Oceanologia (2017) 59, 565—575

Available online at www.sciencedirect.com

ScienceDirect

journal homepage: www.journals.elsevier.com/oceanologia/

ORIGINAL RESEARCH ARTICLE

Benthic *Crustacea* and *Mollusca* distribution in Arctic fjord — case study of patterns in Hornsund, Svalbard

Anna Drewnik [a,b,*], **Jan Marcin Węsławski** [a], **Maria Włodarska-Kowalczuk** [a]

[a] *Institute of Oceanology, Polish Academy of Sciences, Sopot, Poland*
[b] *GIS Centre, University of Gdańsk, Poland*

Received 26 September 2016; accepted 6 January 2017
Available online 4 July 2017

KEYWORDS
Arctic;
Fjord;
Benthos;
Species distribution modeling;
Near-bottom waters

Summary We present the results of species distribution modeling conducted on macrobenthic occurrence data collected between 2002 and 2014 in Arctic fjord — Hornsund. We focus on species from *Mollusca* and *Crustacea* taxa. This study investigates the importance of individual environmental factors for benthic species distribution, with a special emphasis on bottom water temperature. It aims to verify the hypothesis that the distribution of species is controlled by low water temperatures in the fjord and that the inner basins of the fjord serve as potential refugia for Arctic species threatened by the climate change-related intensification of warmer water inflows. Our results confirm the importance of bottom water temperature in regulating the presence of benthic fauna in the Hornsund fjord. The distribution of studied species is clearly related to specific water mass — colder (<1°C) or warmer (>1°C); and the preferred temperature regimes seem to be species specific and unrelated to analyzed groups. This study supports the notion that inner basins of the Hornsund fjord are potential refugia for cold water Arctic fauna, while the outer and central basins provide suitable habitats for fauna that prefer warmer waters.
© 2017 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier Sp. z o.o. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Svalbard archipelago is one of the most rapidly warming regions in the Northern hemisphere (Acia, 2005). One of the main drivers of this warming is the West Spitsbergen Current (WSC). Recently, studies have shown that the WSC is responsible for the majority of Atlantic Water (AW) fluxes, which carries heat into the central Arctic (Pavlov et al., 2013; Schauer et al., 2008; Smedsrud et al., 2010; Walczowski and Piechura, 2007). Moreover, warming and northernmost extension of these waters has been observed (Schauer

* Corresponding author at: Institute of Oceanology, Polish Academy of Sciences, Powstańców Warszawy 55, 81-712 Sopot, Poland.
E-mail address: drewnik.anna@gmail.com (A. Drewnik).
Peer review under the responsibility of Institute of Oceanology of the Polish Academy of Sciences.

Production and hosting by Elsevier

http://dx.doi.org/10.1016/j.oceano.2017.01.005
0078-3234/© 2017 Institute of Oceanology of the Polish Academy of Sciences. Production and hosting by Elsevier Sp. z o.o. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

et al., 2008; Spielhagen et al., 2011; Walczowski and Piechura, 2006, 2007). Inflows from the WSC have been noted in the fjord systems around Svalbard (Berge et al., 2005; Cottier et al., 2005; Nilsen et al., 2006, 2008; Pavlov et al., 2013; Skogseth et al., 2005; Teigen et al., 2011) and account for the instability and increasing temperatures in the fjords' waters (Pavlov et al., 2013).

Atlantic water carried from a region of higher biodiversity (Norwegian Sea) may also affect the Arctic ecosystem by mediating the northern expansion of certain boreal taxa (Węsławski et al., 2009). The WSC that flows along the Norwegian coast is one of the primary pathways of boreal species advection to the Arctic (Berge et al., 2005; Węsławski et al., 2011). Poleward shifts of pelagic as well as benthic species and communities have been broadly documented (Beaugrand et al., 2002; Berge et al., 2005; Drinkwater, 2006; Grebmeier et al., 2006; Piepenburg, 2005). Initial observations have also demonstrated that boreal fauna starts to dominate near the mouths of Spitsbergen fjords (Svalbard archipelago) (Węsławski et al., 2011). Overall, climate change may significantly affect the physical conditions and local Arctic ecosystems. Examples of such impacts on these ecosystems' structure and functioning (Basedow et al., 2004; Berge et al., 2005, 2009; Hop et al., 2002), as well as of fauna migrations and changes in species composition (Falk-Petersen et al., 2007; Jónsson and Valdimarsson, 2005; Wassmann et al., 2011), have already been noted. These changes may affect Arctic biodiversity and even lead to the supplanting of indigenous Arctic species (Dawson et al., 2011; Węsławski et al., 2009).

On the other hand, species that are relicts of past climate regimes are known to persist in many places. In the Baltic, approximately 5% of the macrofauna species present evolved under former, cold Yoldia sea conditions. Cold, brackish water species have also survived in several large lakes in Scandinavia and Russia (Leppäkoski and Olenin, 2001). Relict populations of cold-water species have also been reported in boreal fjords (Drainville, 1970; Freeland et al., 1980). Norwegian fjords are known to host cold water species in their innermost basins, while the outer basins are dominated by warm water Atlantic species (Freeland et al., 1980). The same distribution of species may occur in the future in the fjords of the European Arctic. Some diversification is already being observed in Spitsbergen fjords, and it may be enhanced further by climate change and continual Atlantic water inflows. Semi-closed fjords or topographically isolated inner basins have more homogeneous and uniform fauna, and they support a greater proportion of Arctic-origin species than outer areas under the influence of shelf waters (Kendall et al., 2003; Kędra et al., 2009; Renaud et al., 2007; Weslawski, 1990; Wlodarska-Kowalczuk et al., 1998; Włodarska-Kowalczuk and Węsławski, 2008). Their isolation enables these fjords to retain cold, dense, oxygen-rich bottom water that is produced in the fjords during annual ice formation (Svendsen et al., 2002; Syvitski et al., 1987; Weslawski et al., 2010; Węsławski et al., 2011; Wlodarska-Kowalczuk and Pearson, 2004). As a result, these sheltered bays create stable conditions and may serve as suitable refuges for cold water Arctic species facing ongoing warming in the region (Lydersen et al., 2014).

One way to investigate the mechanism and potential consequences of climate warming on biocoenosis and its components is through the application of species distribution modeling, a method that is gaining increasing attention in marine environmental studies (Degraer et al., 2008; Glockzin et al., 2009; Gogina et al., 2010; Reiss et al., 2011; Robinson et al., 2011). It has been used frequently to model habitat suitability and the spatial patterns of benthic fauna distribution, inter alia, under different climate change scenarios (Degraer et al., 2008; Ellis et al., 2006; Gogina and Zettler, 2010; Gogina et al., 2010; Inglis et al., 2006; Meißner et al., 2008; Thrush et al., 2003; Willems et al., 2008; Ysebaert et al., 2002). In such cases, a crucial step is to include climatic factors or their proxies in a model. In the case of benthic assemblages, in particular those inhabiting Arctic regions, the bottom water temperature has been identified as the most significant one. The purpose of our study is to investigate whether benthic fauna distribution in one of the Spitsbergen fjords — Hornsund — is controlled by the occurrence of cold water masses. We aim to determine whether and how climate change-related Atlantic warm water inflows affect benthos, and we seek to identify potential refugia for these Arctic communities in the fjord. In doing so, we aim to verify whether inner fjord basins could serve as such shelters. We present data on deeper soft bottom sublittoral (<50 m), with no data from shallows or hard substrata. Summer temperatures were analyzed only, as during winter season an entire water column in the fjord is isothermal and isohaline (Swerpel, 1985; Weslawski et al., 1991). Moreover, benthic fauna is the long-living part of the ecosystem with longer life cycles than planktonic communities, ability to incubate eggs or slowing the growth in the winter (Hop et al., 2002; Warwick, 1993; Weslawski et al., 1991). Hence, benthos can integrate hydrographic processes over the years and is believed to serve as a great indicator of long-term environmental changes (Kröncke, 1995; Renaud et al., 2008). The results of our study are discussed on the background of observed changes in Arctic biodiversity to highlight the need for, and usefulness of, collecting data on the distribution of individual species and communities as indicators of Arctic ecosystem change.

