International megabenthic long-term monitoring of a changing arctic ecosystem: Baseline results

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ABSTRACT

The sustainable development and environmental protection of the Arctic ecosystem is on the agenda globally. The Convention of Biological Diversity (CBD) and the UN Sustainable Development Goals call for conserving at least 10 per cent of coastal and marine areas globally. Management tools to achieve this goal include marine protected areas (MPAs) and "other effective area-based conservation measures" (OECMs) of structural mega-benthic organisms (e.g. corals, sea pens, sponges, anemones, etc.). But large areas of the ocean are lacking information about seabed communities. Here we show that this data gap can potentially be filled by collecting data on megabenthic organisms that are "bycatch" (not the target species) on government research vessels monitoring commercial fish and shellfish. For this paper, several Arctic and sub-arctic nations contributed megabenthos data from a total of 12.569 fish assessment trawls and associated bottom water temperature data. The latter outline areas of warm sub-Arctic inflow versus colder Arctic waters, which we align with temperature affinities of community. We also found that maximum levels of shared taxa were higher between Atlantic and Eurasian Arctic Seas than with Pacific Arctic Seas. Areas of high standardized species richness generally, but not everywhere, coincided with areas of high standardized biomass and/or high current velocity and in transition zones between water masses. We did not find that standardized taxon richness declined with latitude (from 60 to 81°N) as has been previously hypothesized. High biomass was generally associated with Arctic outflow shelves and/ or (within-region) colder water masses. We identify areas with high proportions of sessile and upright taxa that may be susceptible to damage by bottom trawl gear, taxa with calcareous skeletons that may be susceptible to ocean acidification, and 'cold-water' taxa that may be most vulnerable to ocean warming. Our results demonstrate the feasibility and value of international collaboration and cooperation in understanding large-scale patterns of Arctic megabenthic communities and providing scientific advice for management of human activities in the global Arctic ecosystem.

1. Introduction

The sustainable development and environmental protection of the

Arctic ecosystem is on the agenda globally (IPBES 2019; IPCC 2019). Rapid detection of, communication about, and response to significant trends in anthropogenic and climate pressures is crucial, as these

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pressures affect Arctic productivity and biodiversity (CAFF 2017). These concerns are also echoed in the "Ecosystem Approach to management" (EA) which is a "Comprehensive, integrated management of human activities based on best available scientific and traditional knowledge about the ecosystem and its dynamics" (Arctic Council 2013). The sustainable use of the ecosystem while maintaining its integrity involves "knowledge about the ecosystem and its functions" (see also CBD Aichi Biodiversity Target 11 https://www.cbd.int/sp/targets/), and should address both fisheries management and marine biodiversity conservation in an integrated manner (Cochrane et al. 2009).

Arctic marine benthic ecosystems are highly productive and species rich (Grebmeier et al., 2006; Degen et al., 2018). Understanding and conserving seafloor habitats is important for EA in the Arctic because habitats provides structural relief on an otherwise featureless bottom. These can be particularly important to fish for food, reproduction, and shelter from predators. Structural habitat includes boulders, corals, anemones, kelp, and other living organisms attached to the ocean bottom. Such areas are also called Vulnerable Marine Areas (VMEs).

Because fishing gear has the potential to disturb structural habitat, regulations have been implemented to protect areas where critical seabed habitat type is known to occur. Marine protected areas (MPAs) and "other effective area-based conservation measures" (OECMs) are protected areas of the sea. The Convention of Biological Diversity (CBD) Aichi Biodiversity Target 11 and the UN Sustainable Development Goal 14.5 called for, by 2020, to have conserved at least 10 per cent of coastal and marine areas, consistent with national and international law and based on the best available scientific information and several countries have ratified this convention.

There is also a growing awareness of the commercial importance of the non-governmental Marine Stewardship Council (MSC) (msc.org) certifications (Marine Stewardship Council, 2018) that ensures the seafood to come from a sustainable fishery that has met the MSC Fisheries Standard. Such seafood brings a premium price in the marketplace yet requires documentation and mitigation of the potential impact on seafloor habitat and its associated biological communities. Organizations such as the MSC encourage nations to provide evidence of responsible use of the resource. For a fishery to be certified as sustainable by the MSC, documentation of responsible use of the commercial stock is required, as well as measures to limit the impact of fishing on seafloor habitats. This requirement has resulted in increased scientific efforts to monitoring the seafloor habitats.

Implementing long-term monitoring of seafloor habitats is logistically demanding and costly. Almost all Arctic coastal states have regular assessment programs used to collect national data on commercial species, mostly fish and shellfish, in parts of the Arctic. In addition to their main objective of obtaining information about the abundance and distribution of commercial species, these scientific surveys can also provide information on other ecosystem components, such as megabenthic epifaunal invertebrates, on a regular basis (Eriksen et al., 2018). Norway and Russia established a joint ecosystem survey in the Barents Sea that has been ongoing for over a decade and have established benthic bycatch monitoring from the bottom trawl surveys (Jørgensen et al., 2019; Zakharov et al., 2020). Canada has similarly conducted ecosystem surveys in the Northern Labrador Sea and in the Eastern Canadian Arctic for two decades (Nozères et al., 2019; Lacasse et al., 2020). The United States of America (USA) has recorded benthic invertebrate bycatch during the Bering Sea (eastern and northern) fish assessment surveys for decades (Conners et al., 2002), and have in recent years added occasional surveys in the northern Bering, Chukchi and western Beaufort seas where benthic bycatch data are systematically included (Sigler et al., 2017, Lauth et al., 2019). Iceland and Greenland have followed suit and established benthic bycatch monitoring from fisheries surveys (Ólafsdóttir and Gudmundsson, 2019, Blicher et al., 2017). In addition, ongoing surveys in Arctic and sub-Arctic seas focusing on other objectives such as monitoring climate change-related processes have comparable monitoring programs (Zalota et al., 2018; Grebmeier et al.,

2018; Iken et al., 2019).

Benthic monitoring data have demonstrated utility in designing protected marine areas by Arctic nations (see chap 2.1) and while regional management decisions are initiated at the national level, there is increasing awareness among scientists and managers that the Arctic ecosystem operates at a global-scale with tight links to sub-Arctic forcing (Wassmann et al., 2020). Increasingly, Pan-Arctic perspectives illustrate the connectivity of the system and the urgency for joint action (Carmack and Wassmann, 2006; CAFF 2017; Bluhm et al., 2020; Wassmann et al., 2020), and combining multiple surveys has improved the management and conservation of transboundary and migrating marine demersal species (Maureaud et al., 2020).

In this study, we incorporate multiple data sets from national and regional benthos monitoring programs from across the Arctic offshore areas to view the marine ecosystem in an integrated matter. We present the first Pan-Arctic synthesis that establishes a baseline for the long-term monitoring of megabenthic invertebrate fauna using several metrics, such as biomass, abundance, functional traits, and temperature tolerance. Establishing a baseline of these metrics will assist in monitoring temporal changes on a Pan-Arctic scale as both climate, and human activities alter benthic ecosystems. We acknowledge the diverse methods in data collection and analyses used by individual monitoring programs and therefore used standardization strategies per national area and a taxonomic approach combined with a traits-based approach as tools to build upon for future long-term monitoring. Specifically, we map these baseline data to identify areas of relatively high biomass, abundance, or biodiversity. In addition, we show areas where benthic species/communities have greater or lesser tolerance to temperature change, areas where communities have traits vulnerable to sea bottom disturbance, and areas where species have traits that can make them vulnerable to bottom disturbance on a Pan-Arctic scale. Finally, we discuss our findings in the context of Arctic oceanography and biogeography and suggest how our results may integrate with management applications in the future.
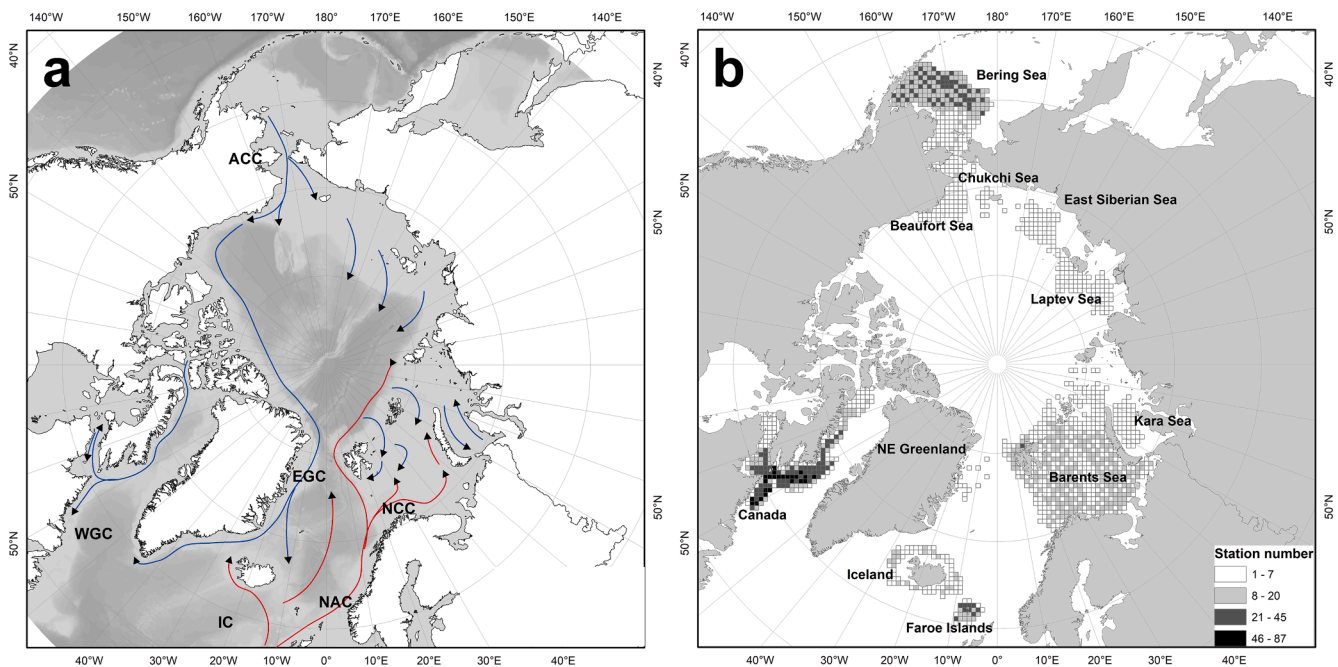
2. Materials and methods

2.1. Study area: hydrography

For the USA (Beaufort, Chukchi, and Bering Seas), Norwegian waters (Barents Sea), and Russia (Barents Sea, Kara-Laptev-East Siberian Seas), sampling stations were located mostly over the continental shelves surrounding the Central Arctic Ocean, while in the Atlantic Ocean the Eastern Canadian Arctic (Northern Labrador Sea, Western Baffin Bay, Davis and Hudson Straits, herein referred to as Labrador-Baffin), Greenland (Northeast Greenland herein referred to as NE Greenland), Iceland and the Faroe Iceland stations were also partly along continental slopes, above 200 m depth (Fig. 1a, b).

On the Pacific side, the dominant sub-arctic Southeastern Bering Sea shelf waters include the nutrient rich Bering Slope-Anadyr water, the Bering Shelf Water and the comparatively fresh Alaska Coastal Water (Coachman, 1986). In contrast to the essentially ice-free waters of Iceland and the Faroe Islands, the Bering Sea is seasonally ice-covered, though ice cover can have large inter-annual variation (Frey et al., 2014).

The Arctic inflow shelves (c.f. Carmack and Wassmann, 2006) are dominated by the inflowing sub-Arctic waters from the warm and saline Atlantic Ocean in the case of the deep Barents Sea shelf (Loeng, 1991) and eastern Baffin Bay (Tang et al., 2004), and the fresher Pacific Ocean in case of the shallow Chukchi Sea shelf (Pisareva et al., 2015; Stabeno et al., 2018).

In eastern Baffin Bay, waters originating from the Irminger and East Greenland Currents flow north through Davis Strait along the eastern side of Baffin Bay as the West Greenland Current (Fig. 1a) (Tang et al., 2004). The broad and generally shallow Siberian interior shelves (Kara, Laptev and East-Siberian Seas) and the narrower North American

Fig. 1. a-b. Pan-Arctic map labeling predominant ocean currents (a), the regional data included in the analyses and the total number of stations used in the analyses (b). In (a) the acronyms are defined as WGC (West Greenland Current), IC (Islandic Current), NAC (North Atlantic Current), EGC (East Greenland Current), NCC (Norwegian Coastal Current), ACC (Alaska Coastal Current).

interior shelf (the Beaufort Sea) are strongly shaped by large amounts of river run-off that add fluvial sediments and terrestrial organic matter to the seafloor over large parts of these shelves (Jerosch, 2013; Lantuit et al., 2012).

The Eastern Canadian Arctic, western Baffin Bay, and east Greenland shelves receive large amounts of cooled Arctic waters, mixed with glacial run-off and high ice cover, yet contain large and seasonally productive polynyas, yielding overall rather variable production

regimes (Michel et al., 2015). These subzero waters from the Arctic Ocean exit towards the sub-Arctic, carrying a substantial amount of melting sea ice. One of these exits is via the East Greenland Current (Michel et al., 2015). Along the East Greenland slope, it mixes with the returning warmer Atlantic Current (Håvik et al., 2017). In the Canadian Arctic, waters come through Nares Strait, Jones and Lancaster Sounds, and exits through Davis Strait. The area consists of a network of islands with water flow through many constrictions, via the Baffin Bay's

Table 1

The table below summarizes the survey gear and sampling effort for each region. Detailed survey descriptions are found in the Supplement.

