

# Pan-Arctic distribution modeling reveals climate-change-driven poleward shifts of major gelatinous zooplankton species

Dmitrii Pantiukhin <sup>1,2\*</sup> Gerlien Verhaegen <sup>1,3</sup> Charlotte Havermans <sup>1,2</sup>

<sup>1</sup>HYIG ARJEL, Benthic Ecology, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research (AWI), Bremerhaven, Germany

<sup>2</sup>BreMarE—Bremen Marine Ecology, FB2, University of Bremen, Bremen, Germany

<sup>3</sup>AG Vogelwarte, Zoological Institute and Museum, University of Greifswald, Greifswald, Germany

## Abstract

Anthropogenic activities, including climate change, are hypothesized to cause increases in gelatinous zooplankton population sizes and blooms. In the most rapidly changing ecosystem, the Arctic Ocean, this hypothesis has not yet been verified, and gelatinous zooplankton is commonly excluded from large-scale modeling studies. Our modeling study is based on an extensive biogeographic dataset, aggregating from four open-source databases (Ocean Biodiversity Information System, Global Biodiversity Information Facility, Jellyfish Database Initiative, and PANGAEA). It includes data on eight of the most reported gelatinous zooplankton taxa of the pan-Arctic region (*Aglantha digitale*, *Sminthea arctica*, *Periphylla periphylla*, *Cyanea capillata*, *Oikopleura vanhoeffeni*, *Fritillaria borealis*, *Mertensia ovum*, and *Beroe* spp.). By coupling three-dimensional species distribution models with oceanographic components from the Max Planck Institute Earth System Model (MPI-ESM1.2), run for historical (1950–2014) and future (2050–2099) periods under the shared socioeconomic pathway SSP370 scenario forcing, we identified species with expanding or contracting habitat ranges in response to climate change. Our projections indicated a general tendency for gelatinous zooplankton distributions to shift, with varying degrees of suitable habitat expansion (largest for the scyphozoan *C. capillata* ~ +180%) or contraction (largest for the hydrozoan *Sm. arctica* ~ –15%). Seven of the eight species modeled, which—similar to the majority of gelatinous taxa occurring in the Arctic Ocean—predominantly represented arcto-boreal and boreal taxa, are projected to shift to northern latitudes. Hence, profound impacts on the Arctic marine environment and associated ecosystem services can be expected.

Jellyfish (cnidarian medusae and ctenophores) and other gelatinous zooplankton (e.g., siphonophores, pelagic tunicates) are generally predicted to benefit from climate change, based on increased numbers or biomass of temperate jellyfish within various seas and coastal regions across the globe (Brotz et al. 2012). Other anthropogenic impacts, such as eutrophication and overfishing, also favor gelatinous zooplankton (Richardson et al. 2009). The combined impact of all these factors might induce “regime shifts” from highly productive,

fish-dominated to jellyfish-dominated, less productive pelagic food webs (Richardson et al. 2009). While there is increasing evidence of a rise in jellyfish abundance in some marine ecosystems, it is not yet clear whether this is a global trend or linked to short-term, oceanography-driven, fluctuations in their abundance (Condon et al. 2013).

This perception of an ocean “jellification” is based on a growing number of records of negative impacts of jellyfish aggregations on human enterprises, including fisheries (e.g., net clogging, gear damage, reduced catch), tourism (stinging jellyfish), and clogging of water-intakes of power production systems (Condon et al. 2013). Gelatinous zooplankton taxa span different trophic levels, from grazers on microplankton (pelagic tunicates) to predators on zooplankton and ichthyoplankton (Júnior et al. 2022). By competing with adult fish for zooplankton prey, and by preying on fish larvae and eggs, jellyfish may outcompete fish in stressful environments or prevent fish stock recovery after overfishing (e.g., Irish Sea, Lynam et al. 2011). Conversely, studies have highlighted the role of increasing gelatinous zooplankton

\*Correspondence: [dmitrii.pantiu@gmail.com](mailto:dmitrii.pantiu@gmail.com)

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

This is an open access article under the terms of the [Creative Commons Attribution](#) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

**Author Contribution Statement:** C.H., D.P.: Conceptualization. D.P., G.V., C.H.: Methodology. D.P., G.V., C.H.: Investigation. D.P.: Visualization. C.H.: Supervision. D.P.: writing—original draft; C.H., G.V., D.P.: writing—review and editing.

blooms for enhancing vertical carbon export, which is well documented for salps (Steinberg et al. 2023) and appendicularians (Jaspers et al. 2023), but also for large jellyfish (Lebrato et al. 2013). Moreover, whereas gelatinous zooplankton have long been considered a dead end of the food chain, an increasing number of studies revealed that these organisms are an important food source for many fish, crustaceans, and other organisms (Hays et al. 2018).

Over recent decades, the Arctic Ocean has experienced more significant changes than any other ocean, including warming of ocean temperatures by four times the global average (Rantanen et al. 2022), increased stratification, altered currents and circulation patterns, as well as a rapid sea ice retreat (Gulev et al. 2021). These alterations cause poleward range shifts of different organisms, from phytoplankton to higher trophic levels, resulting in the restructuring of entire Arctic food webs (Frainer et al. 2017). Most of the studies on range shifts of boreal taxa into the Arctic Ocean have focused on hard-bodied crustacean zooplankton (Edwards et al. 2021; Freer et al. 2021) and fish (Frainer et al. 2017; Dahlke et al. 2018). Studies on the distribution and abundance of gelatinous zooplankton in the Arctic Ocean have mostly been limited to local assessments (Raskoff et al. 2010; Mańko et al. 2022; Pantiukhin et al. 2023). To date, a comprehensive assessment of gelatinous zooplankton communities on the pan-Arctic scale has not been carried out.

One of the most suitable approaches to better understand the ecology of marine organisms and project their spatiotemporal distribution is species distribution modeling, also synonymized as ecological niche modeling (Robinson et al. 2017). Until recently, the majority of marine species distribution modeling case studies were applied in two dimensions (i.e., longitude–latitude), neglecting the third dimension of water depth, and relying on environmental parameters derived from the sea surface layers (Duffy and Chown 2017). The distribution of gelatinous zooplankton communities is, however, highly dependent on water depth (Mańko et al. 2020; Pantiukhin et al. 2023). Moreover, two-dimensional species distribution models average environmental variables over depth layers, resulting in biased results (Duffy and Chown 2017), particularly when studying midwater taxa. Recently, more marine species distribution modeling studies are carried out in three dimensions (i.e., longitude–latitude–depth), including case studies of widespread epipelagic or midwater (e.g., Bentlage et al. 2013; Verhaegen et al. 2023) jellyfish outside the Arctic Ocean. Despite the wide application of such studies worldwide, only 3% of species distribution modeling studies were devoted to the Arctic Ocean and none of these focused on the distribution of gelatinous zooplankton (Robinson et al. 2017).

In this study, we applied species distribution modeling across three dimensions for gelatinous zooplankton species on a pan-Arctic scale to reveal the drivers of their distributions

and shifts in their suitable habitats under future climate change scenarios. We hypothesized that global change is altering pan-Arctic gelatinous zooplankton communities and their suitable habitats, and that boreal-Atlantic species, which are advected into the Arctic Ocean, will become more abundant with warming and sea ice retreat. We selected two key species from each taxonomic group: hydrozoans, scyphozoans, ctenophores, and appendicularians, representing a range from micrograzers to major predators in temperate or Arctic ecosystems. These species are key players in local food webs as major predators (scyphozoans, ctenophores), can reach high abundances and serve as major prey for fish (hydrozoans), and are known to play a major role in carbon export (appendicularians). For the most reported species of each of these groups, we aimed to: (1) identify the environmental factors determining the community structure and distribution of gelatinous zooplankton within the pan-Arctic; (2) describe the geographical and vertical distribution of these communities; (3) project future changes in gelatinous zooplankton communities in the Arctic Ocean using climate change scenarios.

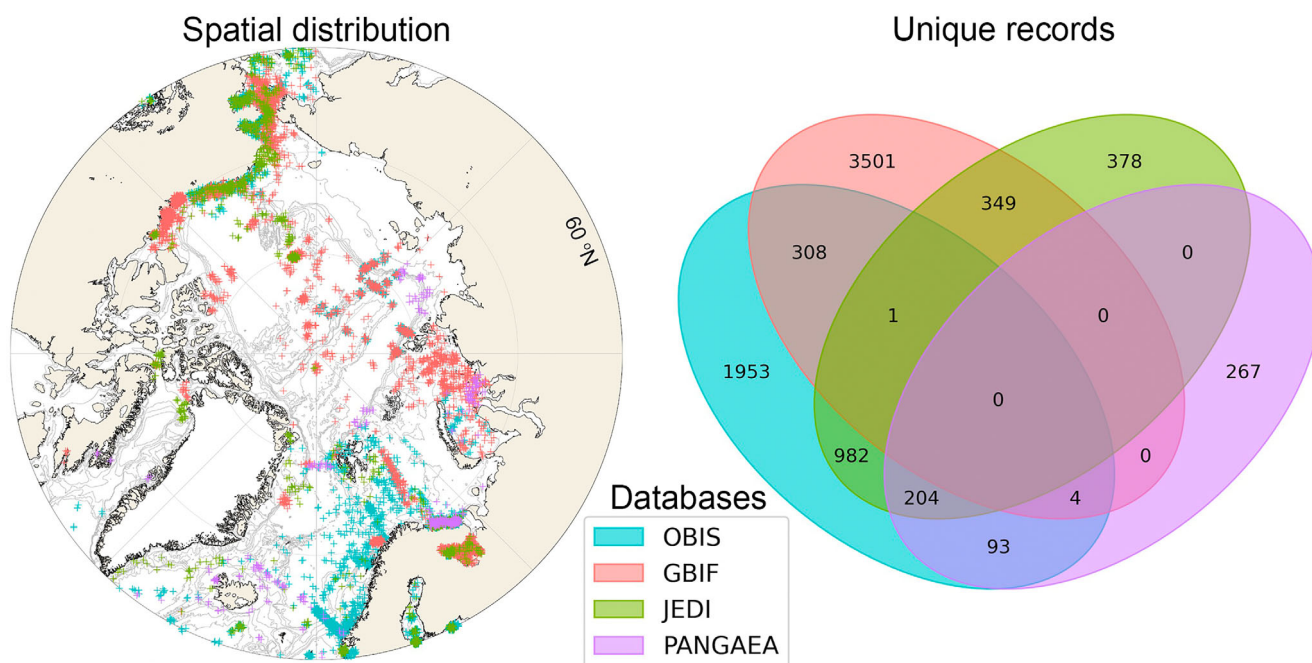
## Materials and methods

### Study area

We chose the pan-Arctic scale, including all marine zones with latitudes  $> 60^{\circ}\text{N}$ , as the study area (Fig. 1). This was done to include gelatinous zooplankton species that could be considered as boreal species commonly occurring in the Arctic Ocean, or species that may expand their distribution poleward from the boreal realm. It also allowed us to examine the mixing zones of the Arctic Ocean with temperate Pacific and Atlantic waters. The oceanographic features of the Arctic Ocean are largely determined by the presence of sea ice, pronounced water stratification, freshening of coastal areas by continental river runoff, and the influence of warm water inflow from the Atlantic and Pacific oceans.

