RESEARCH ARTICLE

Data-driven bioregionalization: A seascape-scale study of macrobenthic communities in the Eurasian Arctic

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Abstract

Aim: We conduct the first model-based assessment of the biogeographical subdivision of Eurasian Arctic seas to (1) delineate spatial distribution and boundaries of macrobenthic communities on a seascape level; (2) assess the significance of environmental drivers of macrobenthic community structures; (3) compare our modelling results to historical biogeographical classifications; and (4) couple the model to climate scenarios of environmental changes to project potential shifts in the distribution and composition of macrobenthic communities by 2100.

Location: Eurasian Arctic seas, in particular Barents, Kara and Laptev Seas.

Taxon: 169 species of macrobenthic fauna; most common taxa are Polychaeta (85 species), Malacostraca (30 species), Bivalvia (26 species) and Gastropoda (10 species).

Methods: We employed the Region of Common Profile (RCP) approach to assess the bioregionalization patterns of Eurasian Arctic seafloor communities. The RCP approach allows the identification of seascape-scale distribution patterns by simultaneously considering biotic and environmental data within one modelling step.

Results: Four RCPs were identified within the Eurasian Arctic. The results showed that water depth, sea-ice cover, bottom-water temperature and salinity, proportion of fine sediments, particulate organic carbon (POC) and depth of the euphotic zone were among the most important driving variables of macrobenthos communities. The projections, driven by the climate-change scenarios, suggested a general north-eastward shift of the RCPs over the 21st century, mainly correlated with retreating sea-ice and increasing sea-bottom temperature.

Main conclusions: The identified RCPs largely match the previously reported large-scale distribution patterns of macrobenthic communities in Eurasian Arctic seas. The spatio-temporal dynamics of RCPs are in agreement with local long-term observation data on macrobenthic resilience/vulnerability in the studied region. The representation of the ecoregions and biotas in a probabilistic form, together with quantitative assessment of potential climate-driven changes, will help to adequately consider macrobenthic biodiversity dynamics in the development of science-based conservation measures.

1 | INTRODUCTION

Human demands for ocean space and resources are rapidly growing, adding to the increasing cumulative impacts of multiple stressors related to climate change (e.g. Ingeman et al., 2019), such as ocean warming and increasing thermal stratification, sea-ice extent and thickness decline, as well as changes in water circulation. These profound environmental shifts lead to far-reaching alterations of the composition and structure of marine populations and communities and cause pronounced quantitative and qualitative changes in ecosystem functioning (McGill et al., 2015; Pecl et al., 2017). Without adequate conservation measures, this will result in a loss of biodiversity, resilience, ecosystem services and functioning (Halpern et al., 2015; Worm et al., 2006).

In the Arctic, global warming is about twice as rapid as worldwide (IPCC, 2014), and sea-ice retreat is the most relevant climate factor for marine ecosystems (Macias-Fauria & Post, 2018; Post et al., 2013). Both climate impacts are causing profound qualitative and quantitative changes in the structure and dynamics of benthic communities (Kedra et al., 2015; Wassmann et al., 2011). However, information on these processes is scarce, due to the challenges of collecting important baseline field data on Arctic biodiversity (e.g. Archambault et al., 2010; Bluhm et al., 2011; Piepenburg et al., 2011), the general lack of open-access large-scale data that can be used to inform biogeographical modelling (e.g. Costello et al., 2018; Renaud et al., 2015), as well as the emphasis of most efforts on easy-accessible and well-researched areas, such as the Barents Sea (e.g. Frainer et al., 2017; Kortsch et al., 2012) or Bering and Chukchi seas (e.g. Grebmeier et al., 2006). Moreover, assessments of biodiversity-ecosystem functions relationship in the Arctic region are scarce (Link et al., 2013) and the use of species and community distribution models (SDM/CDM) to up-scale local or regional analyses has rarely been used in marine ecosystems, particularly in Arctic seas (Kędra et al., 2015; Renaud et al., 2015, 2019; Robinson et al., 2011).

Our knowledge of Arctic benthic ecosystems is geographically unevenly distributed (Piepenburg et al., 2011). However, a comprehensive understanding of the large-scale patterns of Arctic benthic communities can serve as an integrative indicator of the effects of climate change in the region (Birchenough et al., 2015). Studies by Matishov et al., 2012 showed that the macrobenthic fauna of the Barents Sea responds to strong and long-term climatic anomalies and the ratio of boreal-Arctic species composition changes significantly in relation to warm and cold bottom water conditions. In order to shed light on the benthic community dynamics in response to climate change, the use of joint species distribution models that could take into account the multidimensional nature of communities is essential. Such models represent the studied communities as multidimensional spaces where the species respond jointly to the environment and to each other (Foster et al., 2013; Tikhonov et al., 2020). This representation should inform our knowledge of remote areas with insufficient sampling activity (Jetz et al., 2019), a prominent feature of benthic ecosystems in the Arctic (Piepenburg et al., 2011; Renaud et al., 2015) in order to reveal potential shifts of the benthic communities.

Additionally, large-scale knowledge about benthic ecosystems in these largely inaccessible regions is necessary for the establishment of marine protected areas (MPAs). These regions, in addition to climate-change stressors, will experience an increase in economic activities (e.g. Northern Sea Route, increased fishery activities, underwater mining) (Solovyev et al., 2017). Establishing MPAs in the Eurasian Arctic is also important, as currently only about ~2.5% of this area is designated as such (Spiridonov et al., 2012), although about 10% of areas should be designated as protected areas to ensure the sustainability and proper functioning of biomes (Vreugdenhil et al., 2003). In order to establish MPAs, comprehensive knowledge of the water column and the delimitation of biogeographical zones must be combined (Solovyev et al., 2017). The current research should provide a baseline for identifying priority areas for conservation management.

To increase large-scale knowledge of benthic species assemblages in these little explored areas, we employ recent multivariate community models (Foster et al., 2013) underpinned by a novel synthesis of Arctic benthic fauna (Hansen et al., 2019; Casper Kraan, Thomas Brey, Paul Kloss, Jan Hansen & Dieter Piepenburg, unpublished data). We offer the first model-based biogeographical assessment of macrobenthic assemblages in the Eurasian Arctic, with the specific objectives to (1) delineate spatial distribution and boundaries of seafloor communities; (2) assess the significance of a broad selection of environmental drivers on structuring macrobenthic fauna; (3) compare such model-based results to historical biogeographical classifications; (4) use climate-change scenarios to project future distributions of benthic communities.