Nation or Survey	Region	Gear Type	Depth Range (m)	Codend Mesh SizeEstimate (mm)	Year Range	No of Stations	Total Samples	Responsible
USA	Bering Sea (Eastern)	83–112 Eastern otter trawl	50–200	38	1975-present	376	2,313	E. Logerwell
USA	Bering Sea (Northern)	83–112 Eastern otter trawl	50–200	38	2010, 2017	144	177	E. Logerwell
USA	Chukchi Sea	83–112 Eastern otter trawl	50–200	38	2012	71	71	E. Logerwell
USA	Chukchi Sea (Barrow Canyon)	83–112 Eastern otter trawl	50–200	38	2013	31	31	E. Logerwell
USA	Beaufort Sea	83–112 Eastern otter trawl	50–400	38	2008	26	26	E. Logerwell
Canada	W. Baffin Bay-Davis Strait	Alfredo trawl	400–1500	30	2004–2017	1130	12,802	V. Roy (S. Atchison)
Canada	Hudson Strait-Davis Strait-Labrador Sea	Campelen/Cosmos trawls	100–1000	12.7 / 20.0	2005–2017	5085	25,624	V. Roy (S. Atchison)
Iceland	Iceland waters	Golden top research trawl	200–1200	40	2016–2018	374	374	S. Olafsdottir
Norway	Western Barents Sea	Campelen 1800	50–200	24	2007-present	~30–245	1,164	L. Jørgensen
Russia	Eastern Barents Sea	Campelen 1800	50–200	24	2005-present	~0–251	1,117	D. Zakharov
Russia	Kara Sea	Bottom trawl 2387.02.155	50–200	135	2012	93	93	O. Zimina
Russia	Laptev Sea	Bottom trawl 2387.02.155	50–200	135	2014, 2017	101	101	O. Zimina
Russia	East-Siberian sea	Bottom trawl 2387.02.155	50–200	135	2017	62	62	O. Zimina
TUNU VII	NE Greenland	Campelen 1800	200+	40	2015, 2017	18	18	J. S. Christiansen, B. A Bluhm

western basin's narrow shelf and abrupt slope, as well as Northeast Greenland's fjords with adjacent heterogeneous shelf comprising banks and troughs.

Water masses around Iceland differ markedly between regions with warm and saline waters of the North Atlantic Current (NAC) in the south, and the Arctic and Polar waters in the north (Fig. 1a) (Astthorsson et al., 2007, Våge et al., 2015). Similarly, The Faroe shelf and upper slope is mainly influenced by warm Atlantic water coming from the south while on the northern and eastern sides of the Faroes an admixture of cooler East Icelandic water prevails (Hansen and Østerhus, 2000).

2.2. Study area: benthic data

Regional/National seabed depth ranges, gear-types, mesh sizes, and date range for data used in this study are given in Table 1.

2.2.1. Beaufort, Chukchi, and Bering Seas

The megabenthic communities of the Bering Sea, Chukchi Sea and Beaufort Sea were sampled during groundfish assessment and ecosystem surveys conducted by National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service, Alaska Fisheries Science Center (AFSC). Surveys were conducted onboard chartered fishing vessels. While the Southeast Bering Sea has been surveyed annually for megabenthos since 1975, the other areas were covered less often and since the 2000s. The 83–112 Eastern bottom trawl was used for sampling in all years, with noted changes in methodology since 1975 (e.g., added net mensurations, gear modifications, etc.) (Table 1). Bottom water temperatures were collected using a Sea-Bird bathythermograph continuous data recorder attached to the headrope of the net. Catch was enumerated, weighed, and identified to the lowest taxonomic level feasible on board or from voucher specimens and photographs after the surveys, on land. The data are stored at NOAA, Seattle, USA.

2.2.2. Barents Sea

The megabenthic communities of the Barents Sea were sampled during ecosystem surveys conducted by the Institute of Marine Research (IMR) in Norway and the Russian Federal Research Institute for Fisheries and Oceanography (VNIRO) in Russia (Jørgensen et al., 2019; Zakharov et al., 2020). From 2003, the ecosystem survey has been conducted from August to October annually, and covers the ice-free part of the Barents Sea and the Svalbard shelf. Five vessels normally operate in the region: three Norwegian and two Russian. The trawl gear was used in a standardized way by both Norway and Russia in time and space (Table 1). Bottom-water temperatures were measured at all stations each year from vertical casts made with a Sea-Bird CTD. The benthic megafauna was identified to the lowest possible taxonomic level by specialists (on the vessel or on land), counted, and the wet weight measured. Data is stored at IMR, Tromsø, Norway and VNIRO, Murmansk, Russia.

2.2.3. East-Siberian, Laptev, and Kara Seas

The megabenthic communities of the Kara, Laptev and East-Siberian seas were studied during surveys conducted by the Murmansk Marine Biological Institute (MMBI) in 2012 (Kara Sea), 2014 and 2016 (Laptev Sea) and 2017 (East-Siberian Sea) (Table 1). All surveys were conducted on the RV Dalnie Zelentsy of MMBI with a standardized use of trawl equipment (Table 1). Near-bottom water temperatures were taken at most stations with a Sea-Bird CTD. The benthic megafauna was identified to the lowest possible taxonomic level by specialists, counted and weighed onboard. Data is stored at MMBI, Murmansk, Russia.

2.2.4. Western Baffin Bay, Davis Strait, Hudson Strait, Northern Labrador Sea (Labrador-Baffin)

The megabenthic communities of Western Baffin Bay and Davis Strait were sampled during Greenland halibut bottom trawl surveys conducted by the Department of Fisheries and Oceans' (DFO) Central and Arctic Region in NAFO Divisions 0A and 0B (Nozères et al., 2019).

The survey vessel was the RV Pâmiut, a stern trawler owned by the Greenland Institute of Natural Resources. The Alfredo III bottom otter trawl was used each year (Table 1), and temperature data were collected from a Sea-Bird CTD data logger on the trawl. The catch was sorted, weighed and identified in a standardized manner since 2004. In addition, two trawls (Cosmos and Campelen, Table 1) were used to conduct a shrimp survey (Northern and Striped shrimps) since 2005 in Hudson Strait and Northern Labrador Sea in a joint industry-government effort between Northern Shrimp Research Foundation and DFO. Abundance data from all stock surveys are partial (Greenland halibut and shrimp surveys) and were therefore removed because colonial species like sponges were not counted. Bycatch data at the species level have been less well-documented until recently on shrimp surveys (Lacasse et al., 2020), therefore the species data were not used for the temperature sensitivity analysis. Data are stored at DFO's Freshwater Institute (Winnipeg, MB, Canada).

2.2.5. Northeast Greenland

Megabenthic invertebrates were sampled as part of the ongoing international research program TUNU (a program which has sampled fish about every other year since 2002) in August 2015 and September 2017 on board the Arctic University of Norway's RV Helmer Hanssen, a former commercial trawler. The gear used was a Campelen 1800 shrimp trawl, as used in the Barents Sea surveys (Table 1). Temperature was measured with a Sea-Bird CTD at each station. Individuals were sorted from the total or split catch, field-identified, enumerated (both years) and weighed (2017 hauls only). The data are stored at UiT - the Arctic University of Norway, Tromsø, Norway.

2.2.6. Iceland

Megabenthic invertebrates were collected between 2015 and 2018 during the Icelandic Autumn Groundfish Survey (AGS) on board the RV Árni Friðriksson. The AGS survey has been conducted annually in October since 1996 by the Marine and Freshwater Research Institute (MFRI). Benthic invertebrates were sampled from the slope in a standardised way (Table 1). Bottom temperatures were measured with a Scanmar thermometer or similar instrument attached to the trawl. The benthic fauna was identified to the lowest possible taxonomic level on the vessel and specimens were counted and weighed. The data are stored in a benthic database at MFRI.

2.2.7. Faroe Islands

Yearly groundfish surveys have been conducted on the Faroe Plateau since 1983. Over time gear and vessels have changed, but from 1996 the surveys have been conducted by the Faroese RV Magnus Heinason, and gear and methods have been unchanged since then. The yearly groundfish surveys mainly target fish species (cod, haddock and saithe) and are split into a spring survey and an August survey. The gear used was a 112 feet "box" trawl with 40 mm mesh size. Thus far, marine megabenthos has not been measured; however, we document this survey as a potential for future collaborations and data inclusions to Pan-Arctic analyses.

2.3. Data analysis on a pan-arctic scale

A Pan-Arctic map grid of uniform cell size was created in the North-Pole Lambert Azimuthal Equal Area projection, with each grid cell measuring 50 km × 50 km. All sampling locations were allocated to their corresponding grid cell. It is acknowledged that the assignment of each region's survey data to a grid cell does not differentiate those surveys of random (i.e., sample locations randomly allocated) or systematic (e.g., fixed survey sites) or other designs. Also, a grid cell may contain steep depth gradients, such as a cell that may include a portion of the shelf and the slope.

2.3.1. Trawl depth and bottom temperature

In each grid cell, the averages and standard deviations (SD) of bottom depth and bottom temperature were calculated from data obtained from each region's respective trawl surveys. In some regional datasets, values were based on averages of annual sampling at the same location (s) over decades, while other regional datasets were calculated from individual values from single sampling events. Both metrics were mapped on the 50 km × 50 km grid.

2.3.2. Taxa selectivity

As the specimens encountered on the trawl surveys comprised mostly, in terms of catch abundance and biomass, epibenthic (near-surface) species, some effort was made to exclude records of pelagic or endobenthic (buried) taxa. Certain taxa encountered in catches for all data sets used in this study were removed for all subsequent analyses. For example, large pelagic jellies (e. g., Class Scyphozoa) may have been collected, either whole or in fragments, but were not recorded in catch databases. For the whole Barents Sea region, and in Canadian waters where the shrimp survey occurs, the bottom trawl gear that was used is designed to sample shrimp (*Pandalus borealis*, *Pandalus montagui*), hence these species overwhelmingly dominated the catch biomass, and therefore these records were excluded from the data analyses, which may exclude these species from hauls or entire surveys (e.g., Canadian "shrimp surveys").

2.3.3. Megabenthic distribution patterns and the environmental parameters

This study aggregated megabenthos data from all nations' regional levels into a single Pan-Arctic dataset for a spatial illustration of standardized average number of taxa, average biomass (gram wet weight unit area) and average abundance (numbers of individuals per unit area) per trawl haul. Hauls, surveys or taxa (e.g., colonial) that are not enumerated are not included in the abundance analyses. Each taxon name from each region was standardized across all nations/regions using the online Taxon Match tool from the World Register of Marine Species (WoRMS; http://www.marinespecies.org/). Despite standardization to the lowest level possible and decade-long international collaborations and exchange of taxonomic expertise, some level of bias inevitably remains due to different taxonomic resolution and taxonomic expertise within and among regions. Each abundance and biomass estimate was cube-root transformed to reduce the right-sided skewness commonly associated with biomass estimates. Estimates of the total number of taxa, biomass, and abundance were standardized within each region where data were centered by subtracting the average and scaled by standard deviation. The average and standard deviations for each metric were mapped using the 50 km × 50 km grid cell. Although estimates were standardized by area, comparisons between regional estimates lack the possibility for direct comparisons due to varying gear types and associated catchability of those gear types. As noted above, the standardized average abundance estimates for Canada were not used because captures were not always counted, for example colonial species like sponges.

2.3.4. Megabenthic functional traits

Three biological traits were selected: Body Form (BF), Adult Movement (MV), and Skeleton (SK). Within each of the three traits, 3 – 5 categories (also referred to as modalities in the literature, Degen et al., 2018; Sutton et al., 2020) were assigned to each taxon (Table 2, Supplemental material). These traits were chosen as indicators of functions that can respond to both anthropogenic and climatic pressures. For all taxa, traits were associated with the benthic adult organisms and not the meroplanktonic stages.

In cases where species identification was not possible, a taxon was assigned to the next lowest taxonomic level possible such as genus or family. Trait information was first obtained from Degen and Faulwetter (2019) where available and was further expanded on in subsequent workshops where invertebrate expertise, an extensive literature search,

Table 2

Biological traits (e.g. Adult Movement) selected for analyses; each trait has 4–5 respective categories (e.g. Sessile/none) and their accompanying descriptions. A category(s) within all three traits was assigned to each taxon using fuzzy coding where a taxon could be assigned to one or more categories (Table 3). This table is as cited in Degen and Faulwetter (2019).

