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RESEARCH ARTICLE

An estimation of the quantitative impacts of copepod grazing on an under sea-ice spring phytoplankton bloom in western Baffin Bay, Canadian Arctic

Makoto Sampei^{1,2,*}, Louis Fortier^{3,4}, Patrick Raimbault⁵, Kohei Matsuno^{1,6}, Yoshiyuki Abe⁷, Bernard Quéguiner⁵, Augustin Lafond⁵, Marcel Babin^{3,4}, and Toru Hirawake^{1,6,8}

This study aimed to quantify the impact of copepod grazing on the productivity of phytoplankton during an under sea-ice spring phytoplankton bloom (USPB) in western Baffin Bay. To quantify positive and/or negative impacts of copepod grazing on primary production and the interaction between copepod grazing and phytoplankton species, we sampled seawater and zooplankton under the landfast sea ice every 2–3 days between May 24 and July 10, 2016. Samples were analyzed for estimation of primary production, chlorophyll-*a* (chl-*a*) concentration, diatom abundance, and copepod fecal pellet (FP) production/grazing rate. Analyses of chl-*a* concentration, primary production, and FP production/grazing rate revealed clear temporal changes and a mismatch between primary production and copepod consumption. The FP production/grazing rate reached a maximum (9.4/31.2 mg C m⁻² d⁻¹) on June 16 before the USPB phase and suddenly decreased to 0.7/2.4 mg C m⁻² d⁻¹ on June 21, despite an increase in primary production to 74.0 mg C m⁻² d⁻¹. The copepod grazing rate (3.7 mg C m⁻² d⁻¹) was low relative to primary production (344.6 mg C m⁻² d⁻¹) during the USPB phase (after June 20). While our estimates illustrate that copepod grazing did not limit the maximum daily primary production during the USPB, the low grazing pressure (2% of primary production) may have been an additional contributor to the reduction in total primary productivity at the end of the USPB period due primarily to the low supply of regenerated nitrogen-containing nutrients to drive regenerated production.

Keywords: Under sea ice, Grazing, Fecal pellets, Copepod, Top-down control, Spring bloom, Arctic water

1. Introduction

In the context of global change, many studies on the fate of primary productivity have been conducted to quantify the responses of the marine ecosystem and biogeochemical cycling to ongoing alteration of the physical environment, such as sea-ice and glacial ice conditions in Arctic

waters (e.g., Tremblay et al., 2006; Tremblay et al., 2012; Reigstad et al., 2011). Although the ecological and biogeochemical importance of production by ice algae in Arctic waters has been identified (e.g., Gosselin et al., 1997; Lee et al., 2008; Gradinger, 2009), most studies on primary production and its ecological roles in the Arctic seasonal ice zone during the most productive season (i.e., spring) have been conducted in open waters because of the logistical difficulties of working in sea-ice-covered waters. In recent years, massive large-scale under sea-ice spring phytoplankton blooms (USPB) have been observed in Arctic waters (e.g., Arrigo et al., 2012, 2014; Spall et al., 2014). The current estimate of primary production (5–10 g C m⁻² yr⁻¹) may represent a drastic underestimate when compared with a scenario that includes the USPB (>70 g C m⁻² yr⁻¹) in Chukchi shelf water (Arrigo et al., 2014).

Primary production is affected by top-down control (i.e., controlled by feeders) and bottom-up control (i.e., controlled by nutrient availability and photosynthetically active radiation in sea-ice-covered waters) in the water column (e.g., Verity and Smetacek, 1996; Wassmann, 1998). Top-

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down control can affect the taxonomic structure, biomass, and productivity of the primary producers in the water column, the phytoplankton (Campbell et al., 2009; Sherr et al., 2009), while primary production/producers impact the biomass and taxonomic structure of herbivores such as copepods in the water column (Springer et al., 1989).

Despite the ecological importance of the USPB in sea-ice-covered waters under ongoing rapid changes in sea-ice conditions (e.g., sea-ice coverage, thickness, and timing of retreat), the relationships between processes that regulate the USPB (e.g., top-down and bottom-up controls) are

unclear. This article focuses on the top-down control by copepod grazing activity during the USPB period as a part of the Green Edge project. We specifically address the quantitative impacts of copepod grazing on the USPB in southwestern Baffin Bay, Canadian Arctic.

2. Materials and methods

2.1. Study area

Baffin Bay is located between the Canadian Archipelago and Greenland, bordered by the Labrador Sea and the Atlantic Ocean in the south and connected to the Arctic

