



Species composition comparisons and relationships of Arctic marine ecoregions

Joan M. Alfaro-Lucas^{a,b,*}, Chhaya Chaudhary^{a,b}, Angelika Brandt^{a,b}, Hanieh Saeedi^{a,c}

^a Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325, Frankfurt am Main, Germany

^b Institute for Ecology, Evolution and Diversity, Goethe-University of Frankfurt, FB 15, Max-von-Laue-Str. 13, 60439, Frankfurt am Main, Germany

^c OBIS Data Manager, Deep-Sea Node, Frankfurt am Main, Germany

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ABSTRACT

In the context of rapid climate change, a better understanding of the Arctic Ocean (AO) biodiversity patterns is of paramount importance. Here, we integrated and quality controlled the distribution records of well-represented marine taxa from OBIS and GBIF, from shallow (0–200 m) to deeper environments (>200–500 and > 500 m), across fifteen Marine Ecoregions of the World (MEOW) of the AO. We qualitatively compared patterns of species richness and unique species along those ecoregions, and based on species compositions: (i) assessed ecoregions validity by statistically comparing composition differences; and (ii) determined the relationships between ecoregions. We found less significant differences between ecoregion species compositions at greater depths suggesting a highest homogeneity of deeper environments and that the MEOW system, originally defined for shallow water (0–200 m), does not represent well the organization of deep-sea Arctic biodiversity. However, at shallower depths, some regions such as the Canadian and Greenland ecoregions neither showed clear species composition differentiation. At all analyzed depths, Arctic ecoregions cluster in two groups differentiating Eurasian and American ecoregions, respectively. At shallower depths, however, Siberian ecoregions tended to group highlighting their specific environment and more isolated waters. Our results suggest that AO biodiversity patterns and distribution match the paths and influence of the main oceanic currents entering from the Atlantic and Pacific. We identified the Siberian Arctic and the Canadian Arctic to be data scarce highlighting the need for sampling in these regions and mobilization of data to public repositories. This study helps to better understand the organization of the AO biodiversity and to guide future biodiversity assessments and management activities.

1. Introduction

The composition and distribution of species in the Arctic Ocean (AO) are shaped by complex past geologic and climatic events, and its episodes of connection and disconnection with the Atlantic and Pacific Oceans (Dunton, 1992; Piepenburg, 2005). The AO emerged ~150 Myrs ago as a temperate embayment of the Pacific Ocean but the deep-sea connection was interrupted ~80 Myrs ago (Dunton, 1992). Arctic connections with the Atlantic were established uninterruptedly since the Eocene (~50 Myrs). During the last glacial periods, the AO became a deep-sea basin connected to the Atlantic but disconnected from the Pacific Ocean due to a sea level drop of ~100 m. This drop exposed shelves, equivalent to ~50% of the present-day AO area (Jakobsson, 2002), eradicating the majority of their fauna (Dunton, 1992; Piepenburg, 2005; Bluhm et al., 2015). During interglacial periods, the sea

level rose again and the Pacific connection was reestablished. The re-submerged shelves were recolonized by glacial survivors, Pacific and mainly Atlantic immigrants (Bluhm et al. 2011a, 2011b, 2015; Hardy et al., 2011; Bringloe et al., 2020). Thus, fauna of Pacific origin are currently mainly found in shallow waters near the Bering Strait (Bilyard and Carey, 1980; Dunton, 1992; Bluhm et al., 2015), whereas species of Atlantic origin currently dominate in both Arctic shelves and deep sea (Bluhm et al., 2011a, 2011b). Furthermore, the repeated recolonizations after glacial periods explain the current Arctic low endemism and the dominance of widespread eurybathic, boreal-Arctic species (Bluhm et al., 2011a). Nevertheless, species composition differences have been identified throughout the AO and at depth suggesting a more nuanced organization of fauna (Spalding et al., 2007; Piepenburg et al., 2011; Yasuhara et al., 2012; Costello et al., 2017; Vedenin et al., 2018, 2021).

Marine Ecoregions of the World (MEOW) (hereafter ecoregions)

* Corresponding author. Senckenberg Research Institute and Natural History Museum, Senckenberganlage 25, 60325, Frankfurt am Main, Germany.

E-mail address: jmalfarolucas@gmail.com (J.M. Alfaro-Lucas).

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define geographic units of consistent species composition and underlying environmental features, forming an organization system for benthic and pelagic biota of coastal and shelf environments (down to 200 m depth) (Spalding et al., 2007). Arctic ecoregions show distinct environmental regimes, in terms of primary productivity, depth, river runoff and ice cover, but the influence of Atlantic and Pacific currents are arguably the main drivers of ecoregion biodiversity composition and patterns (Grebmeier et al., 2006; Piepenburg et al., 2011; Bluhm et al., 2011a, 2020; Wassmann et al., 2015; Degen et al., 2015; Rybakova et al., 2019; Käb et al., 2019) (Fig. 1). From the Atlantic Ocean, the warmer and saltier West Spitsbergen Current influences the Arctic shelves via the Fram Strait, while the Norwegian Atlantic Slope Current does so via the Barents Sea (Beszczynska-Möller et al., 2011; Bluhm et al., 2015) (Fig. 1). These currents run towards the Siberian shelves and reach the Chukchi Sea and Canadian regions before coming back to the Atlantic Ocean forming the East Greenland Current (Beszczynska-Möller et al., 2011; Bluhm et al., 2015) (Fig. 1). From the Pacific Ocean, the shallower Alaska Coastal Current, as well as Aleutian North Slope, Bering Slope, and Anadyr waters, enter the Chukchi Sea via the Bering Strait, head towards the Canadian ecoregions and ultimately reach the Atlantic Ocean (Grebmeier et al., 2006; Sigler et al., 2011; MacKinnon et al., 2021) (Fig. 1). The dilution of the effect of the warmer and nutrient-rich Atlantic currents from the Barents to the East Siberian Sea, and of the Pacific currents from the Chukchi Sea to the Canadian ecoregions, creates decreasing trends of species diversity (Dunton, 1992; Sirenko, 2001; Wassmann et al., 2015; Bluhm et al., 2011a; Yasuhara et al., 2012, 2012b). Despite these broad trends, species composition differences and relationships between Arctic ecoregions are not well understood (Piepenburg et al., 2011; Bluhm et al., 2011a). Furthermore, the ecoregions defined by MEOW were derived from expert knowledge (Spalding et al., 2007) and statistical tests still remain necessary to prove both their validity as organization system and suitability for greater depths (Piepenburg et al., 2011; Costello et al., 2017; Hadiyanto et al., 2021; Watling and Lapointe, 2022).

