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Herring (*Clupea harengus*) recruitment failure in the western Baltic Sea as a consequence of a drastic zooplankton decline

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ABSTRACT: Climate-induced shifts in zooplankton communities can influence the survival and recruitment of commercially important fishes worldwide by altering the prey field, potentially causing severe food limitation. Due to the recruitment failure of the western Baltic herring stock over the last decade, we investigated the role of zooplankton and potential environmental drivers of early life stage survival in a major nearshore nursery area in the western Baltic Sea. The seasonal synchrony between predator and prey structures annual secondary production. However, studying the cause-and-effect relations is challenging, as many monitoring programs are static in time and limited to a short period every year. We analysed weekly data from 2008 to 2020, including zooplankton density and community composition together with herring larvae survival. Larval herring productivity has been notably low in recent years, particularly since 2014, reaching a record low in 2020. Annual mean total zooplankton density has also decreased drastically, with the largest decline (~84%) occurring between 2012 and 2013. This decrease was predominantly seen in small organisms (copepod nauplii, bivalve veligers, and rotifers). The total density of these major prey organisms was positively correlated with the larval herring survival index for early herring life stages. The decrease in zooplankton taxa density was most likely induced by changes in phytoplankton phenology expressed by earlier seasonal chlorophyll *a* peaks. Using these high-resolution time series, we provide a potential mechanism of cascading climate change effects on the survival of young herring in the western Baltic Sea.

KEY WORDS: Baltic Sea · Climate change · Atlantic herring · *Clupea harengus* · Larval fish · Phytoplankton bloom · Zooplankton

1. INTRODUCTION

Changes in zooplankton community structure and density can affect fish recruitment by reducing the energy supply available for fish larvae by decreasing both the quantity and quality of their prey, potentially impacting their survival (Hjort 1914, Cushing 1990, Llopiz et al. 2014, Burbank et al. 2023). As a consequence, global fish production, which includes fisheries and aquaculture and is valued at USD 406 billion (FAO 2022), is absolutely dependent on an adequate abundance of zooplankton. As climate change progresses, major challenges to ecosystems are anticipated (Beaugrand 2004, Beaugrand & Ibañez 2004, Poloczanska et al. 2016). At the lower levels of the food web, zooplankton is particularly sensitive to environmental changes, resulting in temporal shifts in community composition, structure, and abundance as well as changes in the timing of life cycle events (Richardson 2008, Ji et al. 2010). Zooplankton in higher latitudes may be more exposed to climate warming, including altered seasonal temperature changes. This trend has

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been observed throughout the North Atlantic (Beaugrand & Ibañez 2004, Morse et al. 2017), the North Sea (Beaugrand 2004, Belkin 2009, Dutheil et al. 2022), and the Baltic Sea (Belkin 2009, Dutheil et al. 2022). In particular, inshore systems such as estuaries, bays, and lagoons are characterised by both high levels of productivity and variability in productivity at low trophic levels. This is due, in part, to factors like terrestrial nutrient inputs (Cloern & Jassby 2010, Carstensen et al. 2020) and wind-induced mixing of the water column (Lehmann & Myrberg 2008). These coastal regions in temperate and boreal zones are expected to experience more extreme warming than global averages (Cai et al. 2011, Wallace et al. 2014). Although coastal zooplankton species have mechanisms to cope with high environmental variability (Dam 2013, Dam et al. 2021), such as fast reproductive cycles and the ability to form resting eggs in adverse conditions, the rapid and intense nature of climate change could outstrip their ability to acclimate and adapt.

Among such regions experiencing significant climate-induced impacts, the Baltic Sea stands out (Reusch et al. 2018). In general, this area has endured substantial ecosystem regime shifts due to a combination of warming, overfishing, and eutrophication. Climate warming in particular has affected zooplankton in the central Baltic Sea (Möllmann et al. 2008), and declines in marine taxa and large-bodied copepods have been reported for the 20th century in the northern Baltic Archipelago Sea (Mäkinen et al. 2017). In the southwestern Baltic Sea, this change has been reflected in a decline in copepods, followed by a decline in rotifers (Feike et al. 2007). This pattern shows how climate change can alter marine ecosystems and cause shifts in zooplankton populations. In addition to direct heat stress, even if compensated by a broad temperature tolerance range of some aquatic organisms (Bates et al. 2013, Bennett et al. 2018), shifts in the phenology and corresponding asynchronies in the timing of life history events can be a challenge for marine life in temperate latitudes. Phenology plays a critical role in higher-latitude environments that experience strong seasonal cycles of production (Hjort 1914, Cushing 1990, Edwards & Richardson 2004, Winder & Varpe 2020). In these regions, rising spring temperatures lead to decreasing sea ice cover, a trend that is expected to continue in the future (Prandle & Lane 1995, Haapala et al. 2015, Käyhkö et al. 2015). As sea ice cover declines, more solar radiation reaches the ocean surface, potentially causing key events such as the spring phytoplankton bloom to occur earlier (Kahru et al. 2016). The seasonal development of zooplankton, which occupy the trophic level directly above phytoplankton, is closely tied to the timing of the phytoplankton bloom (Sommer et al. 2012). Climate change can disrupt the timing of these biological events, causing mismatches in phenology that affect relationships across trophic levels (Koeller et al. 2009, Durant et al. 2019, Ferreira et al. 2023).

Due to the unique early life strategies that fish species have evolved in response to prey dynamics (Cushing 1990, Peck et al. 2012), the impact of shifting temperature regimes is increasingly evident in higher-latitude coastal areas, such as Greifswald Bay (Polte et al. 2021). This bay is a critical spawning ground for western Baltic herring, a stock currently experiencing an alarming decline in recruitment (Moyano et al. 2023). This decline compelled the International Council for the Exploration of the Sea (ICES) to issue a recommendation for a complete halt to herring catches from 2019 to 2024 and ongoing (ICES 2023a). Research progress indicates that earlier hatching cohorts do not result in a substantial number of growing larvae, highlighting a critical bottleneck phase tied to prey availability for first-feeding larvae (Polte et al. 2014).

The unexplored connection between larval survival and zooplankton prey availability in Greifswald Bay presents an excellent opportunity to investigate the decline in recruitment. Our 13 yr time series data represents a unique resource in view of the scarcity of comprehensive, long-term data. The data was collected weekly during the spring and summer months from 2008 to 2020 and offers high temporal resolution, with measurements across 3 trophic levels: phytoplankton, zooplankton, and fish larvae. It includes taxonomic and size-specific information on zooplankton along with size-specific metrics for herring larvae. Using this data set, we tested the hypothesis that environmental pressures have driven a regime shift in the zooplankton community of Greifswald Bay, resulting in changes in its composition and abundance from 2008 to 2020. Subsequently, we examined the impact of these changes on the survival of herring larvae in the system.

2. MATERIALS AND METHODS

2.1. Study site

Greifswald Bay (54° 14′ N, 13° 33′ E; Fig. 1) is a 514 km^2 non-tidal, well-mixed, semi-enclosed lagoon in the southern Baltic Sea with an average depth of 5.8 m (maximum depth: 13.6 m), with salinities between 7 and 9 and a seasonal temperature range from sub-0°C in winter to >20°C during summer (German

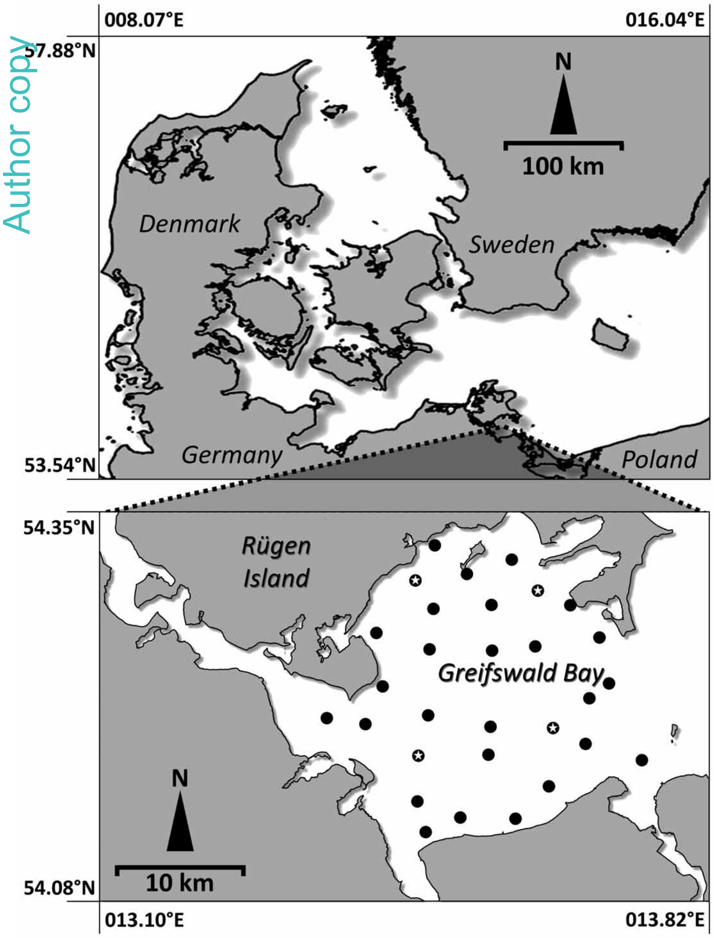

Fig. 1. Location of the larvae sampling sites (black dots) and zooplankton sampling stations (dots with white asterisks) in Greifswald Bay and the positioning of the lagoon in the southern Baltic Sea. The coordinates show the latitude and longitude (in decimal degrees) of the corresponding map edges