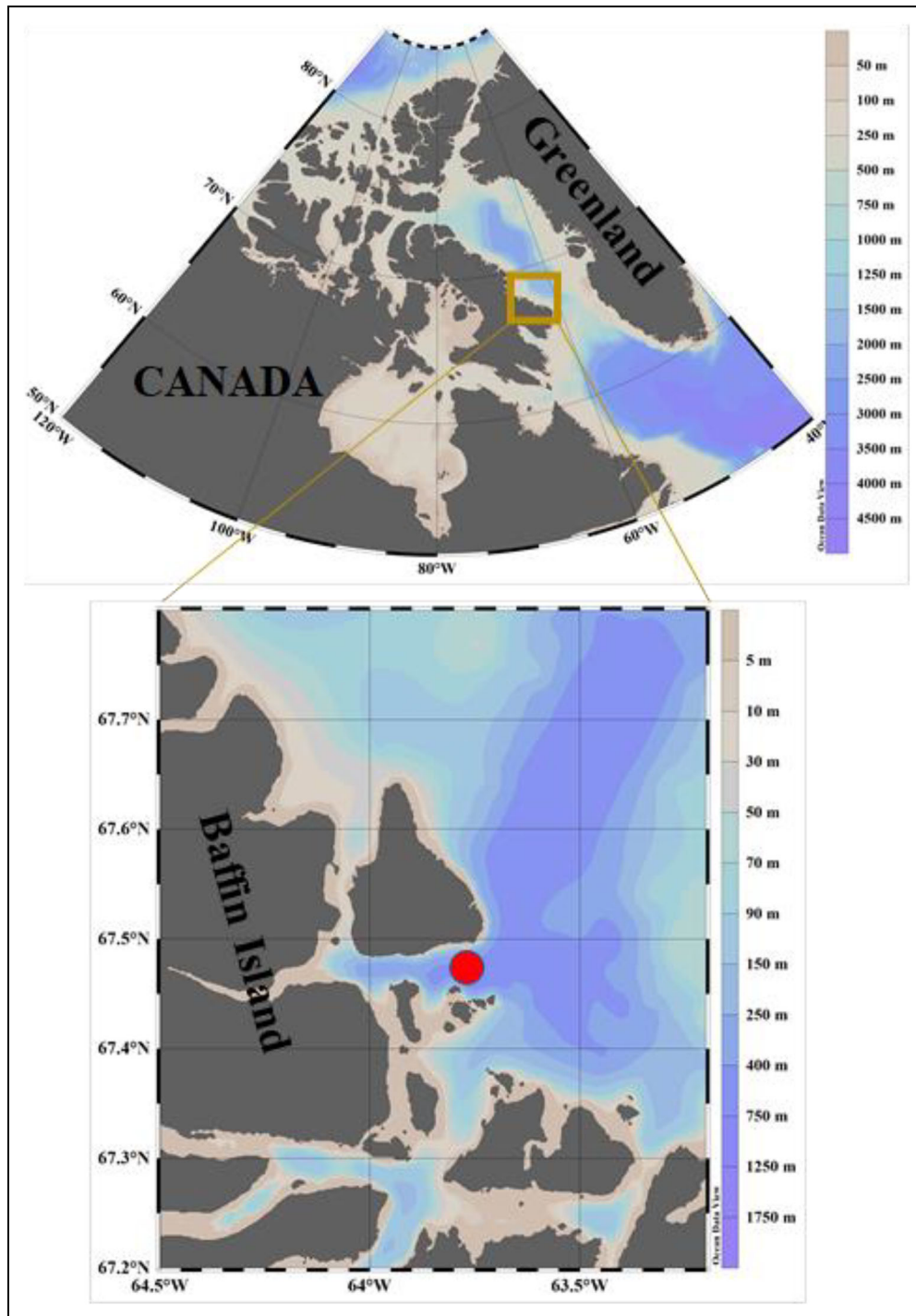


Figure 1. Bathymetrical map with location of the sampling site on landfast ice in western Baffin Bay. Red closed circle shows the sampling site. DOI: <https://doi.org/10.1525/elementa.2019.00092.f1>

Ocean by the Nares Strait in the north (**Figure 1**). The water originating from the Arctic Ocean and the Atlantic Ocean flows, respectively, from north to south on the western side of Baffin Bay and from south to north on the eastern side (Tang et al., 2004). Our study site (ice camp) was located on landfast sea ice on the eastern coast of Baffin Island (67.48°N, 63.79°W, water depth of 350 m) in southwestern Baffin Bay and was representative of the marine conditions prevailing in western Baffin Bay in terms of water masses and sea-ice conditions (see Oziel et al., 2019, and references therein).

Sea-ice thickness was approximately 1.3 m on March 24, 2016 (beginning of the study period), about 1 m on July 8, 2016 (end of the study period), and ranged from 1 to 1.5 m thick during the study period (Oziel et al., 2019). Snow cover thickness on the sea ice was approximately 30 cm before snow melt initiation on June 3, 2016, and gradually decreased to 8 and <1 cm until the appearance of melts pond on June 17, 2016 (Oziel et al., 2019). Concentration of the nutrients nitrate (NO_3^-), phosphate (PO_4^{3-}), and orthosilicic acid ($\text{Si}(\text{OH})_4$) within the upper 20 m before June 16, 2016, were consistently high at >5, >0.8, and >6 $\mu\text{mol L}^{-1}$, respectively (Oziel et al., 2019). These nutrient concentrations decreased gradually between June 16 and July 7, 2016, to <1, <0.6, and <3 $\mu\text{mol L}^{-1}$, respectively (Oziel et al., 2019). The nutrient profiles suggested that the USPB was slowed by nitrogen limitation in the water under landfast ice.

2.2. Chlorophyll-*a* (chl-*a*) concentration in the water column

Water sampling with Niskin bottles was conducted in a heated tent set up over a 1 × 1 m hole on the landfast ice every 2–3 days between May 24 and July 8, 2016, as part of the Green Edge 2016 field campaign in western Baffin Bay. The seawater samples were taken at five depths: 1.5 (bottom of the sea ice), 5, 10, 20, and 40 m. To determine chl-*a* concentration, a subsample of the seawater was filtered through a glass fiber filter (Whatman GF/F, 0.75 μm pore size). Filtered samples were immediately soaked in 90% acetone to extract pigments under dark and freezing (−20 °C) conditions for 24 h (Persons et al., 1984). The fluorescence intensity was measured with a Turner Designs 10AU fluorometer (San Jose, CA) calibrated against a pure chl-*a* standard (Sigma, St. Louis, MO), and chl-*a* concentration was calculated according to the acidification method (Holm-Hansen and Riemann, 1978). The chl-*a* concentration was integrated between 0 and 40 m and expressed in mg chl-*a* m^{-2} .