We use the Region of Common Profile (RCP; Foster et al., 2013) approach to assess multispecies bioregionalization. This method is based on a mixture-of-experts model framework, jointly considering multispecies data and environmental variables. It allows mapping of regions within which species share the same probability of occurrence (Foster et al., 2013; Hill et al., 2017). This is a great advantage compared to traditional methods using some measures of distance or dissimilarity between sampling locations since those do not allow to assess species' individual group membership or propagate uncertainty throughout the modelling process (Warton et al., 2015). Moreover, this approach allows prediction of assemblages in areas where only environmental information is available and their possible shifts in response to climate change (Lyons et al., 2017).

We focus on macrobenthic communities, that is, organisms >500 μm, for four reasons: (1) Macrobenthic fauna consists of rather stationary and long-lived organisms and rely nutritionally almost entirely on the organic flux from euphotic layers. Hence, they reflect changes in surface-layer production in their own dynamics (e.g. Grebmeier et al., 2015). (2) No attempt has yet been made to regionalize Arctic seafloor communities using modern multi-species models. (3) Increased knowledge of such seafloor communities will increase their inclusion and importance in the development of conservation priority areas or other conservation measures (Spiridonov et al., 2017). (4) Our knowledge of the spatial distribution of benthic organisms in the Arctic region is rather limited (Piepenburg et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Study region

Our study region includes three Eurasian shelf seas, that is, Barents, Kara and Laptev Seas (Spalding et al., 2007), covering a total of 3.5 million km^2 (Figure 1). The key environmental feature in this region is sea-ice cover (e.g. Itkin & Krumpen, 2017), lasting between 3–4 months in the Barents Sea to 9–10 months in the Laptev Sea. Sea ice influences many factors that in turn directly influence the distribution and abundance of benthic communities, such as energy and carbon flow from the water column, the effect of desalination in summer, and *vice versa* in winter. Run-off from the Yenisei, Ob and Lena rivers also has an impact on environmental conditions, bringing in a significant amount of heat and freshwater, thereby conditioning coastal water circulation and ice regime, as well as determining biochemical regime (Zenkevitch, 1963).

2.2 | Macrobenthic community data

Biological information was gathered at 354 sampling locations (Figure 1), visited during scientific expeditions in summers between 1991 and 2013 (Hansen et al., 2019; Piepenburg et al., 2011; https://doi.pangaea.de/10.1594/PANGAEA.910004). Data comprise more than 17,000 records of 2086 taxonomic units, characterized as macrobenthic fauna, that is, organisms large enough to remain in the residue of a sieve with a mesh size of 0.5 mm. These records have been quality controlled (see Piepenburg et al., 2011), as well as taxonomically aligned with the world register of marine species (WoRMS Editorial Board, 2019). To reduce bias introduced by various grab-sampling devices, we limited our analysis to presence/absence data (Piepenburg et al., 2011). We ignored temporal variation in benthic species occurrences, since limiting the dataset time frame would severely impact the amount of information available and possibly make this study less valuable or even impossible. However, we matched environmental variables to the time benthic samples were taken (see below).

2.3 | Environmental data

Environmental parameters such as salinity, temperature, sediment composition and food availability were proven to be the most important factors determining the distribution of Arctic benthic communities (Dayton, 1990). It was shown that the similarities of faunal assemblages of benthic communities correlate with different depth zones (Steffens et al., 2006). The steepness of the slope may reflect the structure of benthic communities, being the driving force behind the accumulation of organic sediments (Ichino, 2015). Moreover, environmental factors as apparent oxygen utilization, concentrations of phosphates, silicates and nitrates are considered to represent the benthic remineralization function and, therefore, are assumed to be indicators of benthic activity (Link et al., 2013).

The above-mentioned environmental parameters were extracted from public oceanographical databases and satellite-based remote-sensing data repositories (see Figure A1). Variables were projected to a unified raster graphical format with coordinate reference system WGS84, a spatial resolution of 0.27 × 0.27 latitudinal and longitudinal degrees, and cropped by the bounding box of our study area (Figure 1). To create predictive layers for RCP modelling (see section 2.4 *Statistical modelling*) mean values for the period 1991–2013 were taken. For each biological sampling site, mean annual environmental values were obtained taking into account the sampling time if the environmental data resolution was sufficient.

Temperature (°C), salinity (PSU), apparent oxygen utilization (μmol kg^{-1}), phosphates (μmol kg^{-1}), silicates (μmol kg^{-1}) and nitrates (μmol kg^{-1}), were taken from the World Ocean Atlas (Garcia et al., 2018a, b; Locarnini et al., 2018; Zweng et al., 2018). Water depths (m) were extracted from the bathymetric chart of the Arctic Ocean (Jakobsson et al., 2012). The percentages of 'fine' particles (silt and clay, i.e., particles with grain sizes ≤63 μm) in seafloor sediments were obtained from Pantiukhin et al., (2019). These sediment data, extracted from a geostatistical mapping effort, encompass the period 1935–2016 and represent the only Arctic sediment synthesis that is currently available. The slope of the seafloor (degree of inclination) was obtained from the Global Marine Environment Datasets (Basher et al., 2018).

Values of sea-ice coverage (%) were taken from Walsh et al., (2017). For the period from 1991 to 2013 a stack of averaged annual sea ice cover rasters were created, based on average values from April to September for each year. The summer period captures the largest variability in ice cover, as well as being the most important period for primary production. For each sampling point, mean sea ice concentrations were extracted from the stack of annual layers with an annual delay to accommodate that sea ice concentration has a delayed impact on benthic fauna. For RCP modelling (see section 2.4 *Statistical modelling*), we used mean sea ice concentrations from April to September averaged for the period 1991–2013 as predictive spatial space.

