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Long-term spatio-temporal dynamics of the meroplankton community in the southern Baltic Sea

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Abstract
Meroplankton, the pelagic larvae of benthic invertebrates, are an understudied component of zooplankton communities with particularly large knowledge gaps on interannual variation and long-term changes in meroplankton phenology. This study presents the first long-term assessment of meroplankton in the brackish southern Baltic Sea, spanning 17 years (2005–2021). Data from 11 stations across 33 cruises reveal significant temporal changes in community composition and biomass and encompass three distinct periods. Early in the time series, polychaete larvae typically dominated the spring meroplankton community, contributing most biomass and frequently persisting throughout the summer (June–August). This pattern became rare after 2014, when bivalve larvae dominated during summer. A spring community was present in multiple samples collected in June, only in years following cold winters. A second major shift occurred in 2019, characterized by a dramatic, order of magnitude increase in both meroplankton abundance and biomass, whereas the relative community composition remained largely unchanged. These transitions likely reflect rising water temperatures, and in particular winter sea surface temperatures above the temperature of maximum density for water within our study region. Our study links winter sea surface temperature and meroplankton phenology, with potentially strong implications for benthic recruitment and ecosystem functioning.

Keywords
Planktonic larvae; Seasonality; Invertebrate larvae; Phenology shift; Benthic-pelagic coupling

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1. Introduction

The life cycle of many benthic invertebrate species involves a pelagic larval phase that enables long-distance dispersal, utilisation of food in the productive upper water column, and/or avoidance of competition and predation within benthic communities (Becker et al., 2007; Pechenik, 1999). These pelagic larvae, collectively referred to as meroplankton, are generally less studied than other components of plankton communities and accordingly little is known about their spatio-temporal distribution or their potential ecological importance. Besides their obvious role in the recruitment of benthic invertebrates, past studies have proposed numerous ecological functions for meroplankton: (a) as grazers of autotrophic and heterotrophic micro- and nanoplankton (Pasternak et al., 2008; Turner et al., 2001), (b) as prey for higher trophic levels such as fish larvae (Michelsen et al., 2017b; Silberberger et al., 2021), or (c) as facilitators of the transfer of assimilated organic matter from the water column to the seafloor through synchronized settlement (Kirby et al., 2008; Silberberger et al., 2021; Sommer et al., 2000).

To date, most research on meroplankton has focused on their roles in dispersal and recruitment processes from a benthic perspective (Levin, 2006; Silberberger et al., 2016) and, accordingly, the spatial and/or seasonal distribution of meroplankton has received most attention (Highfield et al., 2010; Michelsen et al., 2017b,a; Silberberger et al., 2016; Weydmann-Zwolicka et al., 2021), while only a few studies have addressed long-term variability (but see Amieva Mau et al., 2026; Fernandes et al., 2012; Highfield et al., 2010; Kirby et al., 2008). One study that explored such long-term changes made use of the Continuous Plankton Recorder (CPR) survey of the North Sea, and reported a climate-induced change in the meroplankton community for the period from 1958 to 2005 (Kirby et al., 2008). During their study period, echinoderms and decapod larvae increased in abundance in parallel with an increase in North Sea sea surface temperatures, whereas bivalve abundance declined. Kirby et al. (2008) attributed this declining trend in bivalve larvae to increased predation on the settled larvae and adult bivalve communities

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by benthic decapods, resulting in lower reproductive output of bivalves and fewer larvae. Accordingly, variation in meroplankton communities can signal broader changes in trophic interactions and ecosystem functioning.

In contrast to other North Atlantic ecosystems, the Baltic Sea ecosystem is strongly shaped by its low salinity, hypoxic and anoxic bottom waters in its deeper basins, as well as quasi-decadal major barotropic inflows of dense oxygen-rich waters from the North Sea (Snoeijs-Leijonmalm and Andrén, 2017). As a consequence of its brackish conditions, the Baltic Sea is characterized by relatively low species diversity, particularly in benthic communities, and is therefore well suited for studying ecosystem processes in a comparatively low-diversity system (Snoeijs-Leijonmalm and Andrén, 2017). Given its relatively low species diversity, the long-term temporal dynamics of meroplankton in the Baltic Sea are likely to differ from those in other systems, including the adjacent North Sea. For example, long periods with high barotropic inflows of oxygen-rich water might lead to colonisation of sediments previously devoid of macrofauna with sufficient time for new colonizers to reach maturity and reproduce. This scenario would not only alter benthic communities in the Baltic Sea but it could also lead to changes in the meroplankton community. Also, the top-down control on North Sea bivalve populations through benthic predators noted earlier is unlikely to play a similar role in the Baltic Sea. The single dominant larger benthic crustacean omnivore in the Baltic Sea, the isopod *Saduria entomon*, contrasts with the North Sea, where diverse and abundant decapod omnivores may control bivalve communities (Kirby et al., 2008). The limited number of benthic species that could potentially prey on adult bivalve communities in the Baltic Sea results in a less likely top-down control. In addition, the absence of other taxa with pelagic larvae, such as echinoderms, from large parts of the Baltic Sea, may indicate different patterns of interspecific competition for food during the larval phase than in more diverse systems. Collectively, this distinction of the Baltic Sea from all other North Atlantic ecosystems suggests a potentially unique Baltic Sea meroplankton community, including its spatio-temporal distribution and associated environmental drivers that cannot be inferred from other locations.

To date, scarce data exist on the spatio-temporal dynamics of the meroplankton community in the Baltic Sea. However, the few studies on the seasonality of the entire mesozooplankton community provide some information about meroplankton seasonality. For the period from September 1999 to August 2000, Mudrak and Żmijewska (2007) reported low meroplankton abundances (<500 ind. m^{-3}) from September to April in the Gulf of Gdańsk, in contrast to high abundances (>1000 ind. m^{-3}) from May to August. In terms of meroplankton composition, polychaete larvae dominated during colder months (October to March), whereas bivalve larvae dominated during warmer months (April–September) (Mudrak and Żmijewska, 2007). Studying the mesozooplankton community in three Polish Baltic Sea ports monthly in 2011, Witalis et al. (2024) reported that high abundances of polychaete larvae and high abundances of cirriped larvae characterisede the spring and summer mesozooplankton community, respectively. In Kalmar Sound (Swedish east coast), Bivalvia larvae dominated from May to October in 2010, but they only occurred in high abundances during June in 2009 (Díaz-Gil et al., 2014). Díaz-Gil et al. (2014) further reported that high abundances of Bivalvia and Gastropoda larvae characterized coastal sites shallower than 40 m. These seasonal patterns generally resemble the seasonal patterns of meroplankton in the southern Baltic Proper from the early 1970s (Hernroth and Ackefors, 1979), suggesting little long-term change in the dynamics of meroplankton in the southern Baltic Sea before 2010. However, these patterns highlight the absence of information about the meroplankton community composition post-2011, and the spatio-temporal distribution of meroplankton over a longer period in the Baltic Sea. Accordingly, the dearth of information on long-term inter-annual variability of meroplankton punctuates a knowledge gap for the majority of marine systems worldwide (but see Amieva Mau et al., 2026; Fernandes et al., 2012; Highfield et al., 2010; Kirby et al., 2008). Climate change and other anthropogenic impacts (e.g., the building of offshore wind parks – new hard bottom habitats for benthic communities, and nuclear power plants – discharge of heated cooling water), underscore the urgent need for such baseline knowledge on interannual variation of meroplankton to detect potential changes in ecosystem functioning.

To fill this knowledge gap, we studied the spatio-temporal structure of the meroplankton community in the southern Baltic Sea during spring and summer over a 17-year period. We assumed that the meroplankton communities differ between areas west and east of the Słupsk Sill, given more diverse benthic communities in the western Baltic Sea (Gogina et al., 2016). Furthermore, we hypothesize that increasing water temperatures (Zalewska et al., 2024) are altering the meroplankton community in the southern Baltic Sea. We predict that changes in meroplankton phenology will result in an earlier disappearance of the spring meroplankton community from the water column under climate change and increasingly warmer water temperatures.

2. Methods

2.1 Study region

The study region comprises the southern Baltic Proper, representing the International Council for the Exploration of the Sea (ICES) Sub-divisions 25 and 26. Accordingly, the study area stretches from the Bornholm Basin in the west, over Słupsk Furrow, to the southern part of the eastern Gotland Basin and the Gdańsk Basin in the east (Figure 1a).

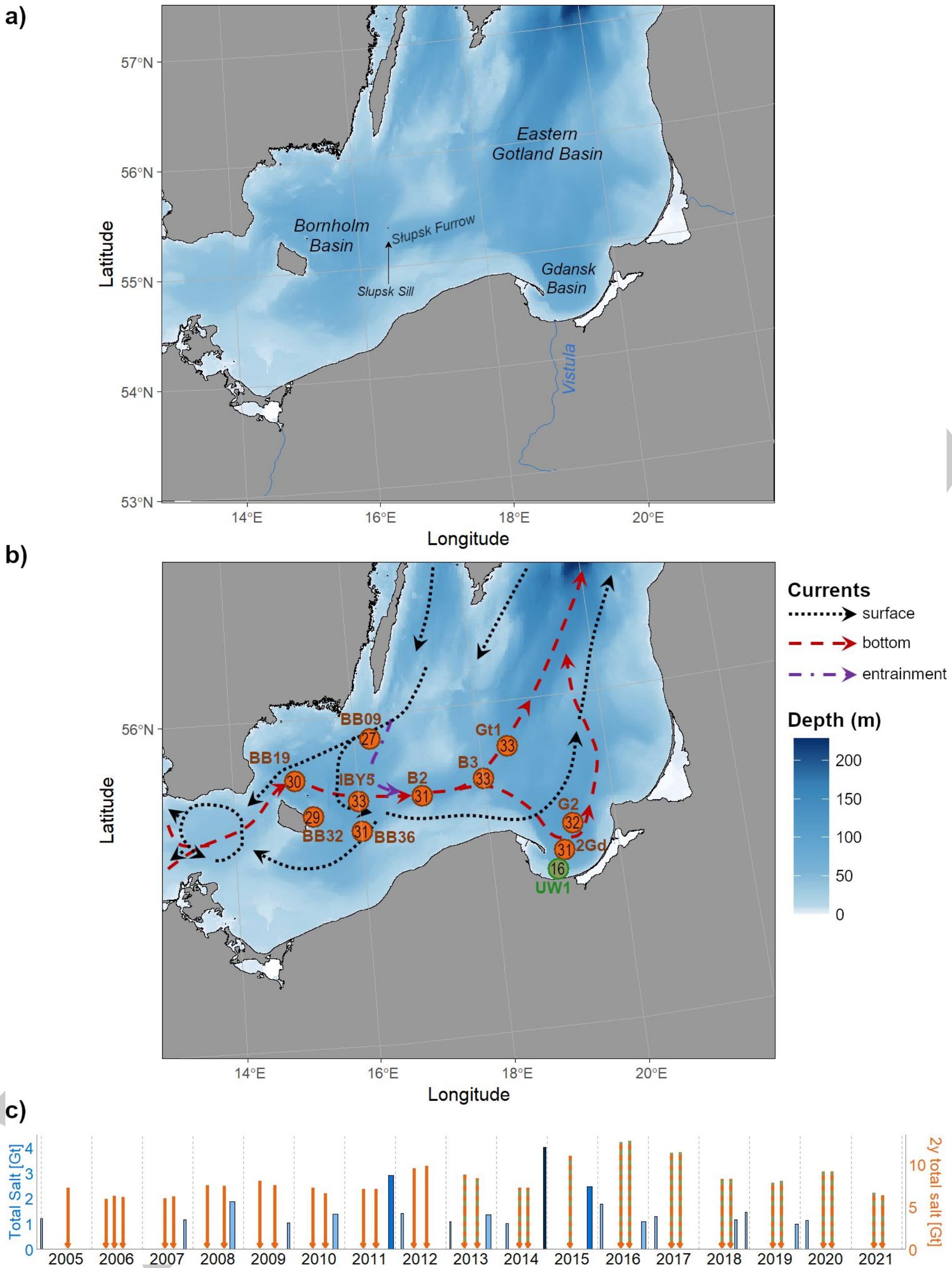


Figure 1. Study area and sampling design. a) Bathymetric map of the southern Baltic Proper. Basin names and the Vistula River are indicated. b) Bathymetric map of the southern Baltic Proper with sampling stations and circulation patterns. Stations sampled from 2005 to 2021 in orange, station UW1 sampled from 2013 to 2021 in green. The black number within each circle gives the total number of samples collected from each station. Schematic illustration of mean circulation patterns drawn after Meier (2007) and Porz et al. (2021). Maps were produced with ggOceanMaps (Vihtakari, 2020). Bathymetry from GEBCO Compilation Group (2023). c) Timeline of the study period. Blue bars indicate all saline barotropic inflow events into the Baltic Sea with more than 1 Gt of imported salt (Mohrholz, 2018). Width and height of the bars indicate duration and intensity of each inflow event (left y-axis). Different shades of blue indicate medium (1–2 Gt salt import), strong (2-3 Gt salt import), and extreme (>3 Gt salt import) inflow events. Arrows indicate sampling campaigns. The length of the arrows is scaled to the total barotropic inflow over the 2-year period prior to the sampling campaign (right y-axis).