2.3. Primary productivity of under sea-ice phytoplankton

Rates of C fixation by phytoplankton (primary production) were measured using a dual $^{13}\text{C}/^{15}\text{N}$ isotopic technique (Raimbault et al., 1999) as described in Massicotte et al. (2020). Column-integrated primary production between 0 and 20 m was calculated on the basis of rates measured at four depths (0.5, 1.5, 5, or 10 m, and 20 m beneath the sea ice). The depth of the integrated water column (i.e., 0–20 m) was chosen on the basis of the in-site euphotic zone

depth. The euphotic zone (>0.415 mol photons $\text{m}^{-2} \text{d}^{-1}$) was always shallower than 20 m before June 15 and was approximately 20 m after June 15 until July 7 (Oziel et al., 2019).

2.4. Diatom composition in the water column

For phytoplankton taxonomy and abundance, 70 mL water samples were taken from the surface (at 1.5, 5, or 10 m depth) through the 1 × 1-m sea-ice hole using Niskin bottles on May 25; June 17, 24, 27, and 29; and July 1. Samples were immediately fixed in 0.3 mL acidified Lugol's solution for storage until microscopic analyses. At the laboratory, phytoplankton taxonomy and abundance were determined by concentrating 70 mL of sample in a sedimentation chamber (Utermöhl, 1931) followed by identification and counting using a Nikon Eclipse TS100 inverted microscope (as detailed in Lafond et al., 2019).

2.5. Copepod sampling, identification, and estimation of fecal pellet (FP) production and grazing rates

Zooplankton sampling was conducted through the 1 × 1-m sea-ice hole every 2–7 days between May 24 and July 7, 2016. A 200- μm mesh, 1-m mouth diameter conical net equipped with a rigid live-capture cod-end was hauled vertically from 100 m (from May 24 to June 21) or 30 m (from June 25 to July 10) to the surface at a towing speed of 0.3 m s^{-1} . The towing depth was changed owing to reasons related to the sampling protocols of other studies, yet the change minimally affected the results of this study because the euphotic zone was about 20 m or less during the study period (Oziel et al., 2019). The filtered volume was estimated using a digital flowmeter with back-run stop (KC Denmark, Holmbladsvej, Denmark) mounted inside the 200- μm mesh net. The filtered volume was an averaged value from vertical net towing (100 m to the surface at a towing speed of 0.5 m s^{-1}) on the days immediately before and after sampling (e.g., estimation of the value for June 16 was the averaged value of readings on June 15 and 17) because the towing speed for the experiments was too low to measure the filtered volume. To remove the effects of variation in the volume filtered because of the difference in net towing depth (30 or 100 m), the FP production rate and abundance of copepod specimens were standardized for those data using a towing distance of 100 m (i.e., the production rate per square meter = raw data × 100/towing depth). The net was deployed from the sea-ice hole at around 12:00 (\pm 4 h) local time.

After retrieval, live zooplankton were rinsed gently with filtered (Whatman GF/F glass fiber filter, pore size 0.8 μm) seawater and sieved into >1 and <1 mm fractions for incubation. The incubation method followed Sampei et al. (2009). Briefly, each fraction was transferred to a plastic cylinder immersed in a 1.5-L incubation jar filled with filtered (Advantec membrane capsule cartridge filter, pore size 0.2 μm) seawater and kept at about 0 °C for >12 h. The bottom of the plastic cylinder was lined with 500- μm mesh (>1-mm live zooplankton fraction) or 200- μm mesh (<1-mm fraction) to reduce feeding on FPs during the

Table 1. Temporal variabilities (in 2016) of copepod abundances in the incubated copepod assemblages (ind. m⁻²). DOI: <https://doi.org/10.1525/elementa.2019.00092.t1>

Copepod Species	May 24	May 28	May 31	June 7	June 11	June 16	June 21	June 25	June 28	June 30	July 2	July 5	July 7	July 10
<i>Calanus glacialis</i> (CI–III)	0	148	73	641	3	66	0	416	922	252	2,257	10	698	2,333
<i>C. glacialis</i> (CIV–VI)	38	296	48	139	316	495	46	222	641	199	484	58	183	288
Pseudocalanus spp. (CI–III)	224	287	0	477	0	0	0	0	2,307	252	503	0	2,433	1,162
Pseudocalanus spp. (CIV–VI)	5,148	9,786	1,287	8,351	1,658	913	625	2,695	7,389	6,080	4,265	417	3,829	1,415
<i>Metridia longa</i> (CI–III)	0	287	0	0	0	0	0	0	0	0	0	0	0	0
<i>M. longa</i> (CIV–VI)	37	67	0	30	209	237	156	8	30	318	38	38	13	70
<i>Calanus hyperboreus</i>	108	9	12	77	77	54	3	2,073	117	1,178	696	1,046	5,283	1,442
<i>Oithona similis</i>	11,855	9,752	508	10,171	3,428	1,051	1,438	12,443	19,392	3,548	10,289	0	6,608	6,754
Copepod nauplii	5,927	6,597	36	10,171	1,347	92	816	8,088	34,628	2,532	11,037	130	6,608	5,592
Others	346	3,874	76	1,443	785	189	306	828	1,407	508	2,013	130	2,087	1,634

incubation. Incubated zooplankton and produced FPs were picked separately and preserved in buffered formalin (5% v/v) for later microscopic observation. This method underestimates FP production rate by fragile gelatinous zooplankton such as appendicularians because they are easily damaged by plankton nets (Sampei et al., 2009).