Adult Movement	Category	Description of category
MV1	Sessile/none	No movement as adult (sponge, coral)
MV2	Burrower	Movement in the sediment (e.g. annelids, echinoderms, crustaceans, bivalves); including tube dwellers
MV3	Crawler	An organism that moves along on the substratum via movements of its legs, appendages or muscles (e.g. crab, snail)
MV4	Swimmer (facultative)	Movement above the sediment (e.g. Amphipoda)
Body Form	*Category*	*Description of category*
BF1	Globulose	Round or oval (e.g. sea urchin, sponge, some bivalves)
BF2	Vermiform, elongate	Worm-like or thin, elongate body form
BF3	Dorso-ventral compressed	Species that are flat or encrusting (e.g. starfish, sponge)
BF4	Laterally compressed	Thin (e.g. isopods, amphipods, some bivalves)
BF5	Upright	(E.g. coral, basket star, sponge)
Skeleton	*Category*	*Description of category*
SK1	Calcareous	Skeleton material aragonite or calcite, e.g. bivalves
SK2	Siliceous	Skeleton material silicate, e.g. siliceous sponges
SK3	Chitinous	Skeleton material chitin, e.g. arthropods
SK4	Cuticle	No skeleton but a protective structure like a cuticle, e.g. sea-squirts
SK5	No skeleton	No form of protective structure, e.g. sea slugs

and the Polytrait database (Faulwetter et al., 2014) were used to delineate each taxon into categories within each of the three traits. Fuzzy coding was used to assign a value of affinity (from none to high) to each taxon for a particular trait category (Chevenet et al., 1994) (Table 3). Specifically, this accounted for plasticity in the sense that a given taxon may exhibit multiple trait categories, for example both 'burrower' and 'crawler'.

To perform a trait analysis, each taxon and their respective fuzzy coded trait categories were weighted by biomass of each taxon within each regional dataset using catch-per-unit-effort (CPUE), which was calculated for each region's survey. This combines two matrices - one with each taxon and its respective trait category codes, and the other of each taxon and their respective CPUE value aggregated to each region's lowest sampling level of either haul or station. Multiplying these two tables produces a third matrix that is a haul/station (rows) by traits (columns) weighted by CPUE (Bremner et al., 2006; Degen et al., 2018). This analysis distils ~2000 taxonomic identifications down to basic functions of those taxa, specifically the three chosen traits with a total of 14 categories. The third matrix was calculated separately for each region yet using the same trait codes. Further, the percentage of each trait category was calculated relative to each region to make comparisons at a Pan-Arctic scale. Both averages per region were estimated, as well as

Table 3

Fuzzy code descriptions where each taxon were assigned a fuzzy code within a trait category (see Table 2). As cited in Degen and Faultwetter (2019).

Fuzzy code	Fuzzy code descriptions
3	Taxon has total and exclusive affinity for a certain trait category.
2	Taxon has a high affinity for a certain trait category, but other categories can occur with equal (2) or lower (1) affinity.
1	Taxon has a low affinity for a certain trait category.
0	Taxon has no affinity for a certain trait category.

percent of categories per grid cell.

To examine those functional trait categories that may be susceptible to bottom disturbance, we selected two categories within two traits: Adult Movement – 'sessile', and Body Form – 'upright' (Foveau et al., 2017, Jørgensen et al., 2019). Organisms that are 'sessile' are often attached to a particular substrate and those that are 'upright' likely feed on particles in the water column. With this combination of trait categories, immobile and upright organisms may be more vulnerable to bottom disturbance (i.e., bottom trawl fishing gear), than 'flat' and highly 'mobile' organisms which may pass under a net or move away from a disturbance. We combine these two categories for a single percent metric, where 100% would indicate 100% of the trait categories at that station were sessile and upright.

2.3.5. Megabenthic temperature preference

The underlying hypothesis for the temperature preference analysis was that species presently occurring at low temperatures and over a narrow temperature range will be most vulnerable to rapid ocean warming. Conversely, species presently occurring at relatively high temperatures and over a broad range will be least vulnerable. A key assumption is that there will be little or no physiological or genetic adaptation to increased temperature. Another key assumption is that observed climate envelopes reflect temperature preferences rather than, for instance, competition, predation, food availability, etc.

The temperature preference of a taxon was defined as the median temperature at all stations where that taxon occurred in our data set. The temperature range of a taxon was defined by the 10th and 90th percentiles of temperatures at all stations where it occurred. Temperature median and range were calculated by combining regional datasets based on geographically contiguous regions: Bering, Chukchi, and Beaufort Seas; West Baffin Bay, Davis and Hudson Straits, Northern Labrador Sea; NE Greenland, and Iceland; Barents Sea; Kara, Laptev and East Siberian Seas. We chose this approach because the spatial scale at which we expect megabenthos to shift their range in response to temperature changes is on the order of within ocean shelves and basins (e.g. from the Bering Sea to the Chukchi Sea), larger than many of the individual survey areas. We did not conduct the analysis at a Pan-Arctic scale because we did not expect taxa to shift their distributions from one shelf or basin area to the next (e.g. from the Chukchi Sea to Baffin Bay).

The distribution of median temperature and range for all observations was skewed, especially for temperature range. This is largely because taxa that were only observed once had a temperature range of 0. Limiting the data to taxa that were observed more than once reduced the skew somewhat and limiting the data to taxa that were observed more than 10 times resulted in fairly normal distributions. Further analyses were therefore conducted on this latter subset of data.

K-means clustering was used to group taxa by median temperature and range separately for each region. K-means clustering is a method of vector quantization that partitions n observations into k clusters in which each observation belongs to the cluster with the nearest mean (Bock, 2008). K-means minimizes the within-cluster variances (i. e. the squared Euclidean distances). The number of clusters (k) or groups was chosen as a balance between the number of groups and the variance within groups. Bigger k results in a lower variance to the extreme case of k = n which results in variance of 0. The final k was selected by plotting the variance (sum of squares) within groups by the number of groups and observing the 'elbow', or the inflection point where the rate of decrease in variance changes from steep to shallow.

The k-means cluster in each region that had the coldest median temperature, and a relatively narrow range was designated as 'cold-water taxa'. The cluster that had the warmest median temperature and a relatively broad range (and thus potentially greater ability to adapt to future warming) was designated as 'warm-water taxa'. The catch of taxa in each of these clusters was converted to % of total catch at each station and mapped. The taxonomic composition of the 'cold-water' and 'warm-water' cluster is presented for each analysis region. The taxonomic composition of all clusters is presented for each analysis region in the Supplement.

3. Results

The average number of regional trawl stations used in this analysis included multiple years, seasons, and various sampling methods, across the study area, as described above (Fig. 1b). In general, sampling was spatially diffuse with relatively low sample numbers varying from 1 to 6 trawl stations per grid cell in the Laptev, and Kara Seas, Iceland, NE Greenland, and northwest Baffin Bay and Hudson Strait. Intermediate (7–51) sampling density occurred on the shelves of the Barents and Bering Seas, while intense sampling (>52 stations) occurred along the slopes in the west Davis Strait and Northern Labrador Sea (Fig. 1b).

3.1. The Arctic seabed environment (depth and temperature)

Our study area comprised a combination of comparatively deep shelves (e.g., >200 m), including upper slope areas in the Atlantic sector, and shallow shelves (e.g., <100 m) of the Pacific sector and interior shelves. The shallowest areas were located in the East-Siberian, Laptev, and inner Kara Seas, and Bering, Chukchi, western Beaufort Seas (Fig. 2a). The standard deviation (SD) of average bottom depth within a grid cell showed the highest values when the areas was associated with steep inclines, notably in western Baffin Bay and Davis Strait, while the shallower areas were associated with flatter shelves (Fig. 2b). The deepest areas in our study were located outside the Baffin Island (western Baffin Bay and Davis Strait), the waters surrounding Iceland, the northwestern portion of the Barents Sea, and a few sites on the NE Greenland shelf and slope (Fig. 2a).

The distribution of average bottom temperature (C°) showed that waters below 0 °C were recorded on the outer shelves in the East-Siberian, Laptev and Kara Seas, and in the eastern Barents Sea. Average bottom temperatures below 0 °C were also found north of Iceland, the narrow and relatively shallow shelf of western Baffin Bay, the Hudson Strait and at the northern end of Labrador because of the cold Labrador Current coming from the north (Fig. 3a). Sub-zero temperatures were also recorded in the offshore Beaufort Sea and the Bering Sea 'cold pool', which is generated locally and not from a current input (Fig. 3a).

Average bottom temperatures above 7 °C were recorded along the path of the North Atlantic drift of the Gulf Stream arriving south of Iceland and mixed into the coastal Norwegian current finally entering the Barents Sea along the coast (Fig. 1a; Fig. 3a). In the Bering and Chukchi Seas, the Alaska Coastal Current maintains the Alaskan west coast comparatively warm. The highest SD values are in the Bering Sea and may reflect interannual fluctuations, e.g., related to the extent of the 'cold pool' and the effects of the Alaskan Coastal Current, where shallower water is subject to greater temperature fluctuations (Fig. 3b).

3.2. Megabenthic distribution patterns

The similarity in the number of taxa between any two given areas is illustrated in Fig. 4; the thickness of the link indicates the value of the Simpson's Index of Similarity (Simpson, 1943), used here because it's low sensitivity to differences in species richness among areas. This depiction acknowledges a bias based on unequal sampling effort, gear selectivity, station depth, and identification efforts, yet it indicates some coarse patterns of taxa connectivity. First, adjacent areas generally showed high levels of common taxa, for example between Iceland and the Barents Sea, between the Laptev, and Kara seas, and between the Bering, and Chukchi Seas. Exceptions included the low levels of common taxa between the Chukchi and Beaufort Seas with the East Siberian Sea, where there is a documented biogeographic boundary (Dunton, 1992; Mironov and Dilman, 2010), and the Beaufort Sea and the Labrador-Baffin region (Canada in Fig. 4), where this may be an artefact of our
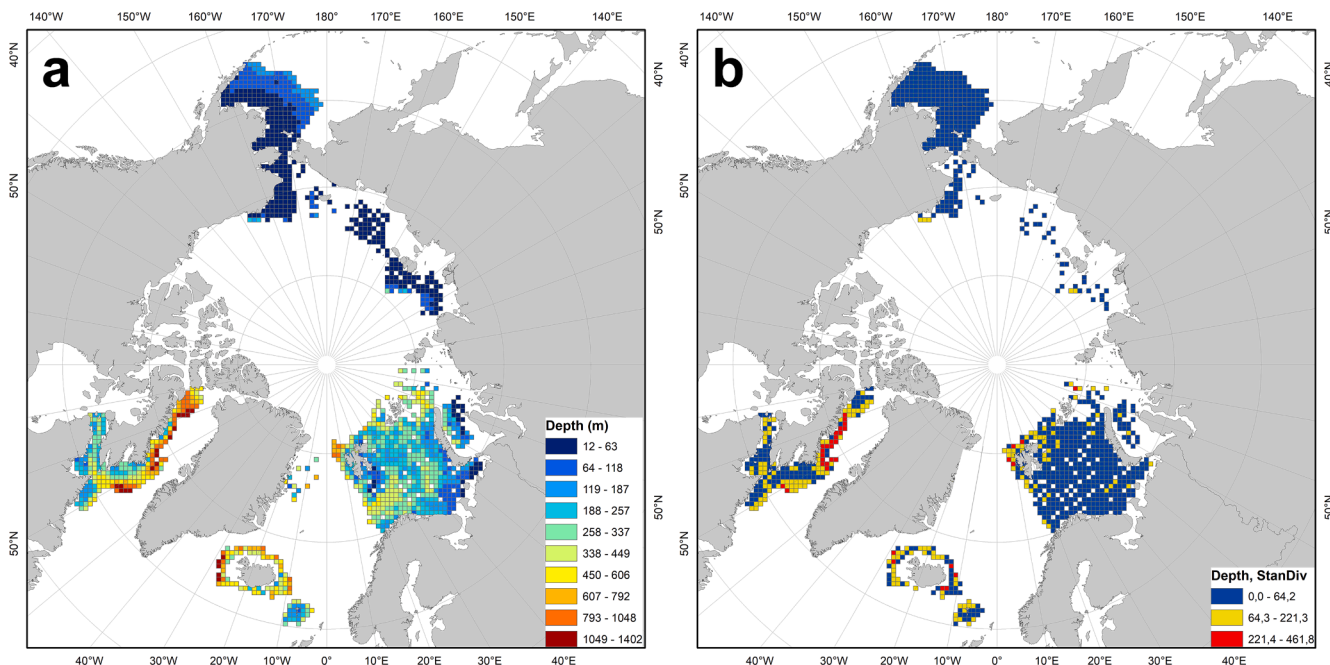
Fig. 2. a-b. Average trawl bottom depth (m) (a), and standard deviation (SD) of average bottom depth (b) calculated as the average across all stations within each grid cell (50 km × 50 km).
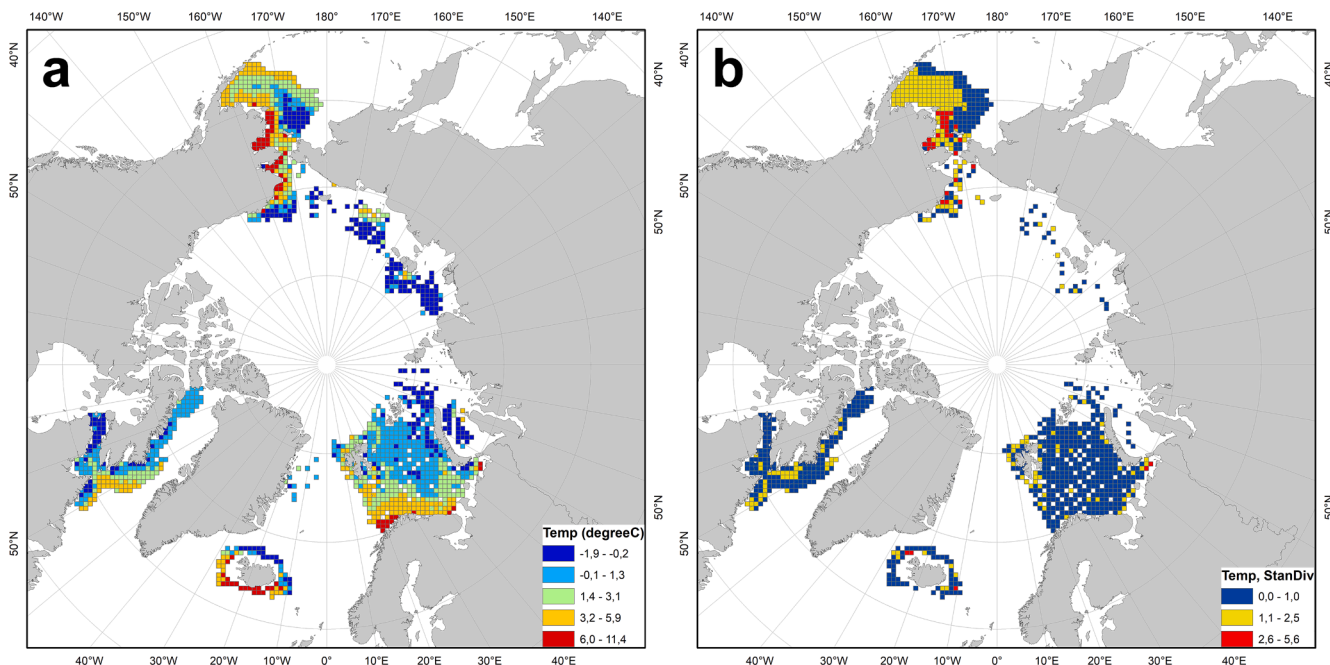

