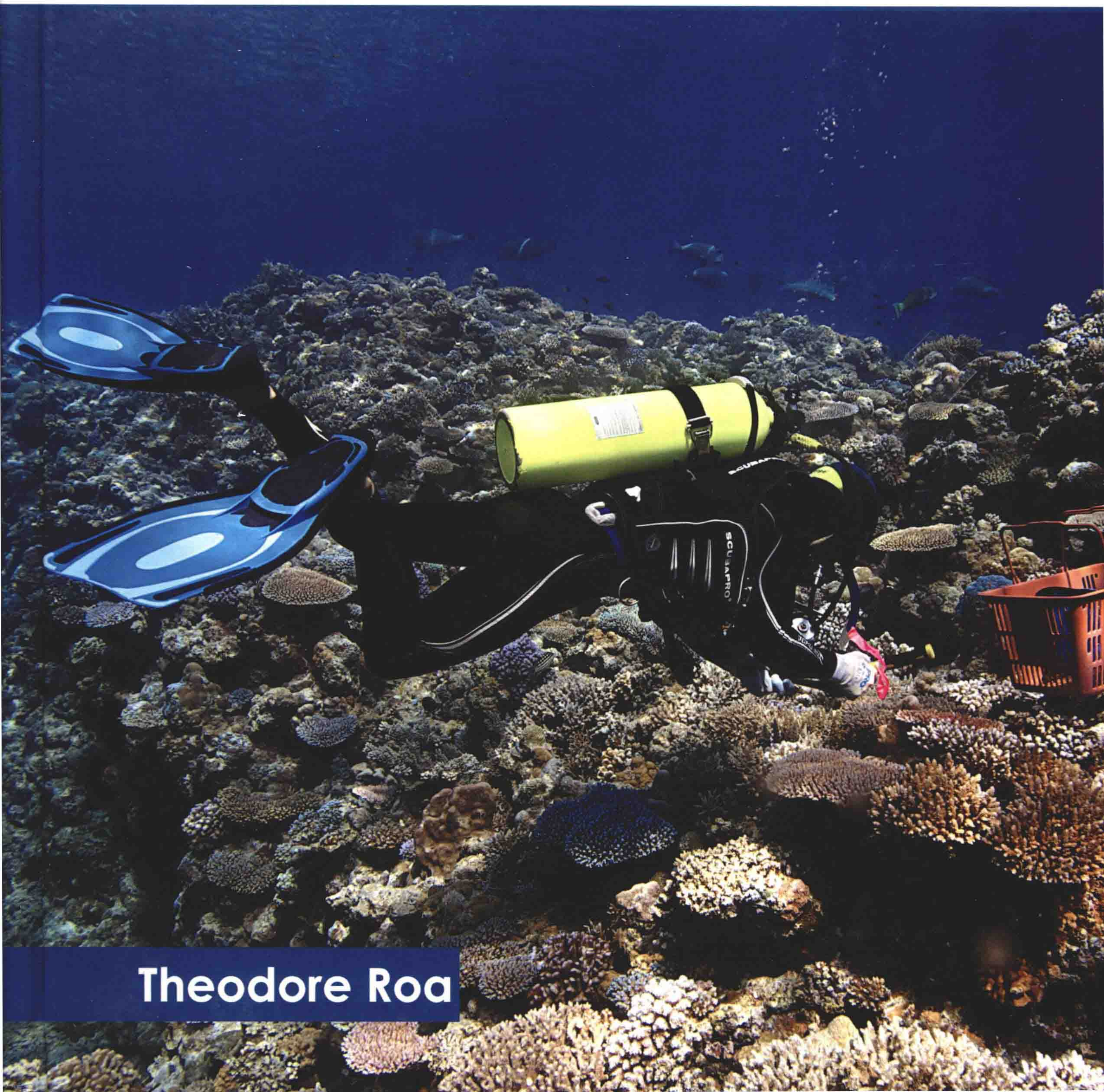
Oceanography

Understanding Oceans



Theodore Roa

Oceanography: Understanding Oceans

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Oceanography: Understanding Oceans

Preface

The aim of this book is to present researches that have transformed the discipline of oceanography, which deals with the study of ocean. From theories to research to practical applications, case studies related to all contemporary topics of relevance to this field have been included in this book. The text highlights important dimensions of oceanography like ecosystem dynamics, ocean currents, waves, plate tectonics, etc. which are important for the readers to get a holistic understanding of this field of study. This book brings forth some of the most innovative concepts and modern applications to elaborate the unexplored aspects of oceanography. This book is an essential guide for both academicians and those who wish to pursue this discipline further. It aims to serve as a resource guide for students and experts alike and contribute to the growth of the discipline.

This book has been a concerted effort by a group of academicians, researchers and scientists, who have contributed their research works for the realization of the book. This book has materialized in the wake of emerging advancements and innovations in this field. Therefore, the need of the hour was to compile all the required researches and disseminate the knowledge to a broad spectrum of people comprising of students, researchers and specialists of the field.

At the end of the preface, I would like to thank the authors for their brilliant chapters and the publisher for guiding us all-through the making of the book till its final stage. Also, I would like to thank my family for providing the support and encouragement throughout my academic career and research projects.

Editor

Table of Contents

Environmental Drivers of the Canadian Arctic Megabenthic Communities

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Abstract

Environmental gradients and their influence on benthic community structure vary over different spatial scales; yet, few studies in the Arctic have attempted to study the influence of environmental gradients of differing spatial scales on megabenthic communities across continental-scales. The current project studied for the first time how megabenthic community structure is related to several environmental factors over 2000 km of the Canadian Arctic, from the Beaufort Sea to northern Baffin Bay. Faunal trawl samples were collected between 2007 and 2011 at 78 stations from 30 to 1000 m depth and patterns in biomass, density, richness, diversity, and taxonomic composition were examined in relation to indirect/spatial gradients (e.g., depth), direct gradients (e.g., bottom oceanographic variables), and resource gradients (e.g., food supply proxies). Six benthic community types were defined based on their biomass-based taxonomic composition. Their distribution was significantly, but moderately, associated with large-scale (100–1000 km) environmental gradients defined by depth, physical water properties (e.g., bottom salinity), and meso-scale (10–100 km) environmental gradients defined by substrate type (hard vs. soft) and sediment organic carbon content. We did not observe a strong decline of bulk biomass, density and richness with depth or a strong increase of those community characteristics with food supply proxies, contrary to our hypothesis. We discuss how local- to meso-scale environmental conditions, such as bottom current regimes and polynyas, sustain biomass-rich communities at specific locations in oligotrophic and in deep regions of the Canadian Arctic. This study demonstrates the value of considering the scales of variability of environmental gradients when interpreting their relevance in structuring of communities.