FP samples were counted and their dimensions measured (width, length, and shape) under a stereomicroscope (20–40× magnification). FP production rate (mg C m⁻² d⁻¹) was estimated on the basis of geometrical data (produced FP volume), a gut clearance time of 33 min for *Calanus glacialis* stages copepodite V (CV) and copepodite VI (CVI: adult female) in northern Baffin Bay (Tremblay et al., 2006), and a conversion factor from FP volume to particulate organic carbon content of 0.048 ± 0.03 mg C mm⁻³ (González and Smetacek, 1994). The FP production rate was estimated for four FP width fractions (<50, 50–100, 100–150, and >150 μm). Zooplankton specimens in a known aliquot (1.6%–100% of total incubated specimens) containing >200 specimens were counted and identified to species and developmental stages under a stereomicroscope (10–40× magnification). The main copepod species likely contributing to a given width class of the produced FPs were identified on the basis of potential FP producers for a given width class (Sampei et al., 2009) and their abundance in the incubated assemblage (ind. m⁻²; **Table 1**).

Grazing rate was estimated from the FP production rate, assuming a digestion efficiency of 70% (Ikeda and Motoda, 1978) as grazing rate = FP production rate × 100/30. Feeding pressure on primary productivity of phytoplankton was further estimated as feeding pressure (%) = grazing rate/primary productivity × 100. Because no primary productivity measurements were conducted on the same days as FP production measurement, primary productivity on the days of FP production measurement were interpolated as averaged values of the productivity on days immediately before and after the date of measurement. All statistical analyses were performed using JSTAT 20.0 J software (Masato Sato, Tokyo, Japan).

3. Results

3.1. Chl-*a* concentration and primary productivity in the water column

The chl-*a* concentration was low (<1.6 mg chl-*a* m⁻³) and stable in the water column (0–40 m depth) between May 24 and June 22. After June 24, chl-*a* concentration peaked at 20 m or shallower depth and stayed relatively high (2.6–7.0 mg chl-*a* m⁻³) until July 8. The column-integrated chl-*a* biomass (**Figure 2**) was constantly low (<9.3 mg chl-*a* m⁻²) until June 15 and then rapidly doubled (to 20.0 mg chl-*a* m⁻²) in 5 days (between June 15 and 20). The concentration gradually increased to 219.7 mg chl-*a* m⁻² by the end of the sampling period (July 8). Temporal variability of the depth-integrated primary productivity (0–20 m) is shown in **Figure 2**. The temporal change was similar to that observed for chl-*a* concentration, with stable low primary productivity (<20 mg C m⁻² d⁻¹) until June 13 and then a doubling (to 48.4 mg C m⁻² d⁻¹) in 7 days (between June 13 and 20). Primary production continued to increase rapidly

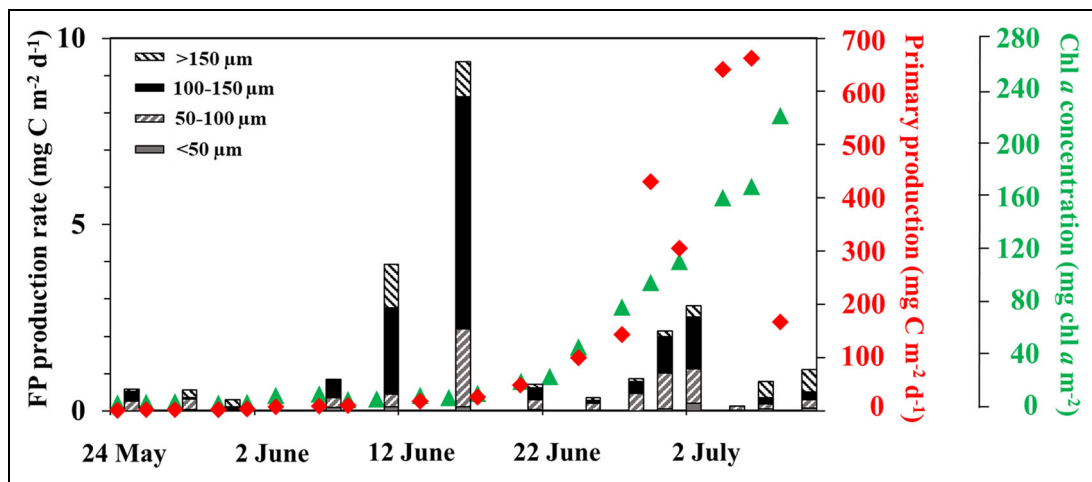


Figure 2. Temporal variabilities of integrated primary production, chlorophyll-*a* (chl-*a*) concentration, and fecal pellet (FP) production rate. Red closed diamonds and green closed triangles show the integrated (0–20 m) primary production ($\text{mg C m}^{-2} \text{d}^{-1}$) and chl-*a* concentration ($\text{mg chl-}a \text{ m}^{-2}$), respectively. Bars show FP production rate ($\text{mg C m}^{-2} \text{d}^{-1}$) for four width ranges (gray: $<50 \mu\text{m}$ and gray stripes sloping up, left to right: $50\text{--}100 \mu\text{m}$; black: $100\text{--}150 \mu\text{m}$ and black stripes sloping up, right to left: $>150 \mu\text{m}$). DOI: <https://doi.org/10.1525/elementa.2019.00092.f2>