### Biogeographic data

We obtained biogeographic data from four databases: Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), Jellyfish Database Initiative (JeDI), and PANGAEA (Data Publisher for Earth & Environmental Science) (Fig. 1). OBIS and GBIF are global repositories of biogeographic data (<https://obis.org/>, <https://www.gbif.org/>), JeDI is a database focused exclusively on gelatinous zooplankton (Lucas et al. 2014), and PANGAEA (<https://www.pangaea.de>) is a data publishing platform-aggregator for earth and environmental sciences (Supporting Information Table S1). Of the total biogeographic data collected, GBIF contributed 43.54% unique occurrences, OBIS 24.29%, JeDI 4.70%, and PANGAEA 3.32%, with the remaining 24.14% consisting of records shared between these databases (Figs. 1, 2). We retrieved data from OBIS, GBIF, and JeDI by sending direct queries to the databases,



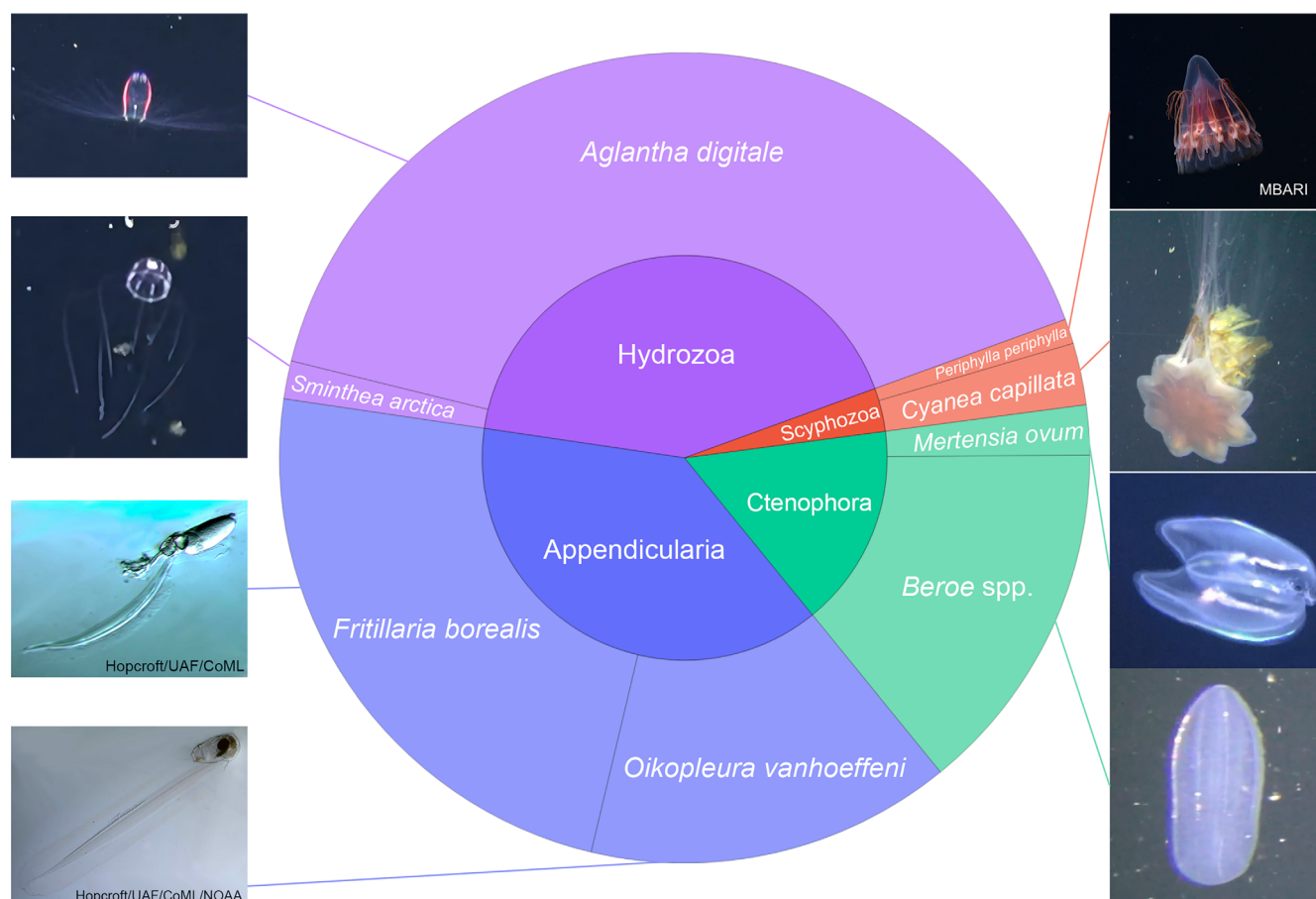
**Fig. 1.** Pan-Arctic distribution of gelatinous zooplankton. Spatial distribution of gelatinous zooplankton based on occurrence data collected between 1950 and 2014. Spatial distribution map and Venn diagram of unique records of eight dominant gelatinous zooplankton species in the Pan-Arctic region. Data sources include GBIF, JEDI, OBIS, and PANGAEA.

and compiled a dataset from individual publications from PANGAEA (Supporting Information Table S1). Furthermore, we selected data for the period 1950–2014 to match the temporal distribution of the environmental data (Supporting Information Fig. S1). The vertical resolution has been set to cover depths from 0 to 3000 m, matching the habitats of the selected taxa. Due to differing quality control mechanisms in the studied databases (Moudrý and Devillers 2020), we rounded spatial longitude and latitude values to one decimal place and depth values to integers. We filtered biogeographic data to remove unreliable coordinates (on land), incorrect depth values, and repeated values. In addition, to avoid spatial autocorrelation during the Maxent model runs, occurrence data within the same spatial cell of the predictive grid ( $50 \times 50$  km) were “thinned” by combining multiple occurrences into a single representative point. We included a total of eight gelatinous zooplankton taxa in the analysis (Supporting Information Figs. S2, S3). These included two species of the class Hydrozoa (*Aglantha digitale* and *Sminthea arctica*), two species of the class Appendicularia (*Oikopleura vanhoeffeni* and *Fritillaria borealis*), two species of the class Scyphozoa (*Cyanea capillata* and *Periphylla periphylla*) and two species of the phylum Ctenophora (*Mertensia ovum* and *Beroe* spp.). We selected these representatives of the different gelatinous zooplankton groups because they (1) span different trophic levels from microplankton grazers to zoo- and ichthyoplankton predators, (2) include species displaying different lifestyles (e.g., holoplanktonic, meroplanktonic),

(3) showed the highest records in most databases (Fig. 2), and (4) are easily identifiable, reducing identification errors. The *Beroe* species were grouped together as *Beroe* spp. due to ongoing taxonomic revisions and controversies in species identification (Shiganova and Abyzova 2022).

### Environmental data

We obtained environmental data from the Max Planck Institute Earth System Model (MPI-ESM1.2, Gutzjahr et al. 2019; Supporting Information Fig. S4; description of the environmental conditions summarized in Supporting Information Text S1), which provided data on historical (Jungclaus et al. 2019), and future projections (Schupfner et al. 2019) of various environmental variables including temperature ( $^{\circ}\text{C}$ ), salinity Practical Salinity Units (PSU), sea ice area coverage (%), dissolved oxygen concentration ( $\text{mol m}^{-3}$ ), and phytoplankton carbon concentration at the ocean surface ( $\text{mol m}^{-3}$ ). We used data from the historical runs (1950–2014) to train the models, while data from two ssp370 emission scenarios were used to generate future projections (O'Neill et al. 2014). The scenarios ssp370 represent shared socioeconomic pathways (SSPs) that describe plausible future trajectories of global societal development, with ssp370 assuming medium-high emission trajectory. To model the distribution of marine species in three-dimensional space, we used a methodology similar to Bentlage et al. (2013). We divided the data into eight depth intervals, based on the most pronounced changes identified for the temperature-salinity gradients, and



**Fig. 2.** Gelatinous zooplankton species proportions. The pie chart shows the relative proportion of occurrence for eight species of gelatinous zooplankton included in the study.

unfolded them into a long predictive raster (Supporting Information Fig. S4). Average depths were taken at 26.5, 103.5, 246.25, 461.25, 865, 1460, 2087, and 2797.50 m (Supporting Information Fig. S4). These depths were averaged over the most distinct sections of the water masses (Supporting Information Fig. S5). We chose these depth thresholds to cover the full range of depths of occurrence of the species studied. This aggregation was also done in order to minimize the bias associated with averaging the depth values in the databases (obtained from the maximum and minimum sampling depths). Furthermore, we checked predictive rasters for multicollinearity. Because of its strong correlation with temperature, we removed oxygen to minimize multicollinearity, thus achieving variance inflation factor values lower than five.

### Maxent model

We used a maximum entropy model (Maxent) to analyze the spatial distribution of the eight selected gelatinous zooplankton taxa. Maxent is a maximum likelihood estimation model that predicts the distribution of species based on the suitability of their habitats (Phillips et al. 2017). We choose the Maxent model because of its high predictive power for

presence-only data (Valavi et al. 2022). We used the R package *ENMeval* v.2.0.4 for fine-tuning and model selection (Muscarella et al. 2014; Kass et al. 2021). We adjusted various parameters during the model parameterization process, such as: (1) the regularization multiplier (RM: 1, 1.5, 2, 2.5, 3, 3.5, and 4), which controls the complexity of the responses in the model; (2) a different combination of the feature classes, including linear (*L*), quadratic (*Q*), product (*P*), threshold (*T*), and hinge (*H*); and (3) the number of background points (10,000, 20,000, and 30,000). Background points were selected to adequately capture distribution of the environmental parameters (Supporting Information Fig. S6). We evaluated the performance of the models by partitioning the occurrence locations into validation and training bins (fourfold cross-validation). We used spatial cross-validation using a pre-built function in the *ENMeval* package—"checkerboard2" (Radosavljevic and Anderson 2014). This method is preferable over random partitioning because it reduces spatial autocorrelation (Roberts et al. 2017). We selected the optimal models based on the following cross-validation evaluation metrics (Supporting Information Fig. S6): (1) average test omission rate (10<sup>th</sup> percentile; OR10p; Kass et al. 2023), (2) continuous Boyce Index (CBI; Di



Cola et al. 2017), (3) area under the receiver operating characteristic curve (AUC; de Hond et al. 2022), and (4) Akaike information criterion (AIC; Cavanaugh and Neath 2019). We preferred metrics that assessed how well the model predicted “presence” points (OR10p, CBI), and after “presence-absence” (AUC). This is because our data did not contain true absences, but instead relied on randomly selected background points. Models with AUC and CBI values below 0.7 and 0.5, respectively, were not considered for further study because of their poor fit (de Hond et al. 2022). We also preferred models with low AIC values to reduce the risk of overfitting. This was also important in the context of our study because we made projections over time (Merow et al. 2014).

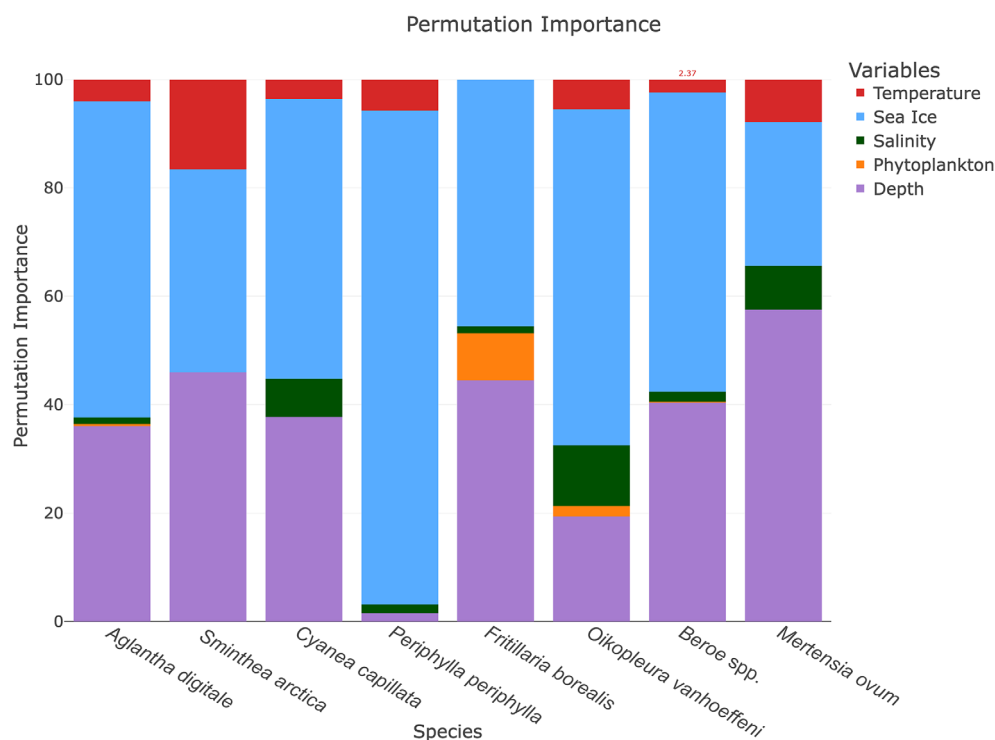
The relative importance of environmental parameters was determined by using the permutation importance metric instead of percent contribution, due to its demonstrated higher accuracy (Searcy and Shaffer 2016) (Fig. 3). We used complementary log–log (cloglog) predictions to construct probability maps for historical time periods (1950–2014), as well as future scenarios (2050–2099). Cloglog was used over the logistic transformation for its stronger theoretical justification (Phillips et al. 2017). Projected grids were interpolated onto an Arctic Polar Stereographic projection (EPSG:3995). For visualization purposes, all depth layers were also averaged across latitudes for the western and eastern hemispheres (Fig. 4). We also produced environmental limiting factor maps that showed the least favorable variables on the spatial scale (Fig. 5). These limiting factors were determined using the

‘limiting’ function from the *rmaxent* package (Baumgartner and Wilson 2023), following the methodology of Elith et al. 2010. This function identifies the limiting factors at a site by calculating the reduction in suitability when each predictor is modified to its mean value across occurrence sites. The factors associated with the greatest reduction in suitability is treated as the most limiting factor at that site.

