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**Food source diversity, trophic plasticity, and omnivory enhance the stability of a shallow benthic food web from a high-Arctic fjord exposed to freshwater inputs**

Guillaume Bridier,1* Frédéric Olivier,2 Laurent Chauvaud,1 Mikael K. Sejr,3,4 Jacques Grall,1,5

1Laboratoire des Sciences de l’Environnement Marin (LEMAR) UMR 6539 UBO/CNRS/IRD/Ifremer, Plouzane, France
2Biologie des Organismes et Écosystèmes Aquatiques (BOREA) UMR 7208 MNHN/SU/UNICAEN/UA/CNRS/IRD, Paris, France
3Arctic Research Centre, Aarhus University, Aarhus, Denmark
4Department of BioScience, Aarhus University, Silkeborg, Denmark
5Observatoire Marin, UMS 3113, Institut Universitaire Européen de la Mer, Plouzané, France

**Abstract**

Under climate change, many Arctic coastal ecosystems receive increasing amounts of freshwater, with ecological consequences that remain poorly understood. In this study, we investigated how freshwater inputs may affect the small-scale structure of benthic food webs in a low-production high-Arctic fjord (Young Sound, NE Greenland). We seasonally sampled benthic invertebrates from two stations receiving contrasting freshwater inputs: an inner station exposed to turbid and nutrient-depleted freshwater flows and an outer station exposed to lower terrestrial influences. Benthic food web structure was described using a stable isotope approach ($\delta^{13}$C and $\delta^{15}$N), Bayesian models, and community-wide metrics. The results revealed the spatially and temporally homogeneous structure of the benthic food web, characterized by high trophic diversity (i.e., a wide community isotopic niche). Such temporal stability and spatial homogeneity mirrors the high degree of trophic plasticity and omnivory of benthic consumers that allows the maintenance of several carbon pathways through the food web despite different food availability. Furthermore, potential large inputs of shelf organic matter together with local benthic primary production (i.e., macroalgae and presumably microphytobenthos) may considerably increase the stability of the benthic food web by providing alternative food sources to locally runoff-impacted pelagic primary production. Future studies should assess beyond which threshold limit a larger increase in freshwater inputs might cancel out these stability factors and lead to marked changes in Arctic benthic ecosystems.

Arctic ecosystems are experiencing strong modifications of abiotic conditions under climate change, including increasing water temperatures and decreasing sea-ice coverage (AMAP 2017). In addition, freshwater inputs to the coastal domain are currently increasing in most locations along the Arctic coastline (Haine et al. 2015; Sejr et al. 2017). The impacts of such inputs on marine systems can be complex and influenced by numerous factors such as the freshwater origin (e.g., marine vs. land-terminating glacier) and local topography (e.g., absence/presence of a sill in fjords; Hopwood et al. 2020). Consequences of increased freshwater on the pelagic compartment include modifications of primary production, water column stratification, turbidity, and nutrient concentrations, but also of organic matter quality (Meire et al. 2017; Paulsen et al. 2017; Bridier et al. 2019), with subsequent impact on food webs (Middelbo et al. 2018).

Surprisingly, impacts on benthic ecosystems have received less attention, with studies mainly focusing on the disturbance generated by high sedimentation close to marine glaciers (e.g., sediment instabilities, bivalve gill clogging, etc.) that may impoverish the specific and functional richness of benthic communities (Sejr et al. 2010; Wródska-Kowalczuk et al. 2019). Some food-web studies have revealed significant contributions of terrestrial organic matter to the diet of benthic organisms, but they have mainly concerned large hydrological systems (e.g., Mackenzie River) over very large spatial scales (i.e., >100 km; Bell et al. 2016). By contrast, fjords and coastal subtidal habitats have been less investigated, although they should be the first to be affected by freshwater inputs (i.e., fjords’ water masses are more confined and surrounded by land than are shelf water masses). Because benthic organisms are essential for the functioning of marine ecosystems (e.g., through carbon and nutrient cycling, and benthic

*Correspondence: guillaume.bridier@univ-brest.fr

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pelagic coupling; Griffiths et al. 2017) and are key resources
for several marine mammal and seabird species
(e.g., Grebmeier et al. 2006), understanding the consequences
e of environmental changes for benthic food webs should be
improved to enable accurate predictions of marine ecosystem
responses to climate change.

In this study, we aimed to understand the effects of local
freshwater inputs on the functioning of a high-Arctic fjord by
investigating carbon pathways through the benthic food web.
For this purpose, we compared stable isotope signatures from
benthic organisms and organic matter sources, using \( \delta^{13}C \) and
\( \delta^{15}N \) measurements from two stations distributed along a gra-
dient of freshwater inputs (controlling other environmental
factors, e.g., turbidity, nutrient depletion, and organic matter
quality; Meire et al. 2017; Paulsen et al. 2017; Bridier et al. 2019).
Ecological studies using stable isotopes have been widely
used to trace transfers of organic matter within benthic
communities (e.g., Abrantes et al. 2014). Numerous studies
have shown the ability of stable isotope mixing models and
trophic position models to quantify the relative importance of
production originating from various origin and to better
understand feeding strategies of benthic invertebrates
(e.g., McTigue and Dunton 2017; Michel et al. 2019). In addition,
several authors recently suggested that the bivariate \( \delta^{13}C – \delta^{15}N \) isotope space (\( \delta \)-space) filled by a community accurately
depicts its isotopic niche (Layman et al. 2007; Jackson
et al. 2011). Several metrics describing such isotopic niches
(e.g., area, dimensions, and shape of the \( \delta \)-space) were then
developed to assess food-web complexity/stability and to deter-
mine the diversity of organic matter sources fueling a
community (Layman et al. 2007; Jackson et al. 2011; Reid
et al. 2016).

