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# Influence of seabird colonies and other environmental variables on benthic community structure, Lancaster Sound Region, Canadian Arctic



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## ABSTRACT

The Canadian Arctic shelters millions of seabirds each year during the breeding season. By the excretion of important quantities of guano, seabirds locally concentrate nutrient-rich organic matter in the marine areas surrounding colonies. Seabirds, acting as biological vectors of nutrients, can markedly affect terrestrial ecosystems, but their influence on the structure of marine benthic communities is still under-studied. Sessile and long-lived megabenthic species can integrate environmental variation into marine food webs over long time frames. The objectives of this study were (1) to characterize the epifaunal and infaunal communities of the Lancaster Sound Region (LSR) and (2) to test the influence of the presence of seabird colonies and other environmental parameters on the structure of those benthic communities. Our prediction was that benthic diversity, number of taxa, total biomass of infauna and total density of epifauna and infauna, would be higher in areas with colonies present. Photos of the seafloor (data on epifauna) and grab samples (data on infauna) were taken at three control areas and at five areas near seabird colonies, within a depth range of 122 to 442 m. A database of 26 environmental parameters was built to study the environment-benthos relationships. Infauna, which was relatively uniform across the LSR, was numerically dominated by Annelida. Epifauna was much patchier, with each study area having unique epibenthic assemblages. Brittle stars were highly abundant in epifaunal communities, reaching 600 individuals per square meter. The presence of seabird colonies was not a major driver of benthic community structure in the LSR at the depths studied. Negative effects of colonies were detected on the density and number of taxa of infauna, perhaps due to top-down effects transmitted by the seabirds which feed in the water column and can directly reduce the quantity of food reaching the seabed. Sediment concentration of pigment, percent cover of gravel and boulders, depth, temperature and duration of open water explained a substantial part of the observed variation across the LSR. Food availability, as expressed by sediment pigment concentration, is a factor driving benthic communities, even if potential pathways through seabirds did not broadly affect the benthos at the point source.

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## 1. Introduction

The transport of nutrients across ecosystem boundaries can profoundly shape recipient food webs. Acting as biovectors, animals that exploit two or more ecosystems to complete their life cycles, such as salmon (Kline et al., 1993), sea lions (Fariña et al., 2003) and seabirds (Ellis et al., 2006), can become effective agents for transfer of marine

nutrients to terrestrial ecosystems. On a planetary scale, seabirds may operate the most significant bio-transportation of such nutrients due to their massive populations that live in dense breeding colonies. They locally concentrate important quantities of nutrient-rich organic matter (guano, feathers, egg shells and carcasses) in seasonal pulses that can enhance terrestrial primary productivity around the colony (Ellis et al., 2006; Zmudczyńska-Skarbek et al., 2013).

Such ornithogenic enrichment is not strictly terrestrial and nutrients derived from guano can return to marine systems through four distinct pathways, summarized by Young et al. (2011): (1) direct excretion by seabirds flying over the sea, (2) run-off from the land, (3) infiltration in ground waters released into the ocean by tidal oscillation and (4) ammonia volatilization followed by precipitation. Several studies have shown that this concentrated input from seabirds can locally

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enhance nutrient content of estuarine and marine waters (Bosman et al., 1986 and references therein; Signa et al., 2012), and create hotspots of biological production (Kolb et al., 2010; Signa et al., 2012).

Through predation (top-down), seabirds control the biological characteristics of their prey such as size (Steinmetz et al., 2003) and biomass (Lewis et al., 2007). Seabirds can also indirectly affect communities of consumers (benthos, phytoplankton) through their fertilized effects that enhance primary production in the water column (bottom-up). Benthic consumer organisms rely on the portion of this production that is not utilized in the water column effecting pelagic-benthic coupling (Iken et al., 2005; Søreide et al., 2013). Little is known about the indirect bird-induced bottom-up effect on abundance and/or biomass of consumers, although a few studies do describe some impacts on marine zooplankton (Zelickman and Golovkin, 1972), polychaetes (Bosman and Hockey, 1986), nematodes (Palomo et al., 1999), chironomids (Michelutti et al., 2009), isopods (Kolb et al., 2010), hermit crabs (Zmudczyńska-Skarbek et al., 2015) and fish (Powell et al., 1991). Studies that focused on the link between seabirds and benthos showed that abundance (Palomo et al., 1999) and biomass (Kolb et al., 2010) of some species are positively influenced by the presence of seabird colonies in shallow waters of coastal ecosystems in Argentina (Palomo et al., 1999) and Sweden (Kolb et al., 2010). Zmudczyńska-Skarbek et al. (2015) demonstrated that seabird bottom-up effects may influence specific benthic organisms (hermit crabs and sea urchins) in shallow waters of an Arctic coastal ecosystem. However, to our knowledge, no one has studied the impacts of seabird presence on the marine benthic community composition over regional scales in the Arctic, where over 10 million seabirds breed each year, generally in recurrent locations (Mallory and Fontaine, 2004).

In the Arctic Ocean, environmental parameters and the way they influence biological communities are characterized by strong seasonality and large inter-annual fluctuations (Hamilton et al., 2013; Link et al., 2013; Michel et al., 2006). The sea-ice cover brings several constraints to primary production by limiting light penetration during a large part of the year. Biological communities are thus dependent on extent, thickness and seasonal melt dynamics of sea ice (Grebmeier et al., 1995). When the ice melts during summer, nutrient availability in the upper euphotic layer may rapidly become a limiting factor to primary production (Harrison and Cota, 1991; Tremblay et al., 2006). Therefore, the magnitude of marine biological production in the Arctic should respond to changes in nutrient inputs (mainly nitrogen) (Ardyna et al., 2011; Tremblay et al., 2015). Seabirds have been shown to locally enhance chlorophyll *a* and organic carbon concentrations, as demonstrated in coastal ponds (Brimble et al., 2009; Signa et al., 2012) and in an intertidal system (Bosman et al., 1986). Moreover, field and laboratory experiments demonstrate that primary production is stimulated when guano is added to seawater (Bosman et al., 1986). Depth also impacts marine benthic communities since it is a proxy of other variables that are characterized by vertical variation such as temperature, salinity or food sedimentation (Smith et al., 2008). Increasing depth is generally linked to a decrease in both quantity and quality of food resources (Roy et al., 2014; Smith et al., 2008), linked with a decreasing strength of pelagic-benthic coupling, which is a key determining force in the Arctic (Gaillard et al., 2015; Soltwedel et al., 2009). Several other parameters of the water column and the seafloor can influence benthic communities such as salinity, temperature, sediment type (e.g.: percentage of mud or gravel, boulder cover), habitat heterogeneity and velocity of bottom currents (McArthur et al., 2010).

Despite their importance in Arctic food webs (Hobson and Welch, 1992), little is known about the structure of Arctic benthic communities and the environmental parameters influencing their distributions. There is a need for baseline data on Arctic benthic communities (Archambault et al., 2010; Piepenburg et al., 2011). In this study, we by-passed the well-documented relationship between seabird colonies and primary production, to focus on their indirect effect on benthic communities. Benthic species are good integrators of environmental

variation (Dauvin, 1993; Pearson and Rosenberg, 1978), since many are sessile and long-lived. Therefore, it is assumed that a change in the structure of benthic communities should be detected if inputs from birds are substantial enough. It is reasonable to expect that the potential mismatch between nutrient load and integration in the benthos could affect the detection of bottom-up effects of seabirds. However, the coupling between surface and bottom processes is thought to be strong in Arctic shelves in general (Ambrose and Renaud, 1997; Clough et al., 2005), particularly in the eastern Canadian Arctic (Darnis et al., 2012), which includes our study site, the Lancaster Sound Region (LSR).

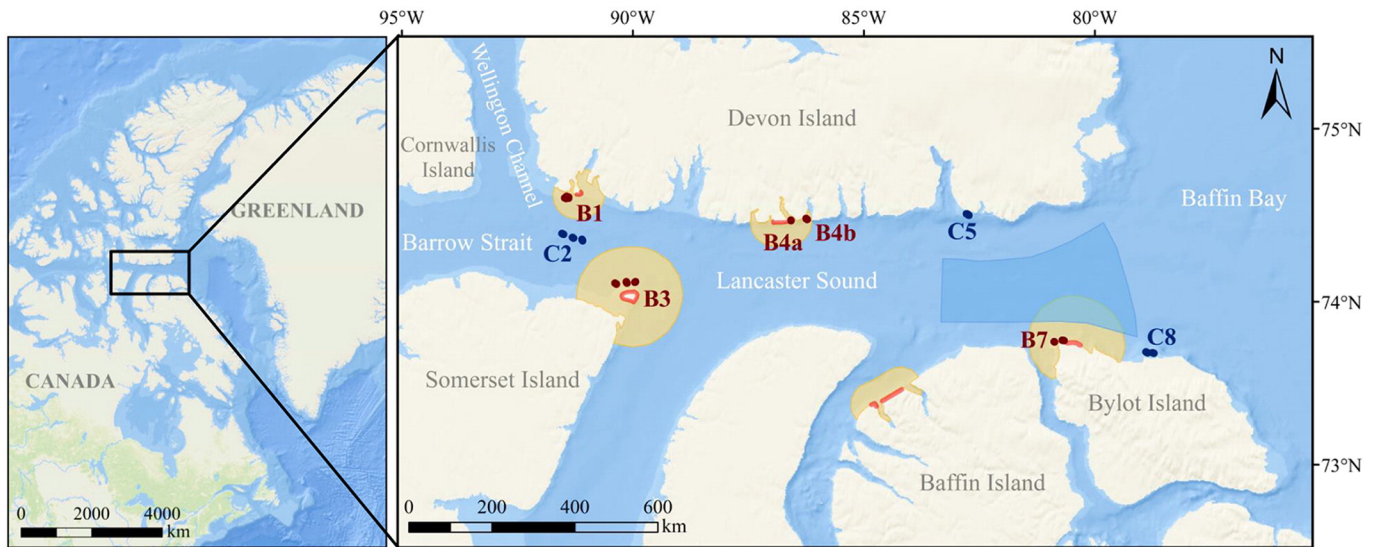
The primary objective of this study was to characterize epifauna and infauna benthic communities of the LSR, Canadian Arctic. The second objective was to identify the potential impacts of seabird colonies (mainly northern fulmar *Fulmarus glacialis* and thick-billed murre *Uria lomvia*) on the structure of benthic communities and also to determine the influence of other environmental parameters. Our hypothesis was that the presence of seabird colonies would partly explain spatial differences in benthic communities at the regional scale of the LSR. This hypothesis is based on the model that the nutrient inputs from the birds increase primary production and can generate bottom-up effects to the benthos (Grebmeier and Barry, 1991). During this study, we did not measure primary production as we could not be at sea at the same time as the birds were present but our objective was to see if a pattern emerged from the benthic community. If the production-diversity relationship is curvilinear as recent studies have suggested (Levin et al., 2001; Witman et al., 2008) and if the pelagic-benthic coupling is as tight as we expect, we anticipated being on the ascending limb of the relationship in the LSR. Hence, we expected that benthic species diversity, number of taxa, total epifauna density (ind. m<sup>-2</sup>), total infauna density (ind. l<sup>-1</sup>) and total infauna biomass (g l<sup>-1</sup>) would be higher in areas where colonies were present.

## 2. Materials and methods

### 2.1. Study site

This study was conducted in the Lancaster Sound Region (LSR), which constitutes about 98,000 km<sup>2</sup> of sea surface (Welch et al., 1992) in the eastern Canadian Arctic (Fig. 1). Arctic water enters Lancaster Sound from the west through Barrow Strait and from the north through McDougall Sound and Wellington Channel (Leblond, 1980; Welch et al., 1992). This water mass then flows along the south coast of Lancaster Sound towards the east to reach Baffin Bay. Typically, ice break-up occurs in June or July and freeze-up usually begins mid-September in channels of the western part and only ends in February or early March because of the strong currents that prevent rapid ice consolidation (Hamilton et al., 2013). Along Devon Island, on the northern side, a seasonal flaw-lead extension of the North Water polynya in north Baffin Bay is formed every winter with annually variable dimensions. Ice conditions in the LSR are variable between years and recent studies showed that some extended periods of land-fast ice conditions in Barrow Strait may characterize one year, while the next year mobile ice conditions are observed throughout the winter (Hamilton et al., 2008, 2013).