Fig. 3. a-b. Average bottom temperature (°C) (a), and standard deviation (SD) of average bottom temperature (b) calculated as the average across all stations within each grid cell (50 km × 50 km).
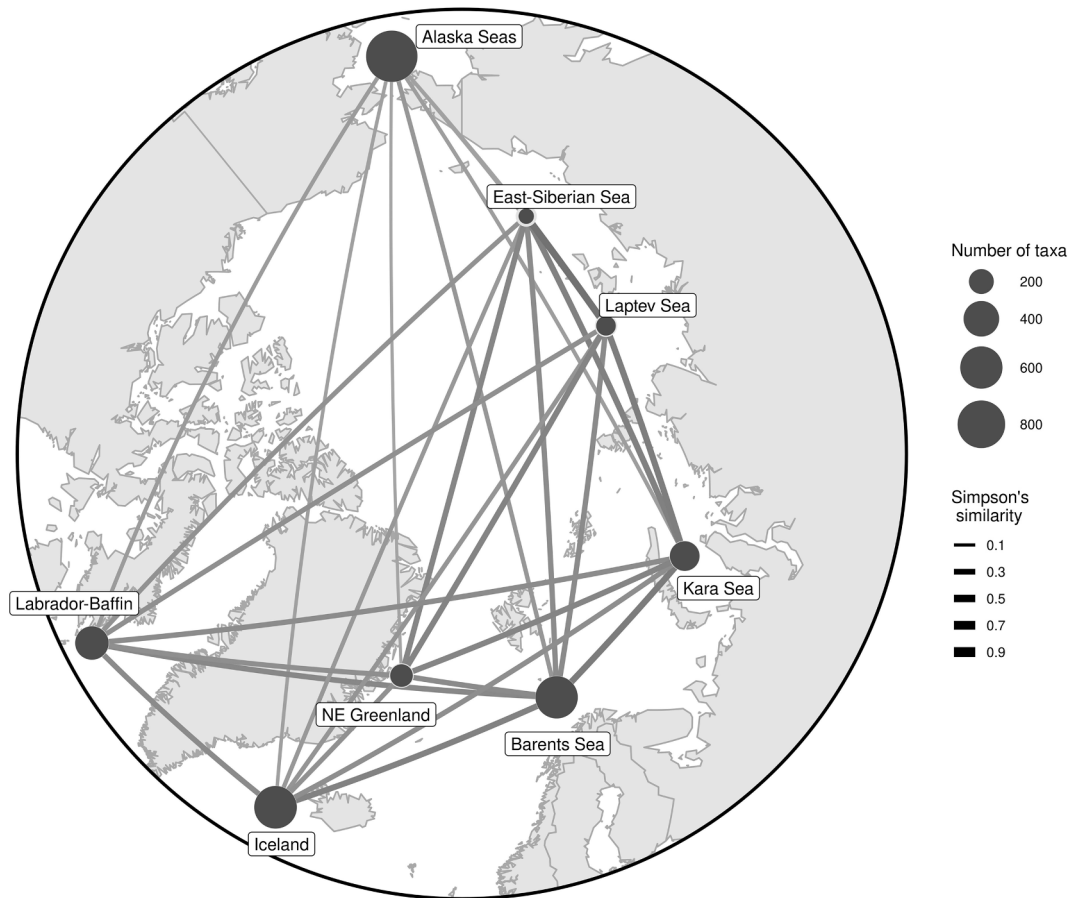
gap in coverage across the Canadian Arctic Archipelago. Finally, maximum levels of shared taxa tend to be higher between Atlantic and Eurasian Arctic Seas than with Pacific Arctic Seas (Fig. 4).
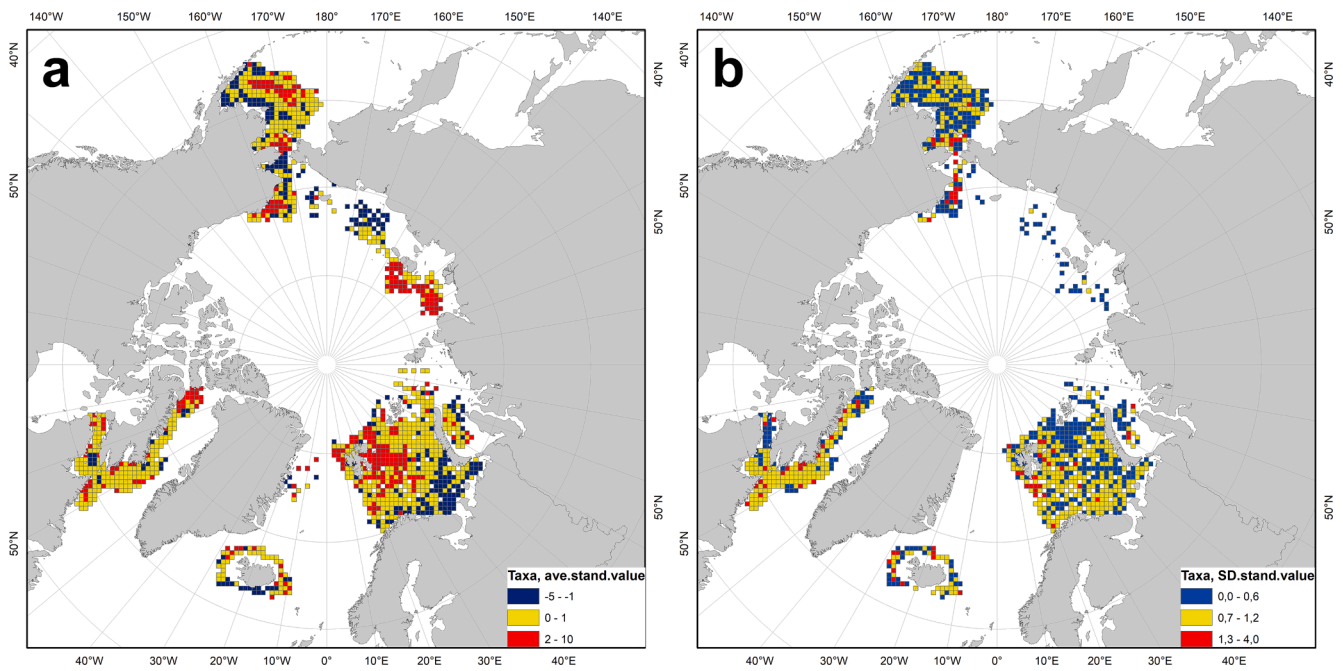
3.2.1. Average standardized total number of taxa

Each of the considered regions showed substantial variation in the number of taxa taken by trawl. The Laptev Sea had high numbers of taxa on its outer shelf whereas those patterns were not present in the East-Siberian Sea, or in the Kara Sea, where above average values occurred in small pockets on the inner shelf (Fig. 5a). The highest numbers of taxa

in the Barents Sea were located in the northwestern and central portion of the Barents Sea shelf compared to the remainder of the Barents Sea shelf (Fig. 5a). Waters north of Iceland had higher number of taxa than waters along the southern slope off Iceland, that could relate to the sampling effort being lesser within the grids along the south shelf; coverage was sparse in NE Greenland, but above average values tended to be at the northern stations (Fig. 5a). High values were also seen on the outer Laptev Sea shelf. Areas of high taxa numbers in Canadian waters appeared in small local patches, with a particularly high portion in northwestern Baffin Bay (Fig. 5a). In USA waters, the highest number of

Fig. 4. Number of taxon and similarities among locations. The size of the circles is proportional to the number of taxon recorded in each study area. The thickness of the links indicates the value of the Simpson's Index of Similarity (Simpson, 1943), used here because its low sensitivity to differences in species richness among areas. The "Alaska Seas" includes the US Bering, Chukchi, and Beaufort Seas.

Fig. 5. a-b. Average standardized number of taxa (a), and standard deviation (SD) of average number of taxon (b) within each grid cell (50 km × 50 km). Note this representation is based on highly uneven effort among (and much less so within) regions, and is intended to give a cautious indication of patterns within regions.

taxa occurred in the Barrow Canyon area, the northern Bering Strait and at the outer shelf and break of the Bering Sea (Fig. 5a).

Only a few areas at the Pan-Arctic scale showed high standard deviations of average number of taxa; a small number of individual grid cells scattered within the Barents, and Icelandic Seas, within the Labrador-Baffin region, and waters within the Chukchi Sea (Barrow Canyon), just south of Bering Strait (Fig. 5b).

3.2.2. Average standardized biomass

General patterns of above average biomass levels by region were somewhat similar to those of standardized taxa richness with exceptions mainly in the Barents Sea where biomass was highest in the eastern portions and off the northwestern Norwegian coast (Fig. 6a). Above average biomass levels also occurred on the outer shelves of the Laptev and East Siberian Seas, and in western Kara Sea in the Atlantic inflow (Fig. 6a). Additionally, a few grid cells with high average taxa biomass occurred in west and south Iceland, south of Faroe Islands, northwest Baffin Bay, off the northern Labrador Sea, in the southern Bering Sea, near the Bering Strait and within Barrow Canyon in the Pacific inflow (Fig. 6a). Relatively large areas had low standardized biomass estimates including the inner East-Siberian Sea, large portions of the western and southern Barents Sea, western Baffin Bay, and the Bering Sea shelf (Fig. 6a). The Standard deviations for standardized biomass estimates show similar patterns with low variability in all sampled regions (Fig. 6b).

3.2.3. Average standardized abundance

The standardized abundance estimates for solitary taxa were, in general, broadly similar to biomass patterns, except for the Barents Sea, the only area where colonial taxa were recorded as counts. Above average abundance estimates with-in region occurred in the northern parts of the Laptev and East Siberian Seas, northwest and central Barents Sea shelf, the Bering Sea shelf, north and south of St. Lawrence Island, and from Barrow Canyon following the Bering Sea Water outflow into the western Beaufort Sea (Fig. 7a). Results were not available for the Canadian regions as abundance data was limited and not done for colonial taxa.

In contrast, the lowest standardized abundance estimates occurred on the inner shelf sections of the East-Siberian, and Kara Seas, southeast portion of the Barents Sea (opposite to the biomass pattern in the Barents Sea), southern waters of Iceland, broadly along the flow of the Alaska Coastal Current (Fig. 1a) in the coastal Bering and Chukchi Seas, with additional below average abundance estimates scattered within each region (Fig. 7a). The standard deviation (SD) estimates of abundance illustrated scattered grid cells of high variation in abundance estimates throughout the region (Fig. 7b).

3.3. Megabenthic functional traits

The relative composition of the categories in each of the three traits, Adult Movement, Body Form, and Skeleton, illustrates some general patterns at the Pan-Arctic scale (Fig. 8). Across all regions combined, 'sessile' and 'crawling' adult movements are more prevalent categories than 'burrowing' and 'swimming' adult movement (Fig. 8, top panel). Burrowers naturally were not well represented due to the trawl sampling mainly epibenthic megafauna. Body Form categories 'globulose', 'dorso-ventro' compressed and 'upright' tended to dominate most areas (Fig. 8, middle panel). The Skeleton category 'calcareous' is prevalent in most regions except the Beaufort Sea, while other categories are highly variable among regions (Fig. 8, bottom panel).