Such advanced approaches have widely shown their ability
to describe the functioning of benthic ecosystems exposed to
high environmental pressures (e.g., flood events; Abrantes
et al. 2014) by tracking changes in organic matter pathways
within communities over time and space. However, these
methods are still rarely used in polar areas (but see Wlodarska-
metrics and stable isotope mixing/trophic position models, we
investigated the small-scale variability (i.e., inner vs. outer
fjord communities) of benthic food-web structures from a
high-Arctic fjord exposed to freshwater inputs. Through this
comparison, our goal is to better understand the effects of
freshwater inputs on Arctic benthic food webs and to identify
the drivers of community resilience and stability in the face of
ongoing climate change.

Materials and methods
Study site and sampling stations
We conducted our study in Young Sound, a high-Arctic
fjord of NE Greenland (Fig. 1). This fjord ranks among the
least-productive coastal ecosystems in the world (pelagic pri-
mary production ~ 10 g C m\(^{-2}\) yr\(^{-1}\); Rysgaard et al. 1999) due
to prolonged sea-ice cover (9–10 months per year; Rysgaard
et al. 1999) and seasonal stratification generated by strong riv-
erine inputs (Holding et al. 2019). This low production is
partly compensated by high benthic primary production in its
shallow coastal areas (i.e., < 30 m) which exceed from 2 to
7 times local phytoplankton production and accounts for
20–40% of the whole outer fjord primary production (Glud
et al. 2002; Krause-Jensen et al. 2007; Attard et al. 2016). On the
other hand, ice-algae contribute only marginally
(i.e., < 1%) to the overall Young Sound primary production,
mainly as a result of high snow cover and low seawater salin-
ity directly under sea-ice (Glud et al. 2002; Limoges
et al. 2018).

Two shallow stations (i.e., depth range = 10–30 m) were
prospected: (1) an inner station (74°24’36”N–20°19’48”W, sur-
veyed in May 2017 and August 2018), close to the Zackenberg
River (river discharge = 0.15–0.25 km\(^3\) yr\(^{-1}\); Citterio
et al. 2017), and (2) an outer station (74°12’36”N–20°6’36”W,
surveyed in May and August 2018), situated at the fjord
mouth. These two localities were selected because of contra-
sted exposure to freshwater inputs associated to an inner/out-
fjord gradient in physical and chemical conditions. Consider-
able freshwater inputs in Young Sound innermost areas (rang-
ing from 0.9 to 1.4 km\(^3\) yr\(^{-1}\); Bendtsen et al. 2014) generate
strong spatial variations in surficial water salinity, ranging
from 8 in the innermost part of the fjord to 30 in the outer-
most part (Rysgaard et al. 2003; Bendtsen et al. 2014). More-
over, the inner station is located at the direct vicinity
(i.e., ~ 500–750 m) of several small deltas and it receives addi-
tional inputs in freshwater and sediment while no deltas were
reported close to the outer station (Kroon et al. 2017). These
contrasted exposure of inner and outer stations to freshwater
inputs and inert particles explain the observed differences in
sediment grain-size distributions between both sites. Pro-
portion of pelites (particles < 63 μm) in the sediment is three-fold
higher at the inner (i.e., 69.2%) than the outer station
(i.e., 21.7%, see Fig. S1, Supplementary Information), reflecting very contrasting loadings of terrestrial material
between these two coastal areas.

This freshwater input gradient leads to contrasting environ-
mental conditions between inner and outer stations. Stronger
stratification at the inner station reduces the size of phyto-
plankton cells (Holding et al. 2019), with potential subsequent
impact on marine primary consumers (Middelbo et al. 2018).
Higher input of terrestrial material and nutrient depletion at
the inner station (Paulsen et al. 2017) is also reported to lessen
the quality of the organic matter (Bridier et al. 2019). Finally,
a two-fold lower pelagic primary production has been
recorded at the inner station compared to the outer station
because of the negative impacts of freshwater inputs on inner
fjord turbidity and nutrient concentrations (Meire et al. 2017).
Benthic consumers were sampled using a triangular dredge (1 mm mesh size, August 2018) or a suction dredge (1 mm mesh size) operated by scuba divers (May 2017 and 2018). All entire individuals were collected for stable isotope analyses in order to meet species diversity requirements for isotopic diversity indices (i.e., \( n > 20 \) species; Brind’Amour and Dubois 2013). Number of replicates varied from 1 to 9 individuals per benthic species. Three potential food sources were sampled in our study: particulate organic matter (POM), sedimentary organic matter (SOM) and terrestrial organic matter (TOM). Bottom POM samples were collected on each site at 1 m above the seabed by using a 10 liter Niskin bottle (May 2017 and August 2018). Scuba divers collected SOM samples by aspirating the first 1–5 mm of the sediment surface delimited in a 25 × 25 cm (i.e., 625 cm²) quadrat with a 450 ml syringe (August 2016). Finally, TOM samples were taken in August 2018 upstream of the Zackenberg River delta (74°28'14.3"N, 20°34'47.4"W, salinity = 0.38) using 10 liter bottles. Sampling replication varied from 3 to 6 samples per food source. Water and sedimentary samples were then filtered on precombusted (5 h at 400°C) GF/F filters (pore size = 0.07 μm) until clogging (for further details, see Bridier et al. 2019). In addition, we used the stable isotope signatures of Fucus sp. and Saccharina latissima measured by De Cesare et al. (2017). All samples were stored at −80°C before laboratory analyses.