LSR is among the most productive ecosystems in the Canadian Arctic (Welch et al., 1992) and supports a large summer zooplankton population (Longhurst et al., 1984; Sameoto et al., 1986). Several marine mammal and seabird populations rely intensively on these food resources (Mallory and Fontaine, 2004). Bird colonies in the vicinity of sampling areas are present each year from May through September and include anywhere between 1100 and 160,000 migratory seabird pairs (all species combined; Mallory and Fontaine, 2004). Generally piscivorous, the thick-billed murre *Uria lomvia* and the northern fulmar *Fulmarus glacialis* are the two main species found in these colonies (Mallory and Fontaine, 2004).



**Fig. 1.** Location of sampling areas in Lancaster Sound Region (LSR), eastern Canadian Arctic. Blue delimited zone is the polynya of eastern Lancaster Sound, pale red lines represent seabird colonies locations and yellow zones are key marine habitat sites for migratory seabirds listed by Mallory and Fontaine (2004). Sampling areas in the vicinity of bird colonies (B = bird colonies) are: Gascoyne Inlet (B1), Prince Leopold Island (B3), Stratton Inlet (B4a), Burnett Inlet (B4b) and Wollaston Islands (B7). Control areas (C = control) are: western part of Lancaster Sound (C2), Croker Bay (C5) and Maud Bight (C8). Dots represent camera deployments done during the mission of 2012. The basemap was provided by Esri, DeLorme, GEBCO, NOAA, NGDC and other contributors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

## 2.2. Study design

To test the hypothesis that bird colonies have an indirect effect on benthic community characteristics (univariate) and community composition (multivariate), eight study areas were sampled: five areas with presence of bird colonies (B = bird colonies: B1, B3, B4a, B4b, B7) and three control areas without colonies (C = control: C2, C5, C8) (Fig. 1). The distances between control areas and areas with colonies were in the order of 50 km to minimize the potential effects of colonies on control areas. Benthic communities from areas with and without colonies were characterized and compared using grab samples for infauna and seafloor photos for epifauna. To do this sampling, an oceanographic mission was carried out aboard the CFAV Quest from August 24th to September 7th, 2012. Water, sediment and imagery samples were collected as close as possible to the 200 m depth contour. All areas were sampled at similar depths to control the effect of depth in order to increase our potential to detect the effect of seabird colonies. Due to high occurrences of Modern and Holocene ice scours above 200 m, shallower depths were avoided (Lewis and Blasco, 1990).

## 2.3. Infauna

Using a 0.15 m<sup>2</sup> Van Veen grab of 20 l volume capacity (maximal penetration depth of 0.18 m), two samples were collected for each study area. The soft sediment at the surface of each grab sample was subsampled in triplicate for organic matter ( $n = 3$ ) and pigment ( $n = 3$ ) analyses (described below). All the remaining sediment was screened through a 1 mm mesh and stored in a 4% seawater-formaldehyde solution buffered with sodium tetraborate to prevent the dissolution of calcified structures. Sorting, taxonomic identification, counting and weighing of benthic infauna were done in the laboratory. Biomass values, with a precision of  $\pm 0.0001$  g, are defined here as formaldehyde wet masses. Identification was done to family level whenever feasible, except for annelids that were only counted and weighed due to time restrictions. In some cases however, even this level of identification could not be ascertained and some taxa were left at the phylum level (e.g., Porifera). Infauna data from each grab sample were divided by the sediment volume associated with that specific grab sample, to obtain density (ind. l<sup>-1</sup>) and biomass (g l<sup>-1</sup>) data. Prior to statistical

analyses, infaunal taxa which were only found in one area were removed to better detect similarities between communities (26 taxa removed) (Clarke and Warwick, 2001).

## 2.4. Epifauna

Photos were taken using a digital camera system referred to as the 4 K Camera (4KCam). This system, built in 2008 by the Geological Survey of Canada, is an aluminium frame that contains a Canon Rebel Eos Ti 12 megapixel camera with two Canon flashes. The 4KCam was lowered with a winch until an attached lead weight hit the bottom, automatically triggering the camera. During the camera operations, the ship was drifting oriented with the surface current and wind speed and direction. Consequently, photos were taken at depths ranging from 122 to 442 m. The 4KCam captured 54 to 146 images per area. For each area, 15 photos were randomly selected after reducing the pool of photos through application of three rules: (1) at least one photo was always skipped between two selected photos taken consecutively to avoid overlap and reduce spatial autocorrelation; (2) blurry images or photos with sediment clouds that hide the bottom were discarded; and (3) the lead weight attached to the camera frame had to be present on all selected photos in order to scale it properly (see Fig. 2 for examples of the photos analyzed). This number of replicates per area ( $n = 15$ ) was sufficient because each area was relatively homogenous and Species Accumulation Curves showed that the addition of new species had slowed and the curves were approaching a plateau after 15 photos analyzed. At the center of each selected and then scaled photo, a surface of 0.692 m<sup>2</sup> ( $0.675 \times 1.025$  m) was delimited based on average area covered by the photos. This delimited surface was scanned to identify and count the epibenthic megafaunal organisms, using the software PhotoQuad (Trygonis and Sini, 2012). Our definition of epibenthic megafauna included all organisms that were on or near the bottom and visible on photos. Fishes, crustaceans and all other mobile or sessile organisms were counted. Each colony of large distinct organisms, such as sponges and soft corals, was counted instead of being only recorded as present or absent as for encrusting species. Organisms were identified to the lowest taxonomic level possible and mutually exclusive names were attributed to each taxon. To compare data between different areas, epifaunal abundance data were converted into density data (ind. m<sup>-2</sup>). A few taxa were found only once, and as for the infauna,



**Fig. 2.** Examples of photos taken by the 4 K Camera (4KCam) during the oceanographic mission in the Lancaster Sound Region (LSR) carried out aboard the CFAV Quest from August 24th to September 7th, 2012. This set of photos gives a representative overview of the types of surface sediment and the epifaunal communities encountered (see Section 3.2). The lead weight attached to the camera frame allowed to scale the photos (length = 14.8 cm, width = 10.2 cm).

these were removed prior to analyses to better detect similarities between communities (9 taxa removed) (Clarke and Warwick, 2001).

### 2.5. Environmental variables

A SBE 39 temperature and pressure recorder was attached to the 4KCam system to provide water depth and temperature associated with each photo. Salinity data closest to the seafloor were extracted from CTD casts done in each area.

To quantify organic matter deposited on the bottom, the three subsamples of surface sediments from each grab sample were dried for 48 h and burned at 450 °C for 6 h (Byers et al., 1978). The pigment concentrations (chl  $a$   $\mu\text{g g}^{-1}$  dry weight and phaeo  $\mu\text{g g}^{-1}$  dry weight) in sediments for each of the three subsamples were determined following the method of Riaux-Gobin and Klein (1993), which is based on a 24 hour acetone extraction and fluorescence readings. Grain size of surface sediment was estimated for each of the analyzed photos (method similar to Hardy et al., 2008). Based on the Gradistat grain size chart, an adaptation of Udden-Wentworth grade scale (Udden, 1914; Wentworth, 1922) by Blott and Pye (2001), percent cover was visually assessed on each photo for each different classes of sediment: fine sediment (FS, <4 mm), fine gravel (FG, 4–8 mm), medium gravel (MG, 8–16 mm), coarse gravel (CG, 16–32 mm), very coarse gravel (VCG, 32–64 mm), very small boulder (VSB, 6.4–12.8 cm), small boulder (SB, 12.8–25.6 cm), medium boulder (MB, 25.6–51.6 cm) and large boulder (LB,  $\geq 51.6$  cm).

To characterize the water column at each area, one to four CTD-Niskin profiles were made and bottom water was sampled 5 m above

the seafloor. Two water subsamples per Niskin bottle were filtered through 25 mm diameter GF/F 0.7  $\mu\text{m}$  filters and frozen at  $-20$  °C on board in 15 ml tubes. Subsamples were later processed to determine nitrite ( $\text{NO}_2^-$ ), nitrate ( $\text{NO}_3^-$ ), phosphate ( $\text{PO}_4^{3-}$ ) and silicates concentrations according to the method of Tréguer and Le Corre (1975). To obtain chlorophyll  $a$  and phaeopigment concentration data, vacuum filtrations, extraction with acetone (20 h, 4 °C) and fluorescence readings were performed for two subsamples per Niskin bottle, according to Parsons et al. (1984).

Based on seabird abundance data from the report of Mallory and Fontaine (2004), an index of bird colony size was created. This index was set at 0 for the control areas, 1 for an area with a colony of 0 to 10,000 bird pairs, 2 for 10,000 to 100,000 pairs and 3 for an area where all colonies put together exceeded 100,000 pairs. The nominal variable Birds is semi-quantitative and ordinal, so it was treated as a single continuous quantitative predictor variable (Anderson et al., 2008; Quinn and Keough, 2002).

Level-3 daily remote sensing reflectances at 4.64 km from the Moderated Resolution Imaging Spectroradiometer (MODIS) were downloaded from the National Aeronautics and Space Administration (NASA, <http://oceancolor.gsfc.nasa.gov>). Remote sensing reflectance was then used to derive chlorophyll  $a$  concentrations using the semi-analytical GSM algorithm (Maritorena et al., 2002) for 2008 to 2012. Daily satellite-derived sea ice concentration data (% 25 km-resolution pixels) from Special Sensor Microwave Imager SSMI/Sounder sensors were obtained from the National Snow and Ice Data Center (NSIDC, <http://nsidc.org>; Maslanik and Stroeve, 1999). For the whole time-series of five years preceding our oceanographic mission in 2012, we extracted yearly mean values of chlorophyll  $a$  concentrations, primary production

(derived from an Arctic-adapted model; see Bélanger et al., 2013 and its validation in Lee et al., 2015) and duration of open water. The latter was defined as the number of days during one year where sea ice concentration represented < 10% of the studied surface (Ardyna et al., 2014).

Yearly maxima and mean velocities data of modelled currents were obtained for the year 2010 using a regional Arctic-North Atlantic ice-ocean system. Based on the CREG12 (Canadian REGIONal) configuration, this system offers a high resolution (1/12°) (Dupont et al., 2015).

In total, 26 environmental variables were collected for the eight sampling areas: index of bird colony size (Birds), phosphate, silicates, nitrate and nitrite, chlorophyll *a* and phaeopigment concentrations of bottom water (respectively [PHO], [SIL], [NIT], [Chl *a*]<sub>BW</sub> and [Phaeo]), depth (D), temperature (T), salinity (S2), organic matter content of sediment (OM), sediment chlorophyll *a* (Sed Chl *a*), sediment phaeopigments (Sed Phaeo), percent cover of different sediment size classes (FS, FG, MG, CG, VCG, VSB, SB, MB, LB), duration of open water (DOW), chlorophyll *a* concentration given by satellite information ([Chl *a*]<sub>SAT</sub>), primary production (PP), maxima velocity and mean velocity of modelled currents (Max\_V and Mean\_V).

## 2.6. Statistical analyses

Impact of the presence of seabird colonies on benthic community characteristics was tested by analyses of variances (ANOVAs) using Bird as a fixed factor (two levels, presence or absence of colonies) and Area as a random factor nested within the Bird factor (five Areas with colonies and three control Areas). Dependent variables related to both infaunal (grab) and epifaunal (images) samples were number of taxa (S), total density of organisms (N, ind. m<sup>-2</sup> for epifauna and ind. l<sup>-1</sup> for infauna), Pielou's evenness index (J') and Shannon-Wiener's diversity index (H'). Total biomass (g l<sup>-1</sup>) of infauna was also included as a dependent variable in an ANOVA. Shapiro-Wilk's test was used to confirm the normal distribution of residuals, and homogeneity of variances of residuals was visually verified. Data were transformed when necessary to respect assumptions of ANOVA and retested for normality of residuals and homogeneity of variances. For dependant variables associated with infauna, no transformation was needed. For epifauna, a logarithmic transformation was done on density (N) data, whereas square-root transformations were done for the three other variables. When transformations did not achieve normality of residuals and/or homogeneity of variances, we still performed the analyses because ANOVAs are robust to small violations of these assumptions, particularly when the number of replicates is high (Underwood, 1997). Tukey's post-hoc multiple comparison tests were used to identify where significant differences found by ANOVAs existed.

