

# A substantial export flux of particulate organic carbon linked to sinking dead copepods during winter 2007–2008 in the Amundsen Gulf (southeastern Beaufort Sea, Arctic Ocean)

Makoto Sampei,<sup>a,\*</sup> Hiroshi Sasaki,<sup>b</sup> Alexandre Forest,<sup>a</sup> and Louis Fortier<sup>a</sup>

<sup>a</sup>Québec-Océan, Département de biologie, Université Laval, Québec, Québec, Canada

<sup>b</sup>Senshu University of Ishinomaki, Ishinomaki, Miyagi, Japan

## Abstract

In the Arctic Ocean, vertical fluxes of particulate organic carbon (POC) remain low during the dark winter period because POC fluxes are derived from photosynthetic production. Passively sinking dead copepods are traditionally excluded from POC fluxes estimated using sediment traps, resulting in the underestimation of the total POC flux. Here, we present the seasonal variability of total POC export flux measured by a sediment trap moored at ~ 100 m in the Amundsen Gulf (southeastern Beaufort Sea) over October 2007–July 2008. Surprisingly, the integrated total POC flux for February (466 mg m<sup>-2</sup>) was the second highest flux during the study period (the highest was in Jul; 1015 mg C m<sup>-2</sup>) due to a contribution of 91% from sinking dead copepods. The total POC flux in February 2008 in the Amundsen Gulf was up to two orders of magnitude higher than the previously reported traditional POC winter fluxes that did not include the contribution of sinking dead copepods. Hence, the POC flux in February only could be equivalent to ~ 18% of the quasi-annual traditional POC flux. Our observations suggest that a substantial POC export flux occurred during winter 2007–2008 due to zooplankton life cycle.

The biological carbon pump drives sequestration of carbon dioxide in the deep sea via sinking particles. Quantifying the export flux of particulate organic carbon (POC) is fundamental to understanding strength of the biological carbon pump. The biological carbon pump, especially the soft-tissue pump, is weak in ice-covered waters during the Arctic winter, because vertical POC fluxes are generally low during the winter (Hargrave et al. 1994; Forest et al. 2010). High POC fluxes occur mainly during spring–autumn periods, because POC fluxes are ultimately derived from primary production in surface waters.

Accurate estimation of the POC export flux and knowledge on processes affecting it in the upper water column are important for understanding the magnitude and efficiency of the biological carbon pump. Sediment traps are widely used to measure vertical POC fluxes in the global ocean. However, the accuracy of POC flux measurements by sediment traps can be affected by ‘swimmers’ (i.e., live organisms that actively swim into the traps as opposed to passively sinking particles [Sampei et al. 2009b]). Most swimmers are metazoans such as copepods, amphipods, and euphausiids, which are generally much larger in size than passively sinking particles. Contamination by swimmers results in the overestimation of the downward POC flux (Sampei et al. 2009b). Hence, undecomposed swimmer metazoans have traditionally been sorted out from trap samples before analysis to prevent overestimation of the POC flux.

Undecomposed copepods in trap samples can either be actively intruding copepods (AICs) that swam into the trap or passively sinking copepods (PSCs) that died in the water

column before sinking into the trap (Sampei et al. 2009b). Contrary to AICs, PSCs should be included in the downward POC flux as sinking particles that would eventually end up in the deep ocean or on the bottom. However, little attention has been given to the potential contribution of PSCs to the export flux because of the difficulty in distinguishing fresh copepod carcasses (i.e., PSCs) from actual swimmers (i.e., AICs). This study extends the work of Sampei et al. (2009b) by investigating the seasonal variability of total POC export fluxes (PSCs + other ‘traditional sinking particles’ [i.e., particles other than undecomposed metazoans in sediment trap samples]) using a long-term mooring carrying a time-programmed sediment trap in the Amundsen Gulf in 2007–2008. We compare our findings with literature data and discuss their significance for Arctic waters. In particular, we tested the hypothesis that a substantial vertical POC flux could occur during the dark Arctic winter due to sinking dead copepods.

## Methods

*Physical and biological environments of the study area*—The Amundsen Gulf is a large channel (~ 400-km length × ~ 170-km width) that connects the southeastern Beaufort Sea to the Canadian Archipelago (Fig. 1). Seasonal sea ice begins to grow in October near the coast and the sea ice cover is usually consolidated by late December over the region (Galley et al. 2008). The sea ice cover gradually thickens over the winter and reaches a maximum thickness of ~ 2 m in late March. The sea ice retreat has typically begun in late May and early June when winds and/or surface circulation push sea ice away from the Amundsen Gulf (Galley et al. 2008). Simplified water masses in the

\* Corresponding author: makoto.sampei@qo.ulaval.ca

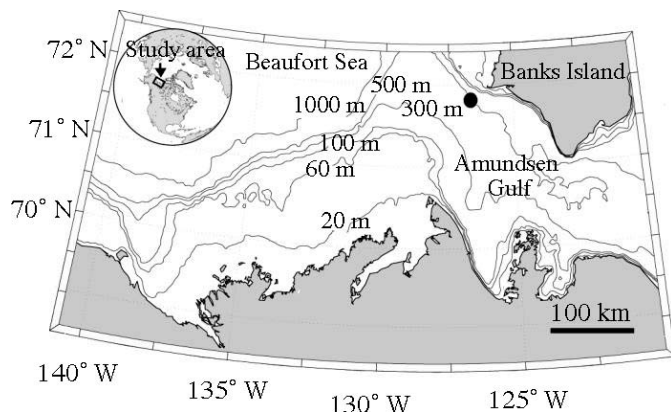


Fig. 1. Bathymetry of the southeastern Beaufort Sea (Arctic Ocean) with the mooring site. The closed black circle corresponds to the mooring site in 2007–2008.

