood S (2020) Package 'mgcv'. R package version 18-39 338