REVIEW

The emerging picture of a diverse deep Arctic Ocean seafloor: From habitats to ecosystems

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Interest in the deep Arctic Ocean is rapidly increasing from governments, policy makers, industry, researchers, and conservation groups, accentuated by the growing accessibility of this remote region by surface vessel traffic. In this review, our goal is to provide an updated taxonomic inventory of benthic taxa known to occur in the deep Arctic Ocean and relate this inventory to habitat diversity. To achieve this goal, we collected data for Arctic metazoan deep-sea taxa from open-access databases, information facilities, and non-digitised scientific literature, limiting the collection to the area north of 66°N and below 500 m depth (excluding all shelf seas). Although notable progress has been made in understanding the deep Arctic using novel technologies and infrastructure, this data gathering shows that knowledge of

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deep-sea benthic Arctic communities remains very limited. Yet, through our compilation of habitat maps, we show that the Arctic contains a high diversity of geomorphological features, including slopes, deep basins, submarine canyons, ridges, and seamounts, as well as chemosynthesis-based and biogenic (biologically engineered) ecosystems. To analyse taxon richness and density, using both morphological and molecular data, we compiled 75,404 faunal records with 2,637 taxa. Phyla with the most records were the Arthropoda (21,405), Annelida (13,763) and Porifera (12,591); phyla with the most documented taxa were the Arthropoda (956), Annelida (566) and Mollusca (351). An overview of the dominant groups inhabiting the different geomorphological features highlights regions in the deep Arctic where data are particularly scarce and increased research efforts are needed, particularly the deep basins of the central Arctic Ocean. This scarcity of deep benthic Arctic biodiversity data creates a bottleneck for developing robust management and conservation measures in a rapidly changing region, leading to a call for international collaboration and shared data to ensure understanding and preservation of these fragile Arctic ecosystems.
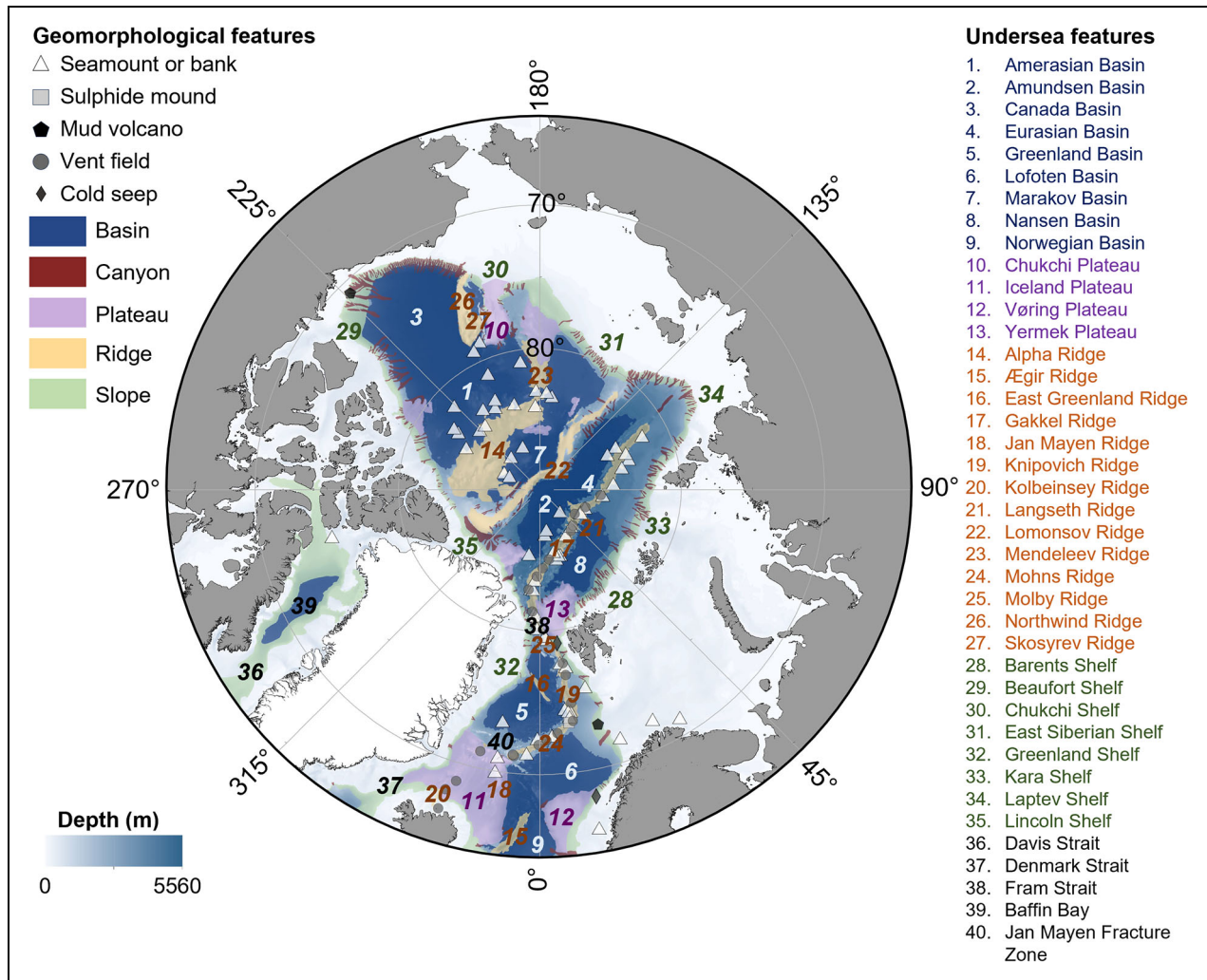
1. Introduction

The focus of researchers, states and industries alike on the Arctic deep sea, defined here as depths below 500 m in the Greenland, Iceland, and Norwegian Seas (GIN Seas/ Nordic Seas) and the central Arctic Ocean (CAO) excluding all shelf seas (**Figure 1**), has been increasing at a rate faster than research efforts can fill knowledge gaps. This surge of interest is related to increasing accessibility by surface vessel traffic (Protection of the Arctic Marine Environment [PAME], 2020), mediated by drastic sea-ice decline in the CAO due to climate warming (Zhang et al., 2023), and by ongoing mapping of potential hydrocarbon, mineral and living resources, which are driving discussions regarding territorial claims (Lambach, 2022). A large part of the research efforts in deep-water areas has focused on sea ice (in the CAO), surface waters and the water column, leaving knowledge gaps surrounding deep benthic environments particularly glaring (Bluhm et al., 2011). Even so, knowledge has been increasing for some deep habitats in the Arctic, especially in the past two decades. For example, new data have been gathered from seamounts housing unexpectedly rich sponge beds and associated benthic biota (Boetius and Purser, 2017; Morganti et al., 2022; Stratmann et al., 2022; Meyer et al., 2023). Continued exploration of ridges in the CAO (Edmonds et al., 2003; Boetius, 2015; Bünz et al., 2019; Bünz et al., 2021) has revealed sparse fauna associated with the hydrothermal vents of the Gakkel Ridge (Ramirez-Llodra et al., 2022) and provided faunal information from other ridges such as the Lomonosov Ridge (Schewe and Soltwedel, 1999) and the Alpha Ridge (Schewe, 2001). Other studies have shown how glacial dropstones can form biodiversity islands (Mayer and Piepenburg, 1996; Meyer et al., 2016; Zhulay et al., 2019). In a thin benthic boundary layer, Arctic deep-sea hyperbenthic taxa (those inhabiting the benthic boundary layer) can encounter abysso-pelagic taxa (Raskoff et al., 2010; Zhulay et al., 2019). There is also evidence of enhanced density and biomass levels associated with the overlying marginal ice zone (Rybakova et al., 2019) in the more 'typical' meio- and macrofauna in Arctic soft sediments of the abyssal plains (Paul and Menzies, 1974; Kröncke, 1994; Kröncke et al., 2000; Renaud et al., 2006; Bluhm et al., 2011). With the current decline of biodiversity and the health status of natural systems, the potential for species going extinct before they have been described is increasing rapidly (Jørgensen et al., 2021).

In recent years, the combination of advanced technology and increasing numbers of research icebreakers and internationally coordinated programs has provided leaps in knowledge gains in the Arctic deep sea (Bluhm et al., 2011; Wiedmann et al., 2020; Ramirez-Llodra et al., 2022). Yet, an updated overview of the diversity of habitats and biodiversity on the deep seafloor is lacking. In the context of increasing anthropogenic exploitation and climate change stressors affecting the deep Arctic Ocean, the objectives of this overview paper are to (1) provide a short summary of how the exploration and study of the deep Arctic Ocean has evolved with the development of technology and methods; (2) raise awareness of the diversity of habitats at the Arctic deep seafloor; (3) document current knowledge on density of faunal records and associated status of species richness in the Arctic deep sea, and (4) highlight knowledge gaps that will inform the need for future research. Herein, we have considered benthic habitats and ecosystems north of 66°N and below 500 m water depth in the GIN Seas and CAO.

1.1. A short history of exploration of the deep Arctic Ocean

Early Arctic expeditions focused mostly on shallow coastal waters or the water column. In particular, the first research expeditions, such as the French R/V *La Recherche* missions around the Faroes, Iceland and Svalbard (1838–1840), barely sampled deeper than 200 m. The *Norwegian North Atlantic Expedition* (1876–1878) and the *Danish Ingolf Expedition* (1895 and 1896) focused on the waters between Greenland, Iceland, Jan Mayen, and Norway (the GIN Seas) and developed winches and tallies to be able to sample deeper. Mapping the bathymetry of the Norwegian Sea was an explicit objective of the *Norwegian North Atlantic Expedition*. The limitations were on both vessel and sampling capacities. All the early expeditions used repurposed naval sail and sail-steam ships, built neither

Geomorphological features
△ Seamount or bank
▢ Sulphide mound
⬠ Mud volcano
● Vent field
♦ Cold seep

Basin
Canyon
Plateau
Ridge
Slope

Depth (m)
0 — 5560

Undersea features
1. Amerasian Basin
2. Amundsen Basin
3. Canada Basin
4. Eurasian Basin
5. Greenland Basin
6. Lofoten Basin
7. Marakov Basin
8. Nansen Basin
9. Norwegian Basin
10. Chukchi Plateau
11. Iceland Plateau
12. Vøring Plateau
13. Yermek Plateau
14. Alpha Ridge
15. Ægir Ridge
16. East Greenland Ridge
17. Gakkel Ridge
18. Jan Mayen Ridge
19. Knipovich Ridge
20. Kolbeinsey Ridge
21. Langseth Ridge
22. Lomonsov Ridge
23. Mendeleev Ridge
24. Mohns Ridge
25. Molby Ridge
26. Northwind Ridge
27. Skosyrev Ridge
28. Barents Shelf
29. Beaufort Shelf
30. Chukchi Shelf
31. East Siberian Shelf
32. Greenland Shelf
33. Kara Shelf
34. Laptev Shelf
35. Lincoln Shelf
36. Davis Strait
37. Denmark Strait
38. Fram Strait
39. Baffin Bay
40. Jan Mayen Fracture Zone

Figure 1. Map of the Arctic Ocean (66−90°N) showing geomorphological features and habitats. Habitats are indicated by symbols; colour-shaded geomorphological features were obtained from Harris et al. (2014), Beaulieu and Szafranski (2020), and GEBCO Undersea Feature Names Gazetteer (https://www.ngdc.noaa.gov/gazetteer/). Bathymetry was obtained from Jakobsson et al. (2020).

for polar waters nor research. The schooner *Fram*, sailing on wind and steam power during Fridtjof Nansen's Norwegian expedition in the Transpolar Drift, was the first vessel especially built for research in sea-ice-covered waters. The French-Swedish *NORBI Expedition* sailed in 1975 on the purpose-built R/V *Jean Charcot*, which was equipped with a diesel-electrical engine but no extra ice protection. The Swedish icebreakers *Ymer* and *Odin* were retrofitted for research in the 1980s (Pfannkuche and Thiel, 1987). R/V *Håkon Mosby* (Norway), purpose-built with ice C-class, could withstand light ice conditions. The latest high-technology expeditions to the CAO are only possible with the use of the purpose-built research icebreakers such as R/V *Polarstern*, R/V *Kronprins Haakon*, I/B *Oden* and U.S., Canadian, and Russian coast guard icebreakers. Examples of recent expeditions to the CAO include the R/V *Polarstern MOSAiC* mission to drift with the ice in 2019–2020 (yet without seafloor sampling; Shupe et al., 2022); the first hybrid remotely operated vehicle (HROV) survey of deep-water seamounts (Karasik Seamount) in the CAO conducted during the *Karasik*

Seamount expedition on board R/V *Polarstern* in 2016 (Boetius and Purser, 2017); the first towed-camera, HROV and ROV surveys of hydrothermal vents (Aurora Vent Field) under permanent ice cover during the *Aurora* expedition in 2014 on board R/V *Polarstern* (Boetius, 2015); the *HACON* expeditions on board R/V *Kronprins Haakon* that surveyed and sampled the Aurora vent field with a towed camera and ROV in 2019 and 2021, respectively (Ramirez-Llodra et al., 2022); as well as a suite of Synoptic Arctic Survey expeditions in the CAO, such as those conducted by the Chinese icebreaker *Xuelong 2* and the Norwegian Nansen Legacy cruise in 2021 (Fransson et al., 2022). All these missions have collected novel data that have contributed to a better understanding of the deep CAO under ice. For example, work undertaken during the Karasik seamount expedition showed for the first time that some deep-sea sponges (in this case, *Geodia parva* Hansen, 1885, *G. hentscheli* Cárdenas, Rapp, Schander & Tendal, 2010 and *Stelletta rhaphidiophora* Hentschel, 1929) can actively move on the seafloor (Morganti et al., 2021). During the Aurora expedition, the first black

smokers on the Gakkel Ridge were discovered (Boetius, 2015), and during the HACON21 cruise to the same location, the first full survey of the Aurora vent field was conducted, resulting in the description of a new limpet species (*Cocculina aurora* sp. nov. C. Chen, Hilário, Rodrigues & Ramirez-Llodra, 2022).

The Nordic Seas, in contrast, are mainly ice-free (except the NE Greenland margin), enabling the modern (and earlier) non-icebreaker research fleet to operate there at times of low ice cover. For example, R/V *Sikuliaq* (USA), R/V *G.O. Sars* (Norway), and R/V *Maria S. Merian* (Germany) are all purpose-built with several specialised laboratories and winches suitable for deep-sea sampling. During these expeditions, new areas including special habitats continue to be discovered, such as the Jøtul vent site on the Knipovich Ridge during an R/V *Maria S. Merian* cruise in 2022 (Bohrmann et al., 2022). Several hydrothermal vent fields have been found on the Mohns Ridge as part of the nearly 2-decade-long exploration of the Norwegian part of the Arctic Mid-Ocean Ridge by the University of Bergen Centre for Deep Sea Research, with Loki's Castle being the first black smoker vent field discovered on the Mohn Ridge in 2008 and several seamounts being surveyed (e.g., Pedersen et al., 2010; Schander et al., 2010; Meyer et al., 2023; Eilertsen et al., 2024). Moreover, the extinct spreading axis Ægir Ridge has been explored in more detail since its discovery (Brix et al., 2022), revealing a new large calliopid amphipod species (*Halirages spongiae* sp. nov. Lörz, Nack & Tandberg in Lörz, Nack, Tandberg, Brix and Schwentner, 2024) inhabiting *Caulophacus* Schulze, 1886 sponges in the neighbouring abyssal plain of the Norwegian Sea (Lörz et al., 2024). Other efforts around Norway, such as Norway's long-term mapping program MAREANO (https://mareano.no/), have done much to improve scientific understanding of the benthic habitats in the Norwegian and Barents seas since the program's origin in 2006 (Buhl-Mortensen et al., 2015b), with its deepest station to date reaching approximately 3,000 m north of Spitsbergen.