Based on Bray-Curtis distance measurements calculated on the square-root-transformed epifaunal density data, permutation multivariate analyses of variances (PERMANOVAs) were conducted with 9999 permutations. These were performed under the same statistical model described above, to test the effect of Bird and Area nested in Bird factors on epifaunal community composition. Square-root transformation was chosen to down-weight the dominant taxa which were prominent in our data set. Pairwise comparisons were carried out to identify where differences within levels of different factors were detected. Multidimensional scaling (MDS) was used to obtain a graphical ordination of the samples, based on the Bray-Curtis similarity matrix. The multivariate dispersion of data was analyzed with a PERMDISP routine. Similarity Percentages Test (SIMPER) was done on the Bray-Curtis similarity matrix of square-root transformed density data to determine the epifaunal taxa that contributed the most to dissimilarities between Areas. Because of the low number of replicates per Area (n = 2), these multivariate analyses were not performed on infaunal data, except for the SIMPER that allowed us to find the infaunal taxa that explained the dissimilarities between the different levels of Area and Bird factors.

To investigate the link between the environmental variables and infaunal and epifaunal communities, multiple linear regressions were

performed. Due to missing data for the Area B1 for organic matter and pigment concentrations of sediment, infauna and epifauna data from this Area were excluded from those analyses. For several environmental variables, only one or two records per Area were available, whereas 15 records (one per photo) were available for other variables. The mean value of each environmental variable in a given Area was attributed to all 15 samples within that Area. For each univariate biological variable calculated (number of taxa, total density, Pielou's evenness index and Shannon-Wiener's diversity index and log-biomass), scatter-plots of AICc (Akaike's Information Criterion corrected) and BIC (Bayesian Information Criterion) values for all possible models was done. The model that offered the best compromise between the AICc criterion and the more severe BIC criterion was selected (Anderson et al., 2008). Number of predictors was always kept smaller than the number of observations (N<sub>tot</sub> = 16) while searching for the best model. The assumption regarding the absence of collinearity (|r| < 0.8) between predictors was reviewed and, where collinearity was evident, the most biologically relevant variables were maintained and the others were removed (Anderson et al., 2008) prior to running the regressions. The predictors [SIL] and [PHO] were collinear together; [SIL] was removed, considering that large influxes in seabird guano can provide an increase in phosphate concentrations in marine systems (Young et al., 2011). The predictor [Phaeo] was collinear with T, [Chl *a*]<sub>BW</sub> and Sed Chl *a*. [Phaeo] was excluded because Chl *a* is a known proxy of food availability for benthic organisms (Carroll et al., 2008; Roy et al., 2014). This also explains the removal of Max\_V, which was collinear with Sed Chl *a* and [Chl *a*]<sub>BW</sub>. The predictor S2 was collinear with MG and PP; S2 was therefore removed since sediment characteristics (e.g.: sediment grain size, organic matter content) are known as relevant predictors in many benthic studies (McArthur et al., 2010). For the same reason, [Chl *a*]<sub>SAT</sub> (collinear with MG and D), PP (collinear with MG, VCG and S2) and Mean\_V (collinear with FG and OM) were eliminated. In summary, among the 26 environmental variables described above, [SIL], [Phaeo], S2, [Chl *a*]<sub>SAT</sub>, PP, Mean\_V and Max\_V were removed, leaving 19 variables for analyses on epifaunal and infaunal communities. Shapiro-Wilk's test was used to confirm the normal distribution of residuals and then homogeneity of variances of the residuals was verified visually.

To better understand which environmental variables are important in explaining differences among Areas in terms of epifaunal community composition, distance-based linear model (DISTLM), represented by distance-based redundancy analysis ordination (dbRDA) (Anderson et al., 2008), was done on the Bray-Curtis similarity matrix with square-root transformed epifaunal density data. Similarly to the approach used for the multiple linear regressions, Area B1 was excluded due to missing data and the spatial resolution of environmental variables was standardized. The DISTLM was performed on 19 variables Birds, [PHO], [NIT], [Chl *a*]<sub>BW</sub>, D, T, OM, Sed Chl *a*, Sed Phaeo, FS, FG, MG, CG, VCG, VSB, SB, MB, LB, DOW, based on the justifications listed above to avoid collinearity. The best selection procedure was run with 9999 permutations and with different selection criteria: AICc, BIC and adjusted R<sup>2</sup>. The best compromise between these three criteria was chosen following the same method used for multiple linear regressions detailed above (Anderson et al., 2008).

SIMPER, PERMANOVA, MDS, PERMDISP, DISTLM and dbRDA were carried out using the software PRIMER-E version 6 with PERMANOVA + (Anderson et al., 2008; Clarke and Gorley, 2006). ANOVA analyses and univariate multiple linear regressions were done with JMP Pro software version 11. For all these analyses, statistical significance was set at  $\alpha < 0.05$ .

## 3. Results

### 3.1. Infaunal communities

Annelida, Crustacea and Echinodermata represented 43%, 22% and 16% of the total abundance of infauna collected across the LSR,

**Table 1**

Results of the ANOVAs testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 Areas with bird colonies, 3 control Areas) on infaunal community characteristics: mean number of taxa (S), mean total density (N), mean Pielou's evenness (J'), mean Shannon-Wiener diversity (H') and mean total biomass. Significant effects ( $p < 0.05$ ) are in bold.

Variable	Source	df	MS	F	p
S	Bird	1	201.67	3.23	0.122
	Area(Bird)	6	62.39	3.02	0.075
	Error	8	20.63		
N	Bird	1	4779.34	12.76	<b>0.012</b>
	Area(Bird)	6	374.60	0.70	0.656
	Error	8	531.69		
J'	Bird	1	0.08	3.12	0.128
	Area(Bird)	6	0.03	3.40	0.057
	Error	8	0.01		
H'	Bird	1	0.04	0.22	0.659
	Area(Bird)	6	0.18	3.01	0.076
	Error	8	0.06		
log-biomass	Bird	1	0.12	1.41	0.280
	Area(Bird)	6	0.09	0.13	0.988
	Error	8	0.66		

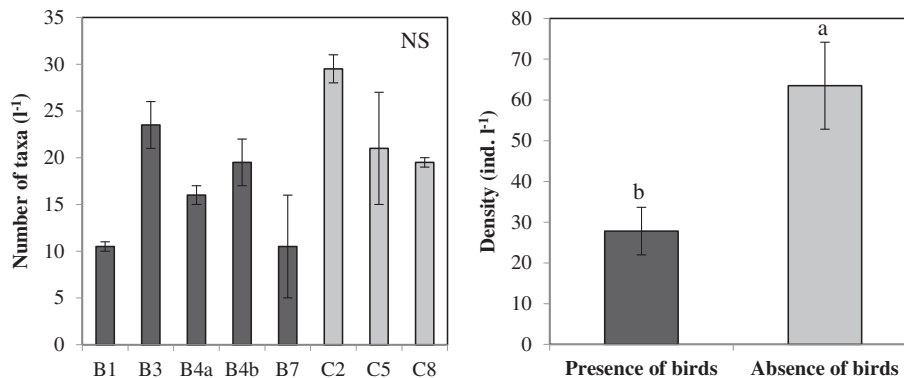
respectively (Appendix A, Fig. A.1). The biomass composition of infauna was highly variable between sampling locations, but generally Echinodermata was the dominant phylum, representing 81% of total biomass (Appendix A, Fig. A.2). The univariate approach to characterize the structure of infaunal communities allowed us to highlight a significant difference between the two levels (presence or absence) of the Bird factor (Table 1). The mean total density of infauna (N) was  $63.5 \pm 10.8 \text{ ind. l}^{-1}$  in control Areas which is significantly higher than in Areas with seabird colonies where the mean was  $27.8 \pm 5.9 \text{ ind. l}^{-1}$  ( $F_{(1,6)} = 12.76$ ,  $p = 0.012$ ) (Table 1 and Fig. 3, right). However, the presence of seabird colonies did not significantly affect the mean number of taxa (S), mean Pielou's evenness index (J'), mean Shannon-Wiener diversity index (H') and mean total biomass (log-biomass) of infaunal communities (Table 1). For all those univariate variables, the eight sampling Areas did not statistically differ from each other (Table 1). The highest number of taxa was recorded in Area C2, which is in the middle of Lancaster Sound, near Barrow Strait (Fig. 3, left). Areas B1 and B7 are characterized by low S, with mean values that are three times lower than that of Area C2 (Fig. 3, left). Biomass data showed large variability between samples located within the same Area, as well as between different Areas (not shown). According to SIMPER analysis, the top five taxa explaining the greatest part of dissimilarity between Areas with seabird colonies and control Areas (Bird factor) were Annelida, the ostracod *Philomedes* sp., *Ophiura robusta*, Ophiuridae spp. and Leuconidae spp. (Cumacea). These taxa together explained 35.57% of the variation between these two groups of Areas and they all had higher mean density in the control Areas. For the Area factor, the results from the SIMPER analysis showed that the mean

contribution of the top five taxa, which were specific to each pairwise comparison, was  $38.26 \pm 1.12\%$  (mean contribution  $\pm$  SE). Annelida and *Philomedes* sp. were the two most important taxa distinguishing Areas, ranking in the top five of 27 and 24 pairwise comparisons (total of 28 comparisons), and explained on average  $11.54 \pm 0.73\%$  and  $9.06 \pm 0.63\%$  of dissimilarities between Areas, respectively.

### 3.2. Epifaunal communities

The order Ophiurida represented 72% to 93% of total abundance of epifaunal organisms depending on the sampling location (Appendix B, Fig. B.1). Considering all Areas, Annelida and other Echinodermata (except Ophiurida) represented 5% and 3%, respectively (Appendix B, Fig. B.1). For epifaunal communities, results of ANOVAs showed no significant difference for S, N, J' and H' between control Areas and Areas with presence of seabird colonies (Table 2). However, the factor Area is associated with significant p values for square-root transformed dependent variables S ( $F_{(6,112)} = 2.89$ ,  $p = 0.012$ ), J' ( $F_{(6,112)} = 19.16$ ,  $p < 0.001$ ) and H' ( $F_{(6,112)} = 15.51$ ,  $p < 0.001$ ) and log-transformed dependent variable N ( $F_{(6,112)} = 21.25$ ,  $p < 0.001$ ) (Table 2). Area C2, in the middle of Lancaster Sound, is characterized by a significantly higher number of epifaunal taxa than Areas B3 and B7 (Fig. 4, left). Areas B1, B4a, B7 and C5 are characterized by similar low N of epifaunal organisms and differed significantly from the Areas C2, B3, B4b and C8 that are showing higher N (Fig. 4, right). The opposite trend was detected in mean values of J', creating the same particular pattern of two groups of Areas (Appendix B, Fig. B.2, left). This trend was also present in the significant differences between the mean values of H', but the pattern was not as clear in this case (Appendix B, Fig. B.2, right).

