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à Rimouski

INFLUENCE DE LA PRÉSENCE DES COLONIES D'OISEAUX MIGRATEURS (*FULMARUS GLACIALIS* ET *URIA LOMVIA*) SUR LES ASSEMBLAGES BENTHIQUES DE LA RÉGION DU DÉTROIT DE LANCASTER, CANADA

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La joie de regarder et de comprendre est le plus beau cadeau de la nature

Albert Einstein

Far better an approximate solution to the right question than… an exact answer to the wrong question, which can always be made precise

John Tuckey

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Article

Bouchard Marmen M., P. Archambault, E. Kenchington (en redaction). Influence of seabird colonies on the structure of benthic communities, Lancaster Sound region, Canadian Arctic.

Affiches et présentations orales

Bouchard Marmen M., P. Archambault, E. Kenchington, 2012. Quand les oiseaux s'en mêlent…! Impact du bioenrichissement engendré par les colonies d'oiseaux migrateurs sur des assemblages benthiques. Réunion annuelle Québec-Océan, Montréal, Canada, 7-9 novembre. (Affiche)

Bouchard Marmen M., P. Archambault, E. Kenchington, 2012. Quand les oiseaux s'en mêlent…! Impact du bioenrichissement engendré par les colonies d'oiseaux migrateurs sur des assemblages benthiques. Forum des Sciences de la Mer, Institut Maurice-Lamontagne, Mont-Joli, Canada, 27-28 novembre. (Affiche)

Bouchard Marmen M., P. Archambault, E. Kenchington, 2013. Can Seabirds Control Benthic Biodiversity in the Arctic? Réunion annuelle Québec-Océan, Rivière-du-Loup, Canada, 13-15 novembre. (Affiche)

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Bouchard Marmen M., P. Archambault, E. Kenchington, 2014. Quel est le régulateur de la biodiversité benthique dans le détroit de Lancaster? Comparaison de deux méthodes d'échantillonnage. Réunion annuelle Québec-Océan, Rivière-du-Loup, Canada, 17-19 novembre. (Affiche)

Bouchard Marmen M., P. Archambault, E. Kenchington, 2014. What is driving benthic biodiversity of Lancaster Sound region? Comparison of two sampling methods. The Arctic Biodiversity Congress, Trondheim, Norvège, 2-4 décembre. (Affiche)

RÉSUMÉ

Agissant en tant que vecteurs biologiques de nutriments, les oiseaux marins peuvent grandement affecter les écosystèmes terrestres, mais leur influence sur les habitats marins est encore méconnue. L'Arctique canadien abrite plusieurs millions d'oiseaux marins chaque année durant la saison de reproduction. Par l'excrétion d'importantes quantités de guano, les oiseaux marins concentrent localement de la matière organique riche en éléments nutritifs dans les zones marines entourant les colonies. Ces apports saisonniers pourraient-ils créer des points chauds de productivité biologique marine et indirectement influencer la faune benthique en augmentant la disponibilité de la nourriture (effets *bottom-up*)? Principalement sessiles et longévives, les espèces benthiques sont capables d'intégrer, à long terme, la variabilité environnementale des réseaux trophiques marins. Les objectifs de cette étude étaient de (1) caractériser les communautés épibenthiques et endobenthiques de la région du détroit de Lancaster (LSR) et de (2) tester l'influence de la présence de colonies d'oiseaux marins et d'autres paramètres environnementaux sur la structure de ces communautés benthiques. Notre hypothèse était que la diversité benthique, le nombre de taxons, la biomasse totale de l'endofaune et la densité totale de l'épifaune et de l'endofaune seraient plus élevés dans les zones avec présence de colonies. À bord du NAFC Quest en 2012, des photos du fond marin (épifaune) et des échantillons provenant d'une benne (endofaune) ont été pris dans trois zones contrôles et cinq zones près de colonies d'oiseaux marins, à une profondeur variant de 122 à 442 mètres. Une base de données de 23 paramètres environnementaux a été construite pour étudier les liens environnement-benthos. L'endofaune, très uniforme à travers LSR, était dominée par les annélides en termes de densité. L'épifaune était distribuée de façon plus hétérogène, chaque zone d'étude étant unique en termes d'assemblages épibenthiques. Les ophiures étaient largement dominantes dans les communautés épibenthiques, atteignant 600 individus par mètre carré. Les résultats ont également montré que la présence de colonies d'oiseaux marins n'était pas un facteur structurant des communautés benthiques dans LSR à une profondeur supérieure à 120 mètres. Des effets négatifs des colonies ont été observés sur la densité et le nombre de taxons de l'endofaune, ce qui pourrait être dû à des effets régulateurs par la prédation (effets *top-down*) engendrés par les oiseaux marins. Globalement, la profondeur, le type de sédiment, la concentration de chlorophylle *a* et le nombre de jours sans glace expliquent une part substantielle de la variabilité spatiale dans la structure des communautés benthiques de LSR. Je conclus que la disponibilité de la nourriture est probablement un facteur structurant les communautés benthiques, bien que les voies de transport associées aux oiseaux marins n'affectent pas largement le benthos situé près de la source de guano.

Mots clés: Communautés benthiques, Colonies d’oiseaux, Vecteur biologique, Arctique, Détroit de Lancaster, Facteurs environnementaux, Structure des communautés

ABSTRACT

Acting as biological vectors of nutrients, seabirds can markedly affect terrestrial ecosystems, but their influence on marine habitats is still unknown. 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. Could these seasonal inputs create hotspots of marine biological productivity and indirectly influence benthic fauna by increasing food availability (bottom-up effects)? Mainly sessile and long-lived, benthic 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 these benthic communities. Our hypothesis was that benthic diversity, numbers of taxa, total infauna biomass and total epifauna and infauna density would be higher in areas with presence of colonies. Aboard CFAV Quest in 2012, photos of the seafloor (epifauna) and grab samples (infauna) were taken at three control areas and at five areas near seabird colonies, within a depth range of 122 to 442 meters. A database of 23 environmental parameters was built to study the environment-benthos relationships. Infauna, which was very uniform across the LSR, was dominated by Annelida in terms of density. Epifauna was much more patchy with each study area being unique in terms of epibenthic assemblages. Brittle stars were however highly dominant in epifaunal communities, reaching 600 individuals per square meter. Results also showed that presence of seabird colonies was not a major driver of benthic communities in the LSR below 120 meters. Negative effects of colonies were detected on density and number of taxa of infauna, perhaps due to top-down effects transmitted by the seabirds. Generally, depth, sediment type, chlorophyll *a* concentration and duration of open water explained a substantial part of spatial variability in structure of benthic communities sampled across the LSR. I conclude that food availability is probably a factor driving benthic communities, even if potential pathways through seabirds did not broadly affect the benthos at the point source.

Keywords : Benthic communities, Seabird colonies, Biological vector, Arctic, Lancaster Sound, Environmental drivers, Community structure

TABLE DES MATIÈRES

LISTE DES TABLEAUX

LISTE DES FIGURES

INTRODUCTION GÉNÉRALE

1.1. TRANSPORT DE NUTRIMENTS ENTRE LES ECOSYSTEMES

Le transport de nutriments entre les habitats est une force clé qui peut profondément modifier la structure des communautés biologiques et la dynamique des réseaux tropiques qu'elles composent (Polis *et al.*, 1997; Anderson et Polis, 1999). Des transferts de nutriments peuvent s'opérer entre deux milieux marins, entre autres par les mouvements de différentes masses d'eau, qu'ils soient verticaux (remontée d'eau profonde, sédimentation vers le benthos) et/ou horizontaux (courants, marées, tourbillons) (Polis *et al.*, 1997). Des échanges peuvent aussi s'effectuer d'un milieu aquatique à un milieu terrestre, comme par exemple d'un lac ou d'une rivière vers ses rives (Pieczynska, 1975). Ce transfert abiotique génère d'ailleurs un enrichissement suffisamment important pour faire de ces milieux des terres généralement très fertiles et donc propices à l'agriculture. La laisse de mer déposée par les vagues et les marées est un autre exemple de transport abiotique de nutriments et de matière organique, s'effectuant cette fois du milieu marin vers le milieu terrestre côtier (Polis et Hurd, 1996; Polis *et al.*, 1997). Particulièrement important dans le budget nutritif des zones côtières arctiques au printemps, le lessivage généré par le ruissèlement suite à la fonte de la neige et des glaciers constitue un exemple de transfert qui se fait plutôt du continent vers la mer (Holmes *et al.*, 2012). Le saumon qui remonte les rivières pour frayer après avoir passé une partie de son cycle vital dans le milieu marin représente un vecteur biotique mer-terre bien documenté (Kline *et al.*, 1993; Polis *et al.*, 1997). Les baleines, les lions de mer, les tortues marines et les oiseaux constituent tous autant d'exemples d'animaux qui transportent des nutriments au-delà des frontières écosystémiques (Fariña *et al.*, 2003; Ellis *et al.*, 2006; Blais *et al.*, 2007; Michelutti *et al.*, 2009). Bien que le rôle des vecteurs abiotiques sur le fonctionnement des écosystèmes côtiers est bien connu (Sara, 2006), ce n'est actuellement pas le cas du rôle des vecteurs biotiques sur le transfert des ressources d'un écosystème à l'autre (Signa *et al.*, 2012).

1.2. L'ENRICHISSEMENT TERRESTRE ET OCEANIQUE DES OISEAUX MARINS

Les oiseaux marins jouent un rôle important de biovecteur en transférant des nutriments d'origine marine vers des écosystèmes terrestres (Bildstein *et al.*, 1992; Polis *et al.*, 1997; Bosman et Hockey, 1986; Ellis *et al.*, 2006; Zmudczyńska-Skarbek *et al.*, 2013). Les migrations de grande envergure et l'établissement colonial de plusieurs centaines de milliers d'individus (Mallory et Fontaine, 2004) donnent de bonnes raisons de croire que les oiseaux marins engendreraient le biotransport le plus significatif autour du globe (Michelutti *et al.*, 2009). Se nourrissant principalement de ressources pélagiques provenant de vastes aires d'alimentation marines et nichant sur des territoires terrestres plus restreints pour muer ou se reproduire (Mallory et Fontaine, 2004), ils concentrent des nutriments marins sur des zones terrestres. Produite de façon variable dépendamment des saisons, la matière organique ornithogénique, riche en azote et en phosphore (Lindeboom, 1984; Bosman et Hockey, 1986 ; Stauton Smith et Johnson, 1995), provient principalement des fécès (guano), mais aussi des plumes, des carcasses, des coquilles d'œufs et des restes de nourriture (Polis *et al.*, 1997; Ellis *et al.*, 2006). Ces nutriments allochtones fertilisent le sol, ce qui stimule la croissance de la végétation terrestre autour de la colonie (Anderson et Polis, 1999; Zmudczyńska-Skarbek *et al.*, 2013). En comparaison avec des sites adjacents non fréquentés par les oiseaux, certains sites terrestres caractérisés par la présence de grandes colonies sont si productifs qu'ils sont même visibles depuis l'espace grâce aux techniques d'imagerie satellitaire (Blais *et al.*, 2007).

L'enrichissement ornithogénique ne se limite pas seulement au milieu terrestre, puisque les nutriments libérés peuvent retourner dans le milieu marin par quatre voies distinctes résumées par Zmudczyńska-Skarbek *et al.* (2015). Premièrement, le guano peut être directement excrété dans l'eau de mer par les oiseaux en vol en quête de nourriture (Wainright *et al.,* 1998). Deuxièmement, l'apport en nutriments peut provenir du ruissellement du milieu terrestre vers le milieu marin suite à des précipitations sur la colonie (Stauton Smith et Johnson, 1995 ; Kolb *et al.*, 2010). Troisièmement, les nutriments dérivés du guano peuvent être déversés dans les eaux souterraines et ensuite être dispersés dans l'océan par le mélange des marées (Stauton Smith et Johnson, 1995). Finalement, l'ammoniac qui se volatilise à partir du guano peut ensuite être dilué dans la pluie et retourné à l'océan (Lindeboom, 1984; Loder *et al.*, 1996). Par contre, même si les nutriments dérivés du guano retournent au milieu marin et sont susceptibles d'être concentrés près de la colonie, les effets de l'enrichissement océanique peuvent être considérablement moins importants que ceux de l'enrichissement terrestre. En effet, les vagues et les courants océaniques mélangent l'eau de mer et peuvent efficacement diluer et déporter les nutriments. Plusieurs études ont tout de même montré que le guano pouvait favoriser la teneur en éléments nutritifs des eaux estuariennes et marines (Bosman *et al.*, 1986 et ses références; Bosman et Hockey, 1986; Powell *et al.,* 1989; Wainright *et al.*, 1998; voir Bédard *et al.*, 1980 pour une perspective différente à large échelle). En augmentant les concentrations en éléments nutritifs dans l'écosystème marin autour des colonies, les oiseaux marins peuvent influencer la production primaire, ce qui se reflète dans des concentrations plus élevées de carbone organique et de chlorophylle *a* (tel que démontré dans des étangs côtiers : Brimble *et al.*, 2009; Keatley *et al.*, 2009; Michelutti *et al.*, 2009, et en milieu intertidal : Bosman *et al.*, 1986). De plus, des expériences menées sur le terrain et en laboratoire ont montré que le guano ajouté à l'eau de mer stimulait la production primaire (Bosman *et al.*, 1986 et ses références). Conséquemment, il est admis que les oiseaux marins peuvent contribuer à la création de points chauds de production biologique (Bildstein *et al.*, 1992; Cocks *et al.*, 1998; Ellis *et al.*, 2006; Brimble *et al.*, 2009; Kolb *et al.*, 2010). Ceci signifie que les oiseaux sont non seulement importants pour leur effet régulateur par la prédation (*top-down*), mais aussi pour leur impact sur le contrôle des ressources nutritives disponibles (*bottom-up*).

1.3. RELATION PRODUCTION-BIODIVERSITE

Selon le modèle théorique des relations productivité-biodiversité qui a été étudié pour la première fois par Pianka (1967), une hausse de production primaire en surface pourrait avoir des répercussions sur la biodiversité des communautés de consommateurs qui en dépendent, telles que les communautés benthiques (Witman *et al.*, 2008). Pour discuter adéquatement des relations productivité-biodiversité, il est important de distinguer la productivité de la production et la biodiversité du nombre d'espèces. Alors que le nombre d'espèces, comme son nom l'indique, tient compte uniquement du nombre de taxons présents, la biodiversité prend également en considération la régularité (*species eveness*) avec laquelle les espèces sont observées dans une communauté (Hurlbert, 1971; Abrams, 1995). Puisque le nombre d'espèces, aussi appelé richesse spécifique, et la diversité d'espèces sont positivement corrélés, le nombre d'espèces est souvent considéré comme un synonyme de la diversité ou alors comme une mesure de celle-ci (exemples : Pianka, 1967; Mittelbach *et al.*, 2001; Witman *et al.*, 2008) (Hurlbert, 1971). La production est une quantité de carbone associée à un temps donné (moment où la mesure a été prise), contrairement à la productivité qui est une quantité de carbone produite en fonction du temps (MacFadyen, 1948; Abrams, 1995). Les auteurs qui s'intéressent à la relation productivité-biodiversité parlent fréquemment de productivité, là où il aurait été plus juste de parler de production en raison de la nature des données récoltées. Dans le cadre de ce mémoire, il sera surtout question de la production et du nombre de taxons puisque ce sont les paramètres qui ont été mesurés. Par contre, le terme populaire «relation productivité-biodiversité» sera employé pour désigner de façon générale l'ensemble des relations reliant la production/productivité à la richesse spécifique/nombre d'espèces/biodiversité.

En 1967, Pianka a été l'un des premiers à décrire une relation positive entre la longueur de la saison de croissance, utilisée ici comme un indicateur de la productivité, et la richesse spécifique des lézards d'un milieu désertique. Selon le modèle théorique, si une hausse de la productivité permet d'élargir l'étendue des ressources disponibles, la biodiversité devrait effectivement augmenter. En effet, une plus grande disponibilité des ressources pourrait augmenter le taux de reproduction des espèces qui dépendent de ces ressources, entraînant une augmentation du nombre d'individus (Wright *et al.,* 1993). Une population de taille plus importante devrait mener à de plus faibles taux d'extinction reliés à la stochasticité démographique (May, 1974) et à une proportion plus élevée d'espèces rares, alors que les taux de spéciation devraient être plus élevés (Preston, 1962; Wright, 1983). De plus, si l'hétérogénéité de ces ressources augmente également, la diversification de niches écologiques permettrait l'établissement de nouvelles espèces (Rosenzweig, 1995). Par contre, cette théorie est encore considérablement controversée en ce qui a trait à la forme générale des relations productivité-biodiversité, aux mécanismes qui produisent ces patrons et aux facteurs d'influence qui entrent en jeu (Abrams, 1995; Waide *et al.*, 1999).

