Benthic faunal assimilation pathways and depth-related changes in food-web structure across the Canadian Arctic

Virginie Roy [a,*], Katrin Iken [b], Michel Gosselin [a], Jean-Éric Tremblay [c], Simon Bélanger [d], Philippe Archambault [a]

[a] Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, 310 Allée des Ursulines, Rimouski, QC, Canada G5L 3A1
[b] School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
[c] Département de biologie, Québec-Océan, Takuvik, Université Laval, Québec, QC, Canada G1V 0A6
[d] Département de biologie, chimie et géographie, BORÉAS, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski, QC, Canada G5L 3A1

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ABSTRACT

Climate changes in the Arctic are expected to decrease the currently tight pelagic–benthic coupling, yet large-scale, regional understanding of the origin of food for benthic organisms across both biological productivity and depth gradients is still missing. The organic matter assimilation pathways of benthic organisms, along with food-web structure, were investigated at shelf and slope locations spanning 2000 km across the Canadian Arctic using stable carbon and nitrogen isotope analysis. Three potential food sources and over 75 benthic taxa belonging to four feeding guilds were analyzed, but the $\delta^{13}C$ end-members for the benthic food-webs could not be clearly discerned. While spatial patterns of $\delta^{13}C$ for pelagic particulate organic matter were linked to phytoplankton biomass at the time of sampling, sediment $\delta^{13}C$ values reflected the relative composition of terrestrial and marine organic matter. On average, benthic primary consumers were enriched in ^{13}C by 5 and 7‰ compared to the potential organic matter sources sampled in sediment and the water column, respectively. The $\delta^{13}C$ discrepancy between identified sources of organic matter and benthic organisms suggests that an uncharacterized food source provided a significant carbon source to these animals. We propose that the ^{13}C enrichment of benthic organisms may be largely caused by the assimilation of ice algae (which were not sampled in this study), particularly in regions of known high ice-algal standing stock such as Barrow Strait and Eclipse Sound. The $\delta^{15}N$ values of bottom-water particulate organic matter and of benthic primary consumers increased with depth due to greater degradation of the settling organic material. The $\delta^{15}N$ values of secondary consumers did not increase with depth, leading to a decrease of their trophic position compared with shallower regions and likely reflecting an increase in omnivory due to scarcity of prey at depth. This study emphasizes the potential importance of sea-ice algae as a carbon source for benthic communities in the Canadian Arctic and suggests that distinct food-web structures prevail over the shelf and slope.

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1. Introduction

Marine benthic shelf and slope ecosystems of the world's oceans rely mostly on the delivery of food produced in the euphotic zone. In polar environments, benthic communities can be sustained by direct sedimentation of sea-ice associated algae and phytoplankton cells and/or through the sinking of organic material processed by pelagic secondary consumers (e.g., fecal pellets, carcasses of animals; Piepenburg, 2005). Pelagic algal production represents the largest fraction of annual primary production in seasonally ice-covered Arctic seas with ice-algal production contributing only 3 to up to 30% (Carmack et al., 2006). The strength of pelagic–benthic coupling and the relative importance of these carbon sources in the diet of Arctic benthic communities are influenced by many environmental and ecological factors. For instance, when the release of ice algae is sudden or when phytoplankton blooms sink abruptly and pelagic grazers are scarce, the vertical export of particulate organic matter (POM) may be efficiently delivered to the benthos, especially over the shallow continental shelves that characterize the Arctic (Tremblay et al., 2006a). As water depth increases, however, benthic communities become subject to increased food limitation as the amount and quality of sinking POM through the water

* Corresponding author.
E-mail address: virginie.m.roy@gmail.com (V. Roy).

column is limited by processes in pelagic heterotrophic food webs (e.g., Mintenbeck et al., 2007; Smith et al., 2008; Bergmann et al., 2009). Despite high temporal variability in particle flux, the labile POM reaching the sediment of polar systems may be consumed upon deposition (Boetius et al., 2013) or may persist for a long time and thus provide a long-term sediment 'food bank' for the benthic communities (Mincks et al., 2005).

Pelagic–benthic coupling strength and its impact on benthic trophic structure is reasonably well understood for certain shallow shelf regions of the Arctic, such as the northern Bering and Chukchi seas (e.g., Dunton et al., 1989; Lovvorn et al., 2005; Iken et al., 2010; McTigue and Dunton, 2013) and the Barents Sea/ Svalbard Archipelago (e.g., Tamelander et al., 2006a; Søreide et al., 2013; Carroll et al., 2014), but less so for deep Arctic regions (Iken et al., 2005; Bergmann et al., 2009), the Beaufort Sea (Dunton et al., 2006) and the Canadian Archipelago. For the latter, which represents a substantial fraction of the total Arctic Ocean area, current knowledge of POM assimilation pathways in shelf and slope benthic ecosystems is rudimentary and limited to only two regional-scale studies of the Barrow Strait-Lancaster Sound area (Hobson and Welch, 1992) and the North Water (NOW) polynya (Hobson et al., 2002). In the face of a rapidly changing Arctic and anticipated impacts on the sympagic and pelagic primary production regimes and on benthic communities (Bluhm and Gradinger, 2008), there is a growing need to establish a large-scale reference baseline of the major organic carbon sources currently sustaining Canadian Arctic benthic communities. The highly diverse bathymetry, pelagic productivity regimes (i.e., oligotrophic vs. eutrophic) and relative proportion of sympagic vs. pelagic primary production that define the Canadian Arctic (Michel et al., 2006; Ardyna et al., 2011) make it an excellent area in which to explore spatial variability in benthic food-web responses.