Table 2. Temporal variability of diatom abundance (cells L^{-1}) in the water column. DOI: <https://doi.org/10.1525/elementa.2019.00092.t2>

Diatom Species	Sampling Date in 2016 (and Sampling Depth)							
	May 18 (1.5 m)	May 25 (1.5 m)	June 17 (5 m)	June 24 (5 m)	June 24 (10 m)	June 27 (10 m)	June 29 (1.5 m)	July 1 (10 m)
Pseudo-nitzschia spp. (delicatissima group)	200	400	2,640	296,516	14,1075	552,012	258,426	350,428
Pseudo-nitzschia spp. (seriata group)	0	0	0	15,840	15,561	49,224	21,096	41,020
Fragilariopsis spp.	280	320	7,040	73,800	58,653	250,222	173,647.5	69,148
Nitzschia spp.	80	1,960	16,720	1,800	513	640	1,370	14,064
Chaetoceros spp.	0	80	120	720	855	11,680	30,482.5	54,498
Thalassiosira spp.	0	80	320	560	855	2,080	1,370	1,172
Other diatoms	840	1,8120	11,880	21,240	72,846	68,278	88,022.5	106,066
Total	1,400	20,960	38,720	410,476	290,358	934,136	574,414.5	636,396

until July 6 ($661.9 \text{ mg C m}^{-2} \text{d}^{-1}$) and then dropped to $166.1 \text{ mg C m}^{-2} \text{d}^{-1}$ by July 8.

3.2. Diatom composition in the water column

The temporal variability of diatom abundance in the water column is shown in **Table 2**. *Nitzschia* spp. and *Pseudo-nitzschia* spp. were the most dominant diatoms in the community before June 17 and after June 24, respectively. There was a clear temporal change as the cell numbers of most diatoms rapidly increased between June 17 and June 24 (approximately 11-fold increase in total diatoms), and the abundances remained high until July 1. Potentially noxious *Pseudo-nitzschia* spp. increased from 2,640 cells L^{-1} to 312,356 cells L^{-1} (>100 -fold) during the same time frame. The contribution of *Pseudo-nitzschia* spp. to the total diatom abundance sharply increased from 2%–7%

(before June 17) to 49%–76% (after June 24), while the contribution of *Nitzschia* spp. decreased from 9%–43% (before June 17) to $<1\%$ –2% (after June 24). These changes reflect the quantitative importance of *Pseudo-nitzschia* spp. in the diatom community after June 24.

3.3. FP production rate, grazing rate, and feeding pressure

Clear temporal variability was observed for the total FP production rate (**Figure 2**). The FP production rate was consistently low ($<0.9 \text{ mg C m}^{-2} \text{d}^{-1}$) until June 7 and suddenly increased on June 11 to $3.9 \text{ mg C m}^{-2} \text{d}^{-1}$ when the integrated chl-*a* concentration and the integrated primary production were still low. The maximum FP production rate was recorded on June 16 ($9.4 \text{ mg C m}^{-2} \text{d}^{-1}$) before dropping sharply to $0.7 \text{ mg C m}^{-2} \text{d}^{-1}$ on June 21

Table 3. Temporal variabilities of interpolated primary production ($\text{mg C m}^{-2} \text{d}^{-1}$), grazing rate ($\text{mg C m}^{-2} \text{d}^{-1}$), and grazing pressure on primary production (%), grazing rate/primary production $\times 100$). DOI: <https://doi.org/10.1525/elementa.2019.00092.t2>

Process	May 24	May 28	May 31	June 7	June 11	June 16	June 21	June 25	June 28	June 30	July 2	July 5	July 7	July 10
Primary production ($\text{mg C m}^{-2} \text{d}^{-1}$)	1.3	2.1	2.6	9.2	14.6	22.3	74.0	122	287	368	474	652	414	166
Grazing rate ($\text{mg C m}^{-2} \text{d}^{-1}$)	1.9	1.9	1.0	2.8	13.1	31.2	2.4	1.2	2.9	7.1	9.4	0.4	2.6	3.7
Feeding pressure (%)	146	90	38	30	90	140	3	1	1	2	2	<1	1	2

when the integrated chl-*a* concentration and the integrated primary production began increasing gradually in the water under the landfast ice. After June 21, the FP production rate stayed relatively low at $<2.8 \text{ mg C m}^{-2} \text{d}^{-1}$, but a second peak was observed on July 2, before decreasing again despite high and gradually increasing chl-*a* concentration and primary production. At least 94% of the FPs produced throughout the study period was cylindrically shaped (data not shown). The temporal variability of the FP production rate was inconsistent with the temporal variability of either the integrated chl-*a* concentration or primary production. There were no significant relationships between the FP production rate and integrated chl-*a* concentration ($r = -.213$, $p > .05$, $n = 14$) or primary production ($r = -.180$, $p > .05$, $n = 14$).