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Introduction

In Arctic systems, megabenthic communities contribute significantly to bulk benthic biomass [1,2] with high oxygen demands [1,3–5] and important roles in carbon cycling on Arctic shelves [6,7]. Megabenthic communities also provide an important link to higher trophic levels as food for many sea birds and marine mammals [8,9]. Despite their importance in Arctic food webs, little is still known, however, about their distributional patterns and the environmental factors driving them across the large spatial extents, such as the Canadian Arctic Archipelago.

The external drivers of benthic community dynamics change with the spatial scale under investigation. At small scales (e.g., within a sampling station), community structure is controlled mainly by ecological factors such as the availability of niches superimposed by competition and predation, while at meso (10–100 km) to large (100–1000 km) scales it is mainly controlled by environmental gradients [10–13]. Depth and geographic gradients generate large-scale benthic patterns that are well known in the World's oceans [14,15]. For Arctic megafaunal communities, depth is often considered one of the most important large-scale structuring variables [1,16–20]. However, depth is mostly a proxy of other environmental variables that vary vertically, such as physical properties of water masses (temperature, salinity) and declining food availability for slope and deep-sea benthic communities [21]. In the highly seasonal Arctic systems, the declining strength of pelagic-benthic coupling and the resultant reduced food supply is thought to be the most important indirect effect of depth in structuring benthic communities [7,18] and benthic processes [22]. In contrast to large-scale gradients, patterns in current regimes and sea-ice cover, by their influence on primary production and on the sedimentation of organic matter out of the water column, produce meso-scale benthic patterns that are typically regionally specific, such as under polynyas and marginal ice zones in the Arctic [13]. In the quest to elucidate the importance of food supply on Arctic benthic communities, and because of the complexity of biological and physical interactions that can increase or reduce pelagic-benthic coupling, various food supply proxies are often used to interpret benthic community patterns [23]. This study tested a variety of food supply proxies, from estimates of particulate organic carbon (POC) fluxes (e.g., derived from primary productivity in surface waters) to estimates of available organic matter for benthic organisms (e.g., sediment pigment). Substrate variability is also an important local- to meso-scale driver of megabenthic taxonomic composition in both Arctic shelf and slope regions [2,24]. By reflecting near-bottom flow regime, substrate variability influences benthic feeding modes and survival of organisms due to specific requirements from larvae to adult stages [25], and thus profoundly affects benthic community composition.

The Canadian Arctic is an excellent candidate area to test whether large-scale and meso-scale environment-benthic community relationships found elsewhere across the World's oceans also apply within a large, topographically and hydrographically complex Arctic marine environment. The Canadian Arctic is characterized by great depth variation, complex flow dynamics [26], contrasting biological productivity regimes [27], and significant freshwater and sediment inflow from the Mackenzie River, by far the most sediment-rich river discharging into the Arctic Ocean [28].

The current project studied how megabenthic community structure is associated with environmental gradients across 70° longitude (2000 km) of the Canadian Arctic marine environment. The specific objectives of this study were: (1) to delineate community clusters and characterize their structure and distribution patterns, and (2) to evaluate the relationships of environmental factors of various spatial scales with megabenthic community characteristics (e.g., richness, biomass) and community distribution. We hypothesized that: (i) megabenthic biomass, density, richness and diversity decrease with depth and increase with food supply proxies, and (ii) community patterns are associated primarily with large-scale environmental gradients (100–1000 km), and secondarily with meso-scale gradients (10–100 km). This study increases our understanding of the Arctic that is experiencing rapid changes and could serve as a benchmark against which future changes in megabenthic diversity and community patterns could be identified (e.g., species range shifts, invasive species).

Materials and Methods

2.1. Study Area

This study was conducted across the Canadian Arctic from the Mackenzie Shelf in the southeastern Beaufort Sea in the west (135°W) to northern Baffin Bay in the east (65°W) (Figure 1). The two main water masses flowing through the Canadian Arctic originate mainly from the Pacific and Atlantic oceans. The colder-fresher Pacific-origin waters (on average<200 m depth) overlie the warmer-saline Atlantic-origin waters below (on average>200 m depth) [26]. The transition between these water masses coincides generally across the study area with the 200 m isobath along the shelf break [28,29]. The Beaufort Sea and Amundsen Gulf regions are highly influenced by the Mackenzie River that drains a watershed of 1.7×10^{6} km^{2} and discharges approximately 340 km^{3} y^{-1} of freshwater [26] and 127×10^{6} Mt y^{-1} of sediment load [30] into the Beaufort Sea. The complex topography of the Canadian Arctic Archipelago with its numerous islands and channels has a profound influence on sea ice circulation and marine biological productivity regimes [31]. During winter the study area is ice-covered and sea ice could be found throughout the summer as landfast ice or first-year and multiyear pack ice [32,33]. Summer sea ice distribution along with ice break-up and freeze-up dates exhibit large inter-annual variations [32,33]. As a general trend, ice in summer remains longer in the central part of the Archipelago than in areas where large and latent heat polynyas open in spring, such as the North Water (NOW), Lancaster Sound-Bylot Island (LS-BI), and the Cape Bathurst (CB) polynyas [31,34] (Figure 1). Polynyas located in the northeastern Canadian Arctic (i.e., NOW and LS-BI) exhibit intense marine biological productivity and tight pelagic-benthic coupling as revealed by field observations of diatom-based communities [27], satellite-derived high annual primary production (PP) estimates [35], and high sediment chlorophyll *a* (Chl *a*) concentrations and benthic boundary fluxes [36,37]. In the CB polynya, in contrast, highly variable intensity, timing and duration of phytoplankton blooms [38], and strong grazing pressure by zooplankton leads to weak pelagic-benthic coupling [37,39,40]. The central Archipelago has been defined as an oligotrophic system [27].

2.2. Ethics Statement

Sampling licenses were obtained for the Northwest Territories (Canada) by the Aurora Research Institute (#14258, #14304, #14543, #14678, #14917), by the Environmental Impact Screening Committee (#06 07 05, #06 03 10, #03 09 03), and by the Department of Fisheries and Oceans (DFO) (#S-07/08-4017-IN, #S-09/10-4013-IN, #S-10/11-3026-YK, #S-11/12-3026-YK). For Nunavut (Canada) permits were provided by the Nunavut Research Institute (#0500907R-M, #0501408R-M, #0504609R-M, #0505510R-M, #0506511R-M) and by DFO (S-07/08-1034-NU, #S-08/09-1043-NU, # S-09/10-1049-NU, #S-10/11-1021-NU, #S-11/12-1029-NU).