Bien que ce patron ne fait pas l'unanimité, les relations productivité-biodiversité sont fréquemment décrites comme étant en forme de cloche, aussi appelée fonction quadratique négative (Grime, 1973, Huston, 1979; Rosenzweig, 1992, 1995; Levin *et al.*, 2001; Witman *et al.*, 2008). Selon ce modèle, la biodiversité augmenterait en suivant un gradient croissant de productivité, jusqu'à atteindre un maximum de biodiversité correspondant à une productivité intermédiaire, pour ensuite diminuer en allant vers des valeurs de forte productivité (Huston, 1979; Rosenzweig, 1992, 1995). En étudiant des communautés benthiques arctiques, Witman *et al.* (2008) ont observé des fonctions quadratiques négatives en analysant des données de nombre d'espèces en fonction de valeurs satellitaires de chlorophylle *a*. Un tel patron serait probablement généré par une combinaison de mécanismes favorables et défavorables à l'augmentation de biodiversité le long du gradient de productivité (Witman *et al.*, 2008). La partie ascendante de la courbe pourrait donc être expliquée par les mécanismes préalablement décrits reliés à la disponibilité et à l'hétérogénéité des ressources. En ce qui concerne la partie descendante, plusieurs mécanismes peuvent engendrer cette baisse de la biodiversité succédant à un maximum (Rosenzweig, 1995). Par exemple, si une ou quelques espèces dominantes arrivent à utiliser plus efficacement la ressource à de fortes productivités (Rosenzweig et Abramsky, 1993), cela pourrait mener à l'exclusion d'autres espèces moins bien adaptées (Huston, 1979). Ce mécanisme semble opérer plus particulièrement pour les communautés de plantes et les communautés benthiques de substrat rocheux (Witman *et al.,* 2008). Aussi, d'importantes perturbations, des stress environnementaux, une baisse de l'hétérogénéité des ressources ou encore de fortes pressions des consommateurs et/ou des individus de plus grande taille constituent d'autres mécanismes qui peuvent expliquer une baisse de biodiversité à des niveaux de productivité élevée (Grime, 1973).

Plusieurs études ont démontré que la relation productivité-biodiversité est dépendante de l'échelle spatiale (Huston, 1999; Mittelbach *et al*., 2001; Chase et Leibold, 2002; Scheiner et Jones, 2002; Witman *et al*., 2008). Le type de communauté joue également un rôle décisif dans la création des patrons de productivité-biodiversité (Witman *et al.*, 2008). De plus, les perturbations et la productivité ont des effets interactifs qui influencent la richesse spécifique (Kondoh, 2001; Svensson *et al*., 2007). Ces différents facteurs d'influence ainsi que leurs interactions devraient davantage être pris en considération dans l'étude des relations productivité-biodiversité. Bien que les études associées aux milieux terrestres soient nombreuses à ce sujet, celles sur les milieux marins sont plutôt rares. La biodiversité des communautés benthiques semble varier en fonction des niveaux de productivité primaire (Witman *et al*., 2008), mais les connaissances acquises à ce sujet doivent être approfondies pour mieux décrire les mécanismes et les patrons associés.

1.4. EFFETS INDIRECTS DES OISEAUX SUR LES COMMUNAUTES BENTHIQUES

Les oiseaux marins sont l'un des groupes les plus importants des environnements côtiers et estuariens, car ils modifient directement et indirectement la structure et la fonction des communautés qui y vivent (Lindeboom, 1984; Palomo *et al*., 1999). Leurs effets via la prédation (*top-down*) contrôlent entre autres la taille (Steinmetz *et al*., 2003) et la biomasse (Lewis *et al*., 2007) de leurs proies. Différemment, les colonies d'oiseaux peuvent aussi affecter indirectement les communautés de consommateurs par l'augmentation de production primaire marine près des colonies. Le benthos étant dépendant des ressources alimentaires en provenance de la surface, une telle augmentation de la disponibilité de nourriture pourrait engendrer des changements dans la structure des communautés benthiques. En effet, la production primaire qui n'est pas consommée dans la colonne d'eau et donc qui sédimente jusqu'au fond marin devient de la nourriture disponible pour les organismes benthiques. Ce phénomène est inclut dans le couplage pelago-benthique, terme qui réfère à l'ensemble des liens entre les environnements benthiques et pélagiques (Iken *et al*., 2005; Renaud *et al*., 2008; Soreide *et al*., 2013). Quelques recherches ont été menées sur les effets indirects des oiseaux marins via le contrôle des nutriments (*bottom-up*) sur la biodiversité, l'abondance et la biomasse des consommateurs. Par contre, les auteurs s'intéressant plus spécifiquement aux répercussions sur le benthos sont très peu nombreux. Des effets de la présence des oiseaux ont été décrits sur le zooplancton marin (Zelickman et Golovkin, 1972), les polychètes (Bosman et Hockey, 1986), les nématodes (Palomo *et al*., 1999), les chironomidés (Michelutti *et al*., 2009), les isopodes (Kolb *et al*., 2010), les bernard-l'hermites (Zmudczyńska-Skarbek *et al*., 2015) et les poissons (Powell *et al*., 1991). Les études ciblant le benthos montrent que l'abondance (Palomo *et al*., 1999) et la biomasse (Kolb *et al*., 2010) de certaines espèces sont positivement influencées par la présence de colonies d'oiseaux dans les eaux peu profondes d'écosystèmes côtiers en Argentine (Palomo *et al*., 1999) et en Suède (Kolb *et al*., 2010). Chez une espèce de crabe (*Chasmagnathus granulata*), une baisse de l'activité de bioturbation a été observée dans des sites où du guano avait été ajouté (Palomo *et al*., 1999). En fait, une meilleure accessibilité aux ressources alimentaires pourrait permettre aux crabes de subvenir à leurs besoins avec un taux d'activité moindre. Dans le cadre d'une autre étude dans un écosystème arctique côtier (Spitzberg, Svalbard), des analyses isotopiques effectuées sur des bernard-l'hermites et des oursins par Zmudczyńska-Skarbek *et al*. (2015) ont fourni certaines évidences que les effets *bottom-up* des oiseaux pourraient influencer certains organismes benthiques vivant dans des eaux peu profondes de 5 à 15 m. Des apports organiques importants provenant des oiseaux dans des étangs côtiers en Italie ont mené à des réponses benthiques similaires à celles retrouvées dans des cas de sévère eutrophisation (Signa *et al.,* 2015). Il était question d'un déclin marqué des suspensivores et des carnivores au profit des déposivores et d'une nette diminution de l'abondance totale et de la diversité (Signa *et al.,* 2015). Cependant, ces cas extrêmes de «guanotrophisation» n'ont été répertoriés que dans des milieux où les échanges sont restreints en raison de caractéristiques géomorphologiques particulières.

1.5. PARAMETRES STRUCTURANT LE BENTHOS ET L'ENVIRONNEMENT ARCTIQUE

La présence des oiseaux fait partie de la longue liste des paramètres environnementaux qui peuvent structurer les communautés benthiques dans un milieu donné. Ces paramètres ont été classifiés par McArthur *et al.* (2010) selon trois catégories de gradients : les ressources, les directs et les indirects/spatiaux. Les gradients de ressources incluent les indicateurs de production primaire, de flux de carbone organique particulaire ou encore de quantité/qualité de nourriture disponible pour le benthos (ex. : concentrations sédimentaires de pigments photosynthétiques). Les gradients directs affectent directement la physiologie, la morphologie et l'histoire évolutive des espèces benthiques. Il est donc question de variables liées à l'eau de fond, comme la température, la salinité et l'oxygène, et au fond marin, comme le type de sédiment. Les gradients indirects/spatiaux ont une influence indirecte sur le benthos, car ils fluctuent en corrélation avec d'autres gradients de ressources ou directs. Chaque paramètre, qu'il appartienne à l'une ou l'autre de ces catégories, a une importance variable en fonction des échelles temporelle et spatiale considérées. Ces trois catégories ont été reprises dans une figure synthèse par Roy *et al.* (2014) qui résume efficacement comment les facteurs environnementaux varient en fonction du temps et de l'espace selon leurs résultats (Figure 1). Cependant, il est important de préciser que les variables environnementales indiquées dans cette figure sont celles mesurées par Roy *et al.* (2014) et ne sont donc pas exclusives. D'ailleurs, les auteurs (Roy *et al.*, 2014) précisent que des paramètres potentiellement importants pour la structure des communautés benthiques seraient manquants (Figure 1, boîte grise). À petite échelle, c'est-à-dire au sein d'une station échantillonnée, les interactions biotiques (non illustrées sur la figure 1), telles que la compétition et la prédation, ne sont pas négligeables. Elles sont même déterminantes, puisqu'elles modifient la disponibilité de niches écologiques (Gray et Elliott, 2009). À une large échelle spatiale (100 à 1000 km), la structure des communautés varient davantage en fonction de facteurs abiotiques (ex. : profondeur, latitude) (Figure 1). La profondeur fait partie des gradients indirects/spatiaux et est donc corrélée à d'autres paramètres variant verticalement (ex. : température, salinité, carbone organique particulaire) (Mayer et Piepenburg, 1996; Roy *et al.*, 2014). Suivant une augmentation de la profondeur, la quantité et la qualité des ressources alimentaires, (Mayer et Piepenburg, 1996; Smith *et al.*, 2008; Roy *et al.*, 2014) ainsi que la force du couplage pélago-benthique, particulièrement déterminante en Arctique, devraient diminuer (Piepenburg *et al.*, 1997, 2000; Piepenburg, 2005 ; Bluhm et Gradinger, 2008 ; Soltwedel *et al.*, 2009).

Dans l'océan Arctique, tous ces paramètres environnementaux et la façon dont ils influencent les communautés biologiques sont caractérisés par une forte saisonnalité et une importante variabilité interannuelle (Melling, 2002; Prinsenberg et Hamilton, 2005; Michel *et al.*, 2006; Hamilton *et al.*, 2013). Le couvert de glace limite la pénétration de la lumière pendant la majeure partie de l’année, ce qui restreint la production primaire. Les communautés biologiques sont donc dépendantes des dynamiques saisonnières de la glace de mer (Grebmeier *et al.*, 1995, Fortier *et al.*, 2002; Tremblay *et al.*, 2006). Comme dans la majorité des milieux côtiers, la disponibilité des nutriments dans la couche de surface peut rapidement devenir limitante (Grebmeier *et al.*, 1995; Tremblay *et al.*, 2006, 2008; Martin *et al.*, 2010). Des apports allochtones de nutriments résultant de la présence de colonies d’oiseaux devraient donc favoriser la production biologique dans l’Arctique.

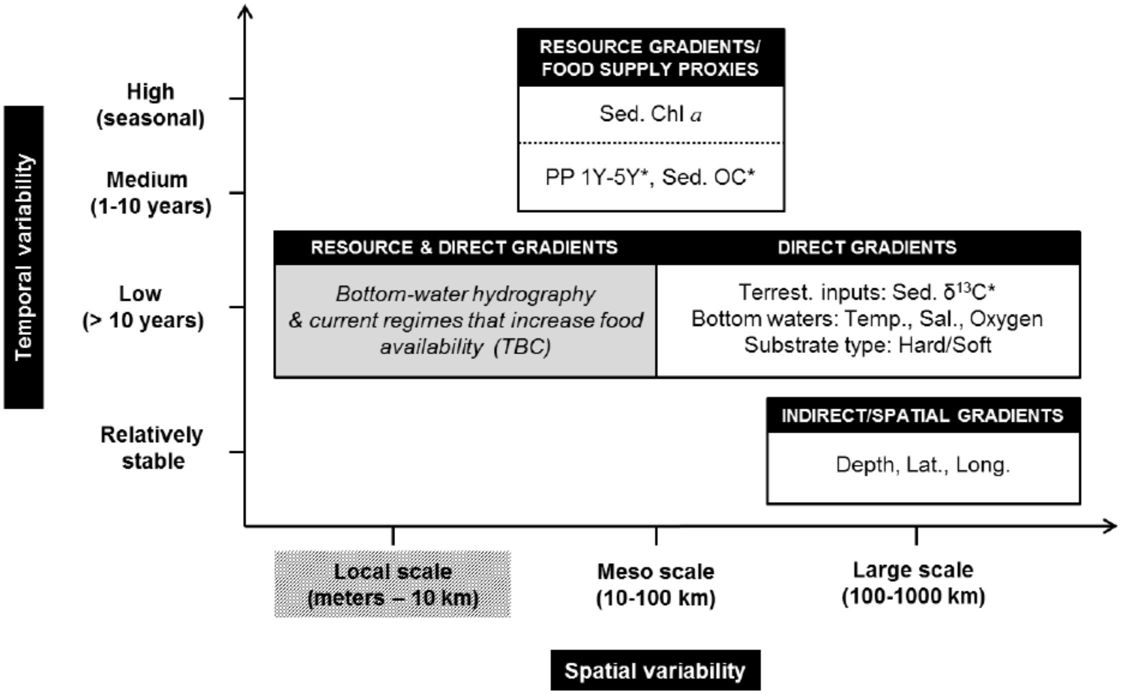

Figure 1. Figure synthèse présentant les principaux résultats de Roy *et al.* (2014) concernant les paramètres environnementaux qui structurent les communautés benthiques (mégafaune) dans l'Arctique canadien en fonction des échelles spatiales et temporelles selon lesquelles ils varient.

1.6. LA REGION DU DETROIT DE LANCASTER (LSR)

Située dans l'Arctique de l'est canadien, LSR comprend la portion est du passage du nord-ouest et représente 98 000 km^2 de superficie marine (Welch *et al.*, 1992). Le détroit de Lancaster est bordé de l'île Devon au nord et de l'île de Baffin au sud. La circulation générale sur la côte nord du détroit va de l'est vers l'ouest, alors que l'inverse se produit le long de la côte sud (Leblond, 1980; Welch *et al.*, 1992). Cette circulation à contre-sens entraîne la formation de tourbillons à l'embouchure du détroit qui s'ouvre sur la baie de Baffin (Fissel *et al.*, 1982). À l'extrémité ouest, le détroit de Barrow est caractérisé par un seuil de 150 m (Welch *et al.*, 1992) qui crée de la turbulence en mélangeant les masses d'eau (Prinsenberg et Bennet, 1987; Welch *et al.*, 1992). La débâcle se produit généralement au début du mois de juin dans la portion est du détroit de Lancaster et vers la mi-juillet dans la partie ouest. À partir de la mi-septembre, la région se couvre progressivement de glace (Welch *et al.*, 1992; Hamilton *et al.*, 2013). Cependant, un prolongement de la polynie des Eaux du Nord se forme sur la côte nord du détroit, la surface libre de glace étant plus ou moins importante en fonction des années (Welch *et al.*, 1992; Hamilton *et al.*, 2013).