Laboratory analyses

Stable isotope analyses (δ\(^{13}\)C and δ\(^{15}\)N) were performed on either one or a pool of complete individuals (guts apart) and muscle tissues from large species (e.g., shrimp, fish; Supplementary Information, Table S1). Animal tissues were freeze-dried for at least 48 h at −50°C and ground to a fine powder in a ball mill (cycles of 10 min at 30 Hz). Half of the carbonate-rich tissues were acidified with hydrochloric acid (10% HCl) for carbon isotope analyses to prevent the bias.
induced by inorganic carbon in $\delta^{13}C$ signatures while the other half remained untreated for nitrogen isotope analyses to avoid acidification bias in $\delta^{15}N$ values (Jacob et al. 2005). Samples were not lipid-extracted, due to the usually low lipid content in Arctic benthic invertebrates (Clarke and Peck 1991) and to avoid potential bias in $\delta^{15}N$ values (Post et al. 2007). No mathematical lipid corrections were done because the large variability of $\delta^{13}C$ lipid bulk signatures among Arctic species makes questionable the use of generalized mathematical equations based on a constant lipid $\delta^{13}C$ value (Mohan et al. 2016).

All stable isotope analyses were performed at the University of California, Davis (UC Davis Stable Isotope Facility, Department of Plant Sciences, CA). Stable isotope measurements were realized with a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer (Sercon, UK). Sample stable isotope ratios were expressed in relation to stable isotope ratios from Vienna Pee Dee Belemnite ($\delta^{13}C$) and atmospheric nitrogen ($\delta^{15}N$), based on following the equation: $\delta X = \frac{[(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000}{R_{\text{sample}}}$, where $X$ is the $\delta^{13}C$ or $\delta^{15}N$ value of the analyzed sample and $R$ the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ molar ratio (Peterson and Fry 1987). Standard deviations of stable isotope measurements were estimated to $\pm 0.2$ for $\delta^{13}C$ and $\pm 0.3$ for $\delta^{15}N$, based on replicated measurements of international standards (run every 15th sample) from the International Atomic Energy Agency (IAEA600) and the United States Geological Survey (USGS40, USGS41, USGS62, and USGS65).

Data analyses

Community convex hulls (areas compassing all the data) and standard ellipses (95% confidence ellipses compassing 40% of the data) were plotted in a $\delta$-space to visualize isotopic niches. Potential shifts on the $\delta^{13}C$ or $\delta^{15}N$ axis between community isotopic niches were investigated by computing the overlap between inner and outer standard ellipses (i.e., the percentage shared by two communities in relation to the smallest ellipse). Community trophic niche widths were assessed by calculating the standard ellipse area and mean distance to centroid (i.e., the mean distance of each species to the $\delta^{13}C$–$\delta^{15}N$ centroid) metrics (Layman et al. 2007; Jackson et al. 2011). Standard ellipses’ eccentricities were also calculated to compare the shapes of isotopic niches (e.g., a lower eccentricity would highlight a narrower community ellipse range on the $\delta^{13}C$ axis; Reid et al. 2016).

The horizontal structure of benthic food webs was described using Bayesian stable isotope mixing models performed on primary consumer stable isotope signatures to assess the diversity and importance of organic matter sources fueling benthic invertebrates (Parnell et al. 2013). Mixing models were calculated using the simmr package (Parnell 2019) to include the variability of consumer and endmember stable isotope signatures as well as the uncertainty in trophic enrichment factors (TEFs) for diet estimates (Parnell et al. 2013). Although $\delta^{13}C$ TEFs are considered to be similar between primary consumers and carnivores (Post 2002; McCutchan et al. 2003), they are known to be highly variable (e.g., ranging from $\sim 0$ to $\sim 4\%$o) among species from a same guild, depending on animal physiology and/or food source quality (e.g., Caut et al. 2009). In order to integer such variability, we used an intermediate $\delta^{13}C$ TEF with a high level of uncertainty (i.e., $2 \pm 2\%$o) which considers that $\delta^{13}C$ fractionation can potentially be very low (e.g., $0\%$o) or very high (e.g., $4\%$o) for some species. Mixing models used Post’s TEF for $\delta^{15}N$ signatures (i.e., $3.4 \pm 1.0\%$o). Stable isotope signatures of POM and SOM sources as well as those of Fucus sp. and S. latissima were combined a posteriori into two unique sources (i.e., ‘POM/SOM’ and ‘Benthic sources’, respectively) because of their close isotopic compositions (Phillips et al. 2014).

Vertical structure was studied using a trophic position model (Quezada-Romegialli et al. 2018) to assess the degree of omnivory in food webs by comparing the trophic positions of consumers in relation to their putative food sources. Trophic positions were calculated using two baseline (i.e., POM/SOM and macroalgae (i.e., Fucus sp. and S. latissima)) Bayesian models from the TrophicPosition package (Quezada-Romegialli et al. 2019) based on the following equations from Quezada-Romegialli et al. (2018):

$$\delta^{15}N_{C} = \Delta N(TP + \lambda) + \alpha(\delta^{15}N_{b1} + \delta^{15}N_{b2}) - \delta^{15}N_{b2}$$

and

$$\alpha = \frac{\delta^{13}C_{b2} - (\delta^{13}C_{c} + \Delta C)}{TP - \lambda}$$

where $\delta^{15}N_{C}$, $\delta^{15}N_{b1}$, and $\delta^{15}N_{b2}$ refer to the $\delta^{15}N$ values of consumers, first and second baselines, respectively; $\delta^{13}C_{C}$, $\delta^{13}C_{b1}$, and $\delta^{13}C_{b2}$ are the $\delta^{13}C$ values of consumers, first and second baselines, respectively; $\Delta N$ refer to the TEF for nitrogen (i.e., $3.4 \pm 1\%$); $\Delta C$ is the TEF for carbon (i.e., $2 \pm 2\%$); TP is the consumer’s trophic position and $\lambda$ is the baseline’s trophic position.

