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Spatial distribution projections of suitable environmental conditions for key Baltic Sea zooplankton species

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Abstract

Environmental changes reshape biological communities, inducing cascading effects throughout the food webs. These changes pressure species either to adapt or to track favorable habitats. Estuaries represent an interesting case study to investigate such responses as species will rapidly reach physical boundaries if they cannot adapt fast enough and need to track suitable conditions. One such estuary is the Baltic Sea, characterized by a salinity and temperature gradient that shapes species distribution and imposes physiological stress on organisms. The Baltic Sea is projected to be affected by substantial modifications in environmental conditions by the end of the 21st century, which could have major consequences for species distribution and community composition. However, despite the impending changes and their potential impact, there is a gap in understanding the potential consequences on pelagic species of the Baltic Sea. This study employs long-term observations of primary zooplankton species in the pelagic food web to model changes in their distribution under future climate projections. We found that the parameters having the largest influence on habitat suitability varied across species, although maximal temperature was the most important for six out of seven species. In addition, there was a shrinkage of suitable area for several key species driven by a decrease in salinity and a rise in water temperature. We discuss the complex interplay between environmental changes and the spatial distribution of pelagic species in the Baltic Sea, highlighting the need for proactive management strategies to mitigate potential ecological impacts in the face of future climate scenarios.

Climate change is modifying the spatial distribution and phenology of species across the globe. Large shifts have been detected in the latitudinal range and community composition of marine ecosystems (Poloczanska et al. 2013; Beaugrand et al. 2013; Lenoir and Svenning 2015; Pinsky et al. 2021), as well as in the phenology of species in order to align key stages of their life cycle with optimal environmental conditions (Parmesan and Yohe 2003; Charmantier et al. 2008;

Bellard et al. 2012). For instance, the rise in water temperature can compel species to track suitable thermal conditions by adjusting their phenology, spatial or vertical distributions (Beaugrand et al. 2002; Burrows et al. 2014; Pinsky et al. 2020). Among marine ecosystems, plankton communities have already experienced major alterations both in distribution and composition due to climate change (Hays et al. 2005). These changes are reshaping aquatic biological communities in terms of biomass, diversity, and composition, with cascading effects throughout the food web, affecting ecosystem functions (Calbet et al. 2014; Reygondeau et al. 2015).

Spatial shifts to track suitable environmental conditions can be constrained due to physical barriers, particularly in estuaries, where species may be pushed beyond the limits of their environmental tolerance, causing extinctions in certain regions. In these enclosed systems, such as the Baltic Sea, factors other than temperature impact environmental suitability and consequently plankton distribution (Gasiunaite et al. 2005). For instance, the Baltic Sea plankton community comprises a diverse assemblage of marine and freshwater species driven by

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Additional Supporting Information may be found in the online version of this article.

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an increasing salinity and temperature gradient from north-east to south-west (Fig. 1, left panel). The brackish water conditions constrain the distribution of marine and freshwater species due to salinity-induced osmotic stress (Vuorinen et al. 1998). This stress further reduces species survival rate and hampers the ability to adapt to other changes in environmental parameters due to interactive effects (Karlsson et al. 2018).

Over the past century, the Baltic Sea has undergone a remarkable increase in water temperature, with an estimated rise of 0.5°C per decade since 1980 of surface water, surpassing the global rate by more than threefold (Belkin 2009; Reusch et al. 2018). Future projections indicate a substantial further increase in temperature, up to 4°C by the end of the century, a decrease in salinity of 1.5–2 (Meier et al. 2012; Andersson et al. 2015; Saraiva et al. 2019). In this brackish system, future changes in multiple hydrographic parameters such as temperature, salinity, and oxygen concentration are projected to exert pressure on species (Gogina et al. 2020), inducing changes in species composition and impacting food webs (Niiranen et al. 2013; Bauer et al. 2019). Additionally, the topographical feature of the Baltic Sea, with a unique and narrow connection to the North Sea, is likely to create a “cul-de-sac” effect for species occupying this estuary, as species are expected to migrate toward the north due to changes in temperature and the connection to the North Sea is located in the south of the Baltic Sea. The abrupt salinity gradient of the Baltic Sea limits the exchange of species with the North Sea, so that the Baltic Sea biodiversity is relatively low compared to other marine systems (Ojaveer et al. 2010). As a result, only a few species transfer primary production toward higher trophic levels. Here we focus on mesozooplankton species that represent a crucial component of the Baltic Sea pelagic food web (Hinrichsen et al. 2002; Möllmann et al. 2004). *Temora longicornis*, *Pseudocalanus elongatus*, and species belonging to the genus *Acartia* spp. are the dominant prey for sprat and herring in the central and southern Baltic Sea (Kornilovs et al. 2001), whereas *Limmocalanus macrurus* supports herring production in the northern Baltic Sea (Hiltunen et al. 2014). Thus, a reduction in the overall habitat suitability as well as a change in the spatial distribution of these mesozooplankton species could have important bottom-up effects on the whole Baltic Sea ecosystem. Projections of the Baltic Sea plankton distribution patterns under future climate scenarios provide crucial information to support effective fisheries management and conservations efforts due to the essential role of plankton in fueling the pelagic food web (Beaugrand and Kirby 2010).

Species distribution models (SDMs) are a popular tool in ecology and biogeography that use species-environmental relationships to estimate the bioclimatic envelope suitable for a species and project its distribution (Peterson et al. 2015). Hence, SDMs are useful for projecting the potential impacts of climate change on species and community distributions (Guillera-Aroita et al. 2015; Benedetti et al. 2018, 2021). To our knowledge, understanding the suitable environmental

conditions of key Baltic Sea zooplanktonic species remains limited and the overall effect of future conditions is only speculative. Moreover, the Baltic Sea zooplankton spatial distributions have never been projected in present or future conditions. Given the ongoing pressures exerted on the Baltic Sea through climate change, there is a need to comprehend the relationship between species and their environment.