Throughout the study area, benthic environments and bottom water may experience low oxygen conditions. However, only rare occurrences of hypoxia affect the Słupsk Furrow, whereas ventilation of the eastern basins (Gotland Basin and Gdańsk Basin) occurs only after strong barotropic inflow events (Meier et al., 2006; Schmidt et al., 2021). The Bornholm Basin in the west of the study area experiences hypoxia and anoxia, but ventilation occurs more frequently than in the eastern basins, resulting in more dynamic oxygen availability in bottom waters than in the east.

In the east of the study area, the Vistula River flows into the Gulf of Gdańsk, where it discharges an average of 1023 m^3/s of water together with nutrients, pollutants, and allochthonous organic matter (HELCOM, 2015). Cyclonic sea surface circulation in the Baltic Sea (Figure 1b) varies in a distinct seasonal pattern (Barzandeh et al., 2024). During autumn and winter, a strong main cyclonic circulation dominates with the formation of cyclonic anomalies. In contrast, a weaker main cyclonic circulation is typical in spring/summer from April to August, along with the formation of anticyclonic anomalies.

Surface temperatures in the Baltic Proper vary strongly seasonally. Historically, during the period 1960–1970, winter sea surface temperatures of 0–2°C occurred commonly, with maximum summer temperatures of 20–22°C (Hernroth and Ackefors, 1979; Zalewska et al., 2024). Since then, however, sea surface temperatures have increased on average by 0.6°C per decade (Zalewska et al., 2024). The warming was strongest in spring–summer with an increase of 0.8–1.0°C per decade, while winter sea surface temperatures increased only by 0.2°C per decade (Zalewska et al., 2024).

In the Baltic Proper, diatoms typically dominate the early phytoplankton spring bloom, gradually transitioning to a dominance by flagellates (Hjerne et al., 2019; Wasmund et al., 1998). This is followed by a summer bloom dominated by Cyanobacteria (Hjerne et al., 2019). In recent decades, however, the growing season of phytoplankton extended (Wasmund et al., 2019). Between 1988 and 2017, the start of the spring bloom in the Bay of Mecklenburg moved earlier at a rate of 1.4 days per year and the end of the autumn bloom was delayed at a rate of 3.1 days per year. Given basin-wide warming and phenological shifts documented across the Baltic Sea (Viitasalo and Bonsdorff, 2022), similar extensions of the phytoplankton growing season can be assumed for the entire study region, although regional hydrographic and biogeochemical differences likely modulate the magnitude and seasonal expression of these changes.

The typical dominants in the Baltic Proper that characterize the holoplankton community in the study region encompass four major taxonomic groups: Copepoda, Cladocera, Rotatoria, and Appendicularia (Díaz-Gil et al., 2014; Mudrak and Żmijewska, 2007; Schulz et al., 2012). Furthermore, the study area is important for spawning and larval development of many Baltic Sea fish species and an abundant ichthyoplankton community often follows the spawning periods (as summarized by Dembek et al., 2019).

2.2 Sampling and sample processing

Stratified mesozooplankton samples were collected at eleven sampling stations in the southern Baltic Sea during 33 cruises with r/v *Baltica* from 2005 to 2021 (Figure 1; Table 1). Two cruises were typically conducted each year, except in 2006 (three cruises), and in 2005 and 2015 (one cruise each). When multiple cruises occurred in a year, the final cruise was always carried out in August. From 2014 onward, the earlier cruise consistently took place in June, following a change in the sampling scheme. Prior to 2014 (2005–2013), the timing of the earlier cruises varied: three in April, four in May, two in June, and one in July. Every cruise targeted ten stations. Station UW1 in the Gulf of Gdańsk was added to the sampling campaigns from 2013 onwards. These modifications to the sampling design were carefully considered throughout our study, particularly in the selection of statistical analyses, the presentation of results, and their interpretation. Table S1 provides the sampling dates of every individual sample. Sample collection was conducted according to the HELCOM guidelines for monitoring of mesozooplankton (HELCOM, 2021). A CTD rosette system was used to acquire a CTD profile during each sampling event, followed by bottom water collection. Dissolved oxygen content of the bottom water was determined using the Winkler method (Hansen, 1999). Subsequently, mesozooplankton samples were collected by means of vertical stratified hauls with a WP2 net (mesh size: 100 μm). The following depth intervals were sampled during each event: (i) 4 m from the bottom to the top of the halocline; (ii) top of the halocline to the top of the thermocline; and (iii) top of the thermocline to the surface. In the absence of either halocline or thermocline, samples were taken from two layers of the water column. Samples were preserved in ~4% seawater-formaldehyde solution buffered with borax.

In the laboratory, the total mesozooplankton community in samples from each depth interval was analysed after each cruise mostly according to the HELCOM guidelines (HELCOM, 2021): consecutive subsamples (sub-sampling by a Motoda splitter) were processed until at least 100 individuals of each of the three dominant taxa of the total mesozooplankton community were counted. Our sample processing deviated from the HELCOM guidelines in two respects. First, we used a Motodo splitter (Motoda, 1959) to subdivide samples, rather than a Kott splitter (Kott, 1953) or a Stempel pipette (Hensen, 1887). Second, we did not consider the addition of detergent to the samples to be necessary. The taxonomic categories used followed the Baltic zooplankton checklist (Telesh et al., 2009) and meroplankton was classified within 7 taxonomic groups: Bivalvia,

Table 1. Station characteristics. Geographic coordinates, depth, distance to land, and sub-basin for every sampling station are given together with the sampling period and the total number of sampling events. Abbreviations for sub-basins: BB – Bornholm Basin, SF – Słupsk Furrow, EGB – Eastern Gotland Basin, GB – Gdańsk Basin.

	IBY5	B2	B3	Gt1	G2	2Gd	BB09	BB19	BB32	BB36	UW1
Longitude [°E]	15.984	17.001	17.999	18.434	19.315	19.139	16.251	15.001	15.250	16.000	19.002
Latitude [°N]	55.233	55.233	55.333	55.600	54.834	54.600	55.791	55.458	55.125	54.958	54.435
Depth [m]	86	84	74	90	105	80	58	77	61	72	50
Distance to land [km]	50.9	57.9	55.6	85.0	38.5	19.6	37.9	19.3	6.4	56.3	9.1
Sub-basin	BB	SF	SF	EGB	GB	GB	BB	BB	BB	BB	GB
Sampling period	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2005–2021	2013–2021
Number of sampling events	33	31	33	33	32	31	27	30	29	31	16

Polychaeta, Gastropoda, Cirripedia, Nemertea, Echinodermata, and Bryozoa. The biomass of meroplankton was calculated according to the standard size classes method (HELCOM, 2021; Witek et al., 1996). For this purpose, each individual was measured under a stereomicroscope for three parameters: length, width, and thickness. Based on these measurements, their volume was calculated and assigned to specific biomass classes. Within a worksheet, we applied the formula:

$$V = \frac{4}{3} \times \pi \times \frac{1}{2} r^1 \times \frac{1}{2} r^2 \times \frac{1}{2} r^3 \tag{1}$$

where V is the calculated volume, and r^1, r^2, and r^3 are the measured length, width, and thickness, respectively.

To complement the meroplankton community data, nine environmental parameters were compiled: surface water temperature, surface salinity, surface chlorophyll *a*, bottom water temperature, bottom salinity, bottom oxygen content, distance to shore, depth, and the sum of all barotropic inflows into the Baltic Sea over a 2-year period preceding each respective sampling cruise (Table 1; Figure 1c; supplementary material Figures S1–6). Surface chlorophyll *a* was extracted from SatBaltyk (https://www.satbaltyk.pl) for each sampling station and sampling event. For the June 2014 cruise, no chlorophyll *a* values were available for the sampling dates and we used the closest preceding date (11 June 2014) with available data. The distance of each sampling station to the closest coastline was determined using the dist2land function of the ggOceanMaps package in R (Vihtakari, 2020). Data for Baltic Saline Barotropic Inflows were obtained from the data products provided by the Leibniz Institute for Baltic Sea Research Warnemünde (Mohrholz, 2018). The remaining variables were measured during the sampling campaigns (see above).

In addition, to further explore interannual thermal variability, daily sea surface temperature data for all sampling locations were obtained from the Copernicus Marine Service (E.U. Copernicus Marine Service Information (CMEMS), 2025) and used to characterize temporal variability and winter temperature patterns over the study period. The temperature of maximum density was calculated from observed surface salinities using the gsw package (Kelley et al., 2024). Specifically, conservative temperature at maximum density was computed using *gsw_CT_maxdensity()*, and subsequently converted to in situ temperature using *gsw_t_from_CT()*.

Temperature and chlorophyll *a* were chosen for analysis because of their known role as environmental drivers of the meroplankton community composition in other systems (Kirby et al., 2008; Stübner et al., 2016), while salinity was used because it reflects water mass origin. Even though not typically included as environmental variables in plankton research, we included depth and distance from shore because of their importance for local benthic communities that are the source populations for meroplankton. These variables also provide surrogates for other environmental factors not measured in our study (e.g., decreased inputs of terrigenous material with distance from shore). We included oxygen content in bottom water because of its importance for the macrobenthic species distribution in the Baltic Sea (Gogina et al., 2016). Stations with hypoxic or anoxic bottom waters generally support very sparse benthic communities; consequently, most meroplankton are likely to originate from sources outside the sampling station. We also included the total barotropic inflows over a 2-year period, given that we assumed all dominant macrobenthic species within the Baltic Proper reach maturity within 2 years. Accordingly, high barotropic inflows over a 2-year period might lead to colonisation of sediments previously free of macrofauna with sufficient time for new colonizers to reach maturity and reproduce.

2.3 Statistical analysis

Although data for stratified samples of the entire mesozooplankton community were collected, our study focuses only on meroplankton. Furthermore, we aggregated all depth intervals for statistical analysis given the focus of our study on spatio-temporal variation and not the vertical distribution of meroplankton. We expressed numbers as individuals/biomass per m^2 surface area to avoid bias in the data associated with different depths of sampling stations. Accordingly, we use the term sample to refer to the meroplankton community integrated over the entire water column, collected from one location during one sampling event.