Standard ellipse area credibility intervals were calculated on species mean isotope signatures through a Bayesian approach using 200,000 posterior iterations. Standard Ellipses Areas without overlap of their 95% credibility intervals were considered significantly different. Unfortunately, this Bayesian approach could not be applied to estimate mean distance to centroid and ellipse eccentricity credibility intervals because these calculations are based on both intra-group (i.e., dispersion between replicates of a single species) and inter-group (i.e., dispersion among species; Jackson et al. 2011) variability and several species had no replicates. Bayesian mixing and trophic position models were performed only on August samples as replication for May samples was too low. Stable isotope signatures of the main abundant
Isotopic niches of outer and inner communities

Isotopic niches of the inner and outer communities were highly similar in both seasons as reflected by their high overlap (74.8% and 77.5% during winter and summer, respectively; Fig. 3a,b). Such seasonal stability and spatial homogeneity of Young Sound food webs is confirmed by the absence of significant differences in standard ellipse areas between both stations and seasons (p > 0.05, see credibility interval overlaps in Supplementary Information, Fig. S2). Although no statistical analyses could be performed on the Layman metrics (mean distance to centroid and eccentricity) due to the absence of replication for several species (i.e., n < 5), the absence of strong variations between seasons and stations suggests no major seasonal or spatial differences of food web structures occurred (Table 1).

Benthic food web horizontal structure

Outputs from our mixing models highlighted a low/insignificant contribution of TOM for all primary consumers, except perhaps for the isopod Arcturus bafinii, Ascidiae and Pectinaria hyperborea which were characterized by large variation in its credibility intervals (Fig. 4). The contribution of other organic matter sources was variable among
primary consumers. Several species considered here as suspension (i.e., *A. baffinii*, *Astarte moerchi*, *Astarte elliptica*, *Balanus* sp., *Hiattella arctica*) or deposit (i.e., *Margarites coastalis*, *P. hyperborea*) feeders appeared to feed in significant proportion on benthic sources (from 18.9% for *Balanus* sp. to 47.4% for *A. moerchi*, modes of the posterior probability distributions), while for other species its contribution remained low (10.4–14.0%, Fig. 4). Aggregated POM and SOM sources showed large contributions for all species (from 43.3% for *A. elliptica* to 85.4% for *Ophiocoma sericeum*, modes of the posterior probability distributions).

### Benthic food web vertical structure

Consumer trophic positions calculated using two-baseline Bayesian models (based on POM and SOM baselines, according to mixing model outputs) were highly variable among species (Fig. 5). The mean trophic position of primary consumers (i.e., suspension and deposit feeders) ranged from 1.7 for *Atylus carinatus* and *Balanus* sp. to 2.6 for *P. hyperborea*, while for predatory/scavenging consumers (combined together as “carnivores”) it ranged from 2.3 for *Metopa glacialis* to 3.8 for *Argis dentata* (Fig. 5). Credibility intervals varied overall over large ranges, exceeding in some cases the extent of one trophic level (e.g., *Colus* sp., *Icelus bicornis*, *P. hyperborea*, Fig. 5).

The modal trophic positions of all primary consumers, except for the crustaceans *A. carinatus* and *Balanus* sp., were higher than 2, with significant values for *A. baffinii*, Ascidiaeae, and *O. sericeum* only (Fig. 5). The modal trophic positions of four taxa initially considered as primary consumers (*A. elliptica*, Ascidiaeae, *A. baffinii*, *P. hyperborea*) were higher than the lowest value of a secondary consumer (*M. glacialis*). In contrast, modal trophic positions of five other species initially considered as secondary consumers (*Colus* sp., *M. glacialis*, *Nereis* sp., *Nymphon hirtipes*, *Ophiura robusta*) were lower than 3 (Fig. 5). Finally, all primary consumers’ credibility intervals overlapped with those of one or several secondary consumers, except for *A. carinatus* (Fig. 5).

### Discussion

**Temporal and spatial variability of the benthic food web**

Although Young Sound experiences an extreme seasonality (Rysgaard et al. 1999; Rysgaard and Nielsen 2006) and strong spatial gradients associated to freshwater inputs (Fig. 2; Meire et al. 2017; Paulsen et al. 2017; Holding et al. 2019), in the present study we did not observe any spatiotemporal variations in the benthic food-web structures. Such similarity between inner and outer standard ellipse areas and positions on the δ¹³C axis (reflected by high standard ellipse area overlaps) suggests that both communities are based mostly on the same organic matter sources. Moreover, high mean distance to centroid and eccentricity values in the inner and outer communities indicate that both trophic webs are based on several...
**Fig. 4.** Boxplots representing relative contributions of benthic sources (left), combined particulate organic matter and sedimentary organic matter sources (middle), and terrestrial organic matter (right) to the diet of main primary consumers. The center line, boxes, and error bars represent the modes and 50% and 95% credibility intervals based on posterior probability distributions, respectively. Outliers were omitted for clarity. POM: particulate organic matter; SOM: sedimentary organic matter.