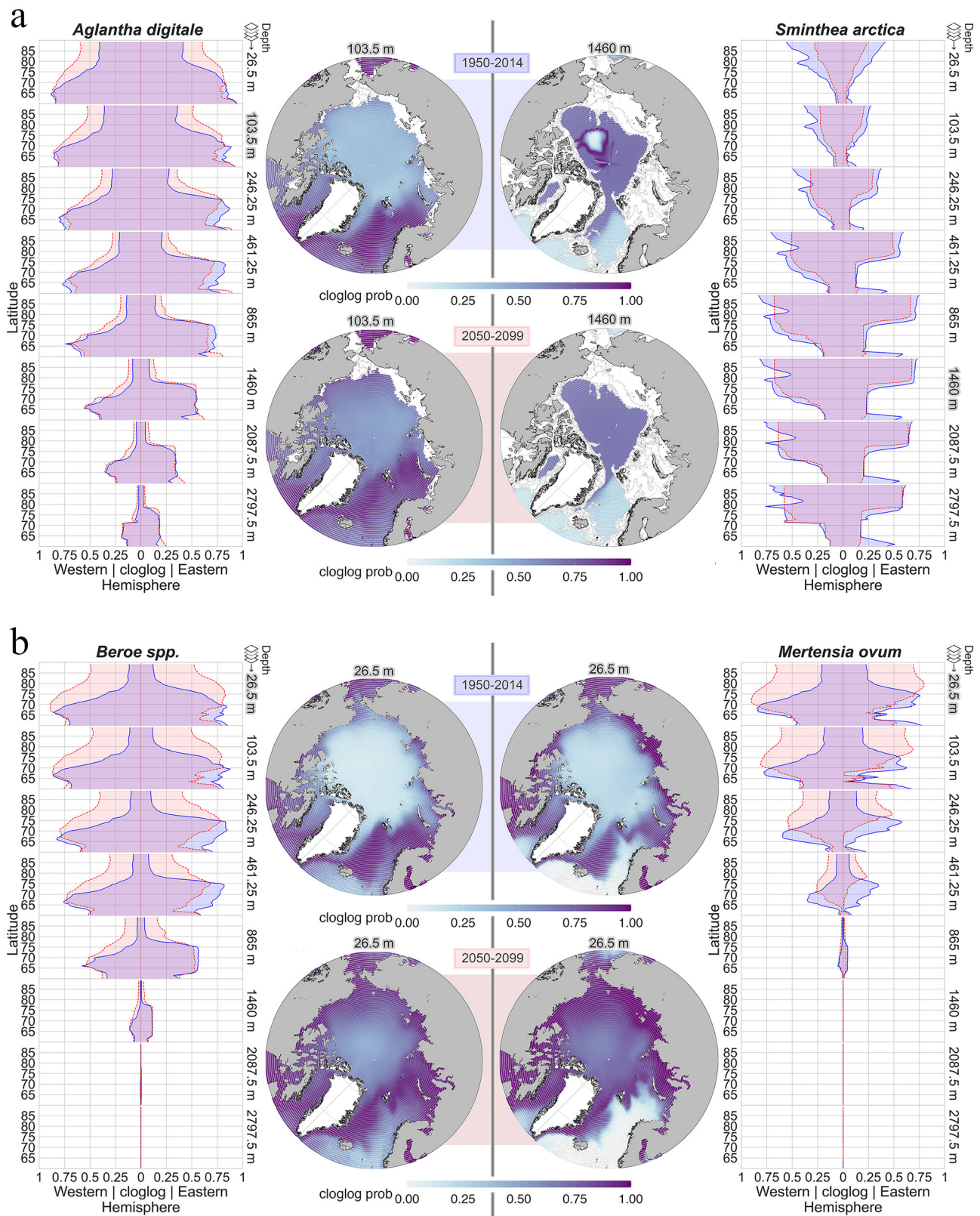
## Results

### Biogeographic data collection

For the eight selected gelatinous zooplankton taxa, we collected 24,160 occurrence points with available metadata on longitude, latitude, and depth from four databases: GBIF, OBIS, JeDI, and PANGAEA (Figs. 1, 2). We observed five temporal peaks of gelatinous zooplankton counts per year over the whole study period: a first 1953–1955 peak, with the highest count of 568 in 1955, 1967 (330 counts), 1976 (568 counts), 1987 (492 counts), and 1995 (484 counts) (Supporting Information Fig. S1; Text S2). Since the 2000s, the gelatinous zooplankton presence data have been more consistently sampled without large fluctuations. While some taxa, such as *A. digitale* and *F. borealis*, showed a rather stable sampling effort throughout our study period, records of other taxa were characterized by more sporadic sampling patterns, such as *Sm. arctica*, *O. vanhoeffeni*, as well as both ctenophore and scyphozoan species.



**Fig. 3.** Permutational importance of the environmental variables for the studied gelatinous zooplankton taxa, based on the best Maxent models.



**Fig. 4.** Projected spatial distribution of gelatinous zooplankton species. Horizontal maps showing the spatial distribution of eight marine gelatinous zooplankton species for the periods 1950–2014 (blue) and 2050–2099 (red) at the most probable depth layers (highlighted in gray). Adjacent to these maps are plots showing the cross-latitude vertical distribution of species at different depth layers.



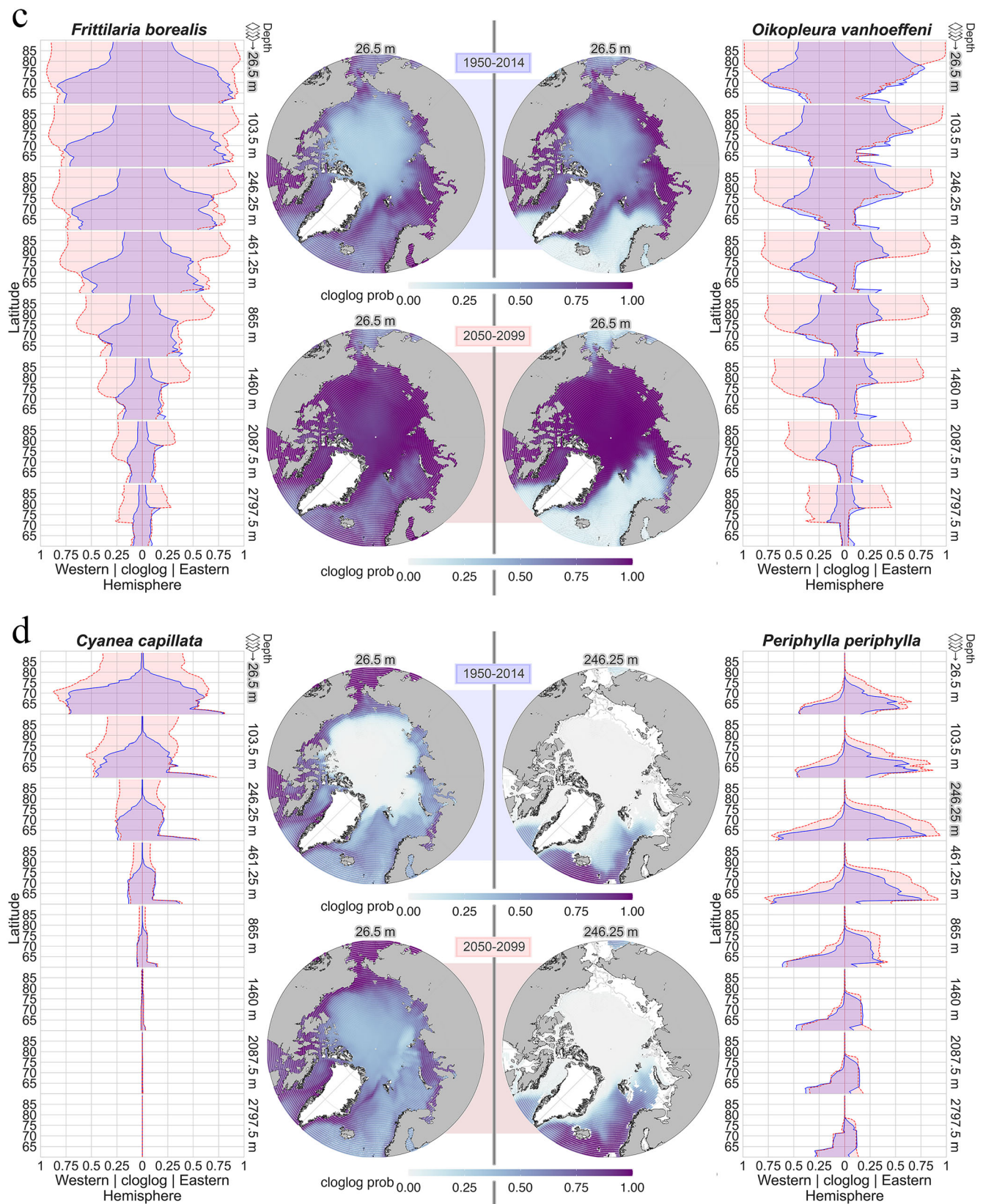
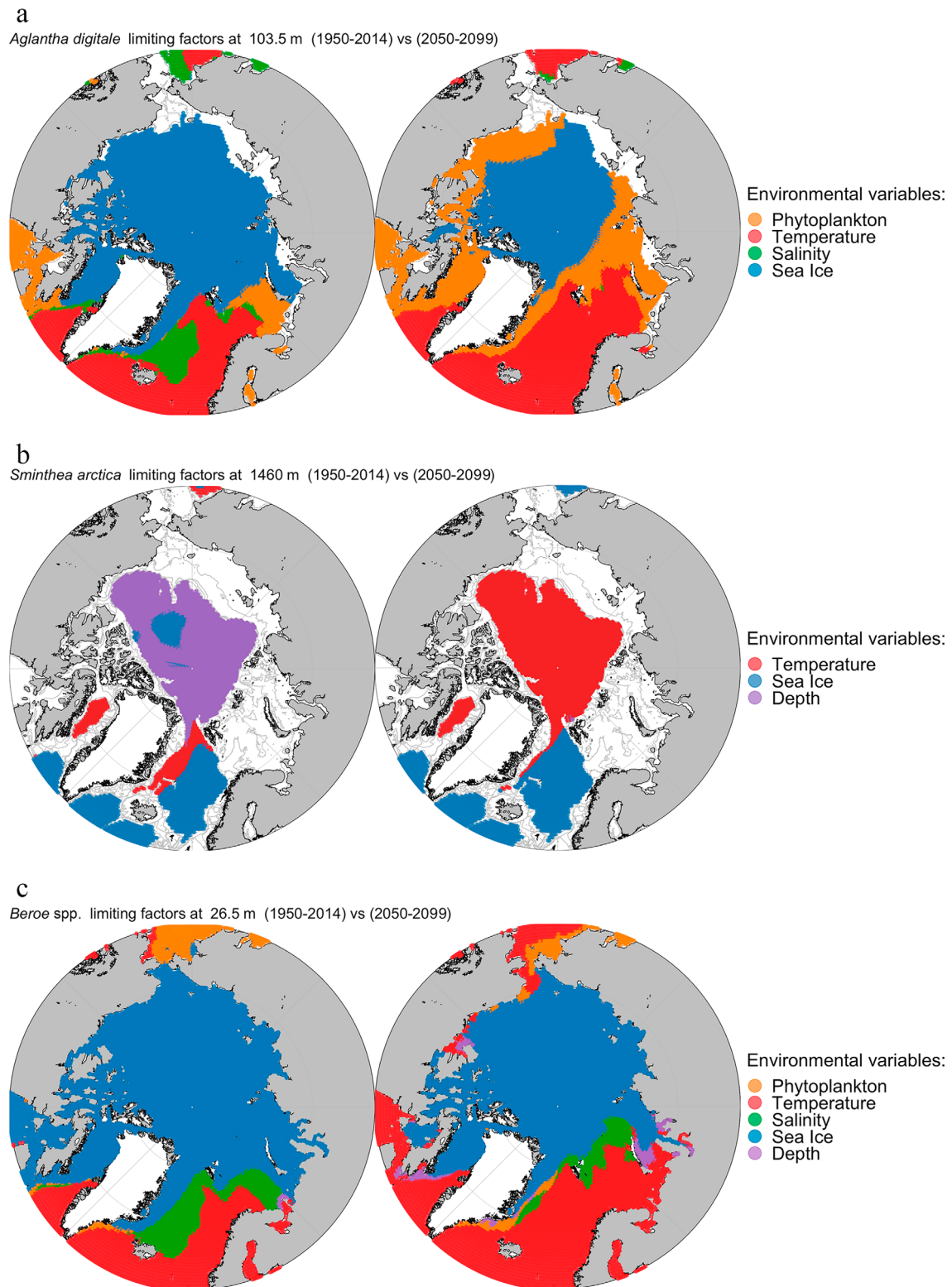
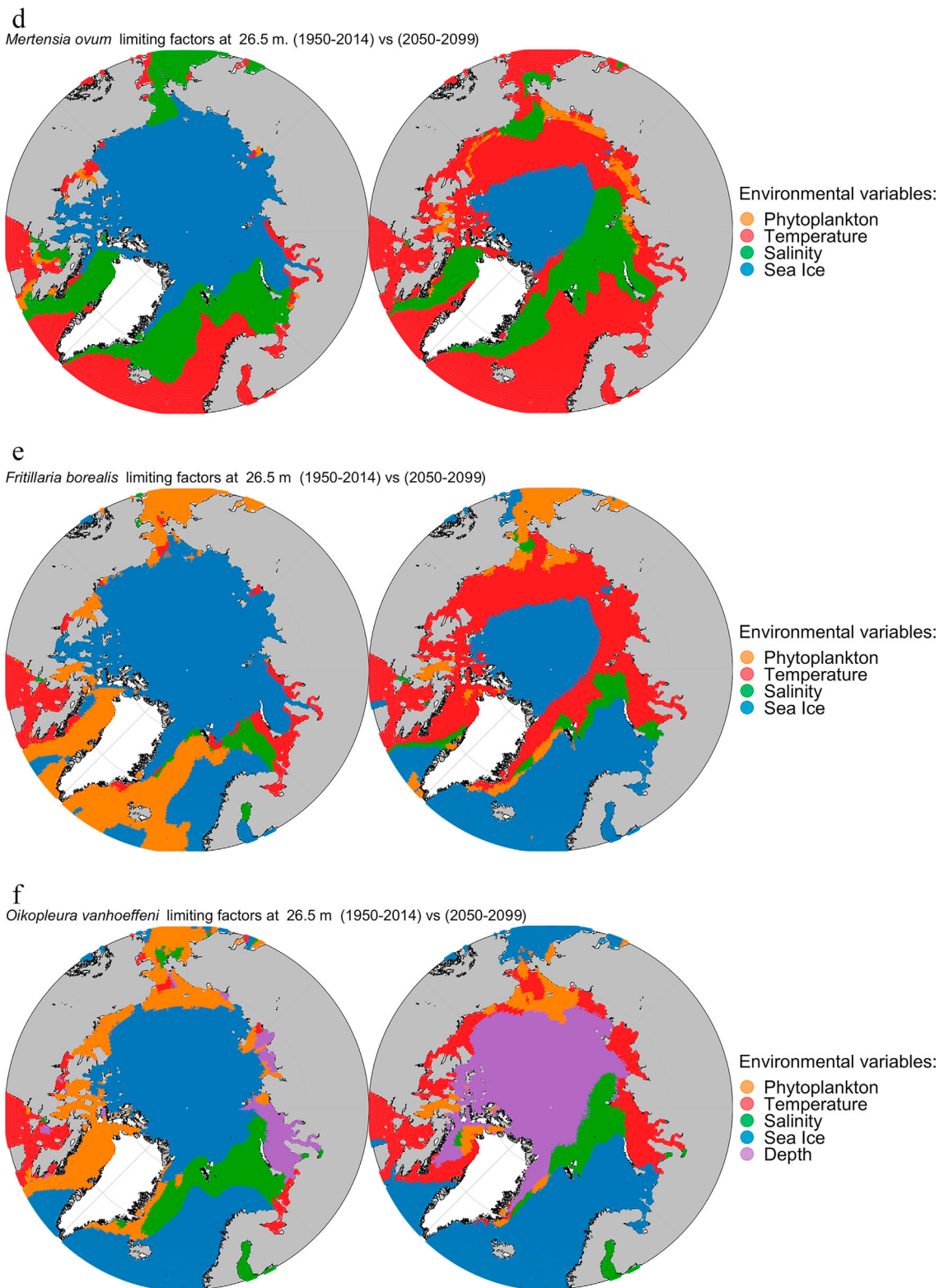