Hydrographic Institute, https://www.bsh.de/EN/DATA/Climate-and-Sea/Sea_temperatures/Sea_surface_temperatures/sea_surface_temperatures_node.html). Due to its shallow littoral zone, which serves as a major spawning ground for western Baltic Sea spring-spawning herring (Polte et al. 2017), this bay is of particular ecological importance for the survival of the early life stages of herring. Positioned mid-latitude, within the northern temperate zone, Greifswald Bay is subject to seasonal ice coverage during the winter months. However, the extent and duration of this ice coverage vary each year, influenced by annual variability in weather conditions (Schmelzer et al. 2014, Schwegmann & Holfort 2018). Thanks to these unique characteristics, the confined waters of Greifswald Bay offer a remarkable opportunity for conducting *in situ* studies on herring early life-stage ecology.

2.2. Field sampling and data generation

2.2.1. Herring larvae

Since 1992, Greifswald Bay has been the subject of regular ichthyoplankton surveys (Fig. 1). These surveys are conducted from February or March to June each year, depending on the time of ice retreat, and provide valuable insights over a substantial period (Oeberst et al. 2009, Polte et al. 2021). The surveys were conducted weekly across a 35-station grid in the bay and the connecting sound (Strelasund). To align larval herring data with the area of zooplankton sampling, the stations in the sound were excluded in this study. Bongo nets (mesh size: 335 µm) equipped with flow meters were used to collect herring larvae samples, performing double-oblique hauls from the surface down to 1 m above the sea floor. Upon collection, all samples were immediately fixated in a 4% borax-buffered formaldehyde solution and transported to a laboratory for further analysis. There, each herring larva was counted and a maximum of 300 larvae per sample were measured to the nearest 1 mm total length (TL). The weekly sampling regime allowed for studying the detailed succession of larval survival and growth patterns using the abundance of early, pre-feeding larval stages as a baseline for calculating a survival index based on the corresponding numbers of resulting advanced larval stages later in the season (see Section 2.3 for details). Due to the way the survival index was calculated for the explicit year-class surviving the critical period, it circumvented potential effects of varying spawning stock biomass and corresponding variation of spawned egg numbers and egg mortality.

2.2.2. Zooplankton

Between 2008 and 2020, zooplankton was sampled weekly from February to June. Vertical Apstein net (mesh size: 55 µm; net mouth diameter: 0.1 m) tows were carried out in 4 different monitoring stations (Fig. 1). At these monitoring stations, the tows were conducted from 1 m above the bottom to the surface. Following the guidelines of the Helsinki Commission (HELCOM 2021) for monitoring mesozooplankton, we preserved the samples in a borax-buffered 4% formaldehyde solution and later analysed them in a laboratory using a light microscope (Leica DMIL LED). Zooplankton was manually sorted to the lowest possible taxonomic level to determine the species composition and the individual abundance of each species.

Within the copepods, we differentiated developmental stages: nauplii, copepodites (early stages C1–C3 and late stages C4–C5), females, and males. Protozoans, meroplankton, and very rare taxa in the samples were not included in the analysis. Because of either their reduced densities due to the low salinity levels or their size and mobility resulting in sporadic catches, excluded taxa were Acari, Amphipoda, Annelida, Appendicularia, Chaetognatha, Cnidaria, Decapoda, Echinodermata, Gastropoda, Insecta, Isopoda, Nematoda, Nemertea, Ostracoda ('Other' in Table S1 in the Supplement at www.int-res.com/articles/suppl/m764p075_supp.pdf).

Over the years, the temporal coverage of the zooplankton data proved to be not uniform across the time series. This inconsistency was caused by several factors. In recent years, as the sea surface temperature (SST) increased, sampling began earlier. There were also instances when certain sampling cruises had to be cancelled due to adverse weather conditions or technical issues (Table S2). To reduce the impact of any inconsistencies caused by shifting start times and interruptions and achieve more consistent temporal data coverage for calculating the annual mean spring zooplankton density, we limited the data to the period between calendar weeks 13 (late March) and 25 (mid-June). For simplification purposes, we use 'mean zooplankton density' throughout the paper.

2.3. Data preparation and numerical analyses

An annual survival index for herring larvae in the bay was calculated using the following procedure: As a baseline for the annual survival, the number of larvae that hatched in the system was calculated as the weekly median of 9 mm larvae per m^3 (a proxy for stage 4 first-feeding larvae with seasonal variable length ranging from 8 to 10 mm according to Fischbach et al. 2023, V. Fischbach et al. unpubl. data) of the 30 stations sampled in the Bay, summed over the number of weeks sampled per year (calendar weeks 13–25; see Polte et al. 2014 for details). A similar procedure was applied to herring larvae in stage 10 (Fischbach et al. 2023) within the size classes 19–20 mm (TL), which were determined survivors of the critical period (Fischbach et al. 2023, Fischbach et al. unpubl. data). This length class also shows a strong positive correlation to the 1 yr old juveniles as sampled in the hydroacoustic surveys in the outer western Baltic Sea 1 yr later (Polte et al. 2021). The percentage of these survivors of the initial number of hatchlings was used in this study as a survival index which is considered independent of spawning stock biomass and egg mortality.

To assess the normal distribution of the zooplankton data, the Shapiro-Wilk test was used ($p < 0.05$). Several of the taxa exhibited a right-skewed density that was not normally distributed. To further normalise and stabilise the variance, the original values were fourth-root transformed. To remove extreme outliers from the data of overall zooplankton density (not for each taxon separately), we determined a cut-off value corresponding to the 99th percentile of the densities and removed the highest 1% of values, applying a trimming method by removing. The selection of the trimming percentage was based on a thorough examination of the data distribution (Wilcox 2017). These high values were identified as rotifers *Synchaeta* spp. in the spring of 2011 and were removed due to their ability to rapidly reproduce parthenogenetically and massively increase in numbers under favourable conditions (Walz 1995). First, we used the trimmed data set to calculate the total zooplankton density per m^3 for each sampled station. Then, the arithmetic mean and standard deviation were calculated for each week of each year. The data was aggregated by calculating the mean abundance for each taxon per week, taking into account the available replicates for each week. The weekly averages were further aggregated to calculate the annual arithmetic mean density and its standard deviation for each year. This technique reduces the extreme values more moderately than a log transformation. The fourth-root transformation is used to minimise the impact of extreme values while preserving the integrity of underlying data relationships (Osborne 2002).

Certain categories of organisms were combined into larger groups for simplification. Copepod species were grouped according to their developmental stage (nauplii, C1–C3, and C4–C5), and both male and female copepods were combined into a single 'adult' category. Rotifera species were combined due to inconsistent taxonomic resolution over the years and included mostly *Synchaeta* spp., but also *Brachionus* spp., *Filinia* spp., *Keratella* spp., and *Notholca* spp. Diplostraca (formerly Cladocera) included *Bosmina* spp., *Cercopages pengoi*, *Chydorus sphericus*, *Daphnia* spp., *Evadne* spp., *Leptodora kindtii*, *Podon* spp., *Pleopis polyplemoides*, and Sididae (Table S1). Zooplankton group data were fourth-root transformed, and weekly and yearly community similarity was assessed using the Bray-Curtis similarity index. Non-metric multidimensional scaling (nMDS) allowed visualisation of annual similarities based on weekly and annual zooplankton community data. The stress value indicated how faithfully the 2D ordination plots represented the high-dimensional relationships observed among the samples (Clarke & Warwick 1994). To test whether the 2 distinct time periods of zooplankton community densities revealed by the hierarchical clustering analysis (constrained incremental sum of squares, CONISS) and the breakpoint analysis were significantly different, we used a 1-factor non-parametric multivariate permutation analysis (PERMANOVA) on weekly and yearly zooplankton community densities (Anderson et al. 2008). Data were fourth-root transformed and a Bray-Curtis similarity matrix was generated. Prior to performing the PERMANOVA, we ran a distance-based test for homogeneity of multivariate dispersions (PERMDISP) to evaluate the homogeneity of the data, which were non-significant for weekly ($F_{1,155}$ =1.679, p(perm) = 0.283) and yearly data ($F_{1,11}$ = 0.217, p(perm) = 0.701). Similarity percentage analysis (SIMPER) was used to identify the species or zooplankton groups that contributed the most to average community similarities between periods, both before and after the zooplankton shift (Clarke & Warwick 1994).