**Fig. 5.** Modal trophic positions of main primary (blue circles) and secondary/tertiary consumers (red circles) with their associated 95% credibility intervals based on posterior probability distributions.
organic matter sources (Layman et al. 2007). Although these metrics might be highly sensitive to sampling effort, all standard ellipse areas had a sample size sufficient to avoid such potential bias (i.e., \(n > 20\), Brind’Amour and Dubois 2013).

The absence of temporal variability in the benthic food webs despite strong seasonal variation of POM and SOM baselines (Fig. 3a,b) and changes in food source availability (Brider et al. 2019) may appear surprising. Indeed, several works on Arctic food webs previously highlighted similar temporal stabilities that authors partly explained by the moderate seasonality of systems that were characterized by multiple pulses of fresh organic matter per year (e.g., Renaud et al. 2011). Considering the extreme seasonality of primary production in Young Sound (i.e., limited to 2–4 months per year; Rysgaard et al. 1999; Holding et al. 2019), there is no evidence for regular input of fresh organic matter in this fjord.

We rather hypothesize that the temporal stability reflects the low tissue-turnover rates (expected to range from 8 months to more than 1 year) observed in Arctic benthic invertebrates, which display long lifespan and slow growth (Kaufman et al. 2008; Weens et al. 2012; McMeans et al. 2015). As a consequence, isotope signatures of benthic invertebrates would reflect environmental conditions over the year rather than during one particular season.

Despite strong environmental gradients, which vary at a seasonal scale, we also did not detect any spatial variation in the benthic food webs in Young Sound. Although the sampled stations in this study cover only a part of the fjord’s length, significant gradients of salinity (Paulsen et al. 2017; Sejr et al. 2017), organic matter quality (Brider et al. 2019), and primary production (Meire et al. 2017) have been reported between the same stations. In a similar spatial and salinity gradient of Hornsund (Svalbard), Wlodarska-Kowalczuk et al. (2019) highlighted a clear \(\delta^{13}C\) shift between benthic food webs of inner and outer fjords, which they attributed to different relative contributions of various organic matter sources. The absence of such a trend in Young Sound may signify that the organic matter pool fueling inner and outer communities is minimally affected by environmental gradients.

Considering that the inner and outer communities displayed similar general functioning, we consider that their related consumers should be in fact part of a single benthic food web. We will discuss below the potential origins of this spatial homogeneity that exists despite strong gradients in freshwater inputs.

**Importance of the diversity of food sources on benthic food web stability**

Based on the horizontal structure of the benthic food web (which extends over 79‰ on the \(\delta^{13}C\) axis) and the high standard ellipse area values coupled to low eccentricity metrics, we conclude that primary consumers feed on several organic matter sources (Layman et al. 2007; Reid et al. 2016). We then hypothesize that some of these food sources may support the resilience of benthic food webs in shallow habitats facing high freshwater inputs and low pelagic primary production.

Contrary to several food-web studies conducted in shallow Arctic areas (e.g., Harris et al. 2018), we did not detect significant contributions of TOM to the diet of primary consumers in the Young Sound fjord. Although stable isotope signatures of terrestrial material may be modified by bacteria, \(\delta^{15}N\) signatures of TOM (\(\sim 2.2\%o\)) appear too depleted to reach the \(\delta^{15}N\) signatures of marine POM and SOM, even after bacterial degradation (Lehmann et al. 2002). Several hypotheses can be proposed to explain such opposite results. The first and simplest would be that we have failed to collect species feeding massively on TOM. However, while the highest reliance on terrestrial material is usually shown by sub-surface deposit feeders (e.g., Orbinidae, Maldanidae; Harris et al. 2018; McGovern et al. 2020), these species exhibited relatively enriched \(\delta^{13}C\) signatures in the present study (Supplementary Information, Table S1) leading us to reject this hypothesis.

Second, both the outer and inner sampling stations could be located too far out of the zone of influence of the Zackenberg River delta to receive significant contributions of TOM. But that is not the case for the inner station, located \(\sim 5\) km from the delta, where Brider et al. (2019) detected a significant influence of terrestrial material inputs. Therefore, we hypothesize that such opposite results might reflect differences in the quality and quantity of TOM inputs across Arctic regions.

Indeed, soils from Scandinavia, Siberia or Canada/Alaska contain much more organic carbon than soils from Greenland (i.e., 100–260 vs. <30 kg m\(^{-2}\), respectively; Parmentier et al. 2017). Moreover, Siberian and Alaskan rivers usually flow through permafrost areas covered with abundant vegetation (Walker et al. 2005) while most of the Young Sound river inputs are from glacial meltwater flowing on rocky sediment basin bare from any vegetation (Bendtsen et al. 2014; Paulsen et al. 2017). These geographical features are likely to reduce the quantity and quality of TOM inputs in Young Sound and may thus explain the poor assimilation of this food source in the benthic food web. Contrary to previous shallow food-web studies (e.g., Harris et al. 2018), this negligible contribution of TOM to the benthic food web implies that the negative impact of freshwater inputs on the Young Sound POM quality and availability cannot be balanced by local additional contribution from terrestrial materials.

In contrast, benthic primary consumers fed substantially on the POM/SOM pool. Although carbon stable isotope signatures usually provide a powerful tool to discriminate organic matter sources in marine ecosystems, POM and SOM sources measured in this study were weakly discriminated which precluded the evaluation of their respective contribution to the benthic food web. Such stable isotope signatures overlap probably reflects strong resuspension of sedimentary materials toward the overlying bottom waters (i.e., 1 m above the seafloor). The relatively low degradation of settled particles in polar ecosystems usually leads to the accumulation of a
persistent sediment food bank of labile detritus (Smith et al. 2006; Mincks et al. 2008). The re-suspension of these labile detritus (through bottom currents or bioturbation) has a considerable importance for arctic benthic food webs facing periods of low food availability by providing an alternative food source for suspension feeders (Smith et al. 2006; Włodarska-Kowalczuk et al. 2019). We hypothesize that such resuspension events in Young Sound might thus partly increase the temporal stability and spatial homogeneity of the benthic food web in the face of strong spatiotemporal variations in primary production and organic matter quality (Meire et al. 2017; Bridier et al. 2019).

