Biogeography, diversity and environmental relationships of shelf and deep-sea benthic Amphipoda around Iceland (#59448)

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Biogeography, diversity and environmental relationships of shelf and deep-sea benthic Amphipoda around Iceland

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The waters around Iceland, bounding the Northern North Atlantic and the Nordic seas, are a region characterized by complex hydrography and seabed topography. This and the presence of the Greenland-Iceland-Faroe-Scotland ridge (GIFR) are likely to have a major impact on the diversity and distribution of the benthic fauna. Biodiversity in this region is also under increasing threat from climate-induced changes affecting the marine realm. The aim of the present study was to investigate the biodiversity and biogeographical patterns of amphipod crustaceans in Icelandic waters and how it relates to environmental variables and depth. A comprehensive data-set from the literature and recent expeditions was compiled constituting distributional records for 357 amphipod species across a major depth gradient (18-4556 m). Using a 1° hexagonal grid to map amphipod distributions and a set of environmental factors (depth, pH, phytobiomass, velocity, dissolved oxygen, dissolved iron, salinity and temperature) we could identify four distinct amphipod assemblages: A Deep-North, Deep-South, and a Coastal cluster as well as one restricted to the GIFR. ~~In addition,~~ salinity and temperature were the main parameters that determined the distribution of amphipods. Diversity differed greatly between the depth clusters and was significantly higher in coastal and GIF assemblages compared to the deep-sea clusters north and south of the GIFR. A variety of factors and processes are likely to be responsible for the perceived biodiversity patterns, which, however, appear to vary according to region and depth. Low diversity of amphipod communities in the Nordic basins can be interpreted as a reflection of the prevailing harsh environmental conditions in combination with a barrier effect of the GIFR. By contrast, similarly low diversity of the deep North Atlantic assemblages might be linked to the variable nature of the oceanographic environment in the region over multiple spatio-temporal scales. Overall, our study highlights the importance of amphipods as a constituent part of Icelandic benthos. The strong responses of amphipod communities to certain water mass variables raise the question of whether and how their distribution will change due to climate change, which should be a focus of future studies.

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Abstract

The waters around Iceland, bounding the Northern North Atlantic and the Nordic seas, are a region characterized by complex hydrography and seabed topography. This and the presence of the Greenland-Iceland-Faroe-Scotland ridge (GIFR) are likely to have a major impact on the diversity and distribution of the benthic fauna. Biodiversity in this region is also under increasing threat from climate-induced changes affecting the marine realm. The aim of the present study was to investigate the biodiversity and biogeographical patterns of amphipod crustaceans in Icelandic waters and how it relates to environmental variables and depth.

A comprehensive data set from the literature and recent expeditions was compiled constituting distributional records for 357 amphipod species across a major depth gradient (18-4556 m). Using a 1° hexagonal grid to map amphipod distributions and a set of environmental factors (depth, pH, phytobiomass, velocity, dissolved oxygen, dissolved iron, salinity and temperature) we could identify four distinct amphipod assemblages: A Deep-North, Deep-South, and a Coastal cluster as well as one restricted to the GIFR. In addition, salinity and temperature were the main parameters that determined the distribution of amphipods. Diversity differed greatly between the depth clusters and was significantly higher in coastal and GIF assemblages compared to the deep-sea clusters north and south of the GIFR.

A variety of factors and processes are likely to be responsible for the perceived biodiversity patterns, which, however, appear to vary according to region and depth. Low diversity of amphipod communities in the Nordic basins can be interpreted as a reflection of the prevailing harsh environmental conditions in combination with a barrier effect of the GIFR. By contrast, similarly low diversity of the deep North Atlantic assemblages might be linked to the variable nature of the oceanographic environment in the region over multiple spatio-temporal scales. Overall, our study highlights the importance of amphipods as a constituent part of Icelandic benthos. The strong responses of amphipod communities to certain water mass variables raise the question of whether and how their distribution will change due to climate change, which should be a focus of future studies.

Introduction

Human impacts on the world's oceans are fundamentally altering the biogeography and biodiversity of marine communities (Lotze et al., 2006; Halpern et al., 2008). Cumulating effects of climate change, resource exploitation and pollution are particularly pronounced in the Northern Hemisphere, and some of these changes have already evoked significant biotic responses, such as shifts in distribution and abundance (e.g., Harley et al., 2006; Jones et al., 2014; Birchenough et al., 2015; Hiddink et al., 2015). The pace and strength of global warming and increased atmospheric CO_2 may be faster and greater in the ocean than in the terrestrial realm (Burrow et al., 2011), but our knowledge of the consequences for the marine biota is limited (Richardson & Poloczanska, 2008). Uncovering distribution patterns of species and the identification of the ecological and evolutionary factors and processes responsible for them is therefore vital for predicting biodiversity responses to global change.

A complex array of mechanisms have been identified to determine the distribution of species on multiple spatial and temporal scales (Leibold et al., 2004). Abiotic variables confine the space that species occupy according to their physiological limits (Chase & Leibold, 2003). Species' dispersal capacity alongside their evolutionary heritage defines the size of their realized distribution (Grantham et al., 2003; Hilário et al., 2015; Baco et al., 2016). Finally, biological relationships are known to structure spatial patterns of species in many ways, such as those associated with competitors, consumers, and facilitators (Jablonski, 2008; Bascompte, 2009).

Environmental differences may be less obvious in the deep sea (>150 m) than in the shallows. It is now clear, though, that there is considerable spatial and temporal variation in the physical and biological properties to which species are exposed and which determine their distribution. Processes associated with sediment properties, temperature, salinity, nutrient input and dissolved oxygen are among the main drivers for structuring biodiversity and its geographical distribution (Levin et al., 2001; Schnurr et al., 2018). However, there is still a lack of understanding of biogeographical boundaries in the marine ~~area~~ and even less so in the deep sea (Louri & Vincent, 2004; Rex et al., 2005), making it difficult to predict how communities will respond in the wake of a changing ocean.

The waters around Iceland and adjoining seas represent a spatially heterogeneous environment with steep gradients that promote distinct habitats and related communities. As a boundary region between temperate North Atlantic, and polar waters, they are also considered to be very susceptible to climatic changes (Astthorsson et al., 2007; Eiríksson et al., 2011). Iceland is located on top of the mid-Atlantic ridge and is criss-crossed by several topographic barriers that determine the flow of water masses and ultimately the distribution of species. At the forefront is the Greenland-Iceland-Faroe ridge (GIFR), which stretches from Scotland and the Faroes via Iceland to Greenland, and hinders the direct flow of warm, salty Atlantic waters into the Nordic seas and *vice versa* (Hansen et al., 2008). As a result, seabed temperature and salinity differ strongly between areas north and south of the GIFR, which in turn can lead to marked differences in species compositions (Weisshappel & Svavarsson, 1998; Weisshappel, 2000; Bett, 2001; Weisshappel, 2001, Brix & Svavarsson, 2010; Dauvin et al., 2012; Jochumsen et al., 2016; Schnurr et al., 2018). Knowledge on the most important environmental parameters structuring ~~the~~ deep-sea benth~~os~~ communities would allow prediction of future changes for those communities.