To identify the subset of environmental variables that best explained the variation of the zooplankton community, we used the BIOENV procedure (PRIMER 7). It searches for high matrix correlations, rank-based, between a similarity matrix (Bray-Curtis similarity) of the zooplankton community and the resemblance matrix (Euclidean distance) generated from a normalised suite of environmental variables (Table S3); namely, the weekly peak chlorophyll *a* (chl *a*) timing and peak chl *a* concentration, the annual number of ice days, daily mean SSTs and hourly total sunshine duration). Unfortunately, data on the seasonal timing of ice days was not available. All analyses were performed using R software (v.4.1.2, R Core Team 2022) and PRIMER (v.7.0.24) with PERMANOVA (Anderson et al. 2008).

To visualise the contribution of the main taxonomic groups to the annual variability in mean zooplankton density, we generated a heatmap (see Fig. 4). The colour code of the heatmap, which indicates the value magnitude, was based on 5 evenly spaced intervals that were consistent across all taxa and years. This approach divided the range of values into 5 equal parts, with each part being assigned a specific colour. To account for short-term data fluctuations, taxonomic groups were sorted using their 5 yr rolling window standardised mean. This method calculates the mean zooplankton density for each taxonomic group over a 5 yr period, advancing the window yearly. The mean values were then standardised by subtracting the overall mean and dividing by the standard deviation.

2.4. Environmental data

We aimed to understand how the magnitude and timing of phytoplankton blooms, represented by peak chl *a* concentration and timing of this peak, could affect zooplankton dynamics. We used multiple data sources to examine the relationship between zooplankton dynamics in Greifswald Bay and various environmental factors (Table S3). Firstly, we analysed chl *a* concentration data (mg m^{-3}) from the Plymouth Marine Laboratory for the period 2008 to 2020 with spatial coverage between 54.14° N, 13.06° E and 54.39° N, 13.72° E (https://polarwatch.noaa.gov/erddap/griddap/pmlEsaCCI60OceanColor8Day.html). We selected data for January through June to align with our zooplankton sampling efforts. We created 2 variables: 'peak chl *a* concentration', the highest average chl *a* level across the bay each year, and 'peak chl *a* timing', the day of the year (DOY) when this peak concentration occurs (Ji et al. 2010). Secondly, we sourced 'annual number of ice days' from the German Weather Service, covering ice conditions in the Mecklenburg-Vorpommern region (DWD Climate Data Center, opendata.dwd.de). Next, we included 'mean SST' data from the UK Met Office, with the same temporal coverage as previous data sets (Copernicus Marine Service, doi:10.48670/moi-00165). We calculated the annual mean SST for this period. Lastly, we calculated the annual sunshine hours from hourly sunshine duration data from the German Weather Service for 2008–2020, likewise acquired for January to June (DWD Climate Data Center, dataset ID: urn:x-wmo:md:de.dwd.cdc::obsgermany-climate-daily-solar). To measure variation in our environmental parameter data, we used the 'scale' function to calculate anomalies. These represented the deviation of each yearly measurement from the mean, expressed in terms of standard deviation units.

2.5. Changepoint analyses

We used 2 different methods to identify change points in zooplankton taxa density data: constrained hierarchical chronological clustering using the 'Rioja' package and the pruned exact linear time (PELT) algorithm in the 'changepoint' package, both implemented in R v.4.1.2 R (Core Team 2022). By using 2 different methods, we aimed to provide a robust comparison and increase the confidence in our results. The input data was the fourth-root-transformed zooplankton taxa density, organised in a temporally ordered Euclidean distance matrix. The constrained hierarchical chronological clustering followed an agglomerative bottom-up approach, treating each year as an individual cluster and preserving the order. As the hierarchy was constructed, pairs of years were merged using the CONISS algorithm, which measures the variability of observations within each cluster. For additional support in identifying change points, we applied the PELT algorithm. We used the multivariate species composition from multiple factor analysis as input data, focusing only on the first dimension, which accounted for 56.7% of the variance. The PELT algorithm calculated the location and number of changes in the mean of a time series and a confidence value for each detected change point, with values closer to 1 indicating a higher level of confidence. Our approach aligns with the recommendation to use multiple change point detection methods for comparison (Andersen et al. 2009).

2.6. Correlation between zooplankton and larval herring survival index

To explore the relationship between the herring larvae and the availability of their prey, we summed the mean densities of different small-sized zooplankton species and their various developmental stages, including rotifers, bivalve veligers, and copepod nauplii and copepodites C1–C3. All of these organisms are small enough to serve as prey for larval herring. We used the Spearman rank correlation coefficient, a non-parametric measure that captures both the strength and direction of the association between the variables.

3. RESULTS

3.1. Herring larvae survival decline

Over the 13 yr period from 2008 to 2020, the total median abundance of the 9 mm length class larvae of the western Baltic spring spawning herring was highly variable (Fig. 2A). However, the percent of survival into the 19–20 mm length class ranged between 4 and 11% from 2008 to 2013 and dropped to 0–2.6% from 2014 onward (Fig. 2B).

3.2. Shift in zooplankton dynamics

The dominant zooplankton taxa found during February to June were copepod life stages of the genus *Acartia* spp., Rotifera, and Bivalvia larvae. The annual mean total zooplankton density and its variability generally decreased from 2008 to 2020. An exceptionally high density was recorded in 2011, while the lowest density was recorded in 2013 (Fig. 2C). Notably, between 2012 and 2013, the mean (±SD) zooplankton density decreased from 659 534 ± 154 599 to 79 199 ± 5173 ind. per m^3. This corresponds to a de-

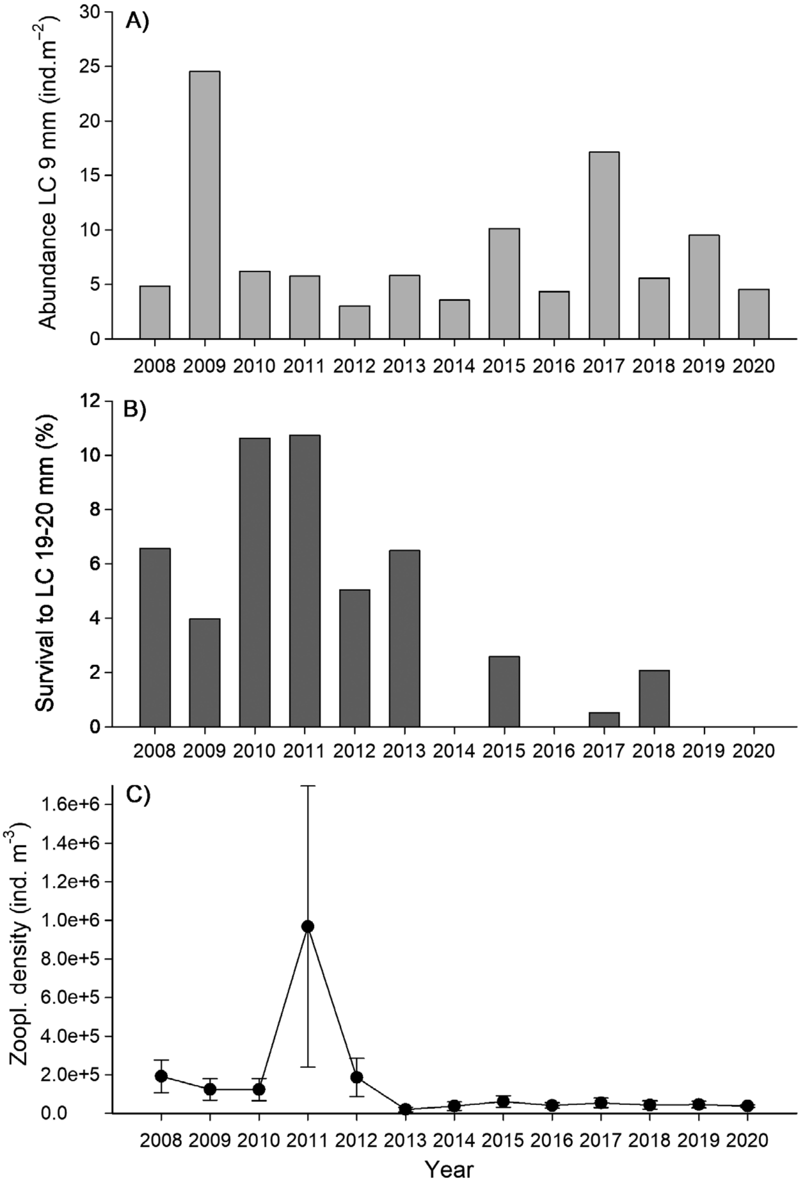

Fig. 2. (A) Annual total abundances of herring larvae in length class (LC) 9 mm (sum of weekly medians), (B) percentage of survival of 9 mm herring larvae into LC 19 and 20 mm (based on the annual sum of weekly medians), and (C) zooplankton yearly mean density from 2008 to 2020. Error bars: 95% CI

crease of 1 order of magnitude or 84% decrease in zooplankton density between those particular years.