2. Material and methods

2.1. Study area

The study area was Hornsund — the southernmost fjord of west Spitsbergen, located at 76 to 77°N. Hornsund is a medium-sized fjord (24 km long, 11 km wide at its mouth) with a strongly developed coastline that includes five secondary bays (see www.iopan.gda.pl/projects/Visual). The Hornsund fjord is under the influence of the coastal Sørkapp Current, which carries cold, less saline Arctic water from the northeastern Barents Sea, and the West Spitsbergen Current, which carries saline Atlantic water from the Norwegian Sea (Cottier et al., 2005; Piechura et al., 2001). Both water masses can penetrate the fjord area because Hornusnd does not have a sill at its entrance. Circulation pattern in Hornsund is similar to other West Spitsbergen fjords. Water entering the fjord tend to inflow along the southern coast and outflow along northern coast (Cottier et al., 2010). Atlantic water (modified by mixing with Arctic Water) is usually observed as a bottom inflow. Its distribution and range differ from

summer to summer; however, a few shallow sills occur throughout the fjord and separate the outer and central parts of Hornsund from its inner basins (Drewnik et al., 2016), thereby limiting the distribution of Atlantic water fluxes (Promińska et al. unpublished data). The deepest layers of isolated basins are reservoirs of cold, saline winter water produced through salt rejection during sea-ice formation (fall-winter period). Tides in Hornsund fjord are regular, semidiurnal with range from 0.8 to 1.8 m (Węsławski et al., 1993; Zagórski et al., 2015). Due to the local climate, topographic conditions and Atlantic water fluxes, the Hornsund region is thought to be more vulnerable to climate-oceanic system changes than the rest of the Svalbard archipelago (Błaszczyk et al., 2013). Hence, it is a hotspot for observations related to the consequences of climate change on Artic ecosystems.

2.2. Benthic data

Sampling was performed during summer R V OCEANIA cruises performed by the Institute of Oceanology Polish Academy of Sciences between 2002 and 2014. Samples were collected using a Van Veen grab (0.1 m^2) at 130 stations dispersed across the Hornsund fjord (Fig. 1). The material was sieved onboard through a 0.5 mm mesh and preserved in a buffered 4% formaldehyde solution. In the laboratory macrofauna individuals were identified to the lowest possible taxonomic level (most often to the species level) using the taxonomic nomenclature after World Register of Marine Species: WoRMS (www.marinespecies.org). For the purposes of this study, only occurrence data for species in the *Mollusca* and *Crustacea* groups were used. Distribution data were compiled for species with at least 5 records of occurrence available for modeling. The "only-presence" occurrence data were imported into ArcGIS 10.1 and Maxent software for further processing and modeling.

2.3. Environmental data

The basic approach to species distribution modeling is to select physical factors (predictors) that are crucial for species persistence and that may control its distribution. For this study, we selected some of the factors known to be important to benthic fauna (Gogina and Zettler, 2010; McArthur et al., 2010; Olenin, 1997; Reiss et al., 2011) — topography and geomorphology (depth, slope, and rugosity), substratum (mean grain size of sediment) and near-bottom water characteristics (temperature, salinity and their derivatives — mean and range). Additionally, we used the distance from the glacier fronts as a proxy for glacier outflow, because no precise data on this predictor were available for the analyzed time period. Organic matter content in sediments was omitted since most of it consists of terrestrial, old carbon (www.iopan.gda.pl/projects/Game/prezentacje/Zaborska_et_al.pdf) that is of very limited use for benthic fauna. Furthermore, our previous studies concerning a detailed analysis of conditions prevailing at the bottom of the Hornsund revealed that organic matter content in sediments is stable across the fjord area (Drewnik et al., 2016). Hence, we consider this factor as insignificant in controlling benthic species distribution in Hornsund.

Sampling was performed during routine summer cruises between 2002 and 2014 (Fig. 1). Sediment grain size analysis was performed on surface (upper 5 cm) sediment samples collected using box corers, analyzed with a Malvern Mastersizer 2000 laser particle analyzer and calculated in GRADISTAT

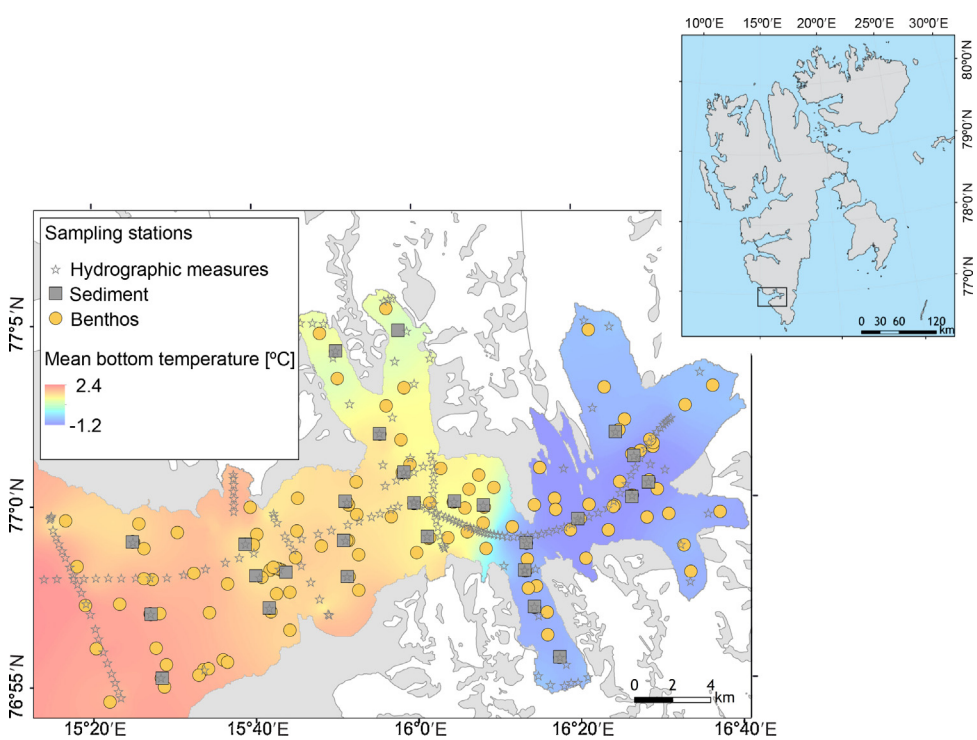

Figure 1 Study area and locations of sampling stations. Circles indicate benthos sampling locations; squares represent sediment collection sites and stars indicate hydrographic measurements; graduated color scale shows mean bottom water temperature.

8.0 using the geometric method of moments. Hydrographic measurements were collected using an SBE 49 probe. Near-bottom measurements were analyzed separately to model the conditions prevailing near the seabed. Water depth was measured simultaneously with other environmental factors at each sampling station (Echotrac MK III 12 kHz, Odom Hydrographic Systems). For more details on sampling and laboratory analysis see Drewnik et al. (2016). All continuous surfaces (raster layers) necessary for modeling were created and processed using ArcGIS 10.1 software.

2.4. Maximum entropy modeling

Maxent (maximum entropy model) is a general-purpose machine learning method used for species distribution modeling (SDM). Species distribution models are used to predict the actual (at present) or potential (at some other time period) distribution of habitats suitable for species survival over the studied area and to explore species—environment correlations. The models require data on species' occurrences in geographical space, as well as digital maps of environmental factors representing conditions encountered by the studied species (Beuchel et al., 2006; Franklin, 2009). The Maxent algorithm estimates a target probability distribution for each species by finding the distribution of maximum entropy (that is closest to uniform) and constraining the expected value of each environmental factor to match its empirical average (Phillips et al., 2006; Reiss et al., 2011). This method is equivalent to finding the maximum-likelihood distribution of a species (Bučas et al., 2013). The Maxent model's reliability has been confirmed in numerous studies (Elith et al., 2006; Hernandez et al., 2006; Hijmans and Graham, 2006; Ortega-Huerta and Peterson, 2008; Pearson et al., 2007; Wisz et al., 2008). The Maxent algorithm was chosen for the analysis because it is a generative, rather than the discriminative tool that allows the use of a limited amount of training data (as few as 4 sampling points; Pearson et al., 2007; Phillips et al., 2006). Benthos was sampled in a fixed net of 130 stations dispersed across the entire Hornsund fjord area (deterministic distribution), however, single species were present at far fewer localities — even 6 (Fig. 4). Moreover, Maxent builds the model using "only presence" biological data. Information about the absence of a species in the study area is not required so possible false absences are avoided. These are incredibly important advantages, especially in benthic marine studies where the capacity to sample at numerous locations is often limited and the species absence is never certain (only a subsample is studied; even several replicates of grab samples can miss the species and falsely provide absence information for the model).