At the regional level, trait composition is similar among some regions; with broadly similar patterns between pairs of directly adjacent geographic areas. For example, the Barents and Kara Seas showed similar percentages of trait categories (e.g. high percent 'sessile' adults, high and broadly equal proportions of 'globulose', 'dorso-ventro' compressed and 'upright', and high and similar proportions of 'cuticle', 'siliceous' and 'calcareous'). Similarly, the adjacent East-Siberian and Laptev seas shared a similar trait composition, but the pattern is markedly different in dominant trait categories when compared to the Barents, and Kara Seas (Fig. 8). The difference lies in high percent of 'crawlers' and organisms with a 'calcareous' skeleton, a pattern shared with the Chukchi, and Bering Seas, which again are contiguous regions. In contrast, the western Beaufort sea was characterized by a predominately 'sessile', 'globulose' and 'dorsal-ventro' community with near-
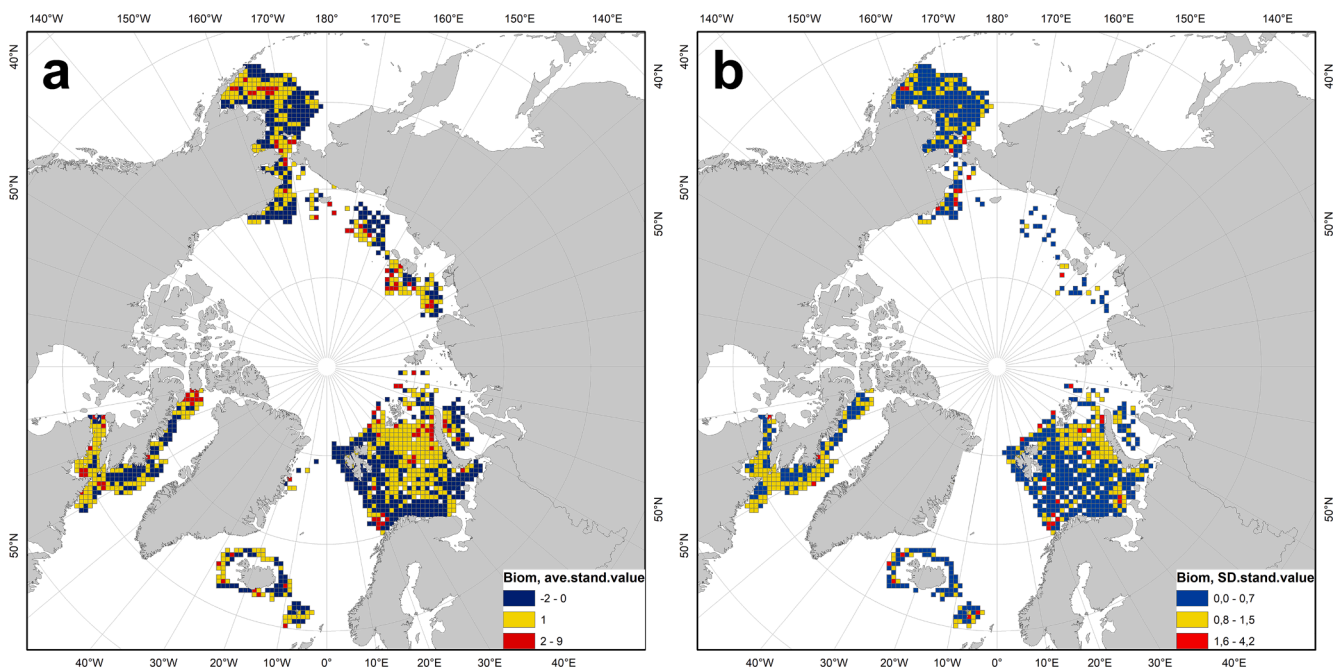

Fig. 6. a-b. Cube-root transformed average standardized biomass estimates (a), and standard deviation (SD) of standardized biomass estimates (b) by area and in case different trawl-gear was used within area (Canada) the transformation was done separately for each of the gears. Estimates were then averaged within each grid cell (50 km × 50 km).
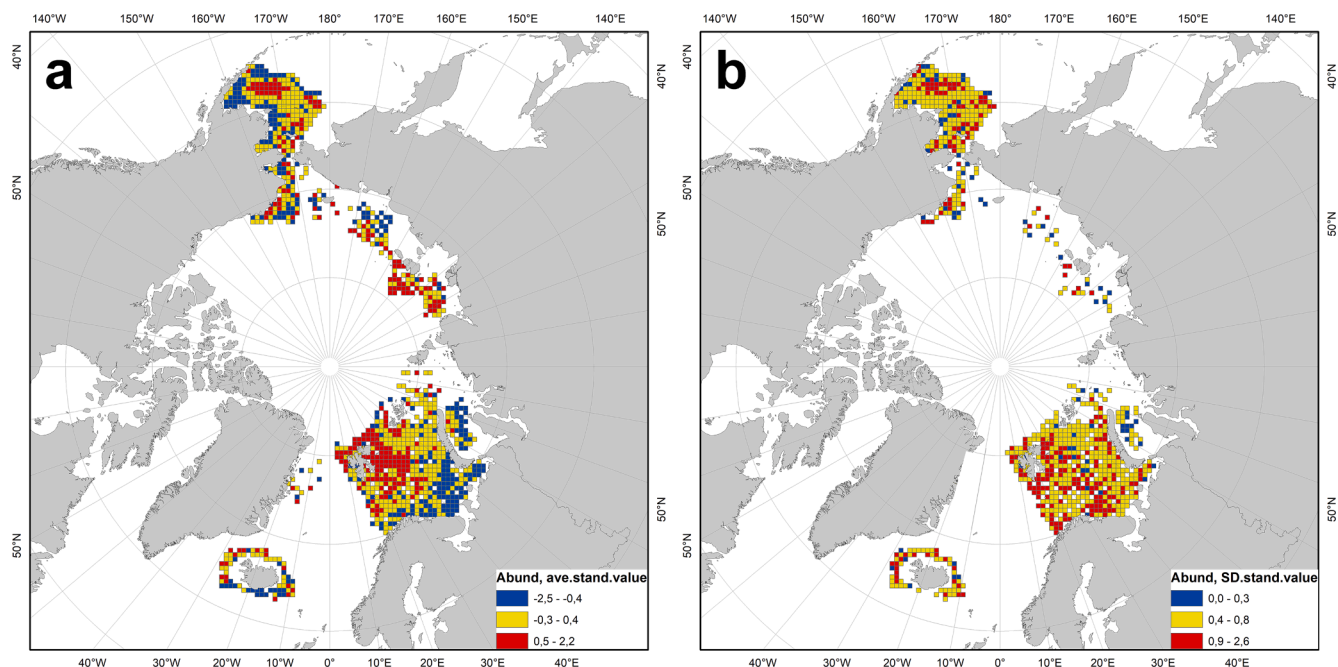
Fig. 7. a-b. Cube-root transformed average standardized abundance estimates (a), and standard deviation (SD) of standardized abundance estimates (b) by area. Estimates were then averaged within each grid cell (50 km × 50 km). Note: Canadian data for total abundance were removed because captures were weighed, but not always counted, for example colonial species like sponges.
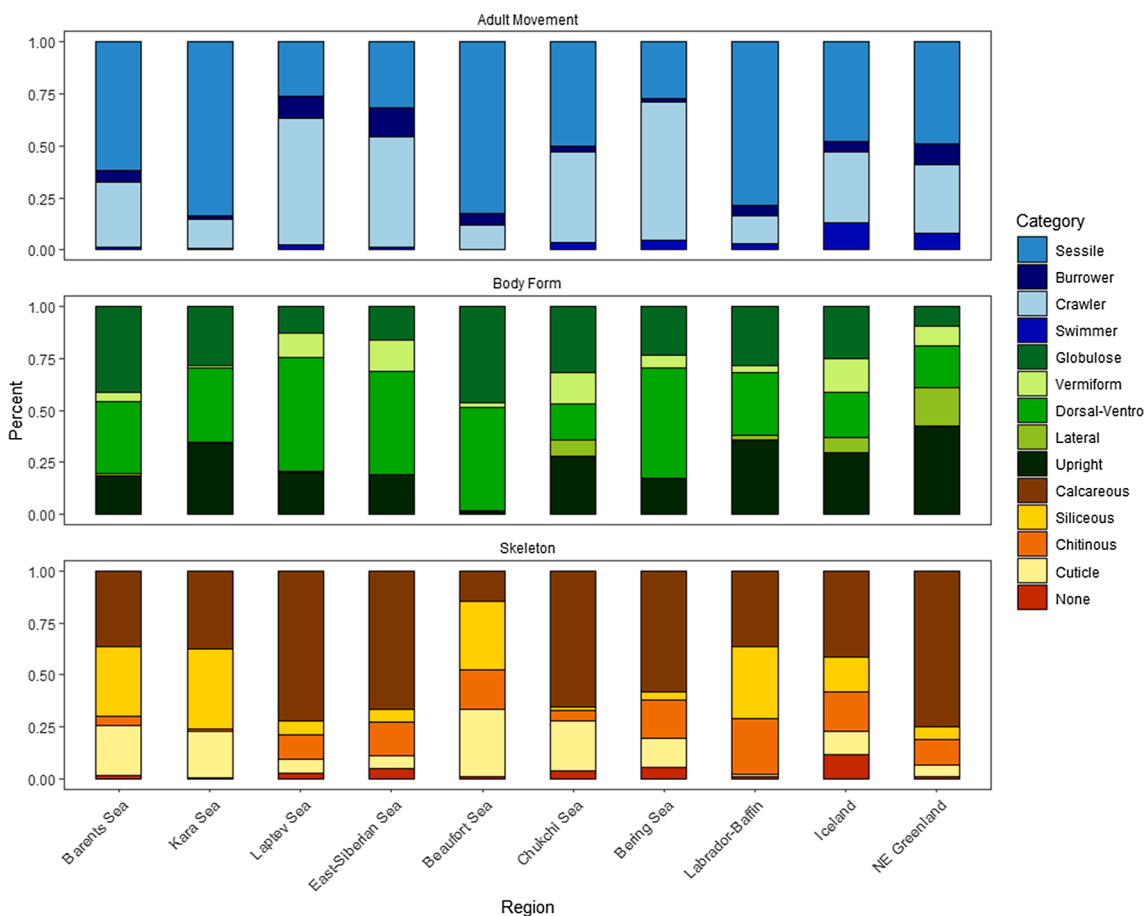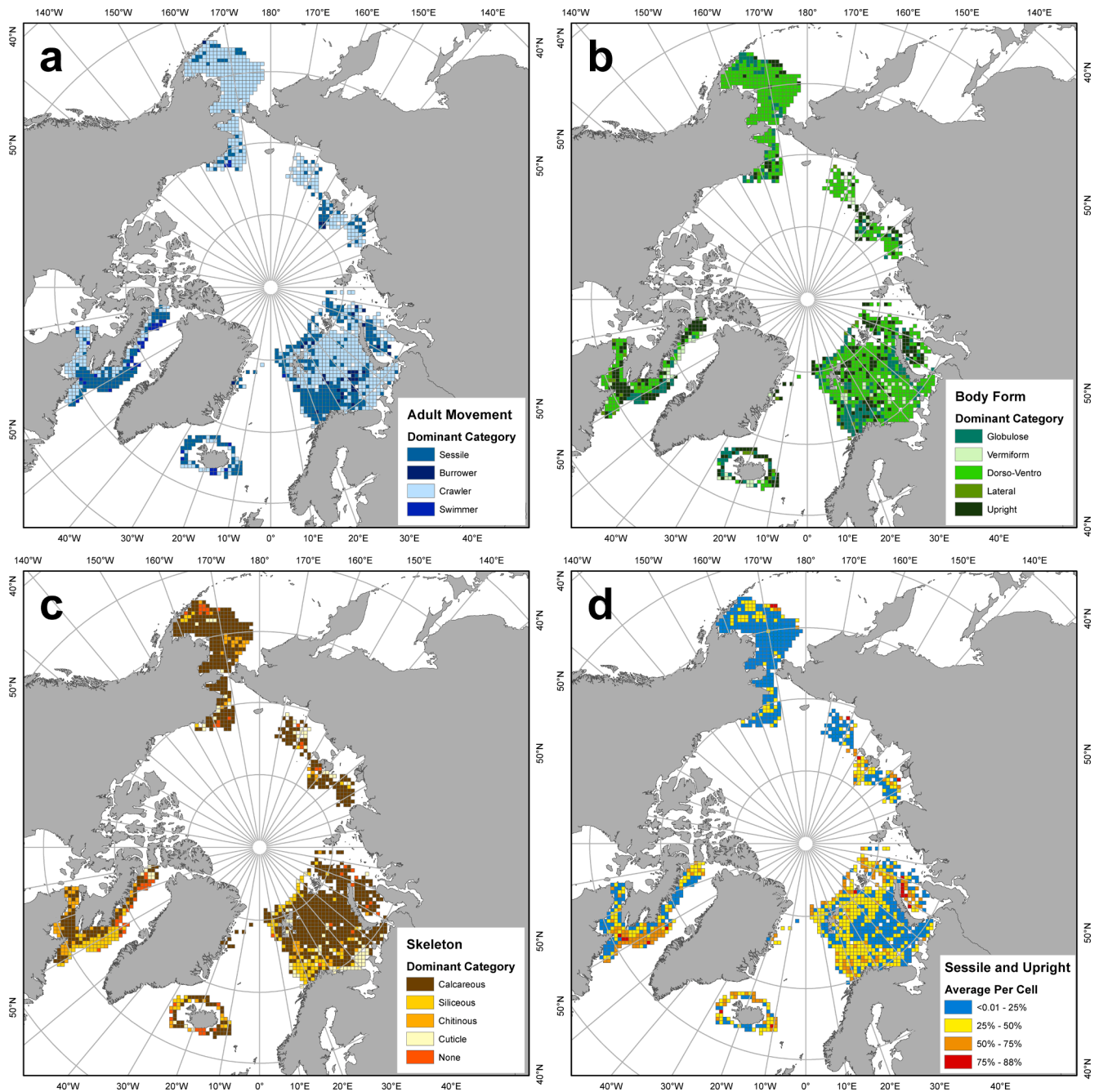

Fig. 8. Average percent by weight for each Region for the three traits: Adult Movement, Body Form, and Skeleton. The shorthand shown on the X-axis (Region) is defined as follows: NE GRL is Northeast Greenland (TUNU VII Survey). Note: the order of the regional areas is different; the Bering-Chukchi-Beaufort Seas, East-Siberian-Laptev-Kara-Barents are considered on continental shelves. The Labrador-Baffin, Iceland and NE Greenland regions are considered off the continental shelves.

equal proportions of four skeleton types, albeit adjacent to the Chukchi Sea (Fig. 8); however, sampling in the Beaufort Sea region likely occurred in waters that oceanographically differed from the Chukchi shelf. Functional traits in the Labrador-Baffin region are similar in composition to traits in the Kara Sea, in particular the deeper western portion of the Kara Sea that is over 200 m in the Novaya Zemlya Trough.