The multivariate analysis PERMANOVA, which tested the differences between Areas in terms of epibenthic community composition, showed significant differences among Areas nested in Bird ( $F_{(6,112)} = 10.20$ ,  $p < 0.001$ ) (Table 3). In fact, the 28 pairwise comparisons were all significant with  $p < 0.001$ , except the ones for Areas B3 and B4b ( $p = 0.013$ ) and for Areas C5 and B7 ( $p = 0.049$ ). This result indicates that each Area is unique with respect to the square-root transformed epifaunal density. These results have been visualized by a MDS plot done on the same square-root transformed data, which presented all samples from each Area grouped together even if the 8 Areas were not highly discrete spatially (Fig. 5). Considering that the stress value of this graphical representation was just beyond the usually accepted threshold (0.2; Clarke and Warwick, 2001), the MDS based on non-transformed data was also reviewed (Appendix B, Fig. B.3). This later graph effectively represented the epifaunal data in 2D (stress value = 0.07), but it attributed an extremely high importance to the dominant species which was why we had undertaken the transformation. Nevertheless, the two MDS plots illustrated the difference between the two groups of Areas which formed a continuum in the data cloud: C2, B3, B4b, C8 on the



**Fig. 3.** Mean number of taxa (S) and mean total density (N) ( $\pm$ SE) of infaunal communities from Areas characterized by the presence of seabird colonies (black) and from control Areas (grey). Different letters (a, b) indicate significant differences between Areas based on Tukey post-hoc multiple comparison tests. NS = nonsignificant.

**Table 2**

Results of the ANOVAs testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 Areas with bird colonies, 3 control Areas) on epifaunal community characteristics: mean number of taxa (S), mean total density (N), mean Pielou's evenness (J') and mean Shannon-Wiener diversity (H'). Significant effects ( $p < 0.05$ ) are in bold.

Variable	Source	df	MS	F	p
$\sqrt{S}$	Bird	1	0.23	0.41	0.548
	Area(Bird)	6	0.56	2.89	<b>0.012</b>
	Error	112	0.19		
log-N	Bird	1	0.30	0.40	0.548
	Area(Bird)	6	0.74	21.25	<b>&lt;0.001</b>
	Error	112	0.03		
$\sqrt{J'}$	Bird	1	0.03	0.12	0.752
	Area(Bird)	6	0.22	19.16	<b>&lt;0.001</b>
	Error	112	0.01		
$\sqrt{H'}$	Bird	1	0.05	0.10	0.763
	Area(Bird)	6	0.51	15.51	<b>&lt;0.001</b>
	Error	112	0.03		

left and B1, B4a, C5, B7 on the right (Fig. 5 and Fig. B.3 of Appendix B). This pattern was also shown by the epifaunal mean total densities (Fig. 4, right). In 32% of all possible comparisons, PERMDISP tests on Area resulted in a significant effect of dispersion ( $F_{(6,112)} = 5.02$ ,  $p < 0.001$ ). Areas B3, B4a, B4b and C8 had high average similarity values (Table 4), meaning that dispersion around the centroid was lower for these Areas in comparison with Areas B1, C2, C5 and B7. Still, considering lower average similarity values for each Area, Areas C2 and B7 had intermediate dispersion whereas Areas B1 and C5 had high dispersion (Table 4). No location or dispersion effect was found for the Bird factor. According to SIMPER analysis on epifaunal density data (square-root transformed) for the factor Area, showed that Ophiurida, Eunicidae, *Ophiacantha* sp., the benthic trachymedusa *Ptychogastrias* sp., *Strongylocentrotus* sp., Patellogastropoda, *Psolus* sp., Gastropoda A (morphotype of a small gastropod similar to *Margarites* sp.), Bivalvia, Worm A (morphotype of a polychaete without tube or any other particular characteristic) and Pycnogonida AB (morphotype of a large pycnogonid) were the most important taxa explaining the dissimilarities for the 28 possible combinations of Areas. Among all these taxa, Ophiurida was by far the most important, since it appeared in the 28 top five lists and contributed a quarter of the dissimilarity between the two Areas levels on average ( $25.73 \pm 1.28\%$ ).

### 3.3. Description of the selected environmental variables

The mean values for Depth were between  $175 \pm 1$  m and  $310 \pm 22$  m, with Area C2 representing the shallower samples and Area C5 the deeper ones (Table 5). The longest open water season was on the south shore of Lancaster Sound with  $111 \pm 7$  days for C7 and  $109 \pm 5$  days for C8. The shortest was limited to  $78 \pm 10$  days in Area C2,

which was located the farthest offshore in the western part of LSR. The OM content of LSR was comprised between  $6.22 \pm 0.39\%$  and  $18.03 \pm 1.25\%$  (Table 5). Areas B4a and B4b appeared to have the highest mean values of OM and Areas C5 and C8 the lowest mean values. For the sediment concentration of pigment, the mean values ranged between  $0.82 \pm 0.10 \mu\text{g g}^{-1}$  and  $0.29 \pm 0.08 \mu\text{g g}^{-1}$  for the chlorophyll *a* and between  $4.24 \pm 0.36 \mu\text{g g}^{-1}$  and  $2.62 \pm 0.16 \mu\text{g g}^{-1}$  for the phaeopigments. Sediment of Areas C2 and B3 had the highest concentrations of pigments (Table 5).

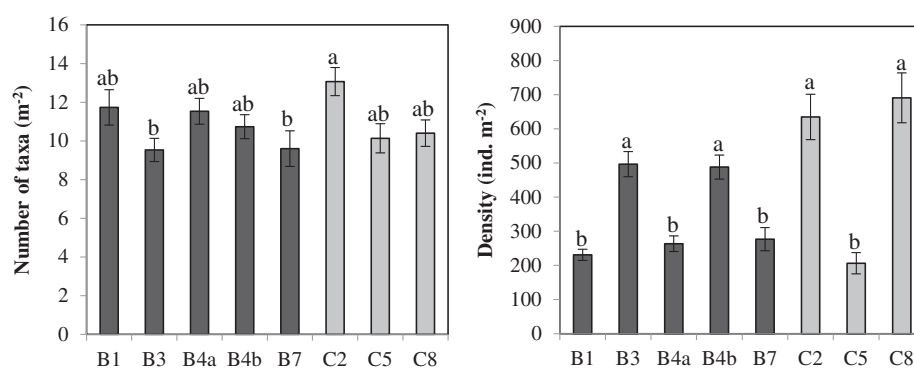
### 3.4. Relation between infauna and the environmental variables

Using environmental variables, the best multiple linear regression models explained from 38% to 68% of variation in the univariate characteristics of infaunal communities S, N, J' and H' (Table 6). The strong explicative power of these models signify that even with only two grab samples, our models were able to explain a significant part of the variation among infaunal communities. S increased with FG and decreased with DOW (Adj.  $R^2 = 0.56$ ,  $p = 0.004$ ), and the same pattern was found for H' (Adj.  $R^2 = 0.38$ ,  $p = 0.029$ ). J' was best predicted by FG and Sed Phaeo and both predictors were negatively correlated to the dependant variable in this regression model (Adj.  $R^2 = 0.68$ ,  $p = 0.001$ ). Sed Phaeo and DOW both negatively influenced H' (Adj.  $R^2 = 0.59$ ,  $p = 0.003$ ). No regression model with the available environmental variables was found to explain variation in log-biomass data.

### 3.5. Relation between epifauna and the environmental variables

The best multiple linear regression models using the environmental variables as covariates explained from 12% to 51% of variation in the univariate characteristics of epifaunal communities S, N, J' and H' (Table 7). A logarithmic transformation was done on density (N) data, whereas square-root transformations were done for the three other variables. S decreased with Birds and increased with OM (Adj.  $R^2 = 0.12$ ,  $p < 0.001$ ). N was negatively correlated to D and T and positively to MG (Adj.  $R^2 = 0.51$ ,  $p < 0.001$ ). J' increased with T and VSB and decreased with SB (Adj.  $R^2 = 0.44$ ,  $p < 0.001$ ). [NIT], T and Sed Phaeo positively influenced H' (Adj.  $R^2 = 0.38$ ,  $p < 0.001$ ).

The best distance-based linear model (DISTLM) for explaining the variation in epifaunal community composition included 5 environmental variables: D, Sed Chl *a*, Birds, MG and SB (Adj.  $R^2 = 0.32$ ) (Table 8, Fig. 6). The two first axes of the dbrDA plot represented together 80.6% of the fitted variation and 28.7% of the total variation and they were mainly built by D and Sed Chl *a* (Table 8, Fig. 6). Less important but still significant, MG also participated to build the two first dbrDA axes. The predictor Birds was mainly associated to the first axis, whereas SB participated more in the construction of the second axis. The first axis, created by the horizontal components of these five predictors,



**Fig. 4.** Mean number of taxa (S) and mean total density (N) ( $\pm$ SE) of epifaunal communities from Areas characterized by the presence of seabird colonies (black) and from control Areas (grey). Different letters (a, b) indicate significant differences between Areas based on Tukey post-hoc multiple comparison tests.



**Table 3**

Results of the PERMANOVA testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 Areas with bird colonies, 3 control Areas) on epifaunal communities (square-root transformed epifaunal density data). Significant effects ( $p < 0.05$ ) are in bold. \* indicates that Monte Carlo  $p$  value was used because the number of permutations was below 100.

Source	df	MS	F	$p$ (perm)
Bird	1	4408.90	0.83	0.577*
Area(Bird)	6	5329.40	10.20	<b>&lt;0.001</b>
Error	112	522.62		

separated the same two groups of Areas: B4a, C5, B7 and C2, B3, B4b, C8 (Area B1 was excluded because of missing data). This pattern was also revealed by ANOVA on N (Fig. 4, right) and by the MDS (Fig. 5, line).

## 4. Discussion

### 4.1. Description of benthic communities

Among the very few studies published to date on the structure of benthic communities in the eastern Canadian Arctic (Roy et al., 2015a; Thomson, 1982), the one recently conducted by Roy et al. (2015a) showed that approximately 60% of megabenthic taxa are still to be documented in this region. Thus, the present contribution is highly relevant, especially as the LSR could become a marine protected area in the near future (Archambault et al., 2016). Over 30 years ago, Thomson (1982) worked at the mouth of Lancaster Sound, at the easternmost range of our sampling Areas. He characterized, through sampling done with a Van Veen grab, an assemblage composed of several species of Ophiurida, *Macoma* sp. and *Astarte* sp.; common taxa that were also collected in our study with the same sampling gear. However, our study revealed that annelids represented approximately half of the relative abundance composition of infauna over the LSR, whereas Thomson (1982) found that crustaceans were the most dominant in the wider eastern Canadian Arctic. This dissimilarity is likely due to a difference in depth range and spatial extent. The infaunal samples from Areas C5 and C8 which were at the eastern limit of our sampling, and therefore most comparable to those of Thomson (1982), presented the highest proportion of crustaceans consistent with the earlier results. Anthropogenic and climatic factors should also be considered when

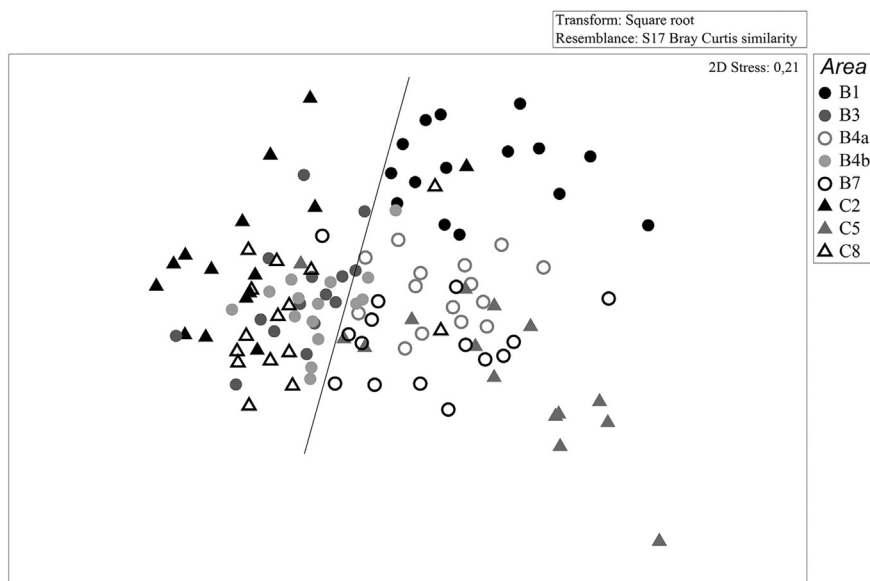
**Table 4**

Average similarity within the same Area (grey) and average dissimilarity between different Areas based on epifaunal communities (square-root transformed epifaunal density data).