2.5. Model processing and interpretation

In this study, we used Maxent software version 3.3.3k (http://www.cs.princeton.edu/~schapire/maxent). The description of the maximum-entropy approach for species habitat modeling as well as equations implemented in the software can be found in Elith et al. (2011), Phillips et al. (2004, 2006). The models were created using 10,000 pseudo-absence points; the convergence threshold was set at 10^{-5}, and the maximum iteration value was set at 500. Features (environmental factors or their functions) were selected automatically by the program depending on the number of presence records. A regularization value was also matched automatically to reduce over-fitting. The cumulative probability output format was chosen for the models' predictions. Cumulative probability ranges from 0 to 100% and indicates relative suitability. The value of a given map cell is calculated as the sum of that cell plus all other cells with equal or lower probability multiplied by 100 (for more details see Phillips et al., 2006). The cumulative output map also uses colors to indicate predicted probability — warmer colors show areas with better conditions predicted (http://www.cs.princeton.edu/~schapire/maxent). In other words, more suitable for that species (Phillips et al., 2006). Maxent automatically creates maps of this suitability that can be later transformed into simpler and clearer binary maps (1 — suitable vs. 0 — not suitable habitat) using a chosen threshold — a value above which model output is considered to be a prediction of presence. We transformed cumulative probability maps (Appendix A) using the ArcGIS 10.1 and the lowest presence threshold (LPT) — the lowest predicted value associated with any one of the observed presence records. It identifies sites that were at least as suitable as those where a species' presence has been recorded (Pearson et al., 2007). There are number of thresholds that are used in Species Distribution Modeling and applying a different one can slightly enlarge or decrease the areas predicted suitable for a species. We chose to use LPT threshold because it reduces false positive predictions, i.e., minimizes the proportion of the study area predicted as present. It is very conservative, hence sometimes the patches of suitability can be as small as a location where the species was recorded, but on the other hand, it enables to illustrate the most suitable sites for species in the studied area.

Supplementary Appendix A related to this article can be found, in the online version, at doi:10.1016/j.oceano.2017.01.005.

LPT values were also used to evaluate the performance of our models. We used the jackknife (or 'leave-one-out') validation approach, which is suitable for testing models with few observed location records available (fewer than 25 locations) (Hernandez et al., 2008; Pearson et al., 2007). We generated multiple models for each species; the number of models generated was equal to the number of occurrence locations of that species (n observed locations, n separate models). During each separate model run, one of the observed locations was removed from the data set and a model was built using the remaining $n - 1$ locations. Then, we assessed the ability of each model to predict the excluded location and calculated the significance of the prediction, and therefore the model, success rate (statistical significance was accepted at $p < 0.05$) (Pearson et al., 2007). For additional details about the jackknife calculation method and the software used see Pearson et al. (2007).

The importance of environmental factors for species distributions was assessed automatically in the Maxent software using a permutation importance measure that determined the contribution of each factor to each model. Values were normalized to give percentages and presented on a stacked bar graph illustrating the percentage contribution of each environmental factor in the creation of every model. Large values indicate that the model depends heavily on that

factor. The more model depends on some factor, the more that factor controls species distribution. To assess a prediction's dependence on individual factors and interpret the influence of those factors on the distribution of a species, we generated response curves. The curves plots present predicted probability of suitable conditions for a species corresponding with each factor value (Merow et al., 2013).

3. Results

In total, we developed 30 Maxent models for benthic fauna species in the *Mollusca* and *Crustacea* taxa found in Hornsund fjord. In each case, the model's success rate and statistical significance were tested to eliminate models with no or poor predictive and explanatory power. Consequently, data on 8 species of Mollusks and 7 species of Arthropods were further analyzed (Table 1).

The relative contributions of all environmental factors to the model predictions vary within and between analyzed groups. However, among all species, the most important predictors were mean grain size, distance from the glaciers, water depth, and mean temperature of bottom water (Fig. 2). The factor importance graphs (Fig. 2) and binary prediction maps (Fig. 4) illustrate the relationship between the importance of water temperature to species distribution and the amount of suitable area predicted. For species that were not significantly affected by temperature (*Dacrydium vitreum*, *Yoldiella solidula*, *Musculus niger*, *Neohela monstrosa*, *Anonyx nugax*, *Pagurus pubescens*), the models identified suitable habitat across most of the fjord. Those species that were more affected by temperature had smaller suitable habitat areas and were generally restricted to either the inner or outer basins of the fjord. The response curves analysis revealed that species representing the first case (distribution not governed by temperature, vast suitable area) are able to tolerate a slightly wider range in water temperature. The model calculated a high probability of suitable conditions for this group both below and above 0°C (Fig. 3). Species whose distributions were influenced by temperature and whose suitable habitat ranges were restricted could be categorized into two groups: (1) species whose response to temperature peaked at low values, mainly between −1 and +1°C (Fig. 3) and whose suitable conditions were located in the inner basins of the fjord, as defined by the algorithm (Fig. 4); and (2) species for whom suitable conditions were predicted at temperature values above 1°C (Fig. 3) and distributed at the fjord mouth and in the outer and central basins of the Hornsund fjord (Fig. 4). Among the

Table 1 Jackknife tests of distribution models for 30 species of *Mollusca* and *Crustacea* collected in Hornsund fjord; LPT — lowest presence threshold — applied. Significant impacts ($p < 0.05$) printed in bold.

Taxon	Class	Order	Species	Success rate	*p* value
Mollusca	*Bivalvia*	—	*Kurtiella tumida* (Carpenter, 1864)	0.9	**0.000**
	Bivalvia	*Nuculanida*	*Yoldia hyperborea* (Gould, 1841)	0.8	**0.001**
	Bivalvia	*Mytilida*	*Dacrydium vitreum* (Møller, 1842)	0.8	**0.001**
	Bivalvia	*Nuculanida*	*Yoldiella solidula* (Warén, 1989)	0.8	**0.002**
	Bivalvia	*Mytilida*	*Musculus glacialis* (Leche, 1883)	0.8	**0.011**
	Bivalvia	*Mytilida*	*Musculus niger* (J.E. Gray, 1824)	0.7	**0.028**
	Bivalvia	—	*Cuspidaria subtorta* (Sars G. O., 1878)	0.7	0.258
	Gastropoda	*Littorinimorpha*	*Onoba mighelsii* (Stimpson, 1851)	0.7	0.750
	Bivalvia	*Nuculanida*	*Portlandia arctica* (Gray, 1824)	0.6	**0.011**
	Bivalvia	*Cardiida*	*Ciliatocardium ciliatum* (Fabricius, 1780)	0.6	**0.019**
	Gastropoda	*Littorinimorpha*	*Frigidoalvania cruenta* (Odhner, 1915)	0.6	0.064
	Bivalvia	*Lucinida*	*Thyasira dunbari* (Lubinsky, 1976)	0.6	0.141
	Bivalvia	*Nuculanida*	*Yoldiella frigida* (Torell, 1859)	0.6	0.226
	Bivalvia	*Cardiida*	*Macoma moesta* (Deshayes, 1855)	0.5	0.136
	Bivalvia	*Lucinida*	*Thyasira gouldi* (Philippi, 1845)	0.5	0.146
	Gastropoda	—	*Margarites costalis* (Gould, 1841)	0.5	0.155
	Gastropoda	*Littorinimorpha*	*Euspira pallida* (Broderip & Sowerby, 1829)	0.4	0.323
Crustacea	*Malacostraca*	*Amphipoda*	*Neohela monstrosa* (Boeck, 1861)	0.9	**0.000**
	Malacostraca	*Amphipoda*	*Anonyx nugax* (Phipps, 1774)	0.9	**0.000**
	Malacostraca	*Amphipoda*	*Lepidepecreum umbo* (Goës, 1866)	0.8	**0.002**
	Malacostraca	*Amphipoda*	*Unciola leucopis* (Krøyer, 1845)	0.7	**0.000**
	Malacostraca	*Amphipoda*	*Orchomenella minuta* (Krøyer, 1846)	0.7	0.485
	Malacostraca	*Cumacea*	*Diastylis goodsiri* (Bell, 1855)	0.6	**0.006**
	Malacostraca	*Amphipoda*	*Melita formosa* (Murdoch, 1866)	0.6	**0.025**
	Malacostraca	*Amphipoda*	*Themisto abyssorum* (Boeck, 1870)	0.6	0.061
	Malacostraca	*Amphipoda*	*Pontoporeia femorata* (Krøyer, 1842)	0.6	0.221
	Malacostraca	*Euphausiacea*	*Thysanoessa inermis* (Krøyer, 1846)	0.6	0.267
	Malacostraca	*Decapoda*	*Pagurus pubescens* (Krøyer, 1838)	0.5	**0.001**
	Malacostraca	*Amphipoda*	*Monoculodes packardi* (Boeck, 1871)	0.5	0.129
	Malacostraca	*Decapoda*	*Sabinea septemcarinata* (Sabine, 1824)	0.4	0.650