We aimed to understand the envelope of suitable conditions for key zooplankton species and to project the variation in the distribution of suitable habitats based on future climate scenarios of the Baltic Sea. We expected salinity and temperature to be the main parameters influencing the biogeography of species in the Baltic Sea and hypothesized that any changes in these two abiotic factors are likely to impact the distribution of zooplankton species. To explore this hypothesis, we used sampled occurrences, across a large North-Atlantic area, of the dominating zooplankton species of the Baltic Sea pelagic food web to train SDMs and determine suitable conditions for each species. Additionally, we projected their distributions on past (2010–2020) and future climates (2040–2050 and 2090–2100). We then explored the projected spatial changes of favorable combinations of environmental conditions by using climate-forced biogeochemical model results.

Materials and methods

Past observed species and environmental data

We extracted occurrence records for seven planktonic species from the Ocean Biodiversity Information System (OBIS, <https://obis.org>) for the period ranging from 2000 to 2020 (Fig. 2). We extracted spatial coordinates and temporal information for the following copepods: *T. longicornis*, *Centropages hamatus*, *L. macrurus*, *Acartia tonsa*, *Acartia longiremis*, *Acartia bifilosa*, and the cladoceran *Evadne nordmanni* due to their central role in the trophic network of the Baltic Sea (Novotny et al., 2023). Occurrences with missing spatial coordinates or dates, as well as occurrences on land, could not be matched with environmental conditions and were discarded.

The values of the environmental predictors were extracted from Bio-ORACLE v3.0 (Assis et al., 2024) at the time and position of sampling of the species occurrence data, whereas the water depth (hereafter called bathymetry) data were obtained from the General Bathymetric Chart of the Oceans 2023 (www.gebco.net). The environmental values were extracted from a layer created by averaging two time periods available in Bio-ORACLE v3.0, years 2000 to 2010 and years 2010 to 2020. In order to reduce potential spatial sampling bias in the occurrence data, we conducted a rasterization of the occurrences, meaning that if one pixel on the biogeochemical model had been sampled more than once during the 2000–2020 period, it counted as one sample. Moreover, we performed variable selection based on three main criteria. First, data for every environmental parameter had to be available at the occurrence sampling date and position to determine the bioclimatic

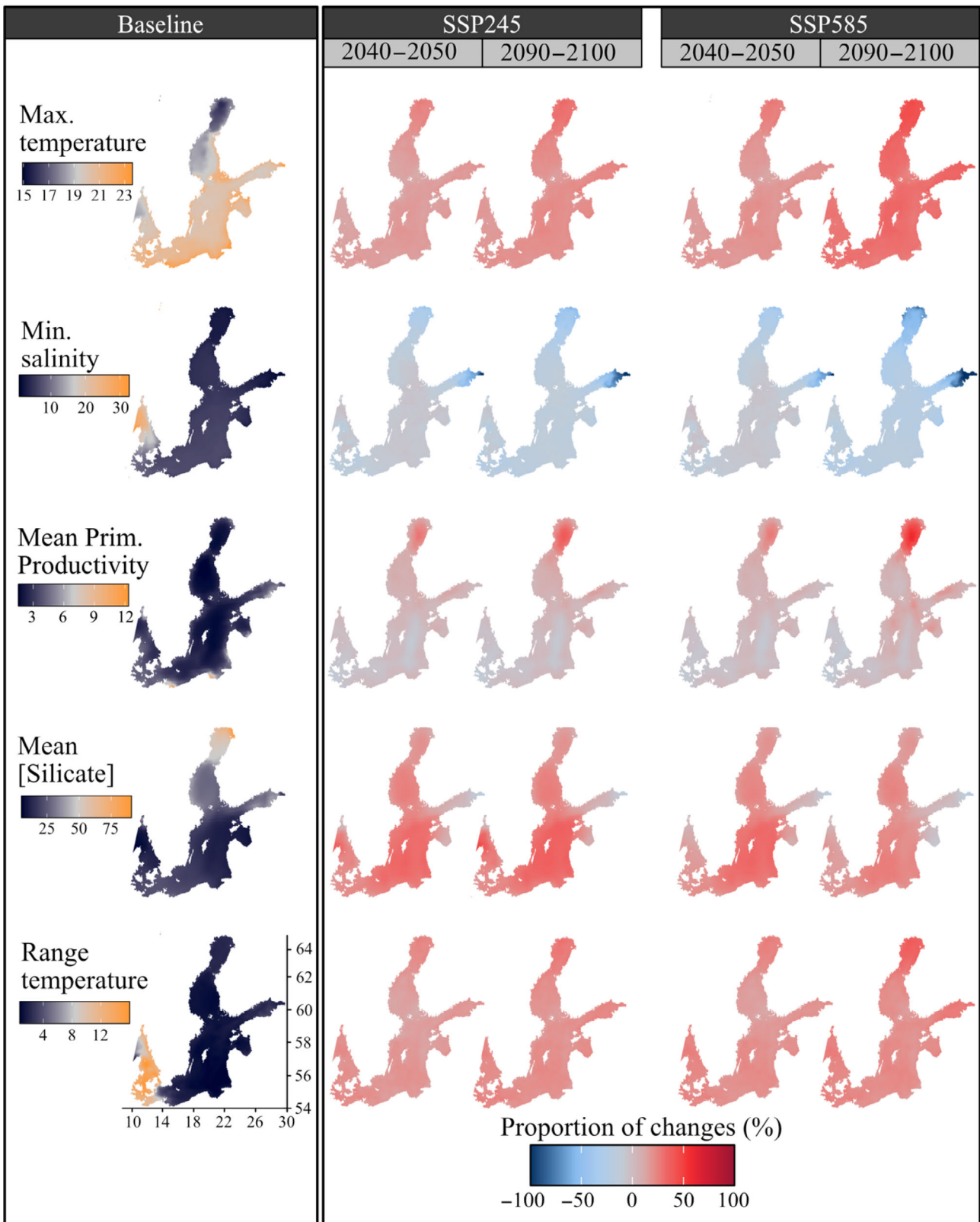


Fig. 1. Environmental conditions used for projections under the baseline scenario (left panel) and the changes in percentages (right panel) across horizons (2040–2050 and 2090–2100) and future scenarios (SSP245 and SSP585). The x-axis represents the longitude and the y-axis the latitude. Temperature parameters are in °C. Primary productivity and silicate concentration are in mmol L^{-3} .