Determining and understanding the Arctic biodiversity patterns is of

paramount importance. The Arctic is warming rapidly under climate change, which is increasing Arctic borealization, i.e., the import of anomalous Atlantic and Pacific waters and biota (Fossheim et al., 2015; Fraimer et al., 2017; Ardyna and Arrigo et al., 2020; Polyakov et al., 2020; Csapó et al., 2021). In the recent years, the exponential increase of data in open-access repositories, such as the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF), has allowed analyses and tests of marine biodiversity and organization systems, respectively, at larger scales (e.g., Costello et al., 2017; Hadiyanto et al., 2021; Watling and Lapointe, 2022). Recently, in the Biogeography of the NW Pacific deep-sea fauna and their possible future invasions into the Arctic Ocean (Beneficial) project, the biodiversity patterns between the NW Pacific and adjacent AO were synthesized and analyzed after an extensive sampling effort integrated with OBIS and GBIF (e.g., Brandt and Malyutina, 2015; Malyutina et al., 2018; Saeedi et al., 2019a, b; Brandt et al., 2020; Saeedi et al., 2020; Saeedi and Brandt, 2020; Saeedi et al., 2022a, b). Here, we extended the Beneficial project goals to the whole AO and analyzed fifteen Arctic ecoregions originally proposed by Spalding et al. (2007) for shallow waters (0–200 m) (Fig. 1), and extended these analyses to deeper environments (200–500 and > 500 m). Our goals were (i) to qualitatively discuss and compare the observed biodiversity patterns including the species richness and unique species across Arctic ecoregions with previous findings, (ii) statistically test the species composition differences between Arctic ecoregions, and (iii) determine Arctic ecoregion species composition similarity relationships.

2. Material and methods

2.1. Study area

Our study area ranged from latitude 70°N to 90°N and included a total of fifteen MEOW from the Arctic realm as defined in Spalding et al. (2007) (Fig. 1). We followed Brümmer et al. (2011) and Horvat et al. (2017), whom defined the AO spatial coverage as comprised between longitude –180 to 180 and latitude 70°N to 90°N. We included the Northern Norway and Finnmark ecoregion because of its area north of 70°N, even if it was previously classified as the Temperate Northern Atlantic realm by Spalding et al. (2007). We excluded the Hudson Complex and the White Sea ecoregions from this study due to their negligible area over 70°N.

2.2. Data extraction and quality control

Species records were extracted from the OBIS (<http://www.iobis.org>) and GBIF (<http://www.gbif.org>) repositories. Data extraction and quality control was done in R v. 4.0.2 (R Core Team, 2020) and QGIS v. 3.16 (QGIS Development Team, 2019). Big data repositories, such as OBIS and GBIF, contain records obtained from different methods, sampling efforts, and sampling intensity along distinct regions (Hughes et al., 2021). In order to minimize potential sampling bias, or at least not to exacerbated bias further, we (i) used presence data only, (ii) selected distribution records from taxonomic groups showing an even spatial distribution, and (iii) used appropriate metrics for comparisons (see also section *Species composition comparisons* for β -diversity metrics justification). The selected taxonomic groups were Actinopterygii, Malacostraca (order Amphipoda only), Bivalvia, Polychaeta, and Gastropoda (see Appendix A; Table A1, for citations of the datasets used). Previous studies showed that these groups were extensively sampled and widely distributed throughout the study area (Bluhm et al., 2011a, 2011b; Piepenburg et al., 2011) and our preliminary analyses exploring data distribution along depth, latitude, and taxonomic groups confirmed these patterns (see Appendix A: Figure A1, Figure A2 and Figure A3). We integrated the distribution records across all selected taxonomic classes irrespectively of environment, i.e., benthic or pelagic, to provide an empirical, holistic basis to test ecoregion species composition

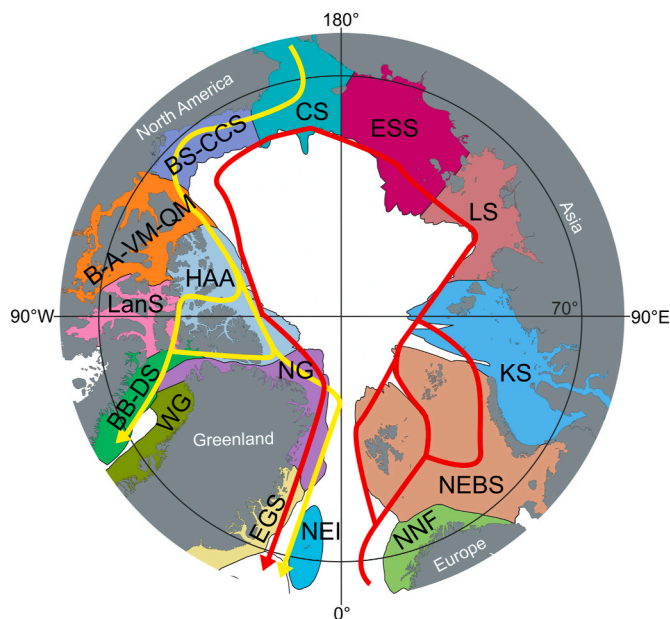


Fig. 1. Analyzed ecoregions and Atlantic and Pacific oceanic currents paths in red and yellow, respectively (see text for details). BB-DS= Baffin Bay - Davis Strait; BS-CCS= Beaufort Sea - continental coast and shelf; B-A-VM-QM = Beaufort-Amundsen-Viscount Melville-Queen Maud; CS= Chukchi Sea; ESS = East Siberian Sea; KS= Kara Sea; LanS= Lancaster Sound; LS= Laptev Sea; NEBS= North and East Barents Sea; NEI= North and East Iceland; NG= North Greenland; NNF= Northern Norway and Finnmark.

differences and relationships as recently done in other studies (e.g., Costello et al., 2017).

Specifically, we extracted distribution records of Animalia from 70°N to 90°N from OBIS using the function *occurrence* in the package *robis* in R (Provoost and Bosch, 2020). We checked and deleted in R the distribution records without coordinates, older than 1899, and with coordinate uncertainty higher or equal to 100 km in order to avoid records of dubious reliability and quality. We then selected only those records belonging to the targeted taxonomic classes in R. Data from the GBIF were downloaded directly from GBIF website following the same criteria mentioned above. OBIS and GBIF data were then merged and duplicate records were deleted. We further matched the species names against the World Register of Marine Species (WoRMS) via the web service from LifeWatch (<https://www.lifewatch.be/data-services>). We corrected species names with spelling errors, and changed not-accepted species names to the currently accepted name in WoRMS. We also selected species classified as “marine” and/or “brackish” independently if they had other affinities. In order to keep extant species only, we retrieved the status of each species from WoRMS using the *wormsbyname* function in the *worms* R package (Holstein, 2018) and deleted all fossil records. The distribution records with depths expressed as negative numbers (e.g., -200 m) and/or exceeding 5,550 m depth (maximum depth in the AO) were also deleted. Species distribution records were visualized with QGIS, and records found on land were removed using the QGIS *Join attributes by location* function. These processes yielded a dataset with 1,750 species and 144,870 distribution records from 0 to 5,540 m depth (Appendix A, Figure A1).