2.3. Faunal data collection

Benthic fauna were sampled at 78 stations between June and October from 2007 to 2011 onboard the Canadian research icebreaker CCGS *Amundsen* (Table S1 in File S1). Station depths ranged from 34 to 1024 m, all below the average ice scouring zone [28,41]. All faunal samples were collected with an Agassiz trawl (effective opening of 1.5 m and a 40 mm net mesh size, with a 5 mm cod end liner) with average trawling time and speed of 5 min and 1.5 knots, respectively. In order to standardize community characteristics among stations (by m^{-2}), bottom trawling time and vessel speed at each station were used to calculate towed area (trawl opening of 1.5 m× distance towed; average trawled area of 372 ± 161 m^{-2}). This trawl design is very effective at collecting both epibenthic and burrowing, large-sized invertebrates. Based on the methodology of Piepenburg et al. [19], invertebrates larger than 2 cm were sorted from the trawl catches directly after capture and classified as megabenthos. In addition, the sediment contained in the catches was washed through a 2 mm sieve under running seawater onboard [19]. Planktonic invertebrates that were accidentally taken by the trawl (e.g., Chaetognatha, Euphausiacea, Scyphozoa) and Pisces were removed to only include benthic invertebrates in the sample analysis. Members of the class Ascidiacea were not considered in this study due to exclusion of this taxon during the first years of sampling. Only large echinoderm taxa that could be reliably identified to species level were counted and wet-weighed in the field given the low precision of on-board mass measurements (detection limit of 5 g). All other taxa were preserved in a 4% seawater-formaldehyde solution buffered with sodium tetraethylborate or frozen for later identification in the lab, and their biomass was determined as formaldehyde wet mass or wet mass (after thawing) at 0.001 g precision. Possible biases in total biomass calculations introduced by different preservation methods were considered minor since all specimens within a phylum were processed the same way and trawl catches were considered semi-quantitative estimates [42,43]. Only specimens with the head-part intact were counted and identified to the lowest possible taxonomic level. However, some taxa were left at the phylum level because no complete identification keys exist for Canadian Arctic waters (e.g., Brachiopoda, Nemertea, Platyhelminthes,

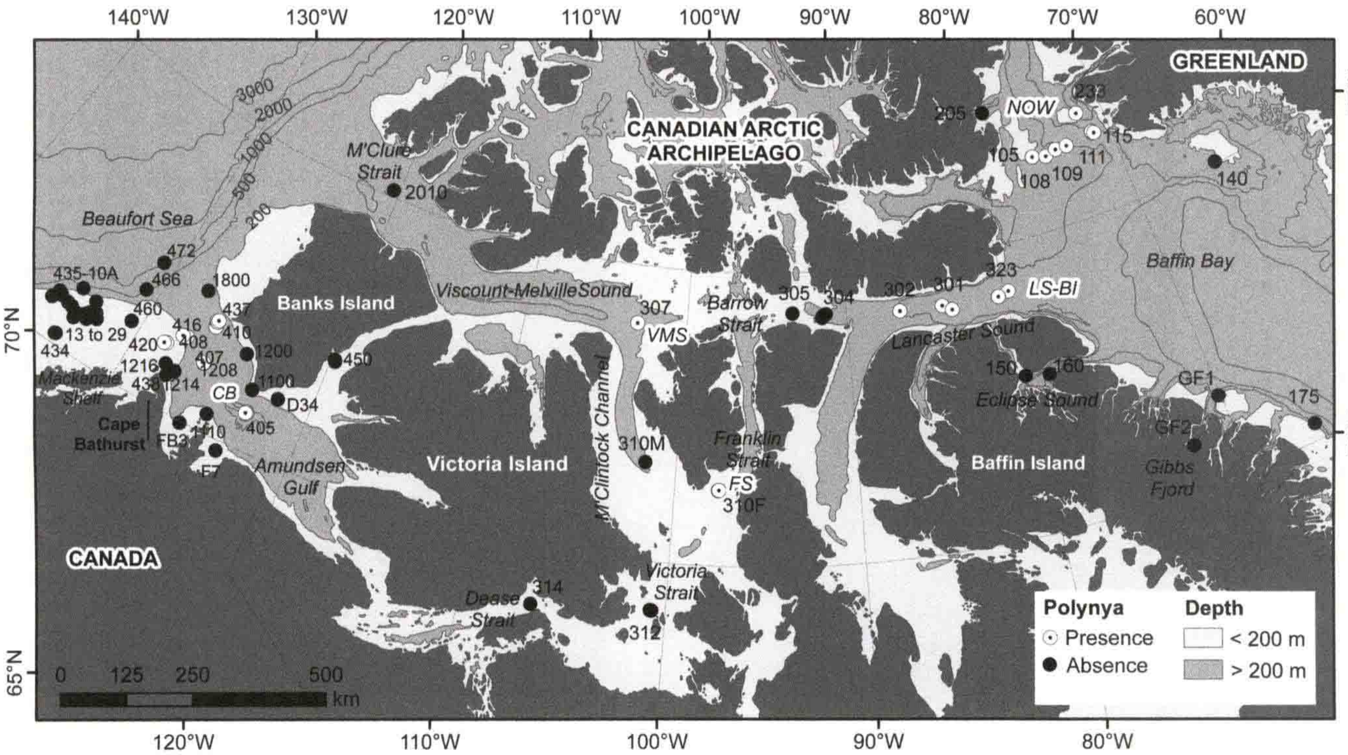

Figure 1. Locations of stations sampled from 2007 to 2011 across the Canadian Arctic. Stations sampled in areas where polynyas are recurrently present (white circles) or absent (black circles). Station codes correspond to ArcticNet expedition labels, sampling years were not added for clarity (see Table S2 in File S1). Names of polynyas are indicated by capital italic letters (*CB*: Cape Bathurst polynya, *FS*: Franklin Strait polynya, *LS-BI*: Lancaster Sound-Bylot Island polynya, *NOW*: North Water polynya, *VMS*: Viscount-Melville Sound polynya). The shelf break and the transition between the Pacific and Atlantic water masses are both around 200 m (<200 m: shelf and Pacific layer; >200 m: slope and Atlantic layer).

Porifera); we acknowledge that their richness will have been underestimated in this study. Taxonomic names were verified using the World Register of Marine Species (WoRMS, [44]). Four species of the phylum Bryozoa and one from the phylum Hydrozoa were not listed in WoRMS but were verified using the Integrated Taxonomic Information System (ITIS, www.itis.gov) (i.e., Bryozoa: *Cellepora smitti, Escharopsis rosacea, Escharopsis sarsi, Porella sacata*; Hydrozoa: *Obelia loveni*).