Within-region spatial trends of dominant categories within the three considered traits were mapped for each regional dataset (Fig. 9a-c). The overall patterns at the Pan-Arctic scale illustrate that dominant body morphological features of the megabenthos, by biomass, over large spatial scales, are 'crawlers' and 'sessile' categories (Fig. 9a), 'dorso-ventro' compressed (Fig. 9b), and 'calcareous' skeleton (Fig. 9c), but within regional variation is substantial. Exceptions to the broad spatial

dominance of 'calcareous' skeletons included the deep slope waters of the Labrador-Baffin region, a substantial portion of Icelandic waters, and a small portion of the southern Barents Sea (Fig. 9c). The 'sessile' category is prominent around much of Iceland, the southwestern and northern Barents Sea, the western and northern Kara Sea, and especially along the continental slope in the Labrador-Baffin region (Fig. 9a). Small patches of the 'sessile' category appear in the central and northeastern Laptev Sea, the southern portion of the Bering Sea, northern Chukchi Sea (Barrow Canyon), and sites in northeastern Greenland (Fig. 9a). The 'dorso-ventro' compressed Body Form trait category, dominated the same areas as the 'crawlers', likewise, patterns in the 'upright' category were broadly similar to those in the 'sessile' category (Fig. 9b).

When the combination of trait categories, 'sessile' and 'upright' was

Fig. 9. a-d. Relative percent by weight of the three traits, Adult Movement (a), Body Form (b), and Skeleton (c), shown as dominant trait (by weight) for each 50 km × 50 km grid cell. In (d), the two traits "Sessile" and "Upright" were combined and expressed as an average relative percent by weight per grid cell to illustrate a combination of traits that could make an organism more susceptible to the effects of bottom disturbance.

mapped, few areas had more than 50% of the biomass comprised of this combination of trait categories with the exception of the Labrador-Baffin region, which showed a large portion of slope waters being dominated by 'sessile' and 'upright' organisms, and the western Kara Sea which corresponds to the deeper Novaya Zemlya Trough (Fig. 9d). Much of the Barents Sea, Icelandic waters, Laptev Sea, and NE Greenland had intermediate levels of this trait combination (Fig. 9d). In contrast, areas with 25% or less of this trait combination included a portion of the southeast Barents, and East-Siberian sea, most of the Bering Sea shelf, and the west Beaufort Sea (Fig. 9d).

3.4. Megabenthic temperature preferences

Variance within cluster groups declined rapidly as the number of groups or clusters increased from 1 to 5 in all regions (Fig. 10). For group numbers larger than five variance decreased less rapidly. So, group size (k) was chosen to be five for further analysis. The five clusters from each regional complex were ranked by median temperature (coldest to warmest) (Table 4). The cluster in each analysis region with the coldest temperature and a narrow range was Cluster A (referred to as 'cold-water taxa') (Table 4).

Median temperatures for this cluster ranged from $-1.5\,°C$ in the Kara-Laptev-East Siberian seas region to $0.5\,°C$ in the Barents Sea. The percent of the number of species defined as ''cold-water'' ranged from 8% in the Barents Sea to 30% in the Kara-Laptev-East Siberian seas. Cluster E, in contrast, had the warmest median temperature and the

broadest range in the Bering-Chukchi-Beaufort seas region and we defined it as the 'warm-water' taxa for this region. In all the other regions, Cluster D had the broadest range and a relatively warm median temperature, therefore, Cluster D was defined as the 'warm-water' taxa in these regions. The median temperature for the warm clusters ranged from $-1.1\,°C$ in the Kara-Laptev- East Siberian Sea region to $4.4\,°C$ in the West Baffin Bay-NE Greenland-Iceland region. The percent of species defined as 'warm-water' ranged from 7% in the Kara-Laptev-East Siberian Seas to 19% in the Barents Sea.

The taxa in the ''cold-water'' and 'warm-water' clusters in each region and their contribution to the catch by weight (except NE Greenland) are shown in Table 5. In the Kara-Laptev-East Siberian Seas, a sea anemone, *Hormathia digitata parasitica*, a sponge, *Craniella cranium*, a sea urchin, *Strongylocentrotus pallidus*, and a gastropod, *Colus* sp., were the most abundant ''cold-water'' species. A sea cucumber, *Myriotrochus rinkii*, was the most abundant 'warm-water' taxon.

Snow crab, *Chionoecetes opilio* along with basketstars, *Gorgonocephalus* spp. and several other echinoderms (contributed the most biomass to ''cold-water'' species in the Barents Sea. *Geodia* sponges, especially *G. barretti* and *G. macandrewii* were the most biomass-contributing 'warm-water' species.

In Iceland, a basket star, *Gorgonocephalus eucnemis*, again dominated the ''cold-water'' species, and a sponge, *Stelletta normani*, dominated the 'warm-water' species.

In northeast Greenland, a brittlestar, *Ophiopleura borealis*, and two shrimp species, *Sabinea septemcarinata* and *Sclerocrangon ferox*, as well as
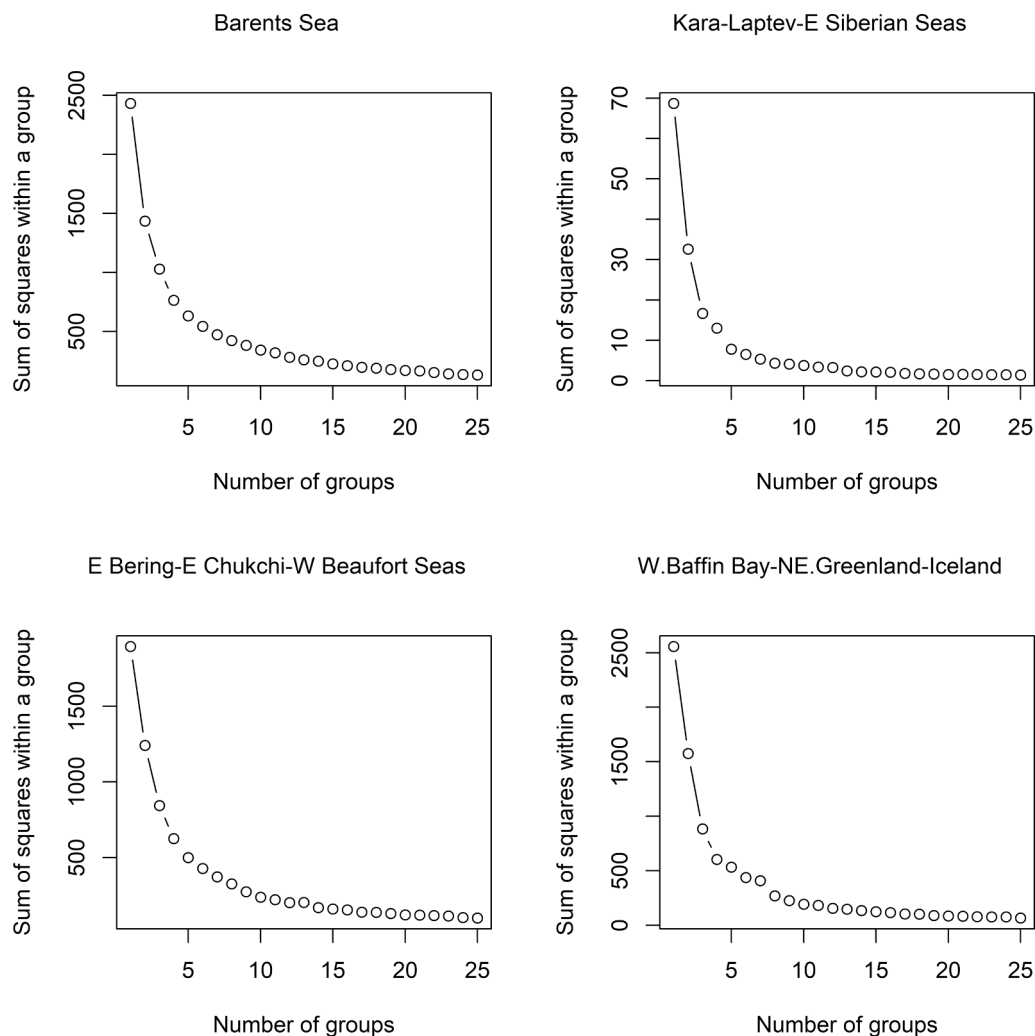

Fig. 10. Relationship between number of groups in k-means clustering and within-cluster variance (sum of squares) for regional datasets.

Table 4

Summaries of temperature clusters in all region groups given as average median temperature and range for each cluster and percent of species in each cluster. Blue cells indicate cold-water taxa, and red cells indicate warm-water taxa.

E Bering-E Chukchi-W Beaufort Seas				W Baffin Bay-NE Greenland-Iceland			
Cluster	Median	Range	% Species	Cluster	Median	Range	% Species
A	−0.3	3.5	12%	A	0.3	1.5	18%
B	0.6	6	21%	B	0.6	6.4	17%
C	3.4	2.8	19%	C	1.4	3.4	26%
D	2.5	5.5	38%	D	4.4	6.1	15%
E	2.8	9	8%	E	4.8	2.0	24%
Barents Sea				Kara-Laptev-E Siberian Seas			
Cluster	Median	Range	% Species	Cluster	Median	Range	% Species
A	0.5	2.7	8%	A	−1.5	0.9	30%
B	1.1	4.5	34%	B	−1.2	2.1	25%
C	2.8	4.0	29%	C	−1.0	1.4	30%
D	3.3	6.4	19%	D	−1.1	3.8	7%
E	4.9	2.8	10%	E	−0.6	0.4	8%

several amphipods were the most abundant ''cold-water'' taxa (note that few biomass data were available and hence abundance was used). There was virtually no catch of 'warm-water' species in northeast Greenland.

An octopus, *Cirroteuthis muelleri,* was the most biomass-rich ''cold-water'' species in the Western Baffin Bay area, followed mostly by echinoderms; and a sponge, *Asconema foliatum,* was virtually the only 'warm-water' species in that area.

Gastropods and the mussel, *Musculus* sp., contributed the most biomass to ''cold-water'' taxa in the Bering-Chukchi-Beaufort seas area, followed by mostly echinoderms and other gastropods. The basketstar, *Gorgonocephalus* cf. *arcticus*, contributed the most biomass to 'warm-water' species, followed by a number of crustaceans mostly.

Patterns in the distribution of cold- and warm-water taxa at the regional scale were as follows. In the Kara-Laptev-East Siberian Sea region, data gaps obscured a clear difference in the distribution of ''cold-water'' and 'warm-water' taxa, though our data suggest 'warm-water' taxa were generally found inshore of, or closer to, river-outflow areas than ''cold-water'' taxa (Fig. 1). In the Barents Sea 'warm-water' taxa were abundant in the south and west while ''cold-water'' taxa were most abundant to the northeast (Fig. 11). In the Iceland area, ''cold-water'' taxa were abundant north of the island, whereas 'warm-water' taxa made up most of the catch south of the island (Fig. 11). Only ''cold-water'' taxa were found in the NE Greenland area in northwestern Baffin Bay area ''cold-water'' taxa dominated catch biomass (Fig. 11). In the Pacific inflow, ''cold-water'' species were most abundant in the north Chukchi Sea, around Barrow Canyon (off Point Barrow) and into the western Beaufort Sea. In addition there were moderate abundances in the outer middle domain of the Southeast Bering Sea (Fig. 11). 'Warm-water' species were mostly found in relatively nearshore waters in the northern Bering, and Chukchi seas.

4. Discussion

This study illustrates the collective efforts of scientists from several nations who combined data sets from surveys which varied considerably in effort, season, time period covered, and trawl-gear types. Despite these biases, by standardizing catch metrics and using traits analyses we were able to combine our data and show patterns in megabenthic fauna spanning the Arctic. Compared to previous studies of Pan-Arctic biodiversity of megabenthos (Piepenburg et al., 2011), we document patterns over a greater area and greater number of taxa. In addition, more varied information is presented here, including catch biomass, abundance, bottom depth and temperature, data which are commonly collected at trawl stations on fisheries, impact and research surveys.

4.1. Megabenthic distribution patterns

4.1.1. The patterns of biomass

The megabenthic biomass were general low within the North Atlantic Current (NAC) as well as in large areas of the western Barents Sea and south Icelandic waters based on the regional estimates of standardized biomass. But in the southern part of Iceland, this might be caused by a low sampling effort. Moderate biomass estimates in Icelandic waters, were associated with and area where the North Atlantic Current mixes with Polar and Arctic waters to the north (Logemann et al., 2013). Relatively high biomass patches are formed by *Geodia* and other similar sponges west of Iceland. In the southwestern part of the Barents Sea, influenced by Atlantic water, the biomass is high, because of *Geodia* sponge fields.