All statistical analyses were performed in R, version 4.3.3 (R Core Team, 2024), mainly using the following packages: vegan (Oksanen et al., 2018) and vegclust (De Cáceres et al., 2010).

To identify differences in total abundance, total biomass, and taxon richness among sampling stations, sampling months, and sampling years, we performed non-parametric Kruskal-Wallis tests (Kruskal and Wallis, 1952) followed by pairwise comparisons using Dunn's test (Dunn, 1964). P-value adjustment used the Benjamini–Hochberg method (Benjamini and Hochberg, 1995).

For all multivariate analyses, we fourth root transformed the abundance and biomass data, running separate analyses for abundance and biomass. In addition, the same analyses (described below) were conducted using square-root-transformed data. As the results were nearly identical across transformations, only those based on fourth-root-transformed data are presented.

Noise clustering, a non-hierarchical fuzzy clustering technique, identified groups of samples with different community composition (Dave and Krishnapuram, 1997). In contrast to traditional clustering methods that focus on discontinuities among objects (i.e., samples), fuzzy clustering methods assess each data entry (i.e., each taxon in the sample) and an object may be, to different degrees, a member of two or more groups (Borcard et al., 2018). Such fuzzy clustering aligns better with ecological samples representing a continuum among different community types. Noise clustering, in contrast to other fuzzy clustering methods, also allows inclusion of outlier samples that are not representatives of any sample group (Borcard et al., 2018). Following the noise clustering, correlation indices and similarity profile analysis (SIMPER) identified the typical community composition of the different sample groups. The number of clusters used in this noise clustering approach was determined exploratively. We first ran the analysis with two clusters, and then increased the number of clusters by one in consecutive analyses until correlation indices and SIMPER analysis showed that two sample groups resembled each other closely.

To identify the main environmental drivers responsible for the observed patterns, we created a triangular dissimilarity matrix of the fourth-root-transformed abundance data using Bray-Curtis dissimilarities (Bray and Curtis, 1957) and ran a non-metric multidimensional scaling (nMDS) ordination. Vectors for the different environmental variables were then fitted to the nMDS ordination. Further, variation partitioning identified the variation in the meroplankton data explainable by the environmental variables that reflected spatial (i.e., stations), seasonal (i.e., months), or interannual (i.e., years) variation. Environmental variables comprised both static (e.g., depth, distance to shore) and dynamic (e.g., temperature, salinity, oxygen) variables. Static variables were not treated as a separate predictor group; instead, their spatially structured effects were accounted for through shared variation with the spatial predictor set (stations) in the variation partitioning. Collinearity among environmental variables was assessed using pairwise Spearman correlations. No strong correlations were observed (maximum $|r| = 0.63$), and all variables were therefore retained. Distance-based redundancy analysis (db-RDA) was used for variation partitioning. Prior to variation partitioning, environmental variables were subjected to forward selection using a double-stopping criterion (Blanchet et al., 2008), which limits the inclusion of explanatory variables to those that significantly contribute to explaining community variation while controlling for inflated Type I error and overfitting. Variation partitioning was conducted twice: first using the full set of selected environmental variables, and second using surface temperature as the sole environmental predictor.

3. Results

Meroplankton in this study encompassed a total of eight higher taxa. Bivalvia accounted for the majority of all individuals (94.7%) and biomass (86.8%), followed by

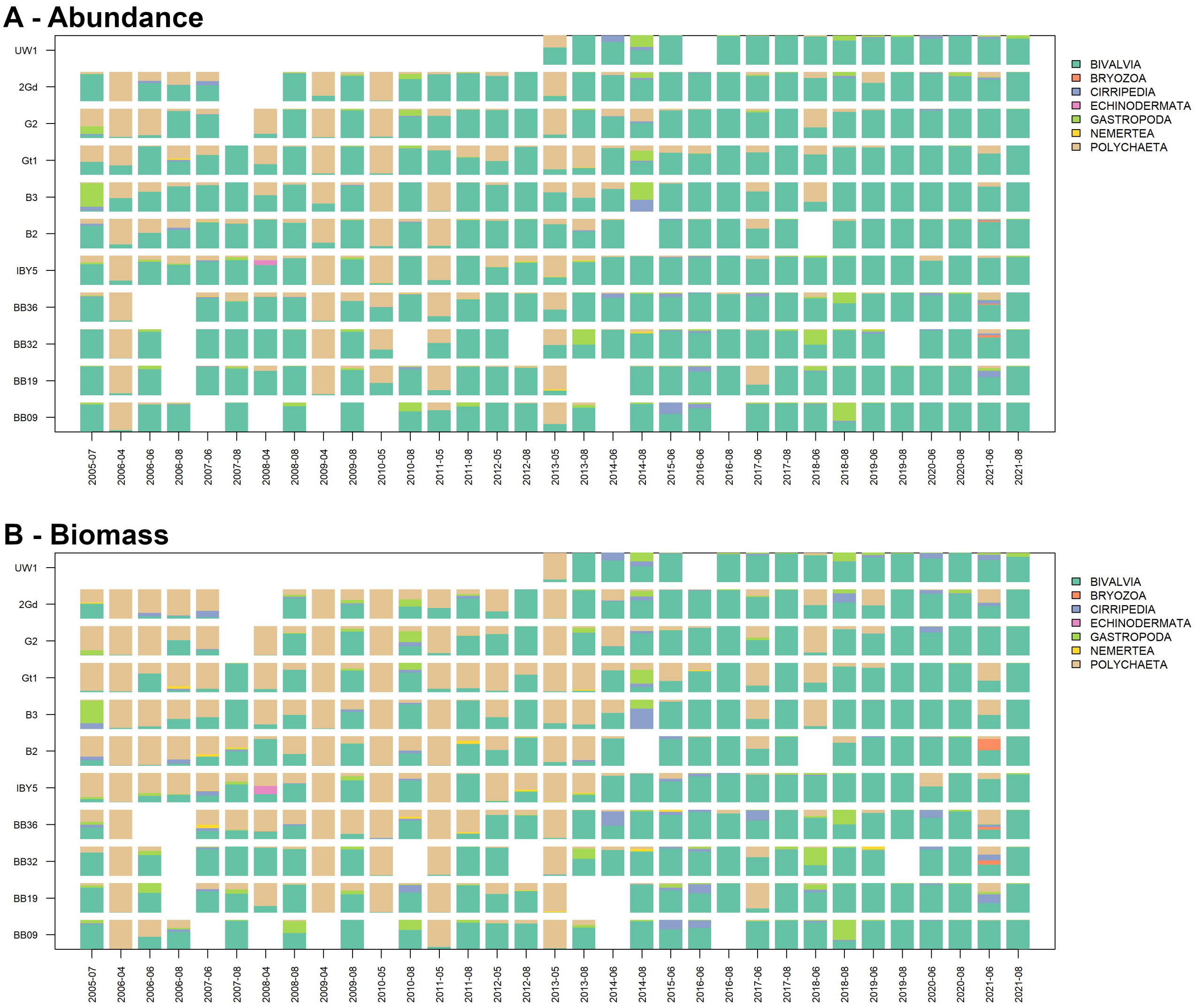


Figure 2. Spatio-temporal variation in meroplankton community composition based on relative abundance (A) and biomass (B). Each cell represents a single sample defined by station (y-axis) and cruise (x-axis). Within each cell, stacked bars indicate the proportional contribution of the seven meroplankton taxa to total community abundance and biomass. If the month changed during the sampling campaign, only the month during which the sampling campaign started is given.

Polychaeta (3.7%; 10.0%), Gastropoda (0.9%; 1.6%), and Cirripedia (0.6%; 1.5%). The other three taxa (Bryozoa, Echinodermata, Nemertea) were very rare and each represented less than 0.1% of total meroplankton abundance or biomass. Bivalvia were present in 99.1% of all samples, followed by Polychaeta (75.5%), Gastropoda (47.9%), and Cirripedia (36.8%). Among the rare taxa, Nemertea were encountered most frequently (9.5% of all samples), followed by Bryozoa (1.2%) and Echinodermata (0.3%) (Figure 2).

A clear spatial difference emerged in terms of total abundance, with higher total abundances at stations in the Gulf of Gdańsk (G2, 2Gd, UW1) than at all other stations. Dunn's test indicated that this difference was significant for most stations (BB09, IBY5, B2, B3, Gt1), in contrast to three stations (BB19, BB32, BB36), that did not differ significantly from any other station (Figure 3). Total biomass yielded similar groupings, except for an exchange of group memberships of stations BB32 and Gt1 (Figure 3). No clear spatial pattern for taxon richness emerged. With little variation in taxon richness overall, Dunn's test identified no distinct station groups.

For comparisons across months and years, we included station UW1 in the Gulf of Gdańsk – sampled only since 2013 – given the consistent spatial pattern that grouped it with the other two stations in the Gulf of Gdańsk (G2 and 2Gd). In terms of seasonality (i.e., sampling months in Figure 3), only the number of taxa differed significantly,