2.4. Environmental data collection

Explanatory environmental variables available for the present study (Table S2 in File S1) were divided into three categories: resource, direct and indirect/spatial gradients (following McArthur et al. [14]). Resource gradients included estimates of vertical POC fluxes derived from primary productivity in surface waters (e.g., phytoplankton biomass, PP estimates) to sediment variables that were proxies of the energy available for benthic consumers (e.g., sediment pigments, sediment organic carbon). Resource gradient variables are called hereafter 'food supply proxies'. Direct gradients included bottom oceanographic variables (i.e., temperature, oxygen, salinity), seabed substrate type (hard vs. soft) and terrestrial influence on the benthic habitat (i.e., sediment $\delta^{13}C$), these variables selecting for the type of physiology, morphology and/or life history of species residing there. Finally, indirect/spatial gradients consisted of purely spatial variables (depth, latitude and longitude) that often correlate with direct and resource variables but with no direct physiological influence on the species. All these environmental gradient categories vary on different temporal scales and we assessed their temporal variability as follow (Table 1). Spatial variables were assumed temporally stable, except on geological time scales. Direct variables were overall assumed to be unchanging on less than a decadal scale [31]. Food supply proxies fluctuate either on a seasonal basis (e.g., phytoplankton biomass [27] and sediment Chl *a* [45,46]) or on a multi-annual basis (e.g., PP estimates integrated over years, sediment organic carbon [47,48]). Additionally, these environmental categories exhibit measurable heterogeneity at different spatial scales, from study area extent to distance between stations. In a continental-scale study such as this one, indirect/spatial and direct gradients should mostly influence benthic community patterns over large geographic scales (100–1000 km), while resource gradients should induce environmental heterogeneity mainly at meso-geographic scales (10–100 km) (Table 1) [13].

2.4.1. Food supply proxies - primary productivity. We used pelagic primary productivity estimates as food supply proxies for benthic organisms based on the assumption that areas with higher pelagic primary productivity should generally have higher vertical POC fluxes [14]. We consequently evaluated if the spatial variability in primary productivity of surface waters was linked to the spatial variability observed in benthic community patterns. Various estimates of primary productivity differ in their temporal integration of the variability of a system. For seasonal variability, we used phytoplankton biomass estimates based on water Chl *a* concentrations measured at the time and locations of faunal sampling and integrated over the euphotic zone (from surface to 0.2% surface light level). We also tested if different size fractions of phytoplankton biomass estimates would be linked with the same strength to benthic community patterns, as large cells sink rapidly and are therefore supposed to contribute most to the carbon flux reaching the seafloor [49]. We estimated the following phytoplankton biomass size fractions: euphotic BT = total phytoplankton biomass (cells $\geq$ 0.7 μm; mg Chl *a* m^{-2}); euphotic BS =

Table 1. Spearman rank correlation coefficients for relationships between benthic univariate community characteristics and environmental variables. Significant correlations ($p<0.01$) are indicated in bold.

Spatial variability	**Meso to large scale (in continental-scale study)**						**Large scale (100–1000 km)**							**Meso scale (10–100 km)**						
Temporal variability	**Years to decades**						**Relatively stable**			**Low (>10 years)**			**Medium (1–10 years)**				**High (seasonal)**			
Variable type	**Benthic community characteristic**						**Indirect/spatial gradient**			**Direct gradient**				**Resource gradient/food supply proxy**						
	Biomass	**Density**	**$S_{density}$**	**H′**	**J′**	**Δ***	**Latitude**	**Longitude**	**Depth**	**Temperature**	**Salinity**	**Oxygen**	**Sed. $\delta^{13}C$**	**Sed. OC**	**PP 5Y**	**PP 1Y**	**Sed. phaeo**	**Sed. Chl *a***	**Euphotic B_T**	**Euphotic B_S**	**Euphotic B_L**
Biomass	1.00																				
Density	**0.84**	1.00																			
$S_{density}$	**0.64**	**0.73**	1.00																		
H′	−0.05	0.20	**0.30**	1.00																	
J′	**−0.40**	−0.15	−0.20	**0.79**	1.00																
Δ*	−0.11	−0.07	0.00	−0.12	−0.05	1.00															
Latitude	0.07	−0.11	−0.11	**−0.44**	**−0.35**	−0.06	1.00														
Longitude	0.01	−0.16	−0.07	−0.27	−0.16	0.04	**0.57**	1.00													
Depth	−0.25	**−0.34**	−0.26	**−0.39**	−0.20	−0.02	**0.66**	**0.65**	1.00												
Temperature	−0.12	−0.19	−0.18	**−0.37**	−0.19	−0.11	**0.46**	**0.46**	**0.76**	1.00											
Salinity	**−0.38**	**−0.44**	**−0.51**	**−0.45**	−0.11	−0.04	**0.47**	0.29	**0.79**	**0.71**	1.00										
Oxygen	0.22	**0.30**	**0.43**	**0.38**	0.08	0.02	**−0.50**	**−0.55**	**−0.67**	**−0.61**	**−0.65**	1.00									
Sed. $\delta^{13}C$	−0.06	−0.25	−0.25	−0.28	−0.20	0.03	**0.59**	**0.76**	**0.60**	**0.37**	**0.37**	**−0.55**	1.00								
Sed. OC	0.01	0.00	−0.02	0.15	0.12	−0.01	0.26	−0.09	0.16	0.12	0.15	−0.17	0.06	1.00							
PP 5Y	**0.45**	**0.38**	0.26	0.16	−0.01	−0.10	−0.07	−0.30	nr	nr	nr	nr	−0.31	**0.57**	1.00						
PP 1Y	**0.44**	**0.35**	0.30	0.20	−0.01	−0.22	−0.07	−0.30	nr	nr	nr	nr	−0.29	**0.51**	**0.92**	1.00					
Sed. phaeo	0.25	0.17	0.09	0.17	0.05	0.02	0.24	0.10	−0.01	−0.08	−0.19	−0.06	0.17	**0.65**	**0.56**	**0.44**	1.00				
Sed. Chl *a*	**0.36**	0.31	0.25	0.28	0.05	−0.08	−0.03	−0.15	**−0.38**	−0.33	**−0.54**	0.28	0.03	**0.51**	**0.58**	**0.55**	**0.80**	1.00			
Euphotic B_T	−0.18	−0.21	−0.15	−0.20	−0.15	−0.04	0.17	**0.45**	nr	nr	nr	nr	**0.61**	−0.18	**−0.35**	**−0.40**	−0.03	−0.12	1.00		
Euphotic B_S	−0.12	−0.07	0.06	−0.04	−0.08	−0.06	−0.12	0.05	nr	nr	nr	nr	−0.10	−0.06	−0.24	−0.31	−0.21	−0.31	**0.55**	1.00	
Euphotic B_L	0.18	0.13	0.10	−0.03	−0.19	−0.12	0.13	0.24	nr	nr	nr	nr	**0.55**	0.13	0.07	−0.03	**0.36**	**0.40**	**0.89**	0.21	1.00
Euphotic B_L:B_T	0.28	0.25	0.04	0.06	−0.01	−0.08	0.05	0.10	nr	nr	nr	nr	**0.50**	0.19	0.30	0.24	**0.47**	**0.56**	**0.45**	−0.34	**0.78**