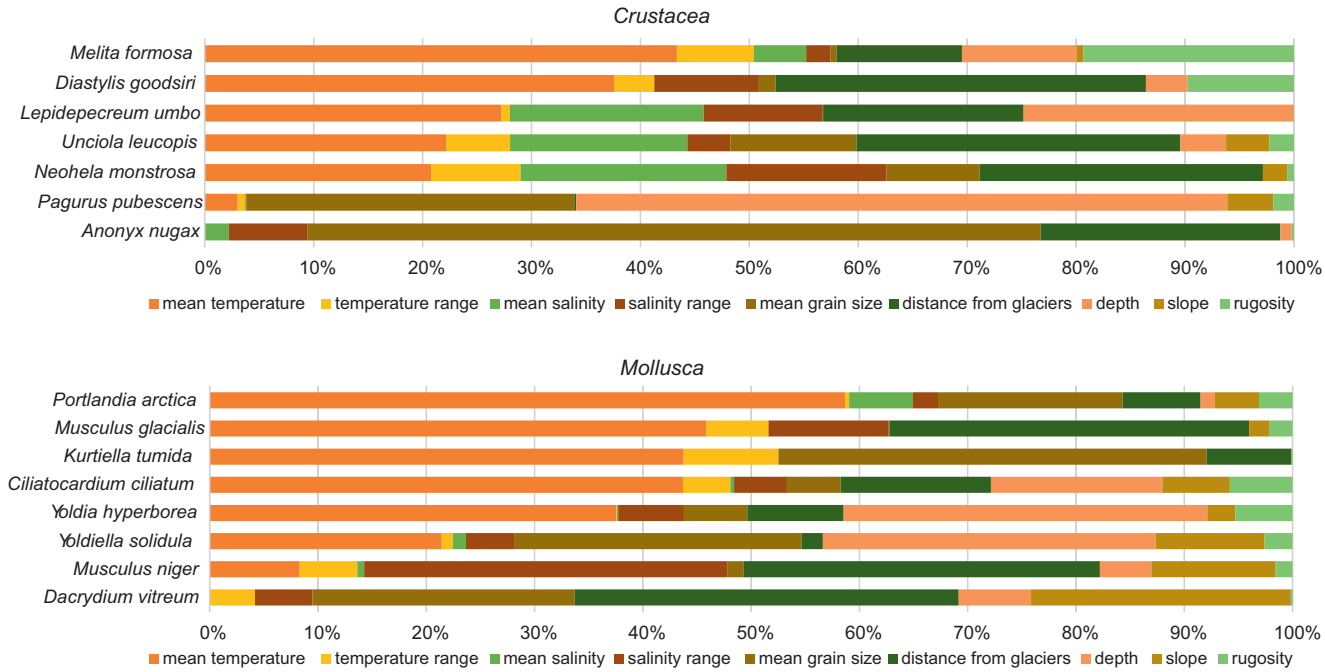

Figure 2 Environmental factors potentially affecting benthic species collected in the Hornsund fjord and those factors' percent contribution to species distribution, as determined in the Maxent models.

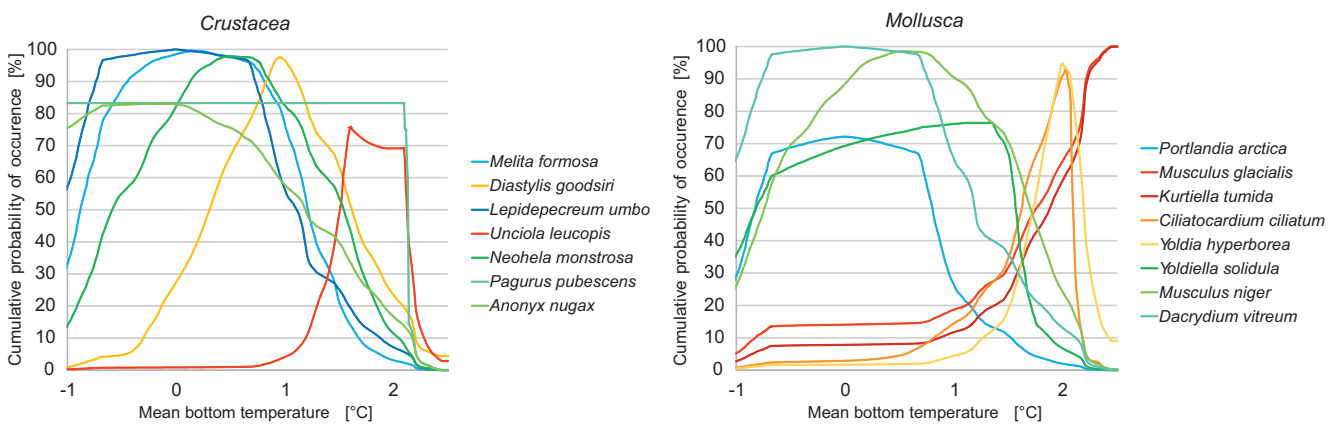

Figure 3 Response curves of benthic species collected in the Hornsund fjord to mean bottom water temperature (derived in Maxent).

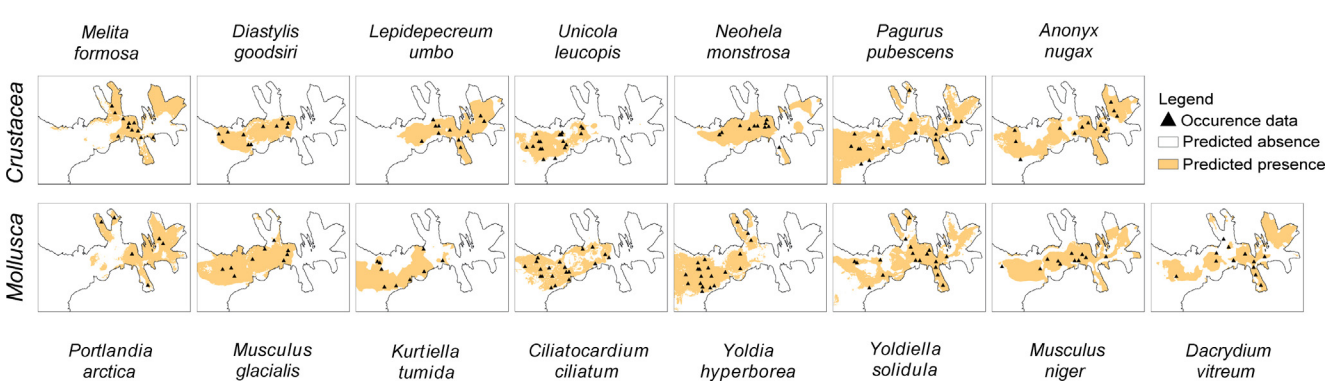

Figure 4 Modeled distributions for selected benthic species collected in Hornsund fjord; modeled using Maxent and applying LPT — the lowest presence threshold. Predicted areas are shaded; locations of observed occurrences are shown as black triangles.

latter group, differences in the influence of temperature on the probability of species occurrence were also observed. For certain species (*Yoldia hyperborea*, *Ciliatocardium ciliatum*, *Unciola leucopis*), the range of water temperature tolerance was incredibly narrow. In other cases (*Kurtiella tumida*, *Musculus glacialis*), the probability of finding a suitable habitat for a species continuously increased with temperature (Fig. 3).

In general, the importance of water temperature on benthic fauna distribution was demonstrated. However, the exact influence of this factor on benthos distribution and potential habitat preferences varied by species.

4. Discussion

Our study confirms the importance of bottom water temperature in the distribution of benthic fauna inhabiting an Arctic fjord — Hornsund. This was one of the most important factors controlling the distribution of the majority of analyzed species, along with the mean grain size, depth, and distance from the glaciers. Sediment characteristic is one of the most important factors for benthic fauna persistence and distribution. The fact that mean grain size is a vital factor in our analysis confirms this statement. However, Hornsund seafloor is quite homogenous in terms of granulometry. The fine fraction of sediment dominates throughout the fjord, with only single patches of coarse sediment. Our previous studies revealed no significant differences between individual fjord basins in terms of this factor (Drewnik et al., 2016). Hence, mean grain size of sediment is of minor importance in controlling benthic species distribution in Hornsund fjord (Drewnik et al., 2016). Same as depth which, although variable across fjord area, is rather stable parameter over time. Yet, the glacier movement (Błaszczyk et al., 2009, 2013) results in the appearance of new shallows (Moskalik et al., 2013) that may potentially serve as new habitats for benthic fauna. Distance from the glacier was used as a proxy for glacier outflow in order to confirm its importance and the need for extensive sampling of this parameter. Our results state this need, as a distance from the glacier fronts was an important predictor for some analyzed species. This will be the subject of our future research. Mean bottom temperature, on the other hand, was a very significant factor for most of analyzed species. Moreover, according to our previous findings, water temperature is the most spatially and temporally variable factor in the bottom habitat of the Hornsund fjord (Drewnik et al., 2016). Given that, bottom water temperature is potentially the most crucial determinant of benthic fauna distribution and habitat suitability in Hornsund. The importance of water temperature for benthic fauna persistence and distribution has also been emphasized in many previous studies (Callaway et al., 2002; Gray, 2002; McArthur et al., 2010; Neumann et al., 2009; Reiss et al., 2011; Snelgrove, 2001). Its influence may be even more visible and striking in semi-closed fjords (Freeland et al., 1980) with specific fauna compositions (Freeland et al., 1980; Görlich et al., 1987; Renaud et al., 2007; Sejr et al., 2000; Włodarska-Kowalczuk and Węsławski, 2008; Wlodarska-Kowalczuk et al., 2005; Włodarska-Kowalczuk et al., 2013) and unique environmental conditions (shelf water inflows). Our results support the significance of observed Atlantic warm water fluxes in benthic fauna persistence and composition in the Hornsund fjord.