The contribution of FPs in the width range of 50–150 μm (33%–91%) was generally higher than the contribution of other width range fractions (i.e., $<50 \mu\text{m}$ and $>150 \mu\text{m}$) over the entire study period. The FP width ranges of 50–100 μm and 100–150 μm dominated (89%) the total FP production on June 16 when the highest FP production rate was recorded; FPs in the 100–150 μm fraction accounted for 67% of the total produced FPs. The FP width range of 50–150 μm was also dominant (68%) on June 11 when the second highest FP production rate was recorded; again, the 100–150- μm fraction occupied a substantial proportion (59%) of the total produced FPs.

Grazing rate ($\text{mg C m}^{-2} \text{d}^{-1}$) and feeding pressure (%) on primary productivity of phytoplankton (i.e., grazing rate/primary productivity $\times 100$) is presented in **Table 3**. The grazing rate showed a similar pattern with FP production rate, given that the grazing rate was estimated based on the FP production rate. The feeding pressure on phytoplankton was one–two orders of magnitude higher before June 11 (30%–146%) than after June 21 ($<1\%$ –3%).

3.4. Taxonomic composition in the incubated assemblage

Oithona similis, unidentified copepod nauplii, *Pseudocalanus* spp., *C. glacialis*, *Triconia borealis*, and *Calanus hyperboreus* were the most abundant specimens in the copepod assemblage (**Table 1**). Another common large Arctic copepod species, *Metridia longa*, also appeared with comparably low abundance. *C. glacialis* CIV–CVI and *M. longa* CIV–CVI had comparably high abundances on June 11 and 16 when higher FP production rates were observed. Apart from these two copepod groups, no other groups had higher abundances on June 11 and 16 than on other dates. A significant positive correlation was observed between the abundance of *C. glacialis* CIV–CVI plus *M. longa* CIV–CVI and FP production rate ($r = .705$, $p < .01$, $n = 14$). These results highlight the importance of the more mature stages of two large Arctic copepod species on FP production under the landfast ice.

4. Discussion

4.1. Important contributors to FP production rate

We found a temporal change in the FP production rate during the conditions of an under sea-ice phytoplankton

bloom, with the highest FP production rate recorded on June 16 when chl-*a* concentration and primary production were still low. These results raise the question of which zooplankton species were primarily responsible for the high FP production rates on June 11 and 16. Crustaceans such as copepods and mysids produce cylindrical FPs (Wexels Riser et al., 2002; Wilson et al., 2008), and >99% of the FPs produced in this study were cylindrical. Additionally, potential producers of the dominant cylindrical FPs in the width range of 100–150 µm were copepods with prosome lengths of 2.5–3.9 mm (*C. glacialis* CIV–CVI, *M. longa* CIV–CVI, and *C. hyperboreus* CI–CVI; Sampei et al., 2009), and these copepods were present at relatively high abundances in the copepod assemblages. The cylindrical pellets could not have been produced from the in vitro predation of large carnivores such as *Pareuchaeta glacialis* on small copepods because none of the cylindrical FPs from the incubations contained copepod remnants such as spines (see also Sampei et al., 2009). Thus, these results, combined with the significant positive correlation between FP production rate and abundances of the two large Arctic copepod species, suggest that *C. glacialis* CIV–CVI and *M. longa* CIV–CVI were the main contributors to FP production. In other words, *C. glacialis* CIV–CVI and *M. longa* CIV–CVI were the main feeders on phytoplankton in water under the landfast ice.

4.2. Grazing impact on primary production

To quantify grazing impact (i.e., top-down control) on the primary productivity of under sea-ice phytoplankton, grazing rate, and feeding pressure were estimated in this study (Table 3). The feeding pressure on phytoplankton was >100% on May 24 (146%) and June 16 (140%). These values may reflect errors in the assumed values for converting FP volume to particulate organic carbon and for digestion efficiency. These values may also indicate that ice algae provided an additional food source for copepods because the presence of ice algae was confirmed by substantial chl-*a* concentrations in the bottom part (0–3 cm) of the sea ice (5.9 mg m⁻² on May 23 and 5.3 mg m⁻² on June 15; Massicotte et al., 2020). A change in ice-algal biomass, however, is not likely the main factor controlling the increase in copepod grazing rates between June 11 and 16 (>2 times) and the sudden decrease in the grazing rate between June 16 and 21 (approximately one-tenth) because the change in chl-*a* concentration in the sea ice did not match the change in grazing rate, that is, an approximate 30% decrease occurred between June 11 and 16 (5.3 mg m⁻² and 3.7 mg m⁻², respectively) and approximate 10% decrease between June 16 and 21 (3.7 mg m⁻² and 3.3 mg m⁻², respectively). Sea-ice algal chl-*a* concentrations were interpolated as described above using chl-*a* concentration data from Massicotte et al. (2020) because no chl-*a* measurements were conducted on those particular dates. As phytoplankton biomass might remain only 33 min in the gut of copepods (for *C. glacialis* CV and CVI: Tremblay et al., 2006), the time lag between feeding and evacuation has no effect on a consideration of this match or mismatch.