Parmi les écosystèmes les plus productifs de l'Arctique (Milne et Smiley, 1978; McLaren, 1982; Welch *et al.*, 1992; Michel *et al.*, 2006; Ardyna *et al.*, 2011), LSR est intensivement exploitée par plusieurs populations d'oiseaux et de mammifères marins (Welch *et al.*, 1992; Mallory et Fontaine, 2004). Le rapport de Mallory et Fontaine (2004) répertorie 34 habitats marins clés pour les oiseaux migrateurs au Nunavut et dans les Territoires du Nord-Ouest. De ce nombre, 8 se retrouvent dans LSR. Selon leur définition, «un habitat marin clé désigne une aire fréquentée par au moins 1 p. 100 des effectifs canadiens d'au moins une espèce d'oiseau migrateur» (Mallory et Fontaine, 2004). Ces habitats sont majoritairement constitués de portions de falaises utilisées pour la nidification et d'une zone marine adjacente leur offrant les ressources nutritives dont ils dépendent. Les colonies exploitant ces habitats sont composées de 1100 à 160 000 couples d'oiseaux (Mallory et Fontaine, 2004). Ces chiffres englobent toutes les espèces présentes dont les principales sont : le fulmar boréal (*Fulmarus glacialis*), le guillemot de Brünnich (*Uria lomvia*), le guillemot à miroir (*Cepphus grylle*), la mouette tridactyle (*Rissa tridactyla*), le goéland bourgmestre (*Larus hyperboreus*) et le mergule nain (*Alle alle*) (Mallory et Fontaine, 2004). Le fulmar boréal et le guillemot de Brünnich sont toutefois les deux espèces coloniales les plus communes et abondantes qui utilisent les ressources diversifiées du détroit. Avec la diminution du couvert de glace en Arctique, ces espèces ainsi que toutes celles retrouvées dans LSR, sont de plus en plus vulnérables, surtout considérant la pression anthropique grandissante (Welch *et al.*, 1992; Melling, 2002). Effectivement, cette région risque d'éventuellement devenir une voie majeure de navigation maritime et une zone d’exploration et de transformation d’hydrocarbures (Welch *et al.*, 1992; Melling, 2002; Gavrilchuk et Lesage, 2013). Surnommé le «Serengeti de l’Arctique», le détroit de Lancaster a été proposé comme future aire marine nationale de conservation (AMNC) par le gouvernement fédéral canadien en 2010, dans le but de préserver l’importante biodiversité retrouvée à plusieurs niveaux trophiques (Parc Canada. 2015). La concrétisation de ce projet n'est pas encore assurée, mais une étude de faisabilité a bel et bien été amorcée (Parc Canada, 2015).

1.7. OBJECTIFS ET HYPOTHESES

Bien que l'Arctique soit exploité par des millions d'oiseaux marins (Mallory et Fontaine, 2004), pratiquement aucune étude n'a été publiée à propos de l'impact des colonies d'oiseaux sur le benthos arctique. Certes, l'étude de Zmudczyńska-Skarbek *et al.* (2015) démontre certains effets positifs de la présence d'oiseaux dans l'Arctique sur une espèce de bernard-l'hermite, mais une étude plus globale sur la structure des communautés benthiques s'impose pour mieux comprendre les effets *bottom-up* engendrés par les oiseaux. Le premier objectif de la présente étude était de décrire les communautés benthiques de LSR. Le second objectif consistait à identifier l'impact potentiel des colonies d'oiseaux marins et d'autres paramètres environnementaux sur la structure des communautés benthiques. Les effets indirects ornithogéniques ont été étudiés en comparant des zones caractérisées par la présence de colonies d'oiseaux et des zones contrôles non colonisées par les oiseaux. L'hypothèse testée était que la biodiversité benthique, le nombre de taxons, la densité totale de l'épifaune (ind. m^{-2}), l'abondance totale de l'endofaune (ind. l^{-1}) et la biomasse de l'endofaune (g. l^{-1}) seraient plus élevés dans les zones caractérisées par la présence de colonies d'oiseaux, puisque la présence de colonies d'oiseaux serait un facteur important pour expliquer les différences spatiales dans la structure des communautés benthiques à l'échelle régionale du détroit de Lancaster.

INFLUENCE DE LA PRÉSENCE DES COLONIES D'OISEAUX MIGRATEURS (*FULMARUS GLACIALIS* ET *URIA LOMVIA*) SUR LES ASSEMBLAGES BENTHIQUES DE LA REGION DU DÉTROIT DE LANCASTER, CANADA

2.1. PREAMBULE

Cet article, intitulé « *Influence of seabird colonies on the structure of benthic communities, Lancaster Sound region, Canadian Arctic* », a été rédigé en collaboration avec mon directeur Philippe Archambault (UQAR-ISMER) et ma codirectrice Ellen Kenchington (IOB, MPO). Tous deux ont écrit ensemble les grandes lignes du projet et ont travaillé sur le plan de la mission océanographique. Par la suite, j'ai participé à la planification logistique et à la réalisation de l'échantillonnage en mer. J'ai également effectué l'ensemble des analyses et la rédaction de cet article. M. Archambault et Mme Ellen Kenchington m'ont épaulé tout au long de ces étapes et ont révisé l'entièreté de l'article. Je tiens à souligner les contributions de Mathieu Ardyna (Takuvik-U. Laval) et de Youyu Lu (IOB, MPO), Michael Casey (IOB, MPO) et Simon Higginson (IOB, MPO). Ces collaborateurs ont extrait et partagé des données environnementales qui se révélèrent d'une importance biologique notable dans le cadre de cette étude.

2.2. INFLUENCE OF SEABIRD COLONIES ON THE STRUCTURE OF BENTHIC COMMUNITIES, LANCASTER SOUND REGION, CANADIAN ARCTIC

2.3. INTRODUCTION

The transport of nutrients across ecosystem boundaries can profoundly shape recipient food webs. Animals that exploit (or are exploited by) two or more ecosystems to complete their life cycles, such as salmons, sea turtles, sea lions, whales and seabirds, act as biovectors (Kline *et al.*, 1993; Fariña *et al.*, 2003; Ellis *et al.*, 2006; Michelutti *et al.*, 2009). In some cases, biovectors transcend the marine/terrestrial boundary and become effective agents for the transfer of marine nutrients to terrestrial ecosystems. The structure and the function of these ecosystems can then be modified by this biological fertilization (Polis *et al.*, 1997; Anderson and Polis, 1999). On a planetary scale, seabirds may operate as the most significant vectors 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 (Anderson and Polis, 1999; 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 Zmudczyńska-Skarbek *et al.* (2015): (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 enhance nutrient content of estuarine and marine waters (Bosman *et al.*, 1986 and references therein; Powell *et al.*, 1989; Wainright *et al.*, 1998), and create hotspots of biological production (Bildstein *et al.*, 1992; Kolb *et al.*, 2010).

Seabirds control through predation (top-down) biological characteristics of their prey such as size (Steinmetz *et al.*, 2003) and biomass (Lewis *et al.*, 2007), but they can also indirectly affect communities of consumers through their positive effects on 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 and reaches the seabed - a phenomenon included in the pelagic-benthic coupling (Iken *et al.*, 2005; Renaud *et al.*, 2008; Soreide *et al.*, 2013). A hypothesis in ecology, mainly tested through terrestrial research, supports the idea that if production of food resources increase, diversity may increase as well (Pianka, 1967; Begon *et al.,* 1990; Bosman *et al.*, 1986; Mittelbach *et al.*, 2001; Witman *et al.*, 2008). Many mechanisms can explain the positive effect of production on diversity. For example, an increased production of resources can lead to higher resource availability and heterogeneity, which in turn might allow more species to establish (Rosenzweig, 1995). Moreover, recent studies have shown that the pattern can be curvilinear (hump-shaped relationship) (Levin *et al.*, 2001; Witman *et al.*, 2008), with the diversity decreasing after reaching the maximum. The descending limb can be explained for example by the effects of environmental stress (Grime, 1973) or those of competitively dominant species decreasing diversity at high productivity (Rosenzweig and Abramsky, 1993). However, this theory is controversial due to the variety of observed patterns, more scientific work is needed to clarify it. 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), nematods (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 in Sweden (Kolb *et al.*, 2010). To our knowledge, no one has studied the impact of seabird presence on marine benthic community structure over regional scales in the Arctic, where over 10 million seabirds breed each year, generally in recurrent locations (Mallory and Fontaine, 2004). Although, the paper of Zmudczyńska-Skarbek *et al.* (2015) demonstrated that seabird bottom-up effects may influence specific benthic organisms (hermit crabs, sea urchins) in shallow waters of an arctic coastal ecosystem.

In the Arctic Ocean, environmental parameters and the way they influence biological communities are characterized by strong seasonality and large inter-annual fluctuations (Melling, 2002; Prinsenberg and Hamilton, 2005; Michel *et al.*, 2006; Hamilton *et al.,* 2013; Link *et al.*, 2013). Ice cover brings several constraints to primary production by limiting light penetration during the main part of the year. Biological communities are thus dependent on extent, thickness and seasonal melt dynamics of sea ice (Grebmeier *et al.,* 1995; Fortier *et al.*, 2002; Tremblay *et al.*, 2006). When the ice melts during summer, nutrient availability in the upper euphotic layer may rapidly become a limiting factor to primary production (Grebmeier *et al.*, 1995; Tremblay *et al.*, 2006, 2008; Martin *et al.*, 2010). Therefore, the magnitude of primary production in the Arctic should respond to changes in nutrient inputs (mainly N) (Tremblay *et al.*, 2006). Seabirds have been shown to locally enhance chlorophyll *a* and organic carbon concentrations (as demonstrated in coastal ponds: Brimble *et al.,* 2009; Keatley *et al.*, 2009; Michelutti *et al.*, 2009, 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 and references therein). Depth also impacts marine benthic communities since it is a proxy of other variables that are characterized by vertical variation such as temperature or salinity (Mayer and Piepenburg, 1996; Roy *et al.*, 2014). Increasing depth is generally linked with a decrease of both quantity and quality of food resources (Mayer and Piepenburg, 1996; Smith *et al.*, 2008; Roy *et al.*, 2014) and with decreasing strength of pelagic-benthic coupling, which is determining key force in the Arctic (Piepenburg *et al.*, 1997, 2000; Soltwedel *et al.*, 2009). Several other parameters of the water column and the seafloor can influence benthic communities such as salinity, temperature, sediment type, habitat heterogeneity and velocity of bottom currents (reviewed in McArthur *et al.*, 2010).

Despite their importance in carbon cycling and in arctic food webs (Hobson and Welch, 1992), little is known about the structure of arctic benthic communities and the environmental parameters that influence their distributions. There is a need for baseline data on arctic benthic communities (Piepenburg *et al.*, 2011; Wassmann *et al.*, 2011), particularly in the context of climate change, which leads to an increasing anthropogenic pressure via maritime traffic and resources extraction (Welch *et al.,* 1992; Melling, 2002; Gavrilchuk and Lesage, 2013). In this study, we bypassed the well-documented relationship between seabird colonies and primary production, to focus on their indirect effect on benthic communities. Moreover, considering that benthic species are good integrators of environmental variation (Pearson and Rosenberg, 1978; Dauvin, 1993), since many are sessile and long-lived (greater than 1 year), 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 et 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 presence of seabird colonies would explain spatial differences in benthic communities at the regional scale of the LSR. This hypothesis is based on the model that the nutrient inputs increase primary production and can generate bottom-up effects up to the benthos. During this study, we did not measured primary production but our objective was to see if a pattern emerges 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 anticipate being on the ascending limb of the relationship in the LSR. Hence, we expected that benthic species diversity, numbers of taxa, total epifauna density (ind. m^{-2}), total infauna density (ind. l^{-1}) and total infauna biomass (g. l^{-1}) would be higher in areas where colonies were present.

2.4. MATERIALS AND METHODS

Study site

This study was conducted in the LSR, which constitutes about 98 000 km^2 of sea surface (Welch *et al.*, 1992) in the eastern Canadian Arctic (Figure 2). Arctic water enters Lancaster Sound from the west through Barrow Strait and from the north through McDougall Sound and Wellington Chanel (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 (Leblond, 1980; Welch *et al.*, 1992). Along Devon and Cornwallis Islands on the north coast of Lancaster Sound, counter currents are oriented westward and transport water mass from Baffin Bay (Leblond, 1980; Welch *et al.*, 1992). These two opposing currents at the mouth of Lancaster Sound generate eddies (Fissel *et al.*, 1982). 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 (Welch *et al.*, 1992). 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 (Welch *et al.*, 1992; Hamilton *et al.*, 2013). Ice break-up occurs at the beginning of June in the eastern part and around mid-July in the western part facing Resolute, but the LSR is never completely ice-free since ice moves in from the west all summer long (Welch *et al.*, 1992).

The LSR is among the most productive ecosystems in the Canadian Arctic (Milne and Smiley, 1978; McLaren, 1982; Welch *et al.*, 1992; Michel *et al.*, 2006; Ardyna *et al.*, 2011) 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 (Welch *et al.*, 1992; 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 to 160 000 migratory seabird pairs (all species combined; Mallory and Fontaine, 2004). 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).

Study Design

To test the hypothesis that bird colonies have an indirect effect on benthic community characteristics (univariate) and community structure (multivariate), eight study areas were sampled: five areas with presence of bird colonies and three control areas without colonies (Figure 2). The control areas were chosen for their similarities in terms of environmental variables, such as depth and sediment type, with areas in which colonies were present. 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.

Sample Collection

To collect samples, an oceanographic mission was carried out aboard the CFAV Quest from August 24th to September 7th, 2012. For each study area, two to six Van Veen grabs of 20 L volume capacity and one to four CTD-Niskins profiles were made. The water column was sampled 5 m above seafloor. 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. The 4KCam captured 54 to 146 images per area, for a total of 782 photos. Water, sediment and imagery samples were collected as close as possible to the 200 m depth contour, due to safety restrictions. During the camera operations, the ship was drifting along the transect whose orientation was dependent on current and wind speed and direction. Consequently, photos were taken at a depth ranging from 122 m to 442 m.

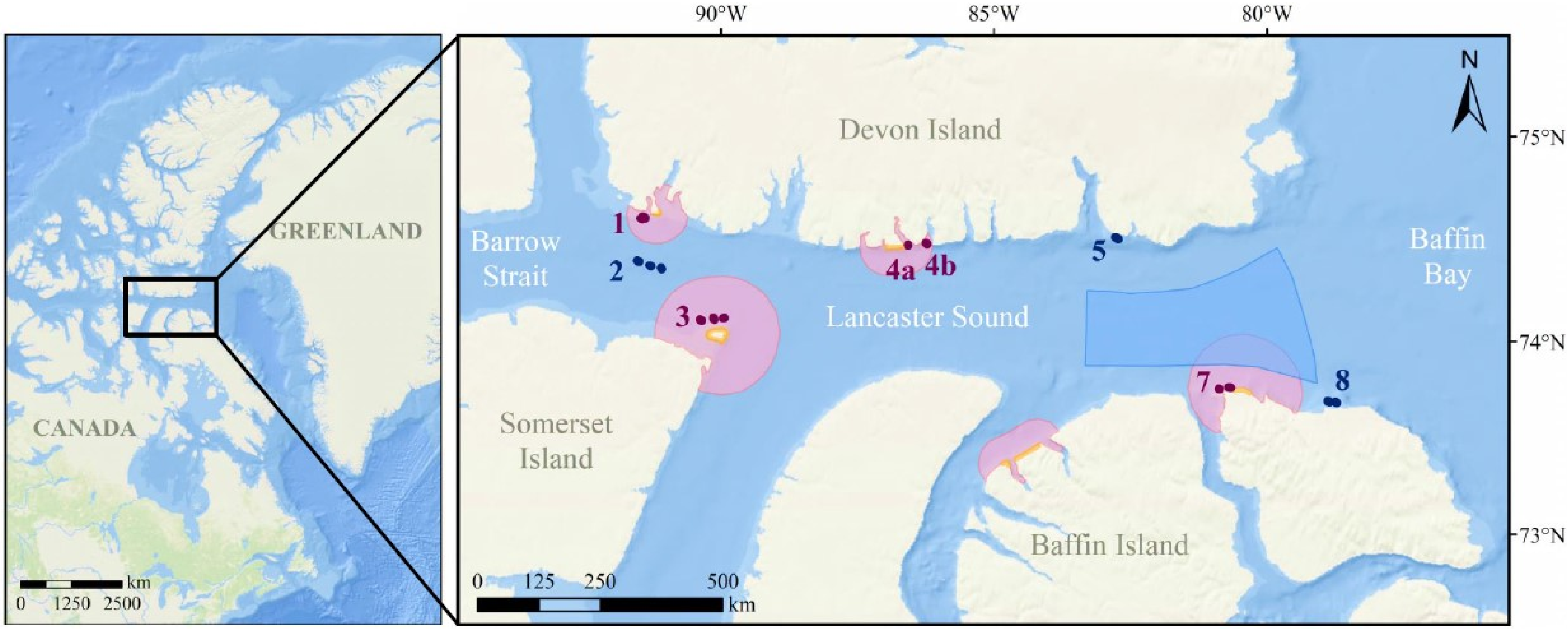

Figure 2. Location of sampling areas in the LSR, eastern Canadian Arctic. Blue delimited area is the polynya of eastern Lancaster Sound, yellow lines represent seabird colonies locations and red zones are key marine habitat sites for migratory seabirds listed by Mallory and Fontaine (2004). Sampling areas in the vicinity of seabird colonies are: Gascoyne Inlet (1, GI), Prince Leopold Island (3, PLI), Stratton Inlet (4a, SI), Burnett Inlet (4b, BI) and Wollaston Islands (7, WI). Control areas are: western part of Lancaster Sound (2, LS), Croker Bay (5, CB) and Maud Bight (8, MB). Area 6 (not shown) was not part of this project. Dots represent camera deployments done during the mission of 2012. The basemap was provided by Esri, DeLorme, GEBCO, NOAA, NGDC and other contributors.