Prior to analyses, we divided our dataset into three different depth categories, including shallow (<=200 m), intermediate (>200 to <=500 m), and deep (>500 m) distribution records. The whole study area was also divided to 50,000 km² equal-area hexagonal cells. For each depth category, distribution records were assigned to their overlapping hexagons, and the hexagons were assigned to an Arctic ecoregion (Spalding et al., 2007) based on the location of their centroid using the *Join attributes by location* function in QGIS. Ecoregion polygon layer was obtained from Spalding et al. (2007). Hexagons with centroids falling outside ecoregions limits and their records were not considered. In total, we analyzed 30,306 distribution records belonging to 1,298 species distributed among 105 hexagons in the shallow dataset; 98,113 records belonging to 1,293 species distributed among 62 hexagons in the

intermediate dataset; and 8,908 records belonging to 647 species distributed among 75 hexagons in the deep dataset (Fig. 1B and C; Table 1).

2.3. Species pattern analyses

We calculated and visualized the number of exclusive and shared species between the three datasets with Venn diagrams using the InteractiVenn web-based tool (Heberle et al., 2015) (Fig. 1B). We calculated the number of shared Arctic species in our datasets with the NW Pacific species (<70°N) reported in Saeedi et al. (2019a, b). To visualize the heterogeneity of the underlying data, we calculated and mapped the number of records and species richness (number of species) per hexagon across the study area in the three datasets (e.g., Costello et al., 2017; Saeedi et al., 2019a, b; Saeedi et al., 2020; Saeedi and Brandt, 2020). We also calculated the number of records (as a proxy of sampling effort) and the number of species (species richness) per ecoregion at each dataset. To explore the endemism patterns, we calculated the percentage of unique species in relation to the total number of species found at each ecoregion. Additionally, we analyzed each taxonomic group separately (Actinopterygii, Amphipoda, Bivalvia, Polychaeta, and Gastropoda) to better understand the nuances of the global patterns and potential deviations. Due to the lack of data standardization, we limited these analyses to qualitatively discuss and compare patterns with those reported in previous studies. In addition, we analyzed the relationship between the number of records and the total species richness, and unique species richness, with linear models using the *lm* function of the package *stats* in R to better understand how sampling intensity (records) affects the observed patterns. These analyses also helped to better identify the under-sampled regions.

2.4. Species composition comparisons

To compare species composition between Arctic ecoregions in each dataset, we produced species presence/absence matrices where hexagons were treated as sites of a given ecoregion and the occurrences of species were 1 (present) or 0 (absent). To avoid potential bias in posterior analyses caused by sampling scarcity, we analyzed hexagons containing ≥10 species and compared ecoregions containing ≥3 hexagons (Table 1). The latter values were set after preliminary data analyses

Table 1

Number of hexagons, records, species richness and percentage and number (in brackets) of unique species per Arctic ecoregion in the shallow (0- ≤ 200), intermediate (>200- ≤ 500) and deep (>500) dataset. NA = not analyzed. Highest numbers are highlighted in bold.

Ecoregion	Shallow				Intermediate				Deep			
	Hexagons	Records	Species	Unique species (%)	Hexagons	Records	Species	Unique species (%)	Hexagons	Records	Species	Unique species (%)
Baffin Bay - Davis Strait	5	229	61	9.84 (6)	4	369	55	18.18 (10)	5	1,449	69	43.48 (30)
Beaufort-Amundsen-Viscount Melville-Queen Maud	2	308	36	11.11 (4)	0	NA	NA	NA	1	37	17	11.76 (2)
Beaufort Sea - continental coast and shelf	7	4,067	467	22.48 (105)	6	902	208	25.48 (53)	5	786	187	41.18 (77)
Chukchi Sea	8	1,909	235	16.17 (38)	5	274	47	44.68 (21)	3	107	43	16.28 (7)
East Greenland Shelf	3	349	93	3.23 (3)	0	NA	NA	NA	0	NA	NA	NA
East Siberian Sea	8	1,189	216	12.5 (27)	3	121	53	0 (0)	3	118	53	7.55 (4)
High Arctic Archipelago	3	991	41	2.44 (1)	0	NA	NA	NA	0	NA	NA	NA
Kara Sea	13	1,086	87	16.09 (14)	10	447	76	9.21 (7)	13	779	85	12.94 (11)
Lancaster Sound	3	365	96	11.46 (11)	0	NA	NA	NA	1	27	17	11.76 (2)
Laptev Sea	10	1,072	158	4.43 (7)	7	170	53	11.32 (6)	3	79	37	5.41 (2)
North and East Barents Sea	31	7,605	558	20.43 (114)	26	29,399	814	16.83 (137)	32	2,784	297	23.57 (70)
North and East Iceland	0	NA	NA	NA	0	NA	NA	NA	2	160	37	35.14 (13)
North Greenland	4	666	133	8.27 (11)	2	120	64	7.81 (5)	2	153	36	13.89 (5)
Northern Norway and Finnmark	7	10,452	693	48.77 (338)	6	66,311	966	33.95 (328)	5	2,429	312	42.63 (133)
West Greenland Shelf	1	18	16	0 (0)	0	NA	NA	NA	0	NA	NA	NA

to maximize the number of ecoregion comparisons per depth. These criteria precluded us to analyze ecoregions focusing on the different taxonomic groups at a time due to the scarcity of data. Nevertheless, integrating all taxonomic groups, we compared a total of 12 ecoregions in the shallow dataset, and eight ecoregions in both the intermediate and deep dataset. We then computed species β -diversity distance matrices between hexagons using Simpson's pairwise dissimilarity index (β_{sim}) (Baselga, 2010). The β_{sim} estimates the species compositional difference between hexagons and ranges between 0 (no species composition difference) and 1 (completely different species composition). β_{sim} is computed as:

$$\beta_{sim} = \frac{\min(b, c)}{a + \min(b, c)}$$

where a is the number of shared species between two hexagons, and b and c are the number of unique species of each hexagon, respectively (Baselga, 2010). β_{sim} was selected in this study because species occurrences derived from OBIS and GBIF data are greatly influenced by both sampling effort and methods (Costello et al., 2017; Hughes et al., 2021). This index is the most appropriate for the quest of analyzing biogeographic units because it only accounts for the species replacement component of β -diversity (i.e., turnover), and thus, is independent of species richness differences (Baselga, 2010; Krefl and Jetz, 2010; Castro-Insúa et al., 2018). These properties are desirable because β -diversity indexes may suffer from species richness differences between sampling units identifying naturally species-poor or uneven-sampled areas as highly dissimilar (Baselga, 2010; Krefl and Jetz, 2010; Castro-Insúa et al., 2018). We computed the β_{sim} distance matrices using the function *beta.pair* in the package *betapart* in R (Baselga and Orme, 2012). Pairwise comparisons of species composition between ecoregions in the three datasets were assessed using permutational multivariate analysis of variance (PERMANOVA), with 999 permutations and false discovery rate (*fdr*) adjusted P value (e.g., Hadiyanto et al., 2021) using the function *pairwise.adonis* in R (Martinez-Arbizu, 2020). In order to check the assumption of multivariate homogeneity of group variances (i.e., at each analyzed ecoregion), we used the *betadisper* function coupled with permutations tests in the package *vegan* in R (Oksanen et al., 2019). Significant differences were set at $P < 0.05$.