We used satellite remote sensing data to shed light on the food input to benthic communities. Averaged annual values of chlorophyll a (mg m^{-3}) were obtained from MODIS (NASA, 2018); euphotic
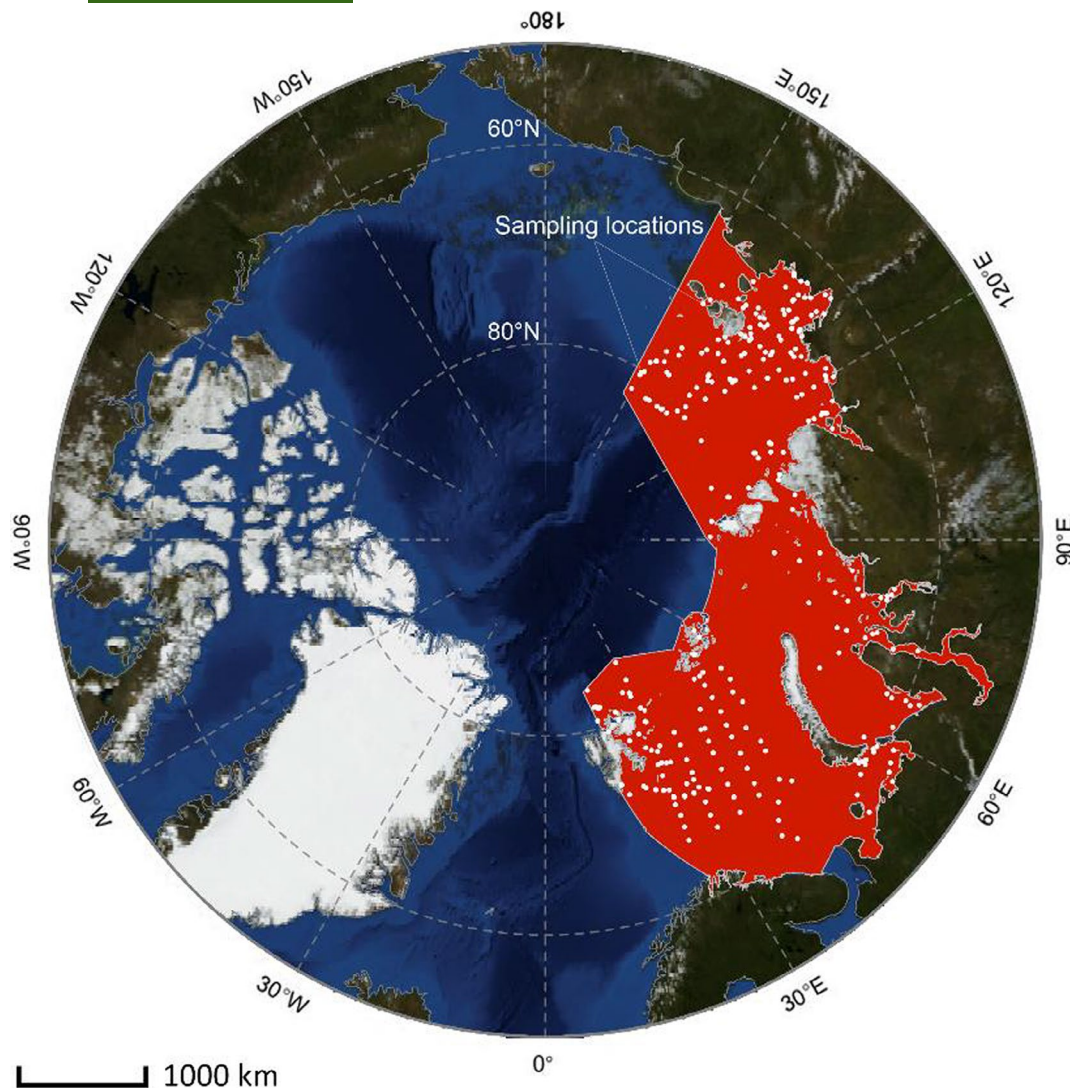
FIGURE 1 Study area. Eurasian Arctic shelf regions in the Barents, Kara and Laptev Seas (red) covering a total of ~3.5 million km^2. White dots mark the locations of the 354 sampling stations, visited during scientific expeditions between 1991 and 2013, from where the macrobenthos data used in our study have been collected

depth (m), particulate organic carbon (POC; mol m^{-3}) in the surface layer and POC integrated over the euphotic depth (mol m^{-2}) were extracted from GlobColour (Maritorena et al., 2010); ocean primary production (mg C m^{-2} day^{--1}) were extracted from www.science.oregonstate.edu/ocean.productivity (accessed September 2019). Additionally, we also estimated POC flux to the sea bottom (g C m^{-2} yr^{-1}) using the empirical function based on mean net primary production in the ocean surface layer and exponential flux decrease with water depth proposed by Suess (1980). The procedure of data extraction for biological samples and the creation of predictive spaces was performed similar to sea ice.

While the effects of global warming and ocean uptake of CO_2 have been well-studied for the surface ocean environment, there are not that many studies that focus on the shelf bottom waters (Holt et al., 2017), especially in the Arctic Ocean (Popova et al., 2014). For obtaining projected future values of near-bottom water temperature and salinity from 2006 to 2099 we used the dynamical downscaling ocean

biogeochemical model 'SINMOD' for Eurasian Arctic Shelves (Wallhead et al., 2017) because its regional scale and high resolution can capture heat and salt transport by Atlantic currents more accurately than other models for the region (Wallhead et al., 2017). Projected concentrations of sea-ice cover were extracted from the Norwegian Earth System Model NorESM1-M (2001–2099; Bentsen et al., 2013), because it was the model of the Coupled Model Intercomparison Project (CMIP5) that correlated best with observed sea ice-cover data.

SINMOD model projections are only available under the greenhouse-gas emission scenario A1B of the Special Report on Emissions Scenarios (SRES); NorESM1-M ran under the Representative Concentration Pathway RCP6.0 (based on the balanced use of all energy sources). These scenarios were chosen because they have the highest similarity to each other (Jubb et al., 2013). We consider the CMIP5 model for projected sea-ice concentrations instead of a more recent CMIP6 model, as there are no comprehensive intercomparison studies of the CMIP6 and SRES

scenarios so far performed. Moreover, it was shown recently that the performance of sea-ice models based on either CMIP5 or CMIP6 projections are similar in many aspects (Notz & Community, 2020).

2.4 | Statistical modelling

The RCP approach performs a one-step classification of multi-species data into groups (assemblages), based on species composition and species' responses to environmental covariates (Foster et al., 2013). Each species of a particular RCP has the same probability of occurrence within this RCP, and each RCP is a latent variable (i.e. it is initially unknown and only revealed by the model), whose distribution varies as a function of the environment. This dependence allows predicting the species' probability of occurrence at locations where no samples, but only environmental data are available (e.g. Foster et al., 2013). RCP models are implemented in the "RCPmod" package in R (Foster et al., 2013; R Core Team, 2019).

Using RCPs requires a number of steps. First, to remove covariates that have limited association with our biological data, generalized additive models (GAM) were used for each environmental variable and each species as a qualitative screening method (Foster et al., 2017; Hui et al., 2013). Environmental covariates with significant values ($p < 0.05$) for at least 66% of the species were included for further analysis (Foster et al., 2017). These GAMs were also used to identify the optimal number of species to be included in the RCP analysis (Figure A2), which was 169 species, occurring at least at 30 sampling locations (Table A1). Finally, correlation analysis of environmental variables that passed this preliminary screening was done (Figure A3), retaining environmental variables with a correlation <0.7 to avoid collinearity (Dormann et al., 2012).

Then, a set of meaningful environmental variables, that is, water depth, sea-ice coverage, near-bottom water temperature and salinity, proportion of fine sediments and POC, were a priori included in each model. The remaining variables were successively added to the RCP analysis, using a forward selection procedure based on a Bayesian information criterion (BIC) to determine the optimal combination of parameters (Hill et al., 2017). Continuous environmental covariates were added as linear and quadratic polynomials.