Benthic community characteristics: biomass (g m^{-2}); density (ind. m^{-2}; without colonial organisms); $S_{density}$: taxon richness density (number of taxa m^{-2}); H′: Shannon–Wiener's diversity index; J′: Pielou's evenness index; Δ*: average taxonomic distinctness. Indirect/spatial gradients: latitude and longitude (km; starting at the most southwestern station); depth (m). Direct gradients: Bottom oceanographic variables: temperature (°C); salinity; oxygen (ml l^{-1}); Terrestrial influence: sediment $\delta^{13}C$ (‰). Resource gradients/food supply proxies: sed. OC: sediment organic carbon (%); PP: sum of monthly satellite-derived primary production estimates over one (PP 1Y) or five years (PP 5Y) before sampling (mg C m^{-2} y^{-1}; model results of Bélanger et al. [35]); sed. phaeo: sediment phaeopigments (μg g^{-1}); sediment Chl *a* (μg g^{-1}); euphotic B_T: total phytoplankton biomass (cells ≥ 0.7 μm; mg Chl *a* m^{-2}); euphotic B_S: biomass of small phytoplankton cells (0.7–5 μm; mg Chl *a* m^{-2}); euphotic B_L: biomass of large phytoplankton cells (≥ 5 μm; mg Chl *a* m^{-2}); euphotic B_L:B_T: relative contribution of large cells to total biomass. nr: biologically not relevant.

biomass of small phytoplankton cells (0.7−5 μm; mg Chl *a* m^{-2}); euphotic BL = biomass of large phytoplankton cells (≥ 5 μm; mg Chl *a* m^{-2}); and euphotic BL:BT = relative contribution of large cells to total biomass (Table 1). Data were available at 73 stations and details on the sampling and analytical methods are found in Ardyna et al. [27]. In addition, we summed satellite-derived monthly PP estimates to assess annual variability of primary productivity (Table 1). Sums of monthly PP estimates over one (PP 1Y) and five years (PP 5Y) before faunal sampling were determined for a 20 km radius around each sampling station based on model results of Bélanger et al. [35] (data available for 71 stations). Sampling stations were also categorized according to presence (n = 30 stations) and absence (n = 48 stations) of a polynya (based on Arrigo and van Dijken [38] and Barber and Massom [50]) as a proxy of ice conditions and primary productivity.

2.4.2. Food supply proxies - surface sediment. We evaluated the seasonal contribution of 'fresh' organic matter inputs to the benthos as sediment Chl *a* and phaeopigments (degraded chlorophyll) concentrations, and by using sediment organic carbon as an estimate of average annual input. From 2008 to 2011, a USNEL box corer (0.25 m^2) was deployed for collecting surface sediments (upper 1 cm) in triplicate using a 60 ml disposable syringe (2.6 cm diameter with a cut off anterior end). Sediment samples for pigment concentration (Chl *a* and phaeopigments) and organic carbon content were immediately frozen at −80°C and −20°C, respectively, for later analysis in the lab. Pigment concentrations were analysed fluorometrically following a modified protocol by Riaux-Gobin and Klein [51] and are expressed as microgram pigment per gram of dry sediment. Sediment organic carbon content was determined after acidification (HCl 10%) with a Costech 4010 elemental analyser (Marine Chemistry and Mass Spectrometry Laboratory, Université du Québec à Rimouski, Canada). Sediment organic carbon content is expressed as % of total sediment dry weight.

2.4.3. Terrestrial organic matter input. Sediment δ^{13}C was used as a measure of the contribution of terrestrial organic carbon input in order to investigate influence of coastal erosion and river sediment discharge on the benthic community structure. Sediment samples were collected and preserved the same way as sediment organic carbon described above. Sediment δ^{13}C was determined after acidification (HCl 10%) with a CF-IRMS (continuous-flow Isotope Ratio Mass Spectrometry) (Marine Chemistry and Mass Spectrometry Laboratory, Université du Québec à Rimouski, Rimouski, Québec, Canada) and is reported in standard delta notation in ‰ with respect to VPDB (Vienna Pee Dee Belemnite). Lighter sediment isotopic δ^{13}C values (−28 to −26‰) are typical of terrigenous organic matter while heavier isotopic δ^{13}C values (−24 to −20‰) are typical of marine production [52].

2.4.4. Bottom oceanographic variables. Bottom water characteristics were measured at all stations from 2007 to 2011. Near-bottom water temperature (°C), salinity and dissolved oxygen concentration (ml l^{-1}) were determined by the shipboard CTD Seabird profiler (SBE911 Plus), combined with a SBE 43 dissolved oxygen sensor, at 10 m above the seafloor.

2.4.5. Substrate type. Because sediment particle size samples could not be consistently sampled during all years, we instead used a qualitative classification based on visual observations of trawls and box corers to assess the substrate type at each station. Substrate category 'hard' was assigned to stations with substantial amounts of gravel and cobbles, and 'soft' assigned to stations with mud (silt and clay), sand and no or little gravel. Overall, fewer hard substrate stations (19 of 78 total stations) were sampled to avoid damaging the trawl and box corer, so that hard bottom stations are under-represented in this study. Near-bottom current speed could not be assessed for this study, but substrate type may be regarded as a proxy for current velocity with coarser substrate indicating a higher near-bottom flow regime [25].

2.5. Data analysis

Benthic community characteristics considered in this study for each of the 78 stations were biomass (g m^{-2}), density (ind. m^{-2}), and four biodiversity metrics (taxonomic richness density ($S_{density}$, number of taxa 1000 m^{-2}), Shannon-Wiener's diversity index (H′, using log$_e$), Pielou's evenness index (J′), and average taxonomic distinctness (Δ*)). H′, J′ and Δ* were calculated based on biomass data including colonial taxa. Density was calculated after removal of colonial taxa because their abundance cannot be recorded (i.e., Bryozoa, Hydrozoa, Nephtheidae (soft corals), Porifera). Δ* estimates the average distance between two randomly chosen organisms through Linnean taxonomy and is considered to be a more genuine reflection of biodiversity than the other diversity indices because it considers taxonomic relationships [53]. Six taxonomic levels were used in Δ* calculations: species, genus, family, order, class and phylum, assuming equal step weights between successive taxonomic levels; when necessary, the lowest taxonomic level available was used for missing level(s) (performed using PRIMER-E software version 6 [54]). Correlations between benthic community characteristics and quantitative environmental variables were assessed using Spearman rank correlations to investigate the intensity of all possible relations following a positive or negative monotonic trend [55]. Prior to correlation analysis, we verified by visual observation that no relationship was quadratic (hump-shape curve). Simple linear regressions were performed to model the relationships between benthic community characteristics and depth as an environmental proxy measure often used in benthic studies. Normality of residuals was examined by plotting theoretical quantiles vs. standardized residuals (Q-Q plots) and homogeneity of variance was assessed by plotting residual vs. fitted (predicted) values. Mann-Whitney *U* tests were used to seek differences in benthic community characteristics between the environmental categories substrate type (hard vs. soft) and polynya (presence vs. absence). Kruskal-Wallis tests with post-hoc multiple comparison tests were carried out to test differences among community clusters (see below).