Infaunal and epifaunal benthic communities

Benthic communities from areas with and without colonies were characterized and compared using grab samples and photos, which respectively sampled primarily infauna and epifauna. In this paper, the term "infauna" refers to all organisms found in grab samples and "epifauna" to all those on photos. Knowing that grab samples included a small proportion of epifaunal organisms and that few taxa, like ophiurids, are part of both infauna and epifauna, this generalization was done solely to simplify the text. Also, Van Veen grab collected macrofauna and megafauna, however photos recorded mainly megafauna.

Whenever possible, the soft sediment at the surface of each grab sample was sub-sampled in triplicate for organic matter ($N = 3$) and pigment ($N = 3$) analyses (described below). Due to missing data for Area 1 and pseudo-replication, these samples were not used as true replicates in statistical analyses. Instead, they were used to characterize the sediments in a descriptive context. To avoid misunderstanding, the term "subsample" will be used to refer to a case of pseudo-replication. All the remaining sediment was screened through a 1 mm mesh and stored in a 4% seawater-formaldehyde solution buffered with sodium tetraethylborate. For two grab samples per area, sorting, taxonomic identification, counting and weighing were done in laboratory. Biomass values, with a precision of ± 0.0001 g, are defined here as formaldehyde wet masses. Identification was done to the 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, Brachiopoda). Infauna data were divided by the sediment volume associated to each grab sample, to obtain density (ind. l^{-1}) and biomass (g l^{-1}) data. Prior to statistical analyses, infaunal taxa which were only found in one area has been removed to better detect similarities between communities (26 taxa) (Clarke and Warwick, 2001).

A total of 120 photos were analysed. 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; (3) The lead weight attached to the camera frame had to be present on all selected photos in order to scale it properly. At the center of each selected and then scaled photo, a surface of 0.692 m^2 (0.675 × 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 some sponges and corals, was counted instead of being only recorded as present or absent as for encrusting species. This method gave a more representative weight to colonial species in the analyses. Organisms were identified at 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^{-2}). A few taxa were found only once, and these were removed prior to analyses to better detect similarities between communities (9 taxa) (Clarke and Warwick, 2001). Organisms that were not visible enough to be identified were not counted due to their poor potential for interpreting biological relevance.

Environmental variables

A Seabird 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 hours and burned at 450°C for six hours (Byers *et al.*, 1978). The pigment concentrations (Chl *a* µg g dry sediment^{-1} and phaeo µg g dry sediment^{-1}) 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 analysed 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, ≥ 51.6 cm).

To characterize the water column at each area, two water subsamples per Niskin bottle were filtered through 25 mm diameter GF/F 0.7 µm filters and frozen at -20°C on board in 15 ml tubes. Analyses were later processed to determine nitrite (NO_2), nitrate (NO_3), phosphate (PO_4^{3-}) and silicates concentrations according to the method of Tréguer and Le Corre (1975). To obtain chlorophyll *a* and phaeopigments concentration data, vacuum filtrations, extraction with acetone (20 hrs, 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 (Quinn and Keough, 2002; Anderson *et al.*, 2008).

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 the oceanographic mission in 2012, yearly mean values of chlorophyll *a* concentrations, primary production (derived from an arctic-adapted model; see Bélanger *et al*., 2013) and duration of open water were extracted. Duration of open water was defined as the number of days during one year where sea ice concentration represented less than 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, 23 environmental variables were collected and available for the eight sampling areas: index of bird colony size (Birds), phosphate, silicates, nitrate and nitrite, chlorophyll *a* and phaeopigments concentrations of bottom water (respectively [PHO], [SIL], [NIT], [Chl a]$_{\mathrm{BW}}$ and [Phaeo]), depth (D), temperature (T), salinity (S2), 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]$_{\mathrm{SAT}}$), primary production (PP), maxima velocity and mean velocity of modelled currents (Max_V and Mean_V). Due to missing data and other logistical reasons, organic matter content (OM), sediment chlorophyll *a* (Sed Chl *a*) and sediment phaeopigments (Sed phaeo) data were not used in the following statistical analyses and were used only in a descriptive context.

Statistical analyses

Impact of presence of seabird colonies on benthic communities 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^{-2} for epifauna and ind. l^{-1} for infauna), Pielou's evenness index (J') and Shannon-Wiener's diversity index (H'). Available for grab samples only, total biomass (g l^{-1}) 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 was visually verified prior to analyses. Data were transformed when necessary to respect basic assumptions of ANOVA and retested for normality of residuals and homogeneity of variances. However, for the data on epifauna, transformations did not achieve normality of residuals and/or homogeneity of variances, but we still performed the analyses because ANOVAs are robust to violations of these assumptions, particularly when the number of replicates is high (N_{tot} = 120 photos) (Underwood, 1997). Tukey's post-hoc multiple comparison tests were used to identify where significant differences found by ANOVAs were.

Based on Bray-Curtis distances 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 structure. Square-root transformation was chosen to down-weight the dominant taxa. Pairwise comparisons were carried out to identify where differences within levels of different factors were. 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 analysed 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 infauna 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 infauna and epifauna communities, multiple linear regressions were performed. For each univariate biological variable calculated (S, N, J', H' and log-biomass), a scatter-plot 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 more generous 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 ($N_{tot} = 16$) while searching for best model. The assumption regarding the absence of collinearity ($|r| \geq 0.8$) between predictors of infauna was verified. Among the 23 environmental variables described before, some predictors were removed prior to run the regressions on infauna: [PHO], [SIL], FS, FG, DOW, [Chl a]$_{SAT}$, PP and Max_V. The predictors [PHO], [SIL] and [NIT] were collinear together; [NIT] was kept rather than the two other ones knowing that it is an important limiting nutrient in marine ecosystems. The classes of sediment size FS and FG were respectively collinear with [Chl a]$_{BW}$ and Mean_V. These sediment classes were removed because the information given by classes of coarser sediment was sufficient and integrative enough. This decision avoided redundant information. DOW, [Chl a]$_{SAT}$ and PP were all collinear with D and MG; D was kept for its integrative nature, thus the three variables acquired by satellite information were not included. Finally, Max_V was collinear with Mean_V, the latter was selected because it captures information contained in the maximal velocities. Following the same approach for regression on epifauna, we eliminated the same environmental variables that we removed for infauna, but we also removed MG and we kept DOW. MG was removed because of collinearity with more than one of the predictors and this decision allowed us to keep DOW which was not collinear with D in this case. Shapiro-Wilk's test was used to confirm the normal distribution of residuals, then homogeneity of variances was verified visually.

To better understand which environmental variables are important in explaining differences among areas in terms of epifaunal community structure, distance-based linear model (DISTLM), represented by distance-based redundancy analysis ordination (dbRDA), was done on the Bray-Curtis similarity matrix with square-root transformed epifaunal density data. To standardize the spatial resolution of environmental data, the same mean value of each environmental variable relative to a given area was attributed to all 15 samples within this area. The absence of collinearity (here assessed at $|r| \geq 0.8$) between predictors was verified (Anderson *et al.*, 2008). Among the 23 environmental variables, we eliminated [PHO], [SIL], FS, FG, MG, [Chl *a*]$_{\mathrm{SAT}}$, PP and Max_V based on the justifications listed above. The best selection procedure was run with 9999 permutations and with different selection criteria: AICc, BIC and adjusted R^2. 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+ (Clarke and Gorley, 2006; Anderson *et al.*, 2008). ANOVA analyses and univariate multiple linear regressions were done with JMP Pro software version 11. For all these analyses, statistical significance was set at $\alpha < 0.05$.

2.5. RESULTS

Infaunal communities

Annelida, Crustacea and Echinodermata respectively represented 43%, 22% and 16% of the total abundance of infauna collected across the LSR (Figure 3). The biomass composition of infauna was highly variable between sampling areas, but generally Echinodermata was a dominant phylum, representing 81% of total biomass (Figure 4). 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 total density of infauna (N) ($F_{(1,6)} = 12.76$, $p = 0.012$) was higher in control areas than in areas with seabird colonies (Figure 5). However, the presence of seabird colonies did not significantly affect the number of taxa (S), Pielou’s evenness index (J’), Shannon-Wiener diversity index (H’) and total biomass (log-biomass) of infaunal communities (Figure 5, Table 1). For all univariate variables (S, N, J’, H’ and log-biomass), the eight sampling areas did not statistically differ from each other (Figure 5, Table 1). Despite finding no significant difference between areas, the highest number of taxa was recorded in Area 2, which is in the middle of Lancaster Sound, near Barrow Strait (Figure 5). Areas 1 and 7 are characterized by low S, with mean values that are three times lower than the one of Area 2 (Figure 5). Biomass data showed large variability between samples located within the same area, as well as between different areas. A SIMPER analysis was done on infaunal density data (square-root transformed) and identified the main taxa that contributed to pairwise dissimilarities between different levels of both factors, Bird and Area. The top five taxa explaining the main part of dissimilarity between areas with seabird colonies and control areas (Bird factor) were *Annelida*, the ostracod *Philomedes* sp., *Ophiura robusta, Ophiuridae* spp. and the *Leuconidae* spp., which is a family of Cumacea. These taxa together explained 35.57 % of the variation between the two groups of 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 ± 1.12 % (mean contribution ± SE). *Annelida* and *Philomedes* sp. were the two most important taxa, ranked in the top five of 27 and 24 pairwise comparisons (total of 28 comparisons) and explaining in average 11.54 ± 0.73 % and 9.06 ± 0.63 % of dissimilarities between areas respectively.

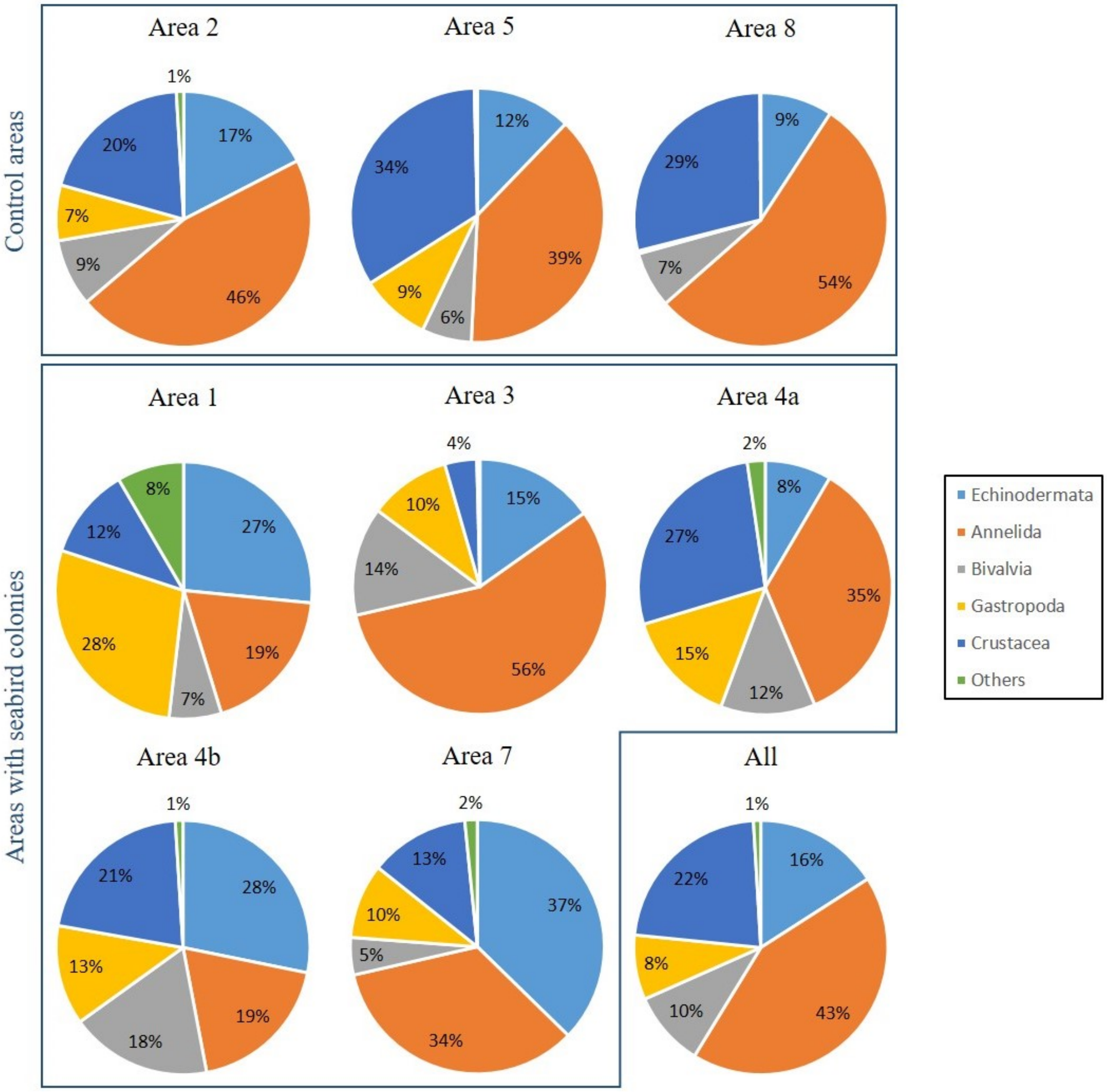

Figure 3. Variation in mean relative abundance composition (%) for the main phyla or class of infaunal communities for the eight sampling areas and for all areas treated as a whole. Control areas are: western part of Lancaster Sound (2, LS), Croker Bay (5, CB) and Maud Bight (8, MB). Sampling areas in the vicinity of seabird colonies are: Gascoyne Inlet (1, GI), Prince Leopold Island (3, PLI), Stratton Inlet (4a, SI), Burnett Inlet (4b, BI) and Wollaston Islands (7, WI).

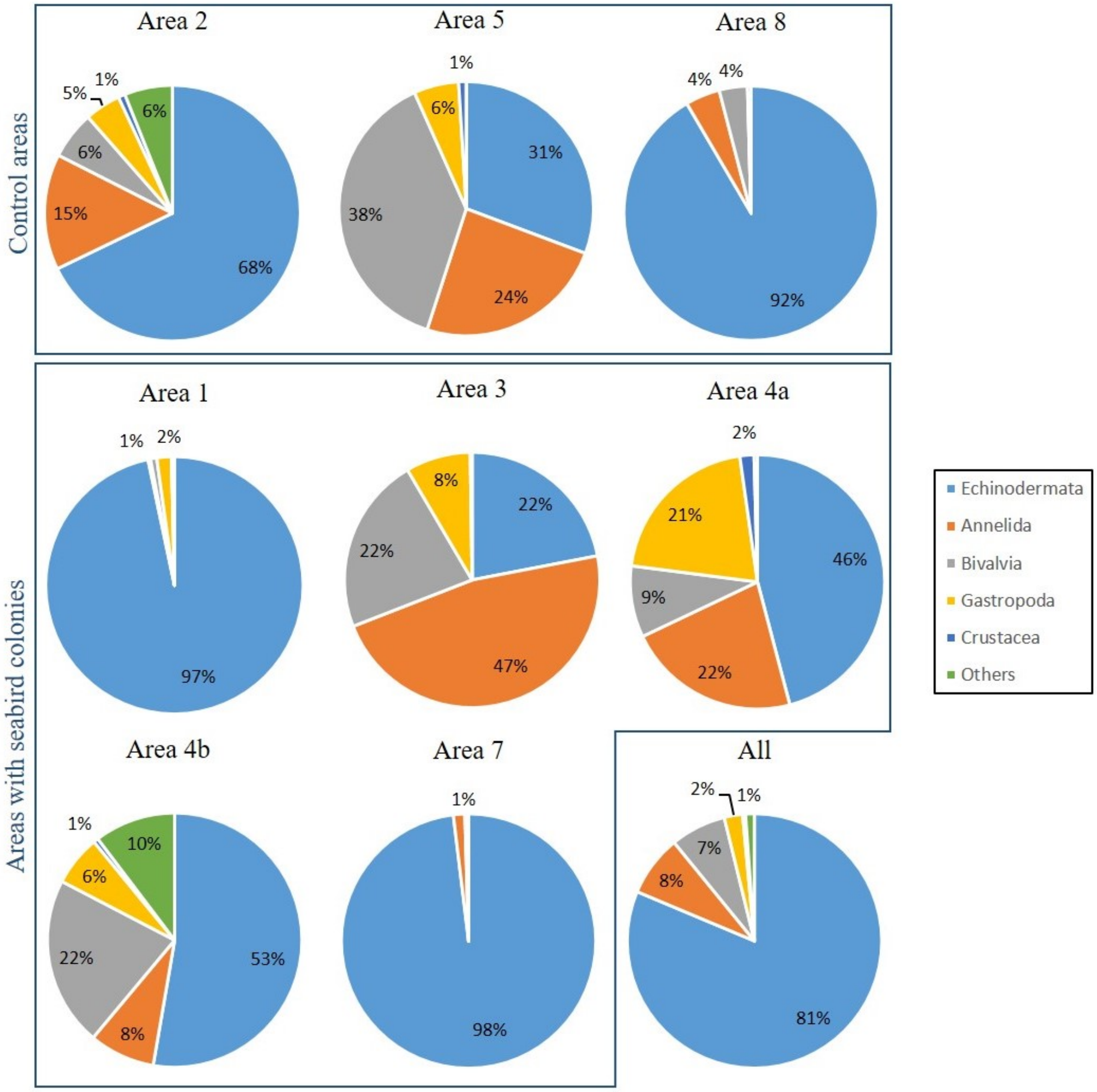

Figure 4. Variation in mean relative biomass composition (%) for the main phyla or class of infaunal communities for the eight sampling areas and for all areas treated as a whole. Control areas are: western part of Lancaster Sound (2, LS), Croker Bay (5, CB) and Maud Bight (8, MB). Sampling areas in the vicinity of seabird colonies are: Gascoyne Inlet (1, GI), Prince Leopold Island (3, PLI), Stratton Inlet (4a, SI), Burnett Inlet (4b, BI) and Wollaston Islands (7, WI).