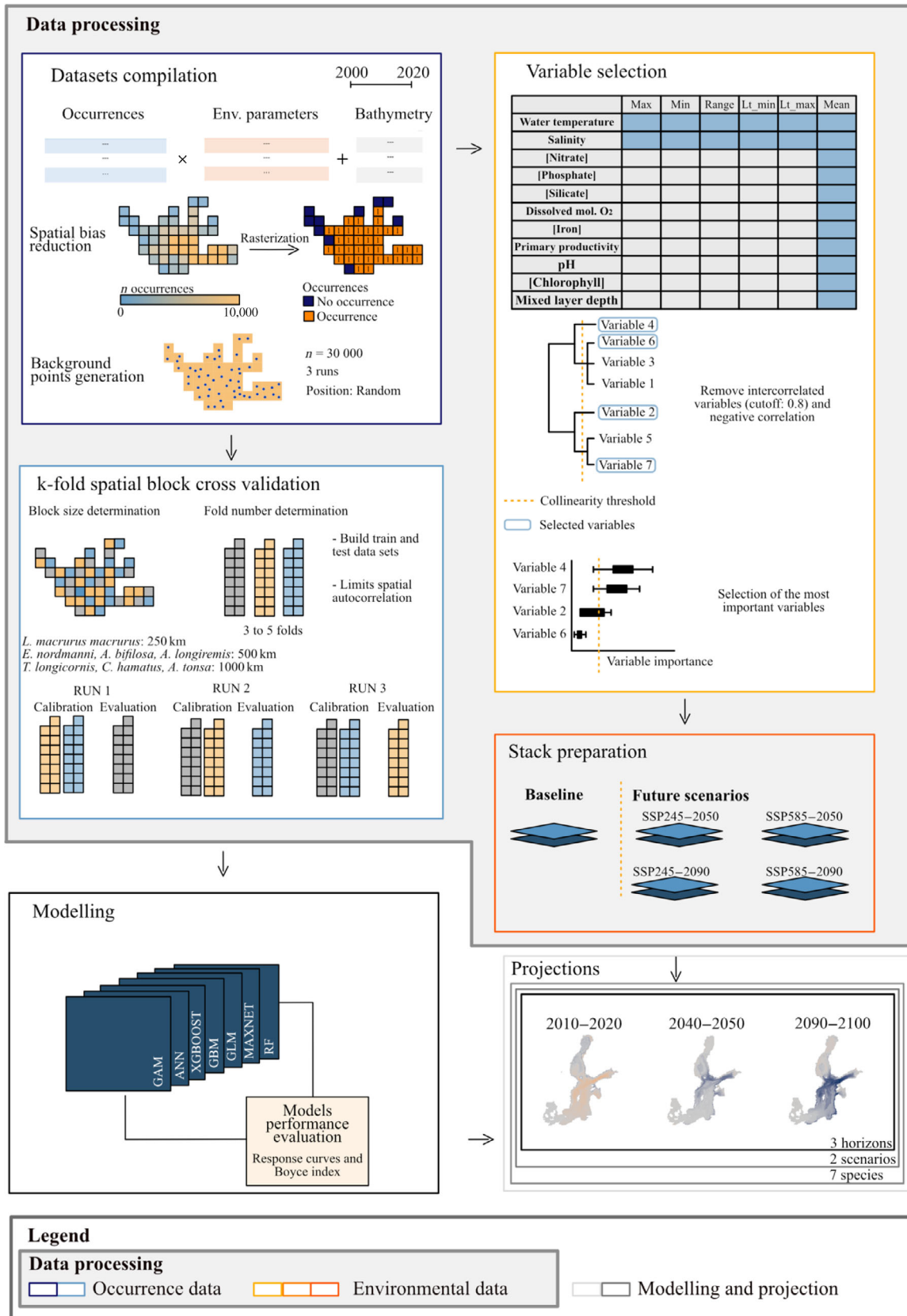


Fig. 2. Methodological framework for data processing, modeling and projection.

envelope of each species. Second, environmental parameters had to exist in the biogeochemical model's future projections. Third, variables could not be collinear. In the case of two parameters being collinear ($|r| > 0.8$) (Dormann et al. 2013; Braunisch et al. 2013), we selected, to our knowledge and based on variable importance in explaining the distribution of the species, the variable with the largest influence on the distribution of the targeted species (Table 1). Variable importance for each species was assessed using a permutation procedure and filtering was then performed based on the importance of the variable for the distribution of each species (Supporting Information Fig. S1).

Future projections

We used future projections of decadal-averaged environmental conditions from Bio-ORACLE v3.0 (Assis et al., 2024). Habitat suitability of each species was projected on three scenarios, one baseline and two future ones. The baseline scenario represented the mean values of environmental parameters from 2010 to 2020. We projected the distribution of habitat suitability for each species on two future horizons spanning the periods from 2040 to 2050 and from 2090 to 2100 (Fig. 2). The 1st future scenario, Shared Socioeconomic Pathway (SSP) 2.4.5, hereafter called SSP245, represents an intermediate trajectory in terms of education, population growth, urbanization and Gross Domestic Product (GDP) in which the current trend would be unchanged, together with the Representative Concentration Pathway (RCP) 4.5. This scenario leads to a radiative forcing increase of 4.5 W m^{-2} by 2100. The 2nd future scenario, SSP5.8.5, hereafter called SSP585, embodies a trajectory characterized by a reliance on fossil fuel-driven growth and a low inclination toward adaptation challenges, aligning with RCP8.5. This combined trajectory is

Table 1. Summary of the environmental variables used for species distribution modeling. Environmental data were extracted from Bio-ORACLE v3.0. and GEBCO 2023 for the period between 2000 and 2020.

Environmental parameters	Unit	Spatial resolution	Source
Maximum temperature	°C	$0.05^\circ \times 0.05^\circ$	Bio-ORACLE v3.0. Assis et al. (2024)
Minimum salinity	—	$0.05^\circ \times 0.05^\circ$	Bio-ORACLE v3.0. Assis et al. (2024)
Mean primary productivity	mmol L^{-3}	$0.05^\circ \times 0.05^\circ$	Bio-ORACLE v3.0. Assis et al. (2024)
Mean silicate concentration	mmol L^{-3}	$0.05^\circ \times 0.05^\circ$	Bio-ORACLE v3.0. Assis et al. (2024)
Range temperature (max–min)	°C	$0.05^\circ \times 0.05^\circ$	Bio-ORACLE v3.0. Assis et al. (2024)
Bathymetry	m	$0.004^\circ \times 0.004^\circ$	GEBCO 2023 www.gebco.net

forecasted to result in a radiative forcing surge to 8.5 W m^{-2} by the end of the century (Assis et al., 2024).