Two main clusters in the zooplankton density data were identified by the CONISS hierarchical chronological clustering algorithm. The analysis showed that (1) data variability decreased within each cluster from 2016 onward and (2) there was a shift from high densities until 2012, decreasing from 2013 onward (Fig. 3A). The change between 2012 and 2013 was also confirmed by the PELT changepoint algorithm, with a confidence value of 0.77, indicating moderately high confidence in the detected change point (Fig. 3B). Visualising the shift and the 2 periods in zooplankton community data, nMDS showed the differentiation on weekly and yearly data (Fig. S1). The zooplankton community compositions were significantly different between the 2 periods (2008–2012 and 2013–2020) (PERMANOVA; pseudo-$F_{1,155\_weekly}$ = 48.841; p(perm) = 0.001; permutation: 999; pseudo-$F_{1,11\_annually}$ = 24.411; p(perm) = 0.001; permutation: 700). Small-sized organisms, such as Rotifera, Copepoda nauplii, Bivalvia veliger, and Copepoda C1–C3 were primarily driving this drastic change and contributed 71% to the differences between the 2 periods (Fig. 4, SIMPER Table S4). These taxa have relatively high densities until 2012, with a minimum value of 229 ind. m^{-3} and a maximum value of 813 469 ind. m^{-3}. However, after 2012, these values sharply decreased, with a minimum of 9 ind. m^{-3} and a maximum of 22 227 ind. m^{-3}. The decrease in Copepoda nauplii was not entirely reflected in the subsequent developmental stages. Although copepodites C1–C3 generally decreased in density, with the exception of 2015 and 2017, there was no clear trend observed for copepodites C4–C5 and adult stages.

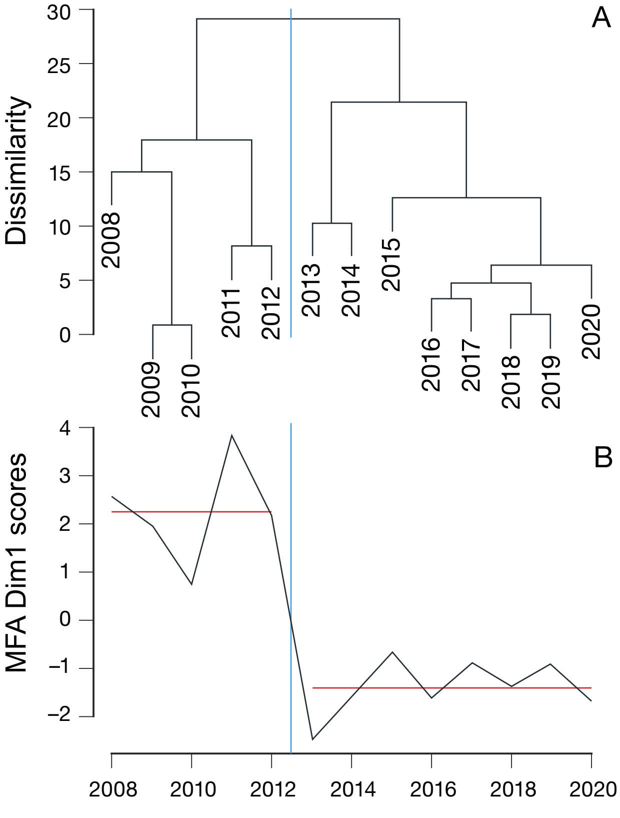

Fig. 3. Mean and change in zooplankton density. (A) Dendrogram of constrained hierarchical clustering analysis (CONISS) showing a significant change in the zooplankton community between 2012 and 2013. (B) Changepoint algorithm (PELT) including a Multi Factor Analysis (MFA) with first dimension factor scores (Dim 1) identifying the transition between 2 different mean zooplankton densities, represented by the red lines (and the identified change point as indicated by the blue vertical lines between 2012 and 2013)

3.3. Correlation between herring larvae prey and survival

To evaluate the putative relationship between prey availability and survival of herring larvae, we used the sum of the mean densities of prey zooplankton species — Bivalvia veliger, Copepoda nauplii and copepodites C1–C3, and Rotifera — and survival into the 19–20 mm length class percentage of the total abundance of 9 mm length class larvae. We found a significant positive correlation between these 2 variables ($r = 0.56$, $p = 0.04$) and a positive linear regression ($R^2 = 0.62$, $p = 0.001$), suggesting that an increase in the density of these ephemeral development stages and rotifer taxa is favourably linked to the survival of herring larvae.

3.4. Key drivers of zooplankton dynamics

To investigate the decrease in zooplankton density and determine its potential causes, we analysed important environmental variables and calculated anomalies for these key determinants (Fig. 5). Our analyses initially focused on chl *a* as an indicator of phytoplankton blooms. We introduced 2 variables: peak chl *a* concentration, the highest annual average level in the bay, and peak chl *a* timing, the DOY when this peak is observed. During the studied season from January to June, the peak chl *a* timing noticeably shifted to an earlier date from 2008 to 2020. The mean ± SD DOY for peak concentration was 99.80 ± 63.47 from 2008 to 2012, but advanced to a mean DOY of 43.13 ± 16.51 from 2013 to 2020, resulting in a shift of

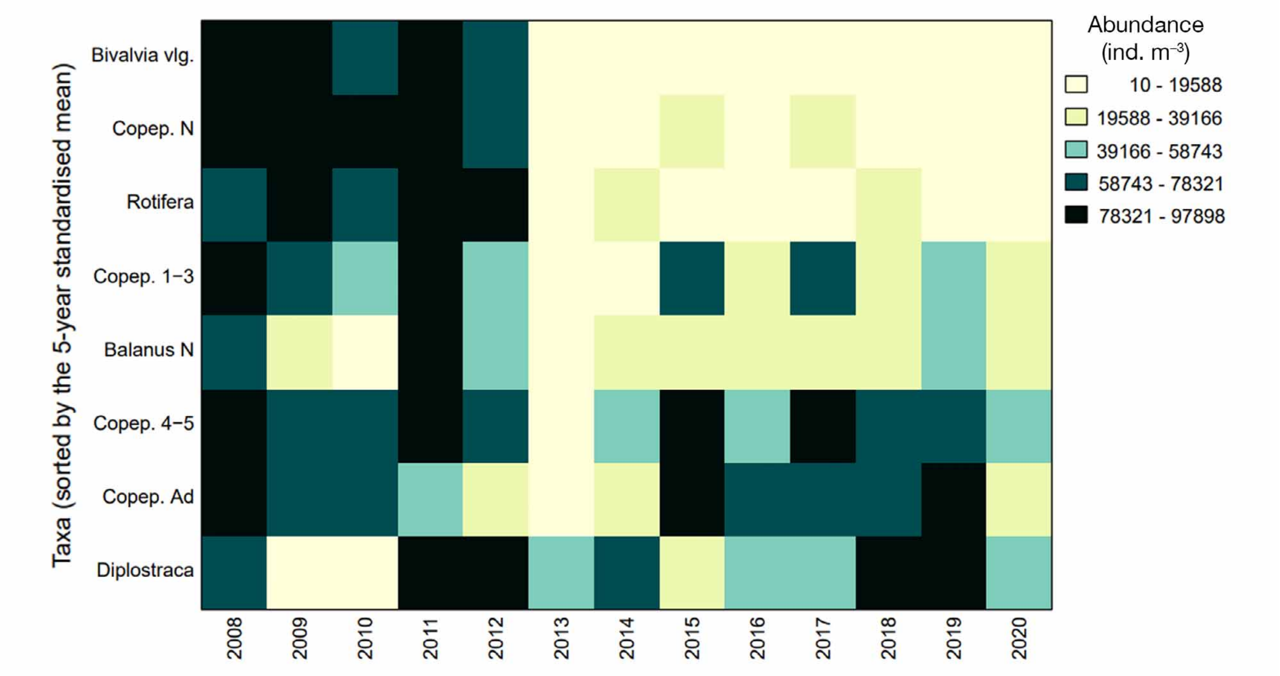

Fig. 4. Heatmap of the fourth-root-transformed original abundance data, divided into 5 intervals and sorted by the 5 yr standardised mean. The plot highlights a yellow-hued cluster in the upper-right corner, representing low values for the small-sized organisms (Bivalvia veliger, Copepoda nauplii, and Rotifera) after 2012. N: nauplii; 1−3 and 4−5: copepod developmental stage groups (copepodites C1−C3 and C4−C5); Ad: adults

approximately 57 d. The mean for peak chl *a* concentration was 12.85 ± 6.72 mg m^{-3} from January to June between 2008 and 2020. The mean concentration decreased from 21.47 ± 10.77 mg m^{-3} in 2008−2012 to 12.85 ± 6.72 mg m^{-3} in 2013−2020, which is a reduction of about 9 mg m^{-3}. However, a higher peak was recorded in 2020. We identified a critical relationship between the timing of peak chl *a* concentrations and zooplankton densities. Specifically, earlier chl *a* peaks are strongly correlated with lower densities of key zooplankton taxa such as Copepoda nauplii, Bivalvia veliger, and Rotifera ($r = 0.60$, 0.58, and 0.58, respectively; $p < 0.05$) (Fig. 6). Conversely, later peaks coincided with higher densities of these taxa. In summary, an earlier chl *a* peak negatively affected the density of these specific developmental stages and rotifer taxa. The multivariate BIO-ENV procedure revealed a positive correlation between the Bray-Curtis similarity matrix of Rotifera, Copepoda nauplii, and Bivalvia veligers and the environmental distance matrix. The best correlation coefficient (0.343) was found with the peak chl *a* concentrations. The other 4 environmental parameters did not increase the explicative power. The annual number of ice days, with a mean of 16.20 d for the period 2008−2020, has decreased over the observational period. Specifically, the mean decreased from 25.13 ± 21.66 d in 2008−2012 to 10.62 ± 7.47 d in 2013−2020 (Fig. 5). This decrease coincided with lower Rotifera densities ($r = 0.59$, $p < 0.05$), whereas the correlations with other zooplankton taxa were variable and not significant (Fig. 6). Meanwhile, both mean SST (10.19°C, Jan−Jun) and total sunshine duration (mean: 56 559 min, Jan−Jun) have been trending upwards in recent years (Fig. 5). Negative correlations were observed between SST and small zooplankton, such as Rotifera, Copepoda nauplii, and Bivalve veligers; however, these were not significant ($r = -0.4$ to -0.1; $p > 0.05$).