As the North Atlantic Current passes through in the Arctic Barents Sea, a complex dynamic of tides, topography and river influx mix the upper layers of warm water, heat dissipate as this water moves further to the east, and mixes with cold waters from the Kara, Laptev and East-Siberian seas along the slope (Bluhm et al., 2020; Fig. 1). These colder temperatures were related to higher megabenthic biomass estimates in the Arctic Barents, Kara, Laptev, and East-Siberian seas. This finding may be counterintuitive since primary production is high in the Atlantic-influenced part of the Barents Sea (Slagstad et al., 2015) and utilized by the sponges in the south west, - while the comparable high biomass in the Arctic Barents Sea is mainly large, but low productive (Degen et al., 2016) echinoderm, crustacean and cnidarian species but large mega-faunal organisms (Jørgensen et al., 2019) while in the Siberian Seas high biomass is formed by large and very numerous echinoderms, mainly Asteroidea (*Urasterias linkii, Icasterias panopla*), Ophiuroidea (*Gorgonocephalus* spp.) and holothurians, cnidaria (soft corals Nephthyidae and actiniarians Hormathiidae). The relatively high megabenthic biomass observed in areas of the northeastern Barents Sea, the outer shelf areas of the Russian Seas and parts of the Bering and Chukchi seas may be the result of high nutrient loads in the inflowing Pacific and Atlantic waters, which result in high primary production and increased export production to benthic communities (Grebmeier et al., 2015a). The low biomass in the western Barents Sea may be modulated by strong grazing and predation in the western part and north of Svalbard. The more productive waters corresponded to both some of the shallowest and some of the deepest stations within the Pan-Arctic shelf regions.

Contrary to the patterns described above, the coldest waters in the Labrador-Baffin region, in particular along the coast, were characterized by low biomass estimates. In contrast, the areas of higher biomass, with massive *Geodia* sponge fields, were associated with deeper water that was also cold, but warmer relative to the inner shelf. Eastern Baffin Bay/West Greenland differed from the broad shelf of the Barents Sea in that it is a deep basin flanked by a relatively deep shelf which in turn is structured by a series of banks and troughs meeting the fjordic and

Table 5

Percent catch by species (or lowest taxon) in each cluster and analysis region. Taxa with percent catch greater than or equal to 0.1% are shown, the rest of the catch is summed and shown as 'Other'.

Barents Sea

Cluster A "cold, narrow range" taxa

Taxon	% g nmi^{-1}
Chionoecetes opilio	2%
Gorgonocephalus arcticus	2%
Ophiopleura borealis	2%
Urasterias lincki	1%
Ophiacantha bidentata	1%
Heliometra glacialis	1%
Gorgonocephalus eucnemis	1%
Sabinea septemcarinata	1%
Ophioscolex glacialis	1%
Icasterias panopla	1%
Gorgonocephalus	1%
Colus sabini	0.3%
Sclerocrangon ferox	0.3%
Ciona intestinalis	0.3%
Gersemia	0.2%
Drifa glomerata	0.2%
Umbellula encrinus	0.2%
Molpadia arctica	0.1%
Solaster	0.1%
Thenea valdiviae	0.1%
Polymastia penicillus	0.1%
Solaster syrtensis	0.1%
Saduria sabini	0.1%
Forcepia	0.1%
Other	0.8%
Grand Total	16%

Cluster D "warm, broad range" taxa

Taxon	% g nmi^{-1}
Geodia barretti	8%
Geodia macandrewii	8%
Geodia	5%
Craniella cranium	0.2%
Mycale lingua	0.1%
Phakellia	0.1%
Other	0.3%
Grand Total	23%

Kara, Laptev and East Siberian Seas

Cluster A "cold, narrow range" taxa

Taxon	% g nmi^{-1}
Hormathia digitata parasitica	1%
Craniella cranium	1%
Strongylocentrotus pallidus	1%
Colus	1%
Thenea muricata	0.4%
Ciona intestinalis	0.3%
Ascidia	0.2%
Hormathia digitata	0.2%
Gersemia fruticosa	0.2%
Craniella polyura	0.1%
Henricia	0.1%
Drifa glomerata	0.1%
Eualus gaimardii	0.1%
Hymenaster pellucidus	0.1%
Pteraster obscurus	0.1%
Pteraster militaris	0.1%
Other	0.1%
Grand Total	6%

Cluster D "warm, broad range" taxa

Taxon	% g nmi^{-1}
Myriotrochus rinkii	3%
Polychaeta	0.3%
Alcyonidium gelatinosum	0.1%
Other	0.1%
Grand Total	3.4%

Bering, Chukchi and Beaufort Seas

Cluster A "cold, narrow range" taxa

Taxon	% kg km^{-2}
Gastropoda	3.8%
Musculus	3.0%
Urasterias lincki	0.4%
Solaster dawsoni	0.3%
Golfingia (Golfingia) margaritacea	0.3%
Myriotrochus rinkii	0.2%
Naticidae	0.2%
Buccinum glaciale	0.1%
Margarites	0.1%
Pandalidae	0.1%
Other	0.2%
Grand Total	9%

Cluster E "warm, broad range" taxa

Taxon	% kg km^{-2}
Gorgonocephalus cf. *arcticus*	2%
Argis lar	0.3%
Balanus	0.3%
Sclerocrangon boreas	0.2%
Urticina crassicornis	0.1%
Argis dentata	0.1%
Stegophiura nodosa	0.1%
Other	0.1%
Grand Total	3%

Labrador-Baffin (Western Baffin Bay, Davis Strait, Hudson Strait, Northern Labrador Sea)

Cluster A "cold, narrow range" taxa

Taxon	% kg km^{-2}
Cirroteuthis muelleri	1.4%

Cluster D "warm, broad range" taxa

Taxon	% kg km^{-2}
Asconema foliatum	1.6%

Table 5 (*continued*)

Labrador-Baffin (Western Baffin Bay, Davis Strait, Hudson Strait, Northern Labrador Sea)

Cluster A "cold, narrow range" taxa			Cluster D "warm, broad range" taxa	
Taxon	% kg km^{-2}		Taxon	% kg km^{-2}
Psilaster andromeda	0.3%		Other	0.1%
Molpadia	0.2%		Grand Total	1.7%
Sclerocrangon ferox	0.2%			
Gorgonocephalidae	0.1%			
Other	0.2%			
Grand Total	2.4%			

Iceland

Cluster A "cold, narrow range" taxa			Cluster D "warm, broad range" taxa	
Taxon	% catch		Taxon	% catch
Gorgonocephalus eucnemis	3.0%		*Stelletta normani*	7.0%
Geodia parva	0.3%		*Stauroteuthis syrtensis*	0.9%
Cirroteuthis muelleri	0.2%		*Actinostola*	0.5%
Bathybiaster vexillifer	0.1%		*Actinauge*	0.3%
Sclerocrangon ferox	0.1%		*Craniella cranium*	0.3%
Allantactis parasitica	0.1%		Axinellidae	0.2%
Colus islandicus	0.1%		*Pasiphaea multidentata*	0.1%
Molpadia borealis	0.1%		*Craniella zetlandica*	0.1%
Other	0.4%		*Asconema foliatum*	0.1%
Grand Total	4.4%		Other	0.3%
			Grand Total	9.7%

Northeast Greenland

Cluster A "cold, narrow range" taxa			Cluster D "warm, broad range" taxa	
Taxon	% ind 1000m^{-2}		Taxon	% ind 1000m^{-2}
Ophiopleura borealis	4%		*Hornera lichenoides*	0.007%
Sabinea septemcarinata	2%		*Hyas coarctatus*	0.007%
Eusirus	1.0%		Nemertea	0.007%
Sclerocrangon ferox	0.9%		*Ophiopholis aculeata*	0.005%
Anonyx	0.7%		Grand Total	0.026%
Themisto libellula	0.5%			
Ctenodiscus crispatus	0.4%			
Ophiocten sericeum	0.4%			
Bythocaris	0.4%			
Molpadia borealis	0.3%			
Rhachotropis aculeata	0.3%			
Pontaster tenuispinus	0.3%			
Zoantharia	0.3%			
Acanthostepheia malmgreni	0.2%			
Colus	0.2%			
Stegocephalus inflatus	0.1%			
Eusirus cuspidatus	0.1%			
Eurythenes gryllus	0.1%			
Poraniomorpha tumida	0.1%			
Pycnogonida	0.1%			
Other	0.1%			
Grand Total	12%			

island-rich coast of west Greenland.

The patterns of benthic biomass relative to water temperature in the USA Arctic seas were in some ways similar and in other ways different than those observed in the Barents Sea, in Icelandic water and in the Russian seas. In the Bering, Chukchi, and Beaufort Seas, the lowest biomass was generally found within the Alaska Coastal Current which follows the Alaskan coastline (Feder et al., 2005; Bluhm et al., 2009) and is characterized by warm, relatively fresh water yet low primary productivity (Fig. 1). The highest biomass estimates were on the Bering Sea shelf, south of the Bering Strait, where echinoderms (*Asterias amurensis, Gorgonocephalus eucnemis, Ophiura sarsii*), and decapods (*Chionoecetes opilio, Pagurus trigonocheirus*) dominate the higher biomass cells. In the north central Chukchi Sea where waters are relatively cold and productive (Springer et al., 1996; Grebmeier et al., 2006), decapods (*Chionoecetes opilio, Pagurus trigonocheirus)*, echinoderms (*Neptunea heros, Leptasterias (Hexasterias) polaris, Asterias amurensis*), and the tunicate, *Aplidium* sp. present the highest benthic biomass. Alternatively, fish biomass is very low in any water mass in the Chukchi Sea, yet benthivorous marine mammals diminish benthic resources (Grebmeier et al., 2015a), while predation on benthos by fish can be substantial in
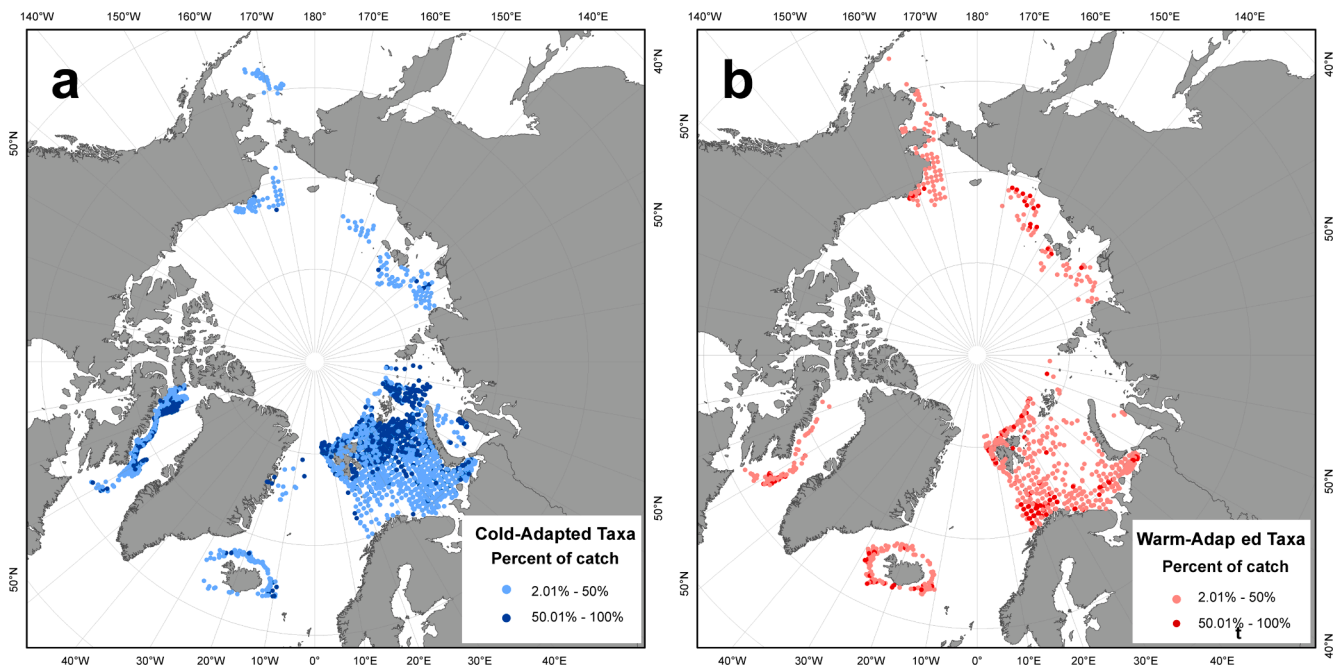
the Bering Sea (Aydin and Mueter, 2007).

4.1.2. The patterns of abundance

Abundance estimates generally tracked biomass estimates; however, there were some exceptions. In the North Atlantic Current of the Barents Sea, and the nearshore Beaufort Sea, abundance estimates were higher than biomass estimates, likely due to smaller organisms inhabiting these waters, for example small crustacean in the coastal Beaufort Sea (Ravelo et al., 2015, 2020). The Barents Sea had numbers for colonial species, which makes the pattern non-comparable to other areas.