Spatial species distribution modeling

Modeling process

Although multiple models can be used to project suitable conditions for a species, predictive outcomes may vary among models (Pearson et al. 2006). As a result, model averaging is recommended for quantifying uncertainty and overreliance on individual models (Araújo and New 2007; Yates et al. 2018). The ensemble of models can produce better predictions than any single one of its model components by exploiting the complementarity and averaging out biases and reducing prediction errors (Dormann et al. 2018). We employed a random subsampling approach to split occurrence data into two groups: the calibration group for model fitting, and the evaluation group for assessing model predictive performance (Roberts et al. 2017). We chose k-fold spatial block cross-validation to design the above splitting, using blockCV R package (Valavi et al. 2019), in order to mitigate the spatial autocorrelation between the calibration and evaluation datasets (Valavi et al. 2019). In this process, the occurrence points are allocated to spatial blocks. These blocks are randomly assigned into folds which are alternatively distributed between the calibration group (containing $n - 1$ folds) and the evaluation group which contains the remaining fold (Valavi et al. 2019). We chose a block size of $1000 \text{ km} \times 1000 \text{ km}$ for *T. longicornis*, *C. hamatus*, and *A. tonsa*, $500 \text{ km} \times 500 \text{ km}$ for *E. nordmanni*, *A. biflosa*, and *A. longiremis*, and $250 \text{ km} \times 250 \text{ km}$ for *L. macrurus* as its distribution is mostly localized in the Baltic Sea and it required a smaller size to keep the number of occurrences across folds balanced. The block size represented a trade-off between a reduction in spatial autocorrelation of the environmental variables and a balanced distribution of presence points between folds. Depending on the species, we assigned the spatial blocks randomly to a number of folds ranging from 3 to 5 (Supporting Information Fig. S2).

Ensemble modeling

Ensemble modeling was used to identify the suitable conditions of each species (Araújo and New 2007). For the ensemble, we chose a combination of seven model algorithms available in BIOMOD2 version 4.2-5 package (Thuiller et al. 2009). The algorithms used were Generalized Additive Model (GAM), Artificial Neural Network (ANN), Generalized Linear Model (GLM), Generalized Boosting Model (GBM), Random Forest (RF), XGBOOST, and MAXNET. We performed 3 runs of cross-validation for each species and 3 rounds of 30,000 background points generation. For each of the 63–105 models per species (3–5 runs of cross-validation * 3 runs of background points generation * 7 algorithms), we projected the habitat suitability on the Baltic Sea map for each horizon and scenario. We combined the outputs of models by calculating the mean of each pixel across models, for each scenario–horizon combination (Thuiller et al. 2009). In order to estimate uncertainty across

models, we calculated the standard deviation among their outputs (Supporting Information Fig. S3).

Models performance

We evaluated model performance using two approaches. First, we assessed the ecological realism of response curves for each species based on expert opinion (Fig. 3). Response curves allow the visualization of the predicted response of species to environmental predictor variables. In this study, we used the evaluation strip method to build the response curves (Elith et al. 2005). Second, we used the Boyce index, which compares the proportion of presences to a random distribution of the occurrences in a given range of suitability values, as this metric is the most appropriate to evaluate presence-only models (Boyce et al., 2002; Leroy et al. 2018). A model should have a higher proportion of presence points for ranges of habitat suitability from 0.5 to 1 in comparison to a random distribution, and a lower proportion for

ranges between 0 and 0.5. Models with a Boyce index higher than 0.25 were considered as good performing. We built the ensemble model by averaging good-performing models (see Supporting Information ODMAP protocol). In order to detect the regions where environmental conditions are outside the range of conditions on which our models were trained, we performed a Multivariate Environmental Similarity Surface (MESS) analysis (Elith et al., 2010), that identifies potential non-analog climatic conditions and therefore regions of higher uncertainty in future projections (Supporting Information Fig. S4). This analysis was performed using the environmental parameters values at the occurrences and carried out on the different projections.

Results

Model performance

Based on our criteria, different sets of environmental parameters were selected for each species (Fig. 3). After a filtering process