Table 1. Results of the ANOVAs testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 areas with colonies, 3 areas without) 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. A logarithmic transformation was done on biomass to meet assumptions of ANOVA. 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	**0.012**
	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		

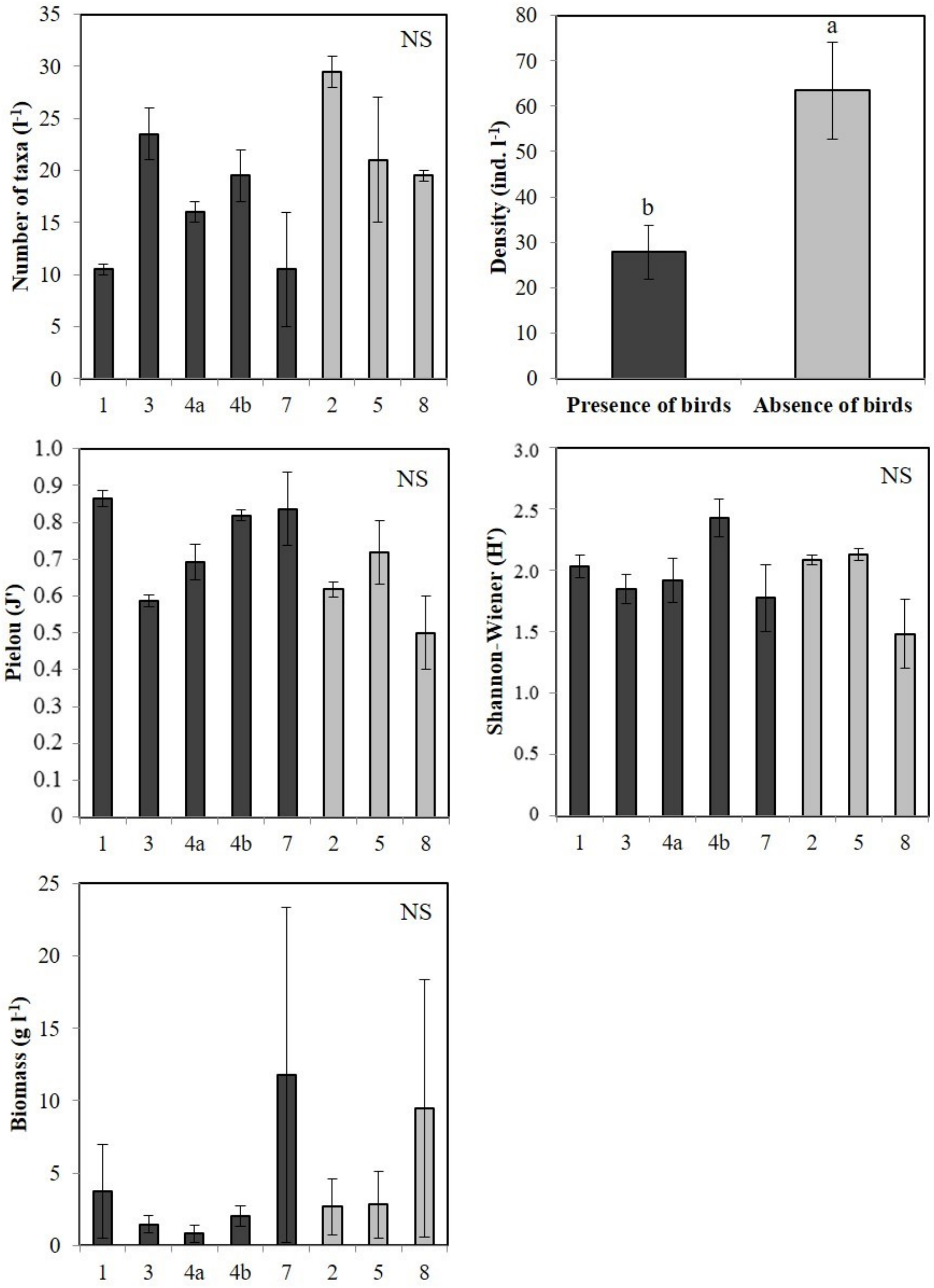

Figure 5. Mean number of taxa, mean total density, mean Pielou's evenness, mean Shannon-Wiener diversity and mean total biomass (± SE) of infaunal communities from areas characterized by the presence of seabird colonies (black) and from control areas (grey). Different letters indicate significant differences between areas based on Tukey post-hoc multiple comparison tests. NS = nonsignificant

Epifaunal communities

The class Ophiuroidea represented 72% to 93% of total abundance of epifaunal organisms depending on the sampling area (Figure 6). Considering all sampling areas as a whole, Annelida and other Echinodermata (except Ophiuroidea) respectively represented 5% and 3% (Figure 6). 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 2, in the middle of Lancaster Sound, is characterized by a significantly higher number of epifaunal taxa than Areas 3 and 7 (Figure 7). Areas 1, 4a, 7 and 5 are characterized by similar low N of epifaunal organisms and similar high values of J' (Figure 7). Areas 2, 3, 4b and 8 are similar together and differed significantly from the other areas, showing higher N and lower J' values (Figure 7). Areas 1, 4a and 5 have similar values of H', which are significantly higher than those of Areas 3, 4b, 2 and 8. Moreover, there is a significant difference of H' between Areas 3 and 7 (Figure 7).

The multivariate analysis PERMANOVA, which tested the differences between areas in term of epibenthic community structure, showed significant differences among areas ($F_{(6,112)} = 10.20$, $p = < 0.001$) (Table 3). In fact, the 28 pairwise comparisons were all significant with $p = < 0.001$, except the ones for Areas 3 and 4b ($p = 0.013$) and for Areas 5 and 7 ($p = 0.049$). This result told us that each area is unique when using the square-root transformed epifaunal density database. These results have been visualized by a MDS, which presented all samples from each area grouped together, with each cloud of dots being relatively distinct from the others (Figure 8). Moreover, the MDS illustrated the difference between the two groups of areas: 2, 3, 4b, 8 on the left and 1, 4a, 5, 7 on the right (Figure 8, dashed line). This pattern was also shown by the epifaunal mean total densities (Figure 7). 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 4b, 3, 8, 4a had high average similarity values (Table 4), meaning that dispersion around centroid was lower for these areas in comparison with Areas 2, 7, 1 and 5. Still considering lower average similarity values for each area, areas 2 and 7 had intermediate dispersion and Areas 1 and 5 had high dispersion (Table 4). No location or dispersion effect was found for the Bird factor. According to SIMPER analysis done on epifaunal density data (square-root transformed) for the factor Area, *Ophiurida, Eunicidae, Ophiacantha* sp., the benthic trachymedusa *Ptychogastrias* sp., *Strongylocentrotus* sp., *Patellogasteropoda, Psolus* sp., *Gasteropoda 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 to explain dissimilarities for the 28 possible combinations of areas (Table 5). These taxa were present at least once in the 28 top five of taxa that explained most of dissimilarity between each comparison of areas. The top five taxa given for each pair-wise comparison explained in average 52.52 ± 0.97 % of dissimilarity between two areas (mean contribution ± SE). Among all these taxa, *Ophiurida* was by far the most important, since it appeared in the 28 top five lists and contributed to explain the quarter of the dissimilarities between two areas in average (25.73 ± 1.28 %) (Table 5).

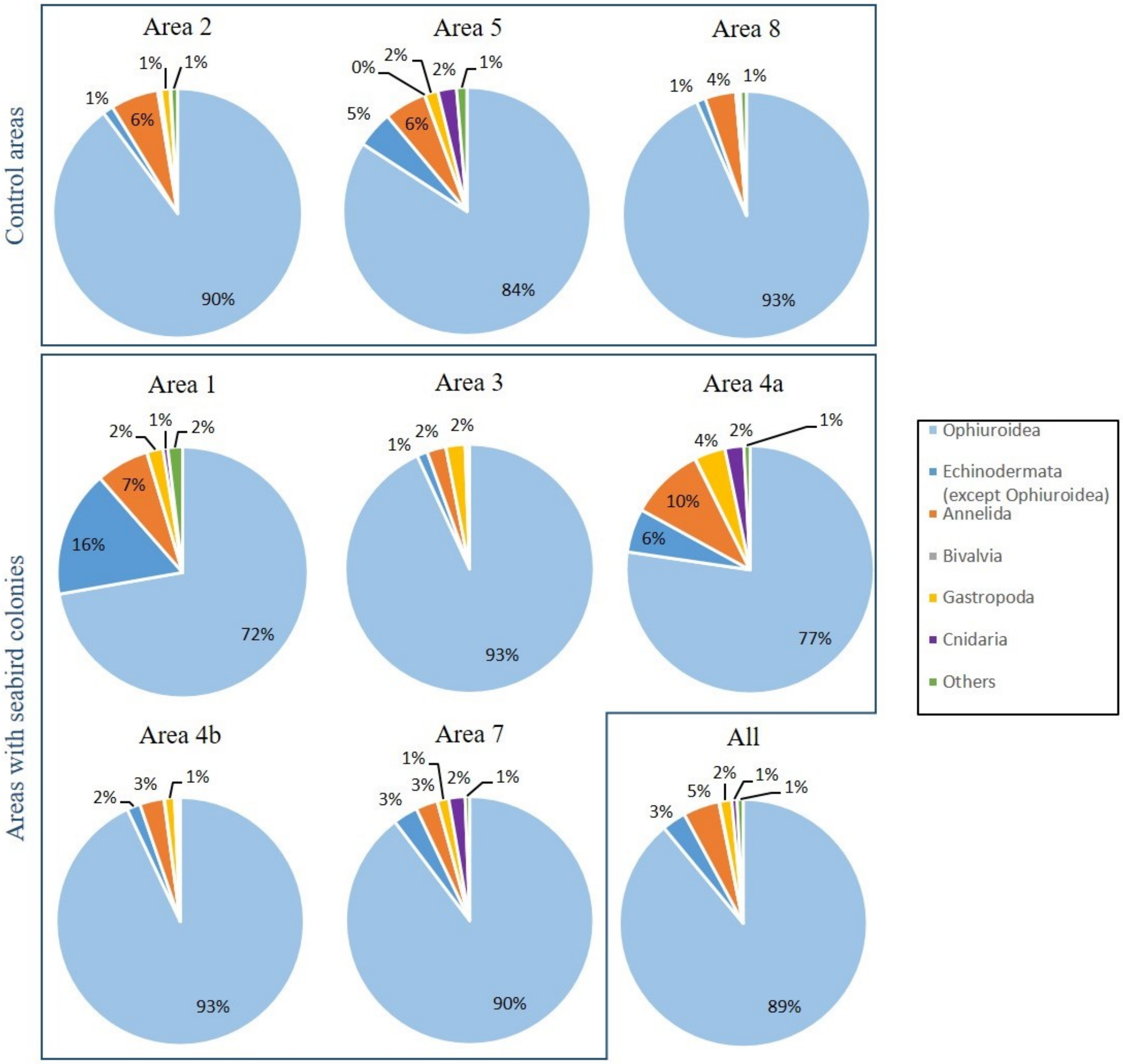

Figure 6. Variation in mean relative abundance composition (%) for the main phyla or class of epifaunal communities from the eight sampling areas and for all areas treated as a whole. The order Ophiuroidea was separated from other Echinodermata to illustrate its importance. Control areas are: western part of Lancaster Sound (2, LS), Croker Bay (5, CB) and Maud Bight (8, MB). Sampling areas in the vicinity of seabird colonies are: Gascoyne Inlet (1, GI), Prince Leopold Island (3, PLI), Stratton Inlet (4a, SI), Burnett Inlet (4b, BI) and Wollaston Islands (7, WI).

Table 2. Results of the ANOVAs testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 areas with colonies, 3 areas without) 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***
√S	Bird	1	0.23	0.41	0.548
	Area(Bird)	6	0.56	2.89	**0.012**
	Error	112	0.19		
log-N	Bird	1	0.30	0.40	0.548
	Area(Bird)	6	0.74	21.25	**<0.001**
	Error	112	0.03		
√J'	Bird	1	0.03	0.12	0.752
	Area(Bird)	6	0.22	19.16	**<0.001**
	Error	112	0.01		
√H'	Bird	1	0.05	0.10	0.763
	Area(Bird)	6	0.51	15.51	**<0.001**
	Error	112	0.03		

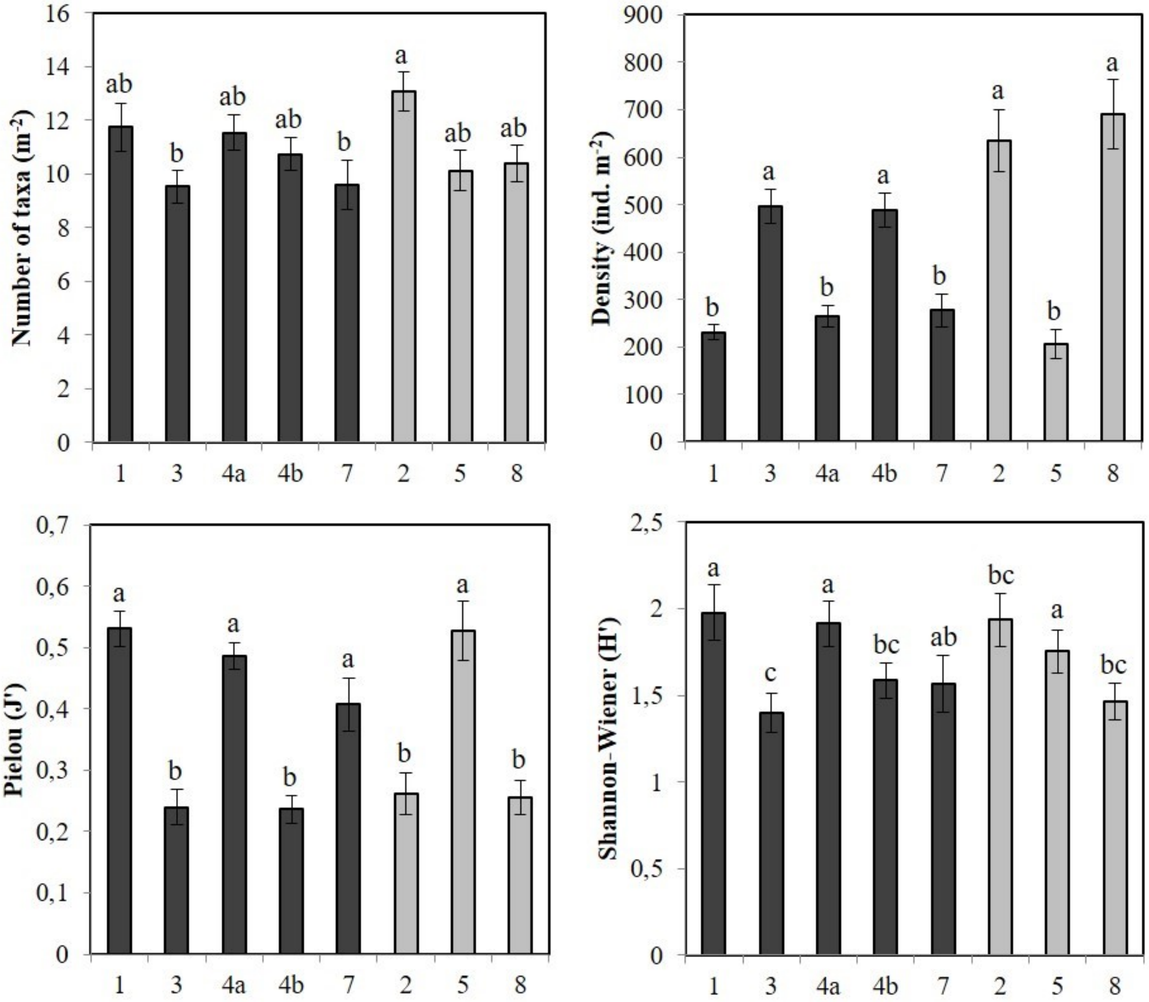

Figure 7. Mean number of taxa, mean total density, mean Pielou's evenness and mean Shannon-Wiener diversity (± SE) of epifaunal communities from areas characterized by the presence of seabird colonies (black) and from control areas (grey). Different letters (a, b) indicate significant differences between areas based on Tukey post-hoc multiple comparison tests.

