

1Contrasting pelagic ecosystem functioning in eastern and western Baffin Bay
2revealed by trophic network modeling

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4Blanche Saint-Béat^{a*}, Brian D. Fath^{b,c}, Cyril Aubry^a, Jonathan Colombet^d, Julie Dinasquet^e, Louis
5Fortier^a, Virginie Galindo^f, Pierre-Luc Grondin^a, Fabien Joux^e, Catherine Lalande^a, Mathieu
6LeBlanc^a, Patrick Raimbault^g, Télesphore Sime-Ngando^d, Jean-Eric Tremblay^a, Daniel Vaultot^h,
7Frédéric Maps^a, Marcel Babin^a.

8

9^a Takuvik Joint International Laboratory, Université Laval (Canada) – CNRS (France),
10 Département de biologie et Québec-Océan, Université Laval, Quebec, Quebec, Canada

11^b Towson University, Department of Biological Sciences, Towson University, Towson, MD,
12 USA

13^c Advanced Systems Analysis Program, International Institute for Applied Systems Analysis,
14 Laxenburg, Austria

15^d LMGE, Laboratoire Microorganismes: Génome et Environnement, UMR CNRS 6023,
16 Clermont Université, Université Clermont- Auvergne, BP 80026, 63171 Aubière Cedex,
17 France

18^e Sorbonne Université, CNRS, Laboratoire d’Océanographie Microbienne (LOMIC),
19 Observatoire Océanologique de Banyuls, 66650 Banyuls/mer, France

20^f Centre for Earth Observation Science, Faculty of Environment, Earth and Resources,
21 University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada

22^g Mediterranean Institute of Oceanography, MIO UMR110, Aix-Marseille Université,
23 CNRS/INSU, Université de Toulon, IRD, 13288 Marseille, France

24^h Sorbonne Université, CNRS, UMR7144, Station Biologique de Roscoff, Roscoff, France

25

26* blanche.saint-beat@takuvik.ulaval.ca

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29

30**Abstract**

31

32Baffin Bay, located at the Arctic Ocean’s ‘doorstep’, is a heterogeneous environment where a

33warm and salty eastern current flows northwards in the opposite direction of a cold and relatively

34fresh Arctic current flowing along the west coast of the bay. This circulation affects the physical

35and biogeochemical environment on both sides of the bay. The phytoplanktonic species

36composition is driven by its environment and, in turn, shapes carbon transfer through the

37planktonic food web. This study aims at determining the effects of such contrasting environments

38on ecosystem structure and functioning and the consequences for the carbon cycle. Ecological

39indices calculated from food web flow values provide ecosystem properties that are not
40accessible by direct in situ measurement. From new biological data gathered during the Green
41Edge project, we built a planktonic food web model for each side of Baffin Bay, considering
42several biological processes involved in the carbon cycle, notably in the biological, lipid, and
43microbial carbon pumps. Missing flow values were estimated by linear inverse modeling.
44Calculated ecological network analysis indices revealed significant differences in the functioning
45of each ecosystem. The eastern Baffin Bay food web presents a more specialized food web that
46constrains carbon through specific and efficient pathways, leading to segregation of the microbial
47loop from the classical grazing chain. In contrast, the western food web showed redundant and
48shorter pathways that caused a higher carbon export, especially via lipid and microbial pumps,
49and thus promoted carbon sequestration. Moreover, indirect effects resulting from bottom-up and
50top-down control impacted pairwise relations between species differently and led to the
51dominance of mutualism in the eastern food web. These differences in pairwise relations affect
52the dynamics and evolution of each food web and thus might lead to contrasting responses to
53ongoing climate change.

54

55**Introduction**

56 The planktonic marine ecosystem is involved in the carbon cycle through several
57biological processes. An important element of the carbon cycle is the fixation of CO₂ by
58phytoplankton in the surface ocean to produce particulate organic carbon (POC), a portion of
59which sinks to the deep ocean by several processes grouped as the “biological pump”. The main
60contributors to the biological pump are i) passively sinking POC and ii) fast sinking fecal pellets
61from zooplankton grazing on primary producers. An attenuation of the carbon exported during
62passive sinking can occur due to the remineralization of organic detritus via bacterial degradation

63(e.g., Kellogg et al., 2011; Le Moigne et al., 2013). Zooplankton are also involved in an active
64transport of carbon, with very limited attenuation, below the sequestration depth (Visser et al.,
652017; Jónasdóttir et al., 2019). The large copepods of the genus *Calanus*, dominating the Arctic
66Ocean (e.g., Auel and Hagen, 2002; Darnis et al., 2008), evolved their life-cycle strategy (Maps
67et al., 2014) in order to survive the winter. In spring–summer, *Calanus* converts assimilated food
68into lipid stores (Hagen and Auel, 2001). Once stores are full, *Calanus* migrates downwards to
69depths of 600–1400 m where they begin diapause, by reducing their metabolism and consuming
70their lipid stores during overwintering. By this trait, copepods contribute to the “lipid pump” and
71allow the sequestration of a similar quantity of carbon to the biological pump (Jónasdóttir et al.,
722015). An additional process, the “microbial carbon pump”, involves Bacteria, Archaea, and
73viruses (Jiao et al., 2010) and refers to microbial processes that transform labile dissolved organic
74carbon (DOC) into refractory DOC, which is resistant to microbial use and can persist in the
75water column for thousands of years (Jiao et al., 2010). Three main mechanisms for production of
76labile DOC have been described: i) direct exudation during growth, ii) release of cell
77macromolecules during viral lysis, and iii) degradation of particulate organic matter. Thus, the
78multiple processes occurring within the planktonic marine ecosystem represent key elements in
79the fate of carbon and its potential sequestration.

80 Planktonic marine ecosystems are supported at their base by phytoplankton that are
81strongly affected by their surrounding environment. Primary producers are especially sensitive to
82the fluctuating light and nutrient conditions that directly control their growth. Because each
83phytoplankton taxonomic group has developed specific strategies to thrive in the nutrient and
84light regime to which they have adapted, the phytoplankton community composition and the
85biogeography of species are largely driven by the physical and biogeochemical oceanographic
86conditions (Falkowski et al., 2004; Boyd et al., 2010). The phytoplanktonic communities exhibit

87a set of traits, each having a specific and distinct role in the biogeochemical cycle (Le Quéré et
88al., 2005). Phytoplankton at the very base of marine ecosystems drive the fate of carbon fixed
89through photosynthesis by favoring some carbon-flow pathways over others. As a result,
90phytoplankton communities shape the functioning of marine ecosystems and the carbon cycle.
91However, an accurate understanding of the complex processes occurring within planktonic
92communities that define the functioning of the planktonic ecosystem is still missing.

93 Baffin Bay, the southernmost gateway of the Arctic Ocean, connects the Atlantic and
94Arctic oceans, forming contrasting physical environments for planktonic communities. The
95northward West Greenland current originates from the merging of North Atlantic waters and the
96Irminger current and carries warm and salty water masses along the Greenland west coast (Tang
97et al., 2004). On the other side and in the opposite direction, the colder and fresher Baffin Island
98current flows outwards from the Canadian Archipelago, following Baffin Island shores. An east
99vs. west contrast in sea-ice freeze-up and melt timing is usually observed, with an early melt in
100the eastern region (Tang et al., 2004). As a result, the eastern and western sides of Baffin Bay
101have differing environments that extend northwards to the North Water, between Greenland and
102Ellesmere Island, where they shape distinct microbial and phytoplanktonic communities (Joli et
103al., 2018). This complex environment was sampled during the Green Edge project during the
104spring-to-summer transition. The *CCGS Amundsen* icebreaker sampled several east–west
105transects by following the sea-ice retreat. Simultaneously, a survey was performed at an ice camp
106site based on the west coast of Baffin Bay in order to catch the initial phases of the spring
107phytoplankton bloom. These efforts gathered large and diverse data sets that were used in the
108present study to build food web models integrating the three carbon pumps and representing the
109western and the eastern Baffin Bay.

110 This paper aims to elucidate how contrasting environments impact the internal flows of
111 carbon, and how they influence, in turn, planktonic ecosystem functioning and carbon
112 sequestration. To build complete food web models, we used linear inverse modelling (LIM) to
113 estimate unmeasured flow values. The application of ecological network analysis (ENA - see
114 Fath and Patten, 1998) provided emergent properties, which cannot be revealed otherwise from
115 simple measurement (Fath et al., 2007). ENA is a powerful tool to reveal and discriminate the
116 functioning of various ecosystems. The combination of both tools (LIM and ENA) revealed
117 major differences in the functioning of both food webs, especially in the fate of carbon fixed by
118 primary producers.

119

120 **Material and methods**

121 *Study area*

122 Baffin Bay is a semi-enclosed sea located at the southern edge of the Arctic Ocean
123 system. It is oriented in the north–south direction with a length of about 1400 km and a maximum
124 width of 553 km, bounded by Greenland in the east and Baffin Island in the west. A central
125 abyssal basin deeper than 2300 m is surrounded by a wider continental shelf on its eastern side,
126 compared to its western side. Baffin Bay acts as an important gateway to the North Atlantic. The
127 large opening on the North Atlantic in the south through Davis Strait contrasts with the three
128 narrow and shallow connections to the Arctic Ocean in the north (Jones Sound, Nares Strait and
129 Lancaster Sound). Its northern end shelters the important North Water polynya, an ecologically
130 productive area that remains mostly free of any sea-ice cover even in the midst of winter
131 (Deming et al., 2002). Baffin Bay is a critical transition zone between both oceans where very
132 different water masses coexist before mixing. The northward West Greenland current originates

133from the merging of North Atlantic waters and the Irminger current that carries warm and salty
134water masses along the west coast of Greenland (Tang et al., 2004). On the other side and in the
135opposite direction, colder and fresher outflows from the Canadian Archipelago follow the shores
136of Baffin Island.

137 Baffin Bay is ice-free in September, whereas melt begins as early as April along its
138Greenland side in the east. In July, more than one-half of the bay is already ice-free. Ice freeze-up
139starts in the northern open water in October and continues southwards until its maximal extent in
140March. The ice cover is always reduced in the eastern part of the Bay, due to the warmer West
141Greenland current. Interannual variations in sea ice extent are mainly due to winter atmospheric
142temperature (Tang et al., 2004; Barber et al., 2015).

143

144*Food web linear inverse modeling*

145**Principle**

146This study aimed at constructing the planktonic food web of each side of Baffin Bay in order to
147determine if the contrasting environments shaped different ecosystem structures and functioning.
148Both food webs were reconstructed by linear inverse modeling (Vézina and Platt, 1988). The
149inverse method assimilates all available in situ data as a linear equation and inequality to solve
150missing flow values. Unmeasured flows are estimated from the combination of three elements: i)
151the food web topology representing the map of flows, ii) the mass balances assuming a null sum
152of inflows (flows received by a compartment) and outflows (flows generated by a compartment),
153and iii) a set of biological parameters, including, for instance, primary production, respiration
154rates, and bacterial production, each of which is integrated into the model as a fixed value
155(referred to as an “equality” hereafter) or as a range of values (referred to as an “inequality”
156hereafter). The set of equalities and inequalities constitutes constraints that delimit a solution

space randomly explored to propose a set of possible solutions that fulfill all constraints. The “mirror” algorithm described by Van den Meersche et al. (2009) and available in the R *limSolve* package as function *xsample*, randomly samples the solution space considering inequalities as reflecting planes, which ensures that proposed solutions are within the solution space. The entire coverage of the solution space is guaranteed by the choice of the jump length and the number of iterations. The convergence of solutions was checked visually as the achievement of the steady state of both the mean and standard deviation of flow values (Niquil et al., 2011). In our case, solution convergence was obtained for a jump equal to 20 mg C m⁻² and 20,000 iterations.