For multivariate analyses, lists of taxa at each station were scaled at the genus level and taxa only found at one station were discarded, for a total of 303 unique taxa found at least at two stations. Singletons in multivariate analysis are prone to random and uninterpretable fluctuations, and it is consequently suggested to remove them to allow better detection of the underlying community similarities [53]. Scaling at the genus level was done because identifications were patchy at the species level among stations; in some cases, specimens were incomplete and missing criteria prevented identification at the species level. Bray-Curtis dissimilarity was calculated for the fourth-root-transformed biomass matrix rather than for the density matrix to be able to include colonial taxa. The fourth-root transformation was chosen to balance the effects of high- and low-biomass taxa to assess responses of the whole communities [53]. The dissimilarity matrix was then subjected to a hierarchical cluster analysis using Ward's minimum variance method, which seeks to define well-delimited groups by minimizing within-cluster sum of squares [56]. Community clusters were determined by selecting a distance where stations were fused in well-defined clusters. To find indicator taxa within each community cluster, the indicator value index (IndVal) method of Dufrêne and Legendre [57] was applied

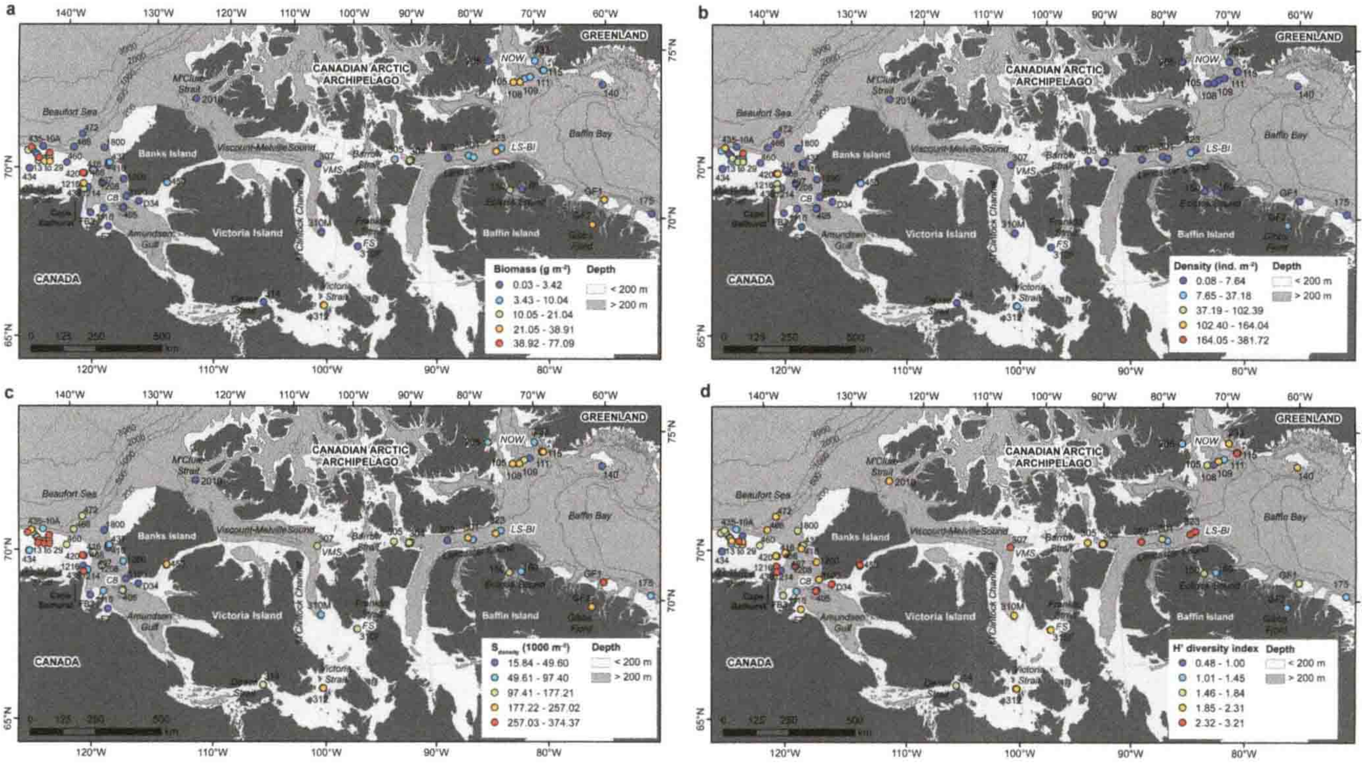

Figure 2. Distributions of benthic community characteristics at 78 stations over 2007–2011. (**a**) biomass (g m^{-2}); (**b**) density (ind. m^{-2}); (**c**) $S_{density}$ (no. of taxa 1000 m^{-2}); (**d**) Shannon-Wiener's diversity index (H').

on the biomass data matrix. IndVal is a measure of association between a taxon and a cluster of stations and is calculated as the product of specificity (mean biomass of a given taxon within a cluster compared to the other clusters) and fidelity (taxon occurrence at stations belonging to a cluster). IndVal is maximal (= 100%) when a given taxon is observed at all stations of only one community cluster and in none of the other clusters. Statistical significances of indicator taxa were tested by random permutation of stations (9999 permutations) and only the five significant indicator taxa with the greatest IndVal value are discussed per community cluster. The influence of all environmental variables on the taxonomic composition was tested on 50 stations (out of 78 stations total) by the use of redundancy analysis (RDA), a direct extension of regression analysis to model multivariate response data. The other 28 stations had to be removed (2007: all 10 stations; 2008: n = 9; 2009: n = 1; 2010 n = 3: 2011: n = 5) because of some missing food supply proxies. A Principal Component Analysis (PCA) plot showing the multivariate similarity among the 50 stations in terms of environmental variables is available in Supporting Information (Figure S1 in File S1). Removing stations for the RDA reduced the total number of taxa found at least at two stations from 303 to 266. The RDA was performed after Hellinger transformation to reduce the importance of dominant taxa [58]. Environmental variables entered into the model were: seven food supply proxies (polynya presence/absence, PP 1Y and PP 5Y, sediment organic carbon, sediment phaeopigments, sediment Chl *a*, and euphotic B_T), five direct variables (three bottom oceanographic variables (bottom oxygen, salinity and temperature), substrate type, sediment $\delta^{13}C$), and three indirect/spatial variables (depth, latitude, longitude). We performed two RDA: one included variables from all types of environmental categories and the other excluded indirect/spatial variables because the latter may mask food supply and direct gradients that have higher ecological significance [14]. Reduction of explanatory variables was performed by forward selection on the basis of their permutation *p* values (9999 permutations) and on Akaike's Information Criterion (AIC) in case of ties. Collinearity of significant forward selected explanatory variables was verified looking at variance inflation factors (VIF)<10 [55].