	B1	B3	B4a	B4b	B7	C2	C5	C8
B1	62.7							
B3	44.8	73.6						
B4a	40.6	38.5	72.0					
B4b	43.4	27.7	35.0	73.7				
B7	42.6	35.8	34.0	35.1	67.6			
C2	49.6	34.4	43.8	34.4	44.4	67.7		
C5	45.6	44.3	37.6	42.4	36.6	50.5	62.4	
C8	45.8	31.1	41.2	30.2	38.4	34.1	45.1	72.3

comparing our results to Thomson (1982) due to the large time interval between studies. With respect to epifauna, the assemblages throughout LSR were completely dominated by ophiuroids, which are known to be very common and abundant in shelf and slope polar environments (MacDonald et al., 2010; Piepenburg et al., 1996; Welch et al., 1992) and in the eastern Canadian Arctic (Roy et al., 2015a). In this study, the density of brittle stars reached six hundred individuals per square meter; numbers similar to those of several other Arctic studies (Ambrose et al., 2001; Ravelo et al., 2014). Low predation pressure is suggested to be one of the reasons for their dominance (Piepenburg, 2000). Moreover, brittle stars have a wide diversity of feeding modes, such as omnivorous and surface deposit feeders (Piepenburg, 2000), and are very mobile in comparison to other benthic invertebrates (MacDonald et al., 2010; Thistle, 2003). This makes them flexible to exploit heterogeneous food inputs. This dominant and abundant benthic group is of fundamental importance in Arctic ecosystems; in particular, in carbon remineralisation processes (Ambrose et al., 2001; Link et al., 2012, 2013).

Each geographic location, as represented by the study Areas, was significantly different from each other in terms of epifaunal community composition; whereas for the infaunal data, no significant difference was found between Areas. This pattern of epifaunal communities is however specific to the spatial scale considered (Cusson et al., 2007; Levin, 1992). Thomson (1982) also worked at a regional scale and



**Fig. 5.** Multidimensional scaling of epifaunal communities (square-root transformed density data) from the eight sampling Areas ( $n = 15$  for each Area). A posteriori pairwise tests showed that all Areas differed significantly from each other. Circles represent samples from Areas characterized by the presence of seabird colonies and triangles represent samples from control Areas. The line separates two groups of Areas, C2, B3, B4b, C8 (left) and B1, B4a, C5, B7 (right), differentiated probably because of their differences in mean total density (Fig. 4, right).

**Table 5**

Mean values of selected environmental variables ( $\pm$ SE) for seven of the eight sampling Areas (missing data for Area B1): index of bird colony size (Birds), phosphate, nitrate and nitrite and chlorophyll *a* concentrations of bottom water (respectively [PHO], [NIT] and [Chl *a*]<sub>BW</sub>), depth, temperature, duration of open water (DOW), organic matter content of sediment (OM), sediment (Sed Chl *a*), sediment phaeopigments (Sed Phaeo) and percent cover of 9 sediment size classes (FS, FG, MG, CG, VCG, VSB, SB, MB, LB).

Area	Birds	[PHO] μmol/l	[NIT] μmol/l	[Chl <i>a</i> ] <sub>BW</sub> μg/l	Depth m				
B3	3	1.44 ± 0.06	13.58 ± 0.39	0.20 ± 0.07	202 ± 1				
B4a	2	1.28 ± 0.01	13.27 ± 2.26	0.04 ± 0.02	187 ± 2				
B4b	2	1.00 ± 0.03	10.41 ± 0.04	0.05 ± 0.02	190 ± 1				
B7	3	1.17 ± 0.06	8.96 ± 0.51	0.11 ± 0.04	284 ± 4				
C2	0	1.07 ± 0.24	8.46 ± 4.27	0.14 ± 0.02	175 ± 1				
C5	0	1.18 ± 0.04	13.16 ± 0.51	0.038 ± 0.002	310 ± 22				
C8	0	1.09 ± 0.09	10.23 ± 0.56	0.17 ± 0.04	242 ± 8				
Area	Temperature °C	DOW nb of days	OM %	Sed Chl <i>a</i> μg g <sup>-1</sup> dw	Sed Phaeo μg g <sup>-1</sup> dw				
B3	-0.78 ± 0.06	91 ± 13	13.63 ± 1.50	0.76 ± 0.11	4.20 ± 0.38				
B4a	0.07 ± 0.01	93 ± 11	18.03 ± 1.25	0.29 ± 0.08	3.54 ± 0.21				
B4b	-0.38 ± 0.01	92 ± 11	16.66 ± 0.79	0.44 ± 0.04	2.62 ± 0.16				
B7	0.23 ± 0.11	111 ± 7	14.66 ± 0.75	0.49 ± 0.07	2.71 ± 0.23				
C2	-0.44 ± 0.02	78 ± 10	12.41 ± 1.08	0.82 ± 0.10	4.24 ± 0.36				
C5	0.08 ± 0.11	91 ± 8	6.57 ± 0.79	0.40 ± 0.09	3.42 ± 0.32				
C8	-0.42 ± 0.13	109 ± 5	6.22 ± 0.39	0.39 ± 0.04	3.13 ± 0.15				
Area	FS %	FG %	MG %	CG %	VCG %	VSB %	SB %	MB %	LB %
B3	19 ± 5	6 ± 1	7 ± 1	14 ± 2	33 ± 4	13 ± 3	7 ± 2	1 ± 1	0 ± 0
B4a	3 ± 1	6 ± 2	10 ± 2	15 ± 3	49 ± 5	11 ± 3	4 ± 1	2 ± 1	0 ± 0
B4b	3 ± 1	5 ± 2	11 ± 3	19 ± 2	53 ± 5	6 ± 1	3 ± 1	1 ± 1	0 ± 0
B7	14 ± 4	4 ± 1	22 ± 5	19 ± 4	24 ± 4	9 ± 2	8 ± 2	0 ± 0	0 ± 0
C2	6 ± 1	7 ± 2	12 ± 2	24 ± 4	31 ± 5	10 ± 2	8 ± 2	1 ± 1	2 ± 2
C5	8 ± 3	9 ± 4	15 ± 4	21 ± 3	34 ± 5	11 ± 3	2 ± 1	0 ± 0	0 ± 0
C8	14 ± 3	30 ± 5	23 ± 4	14 ± 3	14 ± 3	5 ± 1	1 ± 0	1 ± 1	0 ± 0

demonstrated that geographic location was a major predictor of standing stock and density of benthos, indicating environmental heterogeneity in the eastern Canadian Arctic.

4.2. Food supply proxies

In our study, the sediment concentration of phaeopigments was correlated with the diversity (*H'*) of benthic communities, positively for epifauna and negatively for infauna. Moreover, the concentration of organic matter was positively correlated to the number of epifaunal taxa. The concentration of organic matter is a known proxy of the quantity of food available for benthic organisms, whereas the sediment pigment concentrations are frequently used to evaluate the quality (or “freshness”) of organic matter available (Morata and Renaud, 2008; Roy et al., 2014). More specifically, the sediment concentration of phaeopigments provides information on the degraded portion of the organic matter that accumulated on the seabed over years (Renaud et al., 2008). The positive relationships between food supply proxies and

**Table 6**

Results of multiple linear regression models of infaunal community characteristics (*S* = number of taxa, *N* = density of organisms, *J'* = Pielou's evenness index, *H'* = Shannon-Wiener diversity index) against environmental variables associated to the sampling Areas (*n* = 2 for each Area), excluding Area B1. Sed Phaeo = phaeopigment concentration in sediment; FG = percent cover of fine gravel; DOW = duration of open water. For each predictor selected in these models, regression coefficients ( $\pm$ SE) are presented. Absence of regression coefficient means that the environmental variable was not selected in the model. Environmental variables which were not retained in any model are not shown.

	<i>S</i>	<i>N</i>	<i>J'</i>	<i>H'</i>
Intercept	69.55 ± 11.66	132.78 ± 52.76	1.23 ± 0.12	6.80 ± 1.10
Sed Phaeo			-0.13 ± 0.03	-0.46 ± 0.13
FG	0.34 ± 0.15	2.15 ± 0.70	-0.010 ± 0.002	
DOW	-0.56 ± 0.12	-1.13 ± 0.58		-0.035 ± 0.008
Adj. R <sup>2</sup>	0.56	0.38	0.68	0.59
F	9.44	4.93	14.56	10.35
<i>p</i>	0.004	0.029	0.001	0.003
SS <sub>Model</sub>	369.59	3957.33	0.17	1.00

biodiversity metrics could be explained by the wider ecological concept of the productivity-biodiversity relationship. A hypothesis in ecology, mainly tested in land and fresh water habitats (Bosman et al., 1986; Mittelbach et al., 2001), supports the idea that if production of food resources increases, diversity may increase as well (Pianka, 1967; Witman et al., 2008). Recent benthic studies have shown that the pattern can be curvilinear (Levin et al., 2001), as shown in the Arctic (Witman et al., 2008), with the diversity decreasing after reaching the maximum. The descending limb has been attributed to the effects of environmental stress (Grime, 1973) or to competitively dominant species decreasing

**Table 7**

Results of multiple linear regression models of epifaunal community characteristics (*S* = number of taxa, *N* = density of organisms, *J'* = Pielou's evenness index, *H'* = Shannon-Wiener diversity index) against environmental variables associated to the sampling Areas (*n* = 15 for each Area), excluding Area B1. Birds = index of bird colony size; [NIT] = nitrites and nitrates concentration of bottom water; D = depth; T = temperature of bottom water; OM = organic matter concentration in sediment; Sed Phaeo = phaeopigment concentration in sediment; MG = percent cover of medium gravel; VSB = percent cover of very small boulders; SB = percent cover of small boulders. For each predictor selected in these models, regression coefficients ( $\pm$ SE) are presented. Absence of regression coefficient means that the environmental variable was not selected in the model. Environmental variables which were not retained in any model are not shown.

	<i>S</i>	<i>N</i>	<i>J'</i>	<i>H'</i>
Intercept	2.90 ± 0.14	2.70 ± 0.12	0.50 ± 0.04	0.42 ± 0.13
Birds	-0.19 ± 0.05			
[NIT]				0.023 ± 0.009
D		-0.0025 ± 0.0006		
T		-0.45 ± 0.07	0.24 ± 0.03	0.45 ± 0.06
OM	0.05 ± 0.01			
Sed Phaeo				0.09 ± 0.04
MG		0.023 ± 0.004		
VSB				0.020 ± 0.005
SB				-0.015 ± 0.005
Adj. R <sup>2</sup>	0.12	0.51	0.44	0.38
F	8.35	37.08	28.09	21.94
<i>p</i>	<0.001	<0.001	<0.001	<0.001
SS <sub>Model</sub>	2.93	4.06	1.00	2.15

**Table 8**

Distance-based linear model (DISTLM) of epifaunal communities (square-root transformed epifaunal density data) against environmental variables associated to the sampling Areas ( $n = 15$  for each Area), excluding Area 1. Birds = index of bird colony size; D = depth; Sed Chl  $a$  = chlorophyll  $a$  concentration in sediment; MG = percent cover of medium gravel; SB = percent cover of small boulders.