Model topology and constraints

Both Baffin Bay food web models represented trophic interactions and biological processes occurring within the euphotic zone during a summer period (June–July). All flows were expressed in g C m⁻² over the whole period considered. This section only describes how in situ data were integrated into the food web models, whereas methods used for field measurements are described briefly in the supplemental material (Text S1). The food web models were informed by data gathered during (i) an oceanographic campaign aboard the Canadian scientific icebreaker *Amundsen*, and (ii) an expedition on landfast ice off Qikiqtarjuaq in the spring–summer of 2016, both coordinated by the Green Edge Project (www.greenedgeproject.info). The oceanographic campaign surveyed seven east–west transects across Baffin Bay over which a total of > 200 stations were each sampled once. During the landfast-ice expedition, a single station where the ocean depth was nearly 400 m was sampled three times a week during more than three months. We focused on the data covering the period from 9 June to 9 July 2016 for both datasets. The oceanographic campaign data were split into two sets (Figure 1), one for the eastern and one for the western region of Baffin Bay, based on the proportion of Pacific Water found between 0 and 50 m in the bay, determined according to Bergeron and Tremblay (2014). The western side

181presented at least 25% of Pacific Water, whereas eastern Baffin Bay contained less than 20% of
182Pacific Water. The vertical profile of each biological variable considered in the model was
183integrated over the depth of the euphotic zone using the trapezoidal method and then multiplied
184by 30 to obtain a monthly estimate. The 5th and 95th percentile of each variable distribution,
185except net primary production (NPP), was used in the models as lower and upper limits. The
186landfast-ice data were integrated over the euphotic zone and then simply interpolated linearly on
187a daily basis and integrated over the monthly period considered. For NPP in equations, mean
188values of 14.210, 8.462, and 8.770 g C m⁻² month⁻¹ were used for phytoplankton (PHY) in the
189east, PHY in the west, and sea-ice algae (SIA) in the west, respectively. As previously
190mentioned, the ice camp data were relevant for the western Baffin Bay food web model only. The
191eastern food web model only integrated data from the oceanographic campaign. The list of model
192constraints is provided in Table 1.

193

194**Table 1: List of constraints applied to the food web models for inequalities.**

195

Compartment	Process ^a	Min ^b	Max ^b	References
Sea-ice algae (SIA)	Respiration	0.05*GPP ^c	0.3*GPP	Vézina and Platt (1988)
	Exudation	0.08*GPP	0.82*GPP	Gosselin et al. (1997); Klein et al. (2002)
	Grazing by <i>Calanus</i>	- ^d	flow (siaTOomn)	Koski et al. (2017)
		-	flow (phyTOcal)	Søreide et al. (2008)
	Sinking	0.02*flow (phyTOsed ^e)	-	This study
Phytoplankton (PHY)	Respiration	0.05*GPP	0.3*GPP	Vézina and Platt (1988)
	Exudation	0.08*GPP	0.82*GPP	Gosselin et al. (1997) Klein et al. (2002)
	Sinking in west	0.02	0.467	This study
	Sinking in east	0.11	0.586	This study
Bacteria (BAC)	Production in west	0.149	0.334	This study

	Production in east	0.175	0.865	This study
	Bacterial growth efficiency in west (%)	na ^f	2.76	This study
	Bacterial growth efficiency in east (%)	na	2.26	This study
	Respiration	0.2*DOC Uptake	na	Vézina and Pace (1994)
	Respiration in west	na	26.6	Moloney and Field (1989) ^e
	Respiration in east	na	29.8	Moloney and Field (1989) ^e
	DOC uptake in west	na	55.6	Moloney and Field (1989) ^e
	DOC uptake in east	na	63	Moloney and Field (1989) ^e
	Viral lysis in west	0.007	-	This study
	Viral lysis in east	0.020	-	This study
	Flow(bacTOdoc)	-	0.25*(bacTOres ^g) + (bacTOmic)	Suttle (1994, 2005)
Microzooplankton (MIC)	Assimilation	0.50*Ing ^h	0.9*Ing	Vézina and Platt (1988)
	Exudation	0.33*Res ⁱ	Res	Vézina and Platt (1988)
	Respiration	0.20*Ing	-	Vézina and Pace (1994)
	Production	0.10*Ing	0.4*Ing	Straile (1997)
	Production in west	0.028	na	Hirst and Bunker (2003) ^j
	Production in east	0.073	na	Hirst and Bunker (2003) ^j
	Respiration in west	na	9.07	Moloney and Field (1989)
	Respiration in east	na	11.9	Moloney and Field (1989)
	Consumption in west	na	40.58	Moloney and Field (1989)
	Consumption in east	na	53.7	Moloney and Field (1989)
Mesozooplankton (MES)	Assimilation	0.50*Ing	0.9*Ing	Daly (1997); Frangoulis et al. (2010)
	Exudation	0.33*Res	Res	Vézina and Platt (1988)
	Respiration	0.20*Ing	-	Vézina and Pace (1994)
	Production	0.10*Ing	0.4*Ing	Frangoulis et al. (2010); Straile (1997)
<i>Calanus</i> (CAL)	Respiration in west	1.72	3.48	Moloney and Field (1989)
	Respiration in	1.19	3.53	Moloney and Field

	east			(1989)
	Consumption in west	7.72	15.6	Moloney and Field (1989)
	Consumption in east	5.34	15.9	Moloney and Field (1989)
	Production in west	3.95	na	Hirst and Bunker (2003)
	Production in east	3.55	na	Hirst and Bunker (2003)
	Reserve accumulation in west	2.46	3.81	Maps et al. (2014)
	Reserve accumulation in east	1.08	1.96	Maps et al. (2014)
Omnivorous mesozooplankton (OMN)	Respiration in west	2.86	3.84	Moloney and Field (1989)
	Respiration in east	0.75	17.5	Moloney and Field (1989)
	Consumption in west	5.41	31.2	Moloney and Field (1989)
	Consumption in east	3.35	78.8	Moloney and Field (1989)
	Production in west	1.69	na	Hirst and Bunker (2003)
	Production in east	0.51	na	Hirst and Bunker (2003)
Carnivorous mesozooplankton (CAR)	Respiration in west	0.44	1.73	Moloney and Field (1989)
	Respiration in east	0.24	0.84	Moloney and Field (1989)
	Consumption in west	1.99	7.78	Moloney and Field (1989)
	Consumption in east	1.03	3.72	Moloney and Field (1989)
Arctic cod larvae (BSL)	Respiration in west	na	0.003	Hop and Graham (1995)
	Respiration in east	na	0.002	Hop and Graham (1995); Hop et al. (1997)
	Consumption in west	na	0.034	Hop et al. (1997)
	Consumption in east	na	0.015	Hop et al. (1997)
	Production	0.30*Ing	0.70*Ing	Hop et al. (1997)
	Assimilation	0.50*Ing	0.90*Ing	Hop et al. (1997)
Particulate	Sinking in west	0.20* Σ of Inf ^k	0.51* Σ of Inf	This study

detritus (DET)	Sinking in east	$0.32 * \Sigma \text{ of Inf}$	$0.79 * \Sigma \text{ of Inf}$	This study
Dissolved detritus (DOC)	Export	flow (bacTOdoc)	-	Jiao et al. (2011)

196

197^a All processes estimated from in situ data are expressed in $\text{g C m}^{-2} \text{ month}^{-1}$ except for bacterial
198 growth efficiency expressed in %.

199^b Flows between compartments are written like flow (source TO sink).

200^c GPP = gross primary production

201^d Hyphen = data not available.

202^e sed = sediments

203^f na = data not applicable

204^g calculated for the 95th percentile of abundance

205^h Ing = ingestion

206ⁱ Res = respiration^j only considering nauplii

207^k Inf = inflows

208

209 1. Primary producers

210 Over the considered period (9 June to 9 July 2016), western Baffin Bay (WBB) was still
211 ice-covered, whereas eastern Baffin Bay (EBB) was already free of sea ice. Thus, the WBB food
212 web model considered two primary producers: sea-ice algae (SIA) and phytoplankton (PHY), and
213 their associated production. This consideration was the only difference between model
214 topologies.

215 In summer, despite the strong grazing pressure by zooplankton, a portion of the primary
216 producers is assumed to sink. Using data from the sediment traps deployed at 25 m (drifting trap
217 data and both drifting and short-term trap data in the east and in the west, respectively), the
218 relative proportion of the stock of chlorophyll a (Chl_a) sinking to the bottom was calculated.
219 Then this proportion was applied to the 5th and 95th percentiles of Chl_a concentration values
220 found in the euphotic zone in each Baffin Bay region, thus effectively bounding phytoplankton
221 sinking by lower and upper values. The sinking rate of sea-ice algae was estimated using data
222 from long-term sediment traps deployed at 25 m, considering the diatom *Nitzschia frigida* as an
223 indicator of the presence of sea-ice algae. The relative contribution of *N. frigida* to the pool of

total diatoms in the drifting trap was used as minimal constraint of sea-ice algae sinking relative to phytoplankton sinking.

2. Bacteria

Bacterial production was assumed to be fully consumed over the summer period, thus no export to the following season was integrated into the model. Our model also considered the production of dissolved organic carbon (DOC) by bacteria through two processes: i) viral lysis and ii) direct exudation. Viruses use cellular material of their host to support their own reproduction and in the end the host is lysed, releasing new viruses and host cellular material that enriches the DOC pool (Middelboe and Jørgensen, 2006). The main effect of the viral infection relevant to this study is the shunt of carbon from bacteria to higher trophic levels to the detritus pool (DET). To simplify the representation of this process in the model and avoid the explicit addition of a viral compartment, the viral infection was integrated into the model as a flow from the bacteria to DOC. During the Green Edge Project, the frequency of visibly infected cells (FVIC) was estimated to be equal to 1% of the bacterial biomass on average. From this estimate, the frequency of infected cells (FIC) was derived using the equation:

$$FIC = 9.524 FVIC - 3.256$$

described in Weinbauer et al. (2002). Then, virally induced bacterial mortality (VIBM; Binder, 1999) was estimated using:

$$VIBM = (FIC + 0.6 FIC^2) / (1 - 1.2 FIC).$$

As a result, the flow from bacteria to dissolved carbon was constrained by a lower limit equal to 7% of the minimal bacterial biomass observed in situ within the euphotic zone. The 5th percentile of abundance was converted into carbon considering the mean carbon content of 8.5 fg C per cell observed over the period. The maximal bacterial mortality by viral lysis was supposed to be less than the bacterivory by protists (Suttle, 1994; 2005). Moreover direct exudation by bacteria can

represent up to 25% of bacterial respiration (Stoderegger and Herndl, 2001). Consequently, the flow from bacteria to DOC was limited by the sum of maximal mortality due to viruses and maximal exudation.

251

252 3. Microzooplankton

253 This compartment grouped ciliates, heterotrophic flagellates, and copepod nauplii. The biomasses of ciliates and heterotrophic flagellates for each side of Baffin Bay were calculated from their mean abundance and carbon content. The latter was estimated for a specific biovolume range according to the following empirical relationship (Menden-Deuer and Lessard, 2000):

257
$$\text{Carbon content (in pg C cell}^{-1}\text{)} = 0.216 * (\text{Vol in } \mu\text{m}^3)^{0.939}.$$

258 Carbon content for each species of nauplii was determined according to the specific relationship between prosome length and carbon content (references in Bouchard et al., 2014). All were assumed to feed on phytoplankton, bacteria (Pomeroy, 1974; Turner, 2004), and detritus. As a part of their production was assumed to be consumed by predators not considered in the current model, we considered an export of carbon.