Amphipod crustaceans are very common and diverse across marine benthic habitats (Just, 1980; De Broyer & Jazdzewski, 1996; Lörz, 2010; Stransky & Brandt, 2010; Brix et al., 2018; Jażdżewska et al., 2018), and also in Icelandic waters (Weisshappel 2000; Weisshappel, 2001; Dauvin et al., 2012; Brix et al., 2018). Their occurrence in wide variety of marine environments, in turn translates into ~~a~~ diverse feeding types that comprise detritivores, suspension-feeders, predators, and scavengers amongst others (Guerra-García et al., 2014). But they ~~themselves~~ also play a central role in the marine food web (e.g., Loerz, 2010; Nyssen et al., 2002). Amphipods, as a member of the crustacean superorder Peracarida, have a brooding life style, from which a limited dispersal capacity is derived for most species making them potentially very susceptible to environmental change. Exceptions are purely pelagic species (e.g., within the Hyperiidea) or species of the highly mobile scavenging guild.

The aim of this study was to identify the main factors influencing the distribution and biodiversity of marine amphipods in the waters around Iceland. This could provide hints as to which variables could most importantly affect ~~the~~ distribution ~~due to~~ climate change. For this purpose, a comprehensive data~~-~~set from the ~~entire~~ literature and recent expeditions was compiled constituting distributional records for 357 species across a major depth gradient (18-4556 m). Previous investigations of the Icelandic amphipod fauna ~~could identify~~ depth a strong driver of species distributions, but water mass properties were also important (Dauvin et al., 2012; Brix et al., 2018). In this regard, the GIFR appears to act as a major, albeit surmountable distributional barrier (Weisshappel & Svavarsson, 1998; Weisshappel, 2000; Weisshappel, 2001; Dauvin et al., 2012; Brix et al., 2018). Therefore, we tested whether biogeographical regions off Iceland, can be mirrored by benthic Amphipoda.

Materials & Methods

Amphipoda data

We compiled data on occurrences and abundance of 357 Amphipoda species for 501 localities from the literature. The following expeditions and respective data sources were used: extensive literature search, ~~database~~ data from BIOICE and IceAGE expeditions. The assembled dataset was highly heterogenous regarding sampling effort and method, time, location and date of the different expeditions. Many ~~samples~~ only listed one or two species, in particular the historic data from e.g. Boeck (1861), Hansen (1887) and Stephensen (1933, 1938, 1942, 1944a, b) only providing occurrence data. However, other ~~localities~~ had high abundances of individuals (max: 2709) and high species richness (max: 72). Due to the high heterogeneity, we aggregated the data at a coarser spatial resolution.

A common approach is to construct a coarse rectangular grid in which species occurrences are joined. We constructed a hexagonal grid using QGIS (QGIS Development Team, 2019) with a horizontal diameter of 1° per grid cell. Within each grid cell, the occurrence and abundance information were pooled, so that a grid cell ~~had the~~ information ~~of~~ multiple localities but species were not double counted, yet the sum of the abundances per species ~~were~~ calculated. Hexagonal grids have several advantages over rectangular grids, e.g. symmetric neighbourhood relations or reduced edge effects (Birch et al., 2007). For our study the most compelling reason to favour a hexagonal grid was the match of the polygons to the coastlines of Iceland and Greenland. Hexagonal grids much better fit to this jagged pattern with an appropriate size, whereas rectangular grid cells would have to be much smaller and ~~then they~~ would be too small for the purposes of our sampling. Given the case that many of our samples were near the coast, the hexagonal design clearly improved our sampling design.

Environmental layers

We extracted twelve variables from the Bio-Oracle 2.0 database (Assis et al., 2018) using the *sdmpredictors* package (Bosch, 2018). Variables were chosen to represent major environmental deep-sea gradients (Table 1). All variables, except minimum depth, represented long-term maximum values modelled at minimum depths on a raster with 7 km² resolution per cell. In order to use the parameters on the same spatial scale as the species data, we aggregated the raster data to the scale of the hexagonal grid cells by calculating the mean raster value for each grid cell. Hexagons then represented the summed species abundances and averaged environmental data.

We analysed the environmental data for multicollinearity on the level of the hexagons. We calculated a Pearson correlation matrix (AppS1) for all environmental layers and removed all layers with a Pearson's r above 0.75. As expected, we found strong correlation between parameters of the same information type, i.e. Chl-*a* and primary productivity or all nutrient related parameters. Finally, we retained the following parameters: depth, pH, phytobiomass, velocity, dissolved oxygen, dissolved iron, salinity and temperature. We kept salinity although it was correlated with temperature as it is one of the most important parameters structuring deep-sea communities around Iceland (e.g., Weisshappel & Svavarsson, 1998; Brix et al. pers. comm.)

Environmental Cluster Analysis

We hypothesized that deep-sea regions with similar environmental conditions would have a similar benthic fauna. Hence, we clustered the hexagonal grid cells based on the reduced set of the averaged environmental layers into a small set of environmentally homogenous regions. We used the *mclust* package (Scrucca et al., 2016) to conduct model-based hierarchical clustering using finite Gaussian Mixtures. The clustering algorithm compares 14 differently shaped types of Gaussian covariance structures representing different kinds of elliptical shapes ordered by an increasing complexity. The different models are compared using the Bayesian Information Criterion (Burnham & Anderson, 2002) choosing the model with the lowest complexity. Based on the plot of the different BIC models for possible cluster sizes from 2 to 10 (S3), we identified the optimal cluster as that one with highest regionalization capacity, i.e. having a low number of clusters but already touching the plateau of the curve, ~~signalizing~~ little differences in the model fit. We further confirmed the optimal number of clusters using a bootstrapped sequential likelihood ratio test (Scrucca et al., 2016) by comparing an increasing number of cluster sizes. Finally, we calculated mean, standard deviation, minimum and maxima for each parameter and cluster combination. This was done to allow an interpretation of the environmental conditions representing the clusters.