2.5. Cluster analyses

To assess the relationships and similarity between Arctic ecoregions at each dataset, we created species presence/absence matrices per ecoregions for each dataset. We then performed hierarchical cluster analyses based on β_{sim} distances using the Ward cluster algorithm. The Ward algorithm favors clusters internal coherence, i.e., it minimizes the dissimilarities within clusters and maximizes the dissimilarities between them, which is a desirable property for finding coherent groups, and hence for biogeographical analyses (Krefl and Jetz, 2010; Borcard et al., 2018; Castro-Insúa et al., 2018). Additionally, we analyzed each taxonomic group separately (Actinopterygii, Amphipoda, Bivalvia, Polychaeta, and Gastropoda) to better understand the global patterns and potential deviations. To identify robust clusters, we used multiscale bootstrap resampling to calculate the Approximately Unbiased p -values (AU- P) (Suzuki and Shimodaira, 2006). Bootstrap is performed by repeatedly and randomly sampling ecoregions in our datasets and posteriorly performing the cluster analysis (Suzuki and Shimodaira, 2006). Significant AU- P was set at >95 . Cluster and associated bootstrap analyses were implemented with the function *pvclust* in the package *pvclust* in R (Suzuki and Shimodaira, 2006).

3. Results

3.1. Distribution records, species richness, and species uniqueness patterns

Of the total 1,701 species analyzed in our three datasets, there were 962 species shared between the shallow and intermediate dataset; 509 species shared between the shallow and the deep dataset; and 545 species shared between the intermediate and deep dataset (Fig. 2A). A total number of 479 species (~30% of the total) were shared between all three datasets (Fig. 2A). This pattern was also observed on the majority of taxonomic groups (shared species ranging from 27.7% in Polychaeta to 35.7% in Amphipoda) except in Gastropoda where shared species between dataset were only the 13.9% (Appendix B, Figure B1). Comparisons with all species reported in Saedi et al. (2019a, b) revealed that 261 species in our datasets were shared with NW Pacific Ocean (Appendix A, Table A2).

Distribution records and species richness were unevenly distributed among hexagons in the three datasets (Fig. 2B–D), and were mostly concentrated in the Northern Norway and Finnmark, as well as the North and East Barents Sea (Fig. 3A and B). At the ecoregion level and in the shallow dataset, the Northern Norway and Finnmark had the highest number of distribution records (10,452), species (693), and unique species rate (48.77%) (Fig. 3, Table 1). In the intermediate dataset, the Northern Norway and Finnmark also had the highest number of records (66,311), and species (966), but unique species rate was higher at the Chukchi Sea (44.68%) (Fig. 3, Table 1). In the deep dataset, the North and East Barents Sea had the highest number of records (2,784), the Northern Norway and Finnmark had the highest number of species (312), and the Baffin Bay - Davis Strait - had the highest unique species rate (43.48%) (Fig. 3, Table 1). Similar patterns of higher records, species and unique species rate at ecoregions close to the Atlantic and Pacific Ocean were also observed at each taxonomic group (Appendix B, Table B1, B2 and B3). The number of distribution records at ecoregions was significantly correlated with species richness in all datasets (shallow: $P = 5.102 \times 10^{-08}$, $R^2 = 0.92$; shelf-break: $P = 0.0001$, $R^2 = 0.88$; deep: $P = 2.96 \times 10^{-05}$, $R^2 = 0.82$) (Appendix A, Fig. S4). The number of distribution records were only significantly correlated with species uniqueness rate in the shallow dataset ($P = 2.713 \times 10^{-05}$, $R^2 = 0.76$) (Appendix A, Figure A4).

3.2. Species composition differences between Arctic ecoregions

PERMANOVA tests between Arctic ecoregions showed that there were less significant differences between ecoregion species composition in the deep and intermediate datasets than in the shallow dataset (Table 2 and Fig. 4). Specifically, the 42%, 38%, and 25% of the total Arctic ecoregions analyzed in the shallow, intermediate, and deep dataset, respectively, showed significant community composition differences with all other ecoregions (Table 2 and Fig. 4). In the shallow dataset, comparisons between the Canadian and Greenland ecoregions including the East and North Greenland, the Baffin Bay - Davis Strait, the Lancaster Sound, and High Arctic Archipelago, showed the majority of non-significant ($P > 0.5$) community composition differences (Table 2 and Fig. 4). Similarly, the East Siberian Sea and Beaufort Sea - continental coast shelf also showed non-significant differences between them and with the above mentioned Canadian regions (Table 2 and Fig. 4). In the intermediate and the deep dataset, the East Siberian, Laptev, Chukchi and Beaufort Sea - continental coast shelf showed the majority of non-significant community composition differences. The Northern Norway and Finnmark and North and East Barents Sea consistently showed non-significant differences in the intermediate and the deep datasets (Table 2 and Fig. 4).