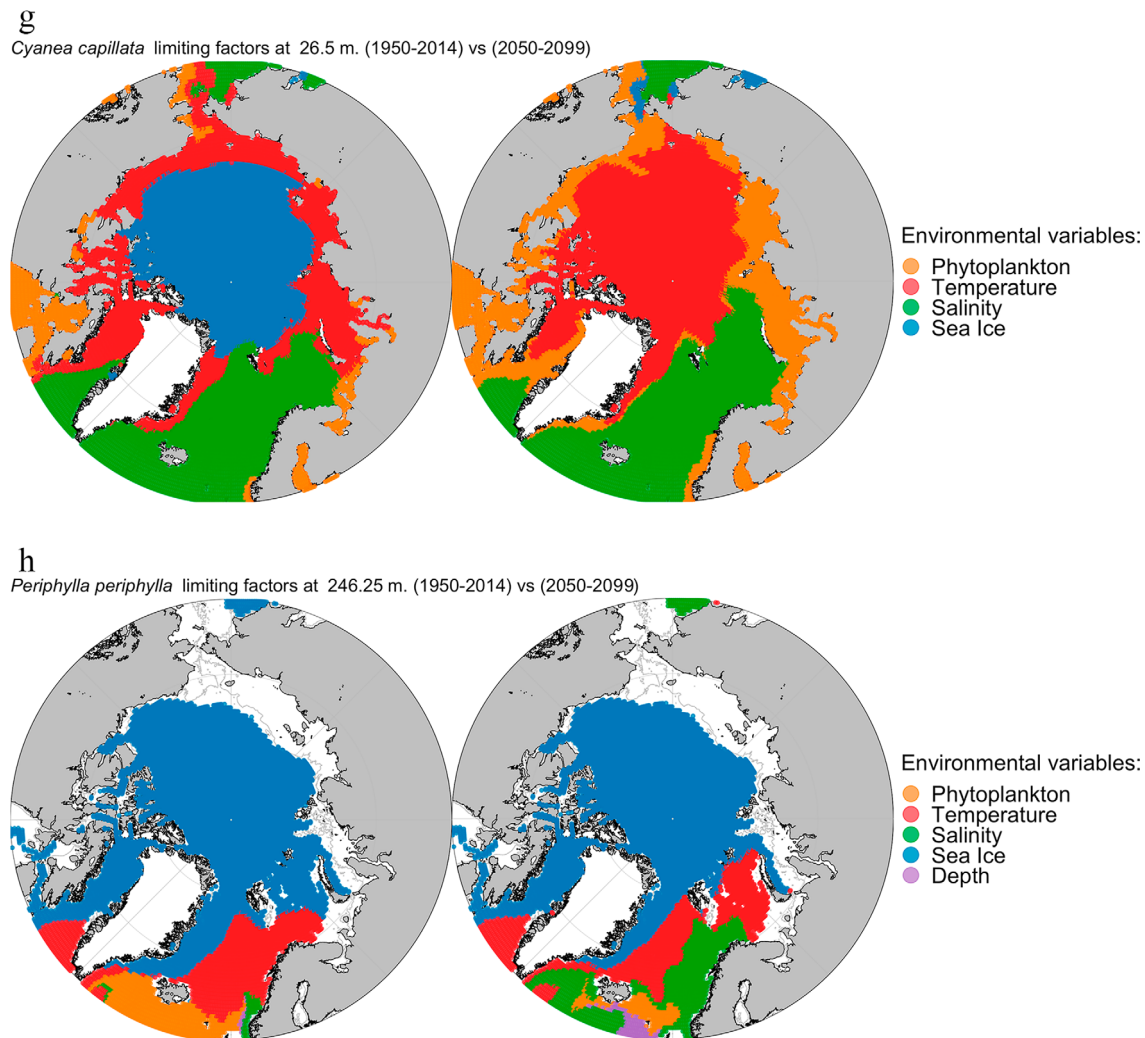
Fig. 4 (Continued)



**Fig. 5.** Environmental limiting factors for gelatinous zooplankton taxa. Maps illustrating environmental limiting factors for eight marine gelatinous zooplankton species for the period 1950–2014 and 2050–2099 (for the most probable depth layers).



**Fig. 5** (Continued)

**Fig. 5** (Continued)

We grouped the gelatinous zooplankton species in our study into three distinct categories based on their major depth distributions (Supporting Information Fig. S2): epipelagic (0–200 m), epi-mesopelagic (0–1000 m), and meso-bathypelagic (200–3000 m). Epipelagic species included *C. capillata* with a mean depth and standard deviation (SD) of  $34.08 \pm 88.56$  m, *M. ovum*— $86.55 \pm 255.61$  m, and *Beroe* spp.— $96.54 \pm 210.99$  m. Epi-mesopelagic species included *P. periphylla* ( $335.92 \pm 330.82$  m), *F. borealis* ( $209.60 \pm 426.09$  m), *O. vanhoeffeni* ( $341.58 \pm 566.06$  m), and *A. digitale* ( $178.93 \pm 365.86$  m). Our only meso-bathypelagic species was *Sm. arctica* ( $850.20 \pm 755.58$  m).

After the pre-processing steps, we included the following number of occurrence points into the species distribution models: *A. digitale* (1060 points), *F. borealis* (623), *O. vanhoeffeni* (381), *Beroe* spp. (245), *C. capillata* (80), *Sm. arctica* (46), *P. periphylla* (41), and *M. ovum* (30).

### Evaluation of the model performance

In total, we ran 49 models (with four replicates each) for each of the 8 selected gelatinous zooplankton taxa. We selected the best performing models with the following feature classes, regularization multipliers, and number of background points (Supporting Information Figs. S7, S8; Table S2). The best model fit according to the OR10p metric was observed for *P. periphylla* (0.052), and *M. ovum* (0.094), while *Sm. arctica* showed the worst fit (0.164; Supporting Information Fig. S7). In terms of CBI values, *A. digitale* (0.954), *F. borealis* (0.936), and *O. vanhoeffeni* (0.915) had the best fitting models. In contrast, *P. periphylla* (0.531) and *Sm. arctica* (0.552) showed the worst CBI results (Supporting Information Fig. S7). Regarding AUC values, the best models were fitted for *P. periphylla* (0.975), *C. capillata* (0.959). Conversely, *Sm. arctica* had the worst fit with an AUC (0.728; Supporting Information Fig. S7). Correlation analysis between the metrics showed the lowest

negative correlation between OR10p and AUC values ( $-0.71$ ) and the highest positive correlation between CBI and AICc ( $0.74$ ; Supporting Information Fig. S9).

### Environmental drivers

Sea ice and depth values showed the highest mean permutational importance (53.5% and 35.4%, respectively; Fig. 3), for the distribution patterns of all studied gelatinous zooplankton taxa, while salinity, temperature, and phytoplankton concentrations had lower mean permutational importance values (4.03%, 5.70%, and 1.39%, respectively; Fig. 3). However, the relative importance of environmental drivers varied along the depth column (Supporting Information Figs. S5, S10, S11). In particular, depth was found to be of higher importance in the deeper parts of the water column, which revealed the nature of its influence on surface zonality. Similarly, the presence of sea ice predominantly restricted the habitable niche for the majority of the studied taxa to the central parts of the pan-Arctic region. In regions where habitable conditions were most favorable, the interplay of temperature, salinity, and surface carbon concentrations was found to limit the distribution of these taxa (summarized per taxon in Table 1).

### Spatial distribution mapping and vertical profiling

Based on the spatial rasters from the MPI-ESM1.2 model, we constructed predictive maps for both observed (1950–2014) and future time periods (2050–2099; Fig. 4). The results of these are summarized in Table 1. We found that both hydrozoan species had a clear segregation of their preferred depth zone at 860 m (Fig. 4; Supporting Information Fig. S8), with *A. digitale* mainly distributed above this depth, and *Sm. arctica* below it. A similar spatial segregation was also observed in the horizontal dimension, with the highest probability of occurrence of *A. digitale* in the region south of 70°N, whereas *Sm. arctica* was mostly recorded in the regions north of 70°N. By the end of the century, the distribution of *Sm. arctica* contracted toward the pole, with the main retreat observed in the Fram Strait and a total loss of preferred suitable habitat of  $\sim -15\%$ . In contrast, *A. digitale* will be characterized by higher occurrences in the central Arctic Ocean by the end of the century with high presence values throughout the study region by 2050–2099, resulting in an overall increase in suitable habitat of  $\sim 29\%$ .