Taxonomic~~al~~ data

To interpret the overlap between clusters in terms of species composition, we first performed a canonical analysis of principal coordinates (Anderson & Willis, 2003) with presence absence information and the Jaccard distance measure. CAP is a constrained ordination technique, that allows to visualize similarities in sites based on species composition and environmental correlates. The ordination diagram was visually inspected by plotting the sites encircled by hulls on the first two axes. We further calculated the ANOSIM statistic on presence/absence transformed species data. ANOSIM is a non-parametric method to measure the community wise overlap between different clusters (Clarke, 1993). It yields a statistic called R that is in the range from 0 to 1 with values of R below 0.5 indicating strong overlap. The statistic is tested for significance using a permuted p-value (n=9999). Values above 0.75 indicate largely non overlapping clusters with strongly different species composition. Both analyses were performed using the vegan package (Oksanen et al., 2019).

To identify characteristic species for each cluster, we identified all species being positively associated with one specific cluster or combinations of clusters using the *multipatt* function of the *indicspecies* package (Cáceres & Legendre, 2009). We used the group-size corrected Indicator Value (IndVal.g) as a measure of association. The null hypothesis tested is that the association of a species is not higher in a specific cluster than in the other clusters. This function calculates a p-value based on 9999 permutations which is not corrected for multiple testing. However, as we are not interested in the number of indicator species, but in whether a species has a high association to a cluster or not, the p-values do not have to be adjusted (De Cáceres et al., 2010). After the analysis, species with high association values were extracted as lists for each cluster combination. The resulting species-cluster relationship was compared with literature and information from the W~~O~~RMS database.

Diversity

We aimed ~~at~~ compar~~ing~~ amphipod diversity between the different clusters. However, due to different numbers of samples, i.e. hexagonal cells, that contained the species data, clusters were not directly comparable in terms of diversity. Hence, we conducted a combined rarefaction-extrapolation analysis based on Hill numbers (Chao et al., 2014). The concept of comparing species diversity using Hill numbers stems from the fact that most diversity indices are measures of entropy such as Shannon or Simpson and do not translate directly into a measure diversity although often applied in such a way (Jost, 2006). Yet three well known measures of diversity i.e. species richness, Shannon and Simpson diversity can be generalized by a formula derived by Hill (Jost, 2006; Chao et al., 2014) which orders the indices along an order of q, i.e. q=0, 1, 2 translating to richness, Shannon and Simpson, respectively. This order reflects an increasing importance of the evenness component of diversity, while the richness component becomes less effective. This means that for richness, there is no effect of abundance on the diversity measure, while the Simpson rare species do not have an effect for the estimated diversity. Hence, the Simpson index is often thought to be the most robust index, when number of individuals strongly differ as is the case here. The diversity information is transformed into a common measure of diversity, the effective number of species, which is the number of species having equal abundances that would be required to reach e.g. the Shannon entropy value of the sample. This measure allows ~~to compare~~ all three different indices having the same unit, the effective number of species. We performed the analysis using the iNEXT package (Hsieh et al., 2016) based on the summed abundance vectors per species and cluster.

Results

General

The assembled dataset contained 357 species from 144 genera and 42 families. From these, 101 species ~~could only be~~ identified to the genus level, where species were given a numerical code. The original number of stations from the expeditions (n=501) were reduced to a set of 136 one-degree wide hexagonal cells in order to reduce the heterogeneity in the dataset. These hexagonal cells were clustered according to their environmental conditions.

Environmental clusters

The *mclust* algorithm identified six clusters to be the optimal configuration according to BIC and the likelihood ratio tests. However, when aggregating the species data to six clusters, this would result in clusters with disproportionally large differences in samples per cluster. Hence, we reduced the final number of clusters to four (Fig.1). As the clustering is hierarchical, and the four-cluster solution is not much worse in terms of BIC we were confident that this aggregation is more informative with regard to the species than the six-cluster solution which would have split the northern and southern clusters into separate regions for the specific basins. The four-cluster solution also provides a good overview of the large-scale spatial pattern. There is a “coastal” cluster (n=34 cells) which is always close to the coastline and is characterized low depth, high amounts of dissolved iron and phytobiomass and warm, oxygen-rich waters with a high current speed (Fig 2). The second cluster resembles the GIFR (n=55), which spreads from west to east and separates the northern and southern basis. In many points it is similar to the coastal cluster but is deeper and with less dissolved iron, oxygen, and phytobiomass. The other two clusters are called “deep south” (n=19) and “deep north” (n=28) as they represent the deep-sea regions of the Atlantic around Iceland. They differ strongly from the first two clusters by having very low values for many parameters. “Deep North” differs from “deep south” by being much colder, with almost no current velocity. Further, “Deep North” has a much higher amount of dissolved oxygen and pH. The lowest depths of around -3400 m are observed in the Aegir ridge. These four clusters thus characterize the environmental conditions around Iceland on a regional spatial scale.

Constrained ordination

We conducted a constrained ordination to verify the amount of variation explained in the species data by the environmental information contained at the level of the hexagonal cells. The constrained axes of the ordination explained 11% of the total variation, while 89% is explained by the 357 unconstrained axes. According to a permutation test of the marginal effects of each environmental variable ~~done with~~ the *anova.cca* function of the *vegan* package, the most important environmental variables were temperature (F=2.34, p<0.001), depth (F=2.123, p< 0.001), and salinity (F=2.01, p<0.001).

The four different clusters strongly overlapped in ordination space (Fig.3a). The ANOSIM-R value of 0.197 signals considerable similarity in species composition between the clusters. All clusters overlap in the centre of the diagram; their large spread indicates strong heterogeneity. The deep-sea clusters overlapped less than the coastal and GIFR-cluster. In general, the first constrained axis represented the depth gradient, which was in contrast to all other variables. Salinity, temperature and pH characterized the second constrained axes, with pH being in contrast to temperature and salinity (Fig. 3a). The species pattern clumped near the centroid of the ordination diagram (Fig 3b) indicating that many species are found in intermediate environmental conditions. ~~Less~~ species have a clear centroid in deeper waters, instead many species favour higher temperatures and an above average salinity. Large variation appears in the direction of pH and dissolved iron, as indicated by the strong scatter of species centroids (Fig. 3b).