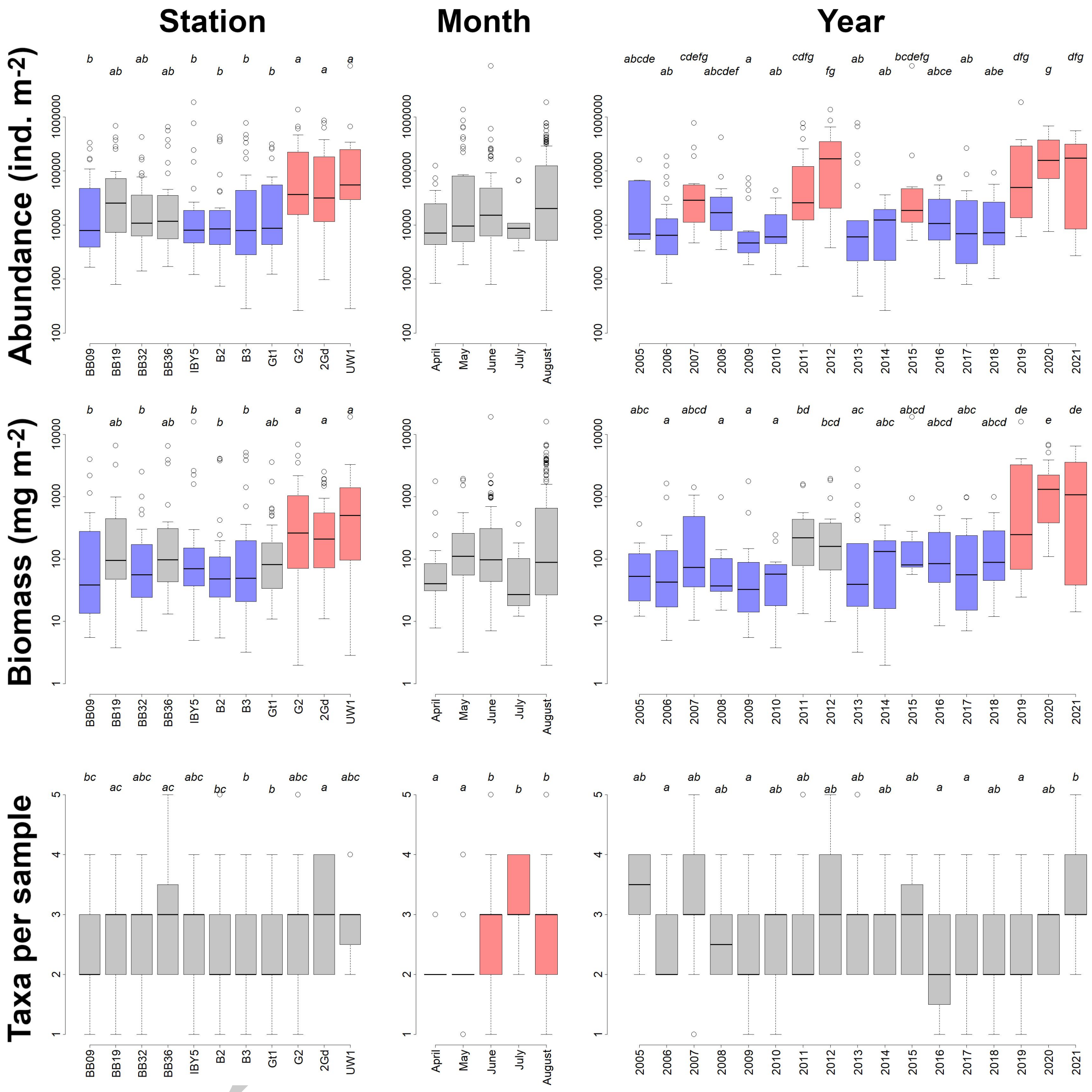
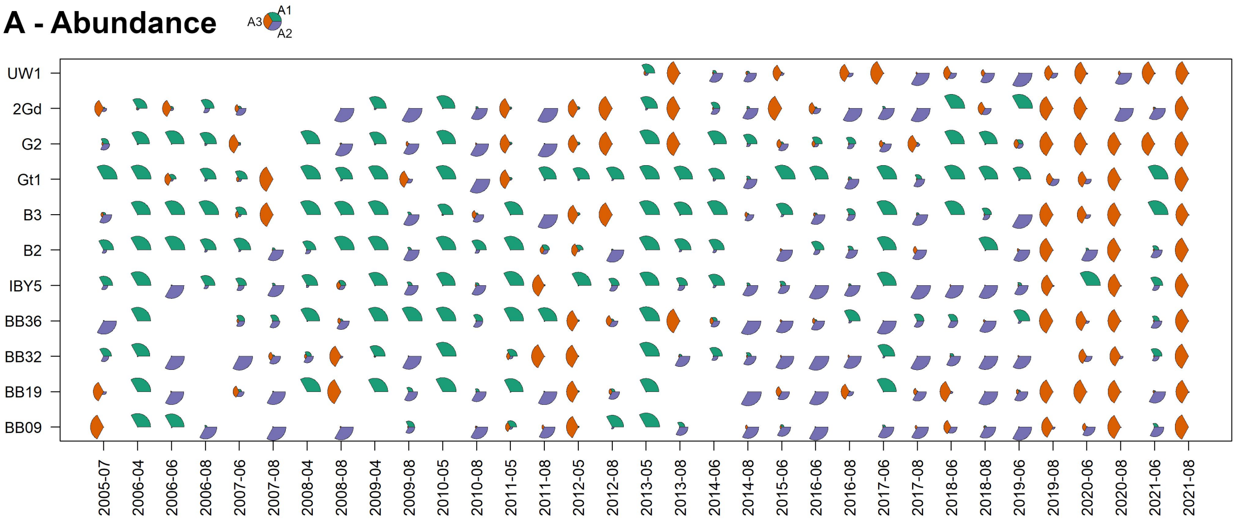


Figure 3. Boxplots showing the median, interquartile range, and outliers of the total abundance, total biomass, and the number of taxa per sample. Letters indicate significant differences among stations/months/years according to Dunn's test ($\alpha = 0.05$). No letters are given for variables with a non-significant Kruskal-Wallis test. Sampling stations/months/years with the same letter are not significantly different. Colors indicate the patterns described in the text. Note: Abundance and biomass are displayed on a logarithmic scale.


A - Abundance

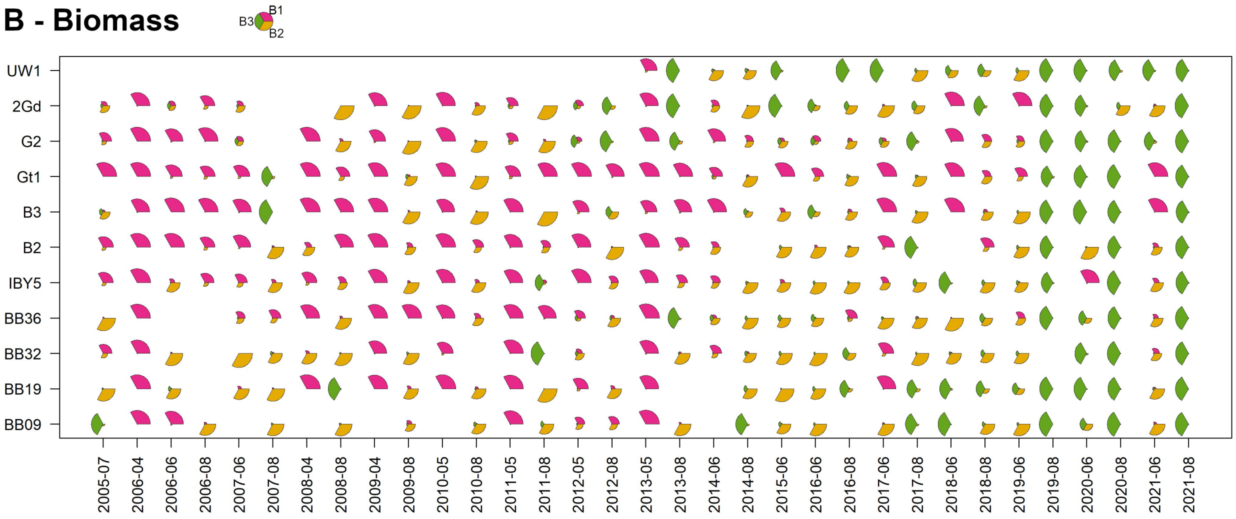

B - Biomass

Figure 4. Overview of the results of the noise clustering for abundance (A) and biomass data (B). The x-axis shows the year and month of each individual sampling campaign. If the month changed during the sampling campaign, only the month during which the sampling campaign started is given. The y-axis shows sampling stations. Relative association of each sample with each of the sample groups is indicated by the size of the different pie parts. Abundance clusters: A1 – green (top-right side), A2 – purple (bottom-right side), and A3 – orange (left side). Biomass clusters: B1 – pink (top-right side), B2 – yellow (bottom-right side), and B3 – olive green (left side).

with fewer taxa per sample in spring (April and May) than in summer (June, July, and August). Kruskal-Wallis tests for total abundance and biomass indicated non-significant differences among sampling months.

Total abundance and biomass varied strongly among years, and pairwise comparisons formed no distinct groups. However, in comparing years that did not differ significantly from the year with the highest and lowest total abundance and total biomass, we found much higher meroplankton abundance and biomass from 2019 to the end of our study period (Figure 3). Total abundance was elevated several times during our study period (Figure 3). In contrast, total biomass remained more stable across the years before 2019. The number of taxa generally remained similar throughout the study years (Figure 3).

Applying noise clustering analysis, we identified three groups of samples, representing three distinct community types. No outlier sample was identified, and all samples aligned to various degrees with these three groups. When we plotted the noise clustering results for each station over time (Figure 4), we found no consistent spatial pattern, but three distinct temporal periods emerged: (i) the A1 and B1 groups dominated from the beginning of the study period until June 2014. (ii) the A2 and B2 groups dominated from

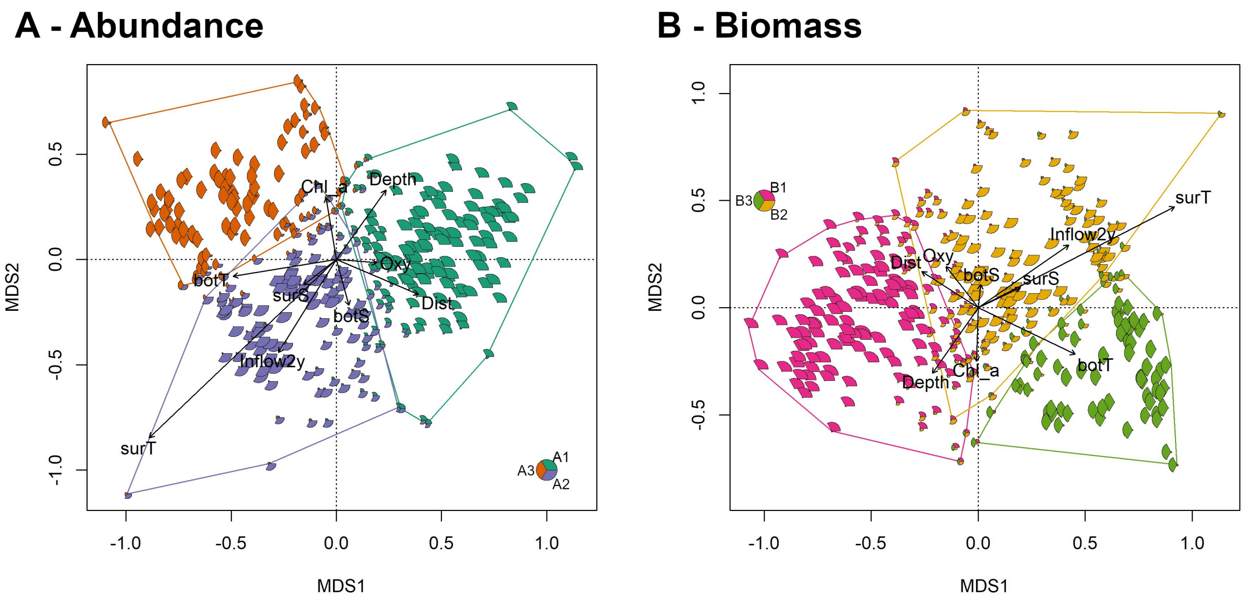


Figure 5. nMDS plot of the fourth-root transformed abundance data (A) and biomass data (B). Stress values of both ordinations are 0.16. Group association of each sample according to noise clustering results is shown and polygons indicate the samples with the main association to the respective group. Fitted vectors for the environmental variables are given in black. Abbreviations for the environmental variables: surT – surface temperature; botT – bottom temperature; surS – surface salinity; botS – bottom salinity; Chl_a – surface chlorophyll *a*; Depth – station depth; Dist – station distance from shore; Oxy – dissolved oxygen in bottom water; Inflow2y – total barotropic saline inflow into the Baltic Sea over 2 years prior to the sampling campaign.

Table 2. Taxa that show a significant ecological preference for groups obtained from noise clustering. + indicates a preference of a taxon for a group. A1–A3 and B1–B3 represent groups obtained from noise clustering of abundance and biomass data, respectively.

	A1	A2	A3	B1	B2	B3
Bivalvia			+			+
Polychaeta	+			+		
Gastropoda		+	+			+
Cirripedia		+	+		+	+
Nemertea				+	+	

August 2014 until June 2019. (iii) the A3 and B3 groups dominated from August 2019 onward. At no point during these periods were all samples assigned to a single cluster; however, the dominant clusters shifted over time. Furthermore, samples collected in August throughout the study period were associated less frequently with the A1/B1 groups than samples collected during other months. These patterns indicate two major temporal shifts in community structure, occurring around 2014 and 2019, separating the study period into three distinct phases.

Only the five taxa observed in more than 5% of our samples (Bivalvia, Polychaeta, Gastropoda, Cirripedia, Nemertea) showed a significant ecological preference for the different sample groups (Table 2).