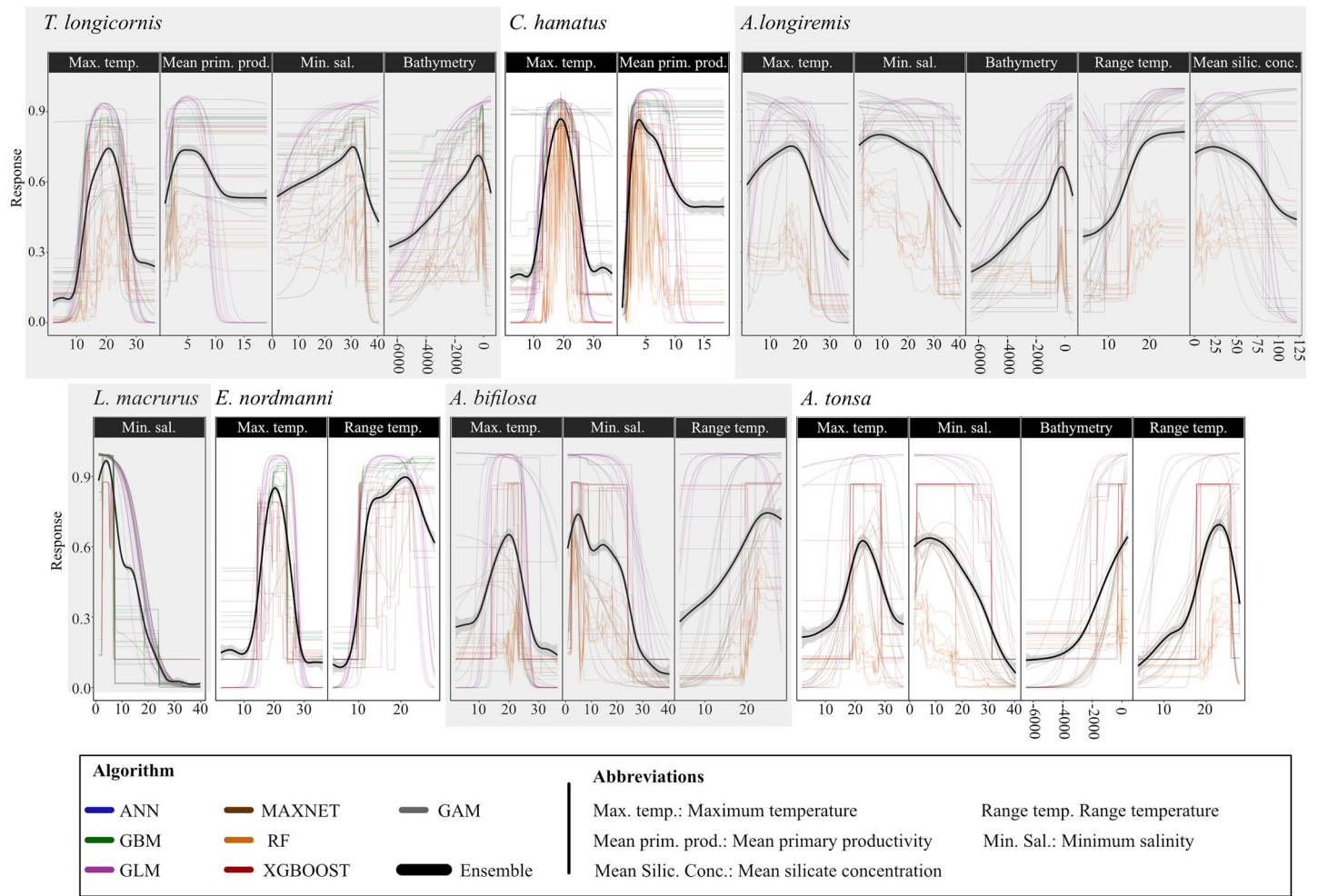


Fig. 3. Responses curve of each species to the environmental parameters used in their ensemble models. The x-axis represents range of values of the parameters in the sampling area and the y-axis indicates the species response in term of habitat suitability, 1 is high suitability and 0 is low suitability. The colored lines represent the different models and the black line is the ensemble model. Each parameter represents either the mean, the maximal or the minimal value for the parameter on the period between 2000 and 2020.

based on the plausibility of the response curve and Boyce index, the ensemble model for *T. longicornis* and *C. hamatus* were based on averaging 45 models, 54 for *L. macrurus*, 28 for *E. nordmanni*, 32 for *A. tonsa*, 40 for *A. bifilosa*, and 37 for *A. longiremis* (Supporting Information Fig. S5). The importance of the environmental variables in predicting habitat suitability for each species varied across models, with salinity and temperature generally having the most influence in the models (Supporting Information Fig. S1).

Determination of suitable environmental parameters

We observed various response patterns to the environment across species (Fig. 3). We found that *T. longicornis* thrived in environments with maximal temperature comprised between 15°C and 25°C and salinities greater than 25. *Centropages hamatus* showed a similar response to water temperature, and both species had high suitability for habitats with a primary productivity between 5 and 10 mmol m⁻³. The habitat suitability of *L. macrurus* was determined by salinity minimum only; the habitat suitability of this species responded negatively to salinity higher than 20. For *E. nordmanni*, suitable habitats comprised maximum temperatures between 15°C and 25°C and a range in temperature between 13°C and 22°C. For *A. bifilosa* and *A. tonsa*, suitable habitats reached a peak at maximal temperature values of 20°C and 23°C, respectively, with an optimal temperature range at 24°C. The two species have the highest suitability for salinity values around 5. Last, *A. longiremis* preferred a maximal temperature of 19°C, brackish water, shallow environments, and a wide range of temperatures.

Projected distribution of suitable conditions

For each species, the models projected a change in the spatial distribution of the suitable environmental conditions in response to future climate scenarios (Fig. 4; Supporting Information Fig. S6). Out of the seven species studied, we found a decrease in environmental suitability for six of them, from 42% ± 8% (mean ± SD) to 98% ± 5% of the pixel showing a decrease in habitat suitability, across time and scenario. The combination of radiative forcing and socioeconomical pathways induced a loss of suitable areas for the marine-originated species *T. longicornis* and *C. hamatus* as well as for the freshwater copepod *L. macrurus* (Fig. 4). Under the SSP245 scenario, *C. hamatus* was projected to experience a decrease in habitat suitability for 95 ± 6% of the pixels by 2050 (Fig. 4a). This proportion increased for the 2090–2100 horizon and its magnitude was greater with the SSP585 scenario, 63% ± 4% of the Baltic Sea presenting more than 30% suitability decrease under the SSP585 projection (Fig. 4b). *Temora longicornis* exhibited a similar trend, both in proportion and magnitude, with a decrease in habitat suitability for periods 2040–2050 to 2090–2100 and from scenario SSP245 to SSP585. For the period 2090–2100, all species except *A. bifilosa* showed a decrease in habitat suitability, a reduction accentuated in the SSP585 scenario.

The reductions in habitat suitability were widespread across the Baltic Sea for *C. hamatus* and *T. longicornis*, with, however, an increase in suitability in the northern part of the Baltic Sea (Fig. 5). *Limnocalanus macrurus* also showed a decrease in habitat suitability, with some areas located close to the North Sea presenting an increased suitability. Notably, *E. nordmanni*, *A. bifilosa*, and *A. longiremis* are the species with a greater increase in habitat suitability in 2050 under scenario SSP245 (respectively 37% ± 8%, 59% ± 6%, and 31% ± 4% of pixels; Fig. 4). These pixels were mostly located on the north-western coast of the Baltic Sea and near the connection to the North Sea. However, this proportion decreased drastically in 2090 with the SSP585 scenario (7% ± 11% for *E. nordmanni*, 3% ± 3% for *A. bifilosa*, and 1% ± 8% for *A. longiremis*). In contrast, the habitat suitability of *A. tonsa* was projected to increase across the Baltic Sea, with few exceptions in coastal areas.