4. DISCUSSION

4.1. Zooplankton decline

We identified a decrease in the mean annual total zooplankton density during the 13 yr between 2008 and 2020. This decrease, however, was not continuous. It was driven by a drastic and sudden shift in zooplankton densities between 2012 and 2013, as demonstrated by the CONISS and changepoint analyses. The decrease in zooplankton was predominantly attributed to small-sized zooplankton organisms, including Rotifera, Bivalvia veligers, and Copepoda nauplii, mainly including nauplii and early copepo-

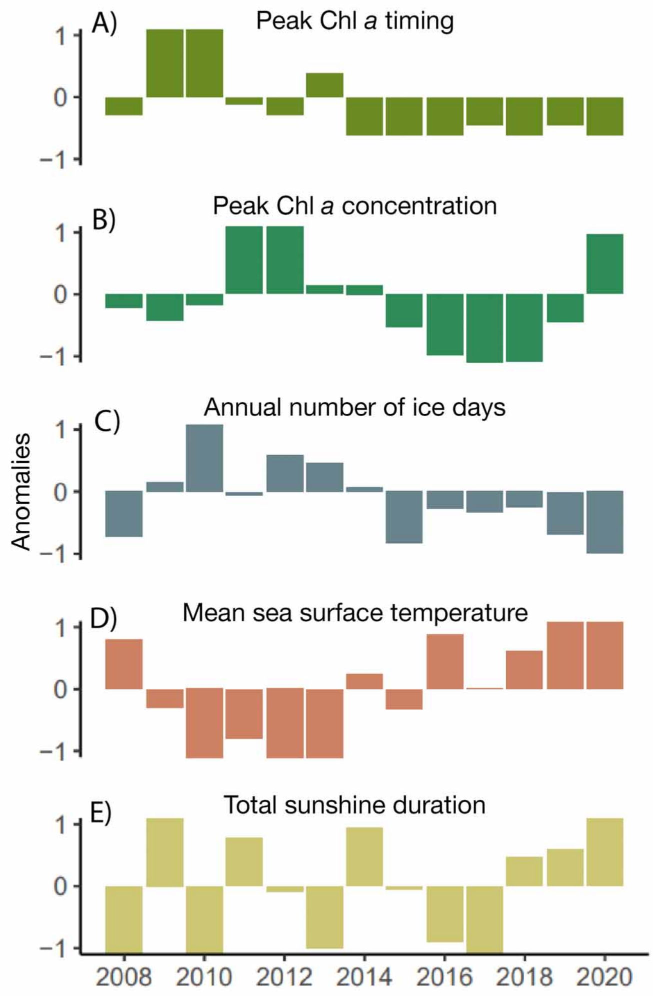

Fig. 5. Annual anomalies of environmental drivers from 2008–2020. (A) Peak chl *a* timing (day of the year), (B) peak chl *a* concentration (mg m^{-3}), (C) annual number of ice days, (D) mean sea surface temperature (°C), (E) total sunshine duration (minutes). The data sources, temporal coverage, temporal resolution, and spatial coverage can be found in Table S3

dites (C1–C3) of *Acartia* spp. Particularly surprising is the decrease in Rotifera abundance, as they can reproduce asexually. This capability leads to high turnover rates and enables them to respond rapidly to environmental changes (Möllmann & Diekmann 2012). Moreover, rotifers can emerge from resting eggs in sediment under suitable light and temperature conditions (Gilbert & Schröder 2004), usually coinciding with periods of high biomass of utilisable food (Starkweather 1980). Despite these adaptive traits, the multi-annual decline in Rotifera may indicate a limit to their ability to adapt to a rapidly shifting environment early in the year. This concept was supported by positive correlations between rotifer density and the later chl *a* peak as well as a trend that higher chl *a* peaks produce higher Rotifera density. However, in the years from 2013 onward, the chl *a* peaks were lower than the mean peak concentration and occurred very early. Therefore, light and temperature conditions may have been inadequate for resting eggs to emerge, resulting in low Rotifera densities.

We also observed a significant reduction in the abundance of early life stages of Copepoda, such as nauplii and copepodites C1–C3. This trend did not extend to later copepodite stages and adults. One possible explanation is that under the current conditions, copepods, such as the dominant species *Acartia* spp., prioritise survival and somatic growth over reproduction (Croll & de Roos 2022). In other words, while *Acartia* spp. may reproduce less, their survival rates remain high. This resource allocation trade-off, favouring somatic growth over reproduction, could potentially create a negative feedback loop. Reduced reproduction could result in lower genetic diversity, making the population more susceptible to environmental changes and ultimately leading to a decrease in overall population density. It appears unlikely that the peak hatching of nauplii would occur as early as January and February, making it improbable that the sampling surveys missed it. Our sampling survey starts when water temperatures reach about 4°C each year, typically aligning with March (calendar weeks 9–11; Table S1). We then continue with weekly sampling until the end of June. Given the low success rate of egg hatching for *A. bifilosa* and *A. tonsa* at temperatures of 5°C and below (Chinnery & Williams 2004, Holste & Peck 2006), it seems improbable that a significant proportion of the nauplii would have reached later developmental stages by March. *A. bifilosa* performs optimally at 10°C and *A. tonsa* at 20°C (Castro-Longoria 2003, Chinnery & Williams 2004). Although our data set lacks information from the late summer months of July and August, accelerated development into the first copepodite stage could potentially have a greater impact on *Acartia* spp. nauplii during that period. Moulting rates are known to increase with rising temperatures, and the transition from the naupliar to the first copepodite stage can occur in fewer than 7 d at 17°C (Peterson 2002). As a result, there may be only a brief window during which nauplii are present in the environment. This rapid development could hinder their detection despite rigorous weekly sampling efforts.

The decline in zooplankton density could potentially be due to increased predation from fish; however, our data indicate otherwise. A recently published study shows that adult herring consume virtually no food during their stay in the spawning

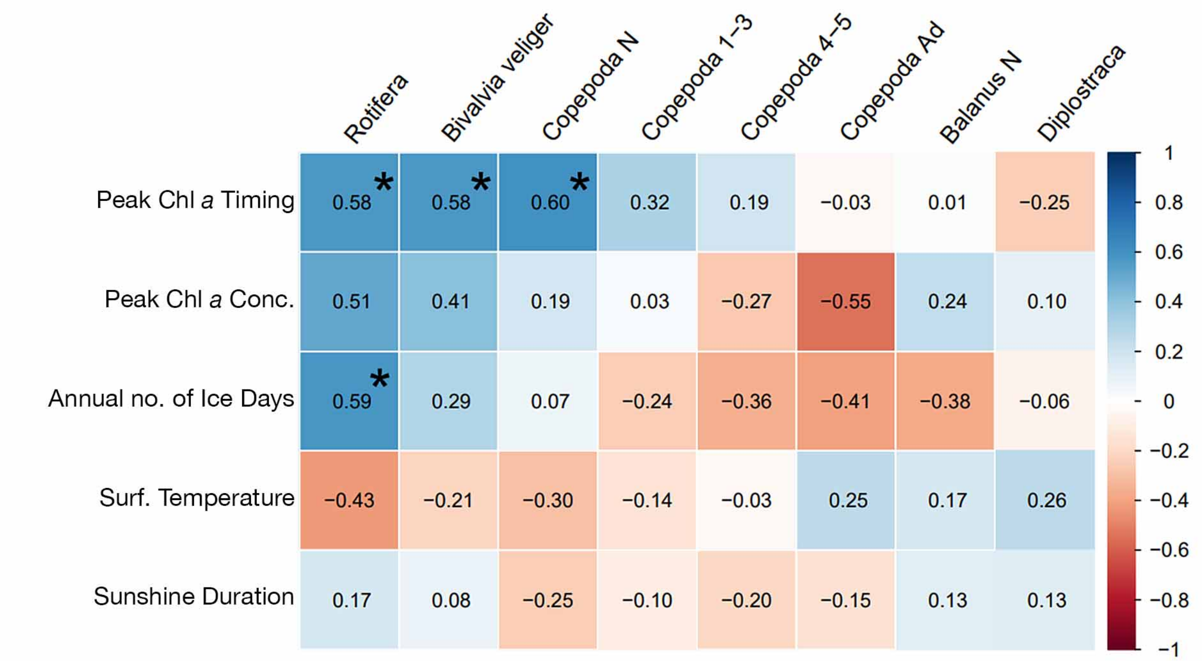

Fig. 6. Correlation matrix of zooplankton groups and environmental factors based on annually aggregated data from various sources (Table S2). N: nauplii; 1–3 and 4–5: copepod developmental stage groups (copepodites C1–C3 and C4–C5); Ad: adults. Colour coding represents the strength of correlations: blue: positive; red: negative. Statistically significant correlations ($p < 0.05$) are marked with an asterisk (*)