3.3. Cluster analyses

We found two significant clusters of ecoregions in the shallow

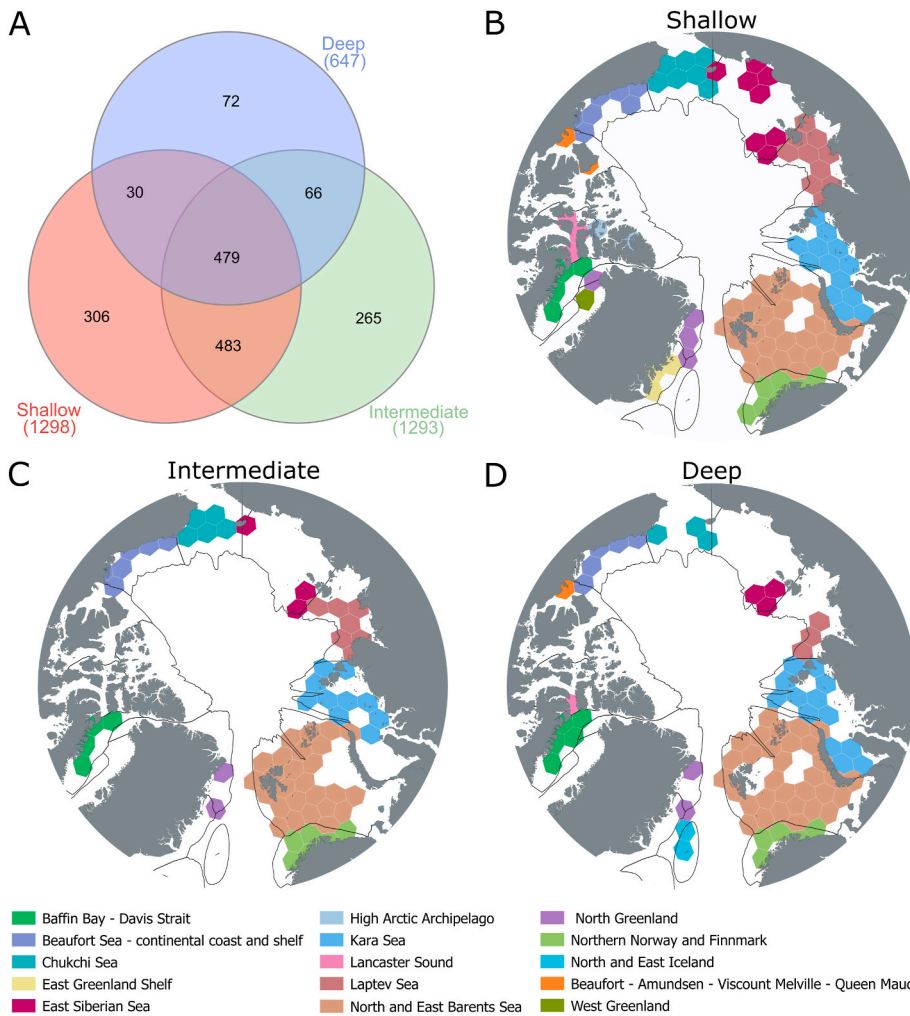


Fig. 2. Venn diagram of species shared between the shallow (≤ 200 m), intermediate (>200 to ≤ 500 m), and deep (>500 m) datasets (A). Colored numbers in brackets are the total number of species per dataset. Number in overlap areas between circles indicate the numbers of shared species. Hexagons ($50,000 \text{ km}^2$) analyzed by ecoregion in the shallow (B), intermediate (C), and deep datasets (D). Note that ecoregions with less than three hexagons were not included in PERMANOVA tests and cluster analyses. Legend for ecoregions in B-D is the same. The venn diagram was created using InteractiVenn web-based tool (<http://www.interactivenn.net>) (Heberle et al., 2015).

dataset. The first cluster was formed by the Northern Norway and Finnmark, the North East Barents Sea and the North and East Greenland ecoregions (AU = 98). The second cluster included the Beaufort - continental coast and shelf and the High Arctic Archipelago (AU = 98) (Fig. 5A). Siberian ecoregions showed a great affinity but their cluster was not significant (AU = 94). No statistically significant clusters were identified in the intermediate dataset. In the deep dataset, two statistically significant clusters were identified (Fig. 5B). One cluster was formed by all Eurasian ecoregions (AU = 100), whereas the other cluster contained all American ecoregions (AU = 100) (Fig. 5C). These patterns were much less clear for each taxonomical group analyzed separately (Appendix B, Figure B2, B3, B4, B5 and B6).

4. Discussion

The warming of the Arctic and its sea-ice thickness reduction directly and indirectly impact the physical and biogeochemical environment (Ardyna and Arrigo, 2020; Csapó et al., 2021), resulting in major changes in both ecosystem functioning and overall biodiversity patterns of the AO (Fossheim et al., 2015; Frainer et al., 2017). This is happening while our knowledge on the AO biodiversity is still limited despite important initiatives of the recent decades (e.g., Bluhm et al., 2011a). Data gaps in the AO cumulatively impair our knowledge on the faunal distribution. Here, we have integrated all data of well represented taxa available in OBIS and GBIF and explored the biodiversity patterns, and tested the community composition of Arctic ecoregions.

4.1. Biodiversity patterns

Due to several extinction/recolonization processes driven by the recent glacial/interglacial periods, many Arctic taxa are amphiboreal, eurybathic species derived from both the Atlantic and the Pacific Oceans (Bilyard and Carey, 1980; Dunton, 1992; Piepenburg, 2005; Bluhm et al., 2011a, 2011b; Rybakova et al., 2019). Our results support the existence of numerous eurybathic species with the $\sim 30\%$ of the total species found at all depths. Past studies suggested similar contribution of the Atlantic and Pacific species to the Arctic fauna (Bilyard and Carey, 1980; Dunton, 1992). However, more recent studies suggest an Atlantic predominance in both shallow and deep-sea Arctic ecosystems (Piepenburg, 2005; Piepenburg et al., 2011; Bluhm et al., 2011a, 2011b). For instance, Saeedi et al. (2019a, b) found only 1% of shared fauna between the Siberian ecoregion and partial Chukchi Sea with the NW Pacific Ocean, but their analyses included the adjacent AO to the NW Pacific, not the entire AO. Here, we found that 261 species ($\sim 15\%$ of the total 1,701 analyzed species) were shared between the entire AO and the NW Pacific area analyzed by Saeedi et al. (2019a, b). This increase is due to the wider Arctic areas analyzed here, which included the entire Chukchi Sea and Beaufort ecoregions, both known to be the regions most-influenced by Pacific currents (Sigler et al., 2011; Bluhm et al., 2015). Considering the direct connection between the Arctic and Pacific Oceans and that we include taxonomic classes with high dispersal capacity, such as Actinopterygii, $\sim 15\%$ of shared fauna might be considered rather low supporting the notion of a moderate Pacific influence. Ecoregions limiting with the Atlantic and the Pacific Oceans, not