Discussion

Our findings underscore the profound impact of projected shifts on the future temporal and spatial distribution of favorable conditions for the zooplankton community of the Baltic Sea. The projected combination of salinity decrease and temperature increase will reduce the proportion of suitable areas for the zooplankton community, which has limited dispersal capability due to the physical borders of the Baltic Sea. Building on the fact that environmental conditions shape zooplankton communities (Otto et al., 2020), our study highlights the changes in the distribution of suitable habitat for essential components of the food web. By observing the bioclimatic envelopes of these species, our research contributes to a better understanding of the drivers of zooplankton community dynamics in the face of ongoing environmental change, thus providing valuable insights for future ecosystem management and conservation efforts in the Baltic Sea.

Niche characterization

The analysis of habitat suitability revealed the overlap of the favorable conditions of *C. hamatus* and *T. longicornis* (Fig. 3), suggesting that these two species may be competing for resources if they feed on similar prey. However, *C. hamatus* and *T. longicornis* occupy different trophic niches (Serandour et al. 2023), which explains their co-existence and supports the view that copepod species of similar sizes may co-occur through niche partitioning (Novotny et al. 2021). These two species presented higher suitability for salinities above 10, which may be explained by their marine origin, thus, the salinity gradient of the Baltic Sea is restraining their distribution in the central and southern basins (Kchlebovitch, 1974). Moreover, the fitness of the Baltic Sea *T. longicornis* population is lower compared to the North Sea population, as illustrated by their decrease in egg production with decreasing salinity (Holste et al. 2009), which aligns with our model outputs (Fig. 3). In contrast, the limnic species *L. macrurus* showed

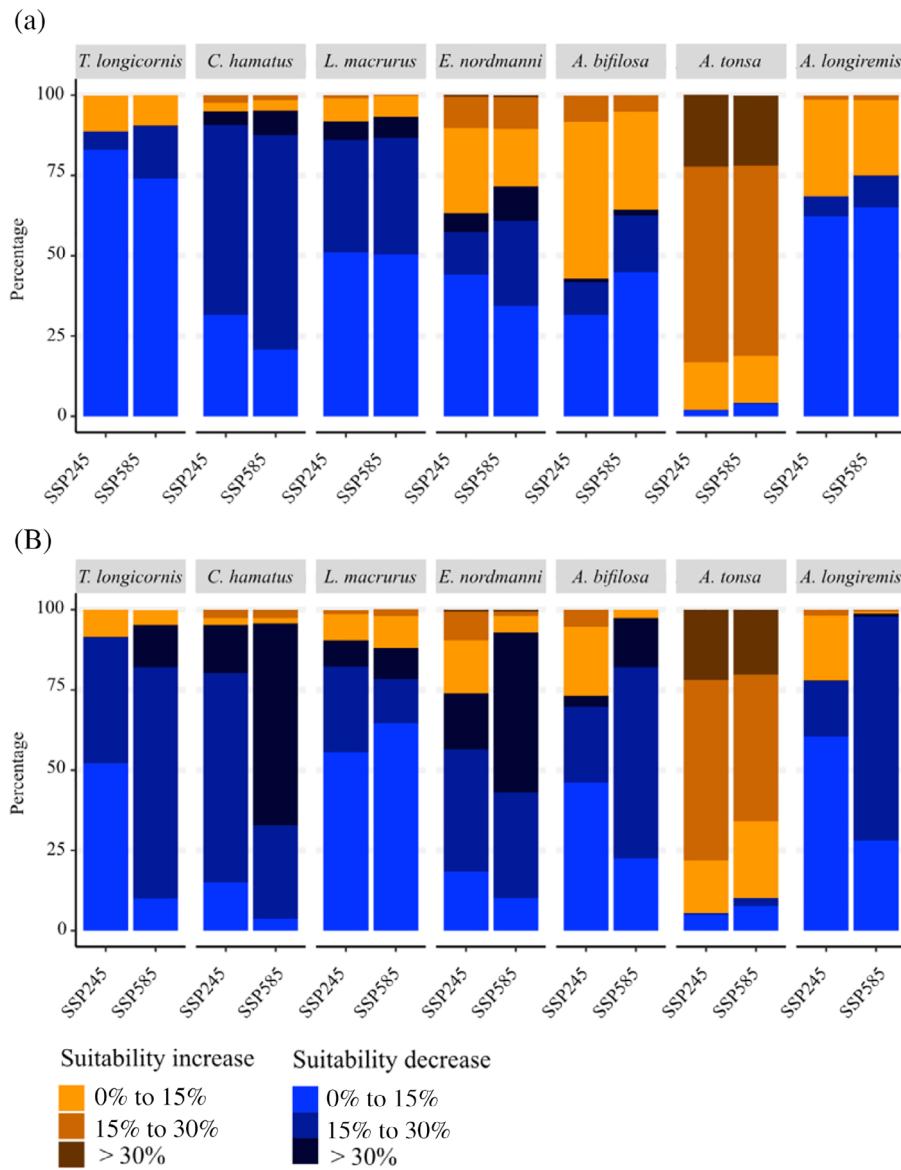


Fig. 4. Difference between future (SSP245 and SSP585) and baseline projections for habitat suitability levels. For each pixel, the value of the baseline scenario has been subtracted from the future scenarios. The percentage of pixel for each category of gain or loss of habitat suitability is shown with colors. An increase in suitability represents a higher suitability level for the future scenario compared to the baseline in the pixel and a suitability decrease represents a lower suitability level compared to the baseline in the pixel. (a) Projections for the 2050 horizon and (b) projections for the period between 2090 and 2100.

greater performance in areas with salinity below 10, explaining its distribution, which is mostly restricted to the northern parts of the Baltic Sea. Our model did not identify salinity as a main driver for *E. nordmanni* occurrence, which is supported by its euryhaline nature (Bryan and Grant 1979), despite the fact that Egloff et al. (1997) considered it as a marine cladoceran confined to higher salinities. Overall, our study confirms that salinity is a strong driver for determining habitat suitability and serves as a major factor for the spatial distribution of Baltic Sea zooplankton (Möllmann et al. 2000).