Although the temperature is widely recognized as a factor limiting the occurrence and performance of Arctic marine invertebrates (Brown and Thatje, 2015; Petersen et al., 2003), many species inhabiting Hornsund are species of very wide thermal tolerance from the subarctic domain. Nevertheless, our studies show that the level of importance of bottom water temperature varies between species and individual species' responses to that factor should not be underestimated. We did not observe clear trends, similarities or differences between crustaceans and mollusc. Further analysis of the species' responses to specific temperature values (response curves graphs) and predicted occurrences in the fjord (binary prediction maps) indicated that interspecific differences were due to the temperature preferences of individual species. We identified species with a broad tolerance range to temperature, and suitable conditions for these species were modeled across a vast area of the fjord (low-temperature importance). We also identified species that preferred only warm (above 1°C) or only cold (below 1°C) waters with suitable habitats predicted in the outer and central, or in the central and inner basins of the fjord, respectively. This latter group's distribution was categorized as being temperature-dependent.

In terms of species physiology, potential consequences related to the continuous inflow of Atlantic warm water into the fjord may be the most severe for cold water species in the temperature-dependent group. However, Atlantic fluxes are believed to be limited to the outer and central basins of the fjords (Swerpel, 1985; Urbański et al., 1980). Long-term measurements of bottom water temperature in Hornsund fjord confirm that those basins, and not the inner basins, are influenced by shelf waters (Drewnik et al., 2016). On the other hand, the innermost basins contain cold water and are more stable (Weslawski et al., 2010). Consequently, cold-water benthic fauna that occupies the innermost basins of the fjord is isolated from the influence of shelf water inflows. Species that also inhabit the central and outer basins may be more vulnerable to the effects of Atlantic fluxes. As a result, their distributions may be limited to the inner basins when exposed to temperatures exceeding their maximum tolerance level. Either way, our results confirm that the inner most basins of Hornsund fjord likely serve as refugia for cold water Arctic fauna, as previously determined in Węsławski et al. (2011). Furthermore, our results show that the outer and central basins of the fjord create suitable habitats for fauna preferring warm Atlantic waters, assuming that they do not have a very narrow range of temperature tolerance. Nevertheless, these species may not tolerate exposure to higher temperatures for extended time periods, and they may become extinct if such conditions persist.

Overall, the constant inflow of warm shelf waters may potentially result in the division of Hornsund fjord into two biologically distinct zones. In this case, cold water fauna would dominate in the inner basins and warm water fauna in outer and central basins of the fjord. Biodiversity would remain stable unless certain species do not survive the changes in prevailing conditions. In that case, a decrease in the species pool would be expected. However, few documented marine extinctions have occurred (Dulvy et al., 2003; McCauley et al., 2015), and regional extinctions are considered unlikely (Carstensen and Weydmann, 2012; Flessa and Jablonski, 1995). Stuart-Smith et al. (2015) indicate the

importance of individual species' responses — particularly their thermal bias — and the need to investigate this topic to predict the future existence of species in warmed up areas. This will be the subject of the next paper to be published based on the present material.

The biodiversity of Hornsund fjord may also be affected by the northward advection of the North Atlantic Current. This current is able to carry boreal taxa from the Norwegian Sea shelf, an area distinctly richer in species than the European Arctic shelf of Svalbard, to the Hornsund fjord (Palerud et al., 2004). One possible scenario involves the increase of Hornsund diversity. Examples of such increases have already been observed in the Pacific Arctic (Grebmeier et al., 2006; Sirenko and Gagaev, 2007), in Svalbard fjord Kongsfjord (Beuchel et al., 2006; Kędra et al., 2009), as well as in Hornsund (Węsławski et al. unpublished data; Grzelak and Kotwicki unpublished data). This species enrichment applies to outer and central basins of Hornsund fjord. Inner, isolated basins of multiple fjords continue to contain less diverse fauna. Decreasing trend in biodiversity has already been observed in glacial impacted regions of Hornsund (Włodarska-Kowalczuk et al., 2013) and other glacial fjords off Spitsbergen (Renaud et al., 2007; Wlodarska-Kowalczuk et al., 2005; Włodarska-Kowalczuk and Węsławski, 2008), Greenland (Sejr et al., 2000), and the Canadian Arctic (Farrow et al., 1983). According to current knowledge, species pools may be enriched because closely related species coexist instead of replacing each other (Kwasniewski et al., 2010; Leppäkoski and Olenin, 2001; Weslawski et al., 2010).

In conclusion, the importance of water temperature in benthic fauna distribution in Hornsund fjord is clear. We have confirmed the significance of observed Atlantic warm water inflows in benthic fauna persistence and composition. Nevertheless, predicted responses to water temperature seem to be species specific. We did not find clear trends or similarities among modeled organisms. To understand and predict the possible consequences of environmental alterations in Arctic regions such as Spitsbergen, knowledge about individual species needs to be considered. For some species, changes in water characteristics may have physical consequences. For others, they may cause new interspecific interactions. Hence, an assessment of Arctic biodiversity should depend on detailed studies of individual species-environment relationships. Overall, the composition of Arctic communities and ecosystems may change in the future and may become more boreal in nature. Studying the distribution of individual species and communities as indicators of Arctic environmental and ecosystem change is of great value and importance.

Acknowledgements

This research was funded by the National Center for Science in Krakow, Poland ("Cold water benthic fauna relicts in warmed up fjords — GIS approach" 2012/05/N/ST10/03856, "GAME" 2012/04/A/NZ8/00661) and the Polish-Norwegian Research Programme operated by the National Centre for Research and Development under the Norwegian Financial Mechanism 2009—2014, Project Contract No POL-NOR/199377/91/2014 ("GLAERE"). IO PAN in Sopot contributed to this study by providing ship time and manpower. We thank Kajetan Deja from IO PAN for assisting with the laboratory analysis, and special thanks go to Agnieszka Promińska and Emilia Trudnowska from IO PAN for providing data on bottom water temperature and salinity.

References

ACIA, 2005. Arctic Climate Impact Assessment. ACIA Overview Report. Cambridge Univ. Press, 1042 pp.

Basedow, S., Eianeb, K., Tverbergc, V., Spindler, M., 2004. Advection of zooplankton in an Arctic fjord (Kongsfjorden, Svalbard). Estuar. Coast. Shelf Sci. 60 (1), 113—124, http://dx.doi.org/10.1016/j.ecss.2003.12.004.

Beaugrand, G., Reid, P.C., Ibañez, F., Lindley, J.A., Edwards, M., 2002. Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296 (5573), 1692—1694, http://dx.doi.org/10.1126/science.1071329.

Berge, J., Johnsen, G., Nilsen, F., Gulliksen, B., Slagstad, D., 2005. Ocean temperature oscillations enable reappearance of blue mussels *Mytilus edulis* in Svalbard after a 1000 year absence. Mar. Ecol.-Prog. Ser. 303, 167—175, http://dx.doi.org/10.3354/meps303167.

Berge, J., Renaud, P.E., Eiane, K., Gulliksen, B., Cottier, F.R., Varpe, Ø., Brattegard, T., 2009. Changes in the decapod fauna of an Arctic fjord during the last 100 years (1908—2007). Polar Biol. 32 (7), 953—961, http://dx.doi.org/10.1007/s00300-009-0594-5.

Beuchel, F., Gulliksen, B., Carroll, M.L., 2006. Long-term patterns of rocky bottom macrobenthic community structure in an Arctic fjord (Kongsfjorden, Svalbard) in relation to climate variability (1980—2003). J. Marine Syst. 63 (1—2), 35—48, http://dx.doi.org/10.1016/j.jmarsys.2006.05.002.

Błaszczyk, M., Jania, J.A., Hagen, J.O., 2009. Tidewater glaciers of Svalbard: recent changes and estimates of calving fluxes. Pol. Polar Res. 30, 85—142.

Błaszczyk, M., Jania, J.A., Kolondra, L., 2013. Fluctuations of tidewater glaciers in Hornsund Fjord (Southern Svalbard) since the beginning of the 20th century. Pol. Polar Res. 34 (4), 327—352, http://dx.doi.org/10.2478/popore-2013-0024.