263 4. Mesozooplankton

264 Mesozooplankton included species that had at least one individual present at half of the stations sampled during the oceanographic campaign in each region of Baffin Bay (Table 2). Species known to stay deeper than 200-m depth were not considered. Furthermore, we assumed that all of the mesozooplankton biomass fed on carbon produced within the euphotic zone. Mesozooplankton species were grouped according to their diet and life-cycle traits. Thus, the *Calanus* genus deserved its own group, while the other species were split into omnivorous mesozooplankton and carnivorous mesozooplankton (Table 2). For each group, the mean abundance of each species was resolved at the developmental stage when applicable, for each

region of Baffin Bay. Then ranges of biomasses (for each stage) were estimated through body length to carbon content relationships (Table 2) based on the minimal and maximal size ranges observed in situ.

275

Table 2: Species composing each mesozooplankton compartment and references used for determining carbon content.

278

Compartment	Species	References
<i>Calanus</i>	<i>Calanus finmarchicus</i>	Madsen et al., 2001
	<i>Calanus glacialis</i>	Forest et al., 2011
	<i>Calanus hyperboreus</i>	Forest et al., 2011
Omnivorous	<i>Boroecia maxima</i>	Appendix C in Mumm, 1991
	<i>Discoconchoecia elegans</i>	Appendix C in Mumm, 1991
	<i>Heterostylites major</i>	Appendix C in Mumm, 1991
	<i>Limacina helicina</i>	Hopcroft et al., 2005
	<i>Metridia longa</i>	Forest et al., 2011
	<i>Microcalanus</i>	Uye, 1982
	<i>Oithona similis</i>	Sabatini and Kiørboe, 1994
	<i>Oncaea notopus/parila</i>	Hopcroft et al., 2005
	Polychaete larva	Uye, 1982
	<i>Pseudocalanus spp.</i>	Liu and Hopcroft, 2008
	<i>Spinocalanus longicornis</i>	Uye, 1982
	<i>Triconia borealis</i>	Sabatini and Kiørboe, 1994
Carnivorous	<i>Aglantha digitale</i>	Hopcroft et al., 2005
	<i>Eukrohnia hamata</i>	Hopcroft et al., 2005
	<i>Gaetanus tenuispinus</i>	Appendix C in Mumm, 1991
	<i>Heterorhabdus norvegicus</i>	Appendix C in Mumm, 1991
	<i>Paraeuchaeta spp.</i>	Appendix C in Mumm, 1991
	<i>Themisto abyssorum</i>	Hopcroft et al., 2005

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Calanus species group together owing to their particular and similar life-cycle traits. These species are able to limit their metabolic costs in winter in order to survive their unfavorable surroundings (Hagen and Auel, 2001). They accumulate energy-rich compounds (lipids) that

form up to 70% of their body mass (e.g., Falk-Petersen et al., 1990; Maps et al., 2014), which allows them to be auto-sufficient during the lean season. By this life trait, they transfer the carbon produced by primary producers during the short summer period to higher trophic levels during the rest of the year. The reserve accumulation in the models ranged between 70% of the minimal and maximal biomass of stages above copepodite IV. *Calanus* was assumed to feed on primary producers (i.e., phytoplankton and sea-ice algae; (e.g., Søreide et al., 2010), detritus and microzooplankton (Calbet and Saiz, 2005) including nauplii (Dufour et al., 2016). In contrast to the *Calanus* group, omnivorous and carnivorous mesozooplankton feed all year around and do not accumulate significant reserves during summer (e.g., Blachowiak-Samolyk et al., 2007). Omnivores feed on primary producers, detritus, bacteria and protists (e.g., Stevens et al., 2004; Turner, 2004), whereas carnivores consume micro- and mesozooplankton (e.g., Blachowiak-Samolyk et al., 2007). The grazing on sea-ice algae by the *Calanus* group was considered to be lower than its grazing on phytoplankton (Søreide et al., 2008) and lower compared to the grazing by omnivorous mesozooplankton (Koski et al., 2017). For these three mesozooplankton groups, we considered an export of carbon corresponding to their production consumed by compartments not incorporated into the model.

5. Arctic cod larvae

Arctic cod (*Boreogadus saida*) larvae that correspond to the young-of-the-year feed on all micro- and mesozooplankton groups (Bouchard et al., 2014). Their production was totally exported in our model, because none of their predators was considered in it. An upper limit of respiration was estimated from experimental respiration rates under satiated feeding conditions (Hop and Graham, 1995). The experimental respiration rates were adapted to the weight of fishes measured in situ according to the empirical relationship given in the same paper. Maximal consumption was constrained using an allometric relationship defined by Hop et al. (1997).

Consumption was first converted to kilojoules using the mean energy content of prey consumed by the Arctic cod in the experiments of Hop et al. (1997), then converted to carbon using the conversion factor of 45.7 J mg C^{-1} (Brey, 2001).

6. Detritus

Two groups of detritus, particulate detritus (DET) and DOC, were considered in the models. The sinking of particulate detritus was estimated as the difference between particulate organic carbon (POC) and Chl a (representing living POC) found in the sediment traps, using a C:Chl a conversion factor of 50. The relative proportion of the POC stock that sunk was applied to the sum of inflows to DET in order to constrain the flow from DET to sediment. The DOC produced by bacteria was considered as refractory (Jiao et al., 2010; 2011). To simulate this process, we considered that the DOC excreted by bacteria was exported.

Ecological network analysis

Once all the flow values were estimated, we performed a network analysis in order to characterize several attributes of the food web and describe the structure and functioning of both Baffin Bay food webs. Ecological network analysis (ENA) revealed emergent properties of the ecosystem via the analysis of the distribution of carbon throughout the various possible pathways. First, the activity of each compartment described by their total inflows assessed the importance of each compartment in the transfer of carbon. A compartment receiving a small amount of carbon contributed little to the transfer of carbon to higher trophic levels. Then, the contribution of each prey to the total inflows of each compartment was analyzed to detect possible differences in the diet composition of each compartment according to the east vs. west side of the Bay. While the prey contribution to the diet of their predators involved only direct flow (i.e., length pathway equal to 1), a complementary approach considering both direct and indirect pathways (i.e., pathways longer than 2) describes the dependency of each compartment on one another (Szyrmer

331and Ulanowicz, 1987). This approach tracks the origin of carbon ingested by consumers. In order
332to determine the impact of the microbial food web on the carbon ingested by higher trophic
333levels, we focused only on the dependency on bacteria and on the direct bacterial consumers:
334microzooplankton and omnivorous mesozooplankton. These attributes of the food webs were
335calculated for the mean flow values by the R package NetIndices (Kones et al., 2009).

336 We further synthesized the information retrieved from our ensemble modeling approach
337by using the Lindeman aggregation routine to compute the carbon transfer between integer
338trophic levels. The Lindeman Spine projected the complex network into a linear food chain
339composed of discrete trophic levels. Nodes of the food web were apportioned into integer trophic
340levels according to their diet (Ulanowicz and Kemp, 1979). The spine represented the transfer of
341carbon received from the previous trophic level and from imports (if applicable), the loss of
342carbon both by respiration and exports. The cycle of detritus was also represented. The Lindeman
343routine was performed for the mean value of the 20,000 possible solutions for each flow by the R
344enaR package (Borrett and Lau, 2014).

345 Some ENA indices reveal the food web architecture (Table 3). Each index and its
346interpretation are presented in Table 3. This set of indices was calculated for the 20,000 sets of
347solution proposed by the limSolve R package in order to assess the uncertainty associated with
348each index. We used the NetIndices R-package (Kones et al., 2009) based on the algorithm
349development by Latham et al. (2006).

350 **Table 3: Ecological network analysis indices describing structure and functioning of**
351**the food web.**

Index name	Abbreviation	Meaning	Reference
Total system throughput	T..	Activity of the entire food web; corresponds to the sum of all flows	Fath et al., 2013
Average mutual information	AMI	Specialization of flows; constraints imposed to a carbon atom; the higher the AMI, the more constrained and specialized the carbon in the food web	Ulanowicz, 1986
Ascendency	ASC	Organization of the system; represents efficient part of the food web	Ulanowicz, 1986; 1997
Relative Ascendency	A/C	Level of organization reached; the higher the A/C, the closer to the maximal ascendency level	Ulanowicz, 1986; 1997
Overhead	(none)	Reserves of the ecosystem limiting ASC; higher overheads associate with lower A/C; overheads have distinct origins: dissipation, export, or redundancy	Ulanowicz, 1986; 1997
Finn cycling index	FCI	Carbon recycling; quantity of carbon involved in a loop	Finn, 1976; 1980
Average path length	APL	Carbon retention; number of compartments visited by an atom of carbon between its entry and its exit	Kay et al., 1989
Compartmentalization	Cbar	Strength of subsystems; 0 indicating the inexistence of any subsystem and 1, a strong compartmentalization	Pimm and Lawton, 1980; Latham, 2006

352

353 Finally, we performed a utility analysis that determined the effects of the network on each
354 pairwise relation. This approach assumes that a compartment is part of two environments: one
355 that drives a given compartment and corresponds to flows received (inflows), and the other that is
356 impacted by and thus refers to the flows originating from the compartment (outflows). Utility
357 analysis captures both top-down (inflows) and bottom-up (outflows) processes (Patten, 1991;
358 1992). It highlights pairwise relations generated by direct interactions. Direct interactions refer to

physical exchanges of carbon between two compartments. Utility analysis also considers the effects of indirect flows on pairwise relations. In this context, indirect flows correspond to interactions between compartments not connected physically, meaning separated by a length pathway equal or greater than 2 (Fath and Patten, 1998). We performed this utility analysis on the mean values of the flows with the R enaR package (Borrett and Lau, 2014).

Results

Some differences in the activity of each compartment, defined as the sum of inflows to each compartment, were observed (Figure 2). The Arctic cod larvae showed the lowest activity in both food webs considered. Activities of some compartments were lower in the eastern food web while others presented higher activity, i.e., bacteria, DOC, phytoplankton and carnivorous mesozooplankton (see flow values in Table S1).

The differences in the activity of some compartments can be related to changes in the relative contribution of the available resources (Figure 3). The western Baffin Bay food web had a supplemental resource (SIA) compared to that from eastern Baffin Bay. In both food webs, compartments fed on the same resources, but their relative contributions changed, except for Arctic cod larvae. Bacteria contributed a greater proportion of the diet of both the microzooplankton and omnivorous groups in the eastern Baffin Bay, which was associated with a decrease in the contribution of primary producers (Figure 3). The contribution of both DET and microzooplankton to the *Calanus* diet in eastern Baffin Bay was lower than in the west. Carnivorous mesozooplankton fed almost exclusively on *Calanus* in the eastern food web, whereas in western Baffin Bay *Calanus* comprised about

38263% of their diet, with the remaining 37% being microzooplankton and omnivorous
383mesozooplankton (Figure 3). The sources of DOC and DET differed between both Baffin Bay
384regions. The main contributors to the DOC pool were the primary producers in both food
385webs, but their relative contribution was higher in the eastern part (48% versus 38%).
386Omnivorous mesozooplankton contributed 9% to the DOC inflows in the eastern Baffin Bay,
387while they represented 22% of the total inflows in the west (Figure 3). The contribution of
388bacteria and microzooplankton to the DOC inflows was higher in the western Baffin Bay
389compared to the eastern food web. *Calanus* and carnivorous mesozooplankton
390contributions remained similar in both food webs. The degradation of DET to DOC was six
391times higher in the eastern Baffin Bay than in the west. The contribution of carnivorous
392mesozooplankton to the DET pool was double in the eastern Baffin Bay, diminishing the
393contributions from microzooplankton and *Calanus*. The latter remained the main
394contributor of DET in both food webs.