Finally, benthic sources (i.e., *Fucus* sp. and *S. latissima*) appear to constitute an additional major source of organic matter for biomass dominating primary consumers (e.g., *A. elliptica*, *H. arctica*, *M. coastalis*). Such contribution is in line with in situ measurements of seabed primary production that revealed substantial production of benthic micro- and macroalgae (2–7 times higher compared with phytoplankton production above 30 m; Glud et al. 2002; Krause-Jensen et al. 2007; Attard et al. 2016). Macroalgae account for the main part of the benthic primary production (Glud et al. 2002; Rysgaard & Glud 2007), mainly through the production of three species (i.e., *Desmarestia aculeata*, *Fucus* sp. and *S. latissima*) together representing more than 90% of the overall macroalgal production (Glud et al. 2002; Krause-Jensen et al. 2007). However, it appears that *Desmarestia aculeata* is unlikely to be a major source of organic matter for the benthic food web because of its poor palatability for benthic invertebrates (e.g., Wessels et al. 2006). In contrast, numerous studies showed that both *Fucus* sp. and *S. latissima* productions are able to provide a considerable part of food web carbon requirements of arctic shallow benthic ecosystems (Renaud et al. 2015; Gaillard et al. 2017). These two macroalgae might thus offer essential alternative food sources to the Young Sound benthic food web in a context of low pelagic primary production.

Benthic macroalgae represent also a non-negligible part of the benthic primary production in Young Sound (i.e., 16% of the overall outer fjord primary production; Glud et al. 2002). These benthic macroalgae are often far neglected in arctic food webs studies, notably because of the great difficulties to obtain accurate isotopic signature in arctic for these primary producers (McTigue and Dunton 2017). Both benthic micro- and macroalgae isotope signatures are known to be $^{13}$C-enriched compared to those from pelagic organic matter sources (France 1995). In the case of Young Sound, we cannot exclude that a part of the enriched $^{13}$C signal in several benthic invertebrates (e.g., *A. elliptica*, *M. coastalis*, *H. arctica*) could also reflect the assimilation of such benthic microalgae as a food source. While enriched-$^{13}$C ice algae would also theoretically constitute an additional potential food source, their extremely low production in Young Sound (i.e., 0.0% of the overall outer fjord primary production; Glud et al. 2002) seems obviously too weak to drive such $^{13}$C enrichment in several biomass-dominant consumers (e.g., *A. moerchi*, *H. arctica*; Sejr et al. 2000).

Overall, the horizontal structure of the food web suggests a significant contribution of carbon of benthic origin to the diet of primary consumers (i.e., species from Fig. 4 fed in average at 25.2% on benthic sources), in accord with what has been reported from other Arctic locations (e.g., Dunton and Schell 1987; Renaud et al. 2015). This finding is also consistent with two annual carbon budgets showing that Young Sound is a net heterotrophic fjord (Rysgaard and Nielsen 2006; Glud and Rysgaard 2007). In this ecosystem, local pelagic primary production provides a minor part of food-web carbon requirements, which are balanced by additional supplies of local benthic primary production and allochthonous inputs from the shelf (both providing ~3 times more organic carbon than local primary production; Glud and Rysgaard 2007). Although this study is not able to distinguish relative contributions from local (i.e., fjord) and shelf primary production to the POM pools, these results suggest that a major part of POM/SOM contributions in primary consumers would actually be related to an assimilation of shelf primary production. Such dominant contributions of both benthic primary production and allochthonous organic matter to the benthic food web would actually signify that both food sources are less impacted by freshwater inputs than are the phytoplankton.

For instance, benthic primary production is not as directly impacted by inputs of turbid and nutrient-depleted freshwaters as pelagic primary production. Benthic primary producers are usually more adapted to nutrient depletion because of the direct access of benthic microalgae to the nutrients released from sediments (MacIntyre et al. 1996) and the relatively low nutrient requirements of perennial macroalgae (Pedersen and Borum 1996). Such adaptations are reflected by the balance of pelagic and benthic primary production by nutrient regimes of shallow coastal ecosystems. Oligotrophic systems generally promote benthic primary production over pelagic primary production, while eutrophic settings favor the dominance of phytoplankton at the expense of benthic micro- and macroalgae (Duarte 1995; Glud et al. 2009). Therefore, we believe that nutrient depletion could affect benthic primary producers to a lesser degree than pelagic producers, which would in turn display homogeneous production along our spatial gradient.

Whereas it may be argued that freshwater inputs impact pelagic and benthic primary production through increased turbidity and sedimentation, several studies have shown that pelagic and benthic primary producers are both well adapted to low-light conditions in Young Sound (Glud et al. 2002; Krause-Jensen et al. 2007; Holding et al. 2019). Similarly, although strong sedimentation may inhibit the settlement of macroalgae (Filbee-Dexter et al. 2019), benthic micro- and macroalgae tolerate moderate sedimentation rates (Wulff et al. 1997; Ronowicz et al. 2020). For these reasons, we believe that nutrient concentration rather than turbidity is
the main factor controlling primary production in the Young Sound fjord.