The two ctenophores taxa *Beroe* spp. and *M. ovum* were aggregated in the upper layers of the water column (Fig. 4). *Beroe* spp. were represented mainly at depths up to 461 m, while *M. ovum* was predominantly found in the epipelagic layers of 26 and 100 m. In historical projections, both species had the greatest presence in the marginal sea ice zones. *Beroe* spp. had the highest probability of occurrence in the Greenland, Barents, Bering, and Norwegian seas. *M. ovum* was also observed in large numbers in these seas, except for the Norwegian Sea. By 2050–2099, the projected distribution of *Beroe* spp. contracted poleward, which is especially noticeable in the

Norwegian and Greenland seas. However, closer to the pole ( $> 75^\circ\text{N}$ ), there was an increase in species occurrence at most sites, and the total suitable habitat increased by  $\sim 110\%$  across the region. *M. ovum* occurrence probability decreased in the Norwegian, Greenland, and Barents seas, but this decrease was more pronounced compared to the *Beroe* species. *M. ovum* became more common near the pole, with the total values of suitable habitat increasing by  $\sim 84\%$ .

The appendicularian species, *F. borealis* and *O. vanhoeffeni*, were observed to have a broad vertical distribution, extending down to depths of 865 m in the historical projection (Fig. 4). Beyond this depth, the probability of occurrence decreased significantly. On the historical projections, *F. borealis* occurred predominantly in the Greenland Sea, Fram Strait, Barents Sea, Kara Sea, and Baffin Bay, with the highest occurrence values between 60°N and 70°N. *O. vanhoeffeni* had a more northern distribution, with the highest occurrence values between 70°N and 75°N. This species was found in the Kara and Laptev Seas, as well as in Baffin Bay. However, both species show a poleward distribution shift. *F. borealis* is projected to extend its presence throughout the entire Arctic Ocean, while *O. vanhoeffeni* narrows its suitable habitats toward the pole, disappearing from the Bering and Barents seas and increasing its presence in the central parts of the Arctic Ocean. The total increase in suitable habitats is 130% and 102% for *F. borealis* and *O. vanhoeffeni*, respectively.

The scyphozoan species *C. capillata* and *P. periphylla* showed highest occurrences at the margins of the Arctic Ocean (Fig. 4). In the historical projections, *C. capillata* had its highest presence in the Bering Sea, Baffin Bay, and in some parts of the Norwegian and Barents seas. *P. periphylla* was found in the North Atlantic and also in the southern parts of the Norwegian and Barents seas. The spatial maps show a shift of *C. capillata* toward the Barents and Kara Seas, also this species becomes more common in Baffin Bay and the Beaufort Sea, with a total increase in suitable habitat of  $\sim 180\%$ . *P. periphylla* also shifts northward and occupies areas in the Svalbard fjords, in parts of the Barents Sea, and becomes more prevalent in the northern parts of the Bering Sea. The total increase in its suitable habitat is  $\sim 62\%$ .

### Discussion

To analyze the potential impact of climate change on gelatinous zooplankton distributions in the Arctic Ocean, we conducted pan-Arctic Species Distribution Models in 3D of the eight most reported taxa of gelatinous zooplankton. We used a maximum entropy model (Maxent) and valuation metrics showed good or excellent model fit for all species. Based on the best models, we projected the distribution of species under the current historical simulation (1950–2014) and under the future SSP370 (mid-high) emission scenario (2050–2100). Our projections show a general trend of poleward shifts in gelatinous zooplankton ranges for seven out of eight taxa studied.



**Table 1.** Future shifts in gelatinous zooplankton habitats and limiting factors in the Pan-Arctic region.

Species	Change in Pan-Arctic habitat niches	Regional habitat changes	Main limiting factors (historical)	Main limiting factors (future)
<i>Aglantha digitale</i>	~ +29%	Expanding in the central Arctic Ocean. In the Fram Strait, abundance is more concentrated in the mid-water column (410–580 m). Increased advection with the eastern branch of the West Spitsbergen Current.	Depth (below 1460 m), sea ice (upper layers in the central Pan Arctic), temperature (North Atlantic, Norwegian Sea), phytoplankton concentrations (sea ice marginal zones).	Decreased importance of sea ice, increased importance of temperature, and phytoplankton (over the shelf zones of the Pan-Arctic).
<i>Sminthea arctica</i>	~ –15%	Contracting toward the pole. Highest retreat observed in the Fram Strait.	Depth (major limiting driver), temperature at 865 m depth, sea ice associated distribution.	Extended temperature importance to 1460 m depth.
<i>Cyanea capillata</i>	~ +180%	Expanding over Arctic Ocean shelf areas, notably the Eurasian shelf.	Sea ice (central regions), temperature, and salinity (marginal sea ice zones, coastal areas).	Decreased importance of sea ice, increased limiting value of temperature in the central regions, increased importance of phytoplankton concentrations in the sea ice marginal zones.
<i>Periphylla periphylla</i>	~ +62%	Shifting northward to Svalbard fjords and parts of the Barents Sea. Also expanding in the Bering Sea.	Sea ice limits over the majority of the Pan Arctic region, phytoplankton concentrations, and temperature (North Atlantic).	Decreased limiting influence of sea ice, proportional shifts in salinity, and temperature limiting zones toward the pole.
<i>Mertensia ovum</i>	~ + 84%	Narrowing habitats toward the central Arctic. Loss of suitable habitat in the Bering and Barents seas.	Depth below 461.25 m, sea ice concentrations (epipelagic layers, Arctic regions), salinity, and temperature (North Atlantic, Norwegian Sea, Barents Sea).	Strong decrease in limiting influence of sea ice, increased limiting importance of temperature and salinity.
<i>Beroe</i> spp.	~ +110%	Expanding to the central Arctic Ocean, but contracting in the Norwegian and Greenland seas.	Depth (below 1460 m), sea ice in the central regions, salinity, and temperature in the North Atlantic, phytoplankton concentrations (Bering Sea).	Proportional shifts in salinity and temperature limiting zones toward the pole.
<i>Fritillaria borealis</i>	~ +130%	Expanding throughout the entire Arctic Ocean.	Sea ice concentrations (upper 1460 m), depth (below 1460 m), phytoplankton concentrations (North Atlantic, Greenland Sea).	Decreasing influence of sea ice and phytoplankton concentrations, poleward shift and increasing importance of temperature and salinity in the sea ice margin.
<i>Oikopleura vanhoeffeni</i>	~ +102%	Expanding into the central parts, but narrowing habitats in the Bering and Barents seas.	Sea ice concentration, phytoplankton concentration and temperature (coastal areas), salinity (Greenland and Barents seas).	Decreasing influence of sea ice, increasing limiting influence of salinity.

Future projections indicate a gradual decrease in the limiting role of sea ice as it retreats, coupled with a corresponding increase in the importance of temperature and phytoplankton concentrations as limiting factors.

The largest range expansion is expected for the scyphozoan *C. capillata* ( $\sim +180\%$ ), whereas the largest range contraction is expected for the hydrozoan *Sm. arctica* ( $\sim -15\%$ ). The distribution patterns of these species were mainly driven by the concentration of sea ice and water depth. However, in the most favorable habitat layers, the interaction of temperature, salinity, and surface carbon concentration was crucial.

### Biogeographic data

The origin and distribution of the biogeographic records showed unevenness in overall records and spatial distribution. Moreover, each of the four databases contributed a considerable number of unique values. The overlap between the values of the largest databases, OBIS and GBIF, was remarkably small ( $\sim 5\%$ ). Moudrý and Devillers (2020) found a rather similar low overlap between OBIS and GBIF in their study, which was explained by different data entry and quality control mechanisms, as well as poor exchange between data aggregators. None of the databases in our study had complete coverage of all studied regions but when combined, spatial coverage improved. With the exception of some parts of the Arctic Ocean, such as Baffin Bay and the East Siberian Sea, the pan-Arctic area was fairly well covered by surveyed stations. Overall, data from JeDI and PANGAEA represented a smaller proportion compared to GBIF and OBIS, but they contributed significantly to the spatial coverage of the region, at poorly studied sites. Ignoring spatial coverage and relying solely on a single database could lead to the underrepresentation of species in certain environments. Therefore, our findings show that the use of a multi-database approach to collect biogeographic data for species distribution modeling increases accuracy, particularly when modeling large-scale spatial distributions.

### Spatial distribution: Limiting drivers and trends

In our analysis, water depth, and sea ice concentrations had the greatest influence on the distribution of gelatinous zooplankton species. The importance of water depth reflects the fact that most of the species appear bound to certain depths (occurring mainly in epi- or epi-mesopelagic layers). As an exception, *P. periphylla* had a eurybathic distribution; for this species, depth had the least importance. In contrast to depth, sea ice coverage had the largest impact in the epi- and mesopelagic layers. This is to be expected since sea ice is considered one of the main factors determining the structure of marine ecosystems in the Arctic (Post et al. 2013). The effect of sea ice cover on the distribution of gelatinous zooplankton species can have both direct and indirect limiting effects (Arrigo 2014). For example, sea ice coverage can affect light penetration, stratification, and nutrient and organic matter supply (Arrigo 2014), which in turn also affects the availability of major prey sources for gelatinous zooplankton such as copepods (Stige et al. 2019).

Following sea ice retreat, we observe a northward expansion of distribution for most species (see Table 1 for details), representing an increase in suitable habitat, with the exception of *Sm. arctica* (habitat reduction of  $-15\%$ ). The observed increase in suitable habitat for most species can be explained by the fact that most species in our study, mirroring the documented biogeographic patterns of gelatinous zooplankton communities in the Arctic Ocean in general, represented boreal or arcto-boreal species (Ronowicz et al. 2015), and their presence in the historical projections is maximal in sea ice-free zones or marginal sea ice zones. Despite the rather low contribution of temperature, salinity, and phytoplankton concentration to the overall explanatory power of gelatinous zooplankton distributions, these parameters had a strong limiting influence at depth and in zones where species were most likely to be found. This was especially noticeable in areas of the North Atlantic without sea ice cover, where, for most of the species, the aforementioned parameters had the greatest importance.

Our distribution models came, however, with some spatio-temporal limitations. While on large spatial scales, the distribution of species is mainly determined by abiotic conditions (Soberón and Nakamura 2009), at finer spatial scales the inclusion of more biotic variables, such as food web interactions and species traits, would likely improve projections. In addition, at finer temporal scales, marine plankton are well known for their seasonal population fluctuations and blooms, hence, integrating these dynamics will further refine future projections (Bian et al. 2023). Nonetheless, current knowledge on gelatinous zooplankton is limited by the lack of species-specific food web data and reliable trait databases. However, with new molecular approaches generating data on prey-predator interactions for gelatinous zooplankton (e.g., Dischereit et al. 2024), it may soon be possible to fit more sophisticated models at finer temporal and spatial scales that explicitly incorporate food web interactions.

### Scyphozoa

With regard to taxonomic groups, the two scyphozoan species were projected to expand their suitable habitat to the greatest extent by 2050–2099. The combined effect of retreating sea ice and pronounced increases in temperature gradients could explain this pattern, as these factors alternated in their limiting importance on the spatial maps. Temperature plays an important limiting role in scyphozoan survival and reproduction (Widmer et al. 2016) and significantly influences their biochemical responses (Thuesen and Childress 1994). Moreover, temperature is the main environmental factor controlling blooms in scyphozoans (Fernández-Alías et al. 2021).

On the spatial maps, *C. capillata* will become more widely distributed over most of the Arctic Ocean shelf areas by 2050–2099. According to Widmer et al. (2016), *C. capillata* can reproduce at temperatures as low as  $4^{\circ}\text{C}$ , which will be characteristic for most parts of the Eurasian shelf, where we also see

the greatest increase in their modeled numbers. Despite the increased freshwater inflow from rivers in some parts of the Eurasian shelf, such desalination is unlikely to greatly limit the distribution of *C. capillata*, because this species can develop and reproduce in estuaries at low PSU values (Holst and Jarms 2010).