395 The relative contribution of the various sources to the diet/inflows of each
396compartment provides information on the direct flows between the components, whereas
397dependency considers both the direct and indirect flows (Figure 4). The dependency of
398consumers and non-living compartments on both bacteria and direct bacterial consumers
399was relatively low (less than 50%) for both food webs (Figure 4). The compartment most
400dependent on bacteria was the DOC in the western food web, whereas the
401microzooplankton compartment was most dependent on bacteria in the eastern food web.
402The most dependent on direct consumers of bacteria (microzooplankton and omnivorous
403mesozooplankton) were Arctic cod larvae in both regions of the Baffin Bay. However, a
404higher dependency on bacteria was observed in the eastern food web for Arctic cod larvae,

405microzooplankton, and omnivorous mesozooplankton. The dependency of other
406compartments on microzooplankton and omnivorous mesozooplankton was thus lower in
407the eastern food web.

408 The Lindeman Spine (Figure 5) summarizes the food web interactions using linear
409food chains containing integer trophic levels. The transfer efficiency at each trophic level
410decreased linearly in western Baffin Bay, whereas transfer efficiency increased at level IV in
411eastern Baffin Bay (Figure 5). The transfer efficiency of the primary producers (Level I)
412refers to the proportion of the total inflows to both Level I and DET that is transferred to
413the following level. The efficiency at this level was similar in both food webs, but the
414contribution of Level I compared to that of DET differed. Indeed, the grazing on primary
415producers was very close to the detritivory in eastern Baffin Bay and was associated with a
416higher loss of carbon fixed by primary producers to detritus ($3.76 \text{ g C m}^{-2} \text{ month}^{-1}$ versus
417 $1.88 \text{ g C m}^{-2} \text{ month}^{-1}$). A lower loss to detritus ($5.61 \text{ g C m}^{-2} \text{ month}^{-1}$ versus 7.63 g C m^{-2}
418 month^{-1}) and lower exports ($1.60 \text{ g C m}^{-2} \text{ month}^{-1}$ versus $4.45 \text{ g C m}^{-2} \text{ month}^{-1}$) in eastern
419Baffin Bay led to a higher transfer efficiency in Level II. The lower losses to detritus,
420respiration and export led to an approximate 6-fold greater transfer efficiency at Level IV in
421eastern Baffin Bay than that observed in western Baffin Bay. Higher exports from detritus
422were observed in the western food web.

423 The emergent properties revealing characteristics of the architecture of the entire
424food web showed some differences between the two regions of Baffin Bay. Despite the
425slightly higher specialization of flows (higher average mutual information, AMI; Figure 6),
426the ascendancy (Table 3) of the eastern food web was lower compared to the western food
427web due to the lower activity of the entire system (total system throughput, T..). However,

the relative ascendancy (A/C; Table 3) was higher in eastern Baffin Bay (Figure 7). The inefficient/unorganized part of the system (1 minus A/C) was higher in the western food web. The uncertainty responsible for the inefficient/unorganized part of the system (overheads; Table 3) can originate from different sources. For both food webs, the uncertainty was dominated by the redundancy of internal flows (excluding respiration and export flows). The uncertainty associated with the dissipation and external overheads was higher in the western food web (Figure 7).

The Finn cycling index (FCI; Table 3) was low in both food webs considered (Figure 6). However, the western food web tended to present a higher FCI index value, ranging from 5 to 15%. The average path length (APL; Table 3) followed a different tendency, being slightly higher in the eastern food web (Figure 6). The compartmentalization index (Cbar), measuring the strength of the subsystems within the ecosystem, was higher in eastern Baffin Bay (Figure 6).

The direct relations were the same in both food webs, but the western food web included 10 additional relations owing to the presence of the supplementary compartment for sea-ice algae. The relations between the compartments (Table 4) differed when considering both direct and indirect flows. The neutralism (0,0) found only for direct relations changed in most instances to indirect mutualism (+,+), which is a beneficial relation for both compartments involved. Some direct predation relations (+,-) were pushed towards another kind of relation (mostly mutualism) when both direct and indirect flows were considered (integral columns in Table 4). This shift represented 26% and 14% of the predation relations for the eastern and western Baffin Bay food webs, respectively. Some of these transformations were similar in both food webs: mutualism for the relation

451between bacteria and omnivorous group (relation 23 in Table 4), and competition between
452microzooplankton and *Calanus* (relation 29 in Table 4). A few others were food web
453specific. For the eastern Baffin Bay food web, indirect mutualism appeared between
454microzooplankton and both carnivorous mesozooplankton and DOC (relations 31 and 34 in
455Table 4) and between bacteria and DET (relation 26). Indirect mutualism emerged between
456bacteria and microzooplankton (relation 21) and between omnivorous mesozooplankton
457and DET (relation 44) in the western Baffin Bay food web. The network of the eastern
458region changed the direct exploitation of *Calanus* by both Arctic cod larvae and DET into
459indirect mutualism (relations 38 and 39 in Table 4). Moreover, the relation between
460omnivorous and carnivorous mesozooplankton completely flipped from predation to
461altruism in the eastern food web. The direct exploitation between sea-ice algae and both
462primary consumers and DOC was not affected by the network, whereas neutralism was
463changed into indirect mutualism (relations 3, 7, and 8), indirect competition (relation 2),
464predation (relation 9) or indirect altruism (relation 4) (Table 4). In conclusion, the eastern
465food web showed a higher proportion of mutualism (about 46%) compared to the western
466food web (36%) at the expense of predation.

467

468**Table 4: Synthesis of pairwise relations within the eastern and western food webs.**

Relatio n ^a	Fro m ^b	To ^b	Dire ct	WBB- Integral ^c	EBB- Integral ^c
1	SIA	SIA PH	(0,0)	(+,+)	na ^d
2	SIA	Y BA	(0,0)	(-,-) C*	na
3	SIA	C	(0,0)	(+,+) M*	na
4	SIA	MIC CA	(0,0)	(-,+) A*	na
5	SIA	L OM	(+,-)	(+,-)	na
6	SIA	N	(+,-)	(+,-)	na
7	SIA	CA	(0,0)	(+,+) M*	na

		R			
8	SIA	BSL	(0,0)	(+,+) M*	na
9	SIA	DET	(0,0)	(+,-) P*	na
		DO			
10	SIA	C	(+,-)	(+,-)	na
		PH			
11	PHY	Y	(0,0)	(+,+)	(+,+)
		BA			
12	PHY	C	(0,0)	(+,+)	(+,+)
13	PHY	MIC	(+,-)	(+,-)	(+,-)
		CA			
14	PHY	L	(+,-)	(+,-)	(+,-)
		OM			
15	PHY	N	(+,-)	(+,-)	(+,-)
		CA			
16	PHY	R	(0,0)	(+,+)	(+,+)
17	PHY	BSL	(0,0)	(+,+)	(+,+)
18	PHY	DET	(0,0)	(+,-)	(+,-)
		DO			
19	PHY	C	(+,-)	(+,-)	(+,-)
		BA			
20	BAC	C	(0,0)	(+,+)	(+,+)
21	BAC	MIC	(+,-)	(+,+) M*	(+,-) P
		CA			
22	BAC	L	(0,0)	(+,+)	(+,+)
		OM			
23	BAC	N	(+,-)	(+,+)	(+,+)
		CA			
24	BAC	R	(0,0)	(+,+)	(+,+)
25	BAC	BSL	(0,0)	(+,-) P*	(+,+) M*
26	BAC	DET	(+,-)	(+,-) P	(+,+) M*
		DO			
27	BAC	C	(-,+)	(-,+)	(-,+)
28	MIC	MIC	(0,0)	(+,+)	(+,+)
		CA			
29	MIC	L	(+,-)	(-, -)	(-, -)
		OM			
30	MIC	N	(+,-)	(+,-)	(+,-)
		CA			
31	MIC	R	(+,-)	(+,-) P	(+,+) M*
32	MIC	BSL	(+,-)	(+,-)	(+,-)
33	MIC	DET	(-,+)	(-,+)	(-,+)
		DO			
34	MIC	C	(+,-)	(+,-) P	(+,+) M*
		CA			
35	CAL	L	(0,0)	(+,+)	(+,+)
		OM			
36	CAL	N	(0,0)	(-, -)	(-, -)
		CA			
37	CAL	R	(+,-)	(+,-)	(+,-)
38	CAL	BSL	(+,-)	(+,-) P	(+,+) M*
39	CAL	DET	(+,-)	(+,-) P	(+,+) M*
		DO			
40	CAL	C	(+,-)	(+,-)	(+,-)
		OM			
41	OMN	N	(0,0)	(+,+)	(+,+)

		CA			
42	OMN	R	(+,-)	(+,-) P	(-,+) A*
43	OMN	BSL	(+,-)	(+,-)	(+,-)
44	OMN	DET	(+,-)	(+,+) M*	(+,-) P
		DO			
45	OMN	C	(+,-)	(+,-)	(+,-)
		CA			
46	CAR	R	(0,0)	(+,+)	(+,+)
47	CAR	BSL	(+,-)	(+,-)	(+,-)
48	CAR	DET	(+,-)	(+,-)	(+,-)
		DO			
49	CAR	C	(+,-)	(+,-)	(+,-)
50	BSL	BSL	(0,0)	(+,+)	(+,+)
51	BSL	DET	(+,-)	(+,-)	(+,-)
		DO			
52	BSL	C	(0,0)	(-,-)	(-,-)
53	DET	DET	(0,0)	(+,+)	(+,+)
		DO			
54	DET	C	(+,-)	(+,-)	(+,-)
		DO			
55	DOC	C	(0,0)	(+,+)	(+,+)

469^a Pairwise relations were obtained by utility analysis.

470^b Abbreviations for compartments as in Table 1

471^c Asterisks indicate direct relations that changed in western Baffin Bay (WBB) and eastern
472Baffin Bay (EBB) when both direct and indirect (integral) flows were considered; relations
473indicated are mutualism (M), predation (P), competition (C), and altruism (A).

474^c Not applicable (na), as sea-ice algae (SIA) were not present in eastern Baffin Bay

475

476 **Discussion**

477

478 This study represents the first one to couple food web modeling and network
479analysis tools to analyze the distribution of carbon through the various pathways of a
480trophic network (all values of flows in Table S1) in order to reveal the mechanisms
481structuring Arctic planktonic food webs and characterize the properties of carbon transfer
482within those food webs. Applying this approach to the contrasting environments of Baffin

483 Bay revealed distinct features in the respective functioning of the eastern and western food
484 webs that affect carbon sequestration through three carbon pumps: biological, lipid and
485 microbial.