In addition to changes in salinity, the earth system model projections indicate an increase in temperature until 2100, with an expected average rise up to 4°C in the northern Baltic Sea during the summer months under scenario RCP8.5 (Meier et al. 2022). Temperature is a critical factor for zooplankton due to its influence on metabolic processes (Dzierzbicka-Glowacka et al. 2009a,b; Musialik-Koszarowska et al. 2019). Our niche models suggest a decrease in habitat suitability for temperatures exceeding 20°C for *T. longicornis* and *C. hamatus*. Previous research on *T. longicornis* identified an optimal temperature of

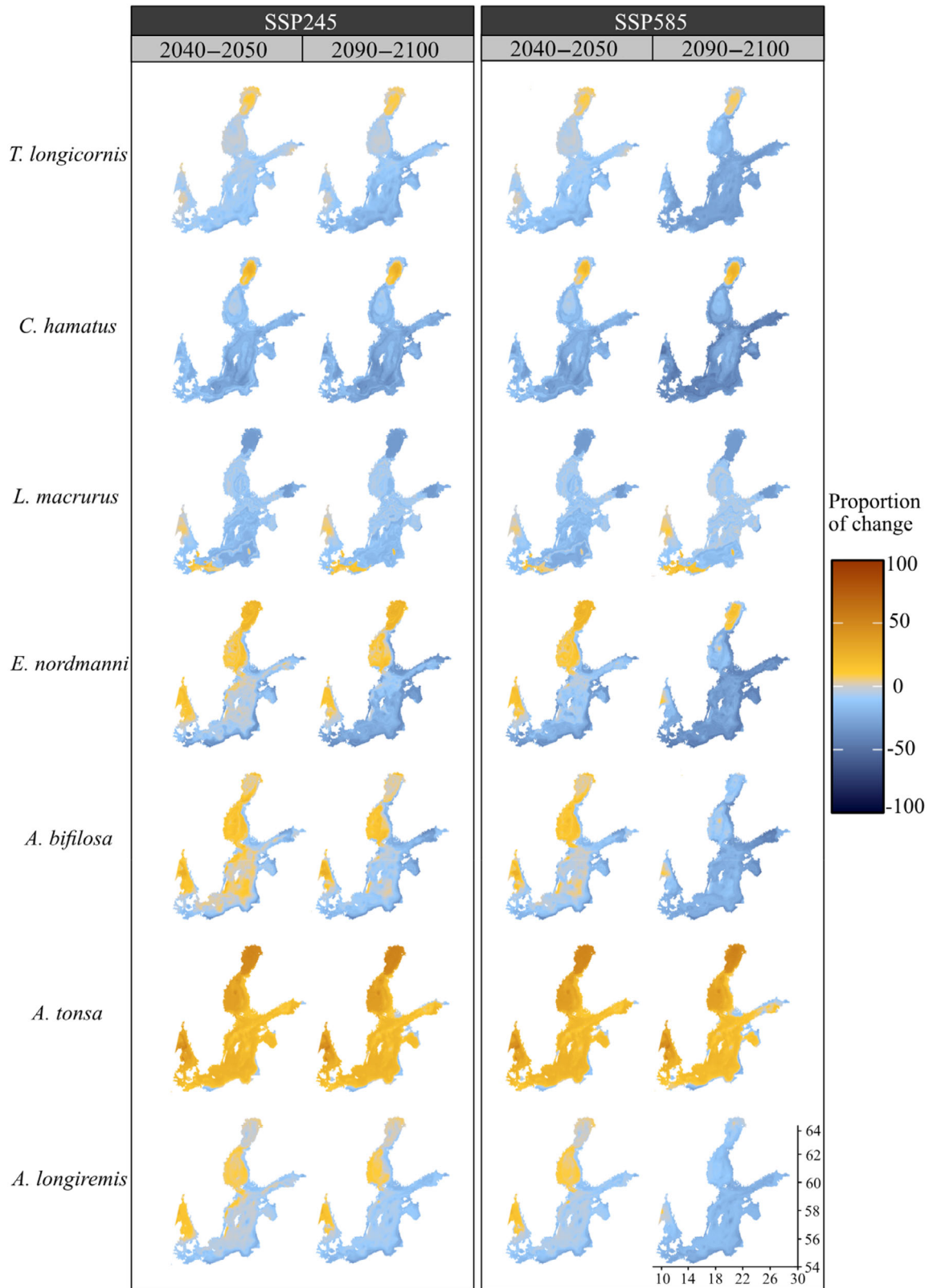


Fig. 5. Relative change between future (SSP245 and SSP585) and baseline projections in habitat suitability levels. For each pixel, the value of the baseline scenario has been subtracted from the future scenario. Negative value indicates a projected decrease in suitability in a given pixel, whereas positive values show a projected increase in the suitability of the conditions within the pixel.

16.6°C for adults, a lethal threshold at 24°C (Holste et al. 2009), and a vertical migration of nauplii from surface water to deeper layers to avoid temperatures warmer than 20°C (Holste et al. 2009). The differences between previously reported and presently modeled thermal optima can be attributed to the drifting nature of zooplankton by water currents (some individuals might have been sampled in water that was beyond their species-specific tolerance limits), the variability in the scale of observation, local adaptation, or intra-species variability. The broad adaptability of *E. nordmanni* across the varying temperature regimes encountered in the Baltic Sea underscores its widespread distribution throughout the study area (Möllmann et al. 2002). Our findings indicate that *E. nordmanni* thrives optimally at 20°C, aligning with its peak phenological period in the Baltic Sea, which typically occurs in early summer (Jan et al., 2024). For *L. macrurus*, a stenothermic species with a preference for temperatures around 11°C or lower (Dahlgren et al. 2012), our models did not identify water temperature as an important factor to explain its distribution. This species dominates the coldest regions of the Baltic Sea (Gulf of Bothnia and Gulf of Finland), despite its important role, the ecological niche of the species remains poorly documented (Einberg et al. 2019). Overall, our model identified temperature as a key parameter for six out of seven species, suggesting that changes in thermal conditions would impact the distribution of these species.