No. vars	Adj R <sup>2</sup>	R <sup>2</sup>	AICc	BIC
5	0.32	0.36	653.99	669.06
Variable	SS (trace)	Pseudo-F	$p$	Prop.
D	9294.1	15.00	<0.001	0.127
Sed Chl $a$	8118.2	12.86	<0.001	0.111
Birds	3028.1	4.45	0.001	0.041
MG	2641.7	3.86	0.003	0.036
SB	2036.6	2.95	0.013	0.027

Axis	Percentage of variation explained by individual axes			
	% explained variation out of fitted model		% explained variation out of total variation	
	Individual	Cumulative	Individual	Cumulative
1	65.7	65.7	23.4	23.4
2	14.9	80.6	5.3	28.7
3	11.2	91.9	4.0	32.7
4	6.2	98.0	2.2	34.9
5	2.0	100	0.7	35.6

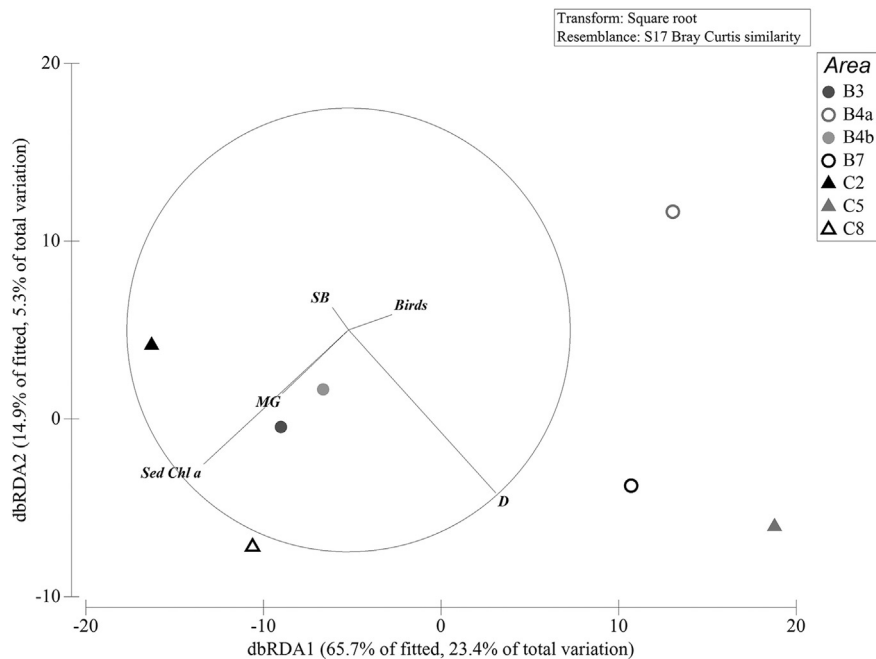
diversity at high productivity (Rosenzweig and Abramsky, 1993). Since the relationship was positive for epifauna and negative for infauna, this indicates that the two assemblages respond differently to food input.

The highest numbers of epifaunal and infaunal taxa were recorded at Area C2, the farthest offshore and the nearest to Barrow Strait of all Areas sampled. Barrow Strait is characterized by a sill of 150 m depth, which mixes the water masses in Lancaster Sound (Prinsenberg and Bennett, 1987). Mixing could allow an efficient replenishment of nutrients in the euphotic layer, increasing primary productivity, as shown with wind-driven upwelling in the coastal Beaufort Sea by Tremblay et al. (2011). These mixing processes probably enhanced food availability for benthic communities located near Barrow Strait via enhanced POC fluxes (McArthur et al., 2010), explaining higher pigment

concentration in sediment and in bottom water found for Area C2 (also shown by Kenchington et al., 2011). This enhanced food input could have led to a higher number of taxa that benefited from these resources (Rosenzweig, 1995; Wright et al., 1993). Also, a recent study near Resolute Bay provided evidence of pelagic blooms under sea ice, with the highest number of cells in Barrow Strait (Duerksen et al., 2014).

For epifaunal communities, density decreased with depth, which is a correlation frequently observed in marine ecosystems and potentially linked with the decreasing fresh food availability along a large depth gradient (MacDonald et al., 2010; Smith et al., 2008). Depth is an indirect factor often correlated with other parameters that vary vertically and convey more biological relevance such as temperature or salinity (Smith et al., 2008). However, depth was not significantly correlated to the abiotic parameters measured in this study, likely because the range was quite narrow as a result of our experimental design. The dbRDA analyses showed depth and the concentration of chlorophyll  $a$  in the sediment to be the most important parameters among those measured to explain the distinction between the two groups of Areas in terms of epifaunal density. However, they were not highly correlated with each other. As the two groups of Areas were directly created by ophiuroid distribution, we conclude that depth, food availability and quality (MacDonald et al., 2010; Morata and Renaud, 2008) drive ophiuroid distribution.

Considering that ice cover is an important limiting factor to primary production in arctic ecosystems, the duration of open water (integrated over five years in this study) can be used as an indirect food availability proxy, such as depth (MacDonald et al., 2010). Several recent studies demonstrated that integrated PP estimates can be significantly correlated to macrofaunal density (Cochrane et al., 2009; Roy et al., 2014) and taxonomic composition (Cochrane et al., 2009), even if it is not always straightforward (Roy et al., 2014). Contrary to our expectations, a longer open water season was associated with a reduced total density of infauna in the LSR. This result is not simple to explain, but it could mean that ice algal production and subsequent export to the seafloor was potentially lower where open water season was longer.



**Fig. 6.** Distance-based redundancy analysis (dbRDA) plot of the DISTLM model based on the environmental variables that better explained variability among epifaunal communities (square-root transformed density data) of the sampling Areas ( $n = 15$  for each Area), excluding Area 1. Circles represent samples from Areas characterized by the presence of seabird colonies and triangles represent samples from control Areas. Birds = index of bird colony size; D = depth; Sed Chl  $a$  = concentration of chlorophyll  $a$  in sediment; MG = percent cover of medium gravel; SB = percent cover of small boulders.

#### 4.3. Percent cover of gravel and boulders

The number of taxa and the total density of infauna were positively correlated to the percent cover of fine gravel. Gravel represents a settlement surface and the large interstices create habitat for cryptical infaunal species (McArthur et al., 2010). By enhancing the total infaunal density, higher proportion of fine gravel may indirectly increase inter-specific competition for resources and promote some opportunistic taxa over other taxa. Therefore, it is consistent to find a negative relationship between percent cover of fine gravel and the evenness index  $J'$ .

The evenness within epifaunal communities was positively correlated with percent cover of very small boulders and negatively associated to cover of small boulders. By increasing habitat heterogeneity and surface for settlement, boulders permit the settlement of less common groups, such as crinoids, basket stars, corals, anemones, tunicates and sponges (Tissot et al., 2006). Since the very small boulders were intermediate between finer and coarser classes of sediment, their presence could allow the different species to coexist in more even proportions. However, it was the percent cover of medium gravel that positively influenced the total density of epifauna, dominated by ophiuroids. During photo analyses, we observed that ophiuroids seemed to prefer gravel and tended to accumulate in the gaps between pebbles, where reduced current velocity probably facilitated their displacement and favored sedimentation of food.

Collectively, our observations support Piepenburg (2000), who summarized that seabed heterogeneity and food availability are important drivers of the structure of ophiuroids assemblages. In our multivariate approach, the percent cover of medium gravel and small boulders explained a significant part of the variation in epifaunal community composition between the Areas sampled. The repetition of these same predictors regardless of the statistical method used, confirms their importance in structuring benthic communities in the LSR.

#### 4.4. The weak link between seabirds and benthos

Our initial hypothesis was on the positive indirect effect of seabird colonies on benthic communities through concentrated nutrient intake and subsequent enhanced food availability (bottom-up effect). This hypothesis was based on relevant results obtained in coastal regions of Argentina (Palomo et al., 1999), Sweden (Kolb et al., 2010) and even in an Arctic ecosystem (Spitsbergen: Zmudczyńska-Skarbek et al., 2015), which demonstrated positive effects on abundance, biomass, trophic characteristics, and/or diversity of benthos (Kolb et al., 2010; Palomo et al., 1999; Zmudczyńska-Skarbek et al., 2015; see Signa et al., 2015 for negative effects in coastal ponds). Food availability is known to influence taxonomic composition, diversity and abundance of benthic communities in the Arctic (Grebmeier and Barry, 1991; Roy et al., 2014). However, in contrast to what was expected, presence of seabird colonies was not a major indirect driver of benthic assemblages in LSR, explaining only a small proportion of the variation between Areas in term of taxonomical composition. Nevertheless, two negative effects of their presence were detected: (1) infaunal communities were less dense in Areas with seabird colonies presence and (2) the number of epifaunal taxa was negatively correlated with the size of seabird colonies. Knowing that the two main species that inhabit LSR cliffs, the thick-billed murre and the northern fulmar, are generally piscivorous (Mallory and Fontaine, 2004), a top-down effect could explain the negative impacts on benthic community structure.

Our study showed that food availability (sediment concentration of pigment and organic matter, depth, duration of open water) structures benthic assemblages in the LSR, but the potential input derived from the seabird colonies did not have large effects on benthic communities. We suggest four hypotheses, not mutually exclusive, to explain this finding. First, the strong currents potentially spread and rapidly exported the indirect input from seabirds. Second, the timing of the input from seabird

colonies may coincide with high ambient nutrient concentrations (as demonstrated by Bédard et al. (1980) in the St. Lawrence Estuary), especially since seabird populations usually follow the ice breakup (Mallory and Fontaine, 2004). Third, the samples were collected too deep and too far from the coast to detect the bottom-up effect expected which has been suggested to be very localized (Bédard et al., 1980; Gagnon et al., 2013). The many processes in the water column can interfere with the organic matter input making it more difficult to detect an effect in deeper water. Fourth, ice algae could play a determining role in the structure of the benthic community in the LSR and could be a more important environmental parameter than phytoplankton production (McMahon et al., 2006), even if nutrient content of seabird guano enhanced it. Only 10% of annual primary production in LSR is produced by ice algae (Michel et al., 2006). It may seem insignificant, but these algal mats, highly concentrated in organic carbon, sink rapidly upon release from the sea ice (Michel et al., 1996) and reach the bottom at a time when there is no other food resource for benthic organisms in the Canadian Arctic (Bradstreet and Cross, 1982; Michel et al., 1996, 2006). Also, numerous past studies suggested the great importance of this resource for benthic organisms in the Arctic (Boetius et al., 2013; Brown and Belt, 2012; Roy et al., 2015b), even at depths beyond 3500 m (Boetius et al., 2013).

#### 5. Conclusion

Benthic communities and benthic processes are driven by complex interactions between biotic and abiotic variables that vary on several spatial and temporal scales (Cusson et al., 2007; Link et al., 2012, 2013; Roy et al., 2014). This study demonstrated that the presence of the large seabird colonies was not a major driver of benthic community characteristics and community structure in the LSR below 120 m, although it did negatively influence the total density of infaunal organisms and influence the number of taxa for epifauna. Food availability proxies and percent cover of gravel and boulders influence the characteristics and the community composition of benthic communities in the LSR. Since food supply proxies had a strong explicative power, a different approach based on feeding traits would be a future research perspective to explore in the LSR. Even though our findings suggested that the effect of seabirds was not a major determining factor for the benthos, more work is needed to clarify their role in Arctic ecosystems. Based on our findings, the first step would be to replicate this sampling in shallower depths, nearer to the coasts, to investigate the influence of the distance from seabird colonies. In a changing Arctic, the bounds between terrestrial and marine environments and between ocean surface and seafloor could be strongly modified with unexpected effects. Accurate predictions of these impacts can only be achieved through a better comprehension of Arctic ecosystems.