A clear difference in the feeding pressure was observed between May 24 and June 16 when primary production was still low (1.3–22.3 mg C m⁻² d⁻¹) and June 21 to July 10 (74.0–651.8 mg C m⁻² d⁻¹) under the USPB phase. The feeding pressure before June 16 was high (30%–146%; average 89%), while the feeding pressure after June 21 was low (<1–3%; average 2%). These variabilities in feeding pressure are consistent with a global comparative analysis indicating that feeding pressure is higher under low primary productivity conditions than under high primary productivity (Calbet, 2001). Grazing pressure has been estimated by previous studies in Arctic waters (e.g., Nielsen and Hansen, 1995; Hanse et al., 2003; Tremblay et al., 2006). The feeding pressures from northern Baffin Bay between April and July (about 79%; Tremblay et al., 2006), the southeastern Beaufort Sea in spring–summer (33%–60%; Forest et al., 2011), and Disko Bay during the bloom (80%; Nielsen and Hansen, 1995) were comparable to the higher feeding pressures before June 16 in this study. The feeding pressure from Disko Bay during bloom development (2.9%; Dünweber et al., 2010) and during the sea-ice breaking period (12%–23%, based on a model calculation; Hansen et al., 2003) were comparable to the lower feeding pressures after June 21 in this study. Thus, the quantitative impact of copepod grazing (i.e., top-down control) on primary productivity by the USPB was low, although copepod grazing could quantitatively impact the primary productivity of phytoplankton under pre-USPB conditions in the water column under landfast ice. We discuss the possible reasons for the low quantitative impact of copepod grazing on the USPB primary productivity in Section 4.4.

4.3. Temporal mismatch between copepod grazing and primary productivity

Match and mismatch scenarios between zooplankton grazing rate and primary production (see also Sakshaug, 2004) have both been reported in Arctic waters (e.g., Sampei et al., 2004, 2011; Reigstad et al., 2008). The relationship between grazing rate and primary production clearly showed a mismatch scenario in the present study. This mismatch (high primary productivity and low grazing rate after June 20) could flush unconsumed organic matter from the local surface ecosystem by vertical/horizontal transport (Reigstad et al., 2008) and result in a slowdown of nutrient supply for regenerated production in the local surface ecosystem. Zooplankton feeding releases dissolved inorganic N into the water column, but not dissolved inorganic Si (Dugdale et al., 1995). N limitation occurred and could have restricted growth of the under sea-ice diatom-dominated phytoplankton. Thus, the low grazing pressure at the beginning to middle of the USPB period (June 20–July 10) may have served as an additional contributor to the reduction in total (i.e., new plus regenerated) primary productivity at the end of the USPB period because of the slowdown in nutrient regeneration by consumers in the local surface water.

4.4. Possible causes for the mismatch between primary production and copepod grazing

The grazing rate and primary production were not significantly correlated ($r = -.180$, $p > .5$, $n = 14$). Two alternative hypotheses exist to explain why the grazing rate did not increase under higher primary production: low abundance of feeders and low grazing activity owing to a lack of suitable food. The former was not likely the primary cause because the difference in the average abundance of the main feeders (i.e., *C. glacialis* CIV–CVI and *M. longa* CIV–CVI) between the periods of June 11–16 and June 21–July 10 (a small difference of 1.8 times: 629 ± 146 ind. m^{-2} , $n = 2$, and 349 ± 202 ind. m^{-2} , $n = 8$, respectively; **Table 1**) was smaller than the difference in the average grazing rate of the main feeders, estimated from the production rate of FPs in the width range of 100–150 μm (a large difference of 10.2 times: 14.3 ± 9.2 mg C $m^{-2} d^{-1}$, $n = 2$, and 1.4 ± 1.6 mg C $m^{-2} d^{-1}$, $n = 8$, respectively). The relatively high abundance of the main feeders from June 21 to July 10 (e.g., 671 ind. m^{-2} on June 28) was comparable to those from June 11 to June 16 (525–732 ind. m^{-2}). Moreover, the average abundance of possible feeders could be much higher in the period of June 21–July 10 ($1,829 \pm 1,610$ ind. m^{-2} , $n = 8$) than in the period of June 11–16 (694 ± 130 ind. m^{-2} , $n = 2$) if the other possible feeder *C. hyperboreus* (CI–VI) is included in the calculation. The increase in the abundance of possible feeders may be attributable to their seasonal vertical migration behavior. These copepods could migrate upward to the surface between June 21 and 25 and stay there until the end of the study period (July 10) because the seasonal vertical (upward) migration of *C. hyperboreus* and *C. glacialis* occurs when the phytoplankton or ice algae begin blooming (early May or early April, respectively) in Arctic waters (Darnis and Fortier, 2014). Those copepods that migrated upward were already actively grazing and reached peak grazing on June 11–16 in the local surface water.

The alternative explanation is that grazing activity was low because of a lack of suitable food. Phytoplankton size is an important variable controlling zooplankton grazing, and some species are too small to be grazed efficiently by zooplankton (see Campbell et al., 2009, and references therein). However, the contributions of small phytoplankton species (flagellates and dinoflagellates) to the total phytoplankton abundance were as low as 14% (May 23), 5% (June 17), 9% (June 24), 4% (June 27), 20% (June 29), and 10% (July 1) at a depth of 5 m below the sea ice (PL Grondin, personal communication, 2019). These low contributions suggest that low grazing pressure during the USPB did not result from the dominance of small phytoplankton in the water column. The phytoplankton species composition in the water column changed drastically after June 20 (PL Grondin, personal communication, 2019). Our results clearly show that the abundance of *Pseudo-nitzschia* spp. increased from $0.4\text{--}2.6 \times 10^3$ cells L^{-1} to $1.6\text{--}6.0 \times 10^5$ cells L^{-1} in the surface (1.5–10 m) water under the landfast ice. The average contribution of *Pseudo-nitzschia* spp. to the entire population of diatom cells also increased by more than one order of