Statistical analyses were performed using the statistical package R version 3.0 [59]. Statistical significance at $\alpha<0.05$ was used for all statistical tests except for Spearman correlations and Kruskal-Wallis post-hoc multiple comparison tests, where a statistical significance at $\alpha<0.01$ was used to account for the increasing probability of type I error in multiple testing [55]. The distribution of biomass, density, $S_{density}$ and H' were mapped with ArcGIS 9.3.1 with color bins defined by the Jenks iterative method which minimizes within class difference and maximizes between class differences [60].

Results

3.1. Community characteristics: biological and environmental linkages

A total of 527 unique taxa were identified at the lowest possible taxonomic level across all 78 stations (430 at the species level) (Table S3 in File S1). Faunal biomass across all stations ranged from<1 to 77 g m^{-2}, density from<1 to 382 ind. m^{-2}, $S_{density}$ from 16 to 374 taxa 1000 m^{-2}, H' from 0.48 to 3.21, J' from 0.16 to 0.85, and Δ^* from 71.8 to 99.4 (Table S1 in File S1). Distribution of benthic biomass, density, $S_{density}$ and H' showed some distinct spatial patterns (Figure 2); J' and Δ^* were not mapped due to their poor association with environmental gradients. Density, biomass and $S_{density}$ were positively correlated with each other, as were H' and J' (Table 1). Biomass and J' were negatively correlated, and Δ^* was not correlated with any community characteristics and also with no environmental variables.

Among the relationships tested with indirect/spatial variables, H′ and J′ were negatively correlated with latitude (from south to north); density and H′ were negatively correlated with depth. Regression models relating benthic biomass, density, $S_{density}$ and H′ with depth had poor explanatory power, in part due to the positive influence of the productive LS-BI and NOW polynyas at deep stations (Figure 3). Among the correlations tested with bottom oceanographic variables, H′ was negatively correlated with temperature; biomass, density, $S_{density}$ and H′ were negatively correlated with salinity; density, $S_{density}$ and H′ were positively correlated with oxygen. Among the correlations tested with food supply proxies, biomass and density were positively correlated with PP 1Y and PP 5Y, and biomass was positively correlated with sediment Chl *a* (Table 1). No benthic community characteristic was significantly correlated with sediment δ^{13}C, sediment organic carbon, sediment phaeopigments, or any descriptors of euphotic phytoplankton biomass. Lower $S_{density}$ and H′ values were found in hard substrate stations than in soft substrate stations (Table 2). H′ was significantly lower at stations located within than outside a polynya (Table 2).

Spatial variables were highly correlated (correlation coefficient>0.5) with all direct gradient variables (bottom oceanographic variables and sediment δ^{13}C) (Table 1). Sediment Chl *a* was the only sediment food supply proxy correlated negatively with depth. Food supply proxies in surface waters representing different temporal integration of primary productivity varied in opposite directions: integrated PP estimates (PP 1Y and PP 5Y) and seasonal euphotic B_T were negatively correlated. However, food supply proxies in sediment varied in the same direction: sediment organic carbon, sediment phaeopigments and sediment Chl *a* were positively correlated. These latter three sediment food supply proxies also were positively correlated with PP 1Y and PP 5Y; only sediment phaeopigments and sediment Chl *a* were positively correlated with the highly seasonal euphotic B_L and euphotic B_L:B_T (Table 1).

3.2. Community clusters and distribution patterns

Ward clustering analysis resulted in six well-defined community clusters (Figure 4). We attributed a 'label' to each community cluster based on three variables (mean biomass, mean depth, proportion of hard/soft substrate stations) and their respective minimal and maximal values among clusters (Table 3). The term 'coldspots' was attributed to the community cluster with the lowest mean biomass, and the term 'hotspots' was given to the community cluster characterized by highest mean biomass. Because the 'hotspots' community type was spatially distributed at discrete locations across the study area, we named it 'local hotspots' community. Substrate type (hard or soft) was added to the name of a cluster when almost all, if not all stations, were of one substrate type. The mean depth around the 200 m shelf break was chosen as the main attribute for the 'shelf break' cluster. Depth was used as a descriptor when all stations were deeper than 200 m (only station 1216 in 'deep soft substrate' cluster was < 200 m, Figure 5). The 'Mackenzie Shelf' community cluster was the only one named based on its geographical location (Figure 5) and was the most dissimilar in terms of taxonomic composition compared with all other clusters (Figure 4). The other five community clusters formed two major groups: one group with two clusters found at deep stations ('deep coldspots' and 'deep soft substrate' clusters) and the second group composed of the remaining three community clusters ('hard substrate', 'shelf break', 'local hotspots') (Figure 4). Across all community clusters, dominant taxa in terms of biomass were often large echinoderms (e.g., sea star, brittle star, basket star, sea cucumber), sea anemones and sponges, but also high biomass of the bivalves *Astarte* spp. and isopods *Saduria* spp. prevailed in some community clusters (Table 3). The distinctiveness of the 'Mackenzie Shelf' taxonomic composition was well represented by the high 'IndVal' index values (≥82%) of the top five significant indicator taxa, meaning that those taxa were almost exclusively found in this community cluster (Table 3). Comparatively, the significant indicator taxa of the other five community clusters had 'IndVal' values between 22% and 62% and occurred in more than one community cluster (Table 3). The 'Mackenzie Shelf' community cluster was composed of stations with significantly higher biomass, density and $S_{density}$ than stations in 'deep coldspots' and 'shelf break' clusters, and with higher H′ than 'deep coldspots' and 'local hotspots' communities (Table 2). 'Local hotspots' community cluster stations had greater biomass than stations in 'deep coldspots' and 'shelf break' communities, and greater density than 'deep coldspots' cluster stations (Table 2). J′ and Δ* were not significantly different among community clusters (Table 2). Relative mean biomass contribution of the main phyla and cumulative total biomass varied between community clusters (Figure 6). The 'Mackenzie Shelf' community cluster was characterized by high biomass of Echinodermata (43%) and Bivalvia (28%). Echinodermata dominated biomass (76%; mostly Ophiuroidea) at almost all stations of the 'deep coldspots' cluster. Biomass of Echinodermata (47%; almost equally Asteroidea, Crinoidea, Holothuroidea and Ophiuroidea), Bivalvia (27%) and Cnidaria (17%; mostly Anthozoa) were high at several stations of the 'deep soft substrate' cluster. For stations of the 'hard substrate' cluster, Porifera (65%) and Echinodermata (23%; mostly Echinoidea) were dominating biomass. 'Shelf break' and 'local hotspots' clusters were similar in relative biomass with high Echinodermata biomass (43–62%; both having predominantly high biomass of Echinoidea, but successively high biomass of Holothuroidea for 'local hotspots' and high biomass of Asteroidea and Ophiuroidea for 'shelf break'), and high biomass of Arthropoda (14–22%) and Mollusca (15–16%). A station-based account of the relative contribution of the main phyla for biomass and taxonomic richness is available in the Supporting Information (Figure S2 in File S1).