Indicator species analysis

To characterize the different clusters with regard to faithful species, i.e. so-called indicator species we conducted a multipattern indicator species analysis. We compared 15 different combinations with an increasing number of clusters. From 357 species, we identified 56 to have a strong association to one or more clusters. 43 species were associated to one cluster only, while 12 and 1 species were associated to 2 and 3 clusters, respectively (Table 2). Only two species were found for the GIFR cluster, but more species from GIFR appear in combination with other clusters. Three of the clusters, the North, the South and the Coastal have indicator species belonging to the genus *Rhachotropis*. While different species of a genus might be specialized on different diets, all *Rhachotropis* species are very good swimmers. The Deep South cluster has four *Rhachotropis* as indicator species. While the GIFR cluster only had two endobenthic species, belonging to the family Ampeliscidae which are not considered strong swimmers, the combined GIFR and coastal cluster indicate *Rhachotropis aculeata* (Lepechin, 1780) as indicator – a species that is known to have a circum-Arctic distribution (Lörz et al., 2018 b). *Caprella microtuberculata* G. O. Sars, 1879 and *Aeginella spinosa* Boeck, 1861 are indicator species of the combined coastal and GIFR cluster~~,~~ these belong to the amphipod group Caprellidae, ghost shrimps, which are known for their clinging lifestyle. The indicator species with the highest values, over 0.5, are *Cleippides quadricuspis* Heller, 1875 from the Deep North, *Eusirus holmi* Hansen, 1887 from the combined Coastal and Deep North cluster and *Rhachotropis thordisae* Thurston, 1980 from the Deep South cluster – these three species are all large amphipods of several cm body length and known as predators.

Diversity

The number of aggregated hexagonal cells differed for each cluster, hence we had to apply a rarefaction and extrapolation analysis to make the three diversity measures comparable. The rarefaction of the summed abundances revealed that the two clusters “coastal” and “GIFR” have ~~around more than~~ twice the number of species than the deep-sea clusters (Fig 4a). This even holds when only the lowest comparable value of approximate 10,000 individuals are considered. Although there were so many individuals per cluster, the curves do not level off, indicating that still more sampling would be required to reach a plateau in species richness. The Shannon diversity (Fig 4b) considers the richness-abundance component of diversity. The “coastal” and “GIFR” clusters are ~~now~~ at the same level of 60 effective species; the deep-sea clusters again have a much lower diversity, i.e. almost three times lower. All curves reach a plateau, indicating that there is little more diversity to expect when abundances are considered. Hence, only rare species might be added by future sampling. Considering the Simpson diversity (Fig. 4c), i.e. when no rare species but only dominant species have an influence on the diversity measure, then the “coastal” cluster becomes the most diverse cluster while ~~also~~ the “GIFR” is only half as diverse as the coastal cluster.

Discussion

The current study built on an extensive data set designed to identify relationships between physical variables and biogeographical patterns in benthic amphipod assemblages around Iceland. We could confirm three distinct biogeographic clusters that occur to the north and south of the GIFR, and along coastal waters. In addition, we could identify a cluster of species confined to the GIFR ~~that, however,~~ had a strong overlap with a coastal assemblage. In earlier studies there were indications of lower diversity for the Nordic basins relative other deep-sea regions (Bouchet & Warén, 1979; Dahl, 1979; Rex et al., 2000; Jöst et al., 2019; but see Egilsdottir et al., 2019). Although we found shelf diversity to be elevated compared to the deep sea, no major differences could be deduced for amphipods for the basins north and south of the GIFR.

Environmental and historical imprints on amphipod distributions

Distributional groupings given in the present study corresponded to earlier findings in which distinctive boundaries between a northern and a southern deep-sea fauna were inferred, while the composition of the shallow-water fauna (> 500 m) around Iceland was very similar (Weisshappel & Svavarsson, 1998; Weisshappel, 2000; Bett, 2001; Weisshappel, 2001). Unsurprisingly, the spatial distribution of amphipods appeared to be most strongly influenced by bathymetry, salinity and seafloor temperature. The latter two were interconnected and indicative of particular water masses (Puerta et al., 2020).

The presence of the GIFR is known as an effective barrier to disrupt the dispersal of benthic organisms between the North Atlantic and the Nordic seas (Weisshappel & Svavarsson, 1998; Brix & Svavarsson, 2010; Schnurr et al., 2018). With a saddle depth averaging 600 m in the Strait of Denmark and 480 m between Iceland and the Faroe Islands and a maximum depth of c. 840 m, the depth increases towards the abyssal basins on each side of the ridge exceeding 3,000 m. Depth, or rather ecological and environmental variables that change with depth, such as hydrostatic pressure, food availability, or competition, have been demonstrated to have a large impact on species distributions (Rex & Etter, 2010; Brown & Thatje, 2011; Tittensor et al., 2011). In contrast, there are several examples of amphipod species, mostly within the more motile scavenger and predator guilds, with large depth distributions and thus at least the intrinsic capability to overcome topographical barriers (Lacey et al., 2018; Lörz et al., 2018a; Weston et al., 2021).

The GIFR also marks the transition between different bodies of water, and hence the effects of depth and water mass properties are intertwined. Generally, physical and chemical water mass attributes such as temperature, salinity, pH, organic matter, and dissolved oxygen play critical roles in structuring benthic communities incl~~.~~ microbes, fish, crustaceans, corals, and sponges

(Koslow, 1993; Weisshappel & Svavarsson, 1998, Brix & Svavarsson, 2010; Schnurr et al., 2018; Puerta et al., 2020; Roberts et al., 2021). Reasons for this involve physiological tolerances of larvae, juveniles and adults towards certain environmental conditions, dispersal constraints invoked by density differences or current shear, as well as enhanced nutrient input linked to hydrography (Puerta et al., 2020; Roberts et al., 2021).

Obviously, cold sub-zero temperatures in the Nordic sea basins restrict species distributions, as ~~only~~ few species are pre-adapted to such low temperatures while withstanding high hydrostatic pressures (Svavarsson et al., 1993; Brown & Thatje, 2011). This is supported by the fact that many amphipod species in our study prefer moderate conditions, at least in terms of temperature. Initially, however, species originating from the North Atlantic had to overcome the GIFR and enter the Nordic seas against the overflow water from the Denmark Strait and Faroe Bank Channel (Yasuhara et al., 2008), the latter being limited to species with broad bathymetric distributions or eurytherm “shallow”-water taxa. The presence of the GIFR is thereby inevitably linked to the opening of the North-east Atlantic about 55 Mya, representing a barrier between the Nordic seas and North Atlantic ever since (Hjartarson et al., 2017). Alternatively, species from the North Pacific had to cross the Bering Strait sill, and experience subsequent trans-Arctic migration (Hardy et al., 2011). While the shelf fauna represents a mixture of North Pacific, North Atlantic and to a lesser extent endemic Arctic fauna (e.g., Svavarsson et al., 1993; Hardy et al., 2011), large parts of the contemporary deep-sea fauna of the Arctic and Nordic seas likely originate from the North Atlantic (e.g. Bluhm et al., 2011 and citations therein; Svavarsson et al., 1993).