Most of the early seafloor sampling equipment was fisheries equipment such as trawls and dredges or gear slightly modified from those. Until the 1970s, these types of pulled samplers were the main equipment used for the epibenthic biological sampling, while the development of corers and grabs provided access to the infaunal biota. Between 1937 and 2015, exploration of the Arctic deep sea and its benthic communities was also conducted by means of temporary, drifting research stations built on ice floes or tabular icebergs by the former Soviet Union/Russia ('North Pole' stations; Frolov et al., 2005) and the United States of America ('Alpha', 'Charlie'/ 'Alpha II', 'T3', and the ARLIS stations; Cabaniss et al., 1965; Belkin and Kessel, 2017). These platforms served for multidisciplinary research activities (e.g., Cabaniss et al., 1965; Belkin and Kessel, 2017), including the collection of sediment and benthos samples by trawls, dredges, buckets, grabs and cores (e.g., Cabaniss et al., 1965; Stendell, 1967; Clark, 1969; Afanasyev and Filatova, 1980) and seafloor imaging by drop-cameras, yielding what probably were the first deep seafloor images

from the CAO (Hunkins et al., 1960). Ongoing warming and multi-annual sea-ice retreat have rendered the establishment and maintenance of drifting stations increasingly difficult in the 21st century, leading to the cessation of the longest-lasting program, the Russian 'North Pole' ice stations, after 2015. The program has since been replaced with the new platform, the *Severny Polyus* (Likhomanov et al., 2022). The only spatially consistent, long-term and hence very valuable deep-sea observatory in the deep Arctic Ocean is the HAUSGARTEN area in eastern Fram Strait, maintained by Alfred Wegener Institute using R/V *Polarstern* (Soltwedel et al., 2020).

Most benthic sampling in the Arctic deep sea has been performed on soft bottoms (Bluhm et al., 2011). Epibenthic sleds were developed in the 1970s for sampling the biota living in and right above the sediments, and these systems have been continually developed for deep-sea sampling, even on slightly coarser bottoms or bedrock (Rothlisberg and Pearcy, 1976; Brandt and Barthel 1995; Brenke, 2005; Brandt et al., 2013). Access to deep-sea hard-bottom fauna has been increasing with the development of subsea sampling vehicles such as landers and subsea laboratories, autonomous underwater vehicles (AUVs), towed cameras, ROVs, and human-occupied vehicles (HOVs). These systems provide visual data through increasingly higher-definition cameras, and ROVs and HOVs can collect physical samples for ground-truthing the observations, confirm specimen identifications and conduct *in situ* experiments (Zhulay et al., 2019; Morganti et al., 2022; Ramirez-Llodra et al., 2022). The visual information obtained from underwater vehicles enables a more detailed understanding of ecosystems, their composition and functioning. Over the past two decades, morphological identification of sampled fauna has been coupled with DNA sequencing (barcoding) to delimit species efficiently (Jażdżewska et al., 2018), discover new cryptic species (Brix et al., 2014) and species complexes through integrative taxonomy (Jennings et al., 2018; Schnurr et al., 2018; Schnurr et al., 2022), which can be used both to develop baseline biodiversity assessments for sustainable management and conservation and as a tool for understanding and developing hypotheses about spatio-temporal biodiversity patterns through phylogenetics (Hobern, 2020). Emerging molecular approaches, including environmental DNA (eDNA), metabarcoding (Laroche et al., 2020) and proteome fingerprinting (Kürzel et al., 2022; Rossel et al., 2023), hold the potential to advance considerably our knowledge of hidden diversity in the Arctic deep sea.

Underlying all these studies has been a significant effort in bathymetric mapping of the Arctic Ocean since 1997, feeding into the International Bathymetric Chart of the Arctic Ocean (IBCAO). In 2020, a joint effort between IBACO and the Nippon Foundation-GEBCO-Seabed 2030 programme has resulted in the IBACO Ver 4.0 map, with a resolution of 200×200 m (in comparison to the 500×500 m of the previous version from 2012). In this latest version, 19.8% of the Arctic Ocean seafloor contains individual depth soundings (versus 6.7% in Ver.3; Jakobsson et al., 2020).

1.2. Diversity of deep Arctic habitats

Mapping the seafloor in the Arctic Ocean has long driven explorers, researchers and, more recently, Arctic states in their efforts to delineate territorial boundaries. Great strides have been made in seafloor habitat mapping in the Arctic, resulting in the recent release of the 4th version of the IBCAO, which now shows details of smaller-scale habitat features as never before (Jakobsson et al., 2020; version 4.2 was released in August 2022). Like the global ocean, the Arctic Ocean area contains a high diversity of geomorphological features (**Figure 1**) subject to specific geochemical and environmental drivers that shape different habitats with their biological communities and interactions (Ramirez-Llodra et al., 2010; Bluhm et al., 2011; Morganti et al., 2022). Unusual compared to the global ocean is the near equal 50% shelf to 50% deep-sea split of the Arctic Ocean, with broad shelves usually reaching to no more than 200 m water depth (in some areas to approximately 500 m, especially in the Barents Sea and on the NE Greenland shelf, which we excluded from this study as they are shelf areas). The shelves break into the continental margin, which is characterised by a wide range of geological and geochemical variables that shape a variety of benthic habitats, including sedimentary slopes, canyons, cold-water coral reefs and cold seeps (Levin et al., 2010; Menot et al., 2010). Below 3,000 m depth, vast expansions of fine sediment cover the abyssal plains in the basins. A semi-continuous mountain chain known as the Arctic Mid-Ocean Ridge (AMOR) runs through the middle of the Atlantic from Kolbeinsey Ridge near Iceland to the Gakkel Ridge in the Eurasian Basin (Johnson and Heezen, 1967; Pedersen et al., 2010), where active and inactive hydrothermal vents can be found, surrounded by seamounts, banks, and knolls (**Figure 1**). In addition, the Lomonosov, Alpha and Mendeleev ridges subdivide the CAO into different basins (**Figure 1**). Only one deep-water connection exists today from the CAO to the North Atlantic, through Fram Strait, providing an important connection amongst ocean basins and associated biogeography (Rudels and Carmack, 2022). The deepest point in the Arctic Ocean is the Molloy Deep at 5,607 m depth (Thiede et al., 1990).

2. Advances in biodiversity knowledge

With the improvement of technology, as well as increasingly advanced approaches to data collection and analysis, knowledge of deep benthic ecosystems in the Arctic has been accumulating at an accelerating rate. The deep sea is far from being the lifeless, monotonous biome once described by early explorers (Forbes, 1844). Here, we present an analysis of available taxonomic data from the deep Arctic, providing a synthesised overview of biodiversity knowledge. Through this analysis, we also identify geographic knowledge gaps that can inform the prioritisation of future research needed for both an improved understanding of the composition and functioning of deep Arctic ecosystems and the development of robust management plans for the region.

2.1. Analytical methods

2.1.1. Data collection and quality control

We compiled taxon occurrence data for Arctic seas (latitude 66–90°N) at water depths equal and greater than 500 m. Although the deep sea is commonly considered to start at 200–250 m depth (Thistle, 2003), below which sunlight can no longer sustain photosynthesis, we chose 500 m as a cut-off to exclude the deeper Arctic shelf seas with typical shelf fauna, namely the Barents Sea and East Greenland shelf which represent Arctic inflow and outflow shelves, respectively (Carmack and Wassmann, 2006).

The data were compiled from three sources: (1) non-digitised scientific literature and previously unpublished field data collections; (2) open-access databases including the Ocean Biodiversity Information System (OBIS; www.iobis.org; for data citations see Table S1); and (3) the Global Biodiversity Information Facility (GBIF; www.gbif.org, for citation see https://doi.org/10.15468/dl.emhhsq). This compilation resulted in a total of 187,003 records prior to cleaning the dataset, where one 'record' refers to an individual taxon occurrence at a georeferenced location. The citation to OBIS and GBIF includes all the datasets extracted before data cleaning; we were not able to remove the dataset citations for data dropped during the cleaning procedure. The merged data were subjected to quality control criteria following Saeedi et al. (2019a; 2019b) and Alfaro-Lucas et al. (2023) as: (1) all taxonomic names were matched against the World Register of Marine Species (WoRMS) and synonyms reconciled (www.marinespecies.org); (2) all pelagic and non-marine taxa were checked based on our taxonomic knowledge and literature, mostly Kosobokova et al. (2011); (3) only data belonging to accepted benthic species were kept in the dataset, with all other unaccepted, pelagic, or non-marine records removed using Rstudio version 4.2.2 packages 'robis' (Provoost and Bosch, 2020) and 'worrms' (Chamberlain and Vanhoorne, 2023); and (4) all records identified at higher taxonomic rankings (e.g., class to kingdom) were removed due to uncertainties of the taxa being truly benthic.

Distribution records were also checked for reliability using quality control tools such as the R packages 'robis' and 'scrubr' (Chamberlain, 2021). Duplicates and dubious records were either removed or corrected (e.g., reversing latitude and longitude fields). Occurrence records with documented depths exceeding the maximum depth of the Arctic Ocean (5,607 m) were excluded from the dataset. The documented depth of the records was checked for reliability by plotting the dataset over a 200 × 200 m bathymetric map produced by the IBCAO project (Jakobsson et al., 2020). Depth values for each record were extracted from the IBCAO map using the 'Extract Values to Point' function in the Spatial Analyst toolbox in ArcGIS v 10.8.1 (Environmental Systems Research Institute [ESRI], 2020) and compared to the documented depth for the record. Records that had a difference between the extracted and documented depth values greater than 1,000 m were excluded from the dataset. After the quality control and the cleaning procedure, the consolidated

dataset contained 75,404 occurrence records in total (40.3% of the original dataset). All the R scripts and the cleaned dataset are available open-access (https://doi.org/10.5281/zenodo.10391404).

2.1.2. Taxon distribution and richness

To identify which geomorphological features corresponded to the records, we mapped the records over the features generated from Harris et al. (2014), Beaulieu and Szafranski (2020), and GEBCO Undersea Feature Names Gazetteer (https://www.ngdc.noaa.gov/gazetteer/). We used the 'spatial join' tool from the Analysis toolbox in ArcGIS (ESRI, 2020) to classify the records that intersected with the five main geomorphological features (basins, canyons, plateaus, ridges, and slopes). Records intersecting the specific features were classified as such, and those not overlapping any geomorphological feature were classified as 'NA.' Due to seamounts and hydrothermal systems (e.g., seeps, vents, and mud volcanoes) overlapping the main geomorphological features, it was not possible to classify the records to the specific seamounts or hydrothermal systems.

We calculated alpha-approximated taxon richness as the number of taxa per each equal-sized hexagon (hexagonal cell = 50,000 km^2) and gamma taxon richness as the total number of taxa per 5-degree latitudinal band and per 100-m depth interval, limiting the data to the benthic taxa in the above defined Arctic Ocean area below 500 m depth. To obtain the number of unique taxa to each corresponding hexagonal cell, we used the 'spatial join' tool in ArcGIS, to intersect each taxon to equal-sized hexagonal cells. All the unique taxa were also assigned to each 5-degree latitudinal bands and 100 m depth intervals (gamma species richness).

Rarefaction curves were generated to examine taxon richness as a result of the number of records across the 5-degree latitudinal belts and the different geomorphological features. The rarefaction curves show the expected number of taxa taken at random in consistent step intervals set at 20 until the total number of records per curve is reached. The curves were drawn using the 'rarecurve' function in the 'vegan' package in R. Prior to creating the rarefaction curves, we generated a matrix where the species were all grouped into their respective grouping (5-degree latitudinal belts or geomorphological features). The samples were not randomised across depth intervals but rather randomised by the sampling steps as explained above.

2.1.3. Barcode data analyses

Records for all marine phyla were downloaded from BOLD to determine how many benthic taxa from the deep Arctic Ocean region have been barcoded to date. Downloaded data were again analysed for records collected north of 66°N and below 500 m after removing all taxa that are not benthic. All these records were collated for analysis, which included phyla and classes represented, barcoding effort of (morpho)species-level data, and depth analysis.

2.2. Deep Arctic biodiversity

The distribution of individual taxon records mapped onto habitat types shows that the five major large geomorphological features (basins, canyons, plateaus, ridges, and slopes) all have a minimum of 4,000 taxon records across the entire study area of the 75,404 records remaining after extensive quality control (**Figure 2**). Over 25,000 occurrence records were from slopes and ridges, while basins, canyons, plateaus and unclassified habitat had less than 8,000 occurrence records each (Table S2). Coverage was not homogeneous across the individual regions of the Arctic Ocean (**Figure 2A**). For example, a large part of occurrence records from the slope and plateau regions are from the frequently studied Iceland and Norwegian Seas, north of Svalbard and the Beaufort Sea. Occurrence records from the large basin areas are largely along a few sparse transects. Spatial sample gaps are particularly prominent along the continental slope (and in canyons) north of the Canadian Arctic Archipelago and of the East Siberian Sea, in the Canada Basin and eastern parts of the Nansen Basin, and in the basin of Baffin Bay. Despite the substantial advances in benthic biodiversity research in the deep Arctic in the past decade (e.g., Vedenin et al., 2022, in the CAO; Lörz et al., 2021, in the GIN), hardly any hexagon in the analysis has more than 50 taxon occurrences recorded (**Figure 2B**) or 200 occurrence records (**Figure 2C**). Those hexagons that do contain over 200 occurrence records and/or 50 taxon records tend to be linked to individual research programmes such as the long-term (25-year) observatory HAUSGARTEN in eastern Fram Strait (Soltwedel et al., 2016). The majority of distribution records are concentrated in the upper 1,500 m (**Figure 3A**, **B**), although clear progress has been made sampling abyssal depths over the past decades.

For the whole deep Arctic dataset, a total of 2,636 metazoan taxa were included in the total of 75,404 distribution records. Most taxa were Arthropoda (956), Annelida (566, including Sipuncula) and Mollusca (352). Echinodermata, Porifera, Cnidaria and Chordata also contributed more than 140 taxa each (**Figure 4A**). These numbers are all higher than those reported in Bluhm et al. (2011) for the region north of 80°N a decade earlier: 366 Arthropoda, 194 Annelida, 70 Mollusca and less than 65 for Echinodermata, Porifera and Cnidaria, yet 140 genera in Nematoda. The greatest number of species barcoded per BOLD were members of Chordata, followed by Arthropoda, Annelida, Mollusca and Cnidaria (**Figure 4A**). There were differences, however, among taxa (**Figure 4B–G**). The current data indicate that the Chordata are the phylum with the greatest percentage of data occurrence in the basins, although data for this group is poor in the Amerasian and Eurasian basins of the CAO (**Figure 4D**). Arthropoda data are well distributed in most regions (**Figure 4C**), while data on sponges are mostly from ridges and slopes (**Figure 4H**). These numbers reflect the current research effort made public, and neither reflect the true taxon richness nor necessarily indicate the actual taxonomic and spatial distribution of the taxa reported.