486 *Explanation of model results by field observations*

487 The difference in food web architecture and functioning in the eastern and western
488 regions of Baffin Bay rested mainly on the distinct fate of primary production. In the eastern
489 food web, twice as much carbon was released as exudate by primary producers, enriching
490 the DOC pool (Figure 5). This higher exudation sustained the higher eastern bacterial production
491 associated with the lower bacterial growth efficiency observed in situ. Some in situ observations
492 in eastern Baffin Bay help to explain model outputs. First, at the time of sampling, the number of
493 days of open water was higher in eastern than western Baffin Bay (Randelhoff et al., 2019).
494 Therefore, the period of the phytoplankton bloom captured was not the same; in the east the
495 bloom was more advanced than in the west where it has just begun. As observed during the post-
496 bloom phase, the simulated eastern food web showed high exudation by phytoplankton, due to
497 nutrient stress (Gosselin et al., 1997; Fragoso et al., 2016) associated with higher bacterial
498 production (Nielsen and Hansen, 1995). On the other hand, the comparison of POC export, which
499 was similar between regions excluding the sinking of sea-ice algae, suggests that the eastern food
500 web was in a transitional state. The community composition was changing from diatoms,
501 understood to be the main player in POC fluxes (Boyd and Newton, 1999), to *Phaeocystis*
502 *pouchetii* (mean abundance 2.8×10^6 cell L⁻¹ versus 4.5×10^5 cell L⁻¹ for the eastern and western food
503 webs, respectively), which form large colonies that do not sink systematically as their sinking
504 depends on physical characteristics of the surrounding environment (Wassmann, 1994). This
505 species is well known to exude a large amount of dissolved organic matter at each stage of its

506growth (Alderikamp et al., 2007) as well as transparent exopolymer particles (Engel et al., 2017).
507Furthermore, despite some controversies regarding the grazing of *Phaeocystis* by copepods
508(Schoemann et al., 2005), large *Calanus spp.* can feed on *P. pouchetii* colonies (Estep et al.,
5091990; Søreide et al., 2008), while smaller copepods cannot (Nejstgaard et al., 2007). Being even
510smaller, copepod nauplii and microzooplankton cannot feed on these colonies (Irigoien et al.,
5112003), but they can ingest free-living cells as *Phaeocystis* colonies break down (Dutz and Koski,
5122006; Nejstgaard et al., 2007). The presence of *Phaeocystis pouchetii* in the eastern region of
513Baffin Bay could explain the model-simulated difference in the fate of primary production; i.e.,
514twice as much exudate, ingestion mainly by *Calanus spp.*, and only a limited quantity of carbon
515flowing to microzooplankton and omnivorous mesozooplankton.

516

517*Phenological connection or spatial decoupling?*

518The eastern and western Baffin Bay food web models simulate two distinct phases of the
519phytoplankton bloom. We thus consider whether the differences observed in food web
520structure and functioning can be attributed to bloom phenology instead of the contrasting
521spatial environments, as originally posed, by focusing on the probability of *Phaeocystis*
522*pouchetii* developing in the western part of the bay. First, colonies of *P. pouchetii* have been
523observed previously in the Arctic (Vogt et al., 2012), in the subarctic Labrador Sea (Fragoso
524et al., 2016), in the Barents Sea (Schoemann et al., 2005), and in Disko Bay on the western
525coast of Greenland (i.e., eastern Baffin Bay, Thøiesen et al., 2015), but they have not been
526observed in western Baffin Bay. Because the temperature niches of *P. pouchetii* and diatoms
527are clearly distinct (Brun et al., 2015) and the extent of *P. pouchetii* blooms is associated
528with northward advection of Atlantic water into the Arctic (Engel et al., 2017), the

529 observation of *P. pouchetii* blooms in western Baffin Bay under the influence of colder
530 Pacific/Arctic waters is unlikely. Second, both regions of the Bay differed by the
531 reconstituted winter stock of nutrients and ratio of elements, which influence the
532 abundance of *Phaeocystis* and diatoms (Jiang et al., 2014). Eastern Baffin Bay was
533 dominated by Atlantic water with a nitrate stock of about $10 \mu\text{mol L}^{-1}$, while the nitrate
534 concentration in the west reached only $5 \mu\text{mol L}^{-1}$ (Randelhoff et al., 2019). An opposite
535 trend was observed for both phosphate and silicate, with deficits in the Atlantic water
536 masses. Because the nutrient winter stock was depleted in silicate in the east, diatom
537 growth was limited, leading to development of *P. pouchetii* colonies in this relatively warm
538 water. The depletion of silicate is not necessary for *Phaeocystis* blooms, however, as *P.*
539 *pouchetii* can dominate or co-dominate in cases where silicate is not limiting. Jiang et al.
540 (2014) showed that a high, pre-bloom nitrate concentration can give the slower growing *P.*
541 *pouchetii* enough time to develop before diatoms deplete the nitrate. In contrast, a more
542 nitrate-limited environment, such as western Baffin Bay, favors diatom growth. Moreover,
543 *Phaeocystis*, which has a higher ammonium uptake capacity, outcompetes diatoms in a rich
544 ammonium environment (Tungaraza et al., 2003). Eastern Baffin Bay with its higher
545 concentration of ammonium in summer compared to western Baffin Bay (Varela et al.,
546 2013) would thus favor the *P. pouchetii* bloom. Based on these arguments and observations,
547 the probability of the functioning of the western food web evolving towards the eastern
548 food web seems very low.

549

550 *Contrasting eastern and western Baffin Bay food webs*

551 The carbon fixed by primary producers in the eastern and western regions of Baffin
552 Bay was distributed very differently throughout the pathways of the two trophic networks.
553 More than 25% of the eastern net production (i.e., $3.76 \text{ g C m}^{-2} \text{ month}^{-1}$; Figure 5) was
554 transferred to the DOC pool to which it contributed 48% (Figure 3). In the contrasting
555 western food web, the exudation of DOC by primary producers represented only 10% of the
556 primary production and contributed to the DOC pool in lower proportion (36%; Figure 3).
557 The rest of the primary production was distributed between *Calanus*, microzooplankton,
558 and omnivorous mesozooplankton in the west, whereas it was almost totally transferred to
559 the sole *Calanus* compartment in eastern Baffin Bay. As a result, the activity of
560 microzooplankton and omnivorous mesozooplankton was lower (Figure 2) in the eastern
561 food web, where microzooplankton diets were more sustained by bacteria and omnivores
562 by both bacteria and DET. This well-defined microbial loop was confirmed by the much
563 higher dependency on bacteria observed in the eastern region (Figure 4) and the higher
564 transfer efficiency between levels II and III (Figure 5). Interestingly, we could also trace a
565 higher dependency on bacteria up to the Arctic cod larvae level, which suggests that a
566 significant fraction of the carbon ingested by Arctic cod larvae had transited through the
567 bacteria compartment in eastern Baffin Bay. Conversely, the overall lower dependency of
568 higher level predators on microzooplankton led to a higher compartmentalization of the
569 eastern food web (Figure 6), characterized by a relative dissociation of the microbial food
570 web from the classical food chain of phytoplankton to *Calanus spp.* to carnivorous
571 organisms.

572 The major difference in the distribution of primary production in the eastern and
573 western regions led to a higher specialization of trophic pathways in the eastern food web.

574The flow of carbon was more constrained through specific pathways, thus minimizing the
575losses caused by the dispersion of carbon through multiple parallel pathways, considered as
576redundant. In this case, direct trophic pathways linking a predator with its main prey were
577preferred (for example, *Calanus* spp. with phytoplankton, and carnivorous
578mesozooplankton with *Calanus* spp.; Figure 3), and accessory prey were neglected favoring
579higher transfer efficiency. The observed higher relative ascendancy value showed that the
580eastern Baffin Bay reached a higher level of both organization and efficiency compared to
581the western food web (Figure 7A). Indeed, eastern primary production was channeled
582towards dissolved carbon and *Calanus* in order to support the large needs of *Calanus* and
583bacteria. The other compartments fed on the latter two according to their preferences,
584leading to the channeling of carbon through some dominant pathways and thus to an
585increase of the organization and transfer efficiency within the system.

586 Some required components of food webs reduce ascendancy and constitute the
587reserves of the system (overheads; Figure 7B), bringing flexibility to it. These reserves have
588several origins and are invested within the following processes: export, dissipation and
589redundancy of trophic pathways. The proportions of redundancy and overhead due to both
590dissipation and export were higher in the western Baffin Bay, which also experienced a loss
591of information corresponding to these flows. This loss implies that the food web is not
592getting the full benefit from the carbon before it is being released by dissipation or export.
593Indeed, the flow values confirm that the higher activity of western compartments (Figure 2)
594associated with a lower transfer efficiency, compared to the east (i.e., the logarithmic mean
595of transfer efficiencies at each level, corresponding to red numbers in Figure 5, was 4.7 in
596the west versus 5.6 in the east), led to a higher proportion of carbon leaving the system. _

597This effect was observed especially at level II (composed mainly of bacteria and
598herbivorous micro- and mesozooplankton) for which export was about three times higher
599in the western food web (Figure 5). At this level of the trophic network, exports refer to the
600production available for predators not considered in this model, as well as to the lipid
601storage accumulated by *Calanus*, which is a very particular feature of Arctic marine
602ecosystems. From this point of view, western Baffin Bay seemed to act according to the
603classical view of Arctic marine ecosystems which are sustained by the large lipid reserves of
604*Calanus* and transfer carbon efficiently towards higher trophic levels like fish and marine
605mammals (not considered in the models). The higher redundancy in the organization of the
606western trophic network also indicates that carbon flowed through alternate trophic
607pathways that favored omnivory, as a consumer can feed on the same prey directly and
608indirectly (Williams and Martinez, 2004). For example, *Calanus* fed directly on
609phytoplankton, while a second pathway indirectly linked *Calanus* to phytoplankton via the
610microzooplankton.

611

612*Interactions between trophic groups*

613 In a network, species interact with each other in various ways: directly by trophic
614exchange between a prey and its predator, but also indirectly through at least one more
615compartment to mediate the transfer of carbon (Wootton, 1994). As the indirect effects are
616often dominant in an ecological network (Higashi and Patten, 1986; 1989), they affect the
617nature of direct relations between species (Ulanowicz and Puccia, 1990; Bondavalli and
618Ulanowicz, 1999). For instance, due to the effect of indirect flows, a predator could be

619beneficial for its prey if it feeds on other predators of this prey (e.g., Bondavalli and
620Ulanowicz, 1999).

621 In both Baffin Bay food webs, the network affected similarly the nature of most
622direct pairwise relations. Direct neutralism (0,0) (i.e., no direct relation between
623compartments) or direct predation was transformed into indirect mutualism (mutually
624beneficial pairwise relations) most of the time. Thus, positive relations became dominant
625when the direct and indirect interactions were considered, as usually emerges in ecological
626networks (Fath and Patten, 1998). Indirect mutualism can occur via various processes
627(Wootton, 1994); we identified at least two kinds of indirect mutualism. The first derived
628from the trophic cascade that involved consumer-resource interactions: the sink
629compartment in the relation (e.g., carnivorous zooplankton) benefits from the source
630compartment (e.g., phytoplankton) as it feeds indirectly on it, while feeding directly on the
631predators of the source compartment, in turn limiting the predation pressure and being
632beneficial for the source compartment. The same mechanism was identified for pairwise
633relations between primary producers or bacteria with trophic levels higher than *Calanus*
634(relations 7, 8, 16, 17, 22–24 in Table 4). The second indirect mutualism involved apparent
635competition mediated by a common predator, like phytoplankton/sea-ice algae and
636bacteria pairwise relations. In this case, the primary producers exuded DOC that was
637mandatory for bacterial growth and bacteria were an alternative resource for grazers.
638Moreover, some direct relations were changed into either i) indirect exploitative
639competition when the compartments involved in the relation exploited the same resources
640(Wootton, 1994), as Arctic cod larvae and DOC (relation 52 in Table 4), which exploited
641micro- and mesozooplankton or ii) apparent competition characterized by a common

642predator (Wootton, 1994). In the latter, a species impacts another one through its influence
643on the abundance of their shared predator (Stige et al., 2018). These two kinds of
644competition are not always easily distinguished. For example, in this study the indirect
645competition between *Calanus* and omnivorous mesozooplankton, as well as between
646microzooplankton and *Calanus*, can be due to the sharing of either a common predator
647(carnivorous mesozooplankton or Arctic cod larvae) or the same resource (phytoplankton
648and microzooplankton or phytoplankton alone, respectively). In this case, further studies
649could reveal which of the top-down or bottom-up effects dominated and led to an indirect
650competition. One approach could consider the network motifs (e.g., Holt et al., 1994; Holt
651and Polis, 1997; Baiser et al., 2016; Klaise and Johnson, 2017), but the challenge is to do so
652in the context of the overall network such that indirect interactions are included. Both
653networks considered in this study obeyed the same processes and thus led to similar
654pairwise relations in the majority of cases.