area and can therefore be ruled out as a controlling top-down factor (Kotterba et al. 2024). Another fish species that must be considered as an important zooplankton predator simply because of its regional dominance in the area is the three-spined stickleback *Gasterosteus aculeatus*. Although in some years sticklebacks show a high spatio-temporal overlap with herring larvae, their diet comprises less than 20% copepods during the herring spawning season (Kotterba et al. 2017), making this species an unlikely major predator of zooplankton. Given this evidence and the fact that jellyfish (mainly *Aurelia aurita*) obviously appear very late in the season (Kotterba et al. 2017), top-down mechanisms appear less likely to be driving the observed decline in zooplankton density. Typically, reduced predator abundance would result in stable or increased prey numbers (Abrams 2000); however, this is not what we observed. Therefore, bottom-up processes emerge as the more plausible explanation for the decline in zooplankton density.

4.2. Earlier phytoplankton blooms linked to zooplankton decline

We identified the shift in phytoplankton bloom phenology as the strongest predictor of changes in zooplankton density. Notably, the mean timing of the phytoplankton peak advanced by an astounding 59 d between 2014 and 2020 compared to the earlier time period from 2008 to 2013. Accompanied by a decrease in peak concentration, this advancement is a substantial change in primary production. A significant relationship supports this finding: an earlier phytoplankton peak correlates with reduced zooplankton density. Earlier bloom initiation is shown in most ocean regions; however, changes vary by region (Yamaguchi et al. 2022).

The advanced timing of the mean phytoplankton peak in this coastal and shallow bay outpaces the phenological shifts observed in the Baltic Proper and the Bay of Mecklenburg (Kahru et al. 2016, Wasmund et al. 2019). It is important to note that the seasonal cycle governs most of the environmental variability encountered by individual organisms at mid and high latitudes (Ji et al. 2010, Kahru et al. 2016). In these latitudes, the development of phytoplankton in spring is primarily limited by light availability (Edwards et al. 2016). Once sufficient light levels (above 50 $\mu E\ m^{-2}\ s^{-1}$) are reached (Chen & Su 2020), phytoplankton can respond to other environmental factors such as nutrient availability and temperature. As unicellular autotrophic organisms, phytoplankton then have the remarkable ability to rapidly reproduce and can double several times a day (Flynn & Raven 2017). At this point, we can only speculate that earlier phytoplankton peaks are a consequence of rare ice-cover events that are also much shorter, if they occur at all.

On the other hand, the reproduction of multicellular zooplankton, such as copepod *Acartia* spp., is largely temperature-dependent. Zooplankton increase fecundity with rising temperatures, and successful hatching typically occurs when the water temperature exceeds 10°C (Castro-Longoria 2003, Chinnery & Williams 2004). In particular, the emergence of *Acartia* nauplii from egg banks in the sediment requires a temperature of around 14°C to contribute to population recruitment (Glippa et al. 2014). At that point, the transformation of these zooplankton from egg to nauplii to copepodite unfolds over several days (Peterson 2002). This disparity in reproduction mechanisms may lead to zooplankton struggling to synchronise with the phytoplankton bloom shifting to earlier in the year and colder water temperatures. Small zooplankton, particularly those with short life cycles or those of ephemeral development stages, depend on phytoplankton blooms for sustenance, making the seasonal synchronisation critical for their survival (Starkweather 1980, Berggreen et al. 1988, Turner et al. 2001, Suchy et al. 2022). Declines in zooplankton productivity due to shifts in the phenology of primary producers could have broader implications for marine ecosystems, considering the crucial role zooplankton play as a primary food source for higher trophic levels.

4.3. Implications of zooplankton decline on herring recruitment

The larval herring survival index used in this study represents the annual abundance of advanced larvae resulting from the number of hatchlings in the system. This index is, in our opinion, the sharpest metric for describing annual reproductive success, provided that larval export from this sheltered non-tidal system is negligible (Bauer et al. 2013). As the annual portion of the spawning stock spawning in the bay is unknown — and even if it were, egg mortality is probably variable — the direct relation of hatchling with advanced larval stages might deliver the strongest proxy for the number of larvae surviving critical periods in larval development (e.g. the transition of yolk consumption to exogenous feeding) until their ability to swim — and therefore hunt, migrate, and escape more efficiently — increases significantly after the formation of the caudal fin (Moyano et al. 2016, Fischbach et al. 2023). Indeed, this is underlined in the study, as the annual abundance time series of hatchlings (Fig. 2A) is unrelated to zooplankton abundance, and the interannual variability of hatched larvae offers an integral over spawning stock size and egg mortality dynamics. Given that the surviving herring larvae from Greifswald Bay are strongly correlated with the number of 1 yr old juveniles in the western Baltic Sea occurring 1 yr later (Polte et al. 2021, ICES 2023b), the investigated bottom-up mechanism can be assumed to be an important driver of recruitment strength on stock level. Zooplankton was monitored simultaneously with larval herring in their major spawning and nursery area. The zooplankton size class that declined in this study represents the main food source for early herring larvae in the system during the critical period when they start exogenous feeding (Busch 1996). Lower prey density might limit energy availability for these early feeding stages, which have been identified as a survival bottleneck in the study area (Polte et al. 2014). This could subsequently lead to lower recruitment success (Peck et al. 2013). Polte et al. (2021) showed that a series of mild winters negatively affected herring recruitment in the western Baltic Sea. However, at the time, they could only speculate on the specific mechanisms driving these patterns. This study provides first insights into specific bottom-up processes related to the changing climate regime. We found a significant correlation between the survival index of herring larvae and the abundance of prey species, implying an increase in herring larvae survival as the density of ephemeral development stages and rotifer taxa increases. The decline in nauplii of the dominant copepod *Acartia* spp. is particularly concerning, given that herring larvae are known to preferentially select copepod nauplii, as shown by stomach content analysis (Checkley 1982, Busch 1996, Hesse 2010, Hufnagl & Peck 2011, Robert et al. 2014). Investigating the processes driving the recruitment failure of western Baltic herring in the context of bottom-up processes is the subject of ongoing research. Nevertheless, this study indicates that shifts in the timing of primary production cascade along the regime, resulting in a decrease in larval herring year-class strength. The annually aggregated data used in the current exploratory analysis effectively conveyed the generally negative trend in zooplankton abundance over more than 10 yr and its dependence on environmental conditions. There remain, however, unexplained patterns, such as the lag phase between the zooplankton decline (2012) and the decline of larval herring survival (2013). This might be a result of specific predator–prey match events in particularly significant weeks which cannot be captured by annual data aggregation. Therefore, future studies should use a narrower temporal scale to analyse seasonal changes in phytoplankton, zooplankton, and ichthyoplankton dynamics, along with the resulting spatio-temporal overlap. Accurately capturing the peak timing of these different trophic levels (phytoplankton, zooplankton, ichthyoplankton) is crucial to quantify mismatches that may be exacerbated by low abundance (Durant et al. 2005, 2007, Moyano et al. 2023).

The interplay between feeding conditions and recruitment success of fish, as seen in Atlantic herring larvae in the Baltic and North Seas (Alvarez-Fernandez et al. 2015, Paulsen et al. 2017, Burbank et al. 2023), is not confined to these regions or species alone. Expanding the scope, a similar interplay between feeding conditions and recruitment success has also been observed in Pacific herring *Clupea pallasii* (Schweigert et al. 2013, Asch 2015). In tropical regions, the future of small pelagic fish communities is imperilled by declining biomass and nutritional value of prey, potentially exacerbating the anticipated decline in small pelagic fish biomass by 2100 (Heneghan et al. 2023). These fundamental ecological processes are of global concern, particularly in light of ongoing climate change driven by continuously rising CO_2 emissions (Friedlingstein et al. 2022). However, it is crucial to consider that specific impacts will be influenced by local ecological conditions, species-specific traits, and differing adaptability of species (Peck et al. 2013, Wilson et al. 2018).