Brown, A., Thatje, S., 2015. The effects of changing climate on faunal depth distributions determine winners and losers. Glob. Change Biol. 21 (1), 173—180, http://dx.doi.org/10.1111/gcb.12680.

Bučas, M., Bergström, U., Downie, A.-L., Sundblad, G., Gullström, M., von Numers, M., Šiaulys, A., Lindegarth, M., 2013. Empirical modelling of benthic species distribution, abundance, and diversity in the Baltic Sea: evaluating the scope for predictive mapping using different modelling approaches. ICES J. Mar. Sci. 70 (6), 1233—1243, http://dx.doi.org/10.1093/icesjms/fst036.

Callaway, R., Alsvag, J., Boois, I., de Cotter, J., Ford, A., Hinz, H., Jennings, S., Kroncke, I., Lancaster, J., Piet, G., Prince, P., Ehrich, S., 2002. Diversity and community structure of epibenthic invertebrates and fish in the North Sea. ICES J. Mar. Sci. 59 (6), 1199—1214, http://dx.doi.org/10.1006/jmsc.2002.1288.

Carstensen, J., Weydmann, A., 2012. Tipping points in the Arctic: eyeballing or statistical significance? Ambio 41 (1), 34—43, http://dx.doi.org/10.1007/s13280-011-0223-8.

Cottier, F.R., Nilsen, F., Skogseth, R., et al., 2010. Arctic fjords: a review of the oceanographic environment and dominant physical processes. Geol. Soc. Lond. Spec. Publ. 344 (1), 35—50, http://dx.doi.org/10.1144/SP344.4.

Cottier, F., Tverberg, V., Inall, M., Svendsen, H., Nilsen, F., Griffiths, C., 2005. Water mass modification in an Arctic fjord through cross-shelf exchange: the seasonal hydrography of Kongsfjorden, Svalbard. J. Geophys. Res. Ocean. 110 (12), 1—18, http://dx.doi.org/10.1029/2004JC002757.

Dawson, T.P., Jackson, S.T., House, J.I., Prentice, I.C., Mace, G.M., 2011. Beyond predictions: biodiversity conservation in a changing

climate. Science 332 (6025), 53—58, http://dx.doi.org/10.1126/science.1200303.

Degraer, S., Verfaillie, E., Willems, W., Adriaens, E., Vincx, M., Van Lancker, V., 2008. Habitat suitability modelling as a mapping tool for macrobenthic communities: an example from the Belgian part of the North Sea. Cont. Shelf Res. 28 (3), 369—379, http://dx.doi.org/10.1016/j.csr.2007.09.001.

Drainville, G., 1970. The Saguenay fjord: the ichtyological fauna and ecological conditions. Nat. Can. 97 (6), 623—666.

Drewnik, A., Węsławski, J.M., Włodarska-Kowalczuk, M., Łącka, M., Promińska, A., Zaborska, A., Gluchowska, M., 2016. From the worm's point of view. I: Environmental settings of benthic ecosystems in Arctic fjord (Hornsund, Spitsbergen). Polar Biol., http://dx.doi.org/10.1007/s00300-015-1867-9.

Drinkwater, K.F., 2006. The regime shift of the 1920s and 1930s in the North Atlantic. Prog. Oceanogr. 68 (2—4), 134—151, http://dx.doi.org/10.1016/j.pocean.2006.02.011.

Dulvy, N., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. Fish Fish. 4 (1), 5—64, http://dx.doi.org/10.1046/j.1467-2979.2003.00105.x.

Elith, J., Graham, C.H., Anderson, R.P., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Townsend Peterson, A., Phillips, S.J., Richardson, K., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S., Wisz, M. S., Zimmermann, N.E., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography (Cop.). 29 (2), 129—151, http://dx.doi.org/10.1111/j.2006.0906-7590.04596.x.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E., Yates, C.J., 2011. A statistical explanation of MaxEnt for ecologists. Divers. Distrib. 17 (1), 43—57, http://dx.doi.org/10.1111/j.1472-4642.2010.00725.x.

Ellis, J., Ysebaert, T., Hume, T., Norkko, A., Bult, T., Herman, P., Thrush, S., Oldman, J., 2006. Predicting macrofaunal species distributions in estuarine gradients using logistic regression and classification systems. Mar. Ecol -Prog. Ser. 316, 69—83, http://dx.doi.org/10.3354/meps316069.

Falk-Petersen, S., Pavlov, V., Timofeev, S., Sargent, J., 2007. Climate variability and possible effects on arctic food chains: the role of Calanus. In: Ørbæk, J., Kallenborn, R., Tombre, I., Hegseth, E., Falk-Petersen, S., Hoel, A. (Eds.), Arctic Alpine Ecosystems and People in a Changing Environment. Springer, Berlin Heidelberg, 147—166, http://dx.doi.org/10.1007/978-3-540-48514-8_9.

Farrow, G.E., Syvitski, J.P.M., Tunnicliffe, V., 1983. Suspended particulate loading on the macrobenthos in a highly turbid fjord: Knight Inlet, British Columbia. Can. J. Fish. Aquat. Sci. 40 (S1), s273—s288, http://dx.doi.org/10.1139/f83-289.

Flessa, K.W., Jablonski, D., 1995. Biogeography of recent marine bivalve molluscs and its implications for paleobiogeography and the geography of extinction: a progress report. Hist. Biol. 10 (1), 25—47, http://dx.doi.org/10.1080/10292389509380512.

Franklin, J., 2009. Mapping Species Distributions: Spatial Inference and Prediction. Cambridge Univ. Press, New York, 340 pp.

Freeland, H.J., Farmer, D.M., Levings, C.D., 1980. Fjord Oceanography. Plenum Press, New York, 715 pp.

Glockzin, M., Gogina, M., Zettler, M.L., 2009. Beyond salty reins — modeling benthic species' spatial response to their physical environment in the Pomeranian Bay (Southern Baltic Sea). Balt. Coast. Zo. 13 (II), 79—95.

Gogina, M., Glockzin, M., Zettler, M.L., 2010. Distribution of benthic macrofaunal communities in the western Baltic Sea with regard to near-bottom environmental parameters. 2. Modelling and prediction. J. Marine Syst. 80 (1—2), 57—70, http://dx.doi.org/10.1016/j.jmarsys.2009.10.001.

Gogina, M., Zettler, M.L., 2010. Diversity and distribution of benthic macrofauna in the Baltic Sea. Data inventory and its use for species distribution modelling and prediction. J. Sea Res. 64 (3), 313—321, http://dx.doi.org/10.1016/j.seares.2010.04.005.

Görlich, K., Węslawski, J.M., Zajączkowski, M., 1987. Suspension settling effect on macrobenthos biomass distribution in the Hornsund fjord, Spitsbergen. Polar Res. 5 (2), 175—192.

Gray, J.S., 2002. Species richness of marine soft sediments. Mar. Ecol. -Prog. Ser. 244, 285—297, http://dx.doi.org/10.3354/meps244285.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., McNutt, S.L., 2006. A major ecosystem shift in the northern Bering Sea. Science 311 (5766), 1461—1464, http://dx.doi.org/10.1126/science.1121365.

Hernandez, P.A., Franke, I., Herzog, S.K., Pacheco, V., Paniagua, L., Quintana, H.L., Soto, A., Swenson, J.J., Tovar, C., Valqui, T.H., Vargas, J., Young, B.E., 2008. Predicting species distributions in poorly-studied landscapes. Biodivers. Conserv. 17 (6), 1353—1366, http://dx.doi.org/10.1007/s10531-007-9314-z.

Hernandez, P.A., Graham, C.H., Master, L.L., Albert, D.L., Hernández Graham, C.H., Master, L.L., Albert, D.L., 2006. The effect of sample size and species characteristics on performance of different species distribution modeling methods. Ecography (Cop.). 29 (5), 773—785, http://dx.doi.org/10.1111/j.0906-7590.2006.04700.x.

Hijmans, R., Graham, C., 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. Glob. Change Biol. 12 (12), 2272—2281, http://dx.doi.org/10.1111/j.1365-2486.2006.01256.x.

Hop, H., Pearson, T., Hegseth, E.N., Kovacs, K.M., Wiencke, C., Kwasniewski, S., Eiane, K., Mehlum, F., Gulliksen, B., Wlodarska-Kowalczuk, M., Lydersen, C., Weslawski, J.M., Cochrane, S., Gabrielsen, G.W., Leakey, R.J.G., Lønne, O.J., Zajaczkowski, M., Falk-Petersen, S., Kendall, M., Wängberg, S.Å., Bischof, K., Voronkov, A.Y., Kovaltchouk, N.A., Wiktor, J., Poltermann, M., Di Prisco, G., Papucci, C., Gerland, S., 2002. The marine ecosystem of Kongsfjorden, Svalbard. Polar Res. 21 (1), 167—208, http://dx.doi.org/10.1111/j.1751-8369.2002.tb00073.x.