Finally, to determine the number of RCPs, we ran preliminary models that indicated that the optimal number of RCPs varied between two and seven regions. Then, full models were run with 2–7 RCPs, all meaningful environmental variables, 50 random starts, and using BIC to determine model fit. Random starts are necessary to avoid getting stuck in a local likelihood maximum (Foster et al., 2013). This then indicated that four RCPs were optimal (Figure A4). Next, we determined the optimal set of environmental variables, by combining all environmental variables (a priori and variable ones) with the preset of four RCPs and 300 random starts, using BIC to determine model fit. Model uncertainty was estimated via 1000 bootstrap replications, providing 95% confidence intervals (CI). Randomized quantile residuals plots (Figure A5) indicated suitable model performance (Foster et al., 2017).

To perform spatio-temporal projections of future shifts in macrobenthic community distribution, the best-trained RCP model was coupled to decadal changes (each decade from 2020 to 2099) of key environmental drivers projected by NorESM1-M (sea-ice cover) and SINMOD (bottom-water temperature and salinity) models. For visualizing, the produced probabilistic maps were transferred into the hard-classed maps (i.e. values of the most probable regions at each spatial point were mapped) (Hill et al., 2017).

3 | RESULTS

3.1 | General bioregionalization

The optimal model consisted of four RCPs: RCP 1 and RCP 2 encompass coastal and offshore shelf areas of the Kara and Laptev Seas, RCP 3 deeper areas in shelf troughs, at the continental slope of the Eurasian basin and in the deep sea of the Kara and Laptev Seas, and RCP 4 the Barents Sea (Figures 2, 3). Seven environmental variables, that is, water depth, sea-ice cover, near-bottom water temperature and salinity, the proportion of fine sediments, and POC ocean surface-layer concentrations, and depth of the euphotic zone showed the best fit based on BIC. Among the 169 species included in the RCP model, the most common taxa were Polychaeta (85 species), Malacostraca (30 species), Bivalvia (26 species) and Gastropoda (10 species). Few species were found in all four regions, that is, the polychaetes *Aglaophamus malmgreni*, *Chaetozone setosa*, *Micronephthys minuta*, *Scoletoma fragilis* and *Terebellides stroemii*, the amphipod *Aceroides (Aceroides) latipes*, the bivalve *Ennucula tenuis*, the brittle star *Ophiocten sericeum* and the gymnolaemate bryozoan *Eucratea loricata* (Table A1).

3.2 | Description of the regions of common profile (RCP)

RCP 1 has a spatial extent of ~570,000 km² with an average probability of occurrence of 73.5%. The region has a predominantly shallow zonation, the euphotic depth reaches the seabed in most places. The probability of occurrence of this region decreased with distance from shore. This RCP had the highest values of and positive correlation with surface-layer POC concentrations, as well as the lowest bottom-water salinities among all regions (Figure 4). Typical species were the polychaetes *Scoloplos armiger*, with a probability of occurrence of 41% and *Tharyx* spp. (37%), the crustacean *Saduria sabini* (33%), as well as the bivalves *Portlandia arctica* (69%) and *Macoma moesta* (27%) (Table A1).

RCP 2 covers ~530,000 km² and has an average probability of occurrence of 62.4%, which is the lowest among all regions. This region mainly represents the offshore Laptev Sea and the eastern Kara Sea, where it intersects with RCP 1. It also encompasses the western coastal Kara Sea, the coastal Barents Sea, as well as the archipelagos of Svalbard and Franz Josef Land (Figure 3). Due to the large longitudinal extent of the region, average sea-ice concentrations vary between 60% and 20%, and euphotic depths
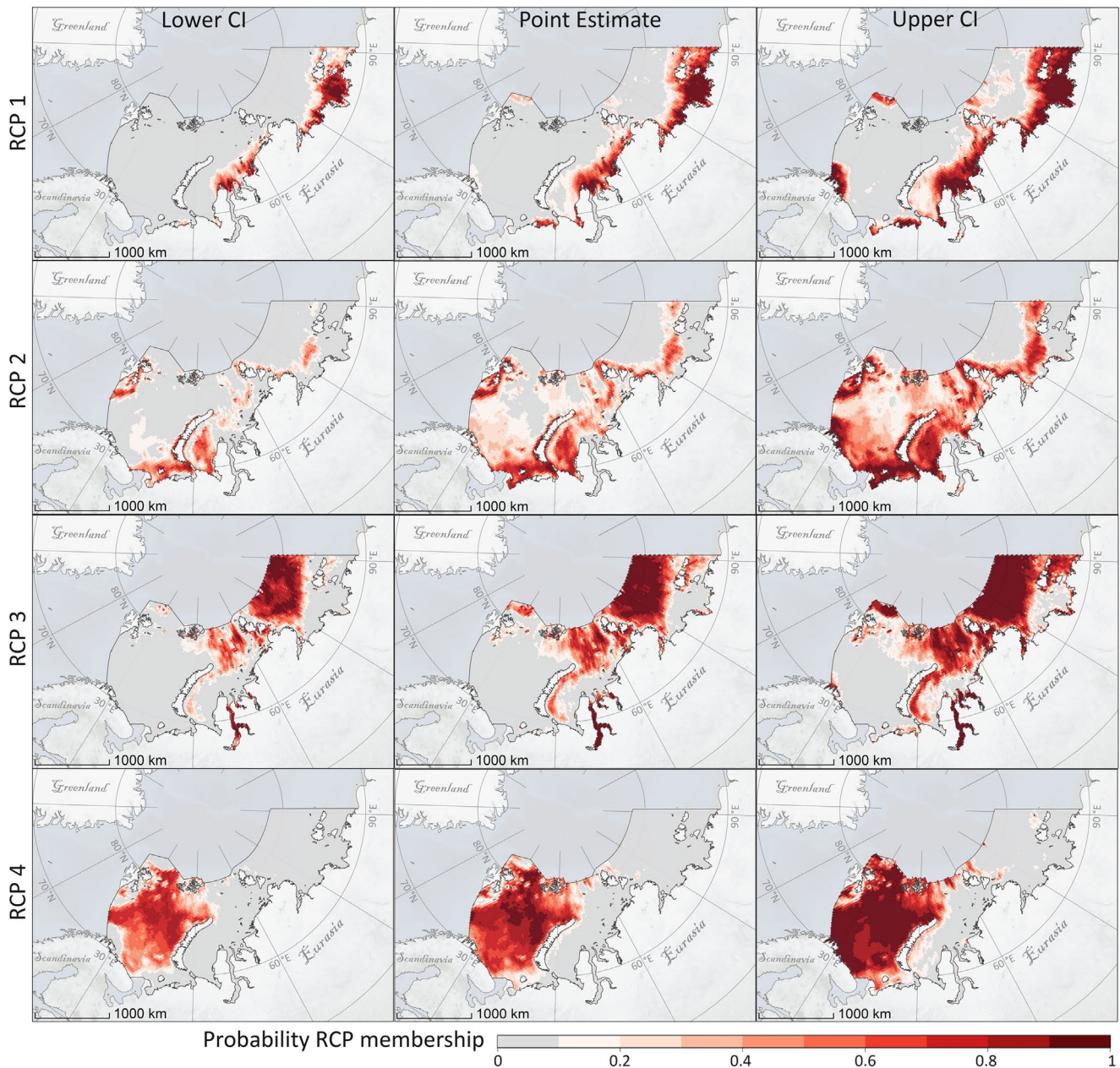
FIGURE 2 Predicted probabilities of occurrence of modelled macrobenthic ecoregions (Regions of Common Profile, RCPs) identified in our study in three Eurasian Arctic seas. The optimal model, based on 354 sampling sites, 169 species and seven environmental variables, comprised four ecoregions (RCP1, RCP2, RCP3 and RCP4). For each RCP (in rows), the point predictions are shown in the middle figure panel, as well as the lower and upper 95% confidence intervals (CI) in the left and right figures panels, respectively