5. CONCLUSIONS

The zooplankton community in Greifswald Bay, a major spawning area for zooplanktivorous herring *Clupea harengus*, has undergone a regime shift in 2013, marked by the lowest levels of zooplankton abundance in the past decade. This significant decrease in zooplankton abundance is primarily attributed to climate change-induced earlier shifts in phytoplankton blooms. These changes in the food web could have critical implications for higher trophic levels, such as the Atlantic herring, and urgently require further investigation. To better understand these ecological dynamics, high-resolution temporal monitoring becomes indispensable. Although associated with high costs, long-term investments in monitoring promise substantial benefits. Advancements in technological solutions, such as machine learning algorithms for image analysis, offer increasingly cost-effective data analytics (Lombard et al. 2019, Giering et al. 2022, Orenstein et al. 2022, Chong et al. 2023). It is essential to recognize that these changes could have severe consequences not only for Greifswald Bay but also for the remaining substantial portion of the herring stocks in the Baltic Sea. Should similar ecological shifts manifest in other critical spawning and nursery grounds, the ramifications for Baltic Sea herring could be devastating.

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LITERATURE CITED

Abrams PA (2000) The evolution of predator–prey interactions: theory and evidence. Annu Rev Ecol Syst 31: 79–105

Alvarez-Fernandez S, Licandro P, van Damme CJG, Hufnagl M (2015) Effect of zooplankton on fish larval abundance and distribution: a long-term study on North Sea herring (*Clupea harengus*). ICES J Mar Sci 72:2569–2577

Andersen T, Carstensen J, Hernández-García E, Duarte CM (2009) Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24:49–57

Anderson MJ, Gorley RN, Clarke KR (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Asch RG (2015) Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. Proc Natl Acad Sci USA 112:E4065–E4074

Bates AE, McKelvie CM, Sorte CJB, Morley SA and others (2013) Geographical range, heat tolerance and invasion success in aquatic species. Proc R Soc B 280:20131958

Bauer KR, Stepputtis D, Gräwe U, Zimmermann C, Hammer C (2013) Wind-induced variability in coastal larval retention areas: a case study on western Baltic spring-spawning herring. Fish Oceanogr 22:388–399

Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. Prog Oceanogr 60:245–262

Beaugrand G, Ibañez F (2004) Monitoring marine plankton ecosystems. II: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. Mar Ecol Prog Ser 284:35–47

Belkin IM (2009) Rapid warming of large marine ecosystems. Prog Oceanogr 81:207–213

Bennett JM, Calosi P, Clusella-Trullas S, Martínez B and others (2018) GlobTherm, a global database on thermal tolerances for aquatic and terrestrial organisms. Sci Data 5:180022

Berggreen U, Hansen B, Kiørboe T (1988) Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: implications for determination of copepod production. Mar Biol 99:341–352

Burbank J, DeJong RA, Turcotte F, Rolland N (2023) Understanding factors influencing Atlantic herring (*Clupea harengus*) recruitment: from egg deposition to juveniles. Fish Oceanogr 32:147–159

Busch A (1996) Transition from endogenous to exogenous nutrition: larval size parameters determining the start of external feeding and size of prey ingested by Ruegen spring herring *Clupea harengus.* Mar Ecol Prog Ser 130: 39–46

Cai WJ, Hu X, Huang WJ, Murrell MC and others (2011) Acidification of subsurface coastal waters enhanced by eutrophication. Nat Geosci 4:766–770

Carstensen J, Conley DJ, Almroth-Rosell E, Asmala E and others (2020) Factors regulating the coastal nutrient filter in the Baltic Sea. Ambio 49:1194–1210

Castro-Longoria E (2003) Egg production and hatching success of four *Acartia* species under different temperature and salinity regimes. J Crustac Biol 23:289–299

Checkley DM (1982) Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Mar Ecol Prog Ser 9:245–253

Chen Z, Su B (2020) Influence of medium frequency light/dark cycles on the cultivation of *Auxenochlorella pyrenoidosa.* Appl Sci (Basel) 10:5093

Chinnery FE, Williams JA (2004) The influence of temperature and salinity on *Acartia* (Copepoda: Calanoida) nauplii survival. Mar Biol 145:733–738

Chong JWR, Khoo KS, Chew KW, Vo DVN and others (2023) Microalgae identification: future of image processing and digital algorithm. Bioresour Technol 369:128418

Clarke KR, Warwick RM (1994) Change in marine communities: an approach to statistical analysis and interpretation. Natural Environment Research Council, Plymouth

Cloern JE, Jassby AD (2010) Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuar Coast 33:230–241

Croll JC, de Roos AM (2022) The regulating effect of growth plasticity on the dynamics of structured populations. Theor Ecol 15:95–113

Cushing DH (1990) Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26:249–293

Dam HG (2013) Evolutionary adaptation of marine zooplankton to global change. Annu Rev Mar Sci 5:349–370

Dam HG, deMayo JA, Park G, Norton L and others (2021) Rapid, but limited, zooplankton adaptation to simultaneous warming and acidification. Nat Clim Chang 11: 780–786

Durant JM, Hjermann DØ, Anker-Nilssen T, Beaugrand G, Mysterud A, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. Ecol Lett 8:952–958

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. Clim Res 33: 271–283

Durant JM, Molinero JC, Ottersen G, Reygondeau G, Stige LC, Langangen Ø (2019) Contrasting effects of rising temperatures on trophic interactions in marine ecosystems. Sci Rep 9:15213

Dutheil C, Meier HEM, Gröger M, Börgel F (2022) Understanding past and future sea surface temperature trends in the Baltic Sea. Clim Dyn 58:3021–3039

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

Edwards KF, Thomas MK, Klausmeier CA, Litchman E (2016) Phytoplankton growth and the interaction of light and temperature: a synthesis at the species and community level. Limnol Oceanogr 61:1232–1244

FAO (2022) The state of world fisheries and aquaculture: towards blue transformation. FAO, Rome

Feike M, Heerkloss R, Rieling T, Schubert H (2007) Studies on the zooplankton community of a shallow lagoon of the Southern Baltic Sea: long-term trends, seasonal changes, and relations with physical and chemical parameters. Hydrobiologia 577:95–106

Ferreira ASA, Neuheimer AB, Durant JM (2023) Impacts of the match–mismatch hypothesis across three trophic levels — a case study in the North Sea. ICES J Mar Sci 80: 308–316

Fischbach V, Finke A, Moritz T, Polte P, Thieme P (2023) A staging system for Atlantic herring (*Clupea harengus*) larvae based on external morphology and skeletal development. Limnol Oceanogr Methods 21:357–376

Flynn KJ, Raven JA (2017) What is the limit for photoautotrophic plankton growth rates? J Plankton Res 39: 13–22

Friedlingstein P, O'Sullivan M, Jones MW, Andrew RM and others (2022) Global carbon budget. Earth Syst Sci Data 14:4811–4900

Giering SLC, Culverhouse PF, Johns DG, McQuatters-Gollop A, Pitois SG (2022) Are plankton nets a thing of the past? An assessment of *in situ* imaging of zooplankton for large-scale ecosystem assessment and policy decision-making. Front Mar Sci 9:986206

Gilbert JJ, Schröder T (2004) Rotifers from diapausing, fertilized eggs: unique features and emergence. Limnol Oceanogr 49:1341–1354

Glippa O, Denis L, Lesourd S, Souissi S (2014) Seasonal fluctuations of the copepod resting eggbank in the middle Seine estuary, France: impact on the nauplii recruitment. Estuar Coast Shelf Sci 142:60–67

Haapala JJ, Ronkainen I, Schmelzer N, Sztobryn M (2015) Recent change — sea ice. In: The BACC II Author Team (eds) Second assessment of climate change for the Baltic Sea Basin. Regional Climate Studies. Springer, Cham, p 145–153

HELCOM (Helsinki Commission) (2021) Guidelines for monitoring of mesozooplankton. https://helcom.fi/action-areas/monitoring-and-assessment/monitoring-guidelines

Heneghan RF, Everett JD, Blanchard JL, Sykes P, Richardson AJ (2023) Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. Nat Clim Chang 13:470–477

Hesse J (2010) Quantitative and qualitative analyses of the food consumption of *Clupea harengus* L. larvae in the Greifswalder Bodden and Strelasund, Baltic Sea, Germany. Diploma thesis, University of Rostock

Hjort J (1914) Fluctuations in the great fisheries of Northern Europe viewed in the light of biological research. Rapp P-V Réun Cons Int Explor Mer 20:1–228

Holste L, Peck MA (2006) The effects of temperature and salinity on egg production and hatching success of Baltic *Acartia tonsa* (Copepoda: Calanoida): a laboratory investigation. Mar Biol 148:1061–1070

Hufnagl M, Peck MA (2011) Physiological individual-based modelling of larval Atlantic herring (*Clupea harengus*) foraging and growth: insights on climate-driven life-history scheduling. ICES J Mar Sci 68:1170–1188

ICES (2023a) Herring (*Clupea harengus*) in subdivisions 20–24, spring spawners (Skagerrak, Kattegat, and western Baltic). Report of the ICES Advisory Committee, 2023. ICES Advice 2023, her.27.20-24