Expected changes in zooplankton distribution

Changes in species distribution with species turnover rates up to 40% are expected in temperate and subpolar planktonic communities (Benedetti et al. 2021), leading to alterations of plankton-mediated ecosystem services. In marine ecosystems, the expansion of species distribution, mostly toward the poles, is occurring faster than its contraction which takes place primarily at the warm margins of their spatial ranges (Poloczanska et al., 2013; Lenoir et al., 2015). However, the enclosed feature of the Baltic Sea hampers the likelihood of expansion for the species and restrains the chance to track suitable habitats. Our results show that most of the species are likely to experience an increase in suitable conditions in the northern part of the Baltic Sea under future scenarios, driven by increasing water temperature. Yet, this improvement may be countered by the projected decrease in salinity levels which would prevent the northern expansion of marine-originated species such as *T. longicornis* and *C. hamatus*. However, new species might fill the ecological niche previously occupied as environmental conditions would exceed tolerance capacity of these two species. Indeed, some euryhaline species can cope with temperatures higher than 20°C, such as the neritic species *A. tonsa*. Additionally, *A. tonsa* demonstrates a remarkable adaptive feeding strategy, alternating between suspension feeding and ambush feeding, in response to variations in the prey community (Kiørboe et al., 1996). This behavioral plasticity may indicate the species' capability to facilitate energy transfer across different

trophic levels in future conditions, in alignment with the seasonal fluctuations of the prey community in the Baltic Sea.

The shrinkage of suitable habitats may cause a substantial reduction in the distribution of key zooplankton species, that could lead to mismatches in the ecosystem and potentially facilitate the establishment of non-indigenous species. Many species in the Baltic Sea already experience osmotic stress and exhibit low intraspecific genetic diversity (Ojaveer, 2017). Additionally, the Baltic Sea hosts low biodiversity due to its ecologically marginal situation that results in limited functional redundancy, and makes it more vulnerable to changes in both biotic and abiotic conditions (Johannesson and André 2006). Among the seven zooplankton species targeted in this study, various functional traits have been identified, particularly related to feeding strategies (Serandour et al., 2023). These functional traits are crucial for elucidating species–environment interactions and understanding species roles in ecosystem functioning and resilience, as functional redundancy can act as a buffer against disturbances (Biggs et al., 2020). Previous studies have highlighted the diversity in physiological and behavioral traits in feeding strategies, further underscoring the importance of functional diversity in maintaining ecosystem stability (Novotny et al., 2021). The observed reduced overlap in primary producer consumption across mesozooplankton species induce inconsistency in terms of roles within the ecosystem, reducing its resistance ability (Biggs et al., 2020). Migration driven by environmental changes could create opportunities for non-native species to occupy newly available niches as indigenous species could be displaced. Nevertheless, it is unlikely that changing conditions in the Baltic Sea will facilitate the migration of non-indigenous marine species from the nearby North Sea and occupation of the ecological niche of native species. This is because the strong salinity gradient of the Baltic Sea will likely be strengthened in future conditions due to an increase in freshwater runoff (Vuorinen et al., 2015; Meier et al., 2022). Furthermore, species occupying similar habitats can have variable ecological tolerances, leading to heterogeneous changes in distribution as a response to variations in abiotic parameters. As a result, spatial disparities may exist between trophically connected species. Due to the central role of mesozooplankton in the pelagic food web (Steinberg and Landry, 2017), this could yield significant ecological and economic ramifications. Specifically, it could disrupt trophic interactions, leading to cascading effects on species abundance, biodiversity, and ultimately, ecosystem stability. Therefore, the reduction of anthropogenic pressures on the Baltic Sea is essential to maintain food web productivity. If climate change cannot be controlled at a local scale, other pressures should be reduced, as species in good conditions are more likely to be able to adapt to climate change.

Model limitations

We identified four main sources of uncertainty in this study. First, variability and uncertainty across the biogeochemical models, particularly regarding salinity projections,

have been reported, with average salinity changes ranging from -45% to $+4\%$ (Meier et al. 2006). Indeed, it is important to note that sea level rise could counteract the expected salinity decrease of the Baltic Sea due to a greater inflow from the North Sea. If most of the models are projecting a salinity decrease in the Baltic Sea, recent climate assessments (e.g., Meier et al. 2022) are uncertain whether salinities will increase, decrease, or remain reasonably constant in the future. Thus, since salinity plays an important role in shaping the distributions of the Baltic Sea species, this inconsistency could increase the uncertainty in our results. Second, spatial distribution modeling relies on niche conservatism, assuming that species are not adapting to their environment, despite the fact that some mesozooplankton species are able to adapt to higher temperatures (Karlsson and Winder 2020). This suggests that the species examined in our study could exhibit adaptations and mitigate the outcomes predicted here by reducing habitat suitability losses. However, the potential adaptation remains a debated field and evidence of widespread adaptation across the different zooplankton species and population are missing (Strack et al., 2022). Third, there is inherent uncertainty in the SDM modeling procedure. We limited this uncertainty with the use of spatial-block cross validation (Valavi et al. 2019). The divergence in the magnitude of the different model outcomes (Supporting Information Fig. S7) illustrates this uncertainty but most of the models, except for *A. tonsa*, agreed in the direction of the change for each species. Therefore, our results provide a reliable estimate that the mesozooplankton communities of the Baltic Sea will experience changes in their suitable habitat which will impact their distributions. Fourth, we did not include biotic variables in the models, which could play a major role in the determination of suitable habitat distribution. We think that the addition of co-occurrences could broaden the distribution through mutualistic interactions or narrower due to competition and predation. If the use of primary productivity in this study marks a step toward incorporating biotic interactions on a large scale, the variability in trophic interactions within zooplankton, which prey on both primary producers and heterotrophic organisms, indicates that further research is needed to better understand this concept.

Conclusion

Our study illustrates the major impact of projected changes under future climate scenarios on the distribution of zooplankton species in the Baltic Sea. We found a potential reduction in suitable habitat conditions for several key zooplankton species that support fish populations. Our results raise concerns about the future composition of the planktonic community and the productivity of the Baltic Sea food web. Moreover, our study underscores the influence of temperature and salinity as drivers of zooplankton distribution. We further emphasize the need to mitigate anthropogenic impacts on the Baltic Sea ecosystem to

safeguard its ecological integrity, as scenario with the most severe climate change pressures predicts the most significant changes in species distributions.

Data availability statement

Both environmental data and occurrence data used in this study can be found at <https://zenodo.org/records/10951348>.

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Conflict of interest statement

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