The rarefaction curves on 5-degree latitudinal bands suggest, first and unsurprisingly, that sampling is
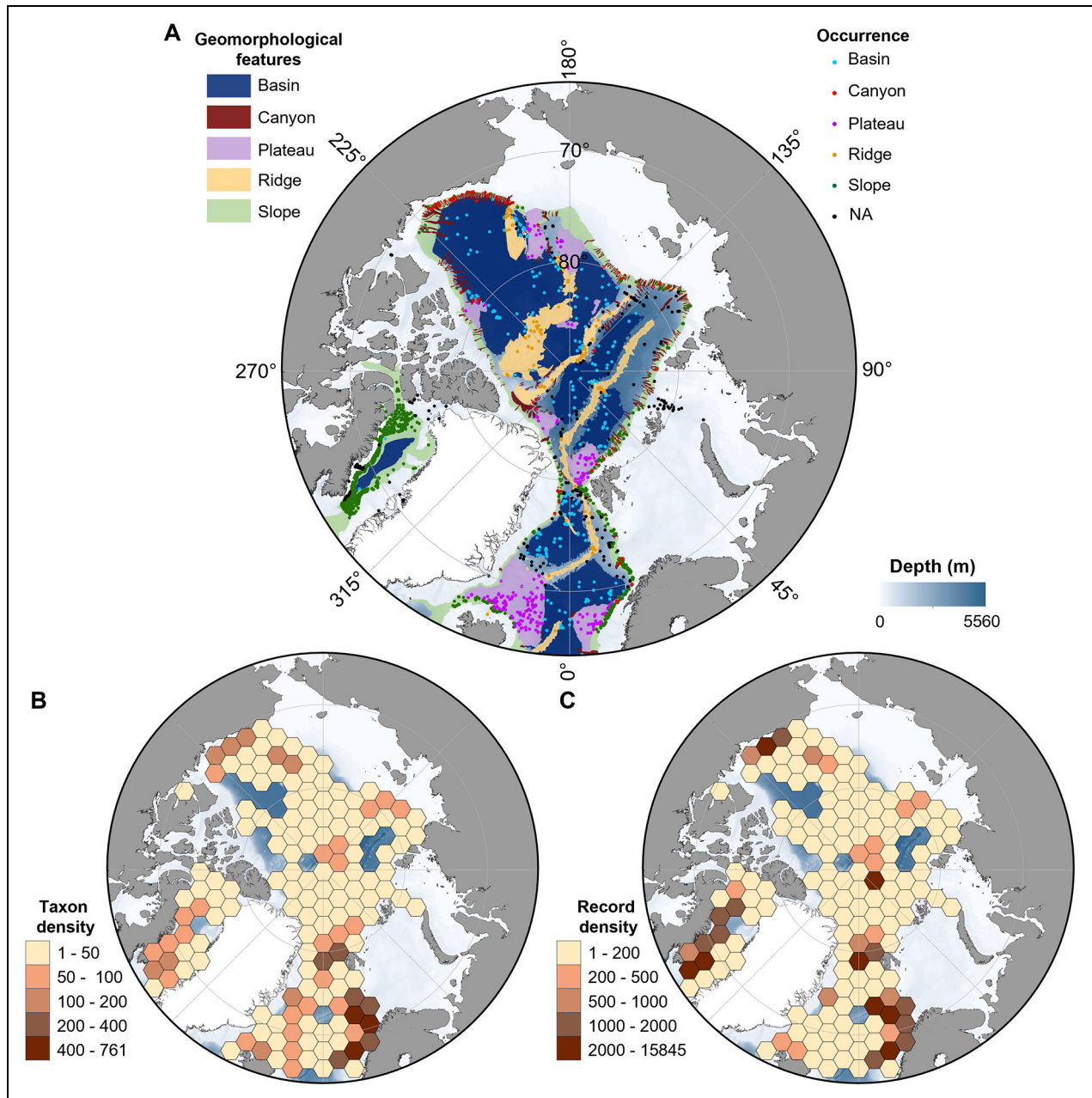
Figure 2. Maps of the Arctic Ocean (66–90°N) showing records in the compiled dataset by geomorphological feature. (A) Each point represents the occurrence of a record from a water depth of >500 m; the colours of the points relate to the habitats they overlap. Not applicable (NA, black points) indicates points that do not overlap entirely with a specific geomorphological feature. (B) Map showing the density of reported taxa per hexagon, where hexagons are equally sized areas of approximately 50,000 km²; transparent hexagons indicate areas where no data were readily available. (C) Map showing the density of reported occurrence records per 50,000 km² equal-sized hexagons.

incomplete in all 5-degree bands between 66°N and 85°N (**Figure 5A**). Second, the patterns suggest a decline in biodiversity with increasing latitude, matching the much-debated latitudinal biodiversity decline hypothesis (Rex et al., 2000). However, this apparent trend should be interpreted with caution, as it may be influenced by a potential diversity-area relationship where there could be a decrease in surface area per degree band as one moves northward. Similarly, the rarefaction curve levelling off between 85°N and 90°N might be influenced by the

diminishing surface area northward within this 5-degree band. Despite the possible bias, the 70–80 degree bands cover the area in the Atlantic sector where, at least on the continental slope, a combination of boreal and Arctic taxa can be found, increasing taxon richness. Taxon richness was higher in the upper 1,500 m than below, with a peak between 500 m and 1,100 m (**Figure 3B**), while a peak in taxon richness is found deeper in some other deep-sea areas and/or taxa (Rex and Etter, 2010), although its location can be variable (Saeedi et al., 2022) or absent
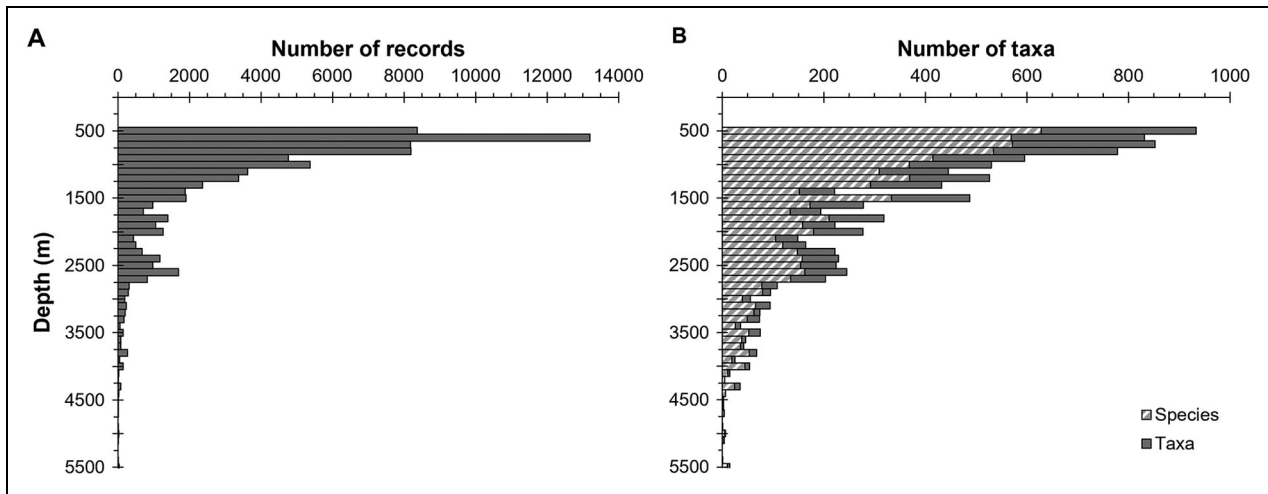
Figure 3. Data availability for the deep Arctic Ocean per 100 m depth interval. (A) Total number of records. (B) Total number of taxa (solid bars; not resolved to species level) and species (hashed bars) per depth interval.

(Wlodarska-Kowalczuk et al., 2004; Renaud et al., 2006). Yet, this pattern may once more be affected by the fact that the highest density of records is also concentrated within the upper 1,500 m.

The rarefaction curves for geomorphological features also suggest undersampling, particularly for the plateaus, canyons, and basins (**Figure 5B**). Undersampling here is unsurprising as numerous factors have made these areas particularly challenging to survey (Bluhm et al., 2011; Huvenne and Davies, 2014; Jørgensen et al., 2022), including ice cover, isolation, sampling logistics, terrain, hydrodynamics, etc. The curves also suggest that ridge areas, which have the highest number of records, have the lowest biodiversity. The sampling efforts on the ridges have been highly concentrated to specific regions, some of which have been revisited over the years, such as HAUS-GARTEN observatory, Aurora Vent Field, Loki's Castle Vent Field, Mohn's Treasure Sulphide Mound, Central Mount, Karasik Seamount, North Mount, and Schulz Bank (**Figure 2**; Soltwedel et al., 2005b; Soltwedel et al., 2009; Pedersen et al., 2010; Roberts et al., 2018; Meyer et al., 2019; Ramirez-Llodra et al., 2020; Soltwedel et al., 2020; Morganti et al., 2021; Morganti et al., 2022; Ramirez-Llodra et al., 2022; Stratmann et al., 2022; Meyer et al., 2023; Eilertsen et al., 2024). While the slope regions have the highest number of taxa and a high number of records, many of the samples are concentrated in Baffin Bay, Davis Strait, and the Norwegian Shelf (**Figure 2**).

2.3. Arctic barcode analysis based on cytochrome c oxidase I

The first review of molecular taxonomy from Arctic environments was conducted just over 20 years ago (Weider and Hobaek, 2000) and summarised research on seven marine mammal species and one marine algal species, using a mixture of mtDNA and rDNA internal transcribed spacers. However, this and later summaries did not involve organisms from the deep sea, which likely indicated that this environment had insufficient research results available at that time. A major review from just over a decade

ago on the status of barcoding molecular diversity in Arctic marine fauna (Hardy et al., 2011) revealed considerable progress, mostly emerging from the Census of Marine Life decadal programme (Costello et al., 2010) and its affiliated Marine Barcode of Life (MarBOL) project (Ratnasingham and Hebert, 2007; Hardy et al., 2011). Hardy et al. (2011) summarised progress of BOLD data from a broad range of Arctic marine organisms, with over 4,300 specimens from 630 species in 11 phyla barcoded. Yet only about 13% of an estimated 5,000+ Arctic marine metazoan species were barcoded, which was proportionally far less than that from the Antarctic marine region for the same time period (Grant and Linse, 2009; Hardy et al., 2011). Few studies of Arctic Ocean deep-sea barcoding had been done before 2012, but several studies conducted on deep-sea polychaetes (Lösekann et al., 2007; Carr et al., 2011), octocorals (Dolan, 2008), fish (Knudsen et al., 2007; Mecklenburg et al., 2011), and crustaceans (Jonsdottir et al., 1998; Martinez et al., 2006) were pioneers in this remote region. Neither of the two recent reviews (Hardy et al., 2011; Walczyńska et al., 2018) noted the proportion of barcodes analysed from deep-sea benthic organisms. However, they both concluded that there was a pressing need to expand barcoding studies into a greater number of taxonomic groups, broader spatial scales, and across all bathymetric ranges (Hardy et al., 2011), particularly in the deep sea (Walczyńska et al., 2018).

Our current review shows that the barcoding effort in the deep Arctic marine region has increased in terms of taxonomic, spatial, and bathymetric efforts in the last decade, with 459 cytochrome c oxidase I (COI) sequences found in BOLD from 5 phyla (Annelida, Arthropoda, Chordata, Echinodermata, and Mollusca), which represent 85 species/morphospecies (Table S3). The greatest number of deep Arctic Ocean sequences (162) are found in the phylum Annelida, representing 20 species in the classes of Polychaeta and Clitellata, and the order Sipuncula. These are closely followed by the phylum Chordata (132), which accounts for 33 species/morphospecies in the classes Teleostei, Ascidiacea and Elasmobranchii. All other phyla
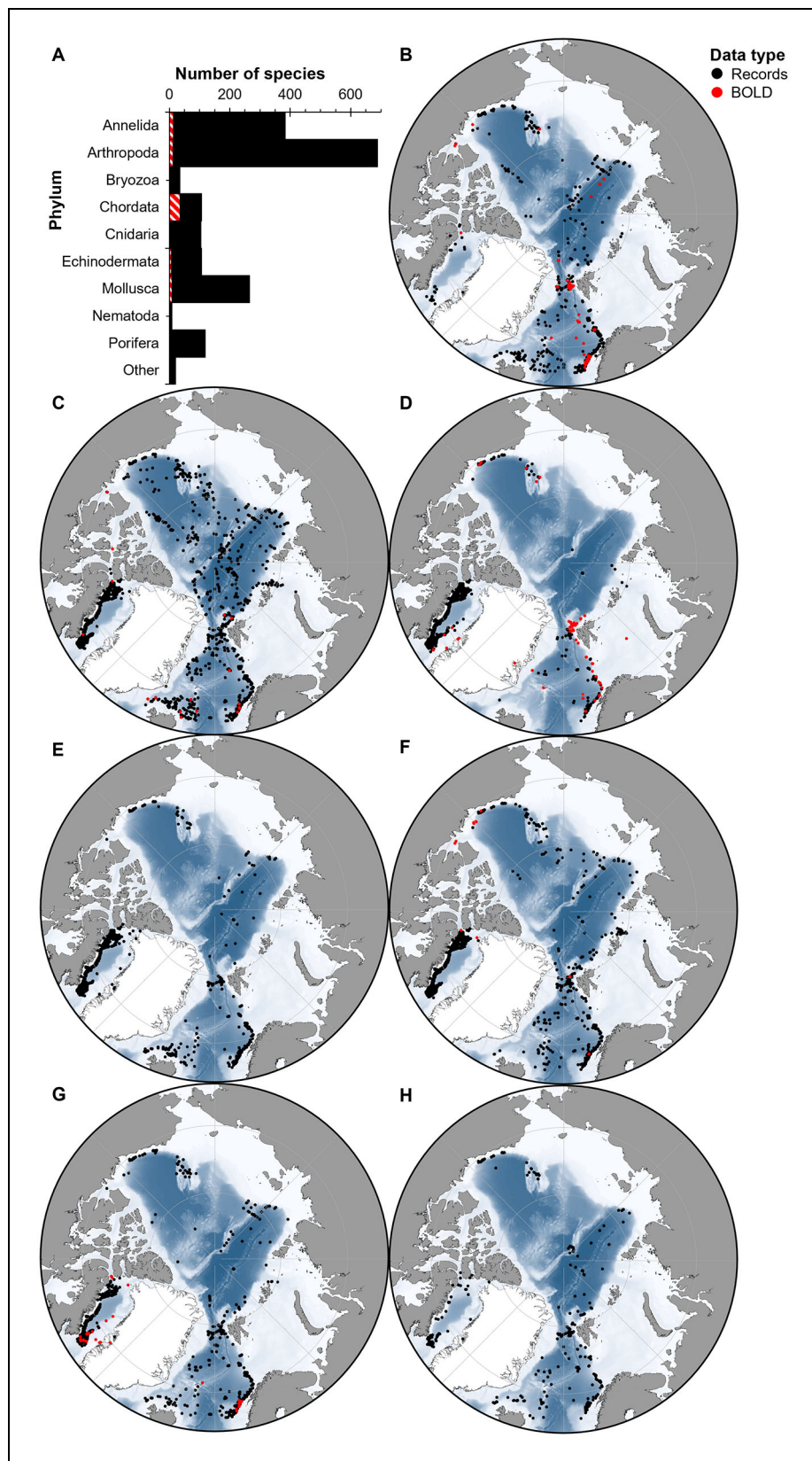
Figure 4. Maps of the occurrence of records and barcoding data by phyla in the deep Arctic Ocean. (A) Total number of species per phylum for the phyla with the most occurrence data, as recorded from the OBIS, GBIF and literature records (black) and BOLD barcoding data (red). 'Other' includes taxa from Brachiopoda, Nemertea, Phoronida, Platyhelminthes, and Priapulida. (B–H) The occurrence data per phylum for (B) Annelida, (C) Arthropoda, (D) Chordata, (E) Cnidaria, (F) Echinodermata, (G) Mollusca, and (H) Porifera.
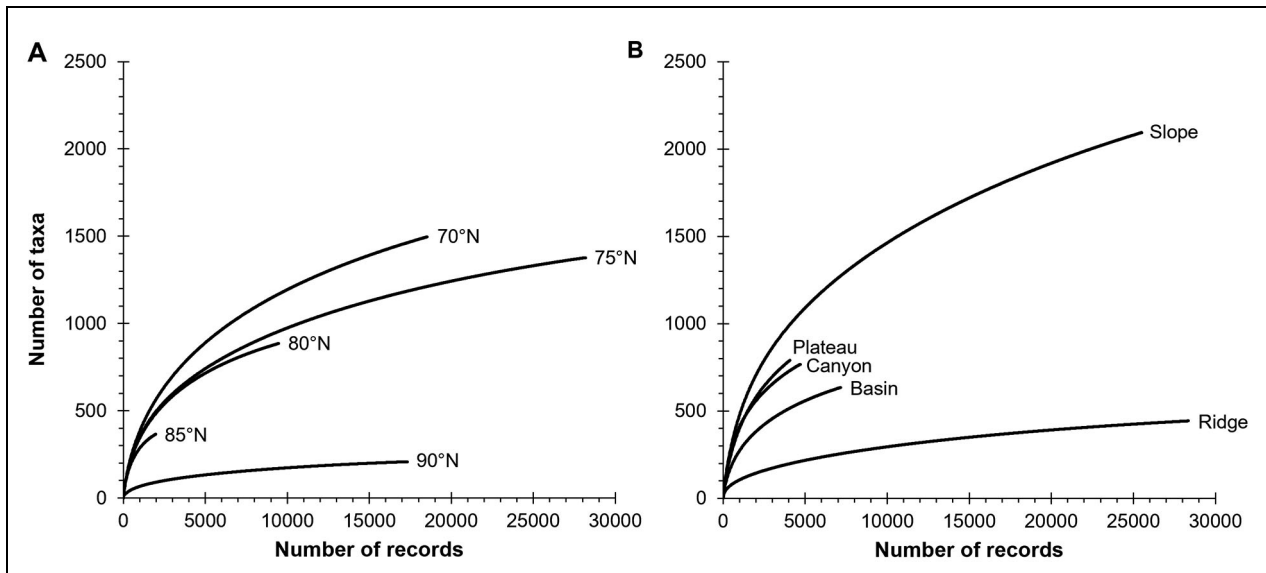
Figure 5. Rarefaction curves of number of taxa against number of records for the deep Arctic Ocean. Rarefaction curves for (A) 5-degree latitudinal bands and (B) geomorphological features.