To elucidate the pathways by which POM is biologically processed and passed on to higher trophic levels, it is useful to explore the functional role of different organismal groups in relation to their functional morphology or feeding mode. Since benthic primary consumers such as suspension and surface deposit feeders rely on different particle sizes (Mintenbeck et al., 2007 and references therein), and secondary consumers may express different predatory and omnivorous feeding habits (Thompson et al., 2007, 2009), their trophic responses along environmental gradients (e.g., marine primary production, depth) can be used to elucidate how environmental forcing of food supply acts on the composition and distribution of benthic communities. The ultimate carbon sources of consumers can be traced using carbon stable isotope ratios ($\delta^{13}C$) if they have distinct $\delta^{13}C$ signatures, since fractionation per trophic step (i.e., the consistent, stepwise enrichment exhibited by stable isotopes during biological processing) is small for carbon (0–1‰; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001; Post, 2002). For example, sea-ice algae are enriched in ^{13}C on average by 4–5‰ compared to phytoplankton (-20 to $-19‰$ vs. -25 to $-24‰$, respectively) (Hobson et al., 2002; Tamelander et al., 2006a; Carroll et al., 2014), so their distinctive $\delta^{13}C$ signatures may serve as a tracer of the main carbon sources in the tissues of consumers in seasonally ice-covered polar systems. Nitrogen stable isotope ratios ($\delta^{15}N$), on the other hand, are used to assess the mean trophic position of organisms in a food web because the enrichment step in ^{15}N between source and consumer is relatively large (3–4‰; Peterson and Fry, 1987; Vander Zanden and Rasmussen, 2001; Post, 2002).

The main objective of this study was to investigate POM assimilation pathways for different benthic primary and secondary consumer guilds, and to assess if and how their carbon and nitrogen stable isotope compositions and food-web structure vary spatially across marine productivity and depth regimes of the Canadian Arctic. We specifically addressed the following research questions. (1) Is the spatial variability in the isotopic signatures of the potential food sources and trophic guilds driven by the same environmental variables? (2) Are the carbon signatures of benthic primary consumers similar to those of the food sources that were available at the time of sampling? (3) Does the nitrogen isotopic signature of different trophic guilds respond to depth, therefore reflecting a change in food-web structure? We hypothesized that (i) stable isotope variability in food sources is driven by different environmental factors than variability in trophic guilds, (ii) the carbon signatures of benthic primary consumers are similar to those of the food sources that were available at the time of sampling, and (iii) a depth-stratified approach is required to study food-web structure across the depth gradient of the study area since we expect $\delta^{15}N$ signatures of trophic guilds to vary with depth.

2. Materials and methods

2.1. Study area

This study was conducted across the Canadian Arctic from the southeastern Beaufort Sea in the west (129°W) to Baffin Bay in the east (70°W), including stations throughout the Archipelago (Fig. 1). The Beaufort Sea and Amundsen Gulf regions in the western study region are highly influenced by the Mackenzie River that drains a 1.7×10^6 km^2 watershed and discharges approximately 340 km^3 y^{-1} of freshwaters (McLaughlin et al., 2004) and 127×10^6 Mt y^{-1} of sediment (Macdonald et al., 2004) into the Beaufort Sea. Two main water masses are layered throughout the Canadian Arctic, with the warmer-saline Atlantic-origin waters on the bottom of the region (on average > 200 m depth) and the colder-fresher Pacific-origin waters directly above (on average < 200 m depth) (McLaughlin et al., 2004). The complex topography of the Archipelago with its numerous islands and channels has a profound influence on sea-ice dynamics and marine biological productivity. During winter the study area is ice-covered and sea ice could be found throughout the summer as landfast ice or first-year and multiyear pack ice (Howell et al., 2009; Environment Canada, 2010). Summer sea-ice distribution along with ice break-up and freeze-up dates exhibit large inter-annual variations (Howell et al., 2009; Environment Canada, 2010). Following a general trend, ice stays longer in summer in the central part of the Canadian Arctic Archipelago than in western and eastern parts where large, latent-heat polynyas open in spring, such as the North Water (NOW), Lancaster Sound–Bylot Island (LS–BI), and the Cape Bathurst (CB) polynyas (Michel et al., 2006; Howell et al., 2008; Fig. 1). Accordingly, field-based and satellite-derived pelagic primary production estimates (PP) are higher in NOW, LS–BI and CB polynyas than in the central part of the Canadian Arctic Archipelago (Ardyna et al., 2011; Bélanger et al., 2013). The study area was divided into three geographical regions (west, center and east; Fig. 1) in order to test for the effects of spatial gradients in ice trends and primary productivity on benthic communities.

2.2. Field sampling

A total of 19 stations was sampled between August and October 2011 onboard the Canadian research icebreaker CCGS *Amundsen* (Fig. 1; Table 1). Two stations were sampled both in August and October to assess seasonal variability in stable isotope composition (stations C.312AB and C.314AB, Fig. 1). Sampling station depths ranged from 35 to 789 m. For analysis purposes, stations were split in two depth categories (shelf < 200 m: $n=8$, and slope ≥ 200 m: $n=11$) with the shelf break assumed to be around 200 m (O'Brien et al., 2006; Spalding et al., 2007) (Fig. 1).