In our indicator analysis, species were identified based on their predominant affiliation to certain oceanographic conditions. Identifying areas of endemicity, Arfianti & Costello (2020) defined our study area as part of a larger region that comprised North American boreal, Arctic and North Pacific areas. Our results, however, are consistent with the view that the deep-sea fauna of the Nordic seas appears to originate from shelf genera or less pronounced deep-sea taxa that were able to cross the GIFR (Dahl, 1979; Just, 1980; Svavarsson et al., 1993). The study by Arfianti & Costello (2020) contained data for the entire Arctic and sub-Arctic regions, encompassing both shelf and deep-sea areas, with the first reportedly representing a mixture of Atlantic, Arctic and Pacific elements (see above). Contrasting distribution patterns in hyperbenthic Eusiridae and Calliopiidae represent good examples to illustrate the barrier effect of the ridge; the family

Eusiridae, which is more prevalent in deep water, has only a few species north of the GIFR, which is in contrast to the shallow water family Calliopiidae, whose species diversity is higher in the north (Weisshappel, 2000; Weisshappel, 2001). Overall, Svavarsson et al. (1993) describes the deep-sea fauna of the Arctic and Nordic seas as very young, probably less than 100,000 yrs. old, due to the presence of the ridge and the adverse conditions prevailing in the northern regions ("topographic and environmental filtering"). Accordingly, little time remained for speciation and formation of endemic species (Svavarsson et al., 1993).

Our coastal amphipod assemblage, as well as the one associated with the GIFR, consisted of indicator species with broad North Atlantic distributions. Over ~~the~~ past millennia the biogeography of northern latitudes had been shaped by recurring glacial cycles (Darby et al., 2006). During the last glacial maximum (ending about 6,000 yrs ago; Darby et al., 2006). Arctic shelves were largely covered by grounded ice sheets forcing the fauna towards more southerly (North Atlantic) ice-free areas or deeper waters (Dunton, 1992; Darby et al., 2006). The latter may have become the ancestors of today's Nordic deep-sea fauna (Nesis, 1984). While evidence exists that at least parts of the shelf had remained ice-free and thus served as glacial refugia, notably here Iceland and the Faroe Islands (Maggs et al., 2008; Hardy et al., 2011), most species must have recolonized the previously ice-covered areas rather swiftly. Given the close overlap of coastal and GIFR fauna in our study, the ridge could have provided a potential shallow-water link for brooding taxa that has promoted the recolonization from suitable ice-free habitats.

Diversity trends

For many taxa, including isopods, molluscs and polychaetes, diversity in deep-sea areas north of the GIFR (encompassing the Norwegian, Greenland and Icelandic seas) is low compared to other deep-sea areas (Svavarsson, 1997; Rex & Etter, 2010; Stuart & Rex, 2009; Oug et al., 2017). Species richness of high northern-latitude shelves appears to be at intermediate levels compared to low latitudes (Piepenburg et al., 2011; Egilsdottir et al., 2019). Thus, we expected amphipod diversity to lower in the northern basins compared to the south and, moreover, a higher shelf diversity that decreases significantly towards the northern basins.

Simply put, comparing the diversity between the distributional clusters showed that the diversity of the shallow clusters (coastal and GIFR) was higher than that of the deep clusters north and south of the ridge. While species richness had the highest number of effective species (Fig. 4a), its sole use is usually not encouraged as it is heavily affected by sample size and shows high sensitivity in recording rare species (Jost, 2006). There were some profound differences between Hill numbers – species richness, Shannon, and Simpson diversity - likely because each of these indices scales rarity differently (Chao et al., 2014; Roswell et al., 2021; Fig. 4 b, c). The fact that none of the richness-based rarefaction curves has stabilized yet, could therefore be an artifact; many species have only been found once, either because they could not be identified or because only a small number of individuals were sampled during the historical missions. The Simpson index, on the other hand, is considered as being most robust when sampling effort differs strongly between samples, since it largely reflects patterns in the most common species (Jost, 2006). Shannon diversity can be seen as a half-way house in terms of its responses to sample size and rarity (Roswell et al., 2021). Overall, though, all estimates applied have their merits and pitfalls, and typically using all three indices provides the best representation of the diversity in a given area (Roswell et al., 2021). Although differences in sampling intensity between grid cells was a confounding factor in our study and the results must be ~~thus~~ carefully weighed, a consistent pattern of a higher diversity in the shallow- relative to the deep clusters was evident in all three indices.

Benthic diversity at high northern latitudes has long been viewed as species-poor reflected in a latitudinal gradient of decreasing diversity from the equator to the poles (Kendall & Aschan, 1993; Piepenburg, 2005). While this may be true for the Nordic basins (Svavarsson et al., 1993; Jöst et al., 2019), it does not apply to the shelf fauna of the Arctic and the Nordic seas (Kendall & Aschan, 1993; Renaud et al., 2009, 2015; Piepenburg et al., 2011; this study). Combined historical and ecological explanations have been utilized to interpret the overall low diversity of the Nordic basins compared to the other deep-sea regions (Svavarsson et al., 1993; Bluhm et al., 2011). In general, it is believed that variation in energy supply (temperature and productivity) affect deep-sea diversity (e.g. Woolley et al., 2016; Yasuhara & Danovaro, 2016; Jöst et al., 2019). Cold temperatures per se do not seem to have a negative impact on diversity, since benthic communities at sub-zero temperatures in the Southern Ocean abyss appear to be extraordinarily rich (Brandt et al., 2007), but when coupled with very low productivity and geographical isolation of the Nordic basins the diversity of invertebrates is relatively low ~~diversity in the cold North~~ (Svavarsson et al., 1993; Egilsdottir et al., 2019; Jöst et al., 2019).

Notably, the diversity of the "Deep South" cluster in our study was ~~similarly~~ low as that of the ~~north~~, which contrasts with the perception of an impoverished Nordic deep-sea fauna (Bouchet & Waren, 1979; Dahl, 1979; Rex et al., 1993; Svavarsson, 1997; Weisshappel & Svavarsson, 1998; Jöst et al., 2019;). Although amphipods are typically less well presented in the deep sea (e.g. when compared to isopods; Lörz et al., 2013), their 'deficiency' in Nordic waters was established earlier. For example, Dahl (1979) found that gammaridean species in the Norwegian Sea is a mere 20% of that in the North Atlantic. Yet, it is not clear whether ~~it~~ is valid, ~~for example, also with regard to~~ the fact that pure richness comparisons are very susceptible to differences in sample sizes and sample effort (see discussion above). In addition, different taxa north and south of the ridge can have different diversity patterns resulting e.g. from their different evolutionary histories, lifestyles (brooding vs. broadcaster) or physiological scope. This becomes very evident in isopods, a sister group of the amphipods, where the diversity of the deep North Atlantic exceeds that of the Nordic seas by far (Svavarsson, 1997).