between 20 and 50 meters (Figure 4). RCP 2 shows fairly strong similarities in biodiversity composition with RCP 4. However, it has some typical species: the polychaetes *Capitella capitata* (36%), *Chone paucibranchiata* (34%), *Clymenura polaris* (40%), *Eteone* spp. (50%), *Leitoscoloplos* (40%), *Pholoe inornata* (47%) and *Polydora* spp. (51%), the cumacean *Diastylis rathkei* (24%), the bivalves *Ciliatocardium ciliatum* (39%), *Montacuta spitzbergensis* (25%), *Yoldiella nana* (32%), and the priapulid *Priapulus caudatus* (43%) (Table A1).

RCP 3 has a spatial extent of ~1,100,000 km^2 and the highest average probability of occurrence amongst all RCPs (77%). It includes mainly deep areas of the Eurasian Basin of the Arctic Ocean and parts of the slopes of the Kara and Laptev Seas. It was positively correlated with water depth, percentage of fine sediments and presence of sea-ice, and negatively correlated with surface-water POC concentrations. Other environmental drivers had rather stable values (Figure 4). The polychaete *Ophelia* spp. (23%) was typical of RCP 3 (Table A1).

FIGURE 3 Prediction map showing the geographical distribution of four macrobenthic ecoregions (Regions of Common Profile: RCP1, RCP2, RCP3 and RCP4) identified in our study within three Eurasian Arctic seas. Each spatial point-estimate cell shown in Figure 2 was mapped in a hard-class approach based on its most likely RCP. Macrobenthos sampling locations are marked by white dots
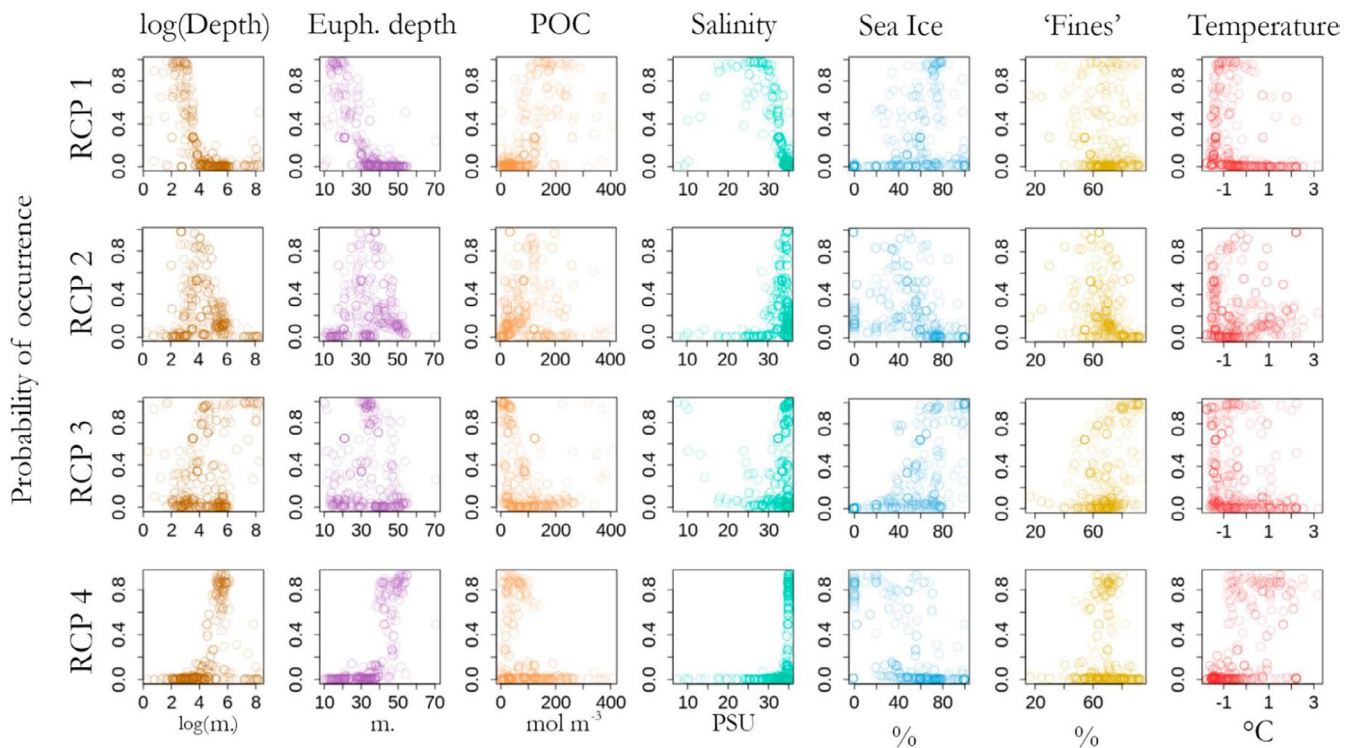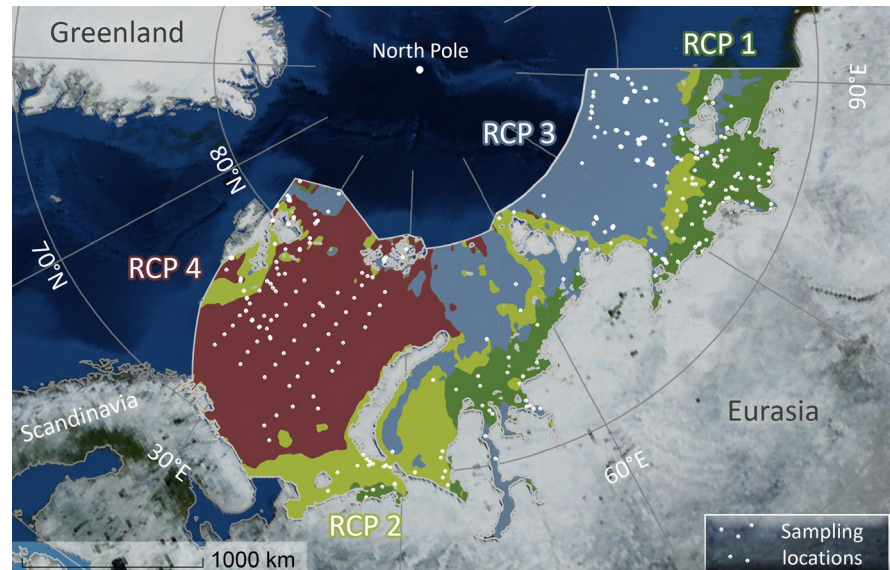
FIGURE 4 Probability of occurrence of each macrobenthic Region of Common Profile (figure panel rows: RCP1, RCP2, RCP3 and RCP4) identified in our study for each of the seven environmental parameters (figure panel columns) considered in our study: water depth (m; logarithmic scale), depth of euphotic zone (m), particulate organic carbon (POC, mol m-3), near-bottom-water salinity (psu), sea-ice cover (% area), proportion of 'fines' (clay and silt) in surficial seabed sediments (%), near-bottom-water temperature (°C)