The SIMPER analysis also supported the groupings obtained from noise clustering and provided additional information about the meroplankton community associated with the groups. Overall, the A3 group was distinct from both other groups because of extremely high abundances, which exceeded the abundances of A1 and A2 by more than a factor of 20. The A3 group had the highest abundances of all four common taxa (Table 3). Nonetheless, the samples were dominated by Bivalvia, which accounted for 97.0% of all the individuals in the samples. The relative composition of the A2 group resembled the A3 group closely, but at much lower total abundance and a slightly lower dominance of bivalves (90.6%). The A1 group differed in relative composition from the other two groups. In these samples, Bivalvia dominance was not so strong, and the number of Polychaeta was similar to that of Bivalvia. Cirripedia and Gastropoda, however, were virtually absent from samples in the A1 group.

The groups identified based on the noise clustering of biomass data were similar to those formed by the abundance data. Polychaeta dominated the biomass of Group B1 (Table 3; Group B1 corresponds to group A1). Bivalves dominated the overall high biomass of Group B3 (Group B3 corresponds to Group A3). The relative biomass com-

Table 3. SIMPER results for fourth-root transformed meroplankton abundance (a–c) and biomass data (d–f) – contrasts for pairwise comparisons of the three cluster groups are given for each data set. Taxa are ordered according to their contribution to between-group dissimilarity. For each taxon, its contribution to the total between-group dissimilarity (Con %) and the cumulative contribution (Cum %) are given (both in %). Furthermore, the average untransformed abundance for samples from each group (Av1, Av2) is reported. Percentages reported next to the letters (a–f) give overall dissimilarities among groups for each pairwise comparison. Percentages reported with each group name in columns Av1 and Av2 give average within-group dissimilarities.

Abundance					Biomass				
Taxa	Av1	Av2	Con %	Cum %	Taxa	Av1	Av2	Con %	Cum %
a) 45.4%	*A1 (27.9%)*	*A2 (31.5%)*			d) 49.3%	*B1 (29.8%)*	*B2 (36.4%)*		
Polychaeta	6053	503	31.8	31.8	Polychaeta	135.9	11.5	37.3	37.3
Bivalvia	6691	14220	26.9	58.7	Bivalvia	34.5	59.0	26.3	63.6
Gastropoda	4	604	22.7	81.4	Gastropoda	0.1	3.3	16.9	80.5
Cirripedia	25	327	14.4	95.8	Cirripedia	1.9	4.5	14.2	94.7
Nemertea	16	10	3.2	99.0	Nemertea	0.3	0.3	4.7	99.0
Bryozoa	4	5	0.7	99.7	Bryozoa	0.0	0.2	0.7	99.7
Echinodermata	10	0	0.3	100.0	Echinodermata	0.1	0.0	0.3	100.0
b) 55.8%	*A1 (27.9%)*	*A3 (27.8%)*			e) 65.9%	*B1 (29.8%)*	*B3 (28.9%)*		
Bivalvia	6691	388200	52.5	52.5	Bivalvia	34.5	2113.0	46.4	46.4
Polychaeta	6053	6325	17.7	70.2	Polychaeta	135.9	12.3	23.3	69.7
Gastropoda	4	3360	17.6	87.8	Gastropoda	0.1	37.1	17.7	87.4
Cirripedia	25	2283	9.8	97.6	Cirripedia	1.9	29.3	10.7	98.1
Nemertea	16	10	2.1	99.7	Nemertea	0.3	0.1	1.7	99.8
Bryozoa	4	0	0.2	99.9	Echinodermata	10	0	0.1	100.0
Echinodermata	0.1	0.0	0.2	100.0	Bryozoa	0.0	0.0	0.0	100.0
c) 43.5%	*A2 (31.5%)*	*A3 (27.8%)*			f) 47.6%	*B2 (36.4%)*	*B3 (28.9%)*		
Bivalvia	14220	388200	51.1	51.1	Bivalvia	59.0	2113.0	49.4	49.4
Polychaeta	503	6325	17.2	68.3	Gastropoda	3.3	37.1	17.7	67.1
Gastropoda	604	3360	16.1	84.4	Polychaeta	11.5	12.3	15.5	82.6
Cirripedia	327	2283	13.4	97.8	Cirripedia	4.5	29.3	15.1	97.7
Nemertea	10	10	1.9	99.7	Nemertea	0.3	0.1	1.8	99.5
Bryozoa	5	0	0.3	100.0	Bryozoa	0.2	0.0	0.5	100.0
Echinodermata	0	0	0.0	100.0	Echinodermata	0.0	0.0	0.0	100.0

position of Group B2 resembled Group B3 (Group B2 corresponds to Group A2).

The nMDS ordinations with fitted environmental variables identified surface temperature as the variable most strongly linked to the meroplankton community (Figure 5; Table 4). Samples associated with the A1/B1 groups were collected when surface temperatures were lower (environmental parameters are presented in supplementary material Figure S1–6). All other variables had very low R^2 values, suggesting little direct importance for the meroplankton community (Table 4).

Based on the results of the forward selection of environmental variables, we selected all variables except surface chlorophyll *a* for variation partitioning of the abundance data and all variables except chlorophyll *a* and bottom water oxygen for variation partitioning of the biomass data. Variation partitioning indicated that approximately 50% of the variation in meroplankton community composition (both abundance and biomass) could be explained by the combined effects of environmental, interannual (year), seasonal (month), and spatial (station) predictors (Figure 6). Seasonal variation was largely captured by the environmental variables, as evidenced by the substantial overlap between the fractions attributed to environmental and seasonal components and the small proportion of variation uniquely attributable to month (3.1% for abundance; 3.7% for biomass). In contrast, interannual variation was only partly explained by the measured environmental variables, with a considerable proportion of variation uniquely attributable to year (13.1% for abundance; 11.8% for biomass). Spatial effects were comparatively weak, accounting for only ∼7% of the variation, indicating that spatial structure was less important than seasonal and interannual dynamics.

When surface temperature was used as the sole environmental predictor, the variation partitioning results differed in three key ways (Figure 6): (i) the total variation explained by environmental variables decreased by 25–30%, (ii) the proportion of unexplained spatial (station) and interannual (year) variation increased, and (iii) nearly all variation attributed to surface temperature overlapped with variation explained by month.

To further characterize interannual variability in thermal conditions, we examined daily sea surface temperature across all sampling locations using data from the Copernicus Marine Service (E.U. Copernicus Marine Ser-

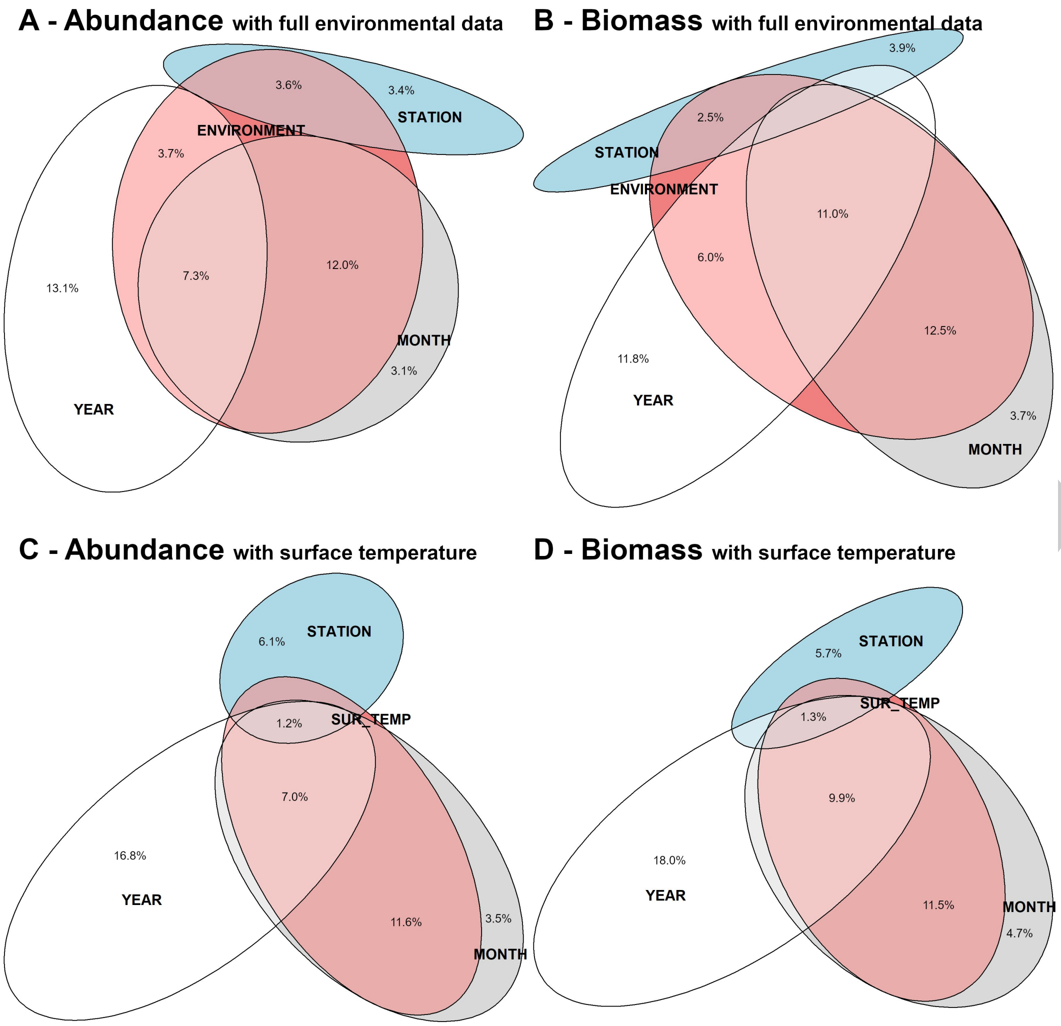


Figure 6. Euler diagram showing the results of variation partitioning for meroplankton abundance (A) and biomass (B). Diagram areas are proportional to the amount of explained variation, with percentages indicating the fraction of total variance attributed to each component. Overlapping areas represent variation jointly explained by multiple sets of predictors. The total variation explained by all predictors was 47.5% for abundance and 53.2% for biomass. Percentages are given for sections accounting for more than 1% of the total variance.