contain between 82 and 37 records (Mollusca, Arthropoda, and Echinodermata), representing 9 taxonomic classes. In four of these five phyla, less than 7% of the species diversity has been barcoded; however, 43% of species diversity in the phylum Chordata has been barcoded.

Only 5% of the documented deep-sea taxonomic species have been barcoded in the Arctic Ocean based on data held in BOLD (**Figure 4**). BOLD data indicated that barcoding efforts have made progress in 5 phyla; however, there are at least 15 phyla recorded for the deep Arctic Ocean. The 5 phyla with barcoding effort are found among the top 7 phyla for deep-sea Arctic species diversity, while current indications are that no barcoding has been undertaken for the phylum with the fourth greatest level of species diversity, Porifera. However, three barcoding studies on sponges have in fact been undertaken in the deep Arctic Ocean (Cárdenas et al., 2013; Hestetun et al., 2017; Plotkin et al., 2018), but the data were not found in BOLD. Two additional phyla that have known barcoded species, which were also not found in BOLD, include Nematoda (De Santiago et al., 2022) and Nemertea (Chernyshev and Polyakova, 2022). Literature on Cnidaria indicates that there are barcodes for the Anthozoa class (Dolan et al., 2013; Neves et al., 2015; Hogan et al., 2019). In the phylum Arthropoda, barcodes from the class Ostracoda are known from the deep Arctic Ocean, too (Karanovic and Brandao, 2016). However, no studies have been identified that have applied DNA barcoding approaches to specimens collected from the deep Arctic Ocean in the 5 phyla of Bryozoa, Brachiopoda, Priapulida, Chaetognatha (pelagic) and Platyhelminthes, which collectively account for about 3% of known species diversity. COI alone is not the best or only marker for DNA barcoding of certain deep-sea taxa, such as sponges and octocorals, with recent technical analysis recommending the use of short sections of ribosomal DNA (18s, 28s), nuclear (ITS), or other mitochondrial DNA genes and

sections, which can be used in conjunction with COI to delimit species and explore phylogenies (McFadden et al., 2010; Yang et al., 2017; Gong et al., 2018). Public BOLD records of deep-sea barcoding efforts are likely providing a less complete overview of deep-sea barcoding efforts than have in fact been accomplished. A more fundamental issue, however, is the lack of spatiotemporal sequence, such as coordinates, time and, particularly, depth, which makes large-scale analyses of deep-sea biodiversity especially difficult until there are concerted community and database efforts to improve the quality of depth metadata for sequence records (Toczydlowski et al., 2021; Crandall et al., 2023).

Geographic coverage of molecular data indicates a clear gap in the Amerasian and Eurasian Basins in the CAO away from the slopes (**Figure 4**) and a concentration in the Norwegian and Greenland Seas and Baffin Bay, with these regions represented by 4 or more phyla with barcoded representatives. Specifically, barcode sampling is limited for the slopes of the Beaufort and Chukchi Seas at >500 m, though the Beaufort Sea slope is represented by 4 barcoded phyla, including most of all Echinodermata barcode records. Only Chordata and Annelida have been sampled in the CAO, as well as across many other regions, while Arthropoda and Mollusca have been sampled well across most deep regional seas and Echinodermata have limited regional sampling for barcodes. By depth, barcodes were generated from fauna collected from 500 m to 4,500 m in the deep Arctic (Table S4), with more than half of these from below 1,000 m depth, yet all phyla are represented down to 2,000 m. However, only Annelida, Arthropoda, and Mollusca have barcode samples recorded from waters deeper than 2,000 m, with all records collected below 3,000 m only representing Annelida. Barcodes generated from records below 2,000 m accounting for 14% of all records indicates a barcoding bias towards the upper bathyal sector.
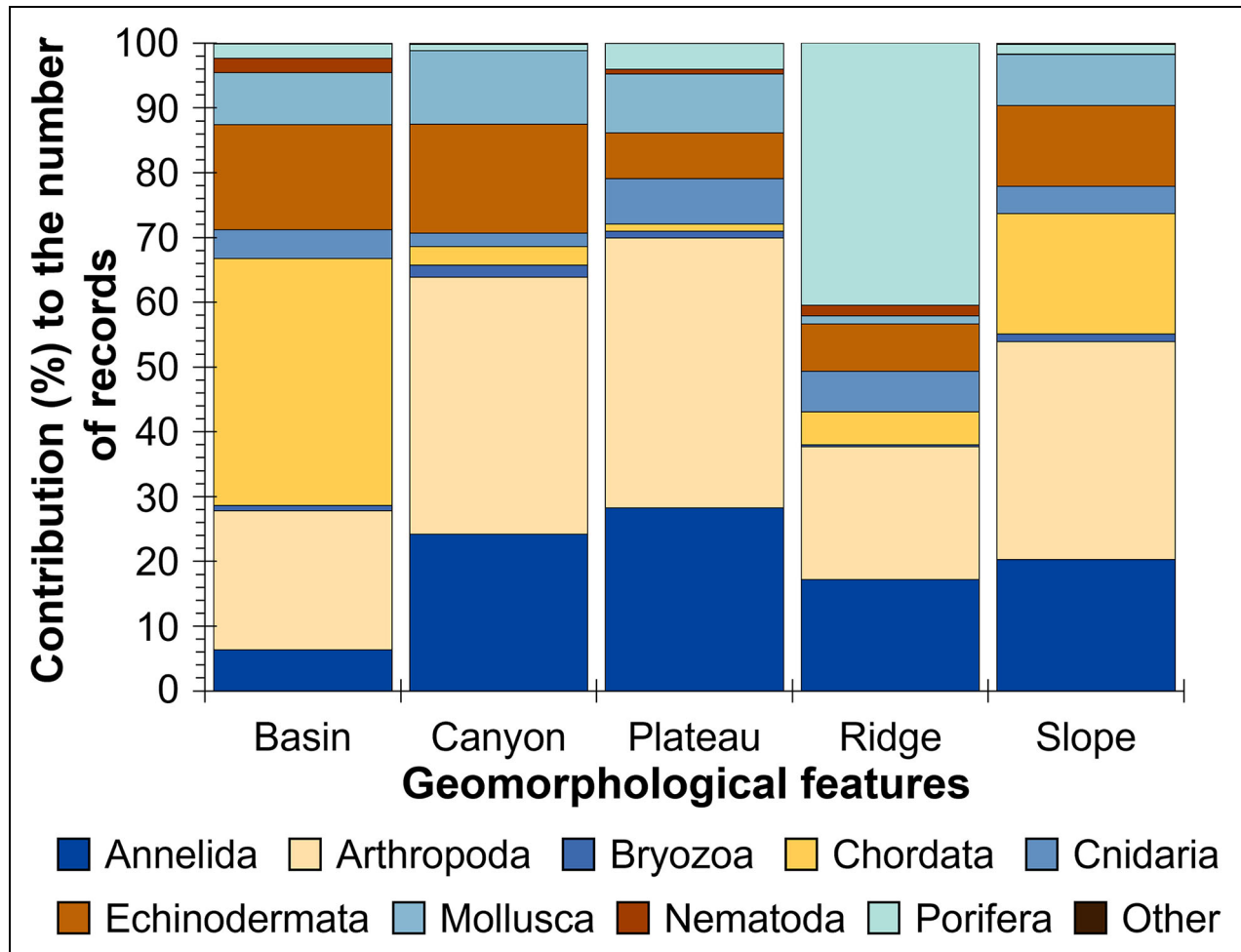
Figure 6. Contribution of phyla to number of records by geomorphological feature in the deep Arctic Ocean. 'Ridge' includes data from different habitats on the ridges (e.g., hard substrate on the ridge, seamounts, hydrothermal vents) because these habitats are too small in size to be separated in the analysis. The specific communities of such habitats are described in the text. 'Other' includes taxa from Brachiopoda, Nemertea, Phoronida, Platyhelminthes, and Priapulida.

3. Habitat diversity and ecosystem composition

Managing ecosystems worldwide, conserving both their functional integrity and the ecosystem services they provide for future generations, requires reliable generalisations and predictions about habitats and the communities they support that can be applied globally (Keith et al., 2020). With the aim to compile available data and contribute new knowledge on Arctic deep-sea ecosystems that can be used in global assessments, we adopted the Global Ecosystem Typology of the International Union for Conservation of Nature (IUCN; Keith et al., 2022). According to this classification scheme, the deep seafloor biomes include continental and island slopes, submarine canyons, abyssal plains, seamounts, ridges and plateaus, deep-water biogenic beds, hadal trenches and troughs, and chemosynthesis-based ecosystems (Keith et al., 2020; 2022). All these biomes exist in the deep Arctic north of 66°N, except hadal trenches. Yet our map is, to our knowledge, the first to show this habitat diversity classification in one figure (**Figure 1**) and the contribution of the different benthic fauna for the main geomorphological features (**Figure 6**). The underlying bathymetry we used is the best available of the Arctic Ocean, IBCAO version 4.2 (4.0 released by Jakobsson et al., 2020).

3.1. Deep continental margins

Deep continental margins of the Arctic Ocean extend between the shelf break (below 500 m depth for this study) and the lower limit of the continental slope and rise at about 2,500–3,000 m depth (Jakobsson et al., 2020; **Figure 7**). Continental margins cover 11% of the global ocean surface and have slope inclinations between 6 and 1 degrees (Menot et al., 2010). They are characterised by a wide range of geological, hydrological and biological conditions that translate into a great diversity of habitats and a significant turnover in species composition downslope. Habitats found on continental margins include several of the biomes in the IUCN marine typology: sedimentary slopes, canyons, cold seeps, and biogenic beds, as described in the following sections.
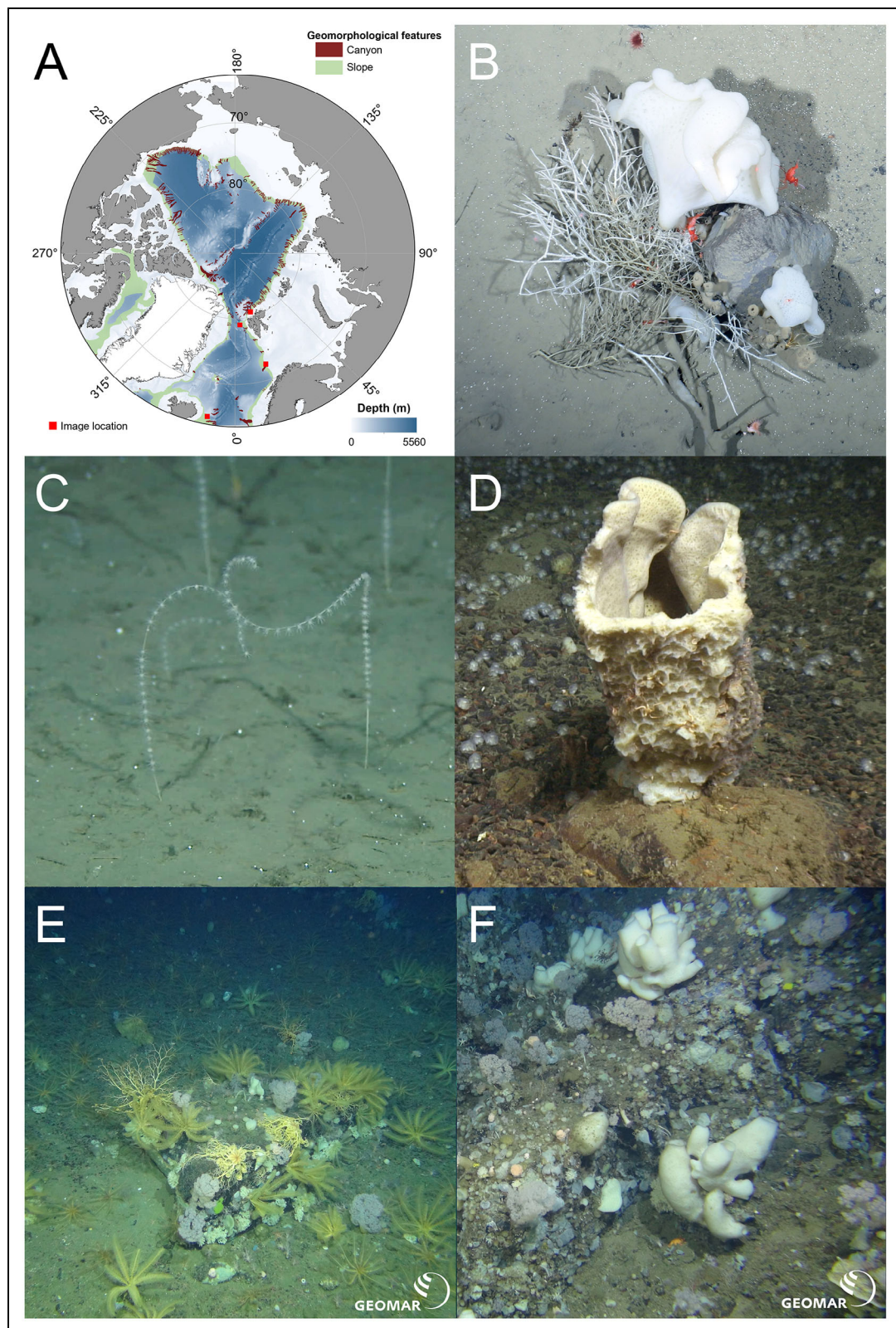
Figure 7. Representative fauna observed around the slopes and canyons in the deep Arctic Ocean. (A) Locations of the representative images; (B) *Caulophacus (Caulophacus) arcticus* (Hansen, 1885) and Cladorhizidae sponges at HAUSGARTEN Observatory (Source: Thomas Soltwedel, AWI, Deep-Sea Research Group); (C) *Radicipes* Stearns, 1883 fields on the continental slopes west of Bear Island; (D) *Haliclona (Gellius) fibulata* (Schmidt, 1862) and *Kukenthalia borealis* (Gottschaldt, 1894) aggregations in a canyon north of Svalbard (Source: Pål Buhl-Mortensen, MAREANO, Institute of Marine Research); and (E) crinoid fields with *Heliometra glacialis* (Owen, 1833 ex Leach MS), *Drifa glomerata* (Verrill, 1869) and *Gorgonocephalus* Leach, 1815 and (F) cauliflower coral gardens with *Drifa glomerata* and *Schaudinnia rosea* (Fristedt, 1887) in a canyon-like section of Ægir Ridge (Source: James Taylor and Saskia Brix, DZMB Senckenberg, GEOMAR Kiel 6000).