RCP 4 is the largest region, covering approximately ~1,300,000 km², with an average probability of occurrence of 76%. It mainly represents the Barents Sea and was characterized by a negative correlation with sea-ice coverage, and highest bottom-water temperatures and salinities (Figure 4). A large number of species occurred only in this RCP, such as the polychaetes *Aricidea (Strelzovia) quadrilobata* (72%), *Glyphanostomum pallescens* (69%), *Maldane arctica*

(59%), *Prionospio cirrifera* (85%) and *Scoloplos acutus* (90%), the malacostracan isopods *Caecognathia elongata* (53%), *Calathura brachiata* (42%), and cumacean *Leucon (Leucon) nathorsti* (44%), the bivalve *Yoldiella lucida* (32%), the gastropod *Punctulum wyvillethomsoni* (42%), the anthozoan *Gersemia fruticosa* (0.32), the sipunculid *Nephasoma diaphanes diaphanes* (50%), the nemertinean *Carinina* spp. (44%), and the molluscan Aplacophora spec. aff. (42%) (Table A1).

3.3 | Climate change-driven projection

The climate-change projections suggested a general eastward shift of the RCPs over the 21st century, mainly correlated with retreating sea-ice and increasing sea-bottom temperature (Figure 5). RCP 1 was projected to experience the most profound shift, disappearing almost completely from the Barents and Kara seas. RCP 3 will be displaced in the trenches of the Barents and Kara Seas by RCP 2 and RCP 4 and will be confined to the deep regions of the continental slope and the deep sea of the Eurasian basins (Figure 5). By the end of the 21st century, RCP 2 will become concentrated in the south of the Barents and Kara Seas, as well as over the offshore shelf of the Laptev Sea (Figure 5). RCP 4 was also projected to expand eastward and northward into the Kara Sea, as well as towards the fjords of Spitsbergen and Novaya Zemlya (Figure 5).

4 | DISCUSSION

Based on our novel synthesis of Arctic benthic fauna (Hansen et al., 2019) and the recently developed model-based bioregionalization method 'RCP' (Foster et al., 2013), we identified four bioregions across the Eurasian Arctic shelves (Figures 2, 3). Each region is represented by characteristic patterns of biodiversity (Table A1) and ranges of environmental conditions (Figure 4). Based on model projections of future climate-driven changes in near-bottom oceanography (Wallhead et al., 2017) and sea-ice cover (Bentsen et al., 2013), we identified the spatiotemporal dynamics of the bioregions by the year 2100 (Figures 5, A6).

While there are long-term data from quite a number of local studies on benthic biota for littoral regions (bays and fjords) in Eurasian-Arctic seas (Wassmann et al., 2011), there are only a few seascape-scale studies, also including offshore regions, that our results can be compared to (Mironov, 2013; Zenkevitch, 1963). Zenkevitch's (1963) bioregionalization, based on data sampled before 1947, overlaps with our Eurasian-Arctic study area, allowing us to put our findings spanning the period 1991 to 2013 into a historical context (Figure 5). Overall, there is a pronounced similarity between Zenkevitch's (1963) spatial structure, which was based on traditional analysis methods, and our RCP model-based results: RCP 1 and RCP 2 largely correspond to the "Shallow brackish-water province" and the "Shallow marine Siberian province", respectively, which are both parts of the "High-Arctic shallow sub-region". RCP 3 aligns with the "Abyssal Arctic sub-region", covering deep-sea parts of the Arctic Ocean and slopes of the Kara and the Laptev Seas. In contrast with Zenkevitch's scheme (1963), RCP 3 also overlaps with other regions and is even found in shelf areas. Zenkevitch's (1963) "Shallow low-Arctic sub-region" largely coincides with RCP 4, mainly encompassing the Barents Sea bounded by Spitsbergen and Franz Josef Land in the north and Novaya Zemlya in the east. Notable dissimilarities between the RCP structure and the classification of Zenkevitch (1963) exist at the southern and northern borders of the Barents Sea. In the RCP model, the southern Barents Sea belongs to RCP 1 and RCP 2

instead of RCP 4, and in the north RCP 4 wedges into the shallow high-Arctic area, separating Franz Joseph Land from Svalbard. The areas around these two archipelagos are characterized by a mosaic of RCP 2 and RCP 4.

The spatio-temporal projections based on the relatively optimistic climate-change scenarios reveal a clear trend of borealization of the major part of the study area. These shifts are strongly related to the retreat of the Arctic sea ice, which is assumed to eventually lead to the weakening of the pelago-benthic coupling and a decrease of the input of organic matter to the sea bottom (Piepenburg, 2005; Wassmann & Reigstad, 2011). Moreover, the warming of the near-bottom oceanic layer, as well as the change of the salinity regime in some Eurasian shelf regions, are projected to partially affect suitable benthic habitat areas (Renaud et al., 2019) and cause poleward migration of species (IPCC, 2014).