Inglis, G.J., Hurren, H., Oldman, J., Haskew, R., 2006. Using habitat suitability index and particle dispersion models for early detection of marine invaders. Ecol. Appl. 16 (4), 1377—1390, http://dx.doi.org/10.1890/1051-0761(2006)016[1377:UHSIAP]2.0.CO;2.

Jónsson, S., Valdimarsson, H., 2005. The flow of Atlantic water to the North Icelandic Shelf and its relation to the drift of cod larvae. ICES J. Mar. Sci. 62 (7), 1350—1359, http://dx.doi.org/10.1016/j.icesjms.2005.05.003.

Kendall, M., Widdicombe, S., Weslawski, J., 2003. A multi-scale study of the biodiversity of the benthic infauna of the high-latitude Kongsfjord, Svalbard. Polar Biol. 26 (6), 383—388.

Kędra, M., Włodarska-Kowalczuk, M., Węsławski, J.M., 2009. Decadal change in macrobenthic soft-bottom community structure in a high Arctic fjord (Kongsfjorden, Svalbard). Polar Biol. 33 (1), 1—11, http://dx.doi.org/10.1007/s00300-009-0679-1.

Kröncke, I., 1995. Long-term changes in North Sea benthos. Senck Marit. 26, 73—80.

Kwasniewski, S., Gluchowska, M., Jakubas, D., Wojczulanis-Jakubas, K., Walkusz, W., Karnovsky, N., Blachowiak-Samolyk, K., Cisek, M., Stempniewicz, L., 2010. The impact of different hydrographic conditions and zooplankton communities on provisioning Little Auks along the West coast of Spitsbergen. Prog. Oceanogr. 87 (1—4), 72—82, http://dx.doi.org/10.1016/j.pocean.2010.06.004.

Leppäkoski, E., Olenin, S., 2001. The meltdown of biogeographical peculiarities of the Baltic Sea: the interaction of natural and man-made processes. Ambio 30 (4—5), 202—209, http://dx.doi.org/10.1579/0044-7447-30.4.202.

Lydersen, C., Assmy, P., Falk-Petersen, S., Kohler, J., Kovacs, K.M., Reigstad, M., Steen, H., Strøm, H., Sundfjord, A., Varpe, Ø., Walczowski, W., Weslawski, J.M., Zajaczkowski, M., 2014. The

importance of tidewater glaciers for marine mammals and seabirds in Svalbard, Norway. J. Marine Syst. 129, 452—471, http://dx.doi.org/10.1016/j.jmarsys.2013.09.006.

McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. Estuar. Coast. Shelf Sci. 88 (1), 21—32, http://dx.doi.org/10.1016/j.ecss.2010.03.003.

McCauley, D.J., Pinsky, M.L., Palumbi, S.R., Estes, J.A., Joyce, F.H., Warner, R.R., 2015. Marine defaunation: animal loss in the global ocean. Science 347 (6219), 247—254, http://dx.doi.org/10.1126/science.1255641.

Meißner, K., Darr, A., Rachor, E., 2008. Development of habitat models for Nephtys species (Polychaeta: Nephtyidae) in the German Bight (North Sea). J. Sea Res. 60 (4), 271—286, http://dx.doi.org/10.1016/j.seares.2008.08.001.

Merow, C., Smith, M.J., Silander, J.A., 2013. A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. Ecography (Cop.). 36 (10), 1058—1069, http://dx.doi.org/10.1111/j.1600-0587.2013.07872.x.

Moskalik, M., Grabowiecki, P., Tęgowski, J., Żulichowska, M., 2013. Bathymetry and geographical regionalization of Brepollen (Hornsund, Spitsbergen) based on bathymetric profiles interpolations. Polish Polar Res. 34 (1), 1—22, http://dx.doi.org/10.2478/popore-2013-0001.

Neumann, H., Reiss, H., Rakers, S., Ehrich, S., Kroncke, I., 2009. Temporal variability in southern North Sea epifauna communities after the cold winter of 1995/1996. ICES J. Mar. Sci. 66 (10), 2233—2243, http://dx.doi.org/10.1093/icesjms/fsp203.

Nilsen, F., Cottier, F., Skogseth, R., Mattsson, S., 2008. Fjord-shelf exchanges controlled by ice and brine production: the interannual variation of Atlantic Water in Isfjorden, Svalbard. Cont. Shelf Res. 28 (14), 1838—1853, http://dx.doi.org/10.1016/j.csr.2008.04.015.

Nilsen, F., Gjevik, B., Schauer, U., 2006. Cooling of the West Spitsbergen Current: isopycnal diffusion by topographic vorticity waves. J. Geophys. Res. Ocean. 111 (8), 1—16, http://dx.doi.org/10.1029/2005JC002991.

Olenin, S., 1997. Benthic zonation of the Eastern Gotland Basin, Baltic Sea. Neth. J. Aquat. Ecol. 30 (4), 265—282, http://dx.doi.org/10.1007/BF02085871.

Ortega-Huerta, M.A., Peterson, A.T., 2008. Modeling ecological niches and predicting geographic distributions: a test of six presence-only methods. Rev. Mex. Biodivers. 79 (1), 205—216, http://dx.doi.org/10.1016/j.biocon.2004.07.008.

Palerud, R., Gulliksen, B., Brattegard, T., Sneli, J.-A., Vader, W., 2004. The marine macro-organisms in Svalbard waters. In: Prestrud, P., Strøm, H., Goldman, H.V. (Eds.), A Catalogue of Terrestrial and Marine Animals of Svalbard. Norwegian Polar Inst., Polar Environ. Centre, Tromsø, 5—56.

Pavlov, A.K., Tverberg, V., Ivanov, B.V., Nilsen, F., Falk-Petersen, S., Granskog, M.A., 2013. Warming of Atlantic Water in two west Spitsbergen fjords over the last century (1912—2009). Polar Res. 32, http://dx.doi.org/10.3402/polar.v32i0.11206.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34 (1), 102—117, http://dx.doi.org/10.1111/j.1365-2699.2006.01594.x.

Petersen, J.K., Sejr, M.K., Larsen, J.E.N., 2003. Clearance rates in the Arctic bivalves *Hiatella arctica* and Mya sp. Polar Biol. 26 (5), 334—341, http://dx.doi.org/10.1007/s00300-003-0483-2.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190 (3—4), 231—259, http://dx.doi.org/10.1016/j.ecolmodel.2005.03.026.

Phillips, S.J., Dudík, M., Schapire, R.E., 2004. A maximum entropy approach to species distribution modeling. In: Proceedings of the Twenty-First International Conference on Machine Learning. ACM, New York, NY, 655—662, http://dx.doi.org/10.1145/1015330.1015412.

Piechura, J., Beszczyńska-Möller, A., Osiński, R., 2001. Volume, heat and salt transport by the West Spitsbergen Current. Polar Res. 20 (2), 233—240, http://dx.doi.org/10.1111/j.1751-8369.2001.tb00061.x.

Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. Polar Biol. 28 (10), 733—755, http://dx.doi.org/10.1007/s00300-005-0013-5.

Reiss, H., Cunze, S., König, K., Neumann, H., Kröncke, I., 2011. Species distribution modelling of marine benthos: a North Sea case study. Mar. Ecol.-Prog. Ser. 442, 71—86, http://dx.doi.org/10.3354/meps09391.

Renaud, P.E., Carroll, M.L., Ambrose Jr., W.G., 2008. Effects of global warming on Arctic sea-floor communities and its consequences for higher trophic levels. In: Duarte, C.M. (Ed.), Impacts of Global Warming on Polar Ecosystems. Fundacion BBVA, Madrid, 139—175.

Renaud, P.E., Włodarska-Kowalczuk, M., Trannum, H., Holte, B., Węsławski, J.M., Cochrane, S., Dahle, S., Gulliksen, B., 2007. Multidecadal stability of benthic community structure in a high-Arctic glacial fjord (van Mijenfjord, Spitsbergen). Polar Biol. 30 (3), 295—305, http://dx.doi.org/10.1007/s00300-006-0183-9.

Robinson, L.M., Elith, J., Hobday, A.J., Pearson, R.G., Kendall, B.E., Possingham, H.P., Richardson, A.J., 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. Glob. Ecol. Biogeogr. 20 (6), 789—802, http://dx.doi.org/10.1111/j.1466-8238.2010.00636.x.

Schauer, U., Beszczynska-Möller, A., Walczowski, W., Fahrbach, E., Piechura, J., Hansen, E., 2008. Variation of measured heat flow through the fram strait between 1997 and 2006. In: Dickson, R.R., Meincke, J., Rhines, P. (Eds.), Arctic-Subarctic Ocean Fluxes. Springer, Netherlands, 65—85.