Table 4. R^2 and p-values indicating the strength of the correlation between each environmental variable and the nMDS analysis according to the envfit analysis. a) and b) give results for abundance and biomass-based analyses, respectively. Variables in a) and b) are given in order of decreasing R^2 values.

a)	surT	Inflow2y	botT	Depth	Dist	Chl_a	botS	surS	Oxy
R^2	0.422	0.076	0.069	0.046	0.050	0.025	0.014	0.011	0.010
p-value	0.001	0.001	0.001	0.002	0.001	0.017	0.105	0.173	0.186
b)	**surT**	**Inflow2y**	**botT**	**Depth**	**Dist**	**Chl_a**	**Oxy**	**surS**	**botS**
R^2	0.402	0.100	0.095	0.053	0.038	0.023	0.022	0.019	0.005
p-value	0.001	0.001	0.001	0.001	0.002	0.028	0.030	0.036	0.445

vice Information (CMEMS), 2025). Sea surface temperature exhibited pronounced seasonal cycles with consistent summer maxima and winter minima (Figure 7). However, substantial interannual variability was evident in winter temperatures, with some years characterized by markedly lower minimum sea surface temperatures than others. In several winters, minimum sea surface temperature fell below the temperature range corresponding to the maximum

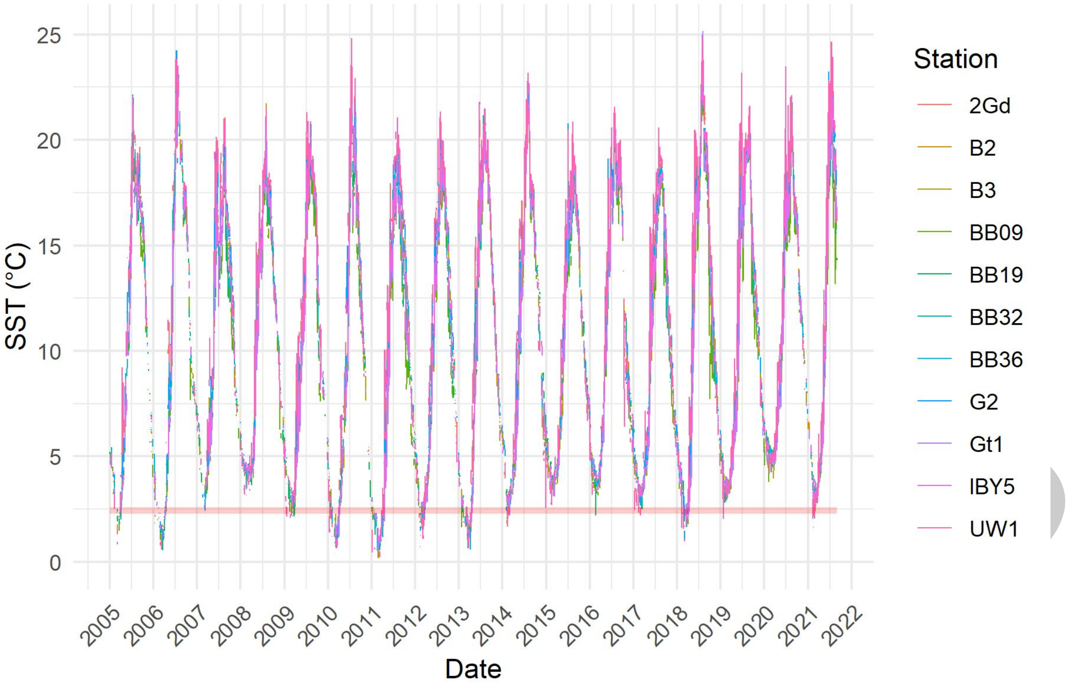


Figure 7. Daily sea surface temperatures (SST) for all sampling locations throughout the study period. SST data from E.U. Copernicus Marine Service Information (CMEMS) (2025). The red horizontal line indicates the range of the temperature of maximum density for the central 95% of the measured surface salinities in our study.

density of surface waters, as defined by the central 95% of observed salinities (Figure 7). In contrast, other years remained consistently above this range.

4. Discussion

We identified three temporally distinct phases in meroplankton community composition, characterized by a shift from a low-abundance community with relatively balanced contributions of Bivalvia and Polychaeta to a system increasingly dominated by bivalve larvae and higher overall abundances. This transition occurred in two major steps, around 2014 and again in 2019, indicating pronounced interannual variability in community structure. In contrast, spatial variation was weak, with consistently higher abundances in the Gulf of Gdańsk, but no clear differentiation between regions west and east of the Słupsk Sill. These findings do not support our initial hypothesis of a strong spatial structuring of meroplankton communities in the study area.

Our results, however, provide partial support for our second hypothesis (earlier disappearance of the spring meroplankton community) in relation to increasing temperatures. We identified sea surface temperature as the main environmental driver of variation in the meroplankton community. Furthermore, we attributed 23.9% and 29.5% of the variation in abundance and biomass data, respectively, to interannual differences. Environmental variation accounted for 11.4% and 17.8% of abundance and biomass differences. However, seasonal variation also explained a large fraction of this variation (7.3% and 11.8%), indicating that it partly reflects the altered sampling scheme, with no sampling earlier than June since 2014. Consequently, our results show that sea surface temperature at the time of sampling reflects seasonal development and also partly explains interannual variability in the meroplankton community. A considerable proportion of interannual variability, however, remained unexplained by the environmental variables included in our models. To further explore potential drivers of this variability, we examined temporal patterns in winter sea surface temperature and their potential influence on stratification dynamics.

4.1 Winter sea surface temperature drives meroplankton phenology

Our nMDS ordinations and the fitting of environmental variables identified surface temperature as the environmental variable most closely related to the differentiation of meroplankton groups. The strong link between surface temperature and the meroplankton community indicates two potentially important temporal scales to consider: (i) seasonality within years and (ii) long-term variability in response to climate warming. Both temporal scales were identified as approximately equally important predictors by the variation partitioning. However, the extent to which this variation was shared with environmental variables differed. Environmental variables – particularly surface temperature – accounted for most of the seasonal variation in both abundance and biomass. In contrast, a larger fraction of interannual variation remained unexplained, and environmental variables other than surface temperature contributed more substantially to the model's explanatory power regarding the interannual variability.

Numerous studies link strong seasonality in benthic reproduction and the occurrence of meroplankton to surface temperatures globally (Fernandes et al., 2012; Silberberger et al., 2016) and also in the Baltic Sea (Hernroth and Ackefors, 1979; Witalis et al., 2024). We also observe a strong seasonal pattern in our data. Virtually all samples collected in April and May (all before 2014) aligned with the A1/B1 group, with high contributions of Polychaeta. Polychaeta typically dominate spring meroplankton in our study area (Hernroth and Ackefors, 1979; Witalis et al., 2024), and accordingly we consider the meroplankton community associated with our A1/B1 group as a typical 'spring' community. Interestingly, samples collected later in the year (June, July, August) frequently aligned with the samples in this group collected prior to August 2014. Samples collected from August 2014 onwards were rarely characterized by such a spring community (A1/B1 group), and consequently our results suggest an earlier disappearance of the spring meroplankton community. Because all samples in this later period were collected in June and August, it is important to disregard samples collected during April and May for the comparison of these two periods. We assessed the frequencies of occurrence of the spring community in June and August samples (the months with sampling campaigns in both periods). Out of 76 samples collected in August in the earlier period, 21 (= 28%) showed the strongest association with group A1 for abundance data and 22 (= 29%) showed the strongest association with group B1 for biomass data. Of 74 samples collected during August in the later period, only 8 (= 11%) and 3 (4%) showed a strong association with group A1 and B1, respectively. A similar trend was observed for June samples. Out of 27 samples collected in the earlier period, 14 (52%) and 15 (56%) aligned with group A1 and B1, respectively, while 23 of 75 samples (31%) collected during the later period aligned with group A1 and 17 (23%) with group B1. Admittedly, June samples in the earlier period were only collected for three years (2006, 2007, 2014) and therefore we cannot rule out that this pattern occurred by chance. However, given that the same trend was observed in August, we consider it unlikely that the pattern in June was coincidental. Such an earlier disappearance of the spring meroplankton community corresponds well with the trend of continuously increasing sea surface temperatures in the southern Baltic Sea (Zalewska et al., 2024). However, we observed an abrupt change in the timing of the disappearance of the spring meroplankton community from the water column, which contrasts with the gradual temperature increase, and therefore we do not consider sea surface temperature at the time of sampling as the main driver of inter-annual variability. Instead, we consider it likely that increased winter sea surface temperatures explain the earlier disappearance of the spring meroplankton community since 2014. As outlined by Zalewska et al. (2024), 2.5°C is the approximate temperature at which water of a salinity of 7, typical for surface waters in the southern Baltic Sea, has its highest density. Consequently, warming after winters with sea surface temperatures above 2.5°C results in the immediate formation of thermal stratification, whereas warming after colder winters results in an unstable water column above the pycnocline. We propose that the earlier stratification in warm winters results in a strong shift in the meroplankton phenology and the observed earlier disappearance of the spring meroplankton community. Comparison with winter sea surface temperature patterns (Figure 7) reveals a clear difference between the early (2005–2014) and later study period. Prior to 2014, winter temperatures generally fell below the temperature of maximum density, with the exception of 2007 and 2008, when temperatures remained comparatively high. Notably, these two years also correspond to the first instances in our samples in which the spring meroplankton community was less dominant. In contrast, in most years after 2014, winter temperatures remained at or above this threshold. The notably cold winter of 2018, during which temperatures clearly dropped below the threshold, coincided with a pronounced persistence of the spring meroplankton community into August. In years such as 2017 and 2021, when minimum temperatures only approached but did not clearly fall below the threshold, this effect was less pronounced and mainly limited to June.

These patterns are consistent with the hypothesis that winter temperature influences the timing of stratification and, consequently, meroplankton phenology. When winter temperatures remain above the temperature of maximum density (~2.5 °C at typical Baltic surface salinities), stratification can establish rapidly during spring warming. In colder years, by contrast, more prolonged mixing may delay stratification. The observed differences between years below and above this threshold suggest that even relatively small differences in winter temperature can lead to substantial shifts in the timing and persistence of meroplankton communities.

4.2 Meroplankton hotspots are produced by multiple source populations

We hypothesized that we would find differences between the meroplankton community in areas to the west and east of the Słupsk Sill. Across all sampling years, however, we observed higher abundances and biomass of meroplankton at the sampling stations in the Gulf of Gdańsk (G2, 2Gd, UW1) than at all other stations. Such a spatial pattern is not reflected in the environmental variables considered in our analysis. Nonetheless, we propose that this spatial pattern in meroplankton abundance is related to the proximity of the sampling locations to shallow coastal communities. In the Baltic Proper, the most abundant benthic macrofaunal communities commonly occur at depths shallower than 30 m depth (Ehrnsten et al., 2020). Below this depth, macrofaunal community biomass is 30% lower on average than at shallower depths (Ehrnsten et al., 2020). Another important shift occurs around 70 m depth (Ehrnsten et al., 2020; Gogina et al., 2016). Below this depth, frequent hypoxia results in very low macrobenthos abundance, mainly represented by the polychaete *Bylgides sarsi* (Gogina et al., 2016). Consequently, the meroplankton in our samples did not originate from our sampling locations, which are mostly deeper than 70 m (Table 1), but rather from source populations in shallower waters. The semi-enclosed nature of the Gulf of Gdańsk places its sampling stations in close proximity to shallow coastal habitats in multiple directions (Figure 1). As a result, these stations are likely to receive high inputs of meroplankton under a wide range of wind and circulation conditions. In contrast, stations outside the Gulf of Gdańsk are only intermittently connected to shallow source areas, and therefore receive substantial meroplankton input only under specific circulation patterns that transport larvae from coastal benthic communities.

4.3 Ecological implications

The dominant meroplankton communities identified for the three periods demonstrate an increasing dominance of bivalves during summer (June–August). Initially, polychaetes and bivalves co-dominated, but from August 2014 onward, bivalves became clearly dominant. From August 2019, meroplankton abundance increased by an order of magnitude, accompanied by a further increase in bivalve dominance. This increase contrasts with the reported declines in bivalve larval abundance in the North Sea associated with ongoing climate change (Kirby et al., 2008). As outlined earlier, we expected differences between the systems due to contrasting predator regimes. In the Baltic Sea, however, top-down control of bivalve populations involves a range of predators across trophic levels, including benthic invertebrates, fish, and birds. While the isopod *Saduria entomon* is often considered an important benthic predator, its feeding preferences suggest that it may not exert strong control on all bivalve species, particularly Macoma balthica (Ejdung and Elmgren, 2001). Other benthic invertebrates, such as amphipods (e.g. *Monoporeia affinis*), can prey on newly settled bivalves (Ejdung and Elmgren, 1998), while demersal fish (e.g. flounders) and seabirds such as Somateria mollissima may exert substantial predation pressure on juvenile and adult bivalves. Consequently, changes in bivalve larval abundance may reflect shifts in a complex predator–prey network rather than a response to a single dominant predator. Environmental change, including warming of bottom waters (Zalewska et al., 2024), may alter this network by affecting predator abundances, feeding rates, or spatial overlap between predators and prey. Such changes could lead to a reduced top-down control on benthic bivalves or their early life stages, potentially contributing to increased larval production. However, alternative mechanisms may also explain the observed increase in bivalve larvae. These include reduced predation on meroplankton in the water column, changes in circulation affecting larval transport and retention, or increased reproductive output of benthic populations. Our data do not allow us to distinguish among these mechanisms, and further studies are needed to resolve the drivers of this pronounced increase in meroplankton abundance. Irrespective of the underlying mechanisms, the observed increase in meroplankton abundance since 2019 has important implications for benthic recruitment and pelagic–benthic coupling in the southern Baltic Sea. High meroplankton biomass suggests that meroplankton may become an increasingly important vector of vertical carbon flux, actively transporting organic matter to the seafloor during larval settlement. Such a role has been proposed for the sub-Arctic Lofoten–Vesterålen shelf (Silberberger et al., 2021). In contrast to that short-term study, our 17-year time series reveals sustained changes in meroplankton communities across the southern Baltic Sea, indicating a potential shift in pelagic–benthic coupling and ecosystem functioning.