Although not strictly comparable, but in line with our results, Egilsdottir et al. (2019), found local diversity of bivalve and gastropod molluscs north and south of the GIFR to be equally low. They attributed this to specific oceanographic conditions prevailing at the deep southern stations. In addition, changes in environmental conditions in the course of past glacial maxima in the northern North Atlantic and in the North Sea were associated with cyclical changes of low (glacial) and relatively increased (interglacial) diversity (Cronin & Raymo, 1997; Yasuhara et al., 2014). The related environmental consequences of these climatic changes, in particular variation in bottom-water temperature, seasonality and meltwater runoff, evidently had a strong impact on deep-sea diversity, with recent deep-sea fauna still in the process of recovering from these events (Rex et al., 1993; Cronin & Raymo, 1997; Wilson, 1998; Yasuhara et al., 2008; Yasuhara et al., 2014; but see Jöst et al., 2019 and citations therein).

Compared to the deep-sea cluster, the diversity of the shallower coastal and GIFR clusters was considerably higher (Fig 4a). This is in stark contrast to an allegedly poor amphipod fauna, for example when compared to the South polar region (Arfianti & Costello, 2020). Although a direct comparison with other regions at complementary depth is still pending, it is already clear that the shelf and upper slope amphipod fauna on the border between the North Atlantic and North Sea, consisting of more than 300 effective species, is not depleted (Fig. 4a). In comparison, De Broyer & Jazdzewska, (2014) counted ~ 560 amphipod species for the entire Antarctic region (south of the Polar front), which is considered a hotspot of amphipod diversity (Arfianti & Costello, 2020). In addition, through the application of molecular techniques, but also additional sampling, especially of the deeper and less frequently explored areas, more species are likely to be discovered for the northern region (Bluhm et al., 2011; Jażdżewska et al., 2018; Lörz et al., 2018a; Schwentner & Lörz, 2020). We admit the comparison is slightly misleading, as cryptic species are discovered across all environments at similar rates (Pfenninger & Schwenk, 2007), plus different geological histories, oceanographic settings, and the size of the Arctic vs. Antarctica, among other things represent additional confounders. Since the Cenozoic Era (c. 65 mya) and more recently, the areas of the northern North Atlantic and the Nordic seas have undergone profound climatic changes, from greenhouse to ice house conditions and vice versa, shaping the composition and biogeography of the marine biota (Piepenburg 2005; Horton et al. 2020). Webelieve that the diversity of the northern regions should not be underestimated and presumably occupies globally at least a middle ranking.

Conclusions

In amphipods, water mass properties appear to be the main force in delineating species distributions at the boundary between the North Atlantic and the Nordic seas, with the GIFR additionally hindering the exchange of deep-sea species between northern and southern deep-sea basins. This pattern is largely congruent for all benthic but also hyperbenthic amphipod families. Different factors are likely responsible for driving deep-sea diversity on each side of the ridge. While impoverished amphipod communities in the Nordic basins are likely to be due to topographical and environmental barrier effects, the southern deep-sea assemblage shows similarly low diversity, presumably a response to variation in the oceanographic environment over a range of temporal and spatial scales. In addition, bathymetric sampling constraints need to be considered. Additional environmental variables may prove important in explaining diversity and distribution, including seasonality in productivity, pH and ice cover.

In our study, amphipods were highlighted as an important benthic component in Icelandic waters. Since climate change is supposed to have an impact on several organizational levels (populations, species, communities), in future studies, we aim to investigate the interaction of local and regional processes on amphipod diversity as well as species-specific responses to better understand potential effects of climate change in Nordic seas.

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Table 1(on next page)

Environmental parameters

Table 1. Environmental parameters initially extracted from the BIO-ORACLE 2.0 database. All parameters are long-term maxima at minimum depth, except bathymetry which represents the deepest (=minimum) depth measured.

Table 1. *Environmental parameters initially extracted from the BIO-ORACLE 2.0 database. All parameters are long-term maxima at minimum depth, except bathymetry which represents the deepest (=minimum) depth measured.*

Acronym	Parameter	Units	Source
depth	Bathymetry	meters	GEBCO URL: http://gebco.net EMODnet Bathymetry URL: http://www.emodnet-bathymetry.eu/
chla	Chlorophyll concentration	mg/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
vel	Current velocity	m/s	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979-2013) URL: http://marine.copernicus.eu/
dO_2	Dissolved oxygen concentration	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dFe	Dissolved iron concentration	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dP	Phosphate concentration	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
dNO_3	Nitrate concentration	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
temp	Sea water temperature	degrees Celcius	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979-2013) URL: http://marine.copernicus.eu/
phybio	Carbon phytoplankton biomass	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
prod	Primary production	g/m²/day	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/
Salinity	Sea water salinity	PSS	Global Ocean Physics Reanalysis ECMWF ORAP5.0 (1979-2013) URL: http://marine.copernicus.eu/

Acronym	Parameter	Units	Source
$Si0_4$	Silicate concentration	µmol/m²	Global Ocean Biogeochemistry NON ASSIMILATIVE Hindcast (PISCES) URL: http://marine.copernicus.eu/

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Table 2(on next page)

Indicator value analysis

Table 2. Indicator value analysis for all combinations of the environmental clusters. The group-size corrected Indicator Value (IndVal.g) represent the association value of a species with a given cluster. The p-value is based on 999 permutations.

Table 2. Indicator value analysis for all combinations of the environmental clusters. The group-size corrected Indicator Value (IndVal.g) represent the association value of a species with a given cluster. The p-value is based on 999 permutations.