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## Appendix A. Supplementary data

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## References

- Ambrose Jr., W.G., Renaud, P.E., 1997. Does a pulsed food supply to the benthos affect polychaete recruitment patterns in the Northeast Water Polynya? *J. Mar. Syst.* 10, 483–495.
- Ambrose Jr., W.G., Clough, L.M., Tilney, P.R., Beer, L., 2001. Role of echinoderms in benthic remineralization in the Chukchi Sea. *Mar. Biol.* 139, 937–949.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. *Permanova + for Primer: Guide to Software and Statistical Methods*. PRIMER-E Ltd, Plymouth.
- Archambault, P., Snelgrove, P.V.R., Fisher, J.A.D., Gagnon, J.M., Garbary, D.J., Harvey, M., Kenchington, E.L., Lesage, V., Lévesque, M., Lovejoy, C., Mackas, D.L., McKindsey, C.W., Nelson, J.R., Pepin, P., Piché, L., Poulin, M., 2010. From sea to sea: Canada's three oceans of biodiversity. *PLoS One* 5, e12182.
- Archambault, P., Grant, C., Berteaux, D., Blanchard, D., Brown, L., Edinger, E., Jensen, O., Lebeau, A., Piot, A., Sahanatien, V., 2016. Marine protected areas and biodiversity conservation in the eastern Arctic. ArcticNet Integrated Regional Impact Study (Eastern Arctic).
- Ardyna, M., Gosselin, M., Michel, C., Poulin, M., Tremblay, J.-É., 2011. Environmental forcing of phytoplankton community structure and function in the Canadian High Arctic: contrasting oligotrophic and eutrophic regions. *Mar. Ecol. Prog. Ser.* 442, 37–57.
- Ardyna, M., Babin, M., Gosselin, M., Devred, E., Rainville, L., Tremblay, J.-É., 2014. Recent Arctic Ocean sea ice loss triggers novel fall phytoplankton blooms. *Geophys. Res. Lett.* 41, 6207–6212.
- Bédard, J., Therriault, J.C., Bérubé, J., 1980. Assessment of the importance of nutrient recycling by seabirds in the St. Lawrence estuary. *Can. J. Fish. Aquat. Sci.* 37, 583–588.
- Bélanger, S., Babin, M., Tremblay, J.-É., 2013. Increasing cloudiness in Arctic damps the increase in phytoplankton primary production due to sea ice receding. *Biogeosciences* 10, 4087–4101.
- Blott, S.J., Pye, K., 2001. Gradstat: a grain size distribution and statistics package for the analysis of unconsolidated sediments. *Earth Surf. Process. Landf.* 26, 1227–1248.
- Boetius, A., Albrecht, S., Bakker, K., Bienhold, C., Felden, J., Fernández-Méndez, M., Hendricks, S., Katlein, C., Lalande, C., Krumpfen, T., Nicolaus, M., 2013. Export of algal biomass from the melting Arctic sea ice. *Science* 339, 1430–1432.
- Bosman, A.L., Hockey, P.A.R., 1986. Seabird guano as a determinant of rocky intertidal community structure. *Mar. Ecol. Prog. Ser.* 32, 247–257.
- Bosman, A.L., Du Toit, J.T., Hockey, P.A.R., Branch, G.M., 1986. A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuar. Coast. Shelf Sci.* 23, 283–294.
- Bradstreet, M.S., Cross, W.E., 1982. Trophic relationships at high Arctic ice edges. *Arctic* 35, 1–12.
- Brimble, S.K., Blais, J.M., Kimpe, L.E., Mallory, M.L., Keatley, B.E., Douglas, M.S.V., Smol, J.P., 2009. Bioenrichment of trace elements in a series of ponds near a northern fulmar (*Fulmarus glacialis*) colony at Cape Vera, Devon Island. *Can. J. Fish. Aquat. Sci.* 66, 949–958.
- Brown, T.A., Belt, S.T., 2012. Identification of the sea ice diatom biomarker IP25 in Arctic benthic macrofauna: direct evidence for sea ice diatom diet in Arctic heterotrophs. *Polar Biol.* 35, 131–137.
- Byers, S.C., Mills, E.L., Stewart, P.L., 1978. A comparison of methods of determining organic carbon in marine sediments, with suggestions for a standard method. *Hydrobiologia* 58, 43–47.
- Carroll, M.L., Denisenko, S.G., Renaud, P.E., Ambrose Jr., W.G., 2008. Benthic infauna of the seasonally ice-covered western Barents Sea: patterns and relationships to environmental forcing. *Deep-Sea Res. II* 55, 2340–2351.
- Clarke, K.R., Gorley, R.N., 2006. *Primer v6: User Manual/Tutorial*. PRIMER-E Ltd, Plymouth.
- Clarke, K.R., Warwick, R.M., 2001. *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*. PRIMER-E Ltd, Plymouth.
- Clough, L.M., Renaud, P.E., Ambrose Jr., W.G., 2005. Impacts of water depth, sediment pigment concentration, and benthic macrofaunal biomass on sediment oxygen demand in the western Arctic Ocean. *Can. J. Fish. Aquat. Sci.* 62, 1756–1765.
- Cochrane, S.K., Denisenko, S.G., Renaud, P.E., Emblow, C.S., Ambrose Jr., W.G., Ellingsen, I.H., Skarðhamar, J., 2009. Benthic macrofauna and productivity regimes in the Barents Sea – ecological implications in a changing Arctic. *J. Sea Res.* 61, 222–233.
- Cusson, M., Archambault, P., Aitken, A., 2007. Biodiversity of benthic assemblages on the Arctic continental shelf: historical data from Canada. *Mar. Ecol. Prog. Ser.* 331, 291–304.
- Darnis, G., Robert, D., Pomerleau, C., Link, H., Archambault, P., Nelson, R.J., Geoffroy, M., Tremblay, J.-É., Lovejoy, C., Ferguson, S.H., Hunt, B.P.V., Fortier, L., 2012. Current state and trends in Canadian Arctic marine ecosystems: II. Heterotrophic food web, pelagic-benthic coupling and biodiversity. *Clim. Chang.* 115, 179–205.
- Dauvin, J.C., 1993. Le benthos: témoin des variations de l'environnement. *Oceanis* 19, 25–53.
- Duerksen, S.W., Thiemann, G.W., Budge, S.M., Poulin, M., Niemi, A., Michel, C., 2014. Large, omega-3 rich, pelagic diatoms under Arctic sea ice: sources and implications for food webs. *PLoS One* 9, e114070.
- Dupont, F., Higginson, S., Bourdallé-Badie, R., Lu, Y., Roy, F., Smith, G.C., Lemieux, J.-F., Garric, G., Davidson, F., 2015. A high-resolution ocean and sea-ice modelling system for the Arctic and North Atlantic Oceans. *Geosci. Model Dev. Discuss.* 8, 1–52.
- Ellis, J.C., Fariña, J.M., Witman, J.D., 2006. Nutrient transfer from sea to land: the case of gulls and cormorants in the Gulf of Maine. *J. Anim. Ecol.* 75, 565–574.
- Fariña, J.M., Salazar, S., Wallem, K.P., Witman, J.D., Ellis, J.C., 2003. Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos sea lion *Zalophus wollebaecki*. *J. Anim. Ecol.* 72, 873–887.
- Gagnon, K., Rothäusler, E., Syrjänen, A., Yli-Renko, M., Jormalainen, V., 2013. Seabird guano fertilizes Baltic Sea littoral food webs. *PLoS One* 8, e61284.
- Gaillard, B., Meziane, T., Tremblay, R., Archambault, P., Layton, K.S.S., Martel, A.L., 2015. Dietary tracers in *Bathycara glacialis* from contrasting trophic regions in the Canadian Arctic. *Mar. Ecol. Prog. Ser.* 536, 175–186.
- Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. *J. Mar. Syst.* 2, 495–518.
- Grebmeier, J.M., Smith, W.O., Conover, R.J., 1995. Biological processes on arctic continental shelves: ice-ocean-biotic interactions. In: Smith, W.O., Grebmeier, J.M. (Eds.), *Arctic Oceanography: Marginal Zones and Continental Shelves*. American Geophysical Union, Washington, D.C., pp. 231–261.
- Crime, J.P., 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242, 344–347.
- Hamilton, J., Pettipas, R., Prinsenberg, S., 2008. Moored current meter and CTD observations from Barrow Strait, 2003–2004. *Can. Data Rep. Hydrogr. Ocean Sci.* 173.
- Hamilton, J.M., Collins, K., Prinsenberg, S.J., 2013. Links between ocean properties, ice cover, and plankton dynamics on interannual time scales in the Canadian Arctic Archipelago. *J. Geophys. Res.* Oceans 118, 5625–5639.
- Hardy, M., Gendron, L., Archambault, P., 2008. Distribution spatio-temporelle du homard au large de Saint-Godefroi (baie des Chaleurs, Québec) et relation avec les activités de pêche au pétoncle. *MPO Rapp. Tech. Can. Sci. Halieut. Aquat.* 2781.
- Harrison, W.G., Cota, G.F., 1991. Primary production in polar waters: relation to nutrient availability. *Polar Res.* 10, 87–104.
- Hobson, K.A., Welch, H.E., 1992. Determination of trophic relationships within a high Arctic marine food web using  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Mar. Ecol. Prog. Ser.* 84, 9–18.
- Iken, K., Bluhm, B.A., Gradinger, R., 2005. Food web structure in the high Arctic Canada Basin: evidence from  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis. *Polar Biol.* 28, 238–249.
- Kenchington, E., Link, H., Roy, V., Archambault, P., Siferd, T., Treble, M., Wareham, V., 2011. Identification of mega- and macrobenthic ecologically and biologically significant areas (EBSAs) in the Hudson Bay complex, the western and eastern Canadian Arctic. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2011/071.
- Kline Jr., T.C., Goering, J.J., Mathisen, O.A., Poe, P.H., Parker, P.L., Scalan, R.S., 1993. Recycling of elements transported upstream by runs of Pacific salmon: II.  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  evidence in the Kvichak River watershed, Bristol Bay, southwestern Alaska. *Can. J. Fish. Aquat. Sci.* 50, 2350–2365.
- Kolb, G.S., Ekholm, J., Hambäck, P.A., 2010. Effects of seabird nesting colonies on algae and aquatic invertebrates in coastal waters. *Mar. Ecol. Prog. Ser.* 417, 284–300.
- Leblond, P.H., 1980. On the surface circulation in some channels of the Canadian Arctic Archipelago. *Arctic* 33, 189–197.
- Lee, Y.J., Matrai, P.A., Friedrichs, M.A.M., Saba, V.S., Antoine, D., Ardyna, M., Asanuma, I., Babin, M., Bélanger, S., Benoît-Gagné, M., Devred, E., Fernández-Méndez, M., Gentili, B., Hirawake, T., Kang, S.-H., Kameda, T., Katlein, C., Lee, S.H., Lee, Z., Mélin, F., Scardi, M., Smyth, T.J., Tang, S., Turpie, K.R., Waters, K.J., Westberry, T.K., 2015. An assessment of phytoplankton primary productivity in the Arctic Ocean from satellite ocean color/in situ chlorophyll-a-based models. *J. Geophys. Res.* 120, 6508–6541.
- Levin, S.A., 1992. The problem of pattern and scale in ecology. *Ecology* 73, 1943–1967.
- Levin, L.A., Etter, R.J., Rex, M.A., Gooday, A.J., Smith, C.R., Pineda, J., Stuart, C.T., Hessler, R.R., Pawson, D., 2001. Environmental influences on regional deep-sea species diversity. *Annu. Rev. Ecol. Syst.* 32, 51–93.
- Lewis, C.F.M., Blasco, S.M., 1990. Character and distribution of sea-ice and iceberg scours. In: Clark, J.L. (Ed.), *Workshop on Ice Scouring and Design of Offshore Pipelines*, Calgary, Alberta, April 18–19, 1990. Canada Oil and Gas Lands Administration, Energy, Mines and Resources Canada and Indian and Northern Affairs Canada, Ottawa, pp. 57–101.
- Lewis, T.L., Esler, D., Boyd, W., 2007. Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. *Mar. Ecol. Prog. Ser.* 329, 131–144.
- Link, H., Chailou, G., Forest, A., Piepenburg, D., Archambault, P., 2012. Multivariate benthic ecosystem functioning in the Arctic – benthic fluxes explained by environmental parameters in the southeastern Beaufort Sea. *Biogeosci. Discuss.* 9, 16933–16976.
- Link, H., Piepenburg, D., Archambault, P., 2013. Are hotspots always hotspots? The relationship between diversity, resource and ecosystem functions in the Arctic. *PLoS One* 8, e74077.
- Longhurst, A., Sameoto, D., Herman, A., 1984. Vertical distribution of Arctic zooplankton in summer: eastern Canadian archipelago. *J. Plankton Res.* 6, 137–168.
- MacDonald, I.R., Bluhm, B.A., Iken, K., Gagev, S., Strong, S., 2010. Benthic macrofauna and megafauna assemblages in the Arctic deep-sea Canada Basin. *Deep-Sea Res. II* 57, 136–152.
- Mallory, M.L., Fontaine, A.J., 2004. Key marine habitat sites for migratory birds in Nunavut and the Northwest Territories. *Canadian Wildlife Service Occasional Paper* 109. Ottawa, Environment Canada.