3.3. Environmental drivers of community clusters

Community clusters were significantly influenced by a set of environmental variables that explained between 19% and 22% ($R^2_{adjusted}$) of the variation in the RDA analysis. These are low but typical variance levels explained for biological systems [61], as the high complexity of these systems rarely makes it conceivable to encompass all the variables that balance the responses of organisms or communities [62]. Among the fifteen explanatory variables (including indirect/spatial variables) employed in the forward selection of the RDA model on 50 stations, seven variables were retained (Table 4, Figure 7a). The final model significantly explained 22% of the taxonomic composition variation ($R^2 = 0.33$, $R^2_{adj} = 0.22$). Depth, longitude, latitude, sediment Chl *a* and bottom oxygen were strongly correlated with the first RDA axis, while substrate type and sediment organic carbon were highly correlated with the second RDA axis (Table 4, Figure 7a). Among the twelve explanatory variables included in the forward selection of the RDA model excluding indirect/spatial variables, six were retained (Table 4, Figure 7b). The final model significantly explained 19% of the mega-epibenthic taxonomic composition variation ($R^2 = 0.29$, $R^2_{adj} = 0.19$). Bottom salinity, oxygen, temperature and sediment δ^{13}C were strongly correlated with

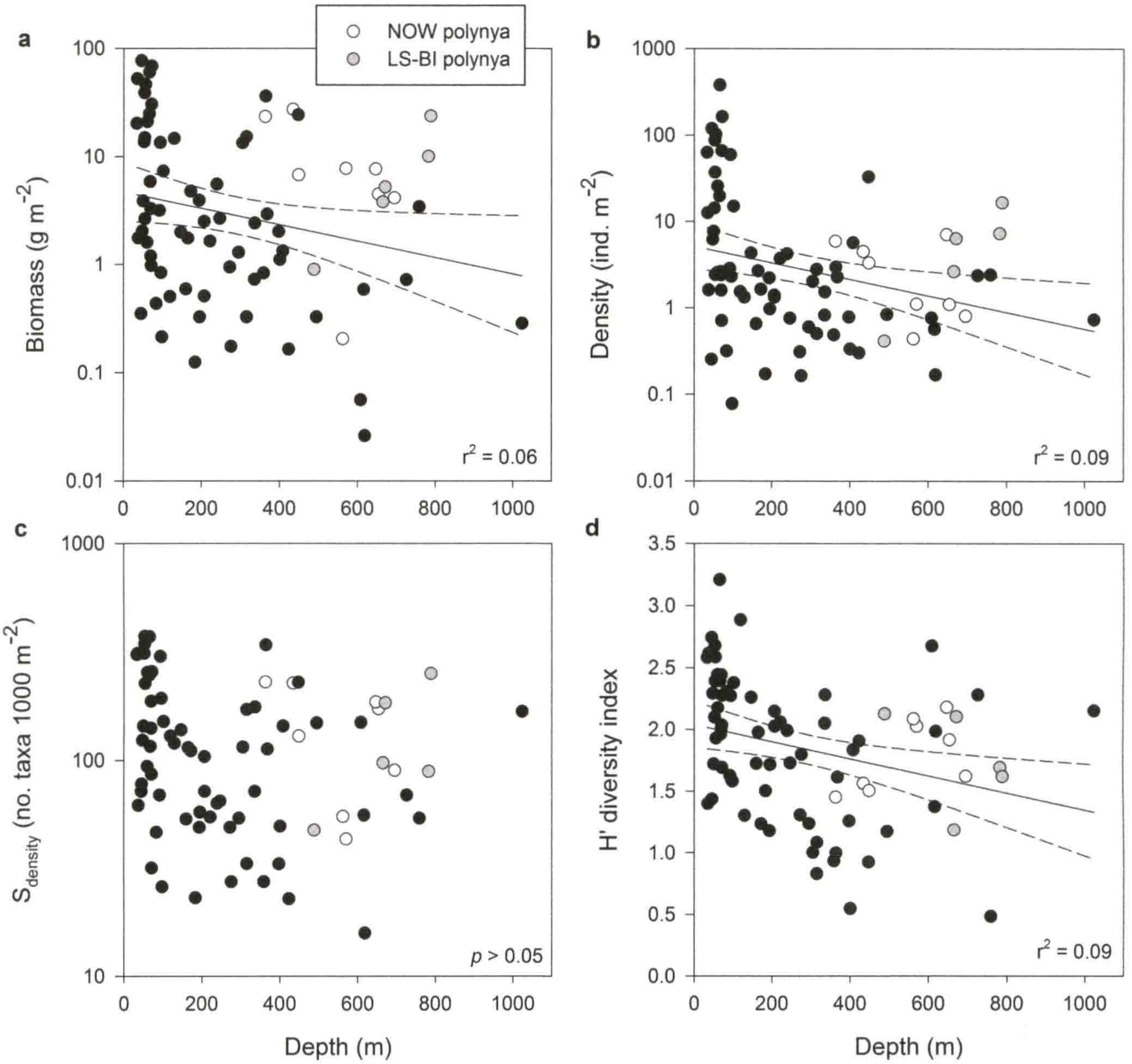

Figure 3. Relationships of benthic community characteristics with depth. Stations sampled underneath Lancaster Sound-Bylot Island polynya (LS-BI; gray circles) and NOW polynya (white circles) are highlighted. (**a**) biomass (g m^{-2}); (**b**) density (ind. m^{-2}); (**c**) $S_{density}$ (no. of taxa 1000 m^{-2}); (**d**) Shannon-Wiener's diversity index (H'). Coefficients of determination of significant linear regressions ($p<0.05$) are shown and dashed lines represent 95% confidence intervals.

the first RDA axis, while substrate type and sediment organic carbon were highly correlated with the second RDA axis (Table 4, Figure 7b). The first RDA axes of both models reflected mostly the distribution of community clusters along two large-scale environmental gradients (100–1000 km): (1) a vertical gradient created by depth, bottom oceanographic variables and sediment Chl *a* variables, and (2) a geographical gradient generated by longitude, latitude and sediment δ^{13}C variables. The second RDA axes of the models reflected the distribution of community clusters along a meso-scale environmental gradient (10–100 km) of the sedimentary environment characterized by the variables substrate type and sediment organic carbon. The six community clusters obtained from the unconstrained Ward clustering analysis (Figure 4) were well segregated within the RDA models, except the 'local hotspots' community cluster with stations scattered along the second RDA axes. The sediment organic carbon content recorded within this community was highly variable, from high values underneath NOW polynya and in Barrow Strait to low values in Victoria Strait and off Cape Bathurst (Table S2 in File S1).

Discussion

This study represents the first continental-scale assessment of the taxonomic composition of megabenthic communities and the relationships of various environmental factors acting at different spatial and temporal scales to their community structure. As we