Cluster	Nr.	Species	IndVal.g	p-value	
Coastal	1	*Rhachotropis oculata*	0.400	0.005	**
	2	*Westwoodilla caecula*	0.383	0.015	*
	3	*Ampelisca macrocephala*	0.368	0.010	**
	4	*Deflexilodes tesselatus*	0.368	0.035	*
	5	*Harpinia* sp. 5	0.343	0.020	*
	6	*Monoculodes* sp.A	0.343	0.015	*
	7	*Westwoodilla megalops*	0.343	0.030	*
	8	*Harpinia pectinata*	0.328	0.020	*
	9	*Bathymedon obtusifrons*	0.319	0.035	*
	10	*Monoculodes latimanus*	0.297	0.045	*
Deep North	1	*Cleippides quadricuspis*	0.642	0.005	**
	2	*Bruzelia dentata*	0.463	0.005	**
	3	*Rhachotropis* sp A	0.392	0.005	**
	4	*Paroediceros curvirostris*	0.375	0.015	*
	5	*Deflexilodes tenuirostratus*	0.349	0.040	*
	6	*Halirages quadridentata*	0.344	0.025	*
	7	*Monoculopsis longicornis*	0.344	0.025	*
	8	*Oedicerina* sp	0.327	0.025	*
Deep South	1	*Rhachotropis thordisae*	0.559	0.005	**
	2	*Rhachotropis proxima*	0.499	0.010	**
	3	*Eusirus bathybius*	0.459	0.010	**
	4	*Lepechinelloides karii*	0.459	0.005	**
	5	*Rhachotropis gislii*	0.459	0.005	**
	6	*Protoaeginella muriculata*	0.401	0.010	**
	7	*Cleonardopsis* sp	0.397	0.005	**
	8	*Lepechinella grimi*	0.397	0.005	**
	9	*Lepechinella helgii*	0.397	0.010	**
	10	*Lepechinella skarphedini*	0.397	0.010	**
	11	*Rhachotropis thorkelli*	0.397	0.010	**
	12	*Neopleustes boecki*	0.365	0.010	**
	13	*Neopleustes* sp	0.324	0.010	**
	14	*Sicafodia* sp	0.324	0.010	**
	15	*Eusirus* sp C	0.300	0.020	*
	16	*Rhachotropis aislii*	0.300	0.040	*
	17	*Rhachotropis gloriosae*	0.300	0.035	*
GFIR	1	*Ampelisca odontoplax*	0.348	0.03	*
	2	*Haploops tenuis*	0.302	0.05	*
Coastal + Deep North	1	*Eusirus holmi*	0.509	0.005	**
	2	*Halirages fulvocincta*	0.490	0.050	*
	3	*Arrhis phyllonyx*	0.458	0.005	**
	4	*Andaniella pectinata*	0.430	0.005	**
	5	*Paroediceros propinquus*	0.372	0.040	*
	6	*Halirages elegans*	0.359	0.030	*
	7	*Harpiniopsis similis*	0.347	0.035	*
Coastal + GFIR	1	*Aeginella spinosa*	0.559	0.005	**
	2	*Rhachotropis aculeata*	0.467	0.025	*
	3	*Caprella microtuberculata*	0.462	0.010	**
	4	*Harpinia propinqua*	0.459	0.030	*
Deep South + Deep North	1	*Liljeborgia pallida*	0.349	0.045	*
	2	*Ampelisca islandica*	0.329	0.025	*

Coastal + Deep South + Deep North	1	*Amphilochus anoculus*	0.424	0.035	*

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Figure 1

Environmental cluster

Figure 1. Map of the outlines four identified environmental clusters in the North Atlantic. The Greenland-Faroe-Iceland ridge (GFIR) extends from west to east and is, like the coastal cluster, partly interrupted due to the coarse resolution of the hexagonal cells of 1° in east-west direction.

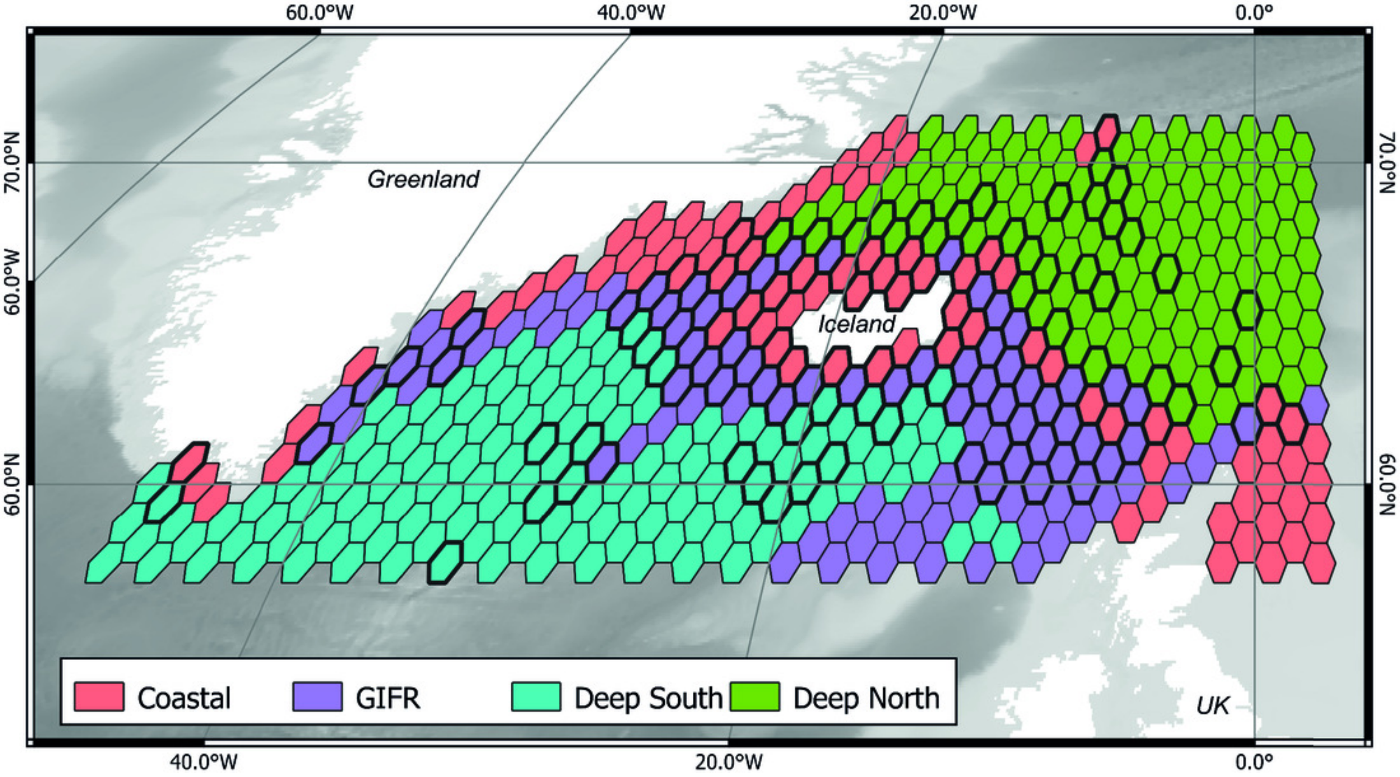

Figure 2

Characterisation of environmental clusters

Figure 2. Characterization of the four environmental clusters by the environmental parameters with box-whisker plots. For abbreviations refer to table 1. An extended table with numeric information can be found in the appendix.