magnitude, from 4% ($n = 2$) to 61% ($n = 5$). Furthermore, the average contribution of *Pseudo-nitzschia* spp. to the total phytoplankton cell abundance could be estimated as 1% (May 25), 3% (June 17), 21%–29% (June 24), 34% (June 27), 24% (June 29), and 33% (July 1) on the basis of the contribution of diatoms to the total phytoplankton abundance (PL Grondin, personal communication, 2019). The contribution of *Pseudo-nitzschia* spp. to total phytoplankton cell biomass could be higher than that of their numerical abundance because the contribution of diatoms to total phytoplankton biomass (mean \pm standard deviation: $68 \pm 10\%$, $n = 6$) was also significantly higher than that of their abundance ($45 \pm 10\%$, $n = 6$) (PL Grondin, personal communication, 2019). *Pseudo-nitzschia* spp. can produce the neurotoxin domoic acid, though only half of the species have been reported as domoic acid producers (Bates et al., 2018) and only *Pseudo-nitzschia arctica*, which has never been reported as a domoic acid producer, is present in the Baffin Bay (Ribeiro et al., 2020). Yet, all strains of *Pseudo-nitzschia* spp. may eventually prove to be domoic acid producers (Bates et al., 2018). *Pseudo-nitzschia obtusa*, which was initially considered a nontoxic species, was later found to be a domoic acid producer (Harðardóttir et al., 2015). Domoic acid production is a chemical defense mechanism against predation (Harðardóttir et al., 2018), and ingestion of the neurotoxin can negatively affect the physiological activities of calanoid copepods like *C. hyperboreus* and *C. glacialis* (Tammilehto et al., 2012). For example, *C. hyperboreus* stopped grazing 6 h after commencing grazing on *Pseudo-nitzschia* (Tammilehto et al., 2012), though Harðardóttir et al. (2015) found no negative impact of domoic acid on copepod grazing over a longer term (8–10 days) and previous studies found no negative impact on copepod grazing (Lincoln et al., 2001; Maneiro et al., 2005; Leandro et al., 2010). Moreover, ingestion of domoic acid reduced the escape responses of *C. hyperboreus* and *C. glacialis* (Harðardóttir et al., 2018). Thus, the large increase in abundance of *Pseudo-nitzschia* spp. might explain the low grazing rate under the USPB conditions. This explanation is consistent with the individual grazing rates of potential feeders (*C. glacialis* CIV–CVI, *M. longa* CIV–CVI, and *C. hyperboreus* CI–VI) from June 21 to July 10 ($0.7 \mu g$ C ind. d^{-1}) being lower than the rates during the period of June 11–16 ($20.6 \mu g$ C ind. d^{-1}), where rates were calculated using the estimated grazing rates for these copepods and their abundances.

5. Conclusions

With intense temporal coverage (once every 2–3 days) of field sampling and comprehensive data sets (e.g., phytoplankton taxonomy, light profiles, and nutrient concentrations) from the Green Edge project from the end of May to the beginning of July (from pre-USPB and progressing into the USPB period), this study successfully illustrated fine-scale temporal variability of grazing impact on phytoplankton and investigated possible processes controlling grazing under landfast sea ice. In summary:

1. Low grazing pressure on phytoplankton during the USPB phase (i.e., mismatch scenario) indicated that copepod grazing did not control daily growth of phytoplankton under the USPB condition, although copepod grazing may have affected the productivity of phytoplankton under pre-USPB conditions.
2. This mismatch scenario might occur because of food quality (i.e., appearance of potentially toxigenic diatoms) rather than abundance of grazers in the surface water under landfast sea ice.
3. The main grazers were large dominant Arctic copepods—*C. glacialis*, *M. longa*, and *C. hyperboreus*—rather than small copepods such as *Pseudocalanus* spp., which are the main grazers in water under landfast sea ice in shallow Canadian Archipelago waters (100–150 m depth; Fortier et al., 2002).
4. Ongoing climate change could bring thinner sea ice, longer open water periods, and less snowfall in the Arctic (Bintanja et al., 2018; Stroeve and Notz, 2018). These environmental changes increase light availability, which affects microalgal growth, and further benefit phytoplankton, rather than ice algae, beneath the sea-ice cover in Baffin Bay (Oziel et al., 2019). These changes suggest that prey accessibility for the main grazers increases in the surface water under sea ice because the sinking speed of phytoplankton (diatoms, $<1\text{--}35\text{ m d}^{-1}$; Miklasz and Denny, 2010) is 1–2 orders of magnitude slower than that of aggregated ice algae ($100\text{--}500\text{ m d}^{-1}$; Riebesell et al., 1991), and aggregated microalgae are not favorable prey particles for grazers (Lürling and Van Donk, 1996). However, the present study indicates that grazers simply could not catch up with the increase in primary production by phytoplankton under the sea ice (i.e., during the USPB). We speculate that grazing pressure on phytoplankton will not increase as expected with an increase in USPB in Baffin Bay, but further studies are required to predict grazing pressure on phytoplankton under the sea ice.

Data accessibility statement

All data are accessible at the Green Edge database (<http://www.obs-vlfr.fr/proof/php/GREENEDGE/greenedge.php>) and will be made public prior to publication.

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Competing interests

The authors have no competing interests to declare.

Author contributions

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Contributed to sampling and analysis: MS, PR, BQ, YA, AL.

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