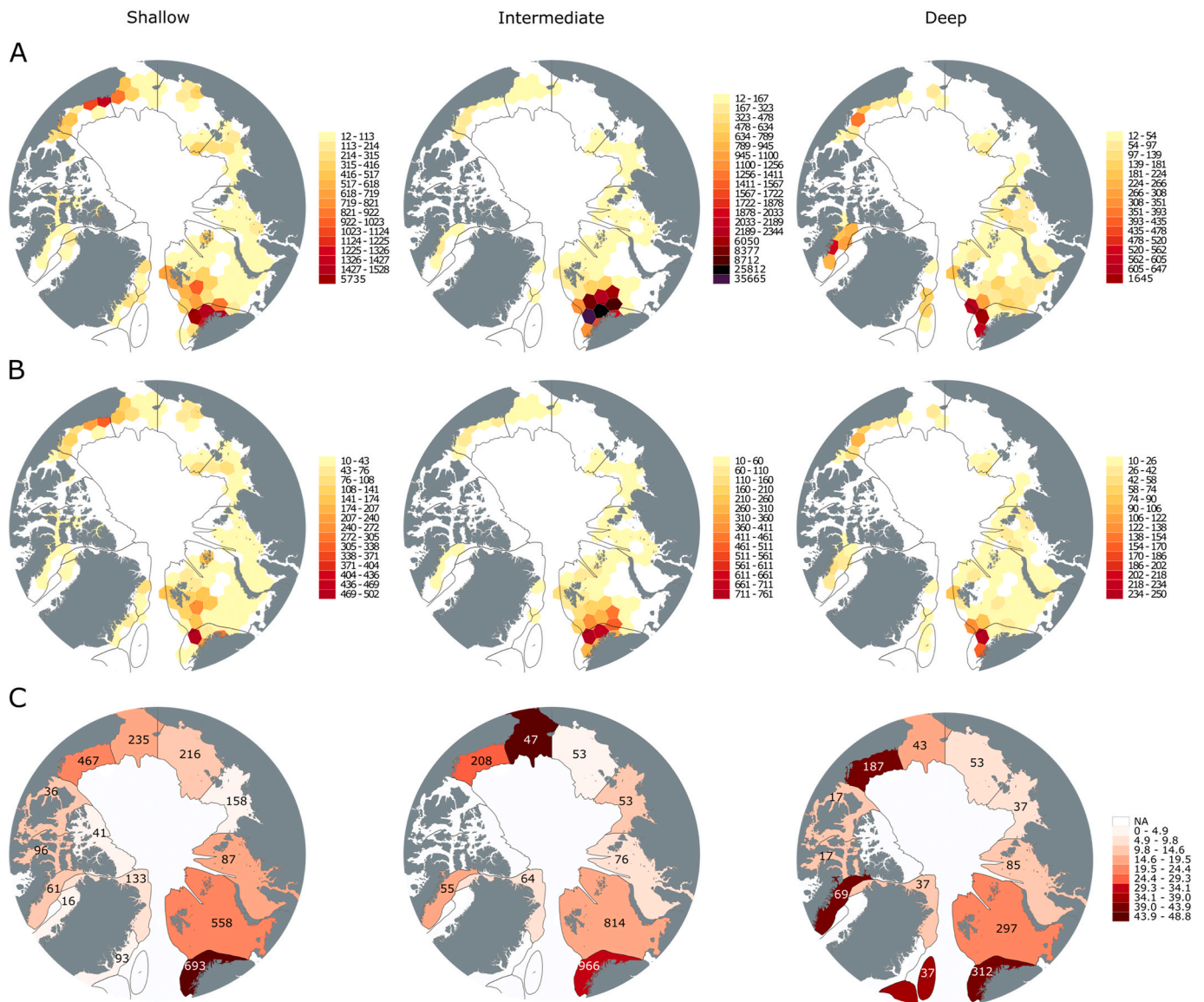


Fig. 3. Number of records (A) and species richness (B) along the 50,000 km² hexagons within Arctic ecoregions in the shallow (≤ 200 m), intermediate (>200 to ≤ 500 m), and deep (>500 m) datasets. Unique species percentage at each ecoregion in the shallow, intermediate, and deep dataset (C). Numbers within ecoregions in C are the total species richness (see Table 1 also).

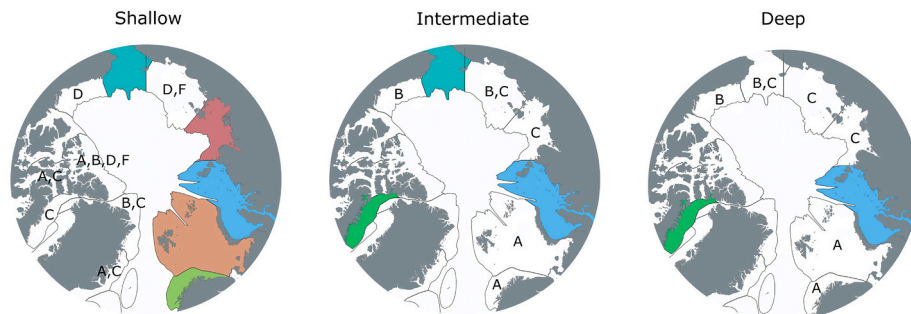


Fig. 4. Validation of Arctic ecoregions in the shallow (≤ 200 m), intermediate (>200 to ≤ 500 m) and deep (>500 m) datasets. Colored ecoregions had species compositions statistically different from all other ecoregions ($P < 0.05$). Ecoregions with letters had species compositions not statistically different from other ecoregions ($P > 0.05$). Shared letters indicate ecoregions without species composition differences. Ecoregions in white and without letter were not analyzed.

considered as Arctic in classical biogeography, such as Baffin Bay-Davis Strait and Northern Norway and Finnmark, and adjacent Arctic ecoregions are considered ecotones supporting higher species richness

(Dunton, 1992; Bluhm et al., 2020). For instance, Piepenburg et al. (2011) analyzed shelf benthic invertebrates and found that the Beaufort region, the Chukchi, and the Barents Sea were among the most diverse

Table 2

P-values obtained from the pairwise PERMANOVA comparisons of Arctic ecoregion species compositions in the shallow (0- ≤ 200), intermediate (>200- ≤ 500) and deep (>500) datasets. Values in bold indicate no statistical differences between species community compositions (P> 0.05).

Shallow	Baffin Bay - Davis Strait	Beaufort Sea - continental coast and shelf	Chukchi Sea	East Greenland Shelf	East Siberian Sea	High Arctic Archipelago	Kara Sea	Lancaster Sound	Laptev Sea	North and East Barents	North Greenland
Beaufort Sea - continental coast and shelf	0.009										
Chukchi Sea	0.005	0.017									
East Greenland Shelf	0.051	0.011	0.009								
East Siberian Sea	0.011	0.021	0.035	0.017							
High Arctic Archipelago	0.032	0.111	0.009	0.105	0.075						
Kara Sea	0.003	0.003	0.003	0.006	0.003	0.008					
Lancaster Sound	0.178	0.011	0.011	0.105	0.011	0.105	0.008				
Laptev Sea	0.005	0.005	0.003	0.006	0.029	0.008	0.003	0.011			
North and East Barents	0.003	0.003	0.003	0.005	0.003	0.003	0.003	0.003	0.003		
North Greenland	0.156	0.006	0.003	0.040	0.017	0.059	0.003	0.049	0.006	0.005	
Northern Norway and Finnmark	0.006	0.005	0.005	0.014	0.003	0.032	0.003	0.011	0.003	0.005	0.010
Intermediate	Baffin Bay - Davis Strait	Beaufort Sea - continental coast and shelf	Chukchi Sea	East Siberian Sea	Kara Sea	Laptev Sea	North and East Barents				
Beaufort Sea - continental coast and shelf	0.013										
Chukchi Sea	0.011	0.012									
East Siberian Sea	0.034	0.059	0.027								
Kara Sea	0.002	0.002	0.002	0.016							
Laptev Sea	0.007	0.002	0.002	0.282	0.002						
North and East Barents	0.004	0.002	0.002	0.002	0.002	0.002					
Northern Norway and Finnmark	0.011	0.002	0.004	0.011	0.002	0.005	0.062				
Deep	Baffin Bay - Davis Strait	Beaufort Sea - continental coast and shelf	Chukchi Sea	East Siberian Sea	Kara Sea	Laptev Sea	North and East Barents				
Beaufort Sea - continental coast and shelf	0.017										
Chukchi Sea	0.033	0.155									
East Siberian Sea	0.031	0.031	0.200								
Kara Sea	0.004	0.004	0.010	0.010							
Laptev Sea	0.030	0.032	0.108	0.108	0.007						
North and East Barents	0.004	0.004	0.009	0.004	0.004	0.012					
Northern Norway and Finnmark	0.021	0.018	0.030	0.031	0.004	0.033	0.092				