All meroplankton in our samples were identified only to a higher taxonomic level. This approach is common in meroplankton studies given the challenge of species-level identification based on the morphology of small specimens (Coyle and Paul, 1990; Stübner et al., 2016). Given the low benthic species diversity in our study region, however, we can constrain the identity of the dominant taxonomic units in our study to a few species.

In the southern Baltic Sea, the four bivalve taxa *Cerastoderma glaucum*, *Macoma balthica*, *Mya arenaria*, and *Mytilus* spp. are widely distributed and extremely abundant. All four taxa reproduce via planktotrophic larvae, and accordingly we assume that the bivalve larvae in our samples represent a mixture of these species. Reproduction in the four bivalves mentioned above is generally closely linked to temperature, but the role of temperature differs markedly among taxa. In *M. balthica*, temperature influences reproduction both indirectly and directly: gametogenesis occurs during autumn and winter and is strongly regulated by winter temperature, with colder conditions promoting energy storage and higher reproductive output (Honkoop et al., 1998). Spawning is subsequently triggered in early spring once temperatures reach a threshold of approximately 8–10°C. In contrast, reproduction in *Mytilus* spp., *M. arenaria*, and *C. glaucum* is more directly controlled by ambient temperature conditions during the productive season. In these species, spawning is typically initiated when water temperatures rise above 10–12°C, often in late spring or summer, and may occur over extended periods or in multiple pulses, particularly in mussels (Honkoop and van der Meer, 1998; Lasota et al., 2014). Consequently, the increased dominance of bivalves in the meroplankton observed since 2014 and the strong increase in bivalve abundance since 2019 indicate changes in the adult populations of *Mytilus* spp., *M. arenaria*, and/or *C. glaucum*.

Of the other three common taxa, we can attribute all Cirripedia to *Amphibalanus improvisus*, the only barnacle species reported from the Baltic Sea (Wrange et al., 2014). *Amphibalanus improvisus* reproduces at water temperatures above 10°C (Meng et al., 2024). Accordingly, *A. improvisus* nauplii rarely occur before June in the southern Baltic Sea, making Cirripedia nauplii a typical component of the summer meroplankton community (Witalis et al., 2024). Cirripedia larvae also occurred almost exclusively from June to August in our samples, confirming their absence from the spring meroplankton community. This absence of Cirripedia from the spring community starkly contrasts with fully marine (saline) systems in Europe. All along the European Atlantic coast, nauplii of the species *Semibalanus balanoides* and *Balanus balanus* dominate the spring meroplankton community (Silberberger et al., 2016). Larval release in these species coincides with onset of the spring diatom bloom and consequently these nauplii are among the first abundant mesozooplankton of the year, sometimes accounting for over 10% of the total mesozooplankton biomass in early spring (Silberberger et al., 2021). The dominance of Cirripedia nauplii in spring suggests potentially important ecological functions, e.g., as prey for larval fish (Amieva Mau et al., 2026; Silberberger et al., 2021). In the Baltic Sea, however, the absence of Cirripedia larvae in spring indicates a potentially important functional difference in the plankton community structure compared to fully marine systems. This observation highlights the need for particular care when transferring knowledge about ecosystem functioning between the Baltic Sea and other marine ecosystems.

Several species within the family Hydrobiidae dominate the Gastropoda in the southern Baltic Sea. Within this family, and even within individual species in this family, the diverse developmental modes also include development via planktonic larvae (Norkko et al., 2010). Accordingly, the Gastropoda in our samples were mostly hydrobiid snails.

Abundant polychaete species in benthic communities in the southern Baltic Sea mainly include spionid polychaetes of the genus *Marenzelleria* and *Pygospio elegans*, the polynoid polychaete *Bylgides sarsi*, and the nereidid polychaete *Hediste diversicolor* (Gogina et al., 2016). The latter species broods offspring and lacks a pelagic larval stage (Breton et al., 2003), and accordingly, Spionidae and *B. sarsi* likely comprise most of the Polychaeta in our study. Within the Spionidae, both *Marenzelleria* spp. and *P. elegans* are potential contributors. In the southern Baltic Proper, the three *Marenzelleria* species show overlapping distributions, with *M. neglecta* and *M. viridis* commonly co-occurring and *M. arctia* occurring more sporadically. Importantly, these species differ in their reproductive strategies, with both autumn and spring spawning reported (Bochert, 1997). Consequently, the timing of larval occurrence in the water column is species-specific. Available evidence suggests that *Marenzelleria* larvae occur predominantly in early spring, as indicated by recruitment peaks in May (Kauppi et al., 2018), implying the pelagic larval phase mainly in April or earlier. While this supports a contribution of *Marenzelleria* spp. to the spring meroplankton community, it suggests a limited direct contribution to the community patterns observed in our data for June and August. We therefore consider it unlikely that the observed changes in Polychaeta larval abundance during summer primarily reflect variability in *Marenzelleria* populations. In contrast, *P. elegans* exhibits a more flexible reproductive strategy, including multiple cohorts and extended periods of larval release (Thonig et al., 2016). This life-history pattern is more consistent with the sustained presence of polychaete larvae observed in our samples during summer months. Accordingly, we consider it more likely that the Polychaeta signal in our data is primarily driven by changes in *P. elegans* populations or their reproductive mode. In particular, shifts toward benthic larval development or asexual reproduction could reduce the presence of larvae in the plankton during summer months, especially following winters with temperatures above the temperature of density threshold (~2.5°C), without necessarily indicating a decline in benthic abundance.

Overall, our results suggest that ongoing environmental change is affecting the functioning of benthic communities in the Baltic Sea, not necessarily through shifts in species composition, but through changes in energy allocation to reproduction and reproductive modes, as reflected in the meroplankton community.

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Supplementary material

Supplementary material associated with this article can be found here.

Data availability

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

Conflict of interest

None declared.

References

Amieva Mau, S., Silberberger, M.J., Tverberg, V., Renaud, P.E., Eiane, K., Krogstad, M., Reiss, H., 2026. *Interannual variability in the spring meroplankton community of a sub-Arctic fjord*. J. Plankton Res. 48. https://doi.org/10.1093/plankt/fbag012

Barzandeh, A., Maljutenko, I., Rikka, S., Lagemaa, P., Männik, A., Uiboupin, R., Raudsepp, U., 2024. *Sea surface circulation in the Baltic Sea: decomposed components and pattern recognition*. Sci. Rep. 14, 18649. https://doi.org/10.1038/s41598-024-69463-8

Becker, B.J., Levin, L.A., Fodrie, F.J., McMillan, P.A., 2007. *Complex larval connectivity patterns among marine invertebrate populations*. Proc. Natl. Acad. Sci. U.S.A. 104, 3267–3272. https://doi.org/10.1073/pnas.0611651104

Benjamini, Y., Hochberg, Y., 1995. *Controlling the False Discovery Rate: A Practical and Powerful Approach to Multiple Testing*. J. R. Stat. Soc. Series B Stat. Methodol. 57, 289–300. https://doi.org/10.1111/j.2517-6161.1995.tb02031.x

Blanchet, G., Legendre, P., Borcard, D., 2008. *Forward selection of spatial explanatory variables*. Ecology 89, 2623–2632. https://doi.org/10.1890/07-0986.1

Bochert, R., 1997. *Marenzelleria viridis (Polychaeta: Spionidae): a review of its reproduction*. Aquat. Ecol. 31, 163–175. https://doi.org/10.1023/A:1009951404343

Borcard, D., Gillet, F., Legendre, P., 2018. *Numerical Ecology with R*. Springer-Verlag, New York.

Bray, J.R., Curtis, J.T., 1957. *An Ordination of the Upland Forest Communities of Southern Wisconsin*. Ecol. Monogr. 27, 325–349. https://doi.org/10.2307/1942268

Breton, S., Dufresne, F., Desrosiers, G., Blier, P.U., 2003. *Population structure of two northern hemisphere polychaetes, Neanthes virens and Hediste diversicolor (Nereididae), with different life-history traits*. Mar. Biol. 142, 707–715. https://doi.org/10.1007/s00227-002-0992-5

Coyle, K.O., Paul, A.J., 1990. *Abundance and biomass of meroplankton during the spring bloom in an alaskan bay*. Ophelia 32, 199–210. https://doi.org/10.1080/00785236.1990.10422031

Dave, R.N., Krishnapuram, R., 1997. *Robust clustering methods: a unified view*. IEEE Trans. Fuzzy Syst. 5, 270–293. https://doi.org/10.1109/91.580801

De Cáceres, M., Font, X., Oliva, F., 2010. *The management of vegetation classifications with fuzzy clustering*. J. Veg. Sci. 21, 1138–1151. https://doi.org/10.1111/j.1654-1103.2010.01211.x

Dembek, M., Bielecka, L., Margoński, P., Wodzinowski, T., 2019. *Changes in the composition and abundance of ichthyoplankton along environmental gradients of the southern Baltic Sea*. Oceanol. Hydrobiol. Stud. 48, 328–336. https://doi.org/10.2478/ohs-2019-0030

Díaz-Gil, C., Werner, M., Lövgren, O., Kaljuste, O., Grzyb, A., Margonski, P., Casini, M., 2014. *Spatio-temporal composition and dynamics of zooplankton in the Kalmar Sound (western Baltic Sea) in 2009–2010*. Boreal Environ. Res. 19, 323–335.

Dunn, O.J., 1964. *Multiple Comparisons Using Rank Sums*. Technometrics 6, 241–252. https://doi.org/10.1080/00401706.1964.10490181

Ehrnsten, E., Norkko, A., Müller-Karulis, B., Gustafsson, E., Gustafsson, B.G., 2020. *The meagre future of benthic fauna in a coastal sea – Benthic responses to recovery from eutrophication in a changing climate*. Glob. Chang. Biol. 26, 2235–2250. https://doi.org/10.1111/gcb.15014

Ejdung, G., Elmgren, R., 1998. *Predation on newly settled bivalves by deposit-feeding amphipods: a Baltic Sea case study*. Mar. Ecol. Prog. Ser. 168, 87–94. https://doi.org/10.3354/meps168087

Ejdung, G., Elmgren, R., 2001. *Predation by the benthic isopod Saduria entomon on two Baltic Sea deposit-feeders, the amphipod Monoporeia affinis and the bivalve Macoma balthica*. J. Exp. Mar. Biol. Ecol. 266, 165–179. https://doi.org/10.1016/S0022-0981(01)00353-7

E.U. Copernicus Marine Service Information (CMEMS), 2025. *Baltic Sea – L3S Sea Surface Temperature Reprocessed*. https://doi.org/10.48670/moi-00312

Fernandes, L.D. d. A., Quintanilha, J., Monteiro-Ribas, W., Gonzalez-Rodriguez, E., Coutinho, R., 2012. *Seasonal and interannual coupling between sea surface temperature, phytoplankton and meroplankton in the subtropical south-western Atlantic Ocean*. J. Plankton Res. 34, 236–244. https://doi.org/10.1093/plankt/fbr106

GEBCO Compilation Group, 2023. *GEBCO 2023 Grid*. https://doi.org/10.5285/f98b053b-0cbc-6c23-e053-6c86abc0af7b

Gogina, M., Nygård, H., Blomqvist, M., Daunys, D., Josefson, A.B., Kotta, J., Maximov, A., Warzocha, J., Yermakov, V., Gräwe, U., Zettler, M.L., 2016. *The Baltic Sea scale inventory of benthic faunal communities*. ICES J. Mar. Sci. 73, 1196–1213. https://doi.org/10.1093/icesjms/fsv265

Hansen, H.P., 1999. *Determination of oxygen*. [In:] Grasshoff, K., Kremling, K., Ehrhardt, M. (Eds.), *Methods of Seawater Analysis*, Wiley, 75–89. https://doi.org/10.1002/9783527613984.ch4

HELCOM, 2015. *Updated Fifth Baltic Sea pollution load compilation (PLC-5.5)*. Baltic Sea Environment Proceedings 145.