Moreover, although turbid and nutrient-depleted freshwater inputs strongly impact primary production toward the fjord head, production on the adjacent shelf remains relatively unaffected due to higher light and nutrient availability (Meire et al. 2017; Holding et al. 2019). Large inflows of shelf water masses into the fjord generated by the seasonal estuarine circulation (Bendtsen et al. 2014) permit the supply of high-quality allochthonous organic matter to the benthic food web (Rysgaard and Nielsen 2006; Glud and Rysgaard 2007). Higher resilience of benthic primary producers and lower exposure of offshore phytoplankton to freshwater inputs may thus explain why these two components make such large contributions to the benthic food web. Therefore, although local pelagic production shows strong spatial variation (Meire et al. 2017), its contribution to the diet of primary consumers is not sufficient to mirror the gradient in the benthic food-web structure.

Potential role of omnivory on benthic food-web stability

The absence of spatial variation in the benthic food web may also result from large trophic adaptations of the community to local carbon availability. According to the benthic food-web structure, the fact that numerous consumers seem to feed on several food sources or several trophic levels could be interpreted as a means to cope with variable resource availability in the ecosystem. We hypothesize that such flexible foraging behavior of benthic invertebrates may enhance the food web’s stability in a context of strong seasonal and spatial variations of food availability and quality.

Several species confirmed our trophic assignments and showed modal trophic positions consistent with their putative trophic levels (e.g., H. arctica or Musculus discors primary consumer, A. dentata predator). One the other hand, the trophic positions of some taxa usually considered suspension or deposit feeders (Ascidiaecea, A. baffini, O. sericatum) were significantly above those of the strict primary consumers. Also, numerous species considered carnivores were actually below the trophic levels of strict secondary consumers (e.g., M. glacialis, Nereis sp., N. hirtipes, O. robusta). Such observed trophic positions could reflect a wide trophic plasticity of primary consumers but also high levels of omnivory in secondary/tertiary consumers. Indeed, when confronted with conditions of low food availability, primary consumers may broaden their forage base by feeding on various δ15N-enriched animal/(macro)algal detritus (Mincks et al. 2008). In addition, secondary consumers may also expand their diet to several trophic levels in summer by feeding on both nutritive prey and abundant primary producers (McMeans et al. 2015). These two feeding strategies (i.e., trophic plasticity and omnivory) may thus considerably increase the stability of benthic communities by sustaining large carbon fluxes through the food web throughout the year despite strong freshwater input gradients and extreme seasonality.

High levels of omnivory highlighted by the trophic position models may also be a result of the TEFs used in this study. For instance, the low modal trophic positions of A. carinatus and Balanus sp. primary consumers (significantly below 2) may indicate that Post’s fractionation factors are actually too high for aquatic consumers (McCutchan et al. 2003). However, neither Post’s nor McCutchan’s fractionation factors seemed appropriate for our trophic position estimates (see McCutchan’s equivalent to Fig. S in Supplementary Information, Fig. S3). The high overlap (not dependent on the applied TEFs) between primary and secondary consumers shows in any case that either trophic plasticity or omnivory is a key feature of the benthic food web. A lower fractionation factor would only imply that more primary consumers would exhibit high trophic plasticity by feeding on δ15N-enriched detritus, while fewer secondary consumers would be omnivorous.

Perspectives

Our study reveals that contributions of alternative food sources (i.e., benthic production and allochthonous inputs of organic matter) and trophic adaptations of benthic consumers (i.e., omnivory, trophic plasticity) are key to the stability of benthic food webs exposed to freshwater inputs. However, future research might assess whether these factors will be able to maintain such stability as these freshwater inputs continue to increase.

For instance, deep communities (i.e., below the euphotic zone) probably have less access to benthic micro- and macroalgae as they rely on the export of benthic production from shallow coastal habitats (Krumhansl and Scheibling 2012). Considering the negative impact of freshwater inputs on phytoplankton productivity (Meire et al. 2017), further studies might thus investigate whether deeper habitats will be more sensitive to forthcoming increases in terrestrial inputs than shallower communities, as their food webs might be less able to adjust their energy requirements to benthic primary production.

In addition, it might be interesting to examine how increasing freshwater inputs would alter supplies of benthic primary production and allochthonous organic matter in benthic food webs. Benthic primary producers will not necessarily be adapted to increased sedimentation under a climate change scenario. Although benthic primary producers can cope with moderate sedimentation (Wulff et al. 1997; Ronowicz et al. 2020), abrupt and extreme sedimentation events may exceed their tolerance threshold, leading to a considerable decline in their productivity (Sahade et al. 2015). On the other hand, increasing freshwater inputs may at the same time enhance the fjord’s estuarine circulation (i.e., surface outflows of turbid freshwater plumes and subsurface inflows of shelf water masses), increasing in turn inputs of allochthonous organic matter to the fjord (Rysgaard et al. 2003; Glud and Rysgaard 2007). The balance between these two scenarios deserves further interest in forthcoming studies, in order to...
better assess the sensitivity of the benthic food web, as well as
the whole system’s functioning, to such changes.

References

isotope-based community metrics as a tool to identify pat-
terns in food web structure in east African estuaries. Funct.

AMAP. 2017. Snow, water, ice and permafrost in the Arctic
(SWIPA). Arctic Monitoring and Assessment Programme
(AMAP).

Benthic primary production and mineralization in a high
Arctic fjord: in situ assessments by aquatic eddy covarianc.

Bell, L. E., M. A. Bluhm, and K. Iken. 2016. Influence of ter-
restrial organic matter in marine food webs of the Beaufort
3354/meps11725

surface layer dynamics and sensitivity to runoff in a high
Arctic fjord (young sound/Tyrolerfjord, 74°N). J. Geophys.