RCP 1 is projected to be most vulnerable to projected climate-change impacts, as it may virtually disappear from the Kara Sea and partly shrink in the Laptev Sea during the 21st century (Figure 5). These Arctic seas are expected to be most affected by sea-ice retreat and warming (Bentsen et al., 2013; Wallhead et al., 2017). However, in the eastern part of the studied region, RCP 1 will still dominate in the Laptev Sea, whilst RCP 2 will become almost absent according to projections for 2020–2050 (Figure A6). It has to be noted, however, that the results need to be interpreted by considering the uncertainty introduced by the sea-ice NorESM1-M model, its resolution did not resolve the occurrence of the rather narrow flaw-lead polynyas in the Laptev Sea (Figures 5, A6), which mostly determines the distribution of RCP 2. After 2050, RCP 2 will expand quite significantly while the extent of RCP 1 will shrink by 2099 due to further sea-ice decline. Therefore, it is quite likely that the projected contraction of RCP 1 and expansion of RCP 2 in this region will be even more pronounced. However, to answer this question, it is necessary to use models with a higher spatial resolution, which are appropriate for reconciling the fine-scale spatial distribution of the sea ice and can reveal the dynamics of formation and distribution of polynyas in the area.

RCP 4 is most expanding its spatial extent throughout the entire climate simulation by 2100 (Figures 5, A6), reflecting that it is most affiliated with higher temperatures and less sea ice (Figure 4) under global warming (IPCC, 2014). However, while it is projected to generally expand northwards, it will not do so towards near-shore zones (Figures 5, A6) because there RCP 2 that is similarly affiliated with increased temperatures and less ice (Figure 4) will persist and impede the expansion of RCP 4. Moreover, RCP 4 is most representative at high salinities, while RCP 2 is more tolerant to the typical strong salinity fluctuations in near-shore zones (Figure 4). The deep RCP 3 will gradually retreat northwards to even deeper regions of the central Arctic Ocean, in response to the projected warming of near-bottom waters in shelf depressions, sea-ice decline (Figure 5) and be gradually replaced by the "warm-water" RCPs 2 and 4 (Figures 5, A6).

The projections suggest that RCP 1 will start occurring in the south-western Barents Sea after 2030 (Figure A6). This prediction is rather surprising, as RCP 1 is actually mostly affiliated
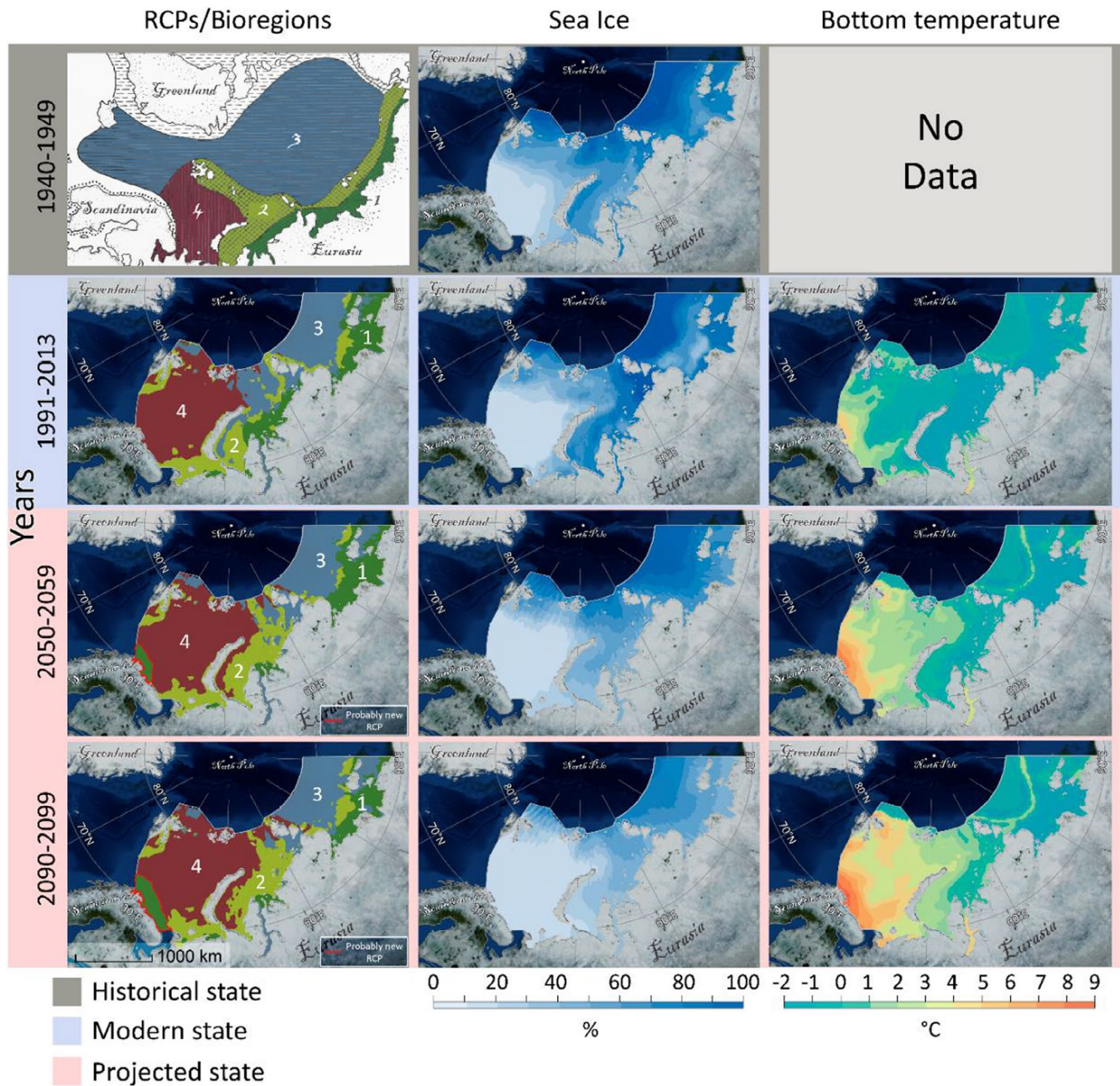
FIGURE 5 Distribution of the four Regions of Common Profile (RCP) identified in our study in three Euasian Arctic seas (left column of figure panel: 1, 2, 3 and 4), sea-ice cover (middle column of figure panel: % area), and near-bottom water temperature (left column of figure panel: °C) for four periods of time: past: uppermost figure panel row (1940–1949) current: second figure panel row (1991–2013); and two projected scenarios (third panel row: 2050–2059; and fourth panel row: 2090–2099). Past distributions are based on the analysis of mid-20th century expeditions (assessed by Zenkevitch (1963)). Current distributions are based on our RCP study and present sea-ice and oceanographical datasets. Future distributions of the four RCPs were estimated by coupling the best-trained RCP model to environmental conditions predicted by projections of NorESM1-M (sea-ice cover) and SINMOD (bottom-water temperature) models that in turn were driven by the climate scenarios Representative Concentration Pathway RCP6.0 of the Coupled Model Intercomparison Project (CMIP5) (for NorEMS1-M) and A1B of the Special Report on Emissions Scenarios (SRES) A1B (for SINMOD)

with the presence of sea ice, cold temperatures and low salinities, while in this area climate change will rather lead to the opposite trends (Figure 4). This artefact highlights the fact that when using RCP models for forecasting, false projections can occur, particularly at the boundaries of the studied regions where potential environmental conditions may exceed the values of the original trained data, and the changes would not involve shifts in the range and extension of delineated RCPs but rather the emergence of novel RCPs that are not foresee by the data analysed. The current RCP approach does not allow for modelling such pronounced

shifts, and an appropriately advanced feature should be implemented within the RCP model.