4.1.3. Patterns of species richness

We found that areas of high species richness roughly coincided with areas of high megabenthic biomass. Exceptions include the western Barents Sea, where richness was greatest in the transition from Atlantic to Arctic Water where the biomass was low, and at the shallowest stations of the Western Baffin Bay, that was low in biomass but high in richness. The northwest Baffin Bay area, albeit deep (~800 m), is recognized as an area of high benthos diversity and productivity, partly due to nearby productive polynyas where strong pelagic-benthic

Fig. 11. a-b. Distribution of a) 'cold-water' and b) 'warm-water' taxa, as percent catch (greater and less than 50% of catch) within each grid cell (50 km × 50 km). Note: Canadian taxa data from shrimp surveys were removed because species identification was limited until recently.

coupling has been reported (Roy et al., 2014). A positive productivity-diversity relationship has been a part of ecological thinking since Tilman (1982) developed a model to predict the number of plant species that can coexist competitively on a limited resource base. The only Arctic-specific study we are aware of, however, refined this concept for multiple benthic components and spatial scales, and showed that negative and curvilinear relationships may exist (Witman et al., 2008). Taxon richness patterns also relate to a number of other factors including evolutionary, biogeographic, and environmental factors such as substrate type, current velocity, and where different water masses meet. On the Pan-Arctic scale, our compiled megafauna data set cannot confirm the often-stated latitudinal decline in biodiversity. Such a pattern would have been visible in lowest values at our northernmost locations throughout the region and highest in the southernmost locations, a pattern that was not observed in any of our study regions. Instead, we found regionally varying patterns of taxon richness. Though caution is warranted, given taxonomic resolution varied within each region and certainly among regions, a few patterns seem to emerge. One pattern observed is likely related to underlying substrate and current velocities: peaks in standardized taxon richness are in areas of high current flow resulting in hard or coarser substrate occurrence such as in Bering Strait, Barrow Canyon, and the area north of Svalbard. These areas have also low/no bottom trawling. In this case, communities containing sessile suspension feeders and other hard-bottom associated taxa increase biodiversity (Bluhm et al., 2009; Pisareva et al., 2015; Jørgensen et al., 2015). Additionally, more patchily distributed hard substrate in the form of glacial drop stones across the study area may also increase biodiversity (Zhulay et al., 2019). A second pattern is one of a biogeographic transition zone where in the central and northern Barents Sea, boreal, Arctic-boreal and Arctic affinities co-occur, to some degree, resulting in a region of enhanced biodiversity measured by taxon numbers (Anisimova, 1989; Jørgensen et al., 2019). A similar pattern is less obvious in the other inflow shelf, the Chukchi Sea. Here, oceanographic influences appear more strongly visible in our data set, namely the above-mentioned cells of higher taxon richness in high current locations. Across the inflow and Siberian interior shelves, taxon richness was lower on the inner parts of the shelves than the central and northern parts, perhaps through (combined) influences of freshwater run-off from

land associated with low salinity, and high turbidity. We likely covered little of the zones where ice gouging also has a negative effect (Ravelo et al., 2020).

4.2. Towards using biological traits as indicators of sensitivity

A biological traits analysis can be useful when evaluating if and how anthropogenic and environmental changes may affect the long term function of benthic invertebrate communities (Bremner et al., 2006; Degen et al., 2018; Rand et al., 2018; Sutton et al., 2020; Hiddink et al., 2020). We considered three types of pressures for which our traits data may be relevant: demersal trawling, ocean acidification and climate warming. We examined traits on a Pan-Arctic scale for large-scale patterns in megabenthic community functions with the goal to move a step closer to identifying areas across the Arctic that might be susceptible to bottom trawling, ocean acidification and ocean warming.

4.2.1. Morphology and movement - trawl sensitivity

Several studies have examined the effects of bottom trawling on high latitude megabenthic invertebrate communities, and they use biological traits as a proxy for community function (Amoroso et al., 2018; Jennings et al., 2001a, b; Tillin et al., 2006; de Juan and Demestre, 2012). But Jørgensen et al., (2019) used a trait-based approach to identify areas in the Barents Sea where megabenthic communities may be especially susceptible to warming, fishing, and predation.

In this study, the sessile and upright trait modalities were highlighted because these modalities may be more susceptible to disturbance by bottom trawl gear than less sedentary and flatter modalities (Jennings et al., 2001a, b; McConnaughey et al., 2005; Jørgensen et al., 2019). Only a few locations hosted more than 75% of sessile and upright megafauna: the western edge of the Kara Sea in the Novaya Zemlya Trough, the outflow of the Hudson Strait, and a few localized spots in Icelandic waters, in the Laptev Sea, and along the shelf edge of the Bering Sea. Yet large areas had between 50 and 75% of sessile and upright megafauna. Of those, areas overlapping most with fishing include the western and southern Barents Sea (Jørgensen et al., 2015), parts of the southeastern Bering Sea shelf (NPFMC, 2020, FAO, 2017) and part of Labrador-Baffin Bay (DFO, 2020; Treble and Nogueira, 2018). These

areas deserve particular attention for future trawl sensitivity studies. Future research on the Pan-Arctic scale should include additional traits such as feeding habits and body size to infer those areas most susceptible to bottom trawling. In addition, it would be useful to quantitatively incorporate fishing effort on a Pan-Arctic scale to compare those areas currently being fished with those areas under protective measures or otherwise unfished (e.g., Chukchi Sea and north-western Barents Sea and the Siberian seas).

4.2.2. Skeleton - ocean acidification

A number of studies have addressed the likely impacts of a warming ocean and increasing CO_2 on the long-term health of marine invertebrate communities (Byrne, 2011). It is believed that, among benthic organisms, in particular calcified Arctic invertebrates are especially vulnerable to changes in ocean acidification in that they depend on a calcified inner or outer skeleton for structure and defense (Kurihara, 2008; Byrne, 2011). However, changes in ocean water chemistry can affect all life history stages of many other taxa, from fertilization through embryo and larvae stages, resulting in changes to the resiliency of adult invertebrates (Byrne, 2011). Certain taxonomic classes with calcareous skeletons in adults, such as gastropods, and echinoids, may be especially vulnerable to the effects of ocean acidification as shell thickness naturally declines with increasing latitude (Watson et al., 2012) since the Arctic has naturally low saturation levels of carbonate.

We used the biological trait category, Skeleton, to help identify those areas in the Pan-Arctic where the megabenthos may be most susceptible to the effects of decreasing calcium carbonate, as a result of ocean acidification. Five of the 11 regions were dominated by the trait category, 'calcareous'. Little is known how the phenotypic response, pace of adaptation, and vulnerable stages of development of Arctic marine invertebrates will respond to decreases in calcium carbonate though studies on individual taxa suggest growth and survival of larvae may be affected, and metabolism and calcification rates in adults respond to pH changes (e.g. Wood et al., 2011; Long et al., 2013). While no difference could be detected in modelled future habitat loss between calcified and non-calcified benthos (Renaud et al., 2019), based on our Pan-Arctic view of calcareous megabenthos, it is clear that research into these changes could be an important tool in monitoring the sensitivity of Arctic invertebrate communities. Future research and monitoring on the Pan-Arctic scale should also incorporate both larval development and propagule dispersal in order to capture those stages that may dictate reproductive success.

4.2.3. Temperature clusters – Ocean warming

Broad shifts in geographic distribution ranges over the past decades across the Arctic and sub-Arctic can partly be explained by ocean temperature increases. For example, Mueter and Litzow (2008) and Alabia et al. (2018) have documented a northward expansion in the distributions of Bering Sea epibenthic / demersal communities from 1982 to 2016 and an increase in community trophic level (more large groundfish) with ocean warming. There is similar evidence for northward range expansions of invertebrate and vertebrate species in the Barents Sea and Western Eurasian Basin (Fossheim et al., 2015, Polyakov et al., 2020).

The temperature range at which species are distributed over a large scale can give an indication of relative tolerance to temperature fluctuations, an approach falling within the field of study known as "macrophysiology" (Chown et al., 2004). Temperature preferences clearly exist between boreal and Arctic taxa (Renaud et al., 2015). Unfortunately, very few laboratory temperature-dependent rate measurements of benthic macrofauna have been made (Renaud et al., 2021). The physiological capacity of benthic organisms to acclimate or adapt to warming or otherwise changing conditions is also understudied (Pörtner, 2010).

We considered 'cold-water' taxa with a narrow temperature range to be the most vulnerable to ocean warming. Many of the 'cold-water' taxa in our study areas are prey for marine mammals, seabirds and commercially fished species (Whitehouse et al., 2016; Bluhm and Gradinger, 2008), thus their loss could have detrimental impacts on Arctic food webs, commercial fisheries and availability of subsistence resources. In the Bering-Chukchi-Beaufort seas the dominant 'cold-water' taxa, gastropods and mussels, are prey to endangered Pacific walrus (*Odobenus rosmarus*), which is harvested as a food resource in native Alaskan communities (Hovelsrud et al., 2008; Sheffield et al., 2001; Sheffield and Grebmeier, 2009). Brittlestars, dominant 'cold-water' taxa in Northeast Greenland and the Barents Sea are prey for sea stars, urchins and demersal fish (Drolet et al., 2004; Packer et al., 1994; Sköld, 1998). Basketstars (gorgonocephalids) are abundant 'cold-water' taxa in Iceland and the Barents Sea where they prey on zooplankton, such as euphausiids (Rosenberg et al., 2005). For snow crab, *Chionoecetes opilio*, one of the most abundant 'cold-water' species in the Barents Sea, a high-value fishery has developed in recent years after the species was first encountered in the ecoregion in 1996. This fishery is mainly carried out by a Russian fleet, in the Russian part of the Barents Sea shelf (International Council for the Exploration of the Sea, 2019).

In general, 'cold-water' species were indicators of the currents of Arctic outflow shelves whereas warm-water species indicated the currents of inflow shelves. In the Barents Sea and northern Iceland warm-water taxa coincided with the North Atlantic Current flowing past southern Iceland and into the south and western Barents Sea bringing warm and high salinity water (Schauer and Fahrbach, 2004, Meißner et al., 2004). 'Cold-water' taxa were most abundant in the northeastern Barents and northern Iceland where cold waters from the Arctic Ocean prevail. 'Cold-water' taxa dominated outflow shelves including NE Greenland and NW Baffin Bay (Michel et al., 2015) and along the shelf-slope to Davis Strait (nearing 50° N), with the warm-water taxa found at greater depths. In the Bering-Chukchi-Beaufort region, as expected, 'cold-water' species were most abundant in the north Chukchi Sea and western Beaufort Sea where cold waters formed locally during winter are located (Danielson et al., 2016). In addition, 'cold-water' species were abundant in the outer middle domain of the southeast Bering Sea where the 'cold pool', the remnant of the previous winter's sea ice, is found (Wyllie-Echeverria and Wooster, 1998). 'Warm-water' species were found nearshore in the area of the warm Alaska Coastal Current which flows from the south (Danielson et al., 2016). In the Kara-Laptev-East-Siberian Sea region there were no obvious patterns relative to latitude or depth. The distribution of benthic fauna in this interior shelf region may be more influenced by freshwater inflows and landfast ice than by Arctic inflow or outflow currents (Mahoney et al., 2007; Jerosch, 2013; Lantuit et al., 2012).

4.3. Data limitations and future directions

There was connectivity suggested across Atlantic areas, in particular among Russian seas, while there was little connectivity between the Pacific Arctic and the Atlantic Arctic. There was also less connectivity between adjacent areas with different ocean environments such as the deep water of Baffin Bay and Davis Strait compared to the shelf systems in other Atlantic Arctic seas. Future analyses could examine species connectivity, diversity and productivity between areas of similar depths, currents and temperatures.

Constraints of this study include the differences in trawl gear, mesh size and trawl depths of the surveys. In addition, there was variation in the taxonomic expertise among surveys and regions. These constraints limited the statistical analyses of biomass, abundance and richness within and across regions in this study. Furthermore, the suitability of including minor taxa should be evaluated for future work, especially before quantitatively analyzing diversity trends over an area (Kenchington and Kenchington, 2013).

The pooling of datasets revealed differences in taxonomic protocols among the regions. Preparing functional traits required comparing and agreeing on taxonomic names and levels between the surveys. Older names were updated and corrected using the WoRMS database as the

standard. Reviewing the names in the data also suggested improvements for future surveys, with either more specific or general names that could be used, based on the shared knowledge of experts. For example, basket stars (*Gorgonocephalidae*) could be recorded to the genus or species level, while sea urchins of *Stronglyocentrotus* might be best left at genus level as the two species (*S. droebachiensis* and *S. pallidus*) are difficult to discriminate.

4.4. Conclusions

We synthesized multiple national data sets from across the Arctic and were thus able to examine the ecosystem in its entirety, showing within-region and Pan-Arctic patterns and trends. We found that spatial patterns in relative biomass estimates of megabenthos were related to Pan-Arctic and local currents and water masses and that higher biomass estimates were generally associated with Arctic outflow currents and colder water masses (with the exception of the Baffin Bay region). We also found that species richness was generally higher in areas of higher biomass, or in transition zones between water masses. We identified areas where there was a very high percentage of sessile and upright taxa that may be more susceptible to damage by bottom trawl gear. These areas were the western edge of the Kara Sea, a few localized areas in Icelandic waters, the Laptev Sea, and along the shelf edge of the Bering Sea. We documented the distribution of taxa with calcareous skeletons that would be most susceptible to ocean acidification. We also identified and mapped 'cold-water' taxa because we considered these to be most vulnerable to ocean warming. The dominant 'cold-water' taxa were generally unique to each national area and were co-located with cold water masses and the currents of Arctic outflow shelves. Our results demonstrate the feasibility and value of international collaboration and cooperation in understanding and providing scientific advice for management of human activities in the global Arctic ecosystem.

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.

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