regions. Similarly, [Bluhm et al. \(2011b\)](#) analyzed annelid communities and showed that the Chukchi and Beaufort Sea slope were among the most diverse Arctic deep-sea environments. In fact, due to the influence of the Atlantic and Pacific currents entering the Arctic, species richness declined from warmer and more productive ecoregions to more isolated ecoregions, such as the Canadian and Siberian ecoregions ([Sirenko, 2001](#); [Bluhm et al., 2011a](#); [Yasuhara et al., 2012](#)) characterized by lower temperatures and light penetration, higher amount of sea ice, freshwater runoff and stratified waters ([Bluhm et al., 2015, 2020](#)). The lack of standardization, prevent from making firm conclusions about our observed biodiversity patterns. Nevertheless, in agreement with the studies discussed above, we also observed higher species richness and unique species in ecoregions near the Atlantic and Pacific, and their decline towards the more isolated Canadian and Siberian ecoregions both in shallow and deeper environments. This suggests that our integration of OBIS and GBIF Arctic records might have captured the expected diversity and distribution trends of the AO.

4.2. Species composition differences between ecoregions

The validity of the Arctic ecoregions proposed in [Spalding et al. \(2007\)](#) has been poorly tested with statistical methods despite their potential implications for conservation initiatives. Furthermore, the development of ecoregions was originally conceived for and based on shallow water environments and biota (0–200 m), and its validity to capture the organization of deeper biodiversity remain also to be tested. The number of statistically validated ecoregions analyzed in this study decreased with depth. Ecoregions showed less significant species composition dissimilarities in the intermediate (38% of analyzed ecoregions validated) and deep dataset (25% of analyzed ecoregions validated) than in the shallow dataset (42% of analyzed ecoregions validated). These results are in agreement with other studies suggesting that deep-sea environments are environmentally more homogenous and show fewer dispersal barriers than shallow waters resulting in less species differences ([Costello et al., 2017](#); [Costello and Chaudhary,](#)

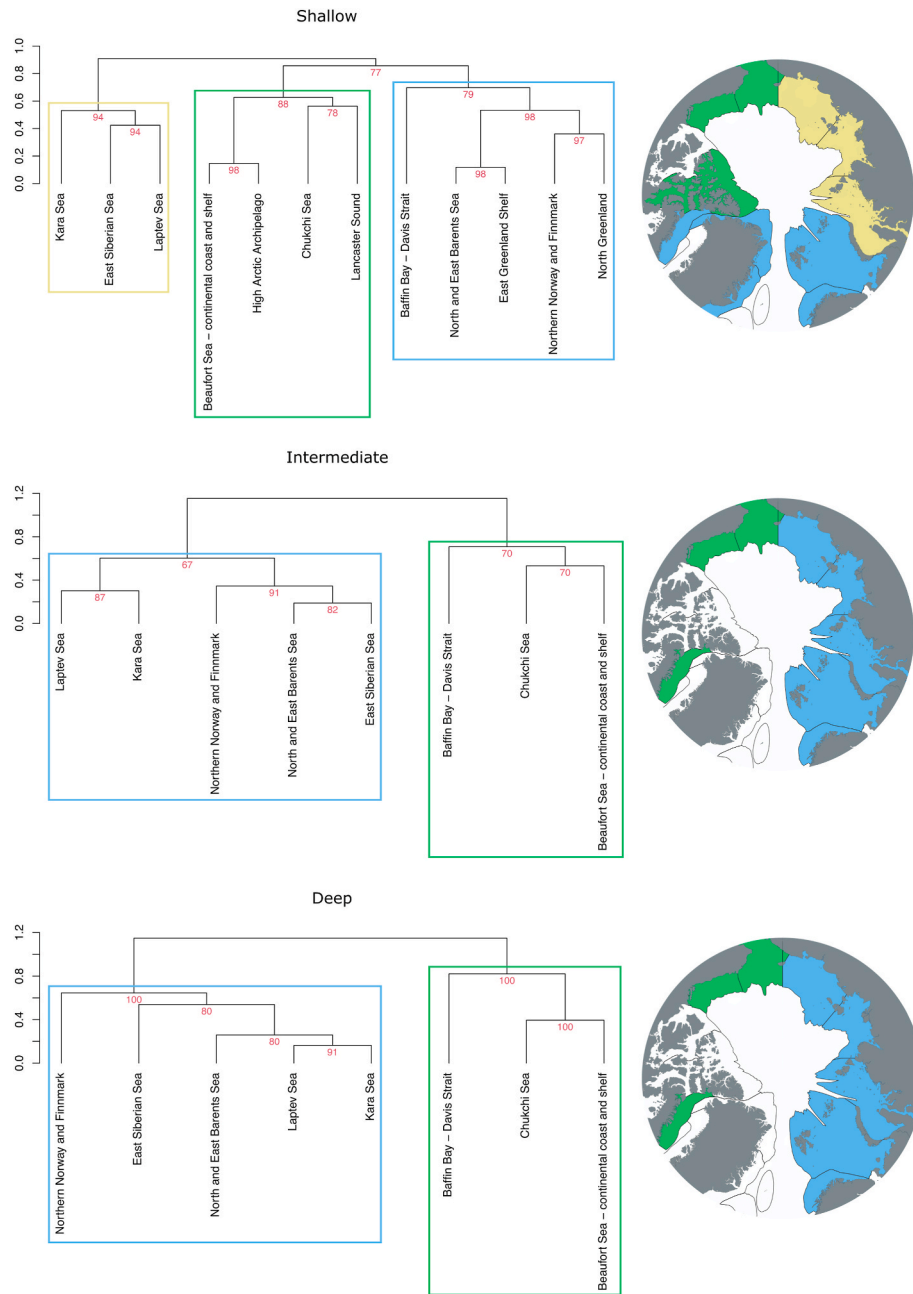


Fig. 5. Hierarchical cluster analyses of species presence/absence in Arctic ecoregions for the shallow (≤ 200 m), intermediate (>200 to ≤ 500 m), and deep (>500 m) datasets. Colored boxes correspond to the ecoregions of the same color in adjacent maps. Numbers in red indicate the Approximately Unbiased p-value (AU-P) derived from multiscale bootstrap resampling. Values of AU-P > 95 were considered statistically significant.