Table 3. Results of the PERMANOVA and pairwise tests testing the effect of Bird (presence or absence) and Area nested in Bird factor (5 areas with colonies, 3 areas without) on epifaunal communities (square-root transformed epifaunal density data). Significant effects ($p < 0.05$) are in bold.

Source	**df**	**MS**	**F**	***p* (perm)**
Bird	1	4408.90	0.83	0.577*
Area(Bird)	6	5329.40	10.20	**<0.001**
Error	112	522.62		
Pair-wise tests			**t**	***p* (perm)**
1, 2			3.93	**<0.001**
1, 3			3.78	**<0.001**
1, 4a			2.90	**<0.001**
1, 4b			3.58	**<0.001**
1, 5			2.77	**<0.001**
1, 7			2.75	**<0.001**
1, 8			3.81	**<0.001**
2, 3			2.38	**<0.001**
2, 4a			4.06	**<0.001**
2, 4b			2.47	**<0.001**
2, 5			4.04	**<0.001**
2, 7			3.63	**<0.001**
2, 8			2.27	**<0.001**
3, 4a			3.92	**<0.001**
3, 4b			1.58	**0.013**
3, 5			3.70	**<0.001**
3, 7			2.78	**<0.001**
3, 8			2.31	**<0.001**
4a, 4b			3.27	**<0.001**
4a, 5			2.32	**<0.001**
4a, 7			2.13	**<0.001**
4a, 8			4.20	**<0.001**
4b, 5			3.42	**<0.001**
4b, 7			2.68	**<0.001**
4b, 8			2.12	**<0.001**
5, 7			1.49	**0.049**
5, 8			3.63	**<0.001**
7, 8			3.08	**<0.001**

* indicates that Monte Carlo *p* value was used because the number of permutations was below 100.

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).

	1	2	3	4a	4b	5	7	8
1	62.7							
2	49.6	67.7						
3	44.8	34.4	73.6					
4a	40.6	43.8	38.5	72.0				
4b	43.4	34.4	27.7	35.0	73.7			
5	45.6	50.5	44.3	37.6	42.4	62.4		
7	42.6	44.4	35.8	34.0	35.1	36.6	67.6	
8	45.8	34.1	31.1	41.2	30.2	45.1	38.4	72.3

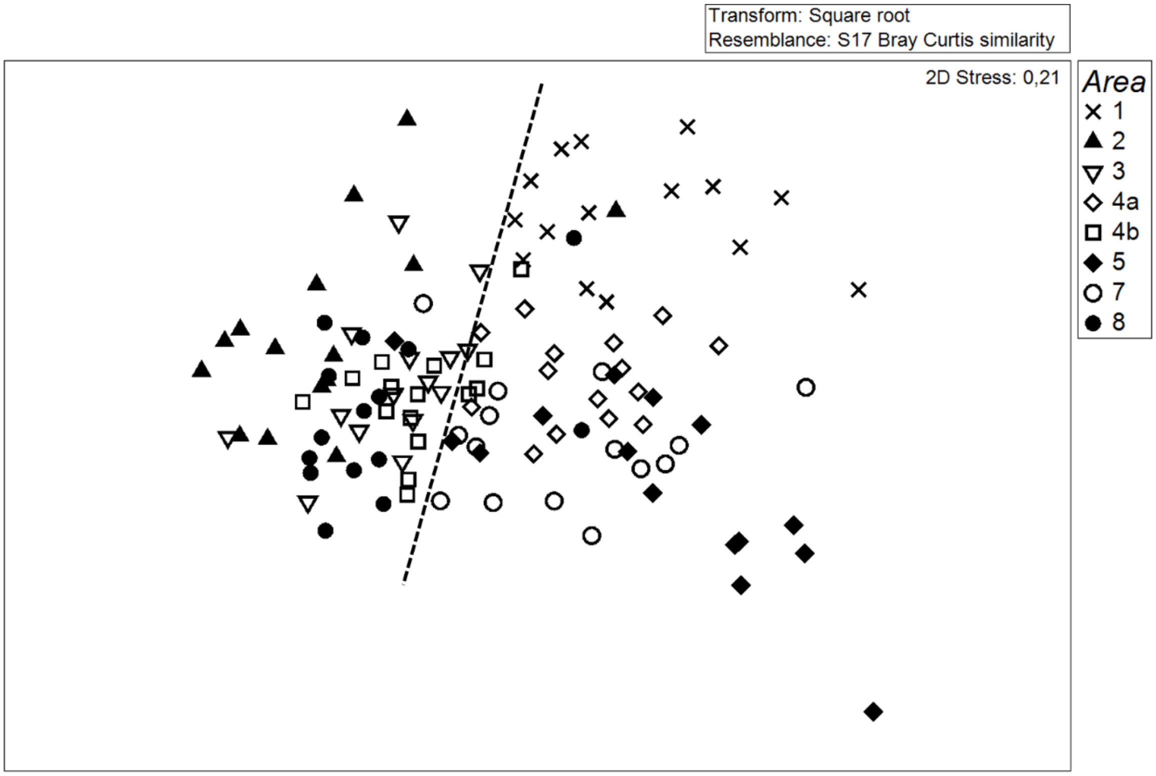

Figure 8. Multidimensional scaling of epifaunal communities from the eight sampling areas (n = 15 for each area). *A posteriori* pairwise tests showed that all areas differed significantly from each other (square-root transformed epifaunal density data). Full black symbols represent areas characterized by the presence of seabird colonies. Empty ones, including × symbols, represent control areas. The dashed line separates two groups of areas, 2, 3, 4b, 8 (left) and 1, 4a, 5, 7 (right), which are shown in this representation probably because of their differences in terms of mean total density (see figure 7).

Table 5. Mean contribution (± SE) of the epifaunal taxa that contributed most to dissimilarity between the eight sampling areas (28 possible combinations). Top five taxa from all pair-wise comparisons in the SIMPER analysis were selected to calculate a mean contribution.

Taxa name or morphototype	**Number of pair-wise comparisons where taxa was among the top five (n/Ntotal)**	**Mean contrib. (%) ± SE**		
Ophiurida	28/28	25.73	±	1.28
Eunicidae	28/28	8.00	±	0.28
Ophiacantha sp.	26/28	6.68	±	0.31
Ptychogastrias sp.	14/28	5.59	±	0.32
Strongylocentrotus sp	12/28	5.58	±	0.26
Patellogasteropoda	10/28	6.09	±	0.40
Psolus sp.	10/28	7.26	±	0.77
Gasteropoda A	8/28	7.13	±	0.87
Bivalvia	2/28	3.95	±	0.06
Worm A	1/28	4.55		-
Pycnogonida AB	1/28	4.19		-

Relation between infauna and environment

OM content of the LSR was comprised between 6.22 ± 0.39% and 18.03 ± 1.25% (Table 6). Areas 4a and 4b appeared to have the highest values of OM and Areas 5 and 8 the lowest ones. Sediment of Areas 2 and 3 seemed to have the highest concentrations of pigments, values ranging between 0.82 ± 0.10 and 0.29 ± 0.08 $\mu g\ g^{-1}$ for the chlorophyll *a* and between 4.24 ± 0.36 and 2.62 ± 0.16 $\mu g\ g^{-1}$ for the phaeopigments (Table 6).

Using environmental variables, the best multiple linear regression models explained from 52% to 71% of variation in the univariate characteristics of infaunal communities S, N, J' and H' (Table 7). 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. A logarithmic transformation was done on density (N) data, whereas square-root transformations were done for the three other variables. S increased with $[\mathrm{Chl}\ a]_{\mathrm{BW}}$ and S2 and decreased with Birds index (Adj. $R^2 = 0.66$, $p = 0.001$). N increased with Mean_V, MB and CG (Adj. $R^2 = 0.52$, $p = 0.008$). J' was best predicted by Mean_V, LB, [NIT] (negative for these three predictors) and CG (positive) (Adj. $R^2 = 0.71$, $p = 0.001$). VCG and MB were the two predictors that influenced H', positively for the first one and negatively for the second (Adj. $R^2 = 0.53$, $p = 0.003$). No regression model with the available environmental variables was found to explain variation in log-biomass data.

Relation between epifauna and environment

Using environmental variables, the best multiple linear regression models explained from 11% to 53% of variation in the univariate characteristics of epifaunal communities S, N, J' and H' (Table 8). S decreased with $[\mathrm{Chl}\ a]_{\mathrm{BW}}$ and CG and increased with LB (Adj. $R^2 = 0.11$, $p < 0.001$). N was negatively correlated to MB, VSB, CG and D (Adj. $R^2 = 0.53$, $p < 0.001$). J' increased with T and VSB and decreased with SB (Adj. $R^2 = 0.49$, $p < 0.001$). T, VSB and SB were the predictors that influenced H', positively for the first two and negatively for the third one (Adj. $R^2 = 0.43$, $p < 0.001$).

Explaining 37% of the overall variation in epifaunal communities structure (Adj. $R^2 = 0.34$, $R^2 = 0.37$) the best distance-based linear model (DISTLM) included 6 environmental variables: LB, D, DOW, SB, MB and S2 (Table 8, Figure 10). The two first axes of the dbRDA plot represented together 74% of the fitted variation and 28% of the total variation (Table 9, Figure 9). Mainly built by MB and LB, the first axis (dbRDA1) separated the same two groups of areas revealed by univariate analyses (Figure 7, N and J') and by the MDS (Figure 8): 1, 4a, 5, 7 and 2, 3, 4b, 8. The second axis (dbRDA2) is strongly correlated with D and S2. The benthic assemblage in Area 1 seemed different from others areas in function of this second axis. Some variability within each of the two groups could also be explained by D and S2. DOW and SB participated significantly to build the first dbRDA axis as well as the second.

Table 6. Mean organic matter content (OM, %), mean sediment chlorophyll *a* (Sed Chl *a*, μg g^{-1}) and mean sediment phaeopigments (Sed phaeo, μg g^{-1}) (± SE) for the eight sampling areas.

Area	**OM**	**Sed Chl *a***	**Sed phaeo**
3	13.63 ± 1.50	0.76 ± 0.11	4.20 ± 0.38
4a	18.03 ± 1.25	0.29 ± 0.08	3.54 ± 0.21
4b	16.66 ± 0.79	0.44 ± 0.04	2.62 ± 0.16
7	14.66 ± 0.75	0.49 ± 0.07	2.71 ± 0.23
2	12.41 ± 1.08	0.82 ± 0.10	4.24 ± 0.36
5	6.57 ± 0.79	0.40 ± 0.09	3.42 ± 0.32
8	6.22 ± 0.39	0.39 ± 0.04	3.13 ± 0.15

Table 7. Results of multiple linear regression models of infaunal communities structure 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 eight sampling areas (n = 2 for each area). Birds = index of bird colony size; [NIT] = nitrate and nitrite concentration of bottom water; $[\text{Chl } a]_{\text{BW}}$ = chlorophyll *a* concentration of bottom water; S2 = salinity of bottom water; CG = percent cover of coarse gravel; VCG = percent cover of very coarse gravel; MB = percent cover of medium boulders; LB = percent cover of large boulders; Mean_V = yearly mean velocity of modelled bottom currents. For each predictors selected in these models, regression coefficients (± 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.

	S	**N**	**J'**	**H'**
Intercept	-484.14 ± 114.60	-66.99 ± 34.68	0.61 ± 0.12	1.23 ± 0.18
Birds	-2.84 ± 0.85			
[NIT]			-0.017 ± 0.006	
$[\text{Chl } a]_{\text{BW}}$	72.09 ± 17.91			
S2	15.04 ± 3.44			
CG		3.71 ± 1.43	0.021 ± 0.008	
VCG				0.028 ± 0.007
MB		22.05 ± 11.33		-0.28 ± 0.13
LB			-0.14 ± 0.05	
Mean_V		1120.18 ± 279.18	-2.92 ± 0.94	
Adj. R^2	0.66	0.52	0.71	0.53
F	10.87	6.43	10.19	9.54
p	0.001	0.008	0.001	0.003
SS_{Model}	541.74	6956.00	0.24	0.92

Table 8. Results of multiple linear regression models of epifaunal communities structure 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 eight sampling areas (n = 15 for each area). D = depth; T = temperature of bottom water; $[\mathrm{Chl}\ a]_{\mathrm{BW}}$ = chlorophyll *a* concentration of bottom water; CG = percent cover of coarse gravel; VSB = percent cover of very small boulders; MB = percent cover of medium boulders; LB = percent cover of large boulders. For each predictors selected in these models, regression coefficients (± 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.

	S	**N**	**J'**	**H'**
Intercept	3.97 ± 0.30	4.52 ± 0.20	0.47 ± 0.02	0.71 ± 0.03
D		-0.0050 ± 0.0005		
T			0.23 ± 0.03	0.33 ± 0.05
$[\mathrm{Chl}\ a]_{\mathrm{BW}}$	-1.96 ± 0.76			
CG	-0.03 ± 0.02	-0.014 ± 0.005		
VSB		-0.036 ± 0.003	0.025 ± 0.003	0.037 ± 0.004
SB			-0.017 ± 0.005	-0.025 ± 0.008
MB		-0.28 ± 0.04		
LB	0.38 ± 0.10			
Adj. R^2	0.11	0.53	0.49	0.43
F	6.11	34.44	39.09	30.33
p	<0.001	<0.001	<0.001	<0.001
SS_{Model}	3.42	4.69	1.30	0.99

Table 9. Distance-based linear model (DISTLM) of epifaunal communities (square-root transformed epifaunal density data) against environmental variables associated to the eight sampling areas (n = 15 for each area). D = depth; S2 = Bottom salinity; SB = percent cover of small boulders; MB = percent cover of medium boulders; LB = percent cover of large boulders; DOW = Duration of open water.