3.1.1. Sedimentary slopes

The sedimentary slopes of Arctic continental margins support benthic ecosystems with a higher species richness than found in the abyssal plains of the basins and, given the soft sediments, a dominance of meio- and macrofaunal infauna but also the occurrence of larger animals such as echinoderms, sponges and arthropods (**Figures 6** and **7B**, **C**; Wlodarska-Kowalczuk et al., 2004; Soltwedel et al., 2009; Brix et al., 2018a; Brix et al., 2018b; Bluhm et al., 2020; Vedenin et al., 2022). When rocks are present, often in the form of glacial drop stones in the CAO, they provide substrate to sessile fauna such as sponges, cnidarians, and their associated fauna (**Figure 7B**; Meyer et al., 2016; Rybakova et al., 2019; Zhulay et al., 2019).

As in other oceans, benthic communities on Arctic slopes show a strong vertical zonation in taxonomic composition, as well as a decline in biomass and abundance associated with decreasing food supply with depth, while they are comparatively homogeneous along bands of similar depth ranges (Bluhm et al., 2020; Brix et al., 2022; Vedenin et al., 2022). Particularly strong community shifts occur around 650–950 m and 2,500–3,000 m water depth in the CAO (Vedenin et al., 2022). These coarsely reflect the transition between the upper, more dynamic slope and the associated water masses (surface water, halocline and Atlantic layer), and the lower, relatively energy-poor and quiescent continental slope and rise immersed in Arctic Deep Water (Bluhm et al., 2020). Taxon richness in our dataset showed a peak between about 500 m and 1,100 m (**Figure 3**), while Vedenin et al. (2022), who included stations shallower than 500 m, found the highest taxon richness at 100–600 m. A peak in taxon richness around 2,000 m often found elsewhere (Rex, 1981; Etter and Grassle, 1992) was not detected in the present Arctic data compilation. While we did not investigate the cause, the extremely oligotrophic nature of these deep layers may offer explanations. The Arctic depth zones of the continental slope described by Vedenin et al. (2022) are characterised by the same species at a virtually pan-Arctic scale (north of Fram Strait): at the upper slope the bivalve *Yoldiella solidula* Warén, 1989, the brittle star *Ophiocten sericeum* (Forbes, 1852), and the polychaetes *Prionospio cirrifera* Wirén, 1883 and *Spiophanes kroyeri* Grube, 1860 are common; at the lower slope the polychaetes *Ophelina opisthobranchiata* Wirén, 1901, *Galathowenia fragilis* (Nilsen & Holthe, 1985), *Prionospio* sp. Malmgren, 1867, and *Siboglinum* Caullery, 1914 and the bivalve *Bathyarca frielei* (Friele, 1877) are frequent.

3.1.2. Submarine canyons

Continental margins are intersected by submarine canyons in some regions (**Figure 7D–F**). These canyons modify the local hydrography and act as conduits for particles from the shelf to the deep seafloor, providing enhanced food supply, as well as refuge and nursery areas for fauna (Fernandez-Arcaya et al., 2017). Overall, the dominant fauna recorded from Arctic canyons belongs to the Arthropoda and Annelida, followed by Echinodermata and Mollusca (**Figure 6**). These are typical deep-sea fauna from sedimentary habitats, which may indicate a certain sampling bias towards the canyon axis rather than the rocky walls where sessile, filter-feeding organisms such as cnidarians and poriferans are often common (Fernandez-Arcaya et al., 2017; **Figure 7F**).

Arguably, the biologically best-studied canyons and troughs around the Arctic basin slopes are (the upper parts of) Barrow Canyon at the Chukchi shelf break and slope and the St. Anna Trough intersecting the eastern Barents Sea (**Figure 1**). Enhanced benthic biomass with a high proportion of suspension feeders was found in upper Barrow Canyon and in the path of the outflowing water in the adjacent western Beaufort Sea shelf break/upper slope (Grebmeier, 2012; Rand et al., 2018). This increased biomass was thought to be mediated by strong northward currents combined with strong downward flows that transport fresh phytoplankton to benthic communities (Pickart et al., 2021). A strong prey base in this area also attracts at times high concentrations of marine mammals (Hauser et al., 2017). Similarly, the benthos from St. Anna Trough was characterised by a comparative prevalence of suspension feeders, which were linked to the strong and persistent bottom currents (Galkin et al., 2015), including a dominance of the seapen *Umbellula encrinus* (Linnaeus, 1758), the echinoderms *Ophiopleura borealis* Danielssen & Koren, 1877 and *Gorgonocephalus arcticus* Leach, 1819, and Porifera and Actiniaria (Jørgensen et al., 2015). Depending on location within the trough, typical boreal-Atlantic invertebrate taxa as well as fish, for example, young Greenland halibut (*Reinhardtius hippoglossoides* [Walbaum, 1792]), occur in the comparatively warm Atlantic Water layer (Galkin et al., 2015; Dolgov and Benzik, 2017), with deep-water species dominating in the deep parts of the trough.

3.2. Abyssal plains

Abyssal plains (of the deep basins) are vast expanses of fine sediment that cover over 75% of the global seafloor between 3,000 and 6,000 m depth (Ramirez-Llodra et al., 2010; **Figure 8**). In our study region, the deepest abyssal plain is the Molloy Deep in Fram Strait (**Figure 8B**), with a maximum depth of 5,607 m (Thiede et al., 1990), while in the CAO, the deepest basin region is in the Amundsen Basin with a maximum depth of 4,400 m (Jakobsson et al., 2020; **Figure 1**). As in the global ocean, the Arctic abyssal sediment is mostly inorganic, except for the surficial layers where organic matter accumulates, deposited from the water column and sea-ice algal falls or advected from continental margins and even river inputs (Gage, 2003; Smith et al., 2008; Boetius et al., 2013; Rybakova et al., 2019). The abyss is characterised by low food availability, with the quantity and quality of the detrital matter sinking from the water column modulating the structure and function of the ecosystem (Gage, 2003; Smith et al., 2008; Wiedmann et al., 2020). Food supply in the Arctic is more seasonal than at lower latitudes and, in the case of the CAO, is also depressed by seasonal or permanent ice cover through light limitation to primary producers (Wiedmann et al., 2020). Thus, benthic abundance and biomass are on the lower side in comparison
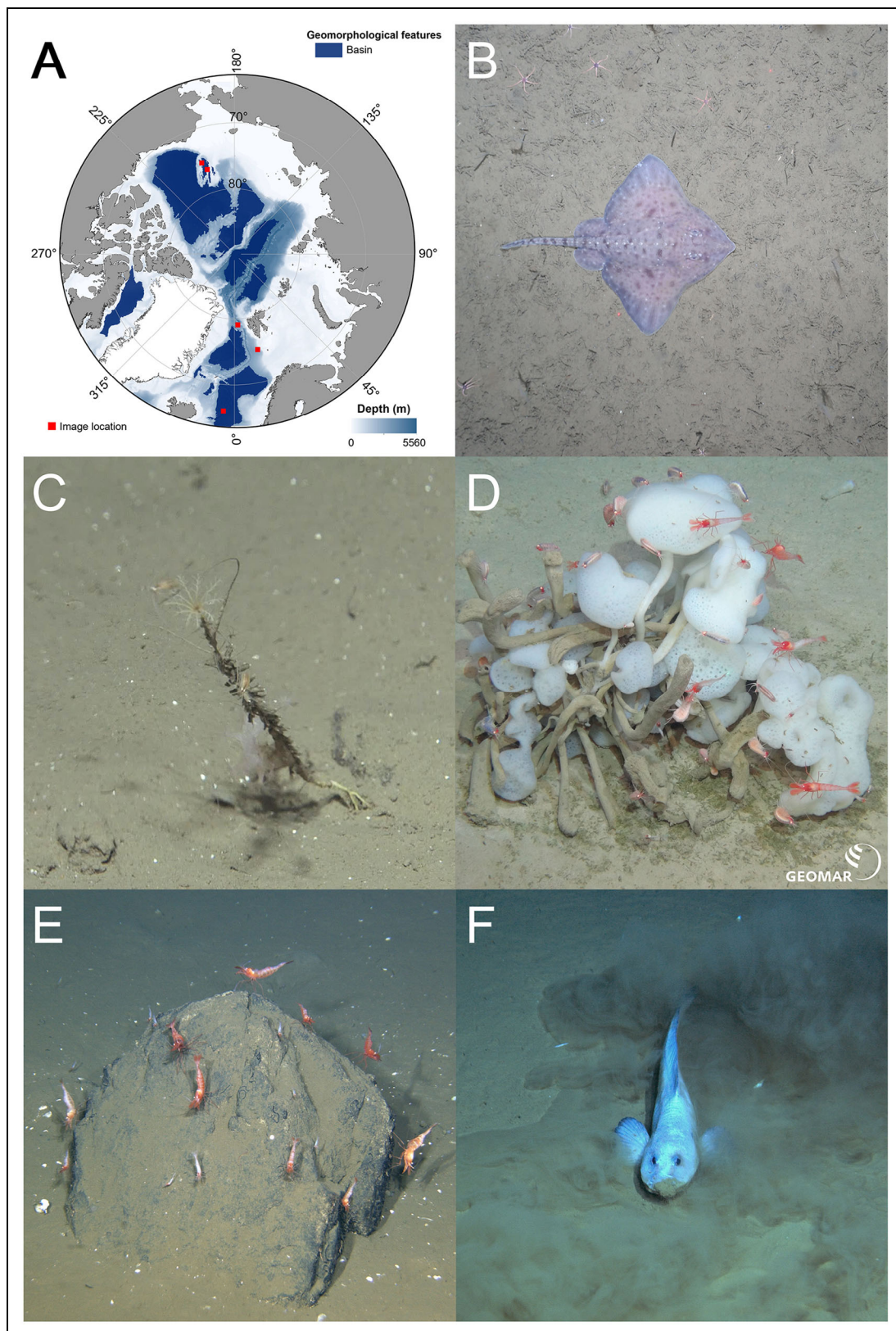
Figure 8. Representative fauna observed around the basins and abyssal plains in the deep Arctic Ocean.
(A) Locations of the representative images; (B) *Amblyraja hyperborea* (Collett, 1879) surrounded by crinoids and ophiuroids in Molloy Deep (Source: Autun Purser, AWI, Deep-Sea Research Group); (C) *Bathycrinus carpenterii* (Danielssen & Koren, 1877) west of Bear Island (Source: Pål Buhl-Mortensen, MAREANO, Institute of Marine Research); (D) *Caulophacus* Schulze, 1886 glass sponges with caridean shrimps and calliopid amphipods (Source: James Taylor and Saskia Brix, DZMB Senckenberg, GEOMAR Kiel 6000); (E) *Bythocaris* G.O. Sars, 1870 on a dropstone; and (F) *Lycodes frigidus* Collett, 1879 in the Chukchi Borderland (Source: Irina Zhulay and Katrin Iken, The Hidden Ocean 2016: Chukchi Borderland, NOAA, University of Alaska Fairbanks, Oceaneering-DSSI).

to the global deep sea (Wei et al., 2010; Bluhm et al., 2011). For example, macrofaunal abundances range from near 0 to near 10,000 individuals (ind) m^{-2} (mean of 937 ind m^{-2}) north of Fram Strait, with most accounted for in the 500–1,000 m range (mean of 2,300 ind m^{-2}) and the smallest contribution at depths >4,000 m (mean of 100 ind m^{-2}; Bluhm et al., 2011). Megabenthic abundances are commonly <10 ind m^{-2} in the abyssal plains of the CAO (Rybakova et al., 2019), though values >30 ind m^{-2} were reported from Hausgarten in Fram Strait (Taylor et al., 2017).