655 Differences observed in food web functioning in both Baffin Bay regions were
656associated with changes in nine pairwise relations that almost all concerned the
657compartments directly involved in the microbial loop, e.g., DET, bacteria, microzooplankton
658and omnivorous mesozooplankton. The relations between omnivorous and carnivorous
659mesozooplankton were opposite between both food webs: beneficial for the carnivores, as
660expected, in the western food web, while omnivores exploited carnivores in the eastern
661food web (relation 43 in Table 4). As carnivores contributed in higher proportion (Figure 3)
662to the detritus that was in turn consumed in higher proportion by omnivores, the
663carnivores became more beneficial than detrimental for omnivores in the eastern Baffin
664Bay. The stimulation of the microbial loop in the eastern region caused indirect mutualism

665between microzooplankton and DOC and between bacteria and Arctic cod due to the higher
666dependency of microzooplankton on bacteria (Figure 4) and the consumption of this main
667bacterial predator by Arctic cod larvae, respectively. Moreover, changes in the origin of
668detritus were involved, with higher contribution of carnivores to DET at the expense of
669*Calanus* contribution causing indirect mutualism between carnivores and
670microzooplankton as well as between *Calanus* and DET. Finally, higher degradation of DET
671to DOC led to indirect mutualism between bacteria and DET in the eastern region. These
672differences led to more indirect mutualistic relations at the expense of predation in the
673eastern food web. Such differences observed in the nature of pairwise relations could affect
674the dynamics of each food web, as well as their responses to environmental perturbations.

675 Describing and understanding interactions between species are key elements in
676determining the dynamics and fate of an ecosystem confronted with environmental
677perturbation such as invasion, climate change, or extinction. Indeed, extinctions rapidly
678affect ecosystem functions and can be involved in later species extinction (Valiente-Banuet
679et al., 2015). Because of the dominating nature of indirect interactions (Higashi and Patten,
6801986; 1989), using an ecosystem approach that includes the entire food web is critical. This
681whole system approach can determine the crucial role of species in the response to
682perturbations (Wootton, 2002). Moreover, the nature of the indirect interaction affects the
683behavior of the ecosystem (Schmitz et al., 2004). The dominance of indirect mutualism over
684competition decreases the risk of secondary extinction (Vandermeer, 2004). Finally,
685interaction strengths also have an impact on the coexistence of species (Borrett et al.,
6862010). A combination of strong and weak interactions dampens resource-predator
687oscillations and thus insures the stability of the ecosystem (McCann et al., 1998; McCann,

6882000). In the case of eastern and western Baffin Bay, the differences observed in the
689integral relations (direct and indirect) let us assume that each region will have a distinct
690fate in the face of climate change. How each region of the bay will evolve and which region
691presents the most robust network remain open questions.

692

693*Insights on the carbon cycle in the Baffin Bay*

694 Trophic network organization and functioning play a role in the biogeochemistry of
695Arctic marine ecosystems. Our network analysis revealed key information on the behavior
696of the biological pump, especially on carbon cycling within the food web. In the network
697analysis framework, cycling refers to the quantity of organic carbon involved in loops.
698Recycling values of less than 15% in both regions of Baffin Bay were low compared to the
699the value of 25% estimated by network analysis for spring–summer in the Amundsen Gulf
700(Saint-Béat et al., 2018). Bacteria play a major role in carbon cycling (Johnson et al., 2009),
701and bacterial processes greatly impact the values of recycling estimated by the Finn cycling
702index (Saint-Béat et al., 2018). Thus, the overall low bacterial production and low growth
703efficiency (< 2.5%) observed in Baffin Bay contributed to the low recycling. The low growth
704efficiency meant re-mineralization of a considerable proportion of the DOC uptake that
705could not be used for the synthesis of particulate bacterial carbon and thus was considered
706a loss to the food web. Detritivory by zooplankton also plays a significant role in carbon
707cycling, and clear differences were observed between the two regions. In the eastern food
708web, 70% of the detrital carbon was transferred to bacteria as DOC, with only 17%
709consumed by zooplankton, whereas 40% of the detrital pool was transfer to zooplankton in

710the western food web. The higher detritivory contributed to the higher carbon recycling
711observed in the western food web, as revealed by the higher FCI values (Figure 6).

712 The origin of the detritus shed new light on the length of loops in the food webs (i.e.,
713number of compartments involved), and regional differences occurred in the origin of the
714detrital pools. In western Baffin Bay, about 90% of the detritus consumed by level II (e.g.,
715bacteria, *Calanus*, microzooplankton and omnivorous mesozooplankton) appeared to be
716returned to the detrital pool (Figure 3; higher flow from level II to detritus in Figure 5),
717while in the east only about one half returned to detritus. This difference suggested shorter
718cycles in western Baffin Bay, which was confirmed by the slightly lower value of APL, an
719measure that provides complementary information on the retention of carbon within the
720system. Generally, the APL value has the same tendency as the FCI index, and thus higher
721APL is expected in a system with high recycling (Baird et al., 1991). This tendency was not
722the case in Baffin Bay. The larger proportion of recycled carbon observed in western Baffin
723Bay was consumed less by the higher trophic levels (i.e., higher FCI, lower APL) and
724confirmed the presence of shorter cycles. In contrast, the low quantity of recycled carbon in
725the east was transferred up to Arctic cod larvae due to higher bacterivory by micro- and
726omnivorous mesozooplankton, as shown by the higher dependency of these compartments
727on bacteria (Figure 4) and the greater transfer efficiency at level IV (Figure 5).

728 Organic carbon can leave the food web by two processes: dissipation and export. In
729both food webs, carbon mainly exited by dissipation as confirmed by the higher dissipative
730overheads (Figure 7). More carbon was exported out of the western Baffin Bay food web
731(Figure 7) and constituted 37% of the carbon exit from this system, whereas carbon export
732represented only 19% in the eastern food web. In the food web models, exports referred to

733several biological processes: i) sinking of both primary producers and particulate detritus
734(DET), ii) accumulation of reserves by *Calanus* to deal with the winter season, iii) the
735generation of refractory DOC by bacteria, and iv) consumption of carbon by higher trophic
736levels not considered in these models. From a biogeochemical point of view, these exports
737do not have the same respective impacts on the carbon cycle. In the last case, carbon
738exported towards higher trophic levels not considered in the model remains within the
739euphotic zone where it could be re-mineralized. The three other processes are involved in
740the possible sequestration of carbon. As a result, in terms of biogeochemical cycles, the
741western food web exported twice as much carbon out of the euphotic zone as the eastern
742food web. Even though the sinking of phytoplankton and DET was similar, the presence of
743sea-ice algae and their sinking stimulated the biological pump, as shown in other studies
744(Lalande et al., 2013). The microbial and lipid pump were more active in the western food
745web, being twelve times and two times higher, respectively, compared to the east. These
746results show that a consideration of the coupling of the three pumps involving planktonic
747components is essential to developing a more realistic view of potential carbon
748sequestration. As a consequence, the in situ quantification of lipid storage by *Calanus* spp.
749and DOC production by bacteria, via viral lysis and exudation, and the regulation of these
750biological processes by environmental factors, represent important challenges for future
751research.

752

753

754**Conclusion**

755

756 The combination of ecological tools applied in this study revealed the impact of
757contrasting environments on the functioning of planktonic Arctic food webs. The western
758and eastern Baffin Bay under Arctic and Atlantic influence, respectively, showed a distinct
759summer food web functioning. Eastern primary production was more exudative and
760supported a stimulated microbial loop. The rest of the carbon fixed by primary producers
761was transferred efficiently through the grazing chain via *Calanus* spp. In the western food
762web, primary production was consumed evenly by the different grazers, which were the
763main contributors to the DOC pool. The architecture of the food webs differed, leading to
764two distinct biogeochemical functionings. In the eastern region, carbon flowed through a
765more complex network (higher relative ascendancy) that favored direct transfer and the
766segregation of the microbial loop. This network channeled carbon throughout longer
767trophic pathways, revealing stimulation of the microbial loop and an efficient transfer
768towards the highest trophic levels, associated with a direct, classical grazing chain. In
769contrast, in the west, organic carbon flowed through short and redundant pathways and
770was more actively exported through both the lipid and microbial pumps. Moreover the
771distinct food web architecture was coupled to the change of some pairwise relations
772considering both direct and indirect pathways, leading to more mutualism in the eastern
773food web. All of these elements suggest distinct ecosystem dynamics and responses to
774ongoing and expected climate change in the Arctic Ocean. Models covering a longer
775temporal scale (seasonal or yearly) need to be developed, however, to further explore the
776stability properties and response of these food webs under both very strong anthropogenic
777and climatic pressures.

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1068 **Authors Contribution**

1069 BSB, FM and MB designed the study. CA, JC, JD, LF, VG, PLG, FJ, CL, ML, PR, TSN,
 1070 JET and DV contributed to the acquisition and curation of the original data collected during the
 1071 international Green Edge project. BSB assembled the data and performed the numerical
 1072 modelling. BSD analysed the output with significant contribution from BDF. BSB led the
 1073 drafting of the manuscript. All co-authors contributed substantially to the discussion of the results
 1074 and the preparation of the submitted manuscript.

1075

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1090

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1102**Data Accessibility statement**

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1104 All data are available at <https://doi.org/10.17882/59892> (Massicotte et al., 2019).

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1106**Competing interests**

1107The authors have no competing interests to declare.

1108**Supplemental Material**

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1110 • Text S1: Protocols for in situ measurements

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1112 • Table S1 : Values of flows in $\text{g C m}^{-2} \text{ month}^{-1}$

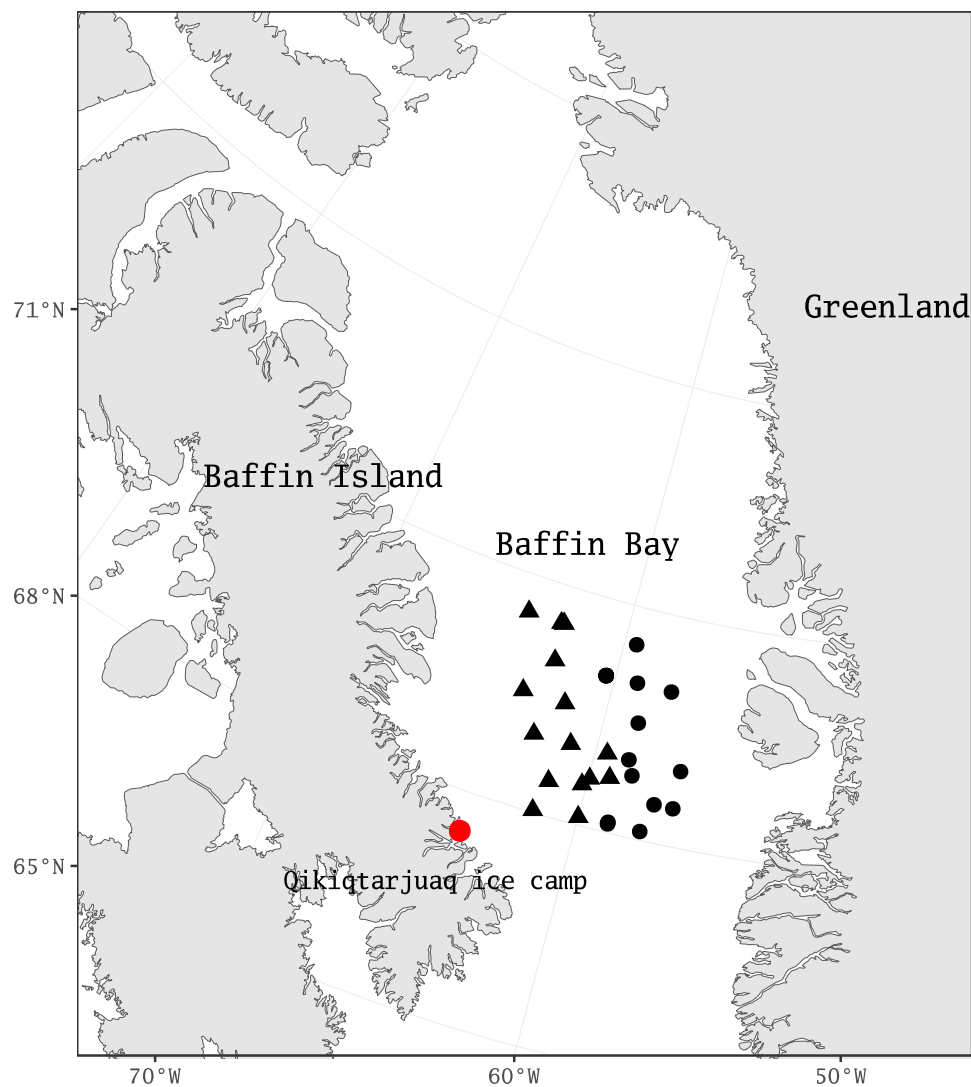
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1117**Figures**



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1119**Figure 1. Map of the sampling stations.**

1120The red circle shows the location of the Qikiqtarjuaq ice camp, and the black circles and triangles
1121indicate the location of stations in the eastern and western region of Baffin Bay, respectively,
1122where data were collected during the cruise onboard the *CCGS Amundsen*.