ICES (2023b) Herring assessment working group for the area south of 62° N (HAWG). ICES Scientific Reports 5.23

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

Kahru M, Elmgren R, Savchuk OP (2016) Changing seasonality of the Baltic Sea. Biogeosciences 13:1009–1018

Käyhkö J, Apsite E, Bolek A, Filatov N and others (2015) Recent change — river run-off and ice cover. In: The BACC II Author Team (eds) Second assessment of climate change for the Baltic Sea Basin. Regional Climate Studies. Springer, Cham, p 99–116

Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S and others (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. Science 324:791–793

Kotterba P, Moll D, von Nordheim L, Peck MA, Oesterwind D, Polte P (2017) Predation on larval Atlantic herring *(Clupea harengus*) in inshore waters of the Baltic Sea. Estuar Coast Shelf Sci 198:1–11

Kotterba P, Moll D, Winkler H, Finke A, Polte P (2024) A wolf in sheep's clothing: planktivorous Atlantic herring preys on demersal fishes in coastal waters. Ecology 105:e4363

Lehmann A, Myrberg K (2008) Upwelling in the Baltic Sea — a review. J Mar Syst 74:S3–S12

Llopiz JK, Cowen R, Hauff M, Ji R and others (2014) Early life history and fisheries oceanography: new questions in a changing world. Oceanography 27:26–41

Lombard F, Boss E, Waite AM, Vogt M and others (2019) Globally consistent quantitative observations of planktonic ecosystems. Front Mar Sci 6:196

Mäkinen K, Vuorinen I, Hänninen J (2017) Climate-induced hydrography change favours small-bodied zooplankton in a coastal ecosystem. Hydrobiologia 792:83–96

Möllmann C, Diekmann R (2012) Marine ecosystem regime shifts induced by climate and overfishing. Adv Ecol Res 47:303–347

Möllmann C, Müller-Karulis B, Kornilovs G, St John MA (2008) Effects of climate and overfishing on zooplankton dynamics and ecosystem structure: regime shifts, trophic cascade, and feedback loops in a simple ecosystem. ICES J Mar Sci 65:302–310

Morse RE, Friedland KD, Tommasi D, Stock C, Nye J (2017) Distinct zooplankton regime shift patterns across ecoregions of the US Northeast continental shelf large marine ecosystem. J Mar Syst 165:77–91

Moyano M, Illing B, Peschutter P, Huebert KB, Peck MA (2016) Thermal impacts on the growth, development and ontogeny of critical swimming speed in Atlantic herring larvae. Comp Biochem Physiol A Mol Integr Physiol 197: 23–34

Moyano M, Illing B, Akimova A, Alter K and others (2023) Caught in the middle: bottom-up and top-down processes impacting recruitment in a small pelagic fish. Rev Fish Biol Fish 33:55–84

Oeberst R, Klenz B, Gröhsler T, Dickey-Collas M, Nash RDM, Zimmermann C (2009) When is year-class strength determined in western Baltic herring? ICES J Mar Sci 66: 1667–1672

Orenstein EC, Ayata SD, Maps F, Becker ÉC and others (2022) Machine learning techniques to characterise functional traits of plankton from image data. Limnol Oceanogr 67:1647–1669

Osborne J (2002) Notes on the use of data transformations. Pract Assess Res Eval 8:6

Paulsen M, Clemmesen C, Hammer C, Polte P, Malzahn AM (2017) Food-limited growth of larval Atlantic herring *Clupea harengus* recurrently observed in a coastal nursery area. Helgol Mar Res 70:17

Peck MA, Huebert KB, Llopiz JK (2012) Intrinsic and extrinsic factors driving match–mismatch dynamics during the early life history of marine fishes. Adv Ecol Res 47: 177–302

Peck MA, Reglero P, Takahashi M, Catalán IA (2013) Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. Prog Oceanogr 116:220–245

Peterson WT (2002) Patterns in stage duration and development among marine and freshwater calanoid and cyclopoid copepods: a review of rules, physiological constraints, and evolutionary significance. In: Lopes RM, Reid JW, Rocha CEF (eds) Copepoda: developments in ecology, biology and systematics. Kluwer Academic Publishers, Dordrecht, p 91–105

Poloczanska ES, Burrows MT, Brown CJ, García Molinos J and others (2016) Responses of marine organisms to climate change across oceans. Front Mar Sci 3:62

Polte P, Kotterba P, Hammer C, Gröhsler T (2014) Survival bottlenecks in the early ontogenesis of Atlantic herring (*Clupea harengus*, L.) in coastal lagoon spawning areas of the western Baltic Sea. ICES J Mar Sci 71:982–990

Polte P, Kotterba P, Moll D, von Nordheim L (2017) Ontogenetic loops in habitat use highlight the importance of littoral habitats for early life-stages of oceanic fishes in temperate waters. Sci Rep 7:42709

Polte P, Gröhsler T, Kotterba P, von Nordheim L and others (2021) Reduced reproductive success of western Baltic herring (*Clupea harengus*) as a response to warming winters. Front Mar Sci 8:589242

Prandle D, Lane A (1995) The annual temperature cycle in shelf seas. Cont Shelf Res 15:681–704

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Reusch TBH, Dierking J, Andersson HC, Bonsdorff E and others (2018) The Baltic Sea as a time machine for the future coastal ocean. Sci Adv 4:eaar8195

Richardson AJ (2008) In hot water: zooplankton and climate change. ICES J Mar Sci 65:279–295

Robert D, Murphy HM, Jenkins GP, Fortier L (2014) Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a 'critical period' driving year-class strength. ICES J Mar Sci 71: 2042–2052

Schmelzer N, Holfort J, Tegtmeier J, Düskau T (2014) Ice winters 2009/2010 to 2013/2014 on the German North and Baltic Sea coasts. Berichte des Bundesamtes für Seeschifffahrt und Hydrographie (Reports of the Federal Maritime and Hydrographic Agency) 53:185. https://www.bsh.de/download/Berichte-des-BSH-53.pdf

Schwegmann S, Holfort J (2018) The ice winter of 2017/18 on the German North and Baltic Sea coasts with a brief description of ice conditions in the entire Baltic Sea region. https://www.bsh.de/EN/DATA/Predictions/Ice_reports_and_ice_charts/_Anlagen/Downloads/Description-ice-winters/Description-of-the-ice-winters-2017-2018.html

Schweigert JF, Thompson M, Fort C, Hay DE, Therriault TW, Brown LN (2013) Factors linking Pacific herring (*Clupea pallasi*) productivity and the spring plankton bloom in the Strait of Georgia, British Columbia, Canada. Prog Oceanogr 115:103−110

Sommer U, Adrian R, de Senerpont Domis L, Elser JJ and others (2012) Beyond the Plankton Ecology Group (PEG) model: mechanisms driving plankton succession. Annu Rev Ecol Evol Syst 43:429−448

Starkweather PL (1980) Aspects of the feeding behavior and trophic ecology of suspension-feeding rotifers. In: Dumont HJ, Green J (eds) Rotatoria. Developments in Hydrobiology, Vol 1. Springer, Dordrecht, p 63−72

Suchy KD, Young K, Galbraith M, Perry RI, Costa M (2022) Match/mismatch between phytoplankton and crustacean zooplankton phenology in the Strait of Georgia, Canada. Front Mar Sci 9:832684

Turner JT, Levinsen H, Nielsen TG, Hansen BW (2001) Zooplankton feeding ecology: grazing on phytoplankton and predation on protozoans by copepod and barnacle nauplii in Disko Bay, West Greenland. Mar Ecol Prog Ser 221:209−219

Wallace RB, Baumann H, Grear JS, Aller RC, Gobler CJ (2014) Coastal ocean acidification: the other eutrophication problem. Estuar Coast Shelf Sci 148:1−13

Walz N (1995) Rotifer populations in plankton communities: energetics and life history strategies. Experientia 51:437−453

Wasmund N, Nausch G, Gerth M, Busch S, Burmeister C, Hansen R, Sadkowiak B (2019) Extension of the growing season of phytoplankton in the western Baltic Sea in response to climate change. Mar Ecol Prog Ser 622:1−16

Wilcox RR (2017) Introduction to robust estimation and hypothesis testing, 3rd edn. Elsevier Academic Press, San Diego, CA

Wilson CJ, Murphy HM, Bourne C, Pepin P, Robert D (2018) Feeding ecology of autumn-spawned Atlantic herring (*Clupea harengus*) larvae in Trinity Bay, Newfoundland: Is recruitment linked to main prey availability? J Plankton Res 40:255−268

Winder M, Varpe Ø (2020) Interactions in plankton food webs: seasonal succession and phenology of Baltic Sea zooplankton. In: Teodósio MA, Barbosa AB (eds) Zooplankton ecology. CRC Press, Boca Raton, FL, p 162−191

Yamaguchi R, Rodgers KB, Timmermann A, Stein K and others (2022) Trophic level decoupling drives future changes in phytoplankton bloom phenology. Nat Clim Chang 12:469−476

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