Despite the general food limitation in the abyss (Smith et al., 2008), abyssal species richness (measured by rarefaction), particularly of macro- and meiofauna, is generally high in the deep sea (Snelgrove and Smith, 2002; Brandt et al., 2007; Rex and Etter, 2010). Among the metazoans, nematodes dominate taxon richness in the meiofauna (yet are underrepresented in the present dataset), and arthropods and polychaetes are the most diverse groups in the macrofaunal size range in Arctic abyssal basins (Bluhm et al., 2011), as they typically live in and on soft sediments. In addition to arthropods, epifaunal species richness is substantial in the echinoderms, sponges, molluscs, and cnidarians (occurrence records in **Figure 6**). Occurrence records are surprisingly high for chordates (**Figure 6**). Common species in the CAO include the polychaetes *Anobothrus laubieri* (Desbruyères, 1978) and *Aricidea* spp., the sponge *Thenea abyssorum* Koltun, 1964, the anemone *Bathyphellia margaritacea* (Danielssen, 1890) and the common sea cucumber *Kolga hyalina* (Danielssen & Koren, 1879) that appears to be able to exploit areas or events of high detrital fluxes (McDonald et al., 2010; Boetius et al., 2013). The stalked crinoid *Bathycrinus carpenterii* (Danielssen & Koren, 1877) forms crinoid fields in the soft-sedimented plains of the Norwegian Sea (Meyer et al., 2014; Ramirez-Llodra et al., 2020; Meyer et al., 2023) and occurs in low densities across the CAO (**Figure 8B**, **C**). Rocky outcrops at abyssal depths, found particularly close to the ridge systems, are often covered by the large glass sponges *Caulophacus (Caulophacus) arcticus* (Hansen, 1885) and *Amphidiscella monai* (Tabachnick & Lévi, 1997) (**Figure 8D**), or by axinellid sponges (Brix et al., 2022; Meyer et al., 2023). Fishes are a dominant group in abyssal Arctic basins (**Figure 6**), with eelpouts and snailfish regularly found in abyssal regions of the CAO, albeit in low densities (Stein et al., 2005; Zhulay et al., 2019; **Figure 8F**). Cephalopods such as the bentho-pelagic cirrate octopod *Cirroteuthis muelleri* (Eschricht, 1838), the nekto-benthic bobtail squids *Rossia* M. Voigt, 1960, as well as the benthic incirrate octopods *Bathypolypus* Grimpe, 1921 and *Muusoctopus* Gleadall, 2004 are an important component of abyssal plain communities (Xavier et al., 2018; Golikov et al., 2023). Despite their (relatively) low taxonomic diversity, they are crucial in food-web functioning linking the benthic to pelagic taxa such as fish and other top predators, due to their high abundance, relatively large size and not entirely benthic lifestyle (Nesis, 1987; Golikov et al., 2017; Golikov et al., 2018; Xavier et al., 2018).

3.3. Mid-ocean ridges

Mid-ocean ridges are a semi-continuous range of volcanic mountains across the ocean floor, where new oceanic crust is formed (**Figure 9**). In the Arctic north of 66°N, the Kolbeinsey Ridge and the inactive Ægir Ridge run from Iceland to the Jan Mayen Fracture Zone (**Figure 1**). From Jan Mayen, the Mohn Ridge runs NE and then bends NW into the Knipovich Ridge up to Svalbard (**Figure 1**). Continuing north, the Molloy Ridge and Lena Trough are followed by the Gakkel Ridge which runs into the CAO in the Eurasian Basin (**Figure 1**). These seven ridge segments form the ultraslow-spreading ridge system known as the AMOR (Johnson and Heezen, 1967; Pedersen et al., 2010). The Lomonosov Ridge separates the Amerasian from the Eurasian Basins, and the former contains the Alpha and Mendeleev Ridges (Jakobsson et al., 2020). The AMOR host numerous geological features and habitat types, including rocky substrates and slopes, sedimented areas, seamounts, and banks, as well as active and inactive hydrothermal vents described below.

Data from the CAO ridges are very sparse, and taxon estimates, hence, incomplete. Outside of seamounts and chemosynthetic-based ecosystems on ridges, existing taxon numbers of soft-bottom meio- and macrofauna reported from the Lomonosov, Gakkel and Alpha-Mendeleev Ridges appear to be perhaps similarly low as surrounding basins, in part related to the very low faunal densities in those remote areas (including the adjacent basins; Kröncke, 1994; 1998; Schewe and Soltwedel, 1999; Schewe, 2001). For example, around 20 macrobenthic species were found at a combined 7 stations at the Lomonosov and Gakkel Ridges in a transect crossing ridges and basins (Kröncke, 1994). At the Lomonosov Ridge (a much higher mountain range than Gakkel Ridge) abundances, however, were slightly enhanced compared to surrounding basins (about 300–500 ind m^{-2} versus 50–200 ind m^{-2}), with a higher fraction of suspension feeders than in the abyssal areas, which was attributed to somewhat higher current velocities at the ridge slopes (Kröncke, 1994; **Figure 6**). Clearly, more detailed studies are needed to better identify patterns on soft sedimentary ridge sections, and making distinctions between such sections and special features of seamounts and vents on these ridges, where densities are higher and fauna is unique, is paramount, as outlined in the following sections.
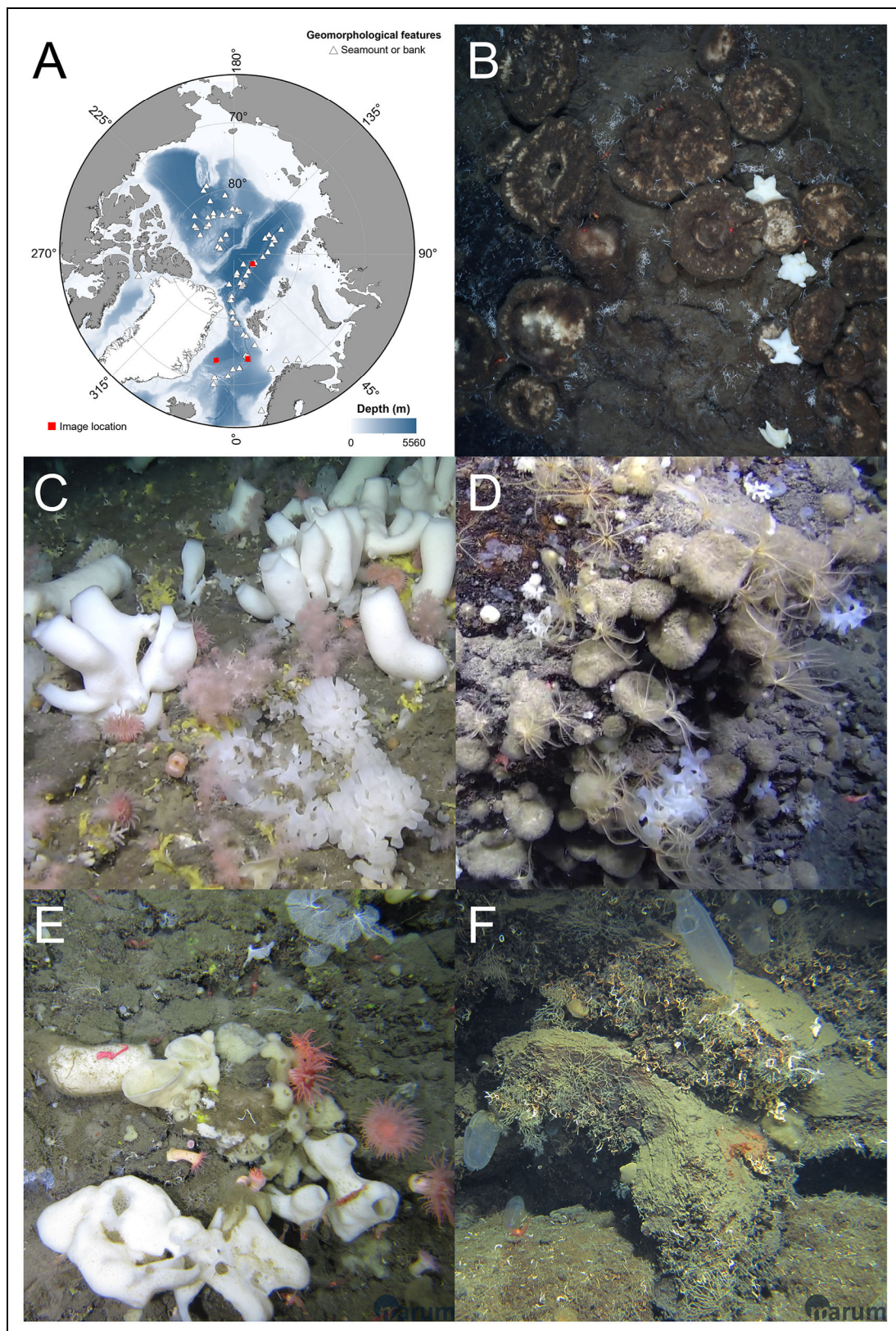
3.3.1. Seamounts

Seamounts are topographic elevations that rise more than 1,000 m from the seafloor without reaching the surface (Harris et al., 2014; **Figure 10**), with smaller structures called banks, knolls, mounds, and also plateaus (**Figure 9D**, **F**; Schlacher et al., 2010; Rogers, 2018). The particular topography of seamounts results in a variety of habitats at a small geographic scale, from sedimented tops or flanks with low inclinations, to rocky outcrops and walls that provide support to filter feeders such as corals and sponges and their associated fauna.

In the Arctic, the majority of the seamounts and banks are of volcanic origin and located on or near AMOR
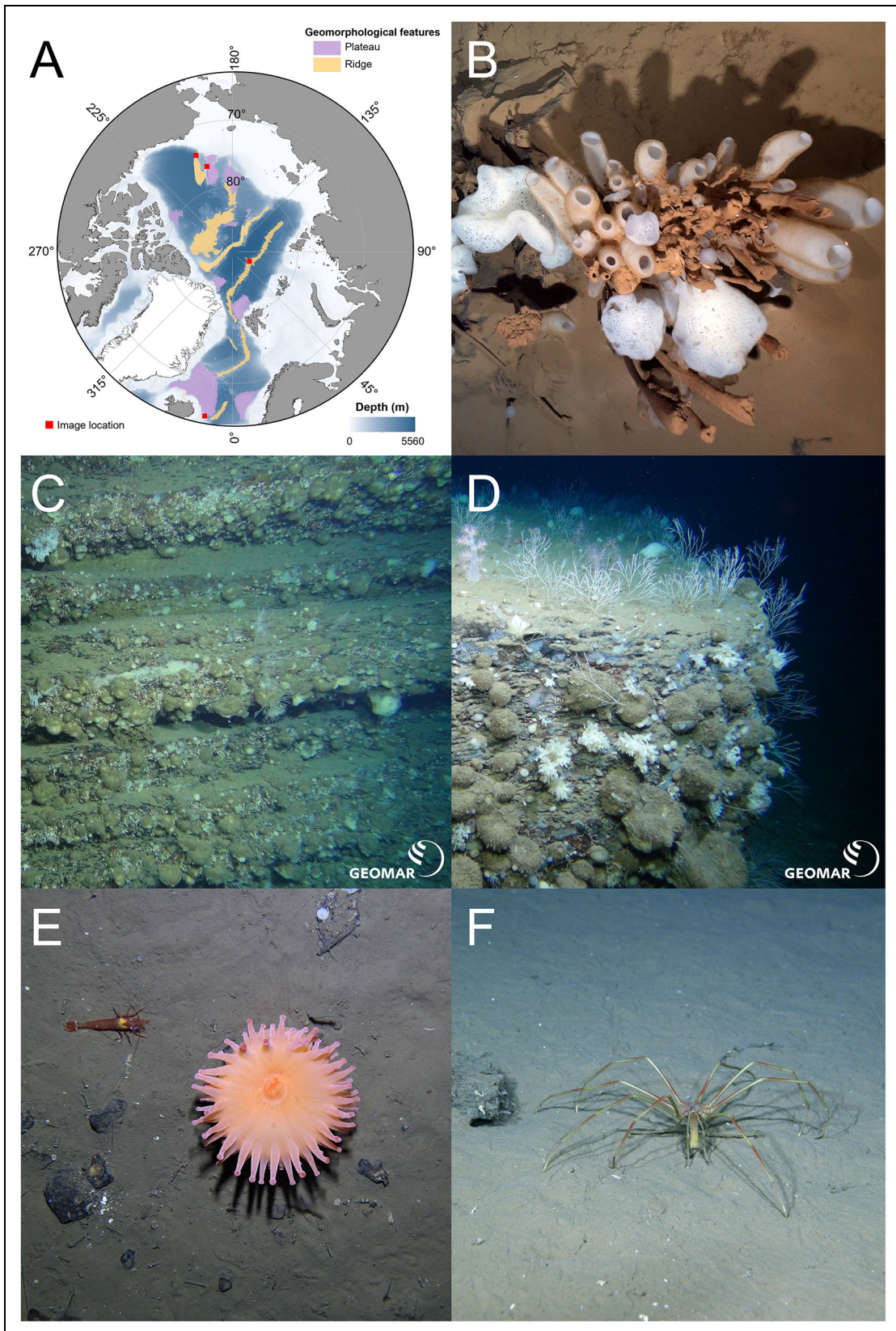
Figure 9. Representative fauna observed on the ridges and plateaus in the deep Arctic Ocean. (A) Locations of the representative images; (B) glass sponges on the Gakkel Ridge (Source: Thomas Soltwedel, AWI, Deep-Sea Research Group); (C,D) vertical *Geodia* walls with *Asbestopluma (Asbestopluma) furcata* Lundbeck, 1905 and *Gersemia* von Marenzeller, 1878 on Ægir Ridge (Source: James Taylor and Saskia Brix, DZMB Senckenberg, GEOMAR Kiel 6000); and (E) *Pycnanthus densus* Carlgren, 1921 and *Bythocaris* on the Northwind Ridge and (F) *Colossendeis proboscidea* (Sabine, 1824) on the Chukchi Plateau (Source: Irina Zhulay and Katrin Iken, The Hidden Ocean 2016: Chukchi Borderland, NOAA, University of Alaska Fairbanks, Oceaneering-DSSI).

Figure 10. Representative fauna observed on seamounts and banks in the deep Arctic Ocean. (A) Locations of the representative images; (B) *Geodia* Lamarck, 1815 and *Stelletta* Schmidt, 1862 with predating seastars on the summit of Karasik Seamount (Source: Autun Purser, AWI, Deep-Sea Research Group); (C) *Schaudinnia rosea* (Fristedt, 1887), *Asconema foliatum* (Fristedt, 1887), *Geodia parva* Hansen, 1885 with associated fauna on the summit; (D) *Geodia* sponges with crinoids and associated fauna on the flanks of Schulz Bank (Source: Heidi Meyer, SponGES project and University of Bergen); and (E) *Schaudinnia rosea* and *Geodia* with associated fauna on the eastern flank and (F) ascidians, bryozoans, and polychaetes on the deep western slope of Vesteris Bank (Source: Jan Steger, copyright: MARUM, University of Bremen, Germany. Cruise MSM86).

(Cochran, 2008). To date, many of these seamounts and banks have remained largely unexplored or unmapped (Kutti et al., 2019; Clark et al., 2021), with only less than 100 Arctic seamounts and banks charted (Figure S5). Out of these, only five have had their biological community composition explored and described: the Northern Mount, Central Mount and Karasik Seamount on the Langseth Ridge (87°N 62°E to 85°N 57°E) in the CAO (Morganti et al., 2021; Morganti et al., 2022; Stratmann et al., 2022; **Figure 10B**), the Schulz Bank (73°52′N, 7°30′E) on the transition point between the Mohn and Knipovich ridges (Roberts et al., 2018; Meyer et al., 2019; Morrison et al., 2020; Hanz et al., 2021; Hanz et al., 2022; Meyer et al., 2023; **Figure 10C**, **D**); and Vesteris Bank (73°30′N, 9°10′W) in the central Greenland Sea (Henrich et al., 1992; Unger Moreno et al., 2021; **Figure 10E**, **F**). These five features host Arctic sponge grounds on their summits, flanks and base (Henrich et al., 1992; Meyer et al., 2019; Morganti et al., 2021; Unger Moreno et al., 2021; Morganti et al., 2022; Stratmann et al., 2022; Meyer et al., 2023). In general, the sponge ground communities on these five seamount summits contain similar characterising taxa, comprised of large glass sponges and demosponges with other associated fauna (e.g., bryozoans, smaller-sized sponges, ascidians, echinoderms, molluscs and cnidarians) settled on sponges (Stratmann et al., 2022; Meyer et al., 2023) or spicule mats on empty siboglinid and serpulid polychaete tubes from extinct seeps (Morganti et al., 2022; **Figures 6** and **10B**, **C**, **E**). These communities extend down to approximately 1,000 m depth and often attain a high standing-stock biomass (Schlacher et al., 2010; Morganti et al., 2022; Meyer et al., 2023). In the deeper regions of the seamounts below 1,500 m, large demosponges with crinoids, ophiuroids, other sponges and decapods are observed settling directly on the large sponges or on the bedrock (Meyer et al., 2023; **Figure 10D**), dominating the steep rocky walls. These deeper communities resemble sponge communities found along AMOR and at several active and inactive hydrothermal areas (Ramirez-Llodra et al., 2020; Brix et al., 2022; **Figure 9C**, **D**).