2017). The limited validation of ecoregions at deeper waters highlights the need for an appropriate system to classify the biodiversity in the AO deep sea. Our results are also in agreement with other literature suggesting that deep-sea environments worldwide may need a specific system to adequately address their classification (Hadiyanto et al., 2021; Watling and Lapointe, 2022).

Despite the higher validation, we found few statistical differences between ecoregions surrounding Greenland and the eastern Canadian Arctic in shallow waters. Such high similarity among ecoregions in the whole Greenland-Canadian region has also been previously reported (Piepenburg et al., 2011; Costello et al., 2017). For instance, Piepenburg et al. (2011) found high similarities between Greenland and Canadian ecoregions for shelf benthic taxa at the family, genus, and species levels. Due to the lack of data, we were unable to test if these affinities were maintained in deeper environments. However, Costello et al. (2017)

found also high similarity in species composition within the whole region in their beta diversity analysis covering both shallow and deep taxa. The Beaufort - continental coast and shelf also showed no statistical differentiation with the eastern Canadian Arctic probably highlighting the common influence of shallow-ocean currents of Pacific origin (Grebmeier et al., 2006; Sigler et al., 2011; Beszczynska-Möller et al., 2011). These currents are highly modified in the Beaufort ecoregions by fresher Arctic water potentially explaining their significant dissimilarity with the Chukchi Sea ecoregion in shallow and intermediate waters more directly influenced by Pacific currents (Dunton, 1992; Grebmeier et al., 2006; Sigler et al., 2011). In contrast, we found that the ecoregions from the Northern Norway and Finnmark to the Laptev Sea showed significant species composition differences in shallow waters. However, deeper environments between the Northern Norway and Finnmark and North and East Barents Sea, and between the Laptev and East Siberian

Sea were comparatively similar. Interestingly, the Kara Sea showed statistical species composition differences at all depths. Evidence suggest that the Polar Front situated in the Barents Sea, a water mass boundary separating Atlantic and Arctic waters, is a strong zoogeographic barrier separating widespread-boreal and strict Arctic species, respectively, potentially explaining the differentiation of the Kara Sea with other ecoregions at all analyzed depths (Fossheim et al., 2015; Frainer et al., 2017; Csapó et al., 2021).

4.3. Ecoregion relationships

Our results showed that Arctic ecoregions clustered into Eurasian and American ecoregions, respectively, at all analyzed depths. These results match the oceanographic patterns described where the Atlantic and Pacific currents entering the Arctic mainly influence Eurasian and American ecoregions, respectively (Grebmeier et al., 2006; Bluhm et al., 2015; Wassmann et al., 2015). Thus, our results extend these patterns to the species composition of ecoregions. In shallow waters, Siberian ecoregions clustered together, yet not significantly. We hypothesize that such pattern highlights the effect of the Polar Front, and/or the higher isolation and different oceanographic conditions of Siberian ecoregions as suggested in previous studies (Sirenko, 2001; Piepenburg, 2005; Bluhm et al., 2011a; Fossheim et al., 2015; Frainer et al., 2017; Csapó et al., 2021; Vedenin et al., 2021). Intriguingly, the Baffin Bay - Davis Strait clustered within the Eurasian group although this ecoregion is considered isolated without direct influence of the Atlantic waters (Dunton, 1992; Bluhm et al., 2011a).

In deeper environments, however, we only found evidence of the two broad Eurasian and American clusters. It has been hypothesized that fewer biogeographic barriers are found in the deep sea compared to coastal and shelf waters (Costello et al., 2017; Costello and Chaudhary, 2017). In fact, previous analyses revealed minor benthic community composition differences along the deep-sea Arctic with no influence of major topographic barriers, such as the Gakkel and Lomonosov ridges (Bilyard and Carey, 1980; Bluhm et al., 2011b). Nevertheless, our results dividing the Arctic deep sea in Eurasian and American ecoregions are somehow surprising. The deep Arctic taxa is considered to be mainly derived from the Atlantic due to the Arctic disconnection with the deep Pacific Ocean ~80 Myrs ago (Dunton, 1992; Piepenburg, 2005; Bluhm et al., 2015; Zhulay et al., 2019). The factors driving our observed geographic division could arise from a variety of hypotheses, and specific studies should tackle this intriguing pattern. In fact, recent studies challenged the view of the Arctic biota as a derivation of the southern temperate regions and highlighted the role of previously unnoticed refuges within the AO suggesting a more complex biogeographical history (e.g., Bringlee et al., 2020). Future analyses including more taxonomic groups and resolving potential cryptic species complexes (Neal et al., 2018) may help to clarify these patterns.

5. Conclusions

Higher species richness and uniqueness were observed in ecoregions near the Atlantic and/or Pacific Ocean decreasing from Norway towards the Siberian ecoregions, and from the Chukchi to the eastern Canadian ecoregions. Although our data lack standardization and might still suffer from sampling bias, the observed biodiversity patterns fit well with previous studies that suggest that latitude (temperature-related) and productivity are major drivers of species diversity in the AO and worldwide (Bluhm et al., 2011a; Yasuhara et al., 2012; Woolley et al., 2016; Yasuhara et al., 2021). Arctic ecoregions showed less statistically differences in species composition in deeper environments highlighting the necessity for a specific Arctic classification of deep-sea regions. Following Atlantic/Pacific current paths, ecoregions tend to cluster into Eurasian and American ecoregions at all depths. Due to climate change and associated sea ice decrease, Atlantic and Pacific fauna influence through borealization processes could likely increase in a near future (e.

g., Fossheim et al., 2015; Frainer et al., 2017; Ardyna and Arrigo, 2020; Polyakov et al., 2020; Csapó et al., 2021; MacKinnon et al., 2021). The importance of the Atlantic and Pacific currents on the Arctic biodiversity highlighted here suggest that borealization could potentially advance following current routes reaching more isolated regions, such as the eastern Canadian and Siberian ecoregions. Species distribution modeling may be a useful tool to test these hypotheses for taxa with contrasting life-history traits (e.g., Renaud et al., 2019). This study used OBIS and GBIF open-access datasets selecting for few, albeit well-represented, taxonomic groups along the AO. Future studies may benefit from more data especially in ecoregions found to be poorly documented, such as the Kara, Laptev and East Siberian Seas, and the Canadian Arctic. Our results may help to understand and uncover the Arctic biodiversity patterns, and are of practical interest for scientists, decision makers, biodiversity working groups of the Arctic Council, (e.g., CAFF (<https://caff.is/>)), and conservation initiatives. Our understanding on the AO diversity is still limited despite the great efforts that have been made so far to uncover its diversity patterns. Our data gap and biodiversity analyses in addition to cross validations with the Arctic ecoregions provide fundamental knowledge for future biodiversity assessments to finally improve the management activities at the AO.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.dsr.2023.104077>.

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