There is evidence of both long-term resilience and vulnerability of benthic communities to climate-driven environmental change in the Eurasian Arctic. Kokarev et al., (2017) studied benthic communities in the Laptev Sea along a latitudinal transect (72–78°N) in the Laptev Sea in 2015 and concluded that their overall spatial distribution corresponded well to that described for this region in preceding decades, indicating the long-term stability of the seabed ecosystems in the region. Our finding that the benthic fauna in the Laptev Sea have not changed much from Zenkezvitch's (1963) assessment, reflecting conditions before 1947, to the 1991–2013 period of our study and the projections until 2100 corroborates this conclusion. Azovsky and Kokarev (2019) reported a strong resilience of benthic communities to climatic changes in the Baydaratskaya Bay (Kara Sea), with no signs of borealization in this region during the last few decades. Similarly, our study indicated a stable dominance of RCP 2 in this area of the Kara Sea that can be traced back to the period of Zenkevitch (1963) and is also visible in the projections up to 2099. Kędra et al., (2013) reported a strong resilience of the benthic communities of Svalbard Bank from 1925 to 2009, indicating adaptation to the historical fluctuation of temperatures. Likewise, the projections in our study also suggest that Svalbard Bank will not change in RCP allocation by 2099. These examples of resilience indicate that the magnitude of change in key environmental conditions was not sufficient to lead to a dramatic shift in the composition of the benthic fauna of these regions.

Despite the resilience of benthic fauna in some Eurasian-Arctic areas, we found a clear trend of eastward shifting biota and ecoregions under climate change (Figure 5), which has also been reported in previous studies. In the Barents Sea, Matishov et al., (2012) recorded a notable correlation between the propagation of boreal benthic fauna and ocean warming, while Fossheim et al., (2015) found the same rapid borealization for fish communities. These trends are not only caused by ocean warming but very likely also in response to indirect impacts resulting from the changes in the pelagic-benthic coupling due to the borealization of the pelagic biota and the shifts in the food-web pathways (Kortsch et al., 2015).

With regard to the projections until 2099, only a subset (sea ice, bottom-water temperature and salinity) of the environmental drivers used in the RCP model were considered. Others, such as POC and the depth of the euphotic zone, had to be kept stationary, due to lack of information about their spatio-temporal dynamics in the future, although their climate-driven change will potentially lead to a shift in benthic fauna.

4.1 | Implications for conservation management

Marine conservation efforts in the Arctic region are considered to be a high priority in the face of recent climatic changes and the concomitant intensification of human activities (Solovyev et al., 2017; Spiridonov et al., 2017). In general, the RCP approach can be considered a powerful model-based mapping tool for informing ongoing and planned spatial conservation management (Hill et al., 2017). For instance, in case of the Eurasian-Arctic study area, it could help improving the identification of conservation priority areas that Solovyev et al., (2017) suggested based on the delineation of biogeographical provinces of benthic invertebrates, by application of a more accurate quantitative approach. The RCP approach is also suitable as a conceptual framework for establishing community-level Essential Biodiversity Variables (EBVs), which have been proposed as a key tool for better understanding the patterns and trends in Earth's biodiversity (Pereira et al., 2013). To this end, multiple current and projected RCPs, modelled for various marine biota (e.g. pelagic, benthic), diversity measures and environmental parameter sets, have to be stacked in a temporal cubic format (Jetz et al., 2019).

4.2 | Data paradigm in biogeographical research

Accelerating climate change is leading to the rapid poleward migration of species in the oceans. Therefore, decisions have to be made for enhancing the efficiency of marine conservation efforts. Moreover, fast progress in the aggregation of biological data (e.g. PANGAEA) and eDNA-based assessments of the 'dark diversity' (Boussarie et al., 2018) will result in rapidly growing data volumes, posing challenges for the efficient analysis of these data that is necessary for further enhancing our knowledge on biodiversity and advancing environmental management. To address these challenges, modelling approaches should be established within the frameworks of the bio-information systems (e.g. PANGAEA). In this context, the integration of RCP approaches is the key to address these tasks. Here, we demonstrated how RCP modelling can be used to extract valuable information from a broad spectrum of datasets, bridging between past, current and future states of the ecoregions.

Overall, the representation of bioregions in the cube-shaped format of layers of RCPs models on the number of different marine communities with underlying environmental layers could give an in-depth level of the ecosystem. Such abstractions will ultimately enhance our knowledge about the functioning of the ecosystems across multiple spatio-temporal scales (Jetz et al., 2019).

4.3 | Conclusions

Building on recent RCP models (Foster et al., 2013), an unrivalled synthesis of seascape-scale data of Arctic seafloor communities and ecologically relevant environmental parameters (e.g. Pantiukhin et al., 2019), we examined the bioregionalization of seafloor communities in the Eurasian Arctic. Our work provides the first model-based quantitative mapping of macrobenthic assemblages based on the spatial distribution of taxa and key environmental drivers, such as water depth, sea-ice cover, bottom-water temperature and salinity, proportion of fine sediments, POC and depth of the euphotic zone. Climate scenario-based spatio-temporal projections

of future RCP distribution allowed for the first time to assess community-level shifts of ecoregions over the course of the 21st century. Applying the RCP approach on a long-term basis would offer an opportunity to identify 'hotspot' regions, which are characterized by particularly pronounced change and particularly little available information, and thus guide future field activities in the Eurasian-Arctic seas.

CONFLICT OF INTEREST
No conflict of interest exists.

DATA AVAILABILITY STATEMENT
All biotic data are available online via https://doi.panga ea.de/10.1594/PANGAEA.910004. Environmental data were taken from open-source online repositories (see main text), with the exception of sediment-data that we compiled for this study (Pantiukhin et al., 2019). The results of the RCP model and raw data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.8pk0p2nn9.

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BIOSKETCH

The authors focus their research on an enhanced understanding of functional biodiversity and biogeography in polar seas under declining sea ice or other environmental stressors, large-scale open-access data and modern statistical models, supported by international cooperation (see 'CATS - The Changing Arctic Transpolar System', https://www.transdrift.info/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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