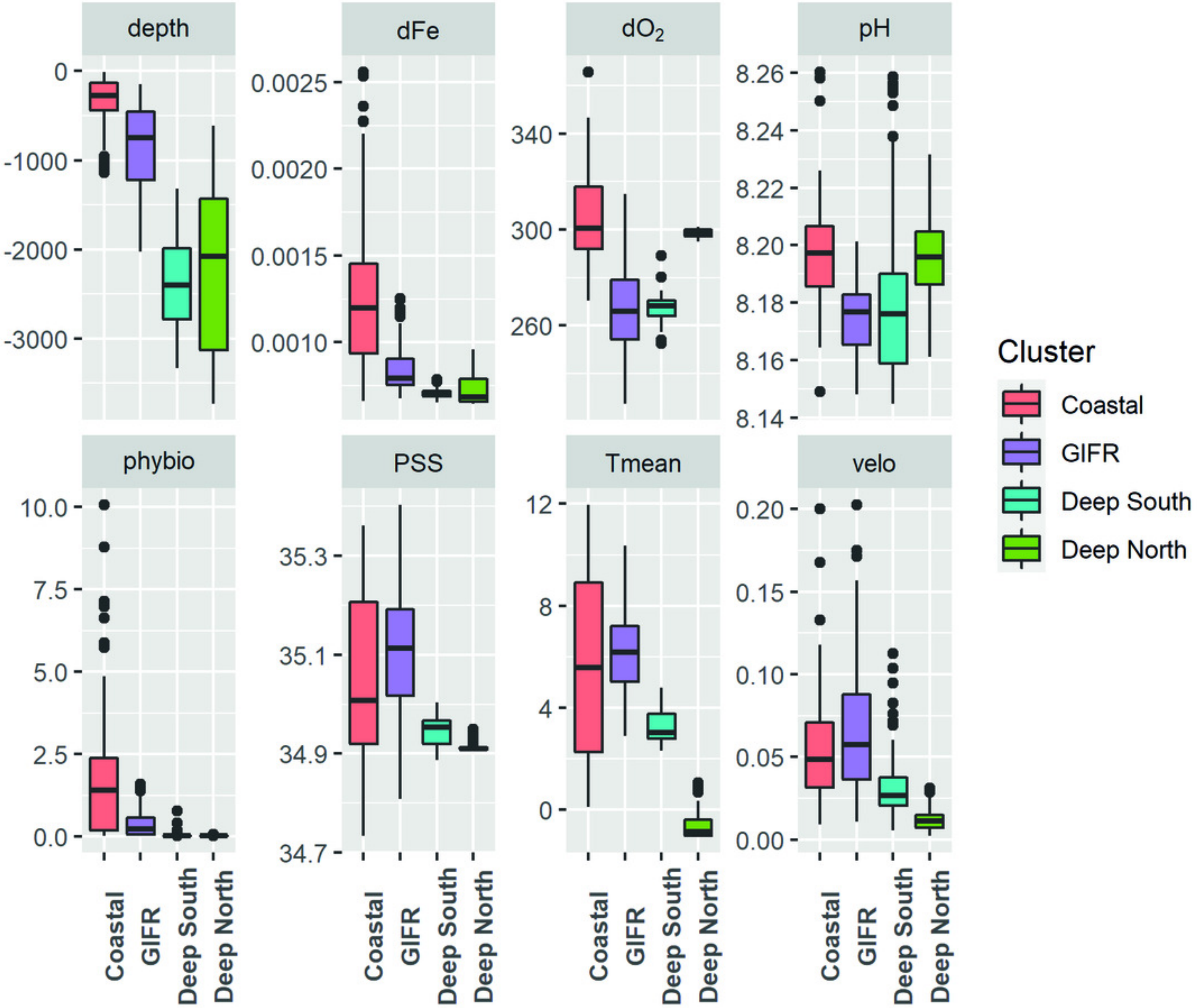

Figure 3

Constrained analysis of principal coordinates (CAP) based on Jaccard distances.

Figure 3. Constrained analysis of principal coordinates (CAP) based on Jaccard distances. a) Scaling is based on site scores, b) scaling is based on species scores (red dots) - note the differences of the axes. Arrows point into the direction of largest correlation with species and site scores. The 0,0 coordinate reflects the centroid of each variable. The environmental clusters still overlap considerably in their species composition as reflected by the low ANOSIM-R statistic.

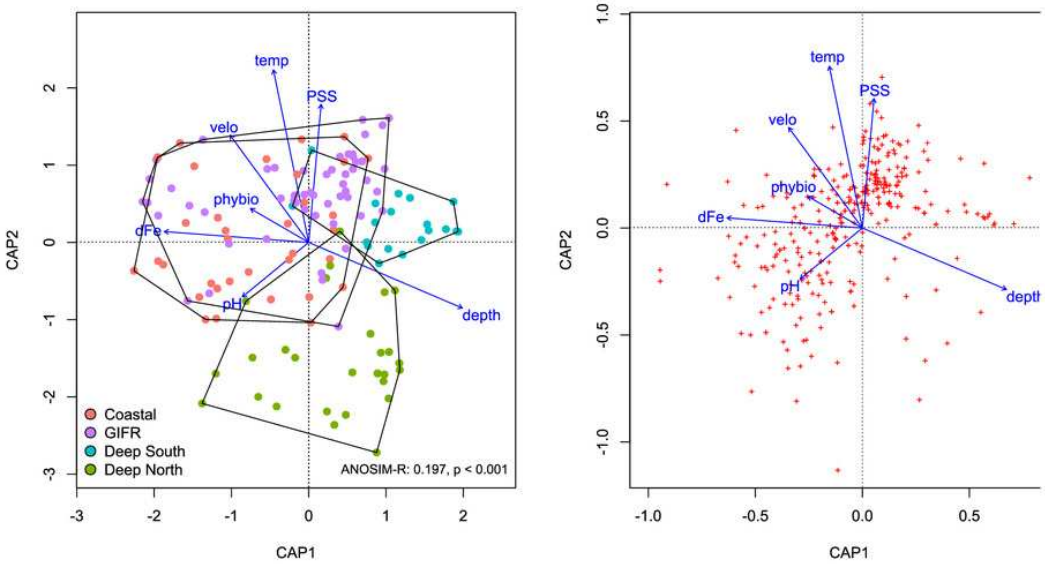
CAP2
CAP1
temp
PSS
velo
phybio
dFe
pH
depth
Coastal
GIFR
Deep South
Deep North
ANOSIM-R: 0.197, p < 0.001
-3
-2
-1
0
1
2
1.0
0.5
0.0
-0.5
-1.0
deptl

Figure 4

Rarefaction-extrapolation of diversity indices per cluster.

Figure 4. Rarefaction-extrapolation of diversity indices per cluster. The diversity indices a) richness, b) Shannon, and c) Simpson, represent an increasing importance of abundant species. The unit of the y-axis is the effective number of species.