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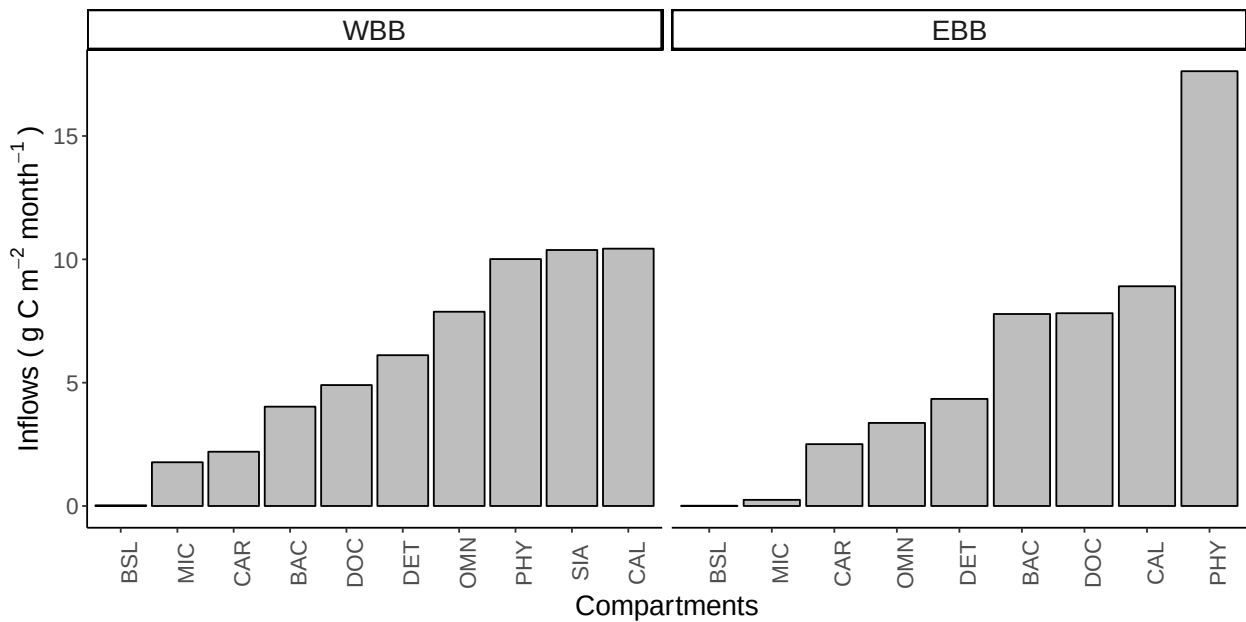


Figure 2. Total inflows for each model compartment in both Baffin Bay food webs

Total inflow was calculated as the sum of mean values of flows received by a compartment and expressed in $\text{g C m}^{-2} \text{ month}^{-1}$ for western (WBB) and eastern (EBB) Baffin Bay. Compartments are bacteria (BAC), Arctic cod (*Boreogadus saida*) larvae (BSL), *Calanus* (CAL), carnivorous mesozooplankton (CAR), omnivorous mesozooplankton (OMN), microzooplankton (MIC), phytoplankton (PHY), dissolved organic carbon (DOC), detrital particulate carbon (DET), and, for WBB only, sea-ice algae (SIA).

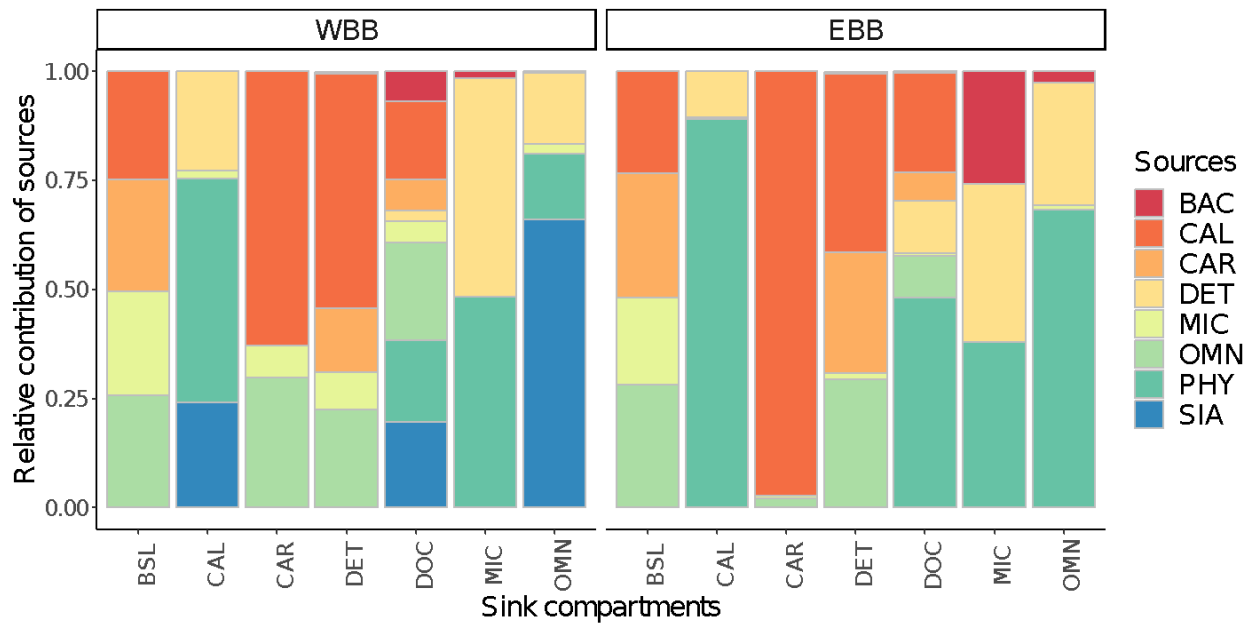
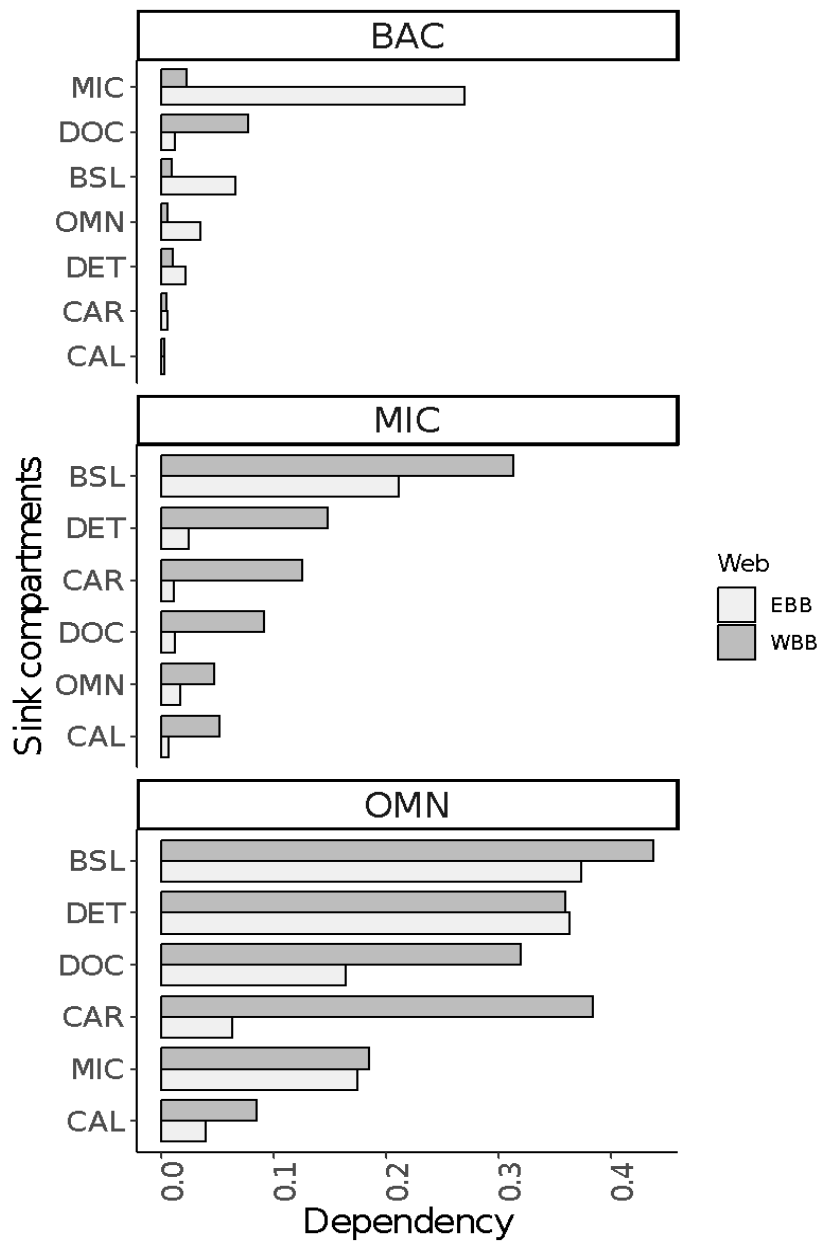


Figure 3. Relative contribution of each carbon source to living and detrital compartments in both food webs.

Sources and sink compartments for the western Baffin Bay (WBB) and eastern Baffin Bay (EBB) food webs are bacteria (BAC), Arctic cod larvae (BSL), *Calanus* (CAL), carnivorous mesozooplankton (CAR), omnivorous mesozooplankton (OMN), microzooplankton (MIC), phytoplankton (PHY), detrital particulate carbon (DET), and dissolved organic carbon (DOC). Sea-ice algae (SIA) were present only in WBB.