The distribution of *P. periphylla* also increases quite significantly, which is especially notable for the northern parts of the Atlantic sector of the Arctic Ocean. Interestingly, despite the lack of data on *P. periphylla* in the Pacific sector of the Arctic Ocean, its distribution is increasing in this area as well. As the species is occurring in the Pacific Ocean south of 60° N (Bentlage et al. 2013), the model's predictions indicating an expansion of suitable habitats in this area underlines its strong extrapolation power. *P. periphylla* is known to maintain stable populations in fjords (Fosså 1992) despite limited prey availability (Youngbluth and Båmstedt 2001). This is corroborated by our spatial limitation maps, where carbon concentrations were of minimal importance.

The recent appearance of this species in Spitsbergen fjords (Geoffroy et al. 2018) could evolve in a potential establishment of year-round populations with increasing warming. This is supported by our modeling results, with most of the fjords in this sector showing relatively high presence values of this species by 2050–2099. The northward expansion of *P. periphylla*'s suitable habitat is mostly restricted by the presence of sea ice and temperature. The known tolerance range of *P. periphylla* ranges from 4°C to 19.8°C (Arai 1997; Bozman et al. 2017; Geoffroy et al. 2018), but this species has also been found in 0°C waters in the Antarctic (Larson 1986). A temperature threshold lower than 4°C would be necessary for their successful overwintering in the high Arctic (Geoffroy et al. 2018). This is well reflected in our predictive curves, with the probability of occurrence of *P. periphylla* limited by 0°C and more strongly increased occurrence at > 4°C. On our predictive maps, we also observe the strongest increase in the presence of these species in regions where temperature values will exceed 4°C. In addition to a persistent presence in Svalbard, the species is also likely to establish year-round populations in the fjords of Novaya Zemlya and Franz-Josef-Land.

### Hydrozoa

The hydrozoan species (*A. digitale* and *Sm. arctica*), both belonging to the family Rhopalonematidae, showed a reverse three-dimensional segregation of suitable habitats, as well as inverse responses to changes in environmental conditions. Such habitat segregation and responses for these species were already highlighted for the Fram Strait (Pantiukhin et al. 2023). Despite a marked increase in the probability of occurrence of *A. digitale* in the northern regions, its suitable habitat slightly narrowed in the southern epipelagic and mesopelagic layers. This may be due to the fact that this species is likely to reach its upper-temperature limit in the

southern parts of the region by 2050–2099, which could be caused by a marked increase in metabolic costs witnessed at temperatures > 10–15°C (Larson 1986). This is also noticeable on the limiting maps, with the limiting importance of temperature increasing in the southern parts of the region by 2050–2099.

### Appendicularia

We found that the distribution of the appendicularian species was the greatest in the marginal sea ice zones. *O. vanhoeffeni* had a normal distribution with a peak at 50% of the sea ice coverage, while *F. borealis* preferred more open areas and had the highest probability of presence at 35% of sea ice coverage. Studies by Arashkevich et al. (2002) and Deibel et al. (2017) confirm this trend, with *O. vanhoeffeni* commonly found in regions near the sea ice edge, while *F. borealis* was more abundant in subpolar habitats. Despite these known differences in habitat preferences, we did not observe substantial habitat segregation where these species co-occurred. Such patterns were confirmed by Deibel et al. (2017), who concluded that *F. borealis* and *O. vanhoeffeni* can successfully coexist in similar habitats due to their utilization of specific food sources.

Appendicularians and other gelatinous filter feeders are projected to become more abundant in the polar regions at the expense of omnivorous copepods decline (Heneghan et al. 2023). We observed similar shifts in distributional patterns by 2050–2099, with both species increasing their presence in the region. Moreover, these two species are becoming more noticeably limited by water depth by 2050–2099, which may indicate that their suitable habitat, in terms of the other environmental conditions, is expanding. Despite this absolute increase, we observe a slight decrease in suitable habitat of *O. vanhoeffeni* in the southern zones. This is largely due to the fact that this species was poorly represented in sea ice free zones.

### Ctenophora

For the ctenophore taxa, we observed a moderate increase in suitable habitats in the central parts of the Arctic region. For *M. ovum*, a slight decrease in suitable habitat in the southern regions was observed, and a pronounced increase in the limiting value of temperature in the marginal sea ice zones by 2050–2099. This could be explained by the fact that the metabolism of this species increases dramatically at temperatures above 7°C (Percy 1988). A similar pattern was also evident on the predictive curves, where the occurrence of *M. ovum* reaches near-zero probability at temperatures of 7–8°C. Similarly, *Beroe* spp. slightly retreat from the southern parts of the region and are also more limited by increasing temperatures, which could presumably be explained by increased metabolic costs at warmer temperatures; however, supporting data from the literature are lacking.



### Potential impact of expanding gelatinous zooplankton communities

Gelatinous zooplankton, in particular cnidarian medusae and ctenophores, can compete with fish, by preying on the same zooplankton prey or by preying on ichthyoplankton (Richardson et al. 2009). Over the past decades, there have been more than 130 reports of adverse impacts of gelatinous zooplankton on marine fisheries and aquaculture, with frequency and severity increasing in recent years (Bosch-Belmar et al. 2020). Our study demonstrates a poleward expansion of suitable habitats for the large, predatory scyphozoan *C. capillata*, which could have a negative impact on local fish populations, including one of the most important Arctic fish species, polar cod (*Boreogadus saida*). At high abundances of *C. capillata*, *B. saida* tends to be replaced from its typical habitat (Crawford 2016). Based on our projections by 2050–2099, the northward expansion of *C. capillata* could significantly affect spawning habitat of *B. saida* (Dahlke et al. 2018), especially in regions around Novaya Zemlya and Spitsbergen, where suitable habitats for *C. capillata* are expected to increase significantly. Moreover, for the other scyphozoan species investigated, *P. periphylla*, suitable temperature conditions around Spitsbergen by 2050–2099 are likely to induce blooming events (Fernández-Alías et al. 2021). Here, this predatory jellyfish may also impact *B. saida* at its spawning sites, in a similarly dramatic way as it affected Atlantic cod populations in the fjords of Norway (Tiller et al. 2015). At the same time, several boreal fish species, many of which being commercially exploited, are known to migrate northward, followed by their fisheries (Mueter et al. 2021), where these species may encounter an increasing competition with gelatinous zooplankton species (Fosså 1992; Tiller et al. 2014). For example, the diet of *C. capillata* shows a high overlap in prey selection with some commercially exploited fish species, such as the pink salmon (*Oncorhynchus gorbuscha*) (Purcell and Sturdevant 2001).

A study by Heneghan et al. (2023) showed that the expansion of filter feeders in the Arctic will lead to a decrease in omnivorous copepods and an increase in carnivorous zooplankton. This, in turn, will lead to an elongation of food chains and, as a consequence, less effective carbon transfer from primary producers to fish (Heneghan et al. 2023). *Oikopleura vaenhoffeni* is known to outcompete copepod secondary producers under certain environmental conditions (Choe and Deibel 2011). Given that the environmental conditions nearer to the pole will become increasingly favorable for the distribution of *O. vaenhoffeni*, it can be assumed that this will make a noticeable contribution to the transformation of the Arctic food web and have a profound impact on local fish populations.

Conversely, gelatinivore species might benefit from the expansion of their prey into the Arctic Ocean. An increasing number of studies report the hitherto neglected importance of gelatinous zooplankton as prey for various Arctic organisms (Urban et al. 2022; Dischereit et al. 2024). As an example, the projected expansion of the Atlantic mackerel, *Scomber*

*scombrus*, into the Arctic realm (Berge et al. 2015), may benefit from the increasing population size of *A. digitale*. This is because *A. digitale* constitutes an important food source for *Sc. scombrus*, which actively preys on this hydrozoan, even in the presence of copepod prey (Runge et al. 1987).

Gelatinous zooplankton are able to form extensive blooms and can contribute significantly to deep-sea carbon transport (Lebrato et al. 2013). A study by Luo et al. (2020) showed that this transport can be as high as 35% of total particulate organic carbon transport on a global scale. In the Pacific sector of the Arctic, the carbon pump has been shown to increase significantly with increasing temperature and retreating sea ice (O'Daly et al. 2020). We can expect that, as habitable areas increase, we will also witness an increase in the efficiency of carbon transfer to the seafloor. As an example, a study in Hudson Bay observed a significant bloom of *A. digitale* in response to increasing temperatures (Lalande and Fortier 2011). This bloom contributed considerably to particulate organic carbon export, while there was a significant decrease in copepods in the sediment traps (Lalande and Fortier 2011). Moreover, two massively bloom-forming species, *C. capillata* and *P. periphylla*, will also experience an increase in habitats suitable for bloom formation (Fernández-Alías et al. 2021), potentially further amplifying carbon export. The aforementioned increase in appendicularians presence will also increase the efficiency of the biological carbon pump (Jaspers et al. 2023). We thus emphasize the need to better understand the ecological impact of gelatinous zooplankton blooms in the Arctic Ocean and the role of gelatinous zooplankton as prey for higher trophic levels and in biogeochemical cycles.

Gelatinous zooplankton span different trophic levels and are characterized by a wide array of ecological habits, hence, poleward expansions of suitable habitats of the different gelatinous zooplankton taxa studied will result in a myriad of potential impacts on the energy flow, trophodynamics, and biogeochemistry in Arctic Ocean ecosystems. At first, we need to better understand their population dynamics, by obtaining accurate estimates of their abundance using modern technologies including pelagic video surveys (e.g., Pantiukhin et al. 2023), and environmental DNA methods (Havermans et al. 2022). Given the expected expansion of gelatinous zooplankton, fisheries need to incorporate these dynamics into their management plans, preventing major impacts on fish stocks, and potentially leading to stock collapses as witnessed elsewhere in the world (Richardson et al. 2009).

### Conclusion

To analyze the potential impact of climate change on the distribution of Arctic gelatinous zooplankton, we performed pan-Arctic species distribution modeling in three dimensions of the eight most reported gelatinous zooplankton taxa in the Arctic Ocean (*A. digitale*, *Sm. arctica*, *P. periphylla*, *C. capillata*, *O. vanhoffeni*, *F. borealis*, *M. ovum*, and *Beroe* spp.). The

synthesis of biogeographic data has demonstrated the need for a multi-database approach, since it significantly improves the spatial coverage of sampling surveys. We used a customized three-dimensional version of the Maximum Entropy Model (Maxent) for the oceanic domain. Our habitat projections under the SSP370 emission scenario suggest a dominant trend toward poleward shifts of seven of the eight modeled gelatinous zooplankton taxa. In particular, the scyphozoan *C. capillata* is likely to shift poleward and expand into most coastal areas of the Arctic Ocean. In contrast, some species, in particular the hydrozoan *Sm. arctica*, may experience a contraction of their range toward the deep basins of the Arctic Ocean. These shifts may lead to a potential displacement of local fish populations and affect the carbon cycle and trophic dynamics. To fully understand such potential impact, it is necessary to gain a more detailed understanding of their population dynamics and their role in the food web, using novel techniques such as molecular analyses (Havermans et al. 2022). In order to assess their interactions with arctic and boreal fish stocks, comprehensive long-term and cost-effective monitoring programs involving the fishing industry are needed (Aubert et al. 2018). The results of this study can be used to guide further observations in areas most vulnerable to change and should also help develop more effective marine resource management strategies in the Arctic by incorporating these dynamics into their management plans, preventing major impacts on fish stocks, and potentially leading to stock collapses as witnessed elsewhere in the world (Richardson et al. 2009).

### Data availability statement

All details on the data retrieval process are available in the main text or in the supplementary materials. Biogeographic data were retrieved from four databases: Ocean Biodiversity Information System (OBIS), Global Biodiversity Information Facility (GBIF), Jellyfish Database Initiative (JeDI), and PANGAEA, with data extracted directly from OBIS, GBIF, and JeDI, and through individual publications from PANGAEA (Supporting Information Table S1). Environmental data were derived from “CMIP6.ScenarioMIP.DKRZ.MPI-ESM1-2-HR” (<https://doi.org/10.22033/ESGF/CMIP6.2450>) and “CMIP6.CMIP.MPI-M.MPI-ESM1-2-HR.historical” (<https://doi.org/10.22033/ESGF/CMIP6.6594>). The results of the major simulations are available at <https://doi.org/10.5061/dryad.f7m0cfz2j>.