Sejr, M.K., Jensen, K.T., Rysgaard, S., 2000. Macrozoobenthic community structure in a high-arctic East Greenland fjord. Polar Biol. 23 (11), 792—801, http://dx.doi.org/10.1007/s003000000154.

Sirenko, B.I., Gagaev, S.Y., 2007. Unusual abundance of macrobenthos and biological invasions in the Chukchi Sea. Russ. J. Mar. Biol. 33 (6), 355—364, http://dx.doi.org/10.1134/S1063074007060016.

Skogseth, R., Haugan, P.M., Jakobsson, M., 2005. Watermass transformations in Storfjorden. Cont. Shelf Res. 25 (5—6), 667—695, http://dx.doi.org/10.1016/j.csr.2004.10.005.

Smedsrud, L.H., Ingvaldsen, R., Nilsen, J.E.Ø., Skagseth, Ø., 2010. Heat in the Barents Sea: transport, storage, and surface fluxes. Ocean Sci. 6 (1), 219—234, http://dx.doi.org/10.5194/os-6-219-2010.

Snelgrove, P.V.R., 2001. Diversity of marine species. In: Steele, J.H., Thorpe, S.A., Turekian, K.K. (Eds.), Encyclopedia of Ocean Sciences. Acad. Press, San Diego, 748—757.

Spielhagen, R.F., Werner, K., Sørensen, S.A., Zamelczyk, K., Kandiano, E., Budeus, G., Husum, K., Marchitto, T.M., Hald, M., 2011. Enhanced modern heat transfer to the Arctic by warm Atlantic Water. Science 331 (6016), 450—453, http://dx.doi.org/10.1126/science.1197397.

Stuart-Smith, R.D., Edgar, G.J., Barret, N.S., Kininmonth, S.J., Bates, A.E., 2015. Thermal biases and vulnerability to warming in the world's marine fauna. Nature 528 (7580), 88—92, http://dx.doi.org/10.1038/nature16144.

Svendsen, H., Beszczynska-Møller, A., Hagen, J.O., Lefauconnier, B., Tverberg, V., Gerland, S., Ørbæk, J.B., Bischof, K., Papucci, C., Zajaczkowski, M., Azzolini, R., Bruland, O., Wiencke, C., Winther, J.G., Dallmann, W., 2002. The physical environment of Kongsfjorden — Krossfjorden, an Arctic fjord system in Svalbard. Polar Res. 21 (1), 133—166, http://dx.doi.org/10.1111/j.1751-8369.2002.tb00072.x.

Syvitski, J.P.M., Burrell, D.C., Skei, J.M., 1987. Fjords. Processes and Products. Springer-Verlag, New York, 379 pp.

Swerpel, S., 1985. The Hornsund Fiord: water masses. Polish Polar Res. 6 (4), 475—496.

Teigen, S.H., Nilsen, F., Skogseth, R., Gjevik, B., Beszczynska-Möller, A., 2011. Baroclinic instability in the West Spitsbergen current. J. Geophys. Res. Ocean. 116 (7), 1—18, http://dx.doi.org/10.1029/2011JC006974.

Thrush, S.F., Hewitt, J.E., Norkko, A., Nicholls, P.E., Funnell, G.A., Ellis, J.I., 2003. Habitat change in estuaries: predicting broad-scale responses of intertidal macrofauna to sediment mud content. Mar. Ecol.-Prog. Ser. 263, 101—112, http://dx.doi.org/10.3354/meps263101.

Urbański, J., Neugenbauer, E., Spacjer, R., Falkowska, L., 1980. Physico-chemical characteristic of the waters of Hornsund Fjord on south-west Spitsbergen (Svalbard Archipelago) in the summer season 1979. Pol. Polar Res. 1 (4), 43—52.

Walczowski, W., Piechura, J., 2006. New evidence of warming propagating toward the Arctic Ocean. Geophys. Res. Lett. 33 (12), 1—5, http://dx.doi.org/10.1029/2006GL025872.

Walczowski, W., Piechura, J., 2007. Pathways of the Greenland Sea warming. Geophys. Res. Lett. 34 (10), 1—5, http://dx.doi.org/10.1029/2007GL029974.

Wassmann, P., Duarte, C.M., Agustí, S., Sejr, M.K., 2011. Footprints of climate change in the Arctic marine ecosystem. Glob. Change Biol. 17 (2), 1235—1249, http://dx.doi.org/10.1111/j.1365-2486.2010.02311.x.

Warwick, R.M., 1993. Environmental-impact studies on marine communities — pragmatical considerations. Aust. J. Ecol. 18, 63—80, http://dx.doi.org/10.1111/j.1442-9993.1993.tb00435.x.

Weslawski, J.M., 1990. Distribution and ecology of south Spitsbergen coastal marine amphipods (*Crustacea*). Pol. Arch. Hydrobiol. 37, 503—519.

Weslawski, J.M., Kwasniewski, S., Wiktor, J., 1991. Winter in a Svalbard fjord ecosystem. Arctic 44 (2), 115—123.

Weslawski, J.M., Wiktor, J., Kotwicki, L., 2010. Increase in biodiversity in the arctic rocky littoral, Sorkappland, Svalbard, after 20 years of climate warming. Mar. Biodivers. 40 (2), 123—130, http://dx.doi.org/10.1007/s12526-010-0038-z.

Węsławski, J.M., Kendall, M.A., Włodarska-Kowalczuk, M., Iken, K., Kędra, M., Legezynska, J., Sejr, M.K., 2011. Climate change effects on Arctic fjord and coastal macrobenthic diversity-observations and predictions. Mar. Biodivers. 41 (1), 71—85, http://dx.doi.org/10.1007/s12526-010-0073-9.

Węsławski, J.M., Kwaśniewski, S., Stempniewicz, L., 2009. Warming in the Arctic may result in the negative effects of increased biodiversity. Polarforschung 78 (3), 105—108.

Węsławski, J.M., Wiktor, J., Zajączkowski, M., Swerpel, S., 1993. Intertidal zone of Svalbard, macroorganism distribution and biomass. Polar Biol. 13 (2), 73—79, http://dx.doi.org/10.1007/BF00238538.

Willems, W., Goethals, P., Van den Eynde, D., Van Hoey, G., Van Lancker, V., Verfaillie, E., Vincx, M., Degraer, S., 2008. Where is the worm? Predictive modelling of the habitat preferences of the tube-building polychaete *Lanice conchilega*. Ecol. Modell. 212 (1—2), 74—79, http://dx.doi.org/10.1016/j.ecolmodel.2007.10.017.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J.R., Lehmann, A., Lohmann, L., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Zimmermann, N.E., 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14 (5), 763—773, http://dx.doi.org/10.1111/j.1472-4642.2008.00482.x.

Wlodarska-Kowalczuk, M., Pearson, T.H., 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). Polar Biol. 27 (3), 155—167, http://dx.doi.org/10.1007/s00300-003-0568-y.

Wlodarska-Kowalczuk, M., Pearson, T.H., Kendall, M., 2005. Benthic response to chronic natural physical disturbance by glacial sedimentation in an Arctic fjord. Mar. Ecol.-Prog. Ser. 303, 31—41, http://dx.doi.org/10.3354/meps303031.

Wlodarska-Kowalczuk, M., Weslawski, J.M., Kotwicki, L., 1998. Spitsbergen glacial bays macrobenthos — a comparative study. Polar Biol. 20 (1), 66—73, http://dx.doi.org/10.1007/s003000050277.

Włodarska-Kowalczuk, M., Pawłowska, J., Zajączkowski, M., 2013. Do foraminifera mirror diversity and distribution patterns of macrobenthic fauna in an Arctic glacial fjord? Mar. Micropaleontol. 103, 30—39, http://dx.doi.org/10.1016/j.marmicro.2013.07.002.

Włodarska-Kowalczuk, M., Węsławski, J.M., 2008. Mesoscale spatial structures of soft-bottom macrozoobenthos communities: effects of physical control and impoverishment. Mar. Ecol.-Prog. Ser. 356, 215—224, http://dx.doi.org/10.3354/meps07285.

Ysebaert, T., Meire, P., Herman, P.M.J., Verbeek, H., 2002. Macrobenthic species response surfaces along estuarine gradients: prediction by logistic regression. Mar. Ecol.-Prog. Ser. 225, 79—95, http://dx.doi.org/10.3354/meps225079.

Zagórski, P., Rodzik, J., Moskalik, M., Strzelecki, M.C., Lim, M., Błaszczyk, M., Promińska, A., Kruszewski, G., Styszyńska, A., Malczewski, A., 2015. Multidecadal (1960—2011) shoreline changes in Isbjørnhamna (Hornsund, Svalbard). Pol. Polar Res. 36 (4), 369—390.