3.3.2. Chemosynthesis-based ecosystems

Chemosynthesis-based ecosystems, mainly hydrothermal vents, cold seeps, and large organic falls, are characterised by primary productivity in the form of microbial chemosynthesis on the deep seafloor (**Figure 11**). In these habitats, chemoautotrophic microorganisms, both free-living and in symbiosis with metazoan fauna, use reduced chemicals as an energy source to produce organic matter (Sweetman et al., 2013; Åström et al., 2022; Eilertsen et al., 2024). This microbial productivity is at the base of the trophic web in these ecosystems, supporting dense aggregations of highly adapted fauna (Tunnicliffe et al., 2003).

Cold seeps, where seafloor sediment is highly concentrated in methane, hydrogen sulphide and other reduced chemicals, are found in the Arctic continental margins and on shelves (Åström et al., 2020; Figure S6). The Håkon Mosby mud volcano, located at 1,200 m depth between

Svalbard and the Norwegian mainland, was the first Arctic cold seep investigated (in the mid-1990s; Gebruk et al., 2003; Soltwedel et al., 2005a; Rybakova et al., 2013). The other known deep Arctic cold seeps include pockmarks on the Vestnesa Ridge (Fram Strait; Åström et al., 2018), the gas hydrate system on the Svyatogor Ridge (Waghorn et al., 2022), and cold seeps in canyons in the Lofoten-Vesterålen margin (Sen et al., 2019). Although outside of our study area, cold seeps are also common on the Arctic shelves, such as the mud volcanoes in the Beaufort Sea, submarine pingos in the Barents Sea and blowout craters in the Barents Sea (Paull et al., 2015; Lee et al., 2019). Recently, a new mud volcano was discovered in the Barents Sea at 380 m depth. The mud volcano was named Borealis, but its communities have yet to be studied (Panieri and Bünz, 2023). Evidence of gas seep sites in the form of echosounder anomalies have also been recorded in several locations around the Svalbard archipelago (Rodes et al., 2023). Arctic seeps have a distinct faunal composition compared to seeps in other oceans, and often host large microbial mats and dense beds of frenulate and moniliferan siboglinid worms (**Figure 11B**), but tend to lack large bodied, chemosynthesis-based fauna (Decker et al., 2012; Åström et al., 2020). Benthic biomass is also higher on the seeps than in adjacent areas (Soltwedel et al., 2005b). Findings of young, often late Pleistocene fossils of vesicomyid, solemyid, and thyasirid bivalves at the Vestnesa and Gakkel Ridges, the Laptev Sea, seeps on the Svalbard margin, and Canning Seafloor Mound in the eastern Beaufort Sea (Valentich-Scott et al., 2014; Åström et al., 2017; Hansen et al., 2017; Hansen et al., 2020), however, indicate the existence of multiple chemosymbiotic bivalves in past Arctic seep environments. Commercially important species such as cod, northern shrimp, and snow crabs have been observed, often in high densities, at shelf Arctic seeps (Sen et al., 2018). Additionally, seeps may coincide with petroleum beds and gas hydrates, therefore holding considerable economic value (Bogoyavlensky et al., 2018; Bernardino et al., 2020; Panieri et al., 2024).

Hydrothermal vents are characterised by hot (commonly up to 300°C–350°C) fluids charged with reduced chemicals that are used by free-living and symbiotic microorganisms to produce organic matter through chemosynthesis (Van Dover, 2000; **Figure 11C–F**). In the Arctic, seven deep-water active hydrothermal vent fields have been discovered and visually confirmed to date. The first vents discovered on the AMOR in 2005 on the southern part of the Mohn Ridge were the Soria Moria and Troll Wall (Schander et al., 2010). Later the Perle & Bruse vent field was discovered in the same area (Stensland et al., 2019; **Figure 11C**). These three sites together are called the Jan Mayen vent fields, and they are located at depths of 550–700 m. The first study of the fauna of the Jan Mayen vent fields found very little vent-specialised fauna, which was hypothesised to be because of their shallow depth (Schander et al., 2010). In contrast to the Jan Mayen vent fields, the deeper Loki's Castle (2,300 m) has a rich and specialised fauna, and several new species to science have been described from this locality (Kongsrud and
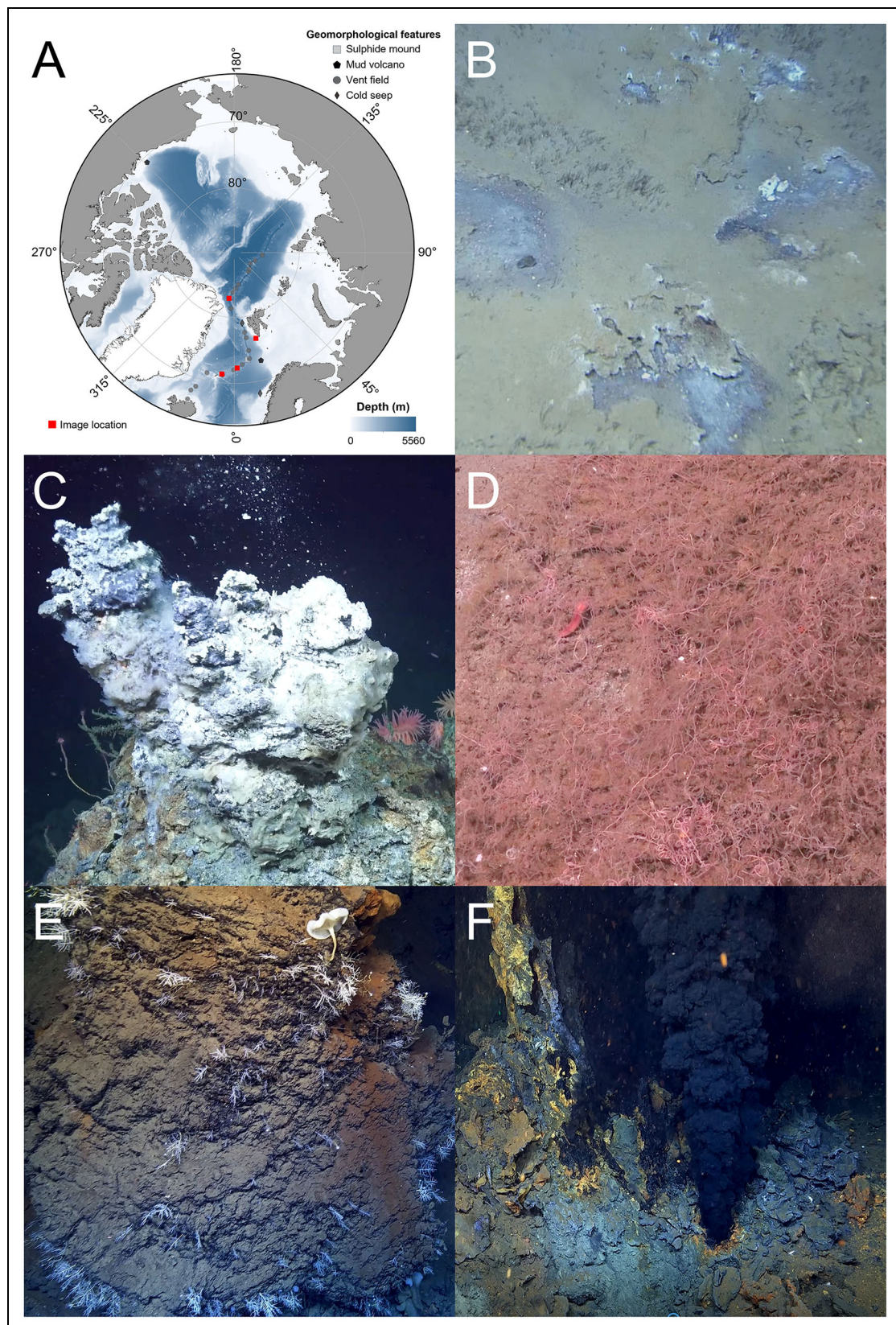
Figure 11. Representative fauna observed on hydrothermal and cold seep systems in the deep Arctic Ocean. (A) Locations of the representative images; (B) microbial mats with siboglinid worm fields at seeps west of Svalbard (Source: Pål Buhl-Mortensen, MAREANO, Institute of Marine Research); (C) microbially covered chimney with associated hydrozoans and actiniarians at Perle & Bruse vent field and (D) *Sclerolinum contortum* Smirnov, 2000 worm field at a diffuse venting region of Ægir vent field (Source: Mari Heggernes Eilertsen, Centre for Deep Sea Research, University of Bergen, Norway); and (E) Cladorhizidae-covered chimney and (F) Enceladus black smoker at the Aurora vent field (Source: Eva Ramirez-Llodra, HACON21 and REV Ocean).

Rapp, 2012; Tandberg et al., 2012; Kongsrud et al., 2017; Tandberg et al., 2018; Eilertsen et al., 2024). Loki's Castle is a sediment-influenced vent field, and the vent fluids show evidence of thermal degradation of organic matter (Baumberger et al., 2016). Two more vent fields have since been discovered on the deeper part of the Mohn Ridge: the Ægir vent field in 2015 and Fåvne vent field in 2018 (Stensland et al., 2019; Sahlström et al., 2023; **Figure 11D**), but the description of fauna of these vent fields has not yet been published. In 2001, hydrothermal venting on the Lucky B site (81°N) was inferred from massive sulphides in peridotites dredged at more than 4,000 m depth (Snow et al., 2001). In 2023, the presence of active black smokers was visually confirmed during an ROV dive, but its biological communities have not yet been studied. In the CAO, the active Aurora Vent Field was located in 2014 (Boetius, 2015), but it was not until 2021 that the first survey and sampling of deep hydrothermal vents under permanent ice cover was successfully conducted with the ROV *Aurora* (Ramirez-Llodra et al., 2022; **Figure 11E**, **F**). The Aurora Vent Field, at 82.5°N on the southern part of the Gakkel Ridge, is dominated by small rissoid and skeneid gastropods, a recently described species of limpet (*Cocculina aurora*; Chen et al., 2022) and melitid amphipods. The phylogenetic relationships of the species from the Aurora Vent Field with species from the Mohn and Knipovich ridges are currently being studied to assess if the CAO vent communities have evolved in isolation or in connectivity with fauna from adjacent basins (Ramirez-Llodra et al., 2022). Ongoing detailed investigations of the faunal community inhabiting the Jøtul hydrothermal vent field, discovered in 2022 at 77°N, will soon help shed light on this scientific question (Bohrmann et al., 2022).

3.4. Biogenic habitats
In general, all these geomorphological features can support biogenic habitats, where ecosystem-engineering fauna such as corals, sponges, crinoids and polychaetes create dense aggregations that provide habitat for a variety of other species (Wright and Jones, 2006) and form Marine Animal Forests (Rossi et al., 2017), often classified as Vulnerable Marine Ecosystems (Food and Agriculture Organization, 2009).

3.4.1. Cold–water corals
Cold-water coral reefs formed by *Desmophyllum pertusum* Linnaeus, 1758 are structurally complex three-dimensional habitats that enhance local biodiversity often comparably to shallow-water counterparts (Roberts et al., 2006). They are found along the Norwegian shelf and continental margin up to 71°N (Buhl-Mortensen, 2017; Burgos et al., 2020; Sundahl et al., 2020), but are generally restricted to water temperatures greater than 4°C, resulting in a general lack of observations further in the CAO basins.

Other hard-bottom cold coral gardens extend farther north than cold-water coral reefs, with occurrences up to 79°N (Tendal, 1992; Roberts et al., 2006; Sundahl et al., 2020; Løkkeborg et al., 2023). Yet, the characterising species (*Primnoa resedaeformis* [Gunnerus, 1763] and *Paragorgia arborea* [Linnaeus, 1758]) are largely associated with relatively warm water masses (e.g., modified Atlantic Water) and therefore do not extend deeper into the water column or northwards into cooler Arctic waters beyond Fram Strait (Buhl-Mortensen et al., 2015a; Sundahl et al., 2020).

Soft-bottom coral gardens are dense aggregations formed by *Isidella lofotensis* Sars, 1868 and *Radicipes gracilis* (Verrill, 1884) and typically occur on sandy mud (Buhl-Mortensen et al., 2015b; **Figure 7C**). These habitats have been documented in higher latitudes north of Spitsbergen at approximately 700 m depth (Burgos et al., 2020; Løkkeborg et al., 2023) and are associated with cooler and fresher water masses such as the Arctic Intermediate Water (Buhl-Mortensen et al., 2020). Low densities of unidentified Keratoisididae species similar to what was observed around Spitsbergen have also been documented along the AMOR at 800–1,000 m depths (Meyer et al., 2023). In the Canadian Arctic, high density bamboo coral gardens (*Keratoisis* sp.) are found at depths of 1,000 m, where they create habitat that increases local infaunal diversity and nutrients in the surrounding ecosystems (Pierrejean et al., 2020).

Cauliflower coral gardens comprised of true soft corals or 'cauliflower corals' (e.g., *Gersemia* von Marenzeller, 1878, *Duva* Koren & Danielssen, 1883, *Drifa* Danielssen, 1887, or *Pseudodrifa* Utinomi, 1961) can form on both hard and soft substrates (Long et al., 2020; **Figure 7F**), and may co-occur with other structure-forming fauna like sponges. Although these coral genera have a wide depth range from 10 m to 2,400 m (Wareham and Edinger, 2007; Neves et al., 2020; Meyer et al., 2023), they have been found in relatively high densities at various points from the Northwest of Iceland to the deep Arctic (Wareham, 2009; Buhl-Mortensen et al., 2019; Long et al., 2020; Brix et al., 2022; Korfhage et al., 2022; Stratmann et al., 2022; Meyer et al., 2023), with observed densities reaching up to 31.3 ind m^{-2} on the slopes of Schulz Bank and up to 9.4 ind m^{-2} on rocky substrates in Davis Strait. However, their distribution and occurrences are likely underrepresented as soft corals are commonly misidentified as *Gersemia*, due their challenging morphology and genetics (Gilkinson and Edinger, 2009; Korfhage et al., 2022), and have been associated with multiple water masses present in the Arctic (e.g., Atlantic Water, Arctic Intermediate Water, and Polar Water; Buhl-Mortensen et al., 2020). These communities have been shown to act as nursery and feeding grounds for many species (Neves et al., 2020), where juvenile basket stars (*Gorgonocephalus*) have been found attached to the soft corals. Commercially fished target species like Greenland halibut, grenadier, and shrimp are found in significantly higher abundance close to these soft corals (Edinger et al., 2009). Thus, these corals not only play an ecologically important role but are also of economic interest to fisheries and the exploited fishery stocks. The structures formed by cold-water corals in both reefs and gardens provide habitat for a myriad of other organisms, such as crustaceans, echinoderms, and fish (Roberts et al., 2006; Schwentner and Lörz, 2021; Eichsteller et al., 2022).