### References

- Arai, M. N. 1997. Functional biology of Scyphozoa. Springer.
- Arashkevich, E., P. Wassmann, A. Pasternak, and C. Wexels Riser. 2002. Seasonal and spatial changes in biomass, structure, and development progress of the zooplankton community in the Barents Sea. *J. Mar. Syst.* **38**: 125–145. doi:10.1016/S0924-7963(02)00173-2
- Arrigo, K. R. 2014. Sea ice ecosystems. *Ann. Rev. Mar. Sci.* **6**: 439–467. doi:10.1146/annurev-marine-010213-135103
- Aubert, A., E. Antajan, C. Lynam, S. Pitois, A. Pliru, S. Vaz, and D. Thibault. 2018. No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management: Concrete cost-effective methodology during routine fishery trawl surveys. *Mar. Policy* **89**: 100–108. doi:10.1016/j.marpol.2017.12.010
- Baumgartner, J., and P. Wilson. 2023. rmaxent: Tools for working with Maxent in R. R package version 0.8.5.9000.
- Bentlage, B., A. T. Peterson, N. Barve, and P. Cartwright. 2013. Plumbing the depths: Extending ecological niche modeling and species distribution modelling in three dimensions. *Glob. Ecol. Biogeogr.* **22**: 952–961. doi:10.1111/geb.12049
- Berge, J., K. Heggland, O. J. Lønne, F. Cottier, H. Hop, G. W. Gabrielsen, L. Nøttestad, and O. A. Misund. 2015. First Records of Atlantic Mackerel (*Scomber scombrus*) from the Svalbard Archipelago, Norway, with possible explanations for the extension of its distribution. *Arctic* **68**: 54. doi:10.14430/arctic4455
- Bian, V., M. Cai, and C. L. Follett. 2023. Understanding opposing predictions of *Prochlorococcus* in a changing climate. *Nat. Commun.* **14**: 1445.
- Bosch-Belmar, M., G. Milisenda, L. Basso, T. K. Doyle, A. Leone, and S. Piraino. 2020. Jellyfish impacts on marine aquaculture and fisheries. *Rev. Fish. Sci. Aquacult.* **29**: 242–259. doi:10.1080/23308249.2020.1806201
- Bozman, A., J. Titelman, S. Kaartvedt, K. Eiane, and D. L. Aksnes. 2017. Jellyfish distribute vertically according to irradiance. *J. Plankton Res.* **39**: 280–289. doi:10.1093/plankt/fbw097
- Brotz, L., W. W. L. Cheung, K. Kleisner, E. Pakhomov, and D. Pauly. 2012. Increasing jellyfish populations: Trends in large marine ecosystems. *Hydrobiologia* **690**: 3–20. doi:10.1007/s10750-012-1039-7
- Cavanaugh, J. E., and A. A. Neath. 2019. The Akaike information criterion: Background, derivation, properties, application, interpretation, and refinements. *Wiley Interdiscip. Rev. Comput. Stat* **11**: e1460. doi:10.1002/wics.1460
- Choe, N., and D. Deibel. 2011. Life history characters and population dynamics of the boreal larvacean *Oikopleura vanhoffeni* (Tunicata) in Conception Bay, Newfoundland. *J. Mar. Biol. Ass.* **91**: 1587–1598. doi:10.1017/S0025315410001876
- Condon, R. H., and others. 2013. Recurrent jellyfish blooms are a consequence of global oscillations. *Proc. Natl. Acad. Sci. USA* **110**: 1000–1005. doi:10.1073/pnas.1210920110
- Crawford, R. E. 2016. Occurrence of a gelatinous predator (*Cyanea capillata*) may affect the distribution of *Boreogadus saida*, a key Arctic prey fish species. *Polar Biol.* **39**: 1049–1055. doi:10.1007/s00300-015-1779-8
- Dahlke, F. T., M. Butzin, J. Nahrang, V. Puvanendran, A. Mortensen, H.-O. Pörtner, and D. Storch. 2018. Northern cod species face spawning habitat losses if global warming exceeds 1.5°C. *Sci. Adv.* **4**: eaas8821. doi:10.1126/sciadv.aas8821

- de Hond, A. A. H., E. W. Steyerberg, and B. Van Calster. 2022. Interpreting area under the receiver operating characteristic curve. *Lancet Digit. Health* **4**: e853–e855. doi:[10.1016/S2589-7500\(22\)00188-1](https://doi.org/10.1016/S2589-7500(22)00188-1)
- Deibel, D., P. A. Saunders, and C. J. Stevens. 2017. Seasonal phenology of appendicularian tunicates in the north water, northern Baffin Bay. *Polar Biol.* **40**: 1289–1310. doi:[10.1007/s00300-016-2053-4](https://doi.org/10.1007/s00300-016-2053-4)
- Di Cola, V., and others. 2017. ecospat: An R package to support spatial analyses and modeling of species niches and distributions. *Ecography* **40**: 774–787. doi:[10.1111/ecog.02671](https://doi.org/10.1111/ecog.02671)
- Dischereit, A., J. Beermann, B. Lebreton, O. S. Wangenstein, S. Neuhaus, and C. Havermans. 2024. DNA metabarcoding reveals a diverse, omnivorous diet of Arctic amphipods during the polar night, with jellyfish and fish as major prey. *Front. Mar. Sci.* **11**: 1327650.
- Duffy, G. A., and S. L. Chown. 2017. Explicitly integrating a third dimension in marine species distribution modelling. *Mar. Ecol. Prog. Ser.* **564**: 1–8. doi:[10.3354/meps12011](https://doi.org/10.3354/meps12011)
- Edwards, M., P. Hélaouët, E. Goberville, A. Lindley, G. A. Tarling, M. T. Burrows, and A. Atkinson. 2021. North Atlantic warming over six decades drives decreases in krill abundance with no associated range shift. *Commun. Biol.* **4**: 644.
- Elith, J., M. Kearney, and S. Phillips. 2010. The art of modelling range-shifting species: The art of modelling range-shifting species. *Methods Ecol. Evol.* **1**: 330–342. doi:[10.1111/j.2041-210X.2010.00036.x](https://doi.org/10.1111/j.2041-210X.2010.00036.x)
- Fernández-Alías, A., C. Marcos, and A. Pérez-Ruzafa. 2021. Larger scyphozoan species dwelling in temperate, shallow waters show higher blooming potential. *Mar. Pollut. Bull.* **173**: 113100. doi:[10.1016/j.marpolbul.2021.113100](https://doi.org/10.1016/j.marpolbul.2021.113100)
- Fosså, J. H. 1992. Mass occurrence of *Periphylla periphylla* (Scyphozoa, Coronatae) in a Norwegian fjord. *Sarsia* **77**: 237–251. doi:[10.1080/00364827.1992.10413509A](https://doi.org/10.1080/00364827.1992.10413509A)
- Frainer, A., R. Primicerio, S. Kortsch, M. Aune, A. V. Dolgov, M. Fossheim, and M. M. Aschan. 2017. Climate-driven changes in functional biogeography of Arctic marine fish communities. *Proc. Natl. Acad. Sci. USA* **114**: 12202–12207. doi:[10.1073/pnas.1706080114](https://doi.org/10.1073/pnas.1706080114)
- Freer, J. J., M. Daase, and G. A. Tarling. 2021. Modelling the biogeographic boundary shift of *Calanus finmarchicus* reveals drivers of Arctic Atlantification by subarctic zooplankton. *Global Change Biol.* **44**: 429–440. doi:[10.1111/gcb.15937](https://doi.org/10.1111/gcb.15937)
- Geoffroy, M., and others. 2018. Increased occurrence of the jellyfish *Periphylla periphylla* in the European high Arctic. *Polar Biol.* **41**: 2615–2619. doi:[10.1007/s00300-018-2368-4](https://doi.org/10.1007/s00300-018-2368-4)
- Gulev, S. K., and others. 2021. Climate change 2021: The physical science basis, p. 287–422. *In* Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, v. **2021**. Cambridge University Press.
- Gutjahr, O., D. Putrasahan, K. Lohmann, J. H. Jungclaus, J.-S. Von Storch, N. Brüggemann, H. Haak, and A. Stössel. 2019. Max Planck institute earth system model (MPI-ESM1.2) for the high-resolution model intercomparison project (HighResMIP). *Geosci. Model Dev.* **12**: 3241–3281. doi:[10.5194/gmd-12-3241-2019](https://doi.org/10.5194/gmd-12-3241-2019)
- Havermans, C., A. Dischereit, D. Pantiukhin, M. Friedrich, and A. Murray. 2022. Environmental DNA in an ocean of change: Status, challenges and prospects. *Arq. Ciencias Mar.* **55**: 298–337. doi:[10.32360/acmar.v55iEspecial.78188](https://doi.org/10.32360/acmar.v55iEspecial.78188)
- Hays, G. C., T. K. Doyle, and J. D. R. Houghton. 2018. A paradigm shift in the trophic importance of jellyfish? *Trends Ecol. Evol.* **33**: 874–884. doi:[10.1016/j.tree.2018.09.001](https://doi.org/10.1016/j.tree.2018.09.001)
- Heneghan, R. F., J. D. Everett, J. L. Blanchard, P. Sykes, and A. J. Richardson. 2023. Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nat. Clim. Change* **13**: 470–477. doi:[10.1038/s41558-023-01630-7](https://doi.org/10.1038/s41558-023-01630-7)
- Holst, S., and G. Jarms. 2010. Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): Is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia* **645**: 53–68. doi:[10.1007/s10750-010-0214-y](https://doi.org/10.1007/s10750-010-0214-y)
- Jaspers, C., R. R. Hopcroft, T. Kiørboe, F. Lombard, Á. López-Urrutia, J. D. Everett, and A. J. Richardson. 2023. Gelatinous larvacean zooplankton can enhance trophic transfer and carbon sequestration. *Trends Ecol. Evol.* **38**: 980–993. doi:[10.1016/j.tree.2023.05.005](https://doi.org/10.1016/j.tree.2023.05.005)
- Jungclaus, J., and others. 2019. MPI-M MPI-ESM1.2-HR model output prepared for CMIP6 CMIP historical. Earth System Grid Federation.
- Júnior, M. N., E. G. Tosetto, L. C. Baldoni, S. Dutto, M. Hidaka, D. J. Lindsay, and R. M. Nagata. 2022. Chapter 7: Gelatinous zooplankton, p. 150–178. *In* J. Pan and P. D. Pratolongo [eds.], *Marine biology a functional approach to the oceans and their organisms*. CRC Press.
- Kass, J. M., R. Muscarella, P. J. Galante, C. L. Bohl, G. E. Pinilla-Buitrago, R. A. Boria, M. Soley-Guardia, and R. P. Anderson. 2021. ENMeval 2.0: Redesigned for customizable and reproducible modeling of species' niches and distributions. *Methods Ecol. Evol.* **12**: 1602–1608. doi:[10.1111/2041-210X.13628](https://doi.org/10.1111/2041-210X.13628)
- Kass, J. M., R. Muscarella, G. E. Pinilla-Buitrago, and P. J. Galante. 2023. ENMeval 2.0: A Vignette. ENMeval: Ecological Niche Modeling Evaluation. <https://jamiemkass.github.io/ENMeval/articles/ENMeval-2.0-vignette.html>
- Lalande, C., and L. Fortier. 2011. Downward particulate organic carbon export and jellyfish blooms in southeastern Hudson Bay. *J. Mar. Syst.* **88**: 446–450. doi:[10.1016/j.jmarsys.2010.12.005](https://doi.org/10.1016/j.jmarsys.2010.12.005)
- Larson, R. J. 1986. Pelagic scyphomedusae (Scyphozoa: Coronatae and Semaestomeae) of the Southern Ocean, p. 59–165. *In* L. S. Kornicker [ed.], *Biology of the Antarctic Seas*, v. **XVI**. Antarctic Research Series.