Bridier, G., T. Meziane, J. Grall, L. Chauvaud, M. K. Sejr, S.
Menneteau, and F. Olivier. 2019. Coastal waters freshening
and extreme seasonality affect organic matter sources, qual-
ity, and transfers in a high Arctic fjord (young sound,
meps12857

Brind’Amour, A., and S. Dubois. 2013. Isotopic diversity indi-
ces: How sensitive to food web structure? PLoS ONE 8:
e84198. doi:10.1371/journal.pone.0084198

Caut, S., E. Angulo, and F. Courchamp. 2009. Variation in dis-
crimination factors (Δ15N and Δ14C): The effect of diet iso-
topic values and applications for diet reconstruction.
01620.x

Citterio, M., M. K. Sejr, P. L. Langen, R. H. Motttram, J.
Towards quantifying the glacial runoff signal in the fresh-
water input to Tyrolerfjord young sound, NE Greenland.

polar.v10i2.6752

De Cesare, S., T. Meziane, L. Chauvaud, J. Richard, M. K. Sejr,
J. Thébault, G. Winkler, and F. Olivier. 2017. Dietary plas-
ticity in the bivalve Astarte moerchi revealed by a multi-
marker study in two Arctic fjords. Mar. Ecol. Prog. Ser. 567:
157–172. doi:10.3354/meps12035

Duarte, C. M. 1995. Submerged aquatic vegetation in relation
1080/00785236.1995.10422039

Dunton, K. H., and D. M. Schell. 1987. Dependence of con-
sumers on macroalgae (Laminaria solidungula) carbon in an
arctic kelp community: δ13C evidence. Mar. Biol. 93:
615–625. doi:10.1007/BF00392799

Filbee-Dexter, K., T. Wernberg, S. Fredriksen, K. M.
Norderhaug, and M. F. Pedersen. 2019. Arctic kelp forests:
Diversity, resilience and future. Global Planet. Change 172:

France, R. L. 1995. Carbon-13 enrichment in benthic com-

Gaillard, B., T. Meziane, R. Tremblay, P. Archambault, M. E.
Food resources of the bivalve Astarte elliptica in a subArctic
567: 139–156. doi:10.3354/meps12036

b16018

budget of young sound, NE Greenland, p. 194–203. In S.
Rysgaard and R. N. Glud [eds.], Carbon cycling in Arctic
marine ecosystems: Case study young sound, v. 58. Meddr.
Grønland. Bioscience.

Benthic diatoms of a high arctic fjord (young sound, NE
Greenland): Importance for ecosystem primary productiv-

2009. Benthic microalgal production in the Arctic: Applied
52: 559–572. doi:10.1515/BOT.2009.074

Grebe, M., and others. 2006. A major ecosystem shift in the
1126/science.1121365

Griffiths, J. R., and others. 2017. The importance of benthic-
pelagic coupling for marine ecosystem functioning in a
changing world. Global Change Biol. 23: 2179–2196. doi:
10.1111/gcb.13642

Haine, T. W. N., and others. 2015. Arctic freshwater export:
Status, mechanisms, and prospects. Global Planet. Change
125: 13–35. doi:10.1016/j.gloplacha.2014.11.013

Harris, C. M., N. D. McTigue, J. W. McClelland, and K. H.
Dunton. 2018. Do high Arctic coastal food webs rely on a
1016/j.foodweb.2018.e00081

Holding, J. M., S. Markager, T. Juul-Pedersen, M. L. Paulsen,
E. F. Moller, L. Meire, and M. K. Sejr. 2019. Seasonal and
spatial patterns of primary production in a high-latitude
fjord affected by Greenland ice sheet run-off. Bio-

Hopwood, M. J., and others. 2020. How does glacier discharge
affect marine biogeochemistry and primary production in

Food-web structure of a Greenland fjord
the Arctic? The Cryosphere \textbf{14}: 1347–1383. doi:10.5194/tc-14-1347-2020
Comparing isotopic niche widths among and within communities: SIBER–stable isotope Bayesian ellipses in R.
doi:10.3354/meps287251

Acknowledgments
A big thanks to Egon Randa Frandsen, Jakob Thyring, Mie Sichlau Windig, Carl Isaksen, Mel Murphy, Erwan Amice, and Jean-Manuel...
Warnet for their contributions in the field, collecting samples for stable isotope analyses. We are greatly indebted to the MarineBasis programme and the Zackenberg/Daneborg staff for their support in the field. Thanks to Jean-Marie Munaron for his help on laboratory analyses. Friendly thanks to Jérôme Jourde, Michel Le Duff, Vincent Le Garrec, Gabin Droual, Caroline Uhlir, Anne-Helene Tandberg, and Natalia Shunatova for their teaching on species identification. We are grateful to Loïc Michel and Nathan McTigue for their advice and assistance with Bayesian analyses. This work was a part of the PhD project of Guillaume Bridier and co-funded by the “Allocation de Recherche Doctorale” from the Brittany Regional Council and the Université de Bretagne Occidentale/LIA BeBEST. Additional funding was provided by the Institut Polaire Français Paul-Emile Victor (IPEV – PRIVARC project), the European H2020 INTAROS program and the Observatoire Marin de l’IUEM (UMS3113). Part of the data included in this manuscript was provided by the MarineBasis programme. We warmly thank the two anonymous reviewers for their extensive constructive comments which greatly improved this manuscript. This study is an international collaboration between the BeBEST International Laboratory (UBO, UQAR, CNRS, and MNHN) and the Aarhus University.

Conflict of interest
None declared.