Sea-pen fields in the Arctic deep sea are characterised by the genera *Kophobelemnon* Asbjörnsen, 1856, *Umbellula* Gray, 1870, or *Virgularia* Lamarck, 1816 and occur on soft-sedimented regions on the continental slope and abyssal plains (Burgos et al., 2020; Ross et al., 2021; García-Cárdenas and López-González, 2023). *Umbellula* and *Virgularia* communities are typically associated with Norwegian Sea Deep Water (Buhl-Mortensen et al., 2020). While much of sea-pen field records in the Arctic are on the continental shelf of Norway and Canada, *Umbellula* communities have been documented on the AMOR and north of Spitsbergen (Morrison et al., 2020; Løkkeborg et al., 2023).

3.4.2. Arctic sponge grounds

Arctic sponge grounds are habitats on soft and hard bottom formed by large structure-forming sponges (*Schaudinnia rosea* [Fristedt, 1887], *Trichasterina borealis* Schulze, 1900, *Scyphidium septentrionale* Schulze, 1900, *Asconema foliatum* [Fristedt, 1887], *Geodia parva*, *G. hentscheli*, *Stelletta rhaphidiophora*, and *Lissodendoryx [Lissodendoryx] complicata* [Hansen, 1885]) from 150 m to more than 2,000 m depth (Klitgaard and Tendal, 2004; Murillo et al., 2018; Meyer et al., 2023). They typically inhabit specific water masses (e.g., cool, dense, fresh water masses like the Arctic Intermediate and Nordic Deep Waters) as well as areas characterised by high current velocities, such as on shelf-breaks, ridges (**Figure 9C**, **D**), seamounts (**Figure 10B**–**F**), and canyons (Klitgaard and Tendal, 2004; Roberts et al., 2018; Hanz et al., 2021; Roberts et al., 2021; Brix et al., 2022; Jørgensen et al., 2022).

Like most sponge grounds, these habitats are similar to cold-water coral reefs by acting as biodiversity hotspots, where associated fauna use sponge grounds as nursery or hatchery grounds, foraging areas, additional substratum, refuge and protection, and microhabitats (Klitgaard and Tendal, 2004; Meyer et al., 2019; Hanz et al., 2022; Morganti et al., 2022; Stratmann et al., 2022; Meyer et al., 2023). The sponges also provide additional substratum by forming dense spicule mats from dead sponges (up to 10 cm thick; Henrich et al., 1992; Klitgaard and Tendal, 2004; Morganti et al., 2022; Stratmann et al., 2022), and play an important role in the local food web throughout their entire life history (from healthy to decaying sponges; Hanz et al., 2022; Stratmann et al., 2022).

3.4.3. Crinoid fields

Crinoid fields are dense aggregations of crinoids that can form on deep Arctic soft-bottom habitats dominated by stalked crinoids *Bathycrinus carpenterii* or harder substrates dominated by *Heliometra glacialis* (Owen, 1833 ex Leach MS; **Figure 8B**, **C**) in the GIN Seas. The soft-bottom habitats are common in cool waters from 480 m to 3,800 m depth in the Arctic Ocean along seamount bases and abyssal plains (Bergmann et al., 2011; Rogacheva et al., 2013a; Rogacheva et al., 2013b). While they tend to host low biodiversity (Ramirez-Llodra et al., 2020; Meyer et al., 2023), they can have high densities (up to 129 ind m^{-2}) forming crinoid fields that can be classified as vulnerable marine ecosystems (Ramirez-Llodra et al., 2020). In contrast, densities of crinoids are low in the CAO (Zhulay et al., 2019).

Little is known about fauna associated with crinoid fields or the ecological role they may play, yet there have been observations of fauna using stalked crinoids in various ways. The eulimid gastropods are highly specialised parasites of echinoderms, and *Crinolamia dahli* Bouchet & Warén, 1979 from the abyssal Norwegian Sea was speculated as likely predating on *Bathycrinus carpenteri* (Bouchet & Warén, 1979). The amphipod *Amathillopsis spinigera* Heller, 1875 was found on stalked crinoids in the Chukchi Borderland, although the relationship is suspected to be commensal (Zhulay et al., 2021). Anemones and octocorals have also been observed using the stalks of crinoids to reach the currents above the seafloor to enhance feeding (Rogacheva et al., 2013a).

3.4.4. Worm forests

Worm forests formed by siboglinid polychaetes (frenulates and monoliferans such as *Sclerolinum contortum* Smirnov, 2000) are often abundant at cold seeps and hydrothermal vents in the Arctic (**Figure 11B**, **D**; Åström et al., 2020; Eilertsen et al., 2024). In some areas, like the Loki's Castle vent field on the Knipovich Ridge, maldanid polychaetes (e.g., *Nicomache (Loxochona) lokii* Kongsrud & Rapp, 2012) also contribute to the structure of the worm forests (Kongsrud and Rapp, 2012). Arctic worm forests have been shown to support a rich associated community of invertebrates (Eilertsen et al., 2024), and the chitin-based tubes of the siboglinids are hypothesised to promote establishment of new communities even after the worms themselves have died out (Morganti et al., 2022).

4. Biodiversity change in the Arctic Ocean

The deep Arctic Ocean fauna has not been constant since the ocean formed. Because a deep-water connection between the Pacific and Central Arctic oceans has been absent for 80–100 million years (Dunton, 1992) and only the shallow Bering Strait exists today, the single modern deep-water connection with adjacent basins is through Fram Strait to the North Atlantic. Today, taxa of Pacific biogeographic affinity hardly occur beyond the shelf break of the Pacific Arctic (Bilyard and Carey, 1979; Zhulay et al., 2019; Ravelo et al., 2020). Maggs et al. (2008) suggested that the existence of unglaciated refugia on the Pacific Arctic shelves allowed those shelf species to persist through glacial periods rather than going extinct or extending their bathymetric distributions down-slope while that was not the case on the Atlantic Arctic side.

To what extent the now ongoing borealisation of the Arctic related to increased inflow of Pacific Water through the Bering Strait (Woodgate, 2018) and Atlantic water through Fram Strait (Ingvaldsen et al., 2021) may change the composition of deep-sea benthos is unclear. While Atlantic and Pacific waters do carry (propagules of) boreal species from sub-Arctic seas into the Arctic Ocean (e.g., Ershova et al., 2019; Descôteaux et al., 2022) and species

distributions have already changed on Pacific and Atlantic Arctic shelves (Mueter and Litzow, 2008; Zakharov et al., 2020), there is little information, to our knowledge, on if or how deep-sea benthic diversity has been affected. There is some evidence, however, of shifts in distribution of deep-sea fishes over the past decades in the deep Greenland Sea (Emblemsvåg et al., 2022) as well as documented temporal variability (on the order of years to decades) in epibenthic community composition at HAUSGARTEN (Svavarsson et al., 1993; Bergmann et al., 2011; Meyer et al., 2013; Taylor et al., 2017; Taylor et al., 2018). First indirect evidence of changes in pelagic-benthic coupling (Bienhold et al., 2022; Zhulay et al., 2023) is likely related to the decline in sea-ice cover and thickness (Arctic Monitoring and Assessment Programme [AMAP], 2021; Landy et al., 2022), which has led to changes in primary productivity in surface waters (Lund-Hansen et al., 2020). Studies in the Chukchi Borderland (Zhulay et al., 2023) and on the Laptev Sea slope (Bienhold et al., 2022) appear to indicate different trends of decreasing and increasing coupling, respectively, though uncertainty is substantial. Potential consequences for benthic biodiversity itself seem more likely to be coming with the deep Atlantic water inflow than the shallow Pacific water inflow as the latter would require very adaptable (larvae of) deep-sea or eurybathic species from the Pacific to be crossing through the shallow Bering Strait into the Amerasian Basin. Sweetman et al. (2017) outlined in detail how deep-sea benthic ecosystems respond to stressors/threats. In their paper, they estimated for polar latitudes that warming will open up new habitats for invasive species or may support warming-induced extensions of the ranges of temperate–subpolar benthic species into polar oceans (Sweetman et al., 2017). Furthermore, bathyal depths (200–3,000 m) worldwide will undergo the most significant reductions in pH in all oceans, and O_2 concentrations will also decline. The greatest declines in pH are projected in the higher latitudes and the Arctic Ocean in particular (Kwiatkowski et al., 2020). How these major changes will affect deep-seafloor ecosystems is, in some cases, very poorly understood (Sweetman et al., 2017).

While the level of connectivity of the Greenland-Norwegian Sea with the CAO is likely gradual and high in the abyssal plain and soft-sediment fauna in general, the more patchy hard-bottom habitats perhaps have less of a continuous gradient in the fauna. The faunal inventory of the Loki's Castle vent field, for example, demonstrates that the fauna of hydrothermal vents of the AMOR is very distinct from the Mid-Atlantic Ridge (Eilertsen et al., 2024). At a higher taxonomic level, there are similarities between the fauna of Loki's Castle and the Aurora Vent Field in the CAO, but there are also taxa that are not shared between these vent fields (Chen et al., 2022; Eilertsen et al., 2024). More detailed studies of the Aurora Vent Field fauna and other vent fields in the Nordic Seas are needed to evaluate the degree of connectivity between vents on the Mohn and Knipovich ridges and the Gakkel Ridge before predictions about climate change effects are feasible.

5. Outlook

This study has shown that much progress has been made in exploring the deep Arctic Ocean, yet knowledge of deep-sea habitats and ecosystems remains limited. This limited knowledge is particularly true for the deep CAO, where ice cover constitutes an additional challenge to research, especially in habitats of complex topography such as submarine ridges. There are, however, heightened levels of interest in the Arctic region by Arctic and non-Arctic states, industry, and researchers alike (Hoel, 2020). These concerns are rooted in the accelerated environmental changes in the Arctic driven by climate change stressors (Arctic Marine Shipping Assessment, 2009; Polyakov et al., 2020; Bergmann et al., 2022). The retreat of sea ice makes the CAO more accessible to vessels (Berkman et al., 2022), thus opening for potential human use. For example, the joint effects of extended open-water areas enhancing both vessel access and primary production (Ardyna and Arrigo, 2020), as well as northward range extensions of various taxa (Snoeijs-Leijonmalm et al., 2022; Ingvaldsen et al., 2023), have ignited a debate on the potential for future fisheries in the CAO. Concerns about potential unregulated fishing occurring before solid ecosystem knowledge is in place have led to an international agreement preventing unregulated fishing (Vylegzhanin et al., 2020), calling for closing data gaps on potential fish stocks and availability of prey. In addition, Arctic and non-Arctic nations are currently investing in developing new ships and shipping routes for the CAO, and tourist vessels now visit the North Pole (Stevenson et al., 2019; Constable et al., 2022). Also, debated territorial claims in the CAO, linked to suspected hydrocarbon, mineral and marine genetic resources from the seafloor (Dodds, 2010; Rapp et al., 2015), require information on the region's biodiversity and ecosystem functioning and their response and resilience to natural and anthropogenic change.

Given the difficulty of accessing and studying the deep Arctic, and in particular the ice-covered CAO, ecosystem knowledge, particularly from deep-water ecosystems, and our ability to predict change are drastically lower than for Arctic shelf environments (Skjoldal, 2022). One of the fundamental conclusions of recent reports produced by the working groups of the Arctic Council (Gill et al., 2011; PAME, 2015; Conservation of Arctic Flora and Fauna, 2017; PAME, 2019; International Council for the Exploration of the Sea, 2021) is that the current state of knowledge on marine ecosystems and biodiversity in the Arctic remains fragmentary and often insufficient for effective science-based decision-making, in particular with regards to deep-sea ecosystems and biodiversity. This limited understanding of the deep Arctic Ocean is a critical bottleneck for the development of robust management and conservation measures in a rapidly changing region. Therefore, improving and expanding the knowledge base and monitoring the status and trends of Arctic biodiversity is listed as the first goal of the Arctic Marine Strategic Plan 2015–2025 (PAME, 2015). Research in the Arctic region should include biodiversity and environmental data. These data are essential to inform the implementation of the Kunming-Montreal Global Biodiversity Framework

adopted during COP15 (December 2022) that aims to halt and reverse biodiversity loss, contributing to the three objectives of the Convention on Biological Diversity and supporting the achievement of several UN Sustainable Development Goals (in particular, SDG13 and SDG14; https://sdgs.un.org/goals). Novel biological and ecological data at the regional scale will be essential towards the operationalisation of the agreement on Marine Biodiversity of Areas Beyond National Jurisdiction (or High Seas Agreement; March 2023) that will place 30% of the ocean into protected areas.

International collaboration is key to address some of the main challenges of conducting research in remote and challenging regions such as the Arctic Ocean. To this aim, the Challenger 150—A decade to study deep-sea life (www.challenger150.world) programme of the UN Decade of Ocean Science for Sustainable Development (Howell et al., 2020; Howell et al., 2021) includes an Arctic working group. This open, global group aims at providing a platform for collaboration, data sharing and enhancing synergies amongst researchers and regional stakeholders. The overall goal is to ensure that scientifically robust data are delivered to managers and decision-makers to support sustainable development in the region and contribute to the UN Sustainable Development Goals. International collaboration and openly shared data are essential to better understand and preserve the fragile ecosystems in the Arctic region. Despite its remoteness and difficult accessibility, the deep sea provides important global ecosystem functioning and services, including CO_2 exchange and sequestration, nutrient cycling, biomass relevant to fisheries, marine genetic resources, hydrocarbons and mineral resources, as well as cultural services, indigenous peoples rights and human well-being (Thurber et al., 2014; Amon et al., 2022). Understanding the ecosystem functions and services provided by the deep Arctic Ocean is thus essential to predict changes in such service provisions under a rapidly changing Arctic.

Data accessibility statement
The cleaned dataset and all the R scripts for biodiversity analyses used in this article are available by open access at https://zenodo.org/records/10391404. The data used in this study were mostly open-access and are accessible from OBIS (Table S1 including dataset IDs) and GBIF (https://doi.org/10.15468/dl.emhhsq).

Supplemental files
The supplemental files for this article can be found as follows:

Tables S1 and S2. Supplementary Materials 1.xlsx

Tables S3 and S4. Figure S5 and S6. Supplementary Materials 2. Docx

Competing interests
None of the authors that have contributed to this manuscript have any competing interests.

Author contributions
ERL, HKM, BAB, SB and HS initiated the idea of this review and have provided substantial contributions to gather data, structure the paper and ensure rigorous analyses and writing contributions from all co-authors. ERL and HKM share first authorship to reflect their equal contributions in leading this review. HS and HKM conducted the data gathering from co-authors and external sources, and

conducted the quality control of the final dataset, as well as the data analyses to produce maps and graphs. RVD collected the molecular data and conducted the analysis of BOLD data. Several co-authors contributed photographs for the figures. All co-authors contributed with the overall design of the review, data gathering, data interpretation, writing specific sections, and critically editing the final manuscript.

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