- Lebrato, M., P. D. J. Mendes, D. K. Steinberg, J. E. Cartes, B. M. Jones, L. M. Birsá, R. Benavides, and A. Oschlies. 2013. Jelly biomass sinking speed reveals a fast carbon export mechanism. *Limnol. Oceanogr.* **58**: 1113–1122. doi:[10.4319/lo.2013.58.3.1113](https://doi.org/10.4319/lo.2013.58.3.1113)
- Lucas, C. H., and others. 2014. JeDI (Jellyfish Database Initiative): A new open-access gelatinous plankton database. *BioScience* **62**: 160–169.
- Luo, J. Y., R. H. Condon, C. A. Stock, C. M. Duarte, C. H. Lucas, K. A. Pitt, and R. K. Cowen. 2020. Gelatinous zooplankton-mediated carbon flows in the global oceans: A data-driven modeling study. *Global Biogeochem. Cycl.* **34**: e2020GB006704. doi:[10.1029/2020GB006704](https://doi.org/10.1029/2020GB006704)
- Lynam, C. P., M. K. S. Lilley, T. Bastian, T. K. Doyle, S. E. Beggs, and G. C. Hays. 2011. Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Glob. Chang. Biol.* **17**: 767–782. doi:[10.1111/j.1365-2486.2010.02352.x](https://doi.org/10.1111/j.1365-2486.2010.02352.x)
- Mańko, M. K., M. Gluchowska, and A. Weydmann-Zwolicka. 2020. Footprints of Atlantification in the vertical distribution and diversity of gelatinous zooplankton in the Fram Strait (Arctic Ocean). *Front. Mar. Sci.* **189**: 102414. doi:[10.1016/j.pocan.2020.102414](https://doi.org/10.1016/j.pocan.2020.102414)
- Mańko, M. K., M. Malgorzata, S. Kwasniewski, and A. Weydmann-zwolicka. 2022. Atlantification alters the reproduction of jellyfish *Aglantha digitale* in the European Arctic. *Limnol. Oceanogr.* **67**: 1836–1849. doi:[10.1002/lno.12170](https://doi.org/10.1002/lno.12170)
- Merow, C., and others. 2014. What do we gain from simplicity versus complexity in species distribution models? *Ecography* **37**: 1267–1281. doi:[10.1111/ecog.00845](https://doi.org/10.1111/ecog.00845)
- Moudrý, V., and R. Devillers. 2020. Quality and usability challenges of global marine biodiversity databases: An example for marine mammal data. *Ecol. Inform.* **56**: 101051. doi:[10.1016/j.ecoinf.2020.101051](https://doi.org/10.1016/j.ecoinf.2020.101051)
- Mueter, F. J., and others. 2021. Possible future scenarios in the gateways to the Arctic for subarctic and Arctic marine systems: II. Prey resources, food webs, fish, and fisheries. *ICES J. Mar. Sci.* **78**: 3017–3045. doi:[10.1093/icesjms/fsab122](https://doi.org/10.1093/icesjms/fsab122)
- Muscarella, R., P. J. Galante, M. Soley-Guardia, R. A. Boria, J. M. Kass, M. Uriarte, and R. P. Anderson. 2014. ENMeval: An R package for conducting spatially independent evaluations and estimating optimal model complexity for MAXENT ecological niche models. *Methods Ecol. Evol.* **5**: 1198–1205. doi:[10.1111/2041-210X.12261](https://doi.org/10.1111/2041-210X.12261)
- O'Daly, S. H., S. L. Danielson, S. M. Hardy, R. R. Hopcroft, C. Lalande, D. A. Stockwell, and A. M. P. McDonnell. 2020. Extraordinary carbon fluxes on the shallow Pacific Arctic shelf during a remarkably warm and low sea ice period. *Front. Mar. Sci.* **7**: 548931. doi:[10.3389/fmars.2020.548931](https://doi.org/10.3389/fmars.2020.548931)
- O'Neill, B. C., E. Krieglér, K. Riahi, K. L. Ebi, S. Hallegatte, T. R. Carter, R. Mathur, and D. P. Van Vuuren. 2014. A new scenario framework for climate change research: The concept of shared socioeconomic pathways. *Clim. Change* **122**: 387–400. doi:[10.1007/s10584-013-0905-2](https://doi.org/10.1007/s10584-013-0905-2)
- Pantiukhin, D., G. Verhaegen, C. Kraan, K. Jerosch, P. Neitzel, H.-J. T. Hoving, and C. Havermans. 2023. Optical observations and spatio-temporal projections of gelatinous zooplankton in the Fram Strait, a gateway to a changing Arctic Ocean. *Front. Mar. Sci.* **10**: 987700. doi:[10.3389/fmars.2023.987700](https://doi.org/10.3389/fmars.2023.987700)
- Percy, J. A. 1988. Influence of season, size, and temperature on the metabolism of an arctic cydippid ctenophore, *Mertensia ovum* (Fabricius). *Sarsia* **73**: 61–70. doi:[10.1080/00364827.1988.10420672](https://doi.org/10.1080/00364827.1988.10420672)
- Phillips, S. J., R. P. Anderson, M. Dudík, R. E. Schapire, and M. E. Blair. 2017. Opening the black box: An open-source release of Maxent. *Ecography* **40**: 887–893. doi:[10.1111/ecog.03049](https://doi.org/10.1111/ecog.03049)
- Post, E., and others. 2013. Ecological consequences of sea-ice decline. *Science* **341**: 519–524. doi:[10.1126/science.1235225](https://doi.org/10.1126/science.1235225)
- Purcell, J., and M. Sturdevant. 2001. Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. *Mar. Ecol. Prog. Ser.* **210**: 67–83. doi:[10.3354/meps210067](https://doi.org/10.3354/meps210067)
- Radosavljevic, A., and R. P. Anderson. 2014. Making better Maxent models of species distributions: Complexity, overfitting and evaluation. *J. Biogeogr.* **41**: 629–643. doi:[10.1111/jbi.12227](https://doi.org/10.1111/jbi.12227)
- Rantanen, M., A. Y. Karpechko, A. Lipponen, K. Nordling, O. Hyvärinen, K. Ruosteenoja, T. Vihma, and A. Laaksonen. 2022. The Arctic has warmed nearly four times faster than the globe since 1979. *Commun. Earth Environ.* **3**: 168. doi:[10.1038/s43247-022-00498-3](https://doi.org/10.1038/s43247-022-00498-3)
- Raskoff, K. A., R. R. Hopcroft, K. N. Kosobokova, J. E. Purcell, and M. Youngbluth. 2010. Jellies under ice: ROV observations from the Arctic 2005 hidden ocean expedition. *Deep Sea Res. II Top. Stud. Oceanogr.* **57**: 111–126. doi:[10.1016/j.dsr2.2009.08.010](https://doi.org/10.1016/j.dsr2.2009.08.010)
- Richardson, A. J., A. Bakun, G. C. Hays, and M. J. Gibbons. 2009. The jellyfish joyride: Causes, consequences and management responses to a more gelatinous future. *Trends Ecol. Evol.* **24**: 312–322. doi:[10.1016/j.tree.2009.01.010](https://doi.org/10.1016/j.tree.2009.01.010)
- Roberts, D. R., and others. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**: 913–929. doi:[10.1111/ecog.02881](https://doi.org/10.1111/ecog.02881)
- Robinson, N. M., W. A. Nelson, M. J. Costello, J. E. Sutherland, and C. J. Lundquist. 2017. A systematic review of marine-based species distribution models (SDMs) with recommendations for best practice. *Front. Mar. Sci.* **4**: 421. doi:[10.3389/fmars.2017.00421](https://doi.org/10.3389/fmars.2017.00421)
- Ronowicz, M., P. Kukliński, and G. M. Mapstone. 2015. Trends in the diversity, distribution and life history strategy of Arctic hydrozoa (Cnidaria). *PLoS One* **10**: e0120204. doi:[10.1371/journal.pone.0120204](https://doi.org/10.1371/journal.pone.0120204)
- Runge, J. A., P. Pepin, and W. Silvert. 1987. Feeding behavior of the Atlantic mackerel *Scomber scombrus* on the

- hydromedusa *Aglantha digitale*. *Mar. Biol.* **94**: 329–333. doi:[10.1007/BF00428238](https://doi.org/10.1007/BF00428238)
- Schupfner, M., and others. 2019. DKRZ MPI-ESM1.2-HR model output prepared for CMIP6 ScenarioMIP. doi:[10.22033/ESGF/CMIP6.2450](https://doi.org/10.22033/ESGF/CMIP6.2450)
- Searcy, C. A., and H. B. Shaffer. 2016. Do ecological niche models accurately identify climatic determinants of species ranges? *Am. Nat.* **187**: 423–435.
- Shiganova, T. A., and G. A. Abyzova. 2022. Revision of Beroidae (Ctenophora) in the southern seas of Europe: Systematics and distribution based on genetics and morphology. *Zool. J. Linn. Soc.* **194**: 297–322. doi:[10.1093/zoolinnean/zlab021](https://doi.org/10.1093/zoolinnean/zlab021)
- Soberón, J., and M. Nakamura. 2009. Niches and distributional areas: Concepts, methods, and assumptions. *Proc. Natl. Acad. Sci. USA* **106**: 19644–19650.
- Steinberg, D. K., and others. 2023. The outsized role of salps in carbon export in the subarctic Northeast Pacific Ocean. *Global Biogeochem. Cycles* **37**: e2022GB007523. doi:[10.1029/2022GB007523](https://doi.org/10.1029/2022GB007523)
- Stige, L. C., E. Eriksen, P. Dalpadado, and K. Ono. 2019. Direct and indirect effects of sea ice cover on major zooplankton groups and planktivorous fishes in the Barents Sea. *ICES J. Mar. Sci.* **76**: i24–i36. doi:[10.1093/icesjms/fsz063](https://doi.org/10.1093/icesjms/fsz063)
- Thuesen, E. V., and J. J. Childress. 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. *Biol. Bull.* **187**: 84–98.
- Tiller, R. G., J. Mork, R. Richards, L. Eisenhauer, Y. Liu, J.-F. Nakken, L. Åshild, and Borgersen. 2014. Something fishy: Assessing stakeholder resilience to increasing jellyfish (*Periphylla periphylla*) in Trondheimsfjord, Norway. *Mar. Policy* **46**: 72–83. doi:[10.1016/j.marpol.2013.12.006](https://doi.org/10.1016/j.marpol.2013.12.006)
- Tiller, R. G., J. Mork, Y. Liu, Å. L. Borgersen, and R. Richards. 2015. To adapt or not adapt: Assessing the adaptive capacity of artisanal fishers in the Trondheimsfjord (Norway) to jellyfish (*Periphylla periphylla*) bloom and purse seiners. *Mar. Coast. Fish.* **7**: 260–273. doi:[10.1080/19425120.2015.1037873](https://doi.org/10.1080/19425120.2015.1037873)
- Urban, P., K. Præbel, S. Bhat, J. Dierking, and O. S. Wangensteen. 2022. DNA metabarcoding reveals the importance of gelatinous zooplankton in the diet of *Pandalus borealis*, a keystone species in the Arctic. *Mol. Ecol.* **31**: 1562–1576.
- Valavi, R., G. Guillera-Aroita, J. J. Lahoz-Monfort, and J. Elith. 2022. Predictive performance of presence-only species distribution models: A benchmark study with reproducible code. *Ecological monographs* **92**: e01486. doi:[10.1002/ecm.1486](https://doi.org/10.1002/ecm.1486)
- Verhaegen, G., M. S. Sangekar, B. Bentlage, H.-J. Hoving, A. G. Collins, and D. Lindsay. 2023. Drivers behind the diversity and distribution of a widespread midwater narcomedusa. *Limnol. Oceanogr.* **68**: 2088–2107. doi:[10.1002/lno.12408](https://doi.org/10.1002/lno.12408)
- Widmer, C., C. Fox, and A. Brierley. 2016. Effects of temperature and salinity on four species of northeastern Atlantic scyphistomae (Cnidaria: Scyphozoa). *Mar. Ecol. Prog. Ser.* **559**: 73–88. doi:[10.3354/meps11879](https://doi.org/10.3354/meps11879)
- Youngbluth, M. J., and U. Båmstedt. 2001. Distribution, abundance, behavior and metabolism of *Periphylla periphylla*, a mesopelagic coronate medusa in a Norwegian fjord. *Hydrobiologia* **451**: 321–333. doi:[10.1023/A:1011874828960](https://doi.org/10.1023/A:1011874828960)

## Acknowledgments

This study has been conducted in the framework of the Helmholtz Young Investigator Group “ARJEL—Arctic Jellies” with the project number VH-NG-1400, awarded to C.H. and funded by the Helmholtz Society and the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research. G.V. was supported by the Deutsche Forschungsgemeinschaft (DFG) by the grants VE 1192/1-1 and VE 1192/3-1, as well as by the grant VE 1192/2-1 in the framework of the priority program SPP 1158 “Antarctic Research with comparative investigations in Arctic ice areas”. We thank Dr. Casper Kraan and Prof. Dr. Dieter Piepenburg for their valuable comments and suggestions on the methodology and the manuscript. Three anonymous reviewers are thanked for their constructive comments on the previous version of the manuscript. We acknowledge support by the Open Access Publication Funds of Alfred-Wegener-Institut Helmholtz-Zentrum für Polar- und Meeresforschung. Open Access funding enabled and organized by Projekt DEAL.

## Conflict of Interest

The authors declare no conflicts of interest.

Submitted 31 August 2023

Revised 18 March 2024

Accepted 30 March 2024

Associate editor: Bingzhang Chen