No. Vars	**Adj R^2**	**R^2**	**AICc**	**BIC**
6	0.34	0.37	754.33	772.84

Variable	**SS(trace)**	**Pseudo-F**	***P***	**Prop.**
LB	7063.2	9.93	<0.001	0.078
D	6556.3	9.16	<0.001	0.072
DOW	3964.5	5.38	<0.001	0.044
SB	3790.2	5.13	<0.001	0.042
MB	3736.5	5.05	<0.001	0.041
S2	3193.7	4.29	<0.001	0.035

Percentage of variation explained by individual axes

	% explained variation out of fitted model		% explained variation out of total variation	
Axis	Individual	Cumulative	Individual	Cumulative
1	55.58	55.58	20.83	20.83
2	18.90	74.48	7.09	27.92
3	11.08	85.57	4.15	32.07
4	8.13	93.70	3.05	35.12
5	4.66	98.36	1.75	36.87
6	1.64	100.00	0.62	37.48

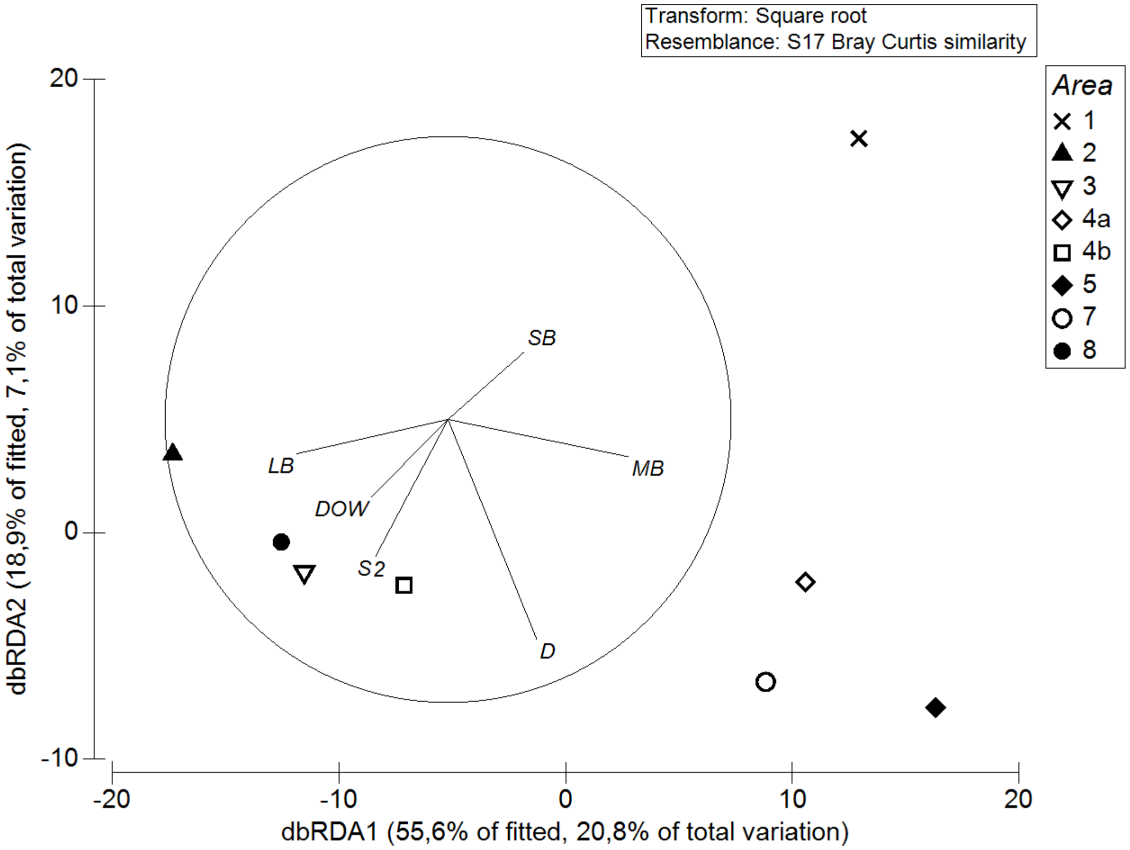

Figure 9. Distance-based redundancy analysis (dbRDA) plot of the DISTLM model based on the environmental variables that better explained variability among epifaunal communities (square-root transformed epifaunal density data) of the eight sampling areas (n = 15 for each area). Full black symbols represent areas characterized by the presence of seabird colonies. Empty ones, including × symbols, represent control areas. D = depth; S2 = Bottom salinity; SB = percent cover of small boulders; MB = percent cover of medium boulders; LB = percent cover of large boulders; DOW = Duration of open water.

2.6. DISCUSSION

This study is the first to test the regional influence of seabird colonies on the structure of benthic communities in the Canadian Arctic. Contrary to our hypothesis, the presence of colonies was not an important factor that positively affected the benthos across the LSR. Furthermore, some negative effects on infauna were detected. Among the various environmental parameters considered in our analyses, depth, sediment type and chlorophyll *a* concentration of bottom waters were the main drivers of epifaunal and infaunal communities of the LSR. We first discuss the structure of benthic communities of the LSR in general and, more specifically, the pattern of high dominance of Ophiuridae among epifaunal assemblages. Second, we discuss how environmental parameters drive benthic communities and generate spatial differences among study areas. Third, we give possible explanations to the weak impact of seabirds shown by all of the analyses. We conclude that food availability is probably one of the main drivers of benthic communities in the LSR.

Description of benthic communities

Since only two other studies on the structure of benthic communities in the eastern Canadian Arctic have been published to date (Thomson, 1982; Roy *et al.*, 2015b), the present contribution is highly relevant. Moreover, approximately 60% of megabenthic taxa are still to be documented in this region (Roy *et al.*, 2015b). Thomson (1982) mainly worked at the mouth of Lancaster Sound, at the easternmost range of our sampling areas. Several common taxa that were collected in our study are similar to those recorded by Thomson (1982), who characterized an assemblage composed of several species of Ophiuroidea, *Macoma* sp. and *Astarte* sp. through a sampling also done with a Van Veen grab. However, our study revealed that the group of Annelida 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 between our results and Thomson's (1982) may be due to different depth range and an offset between the spatial extent of the two studies. The infaunal samples from Areas 5 and 8 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. With respect to epifauna, the assemblages all over the LSR were completely dominated by Ophiuroidea, which are known to be very common and abundant on shelf and slope polar environments (Welch *et al.*, 1992; Piepenburg *et al.*, 1996; Piepenburg, 2005; MacDonald *et al.*, 2010; Ravelo *et al.*, 2014) and in the eastern Canadian Arctic (Roy *et al.*, 2015b). In this study, the density of Ophiuridae reached six hundred individuals per square meter; numbers similar to those of several other studies (Piepenburg, 2000; 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, Ophiuridae includes a diversity of feeding modes, such as omnivorous and surface deposit feeders (Piepenburg, 2000), and are very mobile in comparison to other benthic invertebrates (Thistle, 2003; MacDonald *et al.*, 2010), which makes them flexible to exploit heterogeneous food inputs (for holothurians, Iken *et al.*, 2001). The dominant and abundant group of Ophiuridae is also of fundamental importance in arctic ecosystems, in particular in carbon remineralisation processes (Ambrose *et al.,* 2001; Link *et al.*, 2012, 2013).

Overall, infauna was very uniform and no significant difference was revealed between the different study areas. In contrast, each geographic location, as represented by the study areas, was unique in terms of community structure of epifauna, which was very patchy across the LSR. This pattern is however specific to the spatial scale considered (Levin, 1992; Cusson *et al.*, 2007). Thomson (1982) also worked at a regional scale and demonstrated that geographic location was a major predictor of standing stock and density of benthos, indicating environmental heterogeneity in the eastern Canadian Arctic.

Food supply proxies

In the present study, chlorophyll *a* concentration of bottom water was associated with the number of taxa for both infauna and epifauna. The concentration of chlorophyll *a* is frequently used as a primary production proxy, and indicates fresh food availability for benthic organisms (Grebmeier *et al.*, 1988; Smith *et al.*, 2006; Roy *et al.*, 2014). The relationship between chlorophyll *a* concentration and the number of taxa can be explained by the wider ecological concept of the productivity-biodiversity relationship that may follow a curvilinear (hump-shaped) function (Levin *et al*., 2001) as shown in the Canadian Arctic (Witman *et al*., 2008). Moreover, in our study, the relationship was positive for infauna and negative for epifauna, and this could be explained by the different ways the two assemblages respond to fresh food input, that is, tightly linked with sedimentation of organic matter. Epifaunal communities of the LSR were mostly composed of mega- and macrofaunal organisms associated with hard-bottom, which are more adapted to environments that are insulated from sediment transport and high particle loads (Tissot *et al*., 2006) than infaunal taxa living on soft-bottom such as bivalves or polychaetes which were found in finer sediment. Therefore, at a given place and time and for a given level of primary production, a phase offset could exist between the two benthic compartments: infauna can be on the ascending limb of its respective hump-shaped relationship, whereas epifauna can be on the descending part of its own curve (Levin *et al*., 2001). In fact, sedimentation could become too intense for epifaunal organisms (Gabriele *et al*., 1999), increasing the impact of hard substrate limitation.

Our results also showed that the highest number of taxa in general was recorded in the western part of the LSR (Area 2) and this could be due to food supply as well. Area 2 was the farthest area offshore and the nearest from Barrow Strait of all areas sampled. Barrow Strait is characterized by a sill of 150 m depth which constitutes the western limit of our study site (Prinsenberg and Bennet, 1987; Welch *et al*., 1992). This sill creates an upwelling that mixes the water masses in Lancaster Sound (Prinsenberg and Bennet, 1987; Welch *et al*., 1992). Tidal and bathymetry induced mixing could allow an efficient regeneration of nutrients in the euphotic layer on the eastern side of the sill, increasing primary productivity (Ardyna *et al*., 2011; Tremblay *et al*., 2011). These processes at the western limit of our study site probably enhanced food availability for benthic communities via enhanced POC fluxes (McArthur *et al*., 2010) and this could have led to a higher number of taxa that benefited from these resources (Wright *et al*., 1993; Rosenzweig, 1995). Supporting this explanation, pigment concentrations in sediment from Area 2 were high in comparison with those from other areas sampled in the present study (also shown by Kenchington *et al*., 2011). Higher pigment concentrations are possibly caused by a higher sedimentation rate (Stephens *et al*., 1997). Pigment concentration data of this study can only be compared in a descriptive way though due to pseudo-replication in our sampling and missing data. Moreover, chorophyll *a* concentration of the bottom water was also relatively high in Area 2, substantially above the average for the whole study area.

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 the depth gradient (Smith *et al*., 2008; MacDonald *et al*., 2010). Depth is an indirect factor that is often correlated with other parameters that vary vertically, such as temperature or salinity (Mayer et Piepenburg, 1996; Roy *et al*., 2014) and which convey more biological relevance. However, in this case depth was not significantly correlated to abiotic parameters, likely because the range was quite narrow as a result of our experimental design. Logically, the strength of pelagic-benthic coupling, which is correlated with food supply and usually considered as an important driver structuring arctic benthic communities, should decline when depth increases (Soltwedel *et al*., 2009; Roy *et al*., 2014). For this reason, food availability for benthos might have been lower in deeper areas (Mayer et Piepenburg, 1996; Smith *et al*., 2008; Roy *et al*., 2014), resulting in fewer individuals due to limited resources.

Sediment type and velocity of bottom currents

The percent cover of large boulders was positively linked to the number of taxa. 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). The percent cover of sediment classes "very small boulders" and "very coarse gravel" were intermediate between gravel and boulder and were positively linked with Shannon-Wiener biodiversity index (H'), respectively for epifauna and infauna. Therefore, even if coarser sediment in general structure habitat (Buhl-Mortensen *et al*., 2012), which can explain the positive relationship with the number of taxa, upper classes of sediment (small and medium boulders) were negatively correlated with the Shannon-Wiener index. The reason for this is purely mathematical considering the way this index is calculated and the fact that these percent covers were negatively linked to total density in this study (Magurran, 2005). This was because the sampling success of the grab was heavily compromised in areas where photos revealed that boulders were abundant.

The density of epifauna, which was completely dominated by ophiuroids, was negatively correlated with coarser sediment. During photo analyses, we observed that ophiuroids seemed to prefer finer gravel and tended to accumulate in the gaps between pebbles, where reduced current velocity probably facilitated their displacement and favored sedimentation of food. Our observations support Piepenburg (2000), who summarized that seabed heterogeneity and food availability are important drivers of the structure of ophiuroids assemblages. In our case, these parameters are probably explaining the particular distribution of ophiuroids, but further sampling work would be needed to confirm it.

Differently, percent cover of coarse sediment was positively correlated to the total density of infauna. Gravel and boulders, whose percent cover was estimated on photos, were transported by the action of strong bottom velocity currents (Grebmeier *et al*., 2006; Blanchard and Feder, 2014). This is consistent with the negative relationship between mean velocity of bottom currents and density of infauna. In these areas where currents were stronger and sediment was consequently coarser, the grab probably sampled successfully in particular spots where sedimentation could occur, such as behind a large boulder (McArthur *et al.,* 2010). In these specific spots, infauna was abundant and concentrated, maybe due to the presence of finer sediment and organic matter (Blanchard and Feder, 2014). By increasing total density in these spots, it may increase competition between species for resources and probably promote some opportunistic taxa over other taxa. Therefore, it is consistent to find an indirect negative relationship between mean velocity and the equitability index J', as well as a negative one between percent cover of large boulder and J'. Moreover, findings of Blanchard and Feder (2014) and Blanchard *et al.*

(2013a, 2013b) suggested that local-scale topographically-driven water circulation, which is associated with variation in carbon deposition, influences the structure of macro- and megafaunal communities of the Chucki Sea.

Drivers of epifaunal community structure (multivariate)

The multivariate approach gave another perspective of the complex link between environment and epifaunal community structure. Because we used the mean for each environmental parameter at each area, it is not possible to analyse the similarity among the samples of the same area. Consequently, the interpretation of our results derived from these multivariate analyses is limited to the differences between areas and does not take into account the variation within each area. However, this approach still provided interesting findings. Even if we chose areas at similar depths with the same general type of sediment to try to control the effect of these parameters, they were the two most critical drivers to explain the community structure pattern. Percent cover of boulders (SB, MB, LB) was the most important parameter among those measured to explain the distinction between the two groups of areas in terms of epifauna density. As this important pattern of benthic community structure of the LSR in our results was directly created by ophiuroids distribution, we conclude that surface covered by boulders drives ophiuroids distribution. This finding puts the emphasis on the importance of boulders, which was also detected with the univariate approach. It could be because boulders enhances habitat complexity (Buhl-Mortensen *et al.*, 2012) and/or indicates strong bottom currents (Grebmeier *et al.*, 2006; Blanchard and Feder, 2014) that could increase food availability for filtering species of ophiuroids amongst others. Area 1 was different from other sampling areas in regards to salinity and depth values, which seemed to influence community structure. Salinity and depth may be correlated to other water masses properties that were not sampled in this study, such as oxygen concentration for example. Finally, duration of open water, collinear with the two other satellite-derived parameters (primary production and chlorophyll *a* concentration), was also important to explain epifaunal community structure. Integrated over five years, duration of open water can be used as a 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 (Carroll *et al.*, 2008; 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).

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 the southern hemisphere (Palomo *et al.*, 1999), northern hemisphere (Kolb *et al.*, 2010) and even in an arctic ecosystem (Zmudczyńska-Skarbek *et al.*, 2015). Food availability is known to influence taxonomic composition, diversity and abundance of benthic communities in the Arctic (Grebmeier and Barry, 1991; Piepenburg *et al.*, 1997; Levin *et al.*, 2001; Witman *et al.*, 2008; Roy *et al.*, 2014). However, in contrast to what was expected, presence of seabird colonies did not seem a major driver of benthic assemblages. 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 infaunal taxa was negatively correlated with the size of seabird colonies. Knowing that the diet of thick-billed murre and northern fulmar, the two main species that inhabit the LSR cliffs (Mallory and Fontaine, 2004), consists of fishes during chick-rearing period (Hobson, 1993; Garthe *et al.*, 2004), a top-down effect could explain these negative impacts on benthic community structure. By controlling fish populations, seabirds indirectly contribute to the expansion of zooplankton populations, which are known to be large during the summer in the LSR in comparison with other arctic regions (Longhurst *et al.*, 1984; Sameoto *et al.*, 1986). This could result in a weaker pelagic-benthic coupling, decreasing the quantity of fresh phytoplankton material that reaches the benthic compartment.