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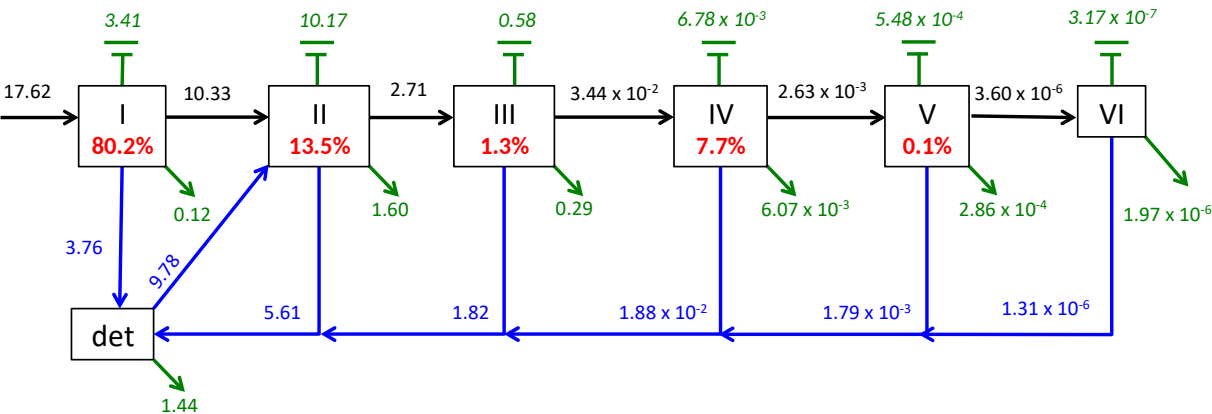
1142**Figure 4. Dependency of compartments on bacteria and direct consumers of bacteria**
 1143**in both food webs.**

1144The dependency for the eastern (EBB, light grey) and the western (WBB, dark grey) Baffin
 1145Bay food webs was calculated for the mean values of flows. Sink compartments are bacteria
 1146(BAC), Arctic cod larvae (BSL), *Calanus* (CAL), carnivorous mesozooplankton (CAR),

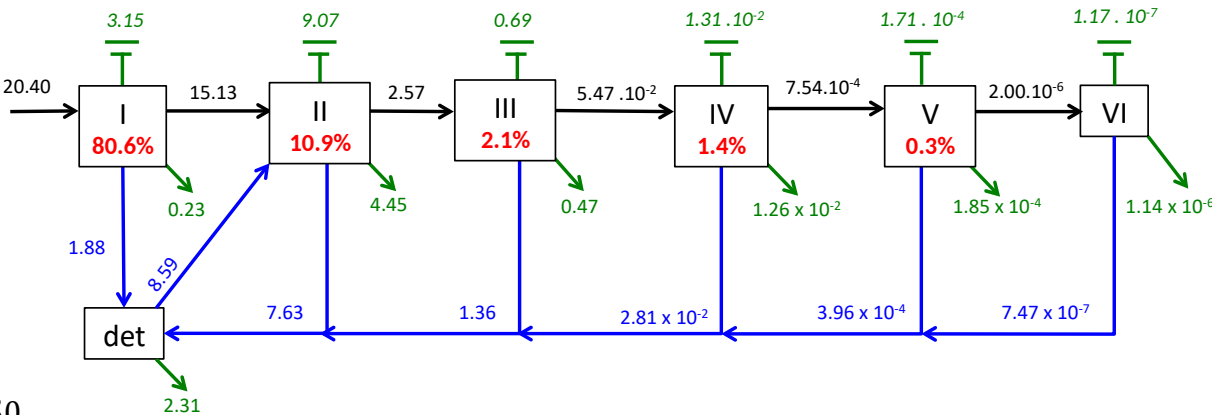
1147omnivorous mesozooplankton (OMN), microzooplankton (MIC), dissolved organic carbon
1148(D)C, and detrital particulate carbon (DET).

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A) Eastern Baffin Bay



B) Western Baffin Bay



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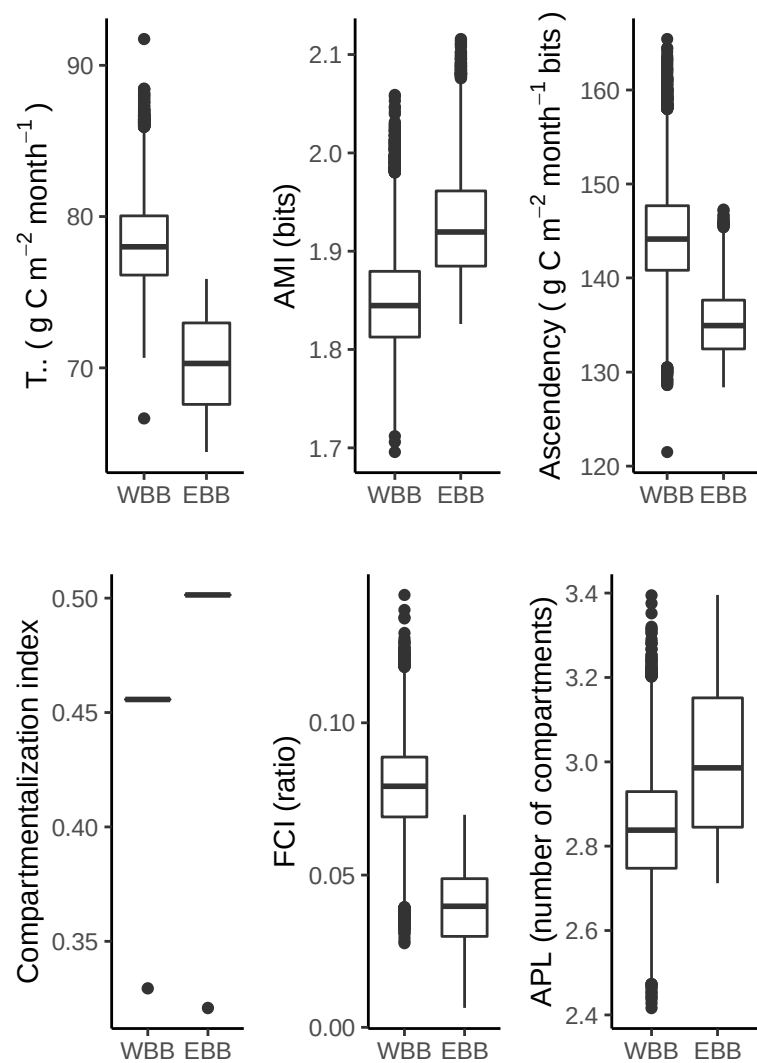
1152Figure 5. Lindeman Spine of carbon transfer in both Baffin Bay food webs

1153All values for A) eastern Baffin Bay and B) western Baffin Bay are in g C m⁻² month⁻¹. Green
1154symbols represent loss at each integer level (arrows for export and ground symbol for
1155respiration). Black and blue arrows refer to the grazing chain and the flows to/from
1156detritus (det; i.e., particulate and dissolved), respectively. Transfer efficiencies
1157corresponding to the proportion of inflows to one level that flows to the next level are given

1158by bold red numbers at each trophic level. Food web components are distributed through
1159the integer trophic levels according to their diets. Level I is composed of primary producers;
1160level II represents bacteria, microzooplankton, *Calanus* and omnivorous mesozooplankton;
1161level III refers to every zooplankton group and Arctic cod larvae; level IV excludes
1162microzooplankton; and level V integrates carnivorous mesozooplankton and Arctic cod
1163larvae, which is the lone constituent of level VI.

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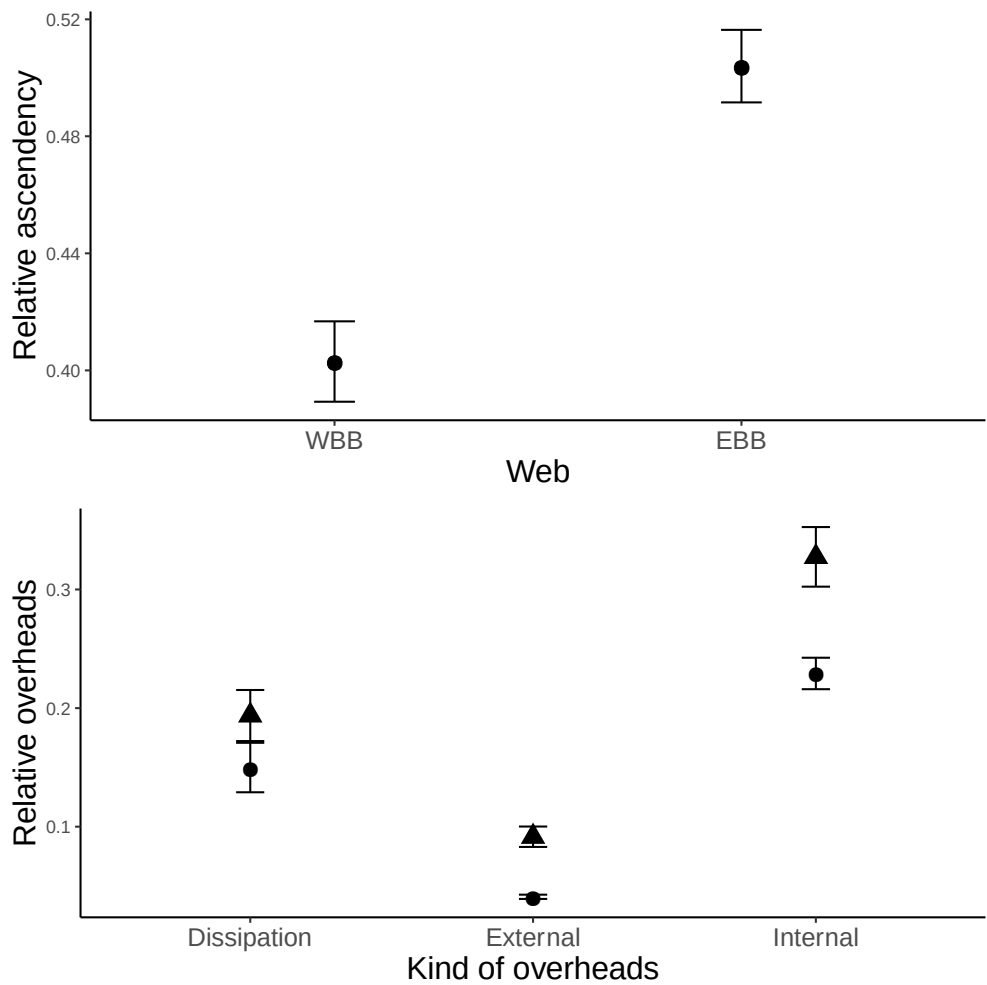
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Web

1168**Figure 6. Ecological network analysis indices describing the architecture of both**
1169**Baffin Bay food webs.**

1170For the food webs in both the eastern Baffin Bay (EBB) and western Baffin Bay (WBB), total
1171throughput (T.), average mutual information (AMI), ascendancy, compartmentalization
1172index , Finn cycling index (FCI), and average path length (APL) were calculated from the set
1173of 20,000 random solutions calculated by LIM-MCMC. Box plots present five statistics: the

1174median, corresponding to the horizontal line inside each box; the first and third percentiles
1175as lower and upper boundaries of the box, respectively; and the values within 1.5 times the
1176interquartile range above the 75% percentile or above the 25% percentile, shown as
1177whiskers. Values outside this frame are represented individually as points along the vertical
1178line. Note that the boxplot for the compartmentalization index presents only the median
1179and one outside value.



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1181**Figure 7. Relative ascendency and reserves associated with each kind of overhead for**
1182**both food webs.**

1183Relative ascendency (upper panel) and relative reserves or overheads (lower panel) for
1184both the western Baffin Bay (WBB) food web (triangles) and eastern Baffin Bay (EBB) food

1185web (circles). Relative overheads correspond to overheads scaled by the maximal possible
1186ascendency. Each symbol represents the mean value with its standard deviation calculated
1187from the set of 20,000 random flows solutions.

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