- Maritorena, S., Siegel, D.A., Peterson, A.R., 2002. Optimization of a semianalytical ocean color model for global-scale applications. *Appl. Opt.* 41, 2705–2714.
- Maslanik, J.A., Stroeve, J.C., 1999. Near-real-time DMSP SSM/I-SSMIS Daily Polar Gridded Sea Ice Concentrations. [2008–2012].
- McArthur, M.A., Brooke, B.P., Przeslawski, R., Ryan, D.A., Lucieer, V.L., Nichol, S., McCallum, A.W., Mellin, C., Cresswell, I.D., Radke, L.C., 2010. On the use of abiotic surrogates to describe marine benthic biodiversity. *Estuar. Coast. Shelf Sci.* 88, 21–32.
- McMahon, K.W., Ambrose Jr., W.G., Johnson, B.J., Sun, M.Y., Lopez, G.R., Clough, L.M., Carroll, M.L., 2006. Benthic community response to ice algae and phytoplankton in Ny Ålesund, Svalbard. *Mar. Ecol. Prog. Ser.* 310, 1–14.
- Michel, C., Legendre, L., Ingram, R.G., Gosselin, M., Levasseur, M., 1996. Carbon budget of sea-ice algae in spring: evidence of a significant transfer to zooplankton grazers. *J. Geophys. Res.* 101, 18–345.
- Michel, C., Ingram, R.G., Harris, L.R., 2006. Variability in oceanographic and ecological processes in the Canadian Arctic Archipelago. *Prog. Oceanogr.* 71, 379–401.
- Michelutti, N., Keatley, B.E., Brimble, S., Blais, J.M., Liu, H., Douglas, M.S.V., Mallory, M.L., Macdonald, R.W., Smol, J.P., 2009. Seabird-driven shifts in Arctic pond ecosystems. *Proc. R. Soc. Lond. B Biol. Sci.* 276, 591–596.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I., Gough, L., 2001. What is the observed relationship between species richness and productivity? *Ecology* 82, 2381–2396.
- Morata, N., Renaud, P.E., 2008. Sedimentary pigments in the western Barents Sea: a reflection of pelagic-benthic coupling? *Deep-Sea Res II* 55, 2381–2389.
- Morata, N., Renaud, P.E., Brugel, S., Hobson, K.A., Johnson, B.J., 2008. Spatial and seasonal variations in the pelagic-benthic coupling of the southeastern Beaufort Sea revealed by sedimentary biomarkers. *Mar. Ecol. Prog. Ser.* 371, 47–63.
- Palomo, G., Iribarne, O., Martinez, M.M., 1999. The effect of migratory seabirds guano on the soft bottom community of a SW Atlantic coastal lagoon. *Bull. Mar. Sci.* 65, 119–128.
- Parsons, T.R., Maita, Y., Lalli, C.M., 1984. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Toronto.
- Pearson, T.H., Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Annu. Rev. Oceanogr. Mar. Biol.* 16, 229–311.
- Pianka, E.R., 1967. On lizard species diversity: North American flatland deserts. *Ecology* 48, 333–351.
- Piepenburg, D., 2000. Arctic brittle stars (Echinodermata: Ophiuroidea). *Oceanogr. Mar. Biol.* 38, 189–256.
- Piepenburg, D., Chernova, N.V., von Dorrien, C.F., Gutt, J., Neyelov, A.V., Rachor, E., Saldanha, L., 1996. Megabenthic communities in the waters around Svalbard. *Polar Biol.* 16, 431–446.
- Piepenburg, D., Archambault, P., Ambrose Jr., W.G., Blanchard, A.L., Bluhm, B.A., Carroll, M.L., Conlan, K.E., Cusson, M., Feder, H.M., Grebmeier, J.M., Jewett, S.C., Lévesque, M., Petryashev, V.V., Sejr, M.K., Sirenko, B.I., Włodarska-Kowalczyk, M., 2011. Towards a pan-Arctic inventory of the species diversity of the macro- and megabenthic fauna of the Arctic shelf seas. *Mar. Biodivers.* 41, 51–70.
- Powell, G.V., Fourqurean, J.W., Kenworthy, W.J., Zieman, J.C., 1991. Bird colonies cause seagrass enrichment in a subtropical estuary: observational and experimental evidence. *Estuar. Coast. Shelf Sci.* 32, 567–579.
- Prinsenberg, S.J., Bennett, E.B., 1987. Mixing and transports in Barrow Strait, the central part of Northwest Passage. *Cont. Shelf Res.* 7, 913–935.
- Quinn, G., Keough, M., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Ravelo, A.M., Konar, B., Trefry, J.H., Grebmeier, J.M., 2014. Epibenthic community variability in the northeastern Chukchi Sea. *Deep-Sea Res. II* 102, 119–131.
- Riaux-Gobin, C., Klein, B., 1993. Microphytobenthic biomass measurement using HPLC and conventional pigment analysis. In: Kemp, P., Sherr, B., Cole, J. (Eds.), *Handbook of Methods in Aquatic Microbial Ecology*. Lewis Publishers, Boca Raton, pp. 369–376.
- Rosenzweig, M.L., 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rosenzweig, M.L., Abramsky, Z., 1993. How are diversity and productivity related? In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 52–65.
- Roy, V., Iken, K., Archambault, P., 2014. Environmental drivers of the Canadian Arctic megabenthic communities. *PLoS One* 9, e100900.
- Roy, V., Iken, K., Archambault, P., 2015a. Regional variability of megabenthic community structure across the Canadian Arctic. *Arctic* 68, 180–192.
- Roy, V., Iken, K., Gosselin, M., Tremblay, J.-É., Bélanger, S., Archambault, P., 2015b. Benthic faunal assimilation pathways and depth-related changes in food-web structure across the Canadian Arctic. *Deep-Sea Res. I* 102, 55–71.
- Sameoto, D., Herman, A., Longhurst, A., 1986. Relations between the thermocline meso and microzooplankton, chlorophyll *a* and primary production distributions in Lancaster Sound. *Polar Biol.* 6, 53–61.
- Signa, G., Mazzola, A., Vizzini, S., 2012. Effects of a small seagull colony on trophic status and primary production in a Mediterranean coastal system (Marinello ponds, Italy). *Estuar. Coast. Shelf Sci.* 111, 27–43.
- Signa, G., Mazzola, A., Costa, V., Vizzini, S., 2015. Bottom-up control of macrobenthic communities in a guanotrophic coastal system. *PLoS One* 10, e0117544.
- Smith, C.R., De Leo, F.C., Bernardino, A.F., Sweetman, A.K., Arbizu, P.M., 2008. Abyssal food limitation, ecosystem structure and climate change. *Trends Ecol. Evol.* 23, 518–528.
- Soltwedel, T., Jaeckisch, N., Ritter, N., Hasemann, C., Bergmann, M., Klages, M., 2009. Bathymetric patterns of megafaunal assemblages from the arctic deep-sea observatory HAUSGARTEN. *Deep-Sea Res.* 1 56, 1856–1872.
- Søreide, J.E., Carroll, M.L., Hop, H., Ambrose Jr., W.G., Hegseth, E.N., Falk-Petersen, S., 2013. Sympagic-pelagic-benthic coupling in Arctic and Atlantic waters around Svalbard revealed by stable isotopic and fatty acid tracers. *Mar. Biol. Res.* 9, 831–850.
- Steinmetz, J., Kohler, S.L., Soluk, D.A., 2003. Birds are overlooked top predators in aquatic food webs. *Ecology* 84, 1324–1328.
- Thistle, D., 2003. The deep-sea floor: an overview. In: Tyler, P.A. (Ed.), *Ecosystems of the World*. Elsevier, New York, pp. 5–38.
- Thomson, D.H., 1982. Marine benthos in the eastern Canadian High Arctic: multivariate analyses of standing crop and community structure. *Arctic* 35, 61–74.
- Tissot, B.N., Yoklavich, M.M., Love, M.S., York, K., Amend, M., 2006. Benthic invertebrates that form habitat on deep banks off southern California, with special reference to deep see coral. *Fish. Bull. NOAA* 104, 167–181.
- Tréguer, P., Le Corre, P., 1975. *Manuel d'analyse des sels nutritifs dans l'eau de mer*. Laboratoire d'océanographie chimique, Université Bretagne Occidentale, Brest.
- Tremblay, J.-É., Michel, C., Hobson, K.A., Gosselin, M., Price, N.M., 2006. Bloom dynamics in early opening waters of the Arctic Ocean. *Limnol. Oceanogr.* 51, 900–912.
- Tremblay, J.-É., Bélanger, S., Barber, D.G., Asplin, M., Martin, J., Darnis, G., Fortier, L., Gratton, Y., Link, H., Archambault, P., Sallon, A., Michel, C., Williams, W.J., Philippe, B., Gosselin, M., 2011. Climate forcing multiplies biological productivity in the coastal Arctic Ocean. *Geophys. Res. Lett.* 38, L18604.
- Tremblay, J.-É., Anderson, L.G., Matrai, P., Coupel, P., Bélanger, S., Michel, C., Reigstad, M., 2015. Global and regional drivers of nutrient supply, primary production and CO<sub>2</sub> drawdown in the changing Arctic Ocean. *Prog. Oceanogr.* 139, 171–196.
- Trygonis, V., Sini, M., 2012. Photoquad: a dedicated seabed image processing software, and a comparative error analysis of four photoquad methods. *J. Exp. Mar. Biol. Ecol.* 424–425, 99–108.
- Udden, J.A., 1914. Mechanical composition of clastic sediments. *Geol. Soc. Am. Bull.* 25, 655–744.
- Underwood, A.J., 1997. *Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance*. Cambridge University Press, Cambridge.
- Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., Hop, H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound Region, Arctic Canada. *Arctic* 45, 343–357.
- Wentworth, C.K., 1922. A scale of grade and class terms for clastic sediments. *J. Geol.* 30, 377–392.
- Witman, J.D., Cusson, M., Archambault, P., Pershing, A.J., Mieszkowska, N., 2008. The relation between productivity and species diversity in temperate-arctic marine ecosystems. *Ecology* 89, S66–S80.
- Wright, D.H., Currie, D.J., Maurer, B.A., 1993. Energy supply and patterns of species richness on local and regional scales. In: Ricklefs, R.E., Schluter, D. (Eds.), *Species Diversity in Ecological Communities: Historical and Geographical Perspectives*. University of Chicago Press, Chicago, pp. 66–74.
- Young, H.S., Hurrey, L., Kolb, G.S., 2011. Effects of seabird-derived nutrients on aquatic systems. In: Mulder, C.P.H., Anderson, W.B., Towns, D.R., Bellingham, P.J. (Eds.), *Seabird Islands: Ecology, Invasion and Restoration*. Oxford University Press, New York, pp. 242–260.
- Zelickman, E.A., Golovkin, A.N., 1972. Composition, structure and productivity of neritic plankton communities near the bird colonies of the northern shores of Novaya Zemlya. *Mar. Biol.* 17, 265–274.
- Zmudczyńska-Skarbek, K., Barcikowski, M., Zwolicka, A., Iłyszko, L., Stempniewicz, L., 2013. Variability of polar scurvygrass *Cochlearia groenlandica* individual traits along a seabird influenced gradient across Spitsbergen tundra. *Polar Biol.* 36, 1659–1669.
- Zmudczyńska-Skarbek, K., Balazy, P., Kuklinski, P., 2015. An assessment of seabird influence on Arctic coastal benthic communities. *J. Mar. Syst.* 144, 48–56.