Only few studies have focused on a seabird effect on benthic communities (Palomo *et al.*, 1999; Kolb *et al.*, 2010; Signa *et al.*, 2015; Zmudczyńska-Skarbek *et al.*, 2015). The results of a recent study in coastal ponds (Italy) showed a typical benthic response of severe eutrophication (clear decrease in total abundance, diversity and trophic functional groups) caused by bird presence (Signa *et al.,* 2015), while another study demonstrated positive effects (abundance, biomass, biodiversity) of seabird colonies on benthic communities in a coastal lagoon (Argentina) (Palomo *et al*., 1999). Kolb *et al.* (2010) worked in shallow waters of an archipelago in the Baltic Sea (Sweden) and their results showed that birds provided a significant nitrogen source at high nest density and positively affected the biomass of three invertebrate taxa (*Jaera albifrons, Gammarus* spp. and Chironomidae) that feed on algae. Also, Zmudczyńska-Skarbek *et al*. (2015) did isotope analyses on hermit crabs and sea urchins below a single seabird colony in Svalbard which suggested that seabird bottom-up effect may influence some benthic organisms. In fact, the hermit crab *Pagurus pubescens* was associated with δ^{15}N and total N enrichment below the colony in comparison with the control site, suggesting that this opportunistic omnivorous feeder depends on detritus derived from ornithogenic nutrient (Zmudczyńska-Skarbek *et al*., 2015). However, dissimilarities between our study and those are not so surprising because of differences in depth and/or geographic location. For example, Zmudczyńska-Skarbek *et al*. (2015) worked in depths ranging between 5 to 15 meters, although we sampled at depths beyond 120 meters. This difference in the methodology decreases our probabilities to detect an effect because of all the processes in the water column that can interfere with the organic matter input. Moreover, the scale-dependence of observed patterns could also be involved in the differences between studies. The shape of the relation productivity-biodiversity is highly variable in the scientific literature and some studies present evidence of the scale-dependence of these patterns that can cause this discrepancy (Huston, 1999; Mittelbach *et al*., 2001; Chase and Leibold, 2002; Scheiner and Jones, 2002; Witman *et al*., 2008). The studies of Palomo *et al*. (1999) and Signa *et al.* (2015) were performed at local scales, while our study was a regional one.

Food availability (depth, chlorophyll *a* concentration, duration of open water) is an important factor that structures benthic assemblages in the LSR, but the potential input derived from the seabird colonies did not have positive effects on benthic communities. We suggest four hypotheses to explain this finding. First, our study site, the LSR, is characterized by strong currents that potentially rapidly spread and export nutrients and phytoplankton farther offshore or toward a neighboring region. Second, the timing of the input from seabird colonies may happen before the phytoplankton bloom and then may coincide with high nutrient concentrations in the marine environment, since seabird populations usually follow the ice breakup (Mallory and Fontaine, 2004). As Bédard *et al.* (1980) demonstrated it in the St. Lawrence Estuary, this input could be insignificant relatively to the nutrients already available at a given time and place or to the other inputs such as land drainage or vertical mixing. Moreover, the relative contribution to abiotic and biotic sources to nutrient budget can vary considerably between years (Bildstein *et al.*, 1992), particularly in Arctic where seasonal and interannual variability are so high (Melling, 2002; Prinsenberg and Hamilton, 2005; Michel *et al.*, 2006; Hamilton *et al.,* 2013). These two first hypotheses imply that benthic communities may be strongly influenced by phytoplankton production and its spatial and temporal variability even if we did not detected positive impact from seabird colonies. Third, it could be that the study areas were too far from the coast due to limitations imposed by safety restrictions and logistics, to detect the bottom-up effect of seabirds on benthos. Perhaps the small impact of seabird colonies on infaunal communities that we detected were the only ones that could be detected at such considerable distance from seabird colonies. Supporting this possibility, it had been suggested that the effect of guano deposition would be very localized and would decrease rapidly with distance from colonies (Bédard *et al*., 1980; Wainright *et al*., 1998). Thus, it could be interesting to replicate this sampling in shallower depths, nearer to the coasts, to clarify the influence of the distance from seabird colonies. 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 the LSR is produced by ice algae (Michel *et al*., 2006). It may seem insignificant, but these algae 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 (Bradstreet and Cross, 1982; Bergmann *et al*., 1991; Michel *et al*., 1996, 2006). Numerous past studies suggested the great importance of this resource for benthic organisms in the Arctic (Renaud *et al.,* 2007; Brown and Belt, 2012; Roy *et al*., 2015a).

2.7. 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 did not seem to be a major indirect driver of benthic community characteristics and community structure in the LSR below 120 meters, although it did negatively influence the total density of infaunal organisms. Several environmental parameters, such as depth, chlorophyll *a* concentration, duration of open water, mean velocity of bottom currents and sediment type, influence density, number of taxa, equitability and biodiversity. Dominated by ophiuroids, epifaunal community structure is mainly controlled by surface covered by boulders and food availability proxies. Based on our findings, food supply proxies had a strong explicative power, hence, 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. In a changing Arctic, the bounds between terrestrial and marine environments and between ocean surface and seafloor could be strongly modified with unexpected repercussions. Accurate predictions of these impacts can only be achieved through a better comprehension of arctic ecosystems.

CONCLUSION GÉNÉRALE

La portée de la présente étude est vaste car elle touche les impacts des colonies d'oiseaux sur le milieu marin, la biodiversité benthique arctique et le lien entre l'environnement et la structure des communautés benthiques (ex. : relation productivité-biodiversité), qui sont tous des sujets caractérisés par des lacunes importantes dans les connaissances actuelles. Les études publiées à ce jour qui portent sur la limitation en nutriments suite à la période estivale de floraison phytoplanctonique (Grebmeier *et al*., 1995; Tremblay *et al*., 2006, 2008; Martin *et al.*, 2010), sur la hausse de production primaire engendrée par les oiseaux (Bosman *et al*., 1986; Brimble *et al*., 2009; Keatley *et al*., 2009; Michelutti *et al*., 2009) et sur le couplage pélago-benthique dans l'Arctique (Piepenburg *et al*., 1997, 2000; Soltwedel *et al*., 2009) soutiennent l'idée que la présence/absence de colonies d'oiseaux engendreraient des différences spatiales au niveau de la structure des communautés benthiques via l'enrichissement en nutriments (*bottom-up*). Cette étude, effectuée à l'échelle régionale du détroit de Lancaster dans l'Arctique canadien, a permis de caractériser la structure des communautés benthiques de la région, de tester l'impact des colonies sur ces dernières et de déterminer les paramètres environnementaux qui influencent significativement les assemblages benthiques décrits. De nombreuses variables reliées à la colonne d'eau et au fond marin ont été prises en considération (ex. : température, salinité, concentrations de pigments et de nutriments, vitesse des courants, type de sédiment). La mission océanographique qui s'est déroulée en 2012 dans le détroit de Lancaster a permis d'échantillonner distinctement l'épifaune et l'endofaune dans des zones situées près de colonies d'oiseaux et dans des zones contrôles. Bien qu'aucun effet indirect positif des colonies d'oiseaux n'ait été démontré en comparant ces deux types de zones, certains effets négatifs ont touchés l'endofaune. Globalement, les indicateurs de disponibilité de ressources alimentaires pour le benthos, le type de sédiment et la vitesse des courants de fond se sont révélés être des paramètres plus importants que la présence de colonies, et ce, autant pour l'épifaune que pour l'endofaune.

Les communautés benthiques : endofaune et épifaune

Les assemblages épibenthiques étaient totalement distincts d'une zone échantillonnée à une autre, alors que les résultats montrèrent l'endofaune comme étant homogène dans toute la région couverte par la présente étude. Le *n* associé à l'endofaune, correspondant seulement à deux échantillons par zone, pourrait jouer un rôle dans le faible nombre de différences significatives détectées pour le compartiment endofaunique. Aussi, la représentativité de ces deux échantillons pour chaque zone d'étude peut être discutable. Le nombre limité de données pour l'endofaune est attribuable au temps limité passé à bord, au substrat grossier rendant le travail avec la benne peu efficace et au traitement des échantillons en laboratoire (tri, identification) qui est particulièrement chronophage par rapport aux analyses photographiques. Malgré cela, cette étude démontre la pertinence d'utiliser deux méthodes d'échantillonnage en parallèle pour étudier deux différents compartiments biologiques. Cela peut être particulièrement intéressant dans le cas des relations avec l'environnement où les réponses endo- et épibenthiques peuvent différer. La distinction de l'endofaune et de l'épifaune est d'autant plus utile lorsque le sédiment est principalement composé de cailloux et de gravier grossier, comme c'était le cas sur les fonds marins du détroit de Lancaster, car des assemblages particuliers s'y retrouvent, combinant des espèces de substrat rocheux et de substrat meuble (Grebmeier *et al.*, 1995). Les forts pouvoirs explicatifs obtenus pour les relations endofaune-environnement démontrent que nos deux échantillons par zone ont pu tout de même donner une bonne représentation de l'influence des facteurs environnementaux. Cette particularité de notre étude, la distinction de l'épifaune et de l'endofaune, a permis une meilleure compréhension générale de l'écosystème benthique dans le détroit de Lancaster. Par contre, pour une caractérisation des communautés endofauniques plus juste et représentative, plus d'échantillons pourraient être collectés en vue de compléter l'état actuel des connaissances.

Lien entre le benthos et son environnement

Les analyses univariées et multivariées ont fourni deux approches statistiques différentes pour décrire les communautés benthiques et déterminer les facteurs structurant leurs assemblages. Tous types d'analyses confondus, la disponibilité des ressources alimentaires dont dépendent les organismes benthiques semble être un paramètre des plus déterminants. Plus spécifiquement trois indicateurs de nourriture ont été mis en évidence par nos analyses. (1) N'étant pas corrélée à une autre variable abiotique de la colonne d'eau (ex.: salinité, température) dans la présente étude, l'influence de la profondeur serait ici probablement liée à la force du couplage pélago-benthique et aux fluctuations de la qualité/quantité de nourriture. (2) La concentration de chlorophylle *a* de l'eau de fond était corrélée au nombre de taxons, positivement pour l'endofaune et négativement pour l'épifaune. Ces deux relations contraires témoignent des préférences différentes de ces deux compartiments biologiques quant aux apports de nourriture. (3) Le nombre annuel de jours sans glace recouvrant la zone, corrélé avec les autres variables calculées à partir d'informations satellitaires (PP, $[\text{Chl } a]_{\text{SAT}}$), a également eu des répercussions sur la structure de la communauté épibentique. Logiquement, une période sans glace plus étendue devrait permettre une production annuelle accrue de cellules phytoplanctoniques, ce qui pourraient influencer directement ou indirectement (*bottom-up*) les organismes benthiques en leur procurant une meilleure disponibilité de nourriture. Considérant l'importance de ces paramètres liés aux ressources alimentaires, les concentrations sédimentaires de pigments photosynthétiques et la quantité de carbone organique dans le sédiment pourraient jouer un rôle particulièrement décisif dans la structure des communautés du détroit de Lancaster, tel que démontré d’autres régions (Morata et Renaud, 2008 ; Roy *et al.*, 2014). Ces paramètres n'ont malheureusement pas pu être intégrés aux analyses statistiques de la présente étude en raison de données manquantes, de pseudo-réplication et du faible succès d'échantillonnage avec la benne.

En ce qui concerne le type de sédiment de surface, le pourcentage de recouvrement des sédiments grossiers a été associé au nombre de taxons de l'épifaune et à la densité totale de l'endofaune et de l'épifaune. Il était initialement prévu de sous-échantillonner le sédiment collecté par la benne pour obtenir la granulométrie des différentes zones d'étude, mais, en raison des difficultés rencontrées avec la benne, des pourcentages de recouvrement ont été déterminés visuellement en utilisant les photos de fond. Si les données sédimentaires utilisées provenaient des bennes, les relations observées entre le type de sédiment et les caractéristiques biologiques des communautés endobenthiques présenteraient probablement des pouvoirs explicatifs encore plus importants. Les courants de fond et les sédiments de surface étant étroitement liés en raison des processus de transports sédimentaires, la vitesse moyenne des courants de fond s'est aussi révélée importante. Les données qui furent utilisées dans cette étude sont issues de modélisation. Il serait pertinent de collecter des données *in situ* dans chaque zone échantillonnée pour comparer et compléter les informations de la base de données environnementales utilisée pour nos analyses.

Perspectives futures : Influence des colonies d’oiseaux

La présence de colonies d’oiseaux n’a pas largement influencé la structure des communautés benthiques selon les résultats des analyses univariées et multivariées présentés dans cette étude. Plusieurs hypothèses ont été formulées pour tenter d’expliquer les effets pratiquement inexistants de ces biovecteurs généralement importants dans les écosystèmes côtiers (Bildstein *et al.*, 1992; Polis *et al.*, 1997; Bosman et Hockey, 1986; Ellis *et al.*, 2006; Zmudczyńska-Skarbek *et al.*, 2013). De ces hypothèses découlent des perspectives de recherche qui pourront être explorées dans le futur. Tout d’abord, il serait particulièrement pertinent de tenter un échantillonnage à de plus faibles profondeurs. Les études existantes démontrant des effets d’enrichissement océanique engendrés par des oiseaux de mer sur le benthos ont toutes été menées à des profondeurs inférieures à 20 mètres (Palomo *et al.*, 1999; Kolb *et al.*, 2010; Signa *et al.*, 2015; Zmudczyńska-Skarbek *et al.*, 2015). Nous estimons que des zones d’échantillonnage plus côtières avec des profondeurs d’environ 50 mètres constitueraient un bon compromis entre ce qui a déjà été démontré et ce qui permettrait d’augmenter les possibilités de détecter les impacts des oiseaux marins sur les communautés benthiques. Dépendamment de la pente du fond océanique, un échantillonnage moins profond serait associé à des distances horizontales moins grandes entre les colonies et la position du navire lors des opérations, ce qui favoriserait également la détection d'impacts.

Bien que la couverture de glace limite l'acquisition de données annuelles de phytoplancton dans l'Arctique, le lien entre la présence de colonies d'oiseaux et la production primaire serait également à caractériser dans le détroit de Lancaster. Les techniques d'imagerie satellitaire constituent des outils adéquats pour suivre à distance les floraisons phytoplanctoniques dans l'Arctique. Les dynamiques de ces floraisons pourraient être étudiées de façon à déterminer si la présence ou la taille des colonies d'oiseaux se répercutent sur celles-ci. Les pistes de discussion de la présente étude ont aussi souligné l'importance potentielle des algues de glace dans la région d'étude. Ce groupe de producteurs primaires est certainement à considérer dans les éventuelles recherches sur le lien entre les oiseaux et la production primaire. De plus, les patrons d'exportation horizontaux et verticaux seraient à étudier pour plus adéquatement définir la zone touchée par l'apport de production primaire.

Puisque la disponibilité de nourriture occupe un rôle important dans l'explication de la structure des communautés benthiques de cette étude, nous avons également analysé les données transformées en fonction des différents modes alimentaires (données non présentées). De façon similaire à nos résultats basés sur les données de densité ou de biomasse, aucun effet de l'enrichissement des colonies d'oiseaux n'a été démontré lors de nos analyses effectuées sur ce trait fonctionnel. Un des rares inconvénients de l'analyse photographique est le faible niveau de précision taxonomique des données biologiques résultantes. L'identification effectuée sur les photos prises dans le détroit de Lancaster n'a pas permis, par exemple, de différencier les nombreuses familles d'ophiures qui peuvent présenter différents modes alimentaires (Piepenburg, 2000). De futures études sur les impacts des oiseaux ou de l'enrichissement organique en général pourraient se concentrer sur ce type de données, couplées à des données isotopiques, qui offrent des informations différentes sur la structure des communautés benthiques et sur la réponse de chaque groupe présentant un comportement alimentaire distinct.

Conclusion

L'importance de la présente étude réside dans le fait qu'elle s'intéresse au lien entre les colonies d'oiseaux marins et la structure des communautés benthiques, sujet de recherche qui n'est que très peu documenté et qui n'a jamais été étudié dans l'Arctique jusqu'à ce jour. De plus, cette étude contribue à la description des communautés benthiques de LSR qui est une région clé dans l'Arctique autant pour de nombreuses espèces que pour le trafic maritime et les compagnies pétrolières. Les résultats, formant un ensemble complet d'analyses univariées et multivariées, sont particulièrement novateurs car ils présentent séparément les deux compartiments biologiques du benthos, l'épifaune et l'endofaune.

Il a été démontré que la disponibilité en nourriture, le type de sédiment et la vitesse des courants de fond sont des paramètres plus importants que la présence des colonies d'oiseaux pour expliquer la structure des communautés benthiques à des profondeurs supérieures à 120 mètres dans LSR. Néanmoins, plusieurs autres tangentes de ce sujet de recherche, telles que celles détaillées dans cette section, doivent être abordées pour mieux comprendre l'impact potentiel de ces colonies sur le milieu marin et ses différentes composantes. Dans l'Arctique canadien, les écosystèmes terrestres et marins sont vraisemblablement voués à des changements significatifs dans le contexte des changements climatiques et de l'intensification des activités anthropiques. Pour efficacement prédire ces modifications et leurs répercussions, une meilleure compréhension de ces écosystèmes et des liens terre-mer qui les unissent est primordiale.

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