HELCOM, 2021. *Guidelines for monitoring of mesozooplankton*, WWW document (accessed 4.10.26). https://helcom.fi/publications/guidelines-for-monitoring-of-mesozooplankton/

Hensen, V., 1887. *Kapitel 1: Über die Bestimmung des Plankton's oder des im Meere treibenden Materials an Pflanzen und Thieren*. [In:] *Jahresbericht Der Commission Zur Wissenschaftlichen Untersuchung Der Deutschen Meere in Kiel*. 1–107.

Hernroth, L., Ackefors, H., 1979. *The Zooplankton Of The Baltic Proper: A long-term investigation of the fauna, its biology and ecology*. Fiskeristyrelsen, Göteborg.

Highfield, J.M., Eloire, D., Conway, D.V.P., Lindeque, P.K., Attrill, M.J., Somerfield, P.J., 2010. *Seasonal dynamics of meroplankton assemblages at station L4*. J. Plankton Res. 32, 681–691. https://doi.org/10.1093/plankt/fbp139

Hjerne, O., Hajdu, S., Larsson, U., Downing, A.S., Winder, M., 2019. *Climate Driven Changes in Timing, Composition and Magnitude of the Baltic Sea Phytoplankton Spring Bloom*. Front. Mar. Sci. 6, 482. https://doi.org/10.3389/fmars.2019.00482

Honkoop, P.J.C., van der Meer, J., 1998. *Experimentally induced effects of water temperature and immersion time on reproductive output of bivalves in the Wadden Sea*. J. Exp. Mar. Biol. Ecol. 220, 227–246. https://doi.org/10.1016/S0022-0981(97)00107-X

Honkoop, P., van der Meer, J., Beukema, J., Kwast, D., 1998. *Does temperature-influenced egg production predict the recruitment in the bivalve Macoma balthica?*. Mar. Ecol. Prog. Ser. 164, 229–235. https://doi.org/10.3354/meps164229

Kauppi, L., Norkko, A., Norkko, J., 2018. *Seasonal population dynamics of the invasive polychaete genus Marenzelleria spp. in contrasting soft-sediment habitats*. J. Sea Res. 131, 46–60. https://doi.org/10.1016/j.seares.2017.10.005

Kelley, D., Richards, C., WG127 SCOR/IAPSO, 2024. *gsw: Gibbs sea water functions. R package version 1.2-0 1*.

Kirby, R.R., Beaugrand, G., Lindley, J.A., 2008. *Climate-induced effects on the meroplankton and the benthic-pelagic ecology of the North Sea*. Limnol. Oceanogr. 53, 1805–1815. https://doi.org/10.4319/lo.2008.53.5.1805

Kott, P., 1953. *Modified Whirling Apparatus for the Subsampling of Plankton*. Aust. J. Mar. Freshw. Res. 4, 387–393. https://doi.org/10.1071/MF9530387

Kruskal, W.H., Wallis, W.A., 1952. *Use of Ranks in One-Criterion Variance Analysis*. J. Am. Stat. Assoc. 47, 583–621. https://doi.org/10.1080/01621459.1952.10483441

Lasota, R., Pierścieniak, K., Miąc, J., Wołowicz, M., 2014. *Comparative study of ecophysiological and biochemical variation between the Baltic and North Sea populations of the invasive soft shell clam Mya arenaria (L. 1758)*. Oceanol. Hydrobiol. Stud. 43, 303–311. https://doi.org/10.2478/s13545-014-0145-8

Levin, L.A., 2006. *Recent progress in understanding larval dispersal: New directions and digressions*. Integr. Comp. Biol. 46, 282–297. https://doi.org/10.1093/icb/icj024

Meier, M.H.E., 2007. *Modeling the pathways and ages of inflowing salt- and freshwater in the Baltic Sea*. Estuar. Coast. Shelf Sci. 74, 610–627. https://doi.org/10.1016/j.ecss.2007.05.019

Meier, H.E.M., Feistel, R., Piechura, J., Arneborg, L., Burchard, H., Fiekas, V., Golenko, N., Kuzmina, N., Mohrholz, V., Nohr, C., Paka, V.T., Sellschopp, J., Stips, A., Zhurbas, V., 2006. *Ventilation of the Baltic Sea deep water: A brief review of present knowledge from observations and models*. Oceanologia 48 (S), 133–164.

Meng, S., Strahl, J., Börner, A., Krienke, K., Zettler, M.L., Wrozyna, C., 2024. *The bay barnacle Amphibalanus improvisus (Darwin, 1854) in the Pleistocene of Europe? A review of Pleistocene Balanidae of northern Central Europe*. J. Quat. Sci. 39, 547–565. https://doi.org/10.1002/jqs.3603

Michelsen, H.K., Nilssen, E.M., Pedersen, T., Reigstad, M., Svensen, C., 2017a. *Spatial patterns of spring meroplankton along environmental gradients in a sub-Arctic fjord*. Aquat. Biol. 26, 185–197. https://doi.org/10.3354/ab00686

Michelsen, H.K., Svensen, C., Reigstad, M., Nilssen, E.M., Pedersen, T., 2017b. *Seasonal dynamics of meroplankton in a high-latitude fjord*. J. Mar. Syst. 168, 17–30. https://doi.org/10.1016/j.jmarsys.2016.12.001

Mohrholz, V., 2018. *Major Baltic Inflow Statistics – Revised*. Front. Mar. Sci. 5, 384. https://doi.org/10.3389/fmars.2018.00384

Motoda, S., 1959. *Devices of simple plankton apparatus*. Mem. Fac. Fish. Hokkaido Univ. 7, 73–94.

Mudrak, S., Żmijewska, M., 2007. *Spatio-temporal variability of mesozooplankton from the Gulf of Gdańsk (Baltic Sea) in 1999–2000*. Oceanol. Hydrobiol. Stud. 36, 3–9. https://doi.org/10.2478/v10009-007-0007-4

Norkko, J., Norkko, A., Thrush, S., Valanko, S., Suurkuukka, H., 2010. *Conditional responses to increasing scales of disturbance, and potential implications for threshold dynamics in soft-sediment communities*. Mar. Ecol. Prog. Ser. 413, 253–266. https://doi.org/10.3354/meps08745

Normant, M., Szaniawska, A., 1996. *The biochemical composition of Saduria (Mesidotea) entomon (Isopoda) from the Gulf of Gdańsk (southern Baltic)*. Oceanologia 38 (1), 113–126.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2018. *vegan: Community Ecology Package. R package version 2.5-2*.

Pasternak, A., Arashkevich, E., Reigstad, M., Wassmann, P., Falk-Petersen, S., 2008. *Dividing mesozooplankton into upper and lower size groups: Applications to the grazing impact in the Marginal Ice Zone of the Barents Sea*. Deep-Sea Res. Pt. II 55, 2245–2256. https://doi.org/10.1016/J.DSR2.2008.05.002

Pechenik, J.A., 1999. *On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles*. Mar. Ecol. Prog. Ser. 177, 269–297. https://doi.org/10.3354/meps177269

Porz, L., Zhang, W., Schrum, C., 2021. *Density-driven bottom currents control development of muddy basins in the southwestern Baltic Sea*. Mar. Geol. 438, 106523. https://doi.org/10.1016/j.margeo.2021.106523

R Core Team, 2024. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Schmidt, B., Wodzinowski, T., Bulczak, A.I., 2021. *Long-term variability of near-bottom oxygen, temperature, and salinity in the Southern Baltic*. J. Mar. Syst. 213, 103462. https://doi.org/10.1016/j.jmarsys.2020.103462

Schulz, J., Peck, M.A., Barz, K., Schmidt, J.O., Hansen, F.C., Peters, J., Renz, J., Dickmann, M., Mohrholz, V., Dutz, J., Hirche, H.-J., 2012. *Spatial and temporal habitat partitioning by zooplankton in the Bornholm Basin (central Baltic Sea)*. Prog. Oceanogr. 107, 3–30. https://doi.org/10.1016/j.pocean.2012.07.002

Silberberger, M.J., Renaud, P.E., Eiane, K., Reiss, H., 2021. *Seasonal dynamics of mesozooplankton biomass over a sub-Arctic continental shelf*. Ecol. Evol. 11, 8713–8729. https://doi.org/10.1002/ece3.7681

Silberberger, M.J., Renaud, P.E., Espinasse, B., Reiss, H., 2016. *Spatial and temporal structure of the meroplankton community in a sub-Arctic shelf system*. Mar. Ecol. Prog. Ser. 555, 79–93. https://doi.org/10.3354/meps11818

Snoeijs-Leijonmalm, P., Andrén, E., 2017. *Why is the Baltic Sea so special to live in?*. [In:] *Biological Oceanography of the Baltic Sea*. Springer Netherlands, Dordrecht, 23–84. https://doi.org/10.1007/978-94-007-0668-2_2

Sommer, F., Stibor, H., Sommer, U., Velimirov, B., 2000. *Grazing by mesozooplankton from Kiel Bight, Baltic Sea, on different sized algae and natural seston size fractions*. Mar. Ecol. Prog. Ser. 199, 43–53. https://doi.org/10.3354/meps199043

Stübner, E.I., Søreide, J.E., Reigstad, M., Marquardt, M., Blachowiak-Samolyk, K., 2016. *Year-round meroplankton dynamics in high-Arctic Svalbard*. J. Plankton Res. 38, 522–536. https://doi.org/10.1093/plankt/fbv124

Telesh, I., Postel, L., Heerkloss, R., Mironova, E., Skarlato, S., 2009. *Zooplankton of the open Baltic Sea: extended atlas*. BMB Publication No. 21 – Meereswiss. Ber.

Thonig, A., Knott, K.E., Kesäniemi, J.E., Winding Hansen, B., Banta, G.T., 2016. *Population and reproductive dynamics of the polychaete Pygospio elegans in a boreal estuary complex*. Invertebr. Biol. 135, 370–384. https://doi.org/10.1111/ivb.12149

Turner, J.T., Levinsen, H., Nielsen, T.G., Hansen, B.W., 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. https://doi.org/10.3354/meps221209

Vihtakari, M., 2020. *ggOceanMaps: Plot Data on Oceanographic Maps using "ggplot2"*. R package version 0.4.3.

Viitasalo, M., Bonsdorff, E., 2022. *Global climate change and the Baltic Sea ecosystem: direct and indirect effects on species, communities and ecosystem functioning*. Earth Syst. Dynam. 13, 711–747. https://doi.org/10.5194/esd-13-711-2022

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. https://doi.org/10.3354/meps12994