region comprise the relatively fresh Polar-Mixed Layer (salinity of  $\sim 26$ – $31$ , 0–50-m depth), the Pacific Halocline and its summer–winter components derived from Bering Sea waters ( $\sim 32$ – $33$ , 50–200 m), and deep waters of Atlantic origin ( $\sim 34$ ,  $> 200$  m; Forest et al. 2010). Sea surface temperature is forced by atmosphere–ice dynamics and spans from  $-1.8^{\circ}\text{C}$  in winter up to usually  $5$ – $6^{\circ}\text{C}$  in summer. Temperature in the Pacific Halocline remains between  $-1.8^{\circ}\text{C}$  and  $-0.5^{\circ}\text{C}$  throughout the year, whereas it increases to  $\sim 0.5^{\circ}\text{C}$  around 400 m in the layer of Atlantic-origin water. Depths of the pycnocline are primarily driven by salinity and usually range from 10 m to 50 m, dependent on wind conditions, ice freeze–melt cycles, and river runoff (Carmack and Macdonald 2002). Ocean circulation in the region is overall influenced by the anticyclonic (clockwise) Beaufort Gyre. Surface waters usually flow southward along Banks Island and northward out of the Amundsen Gulf near Cape Bathurst (Ingram et al. 2008). Below the surface ( $> 50$  m), circulation is reversed and dominated by the eastward Beaufort Undercurrent, which brings waters of both Pacific and Atlantic origin into the Amundsen Gulf along the continental slope (Ingram et al. 2008). Current velocities around 100–200-m depth are usually weak ( $< 10$   $\text{cm s}^{-1}$ ), but can be influenced at times by episodic accelerations and inversions due to the passage of eddies, storms eroding the upper halocline, or internal waves (Barber et al. 2010).

Primary production in the Beaufort Sea traditionally ranges from  $30$   $\text{g C m}^{-2} \text{yr}^{-1}$  to  $70$   $\text{g C m}^{-2} \text{yr}^{-1}$ , indicative of generally oligotrophic conditions (Sakshaug 2004). Ice algae begin to grow in March and their biomass usually peaks in April–May prior to ice break-up (Brown et al. in press). The spring phytoplankton bloom rapidly develops as a subsurface chlorophyll maximum in May–June as a result of typically low nutrient concentrations in the surface layer at the end of winter (Tremblay et al. 2008). A second phytoplankton bloom can occur in late summer or in the autumn as a result of wind-driven mixing and/or coastal upwelling (Brugel et al. 2009).

Mesozooplankton biomass in the southeastern Beaufort Sea is normally comprised of copepods at 80–90%, which, in turn, is dominated at  $\sim 70\%$  by the large calanoids

*Calanus hyperboreus*, *C. glacialis*, and *Metridia longa* (Darnis et al. 2008).

**Sediment trap deployment and sample treatments**—A time-programmed sediment trap was deployed on bottom-tethered mooring at  $71^{\circ}47'\text{N}$ ,  $126^{\circ}30'\text{W}$  (309-m depth) in the Amundsen Gulf (southeastern Beaufort Sea; Fig. 1) through a quasi-annual period (from 21 Oct 2007 to 22 Jul 2008). The cylindrical sediment trap (Technicap PPS.3/3), which has 24 collection cups and collection area at the mouth of  $0.125$   $\text{m}^2$ , was set to collect settling particles at a depth of 112 m. An Acoustic Doppler Current Profiler (Nortek Continental) was deployed at 95-m depth to record current velocity above the sediment trap. The mooring line was recovered earlier than we expected, so that we used 22 collection cups out of 24 cups potentially available on the sediment trap. Collection cups were filled with a solution of  $\sim 5\%$  v:v buffered formalin in GF/F-filtered (Whatman glass-microfiber filter;  $0.75\text{-}\mu\text{m}$  pore size) seawater with final salinity of  $\sim 36$ , so that the density of the solution exceeded that of seawater. The sediment trap continuously collected settling particles between 21 October 2007 and 22 July 2008 (total sampling duration is 275 d). Sampling duration for each collection cup varied from 7 d in spring to 31 d in winter (see Table 1 for the detailed sampling duration for each collection cup).

After recovery of the trap, large undecomposed copepods (adult stages [CVI] of *C. hyperboreus*, *C. glacialis* CVI, and late copepodite [CIV and CV] and CVI of *Pareuchaeta glacialis*) were removed by hand from entire sample (i.e., not from subsamples) under a stereo-microscope and those copepods were kept for determination of PSC (copepod died in the water column before sinking into the trap) flux. The entire sample was then quantitatively split into several fractions for later analyses. Other undecomposed zooplankton were manually removed from the subsamples intended for chemical analyses, under a stereo-microscope.

Vertical POC fluxes (i.e., traditional sinking particles and PSCs) presented here should be considered minimum estimates because we did not correct for the possible solubilization of POC to dissolved organic carbon that could occur in trap sample cups ( $< 10\%$ ; Sampei et al. 2004). Our estimations nevertheless compare with POC fluxes from other sediment trap studies conducted in the Arctic Ocean, within which no correction was applied (Hargrave et al. 1994; Forest et al. 2010; Sampei et al. 2011).

**Traditional sinking-particle flux measurements**—To increase accuracy of the traditional sinking-particle flux quantification, we performed two series of analyses in two different laboratories and we combined their results. The first set of subsamples was filtered through preweighed GF/F filters (precombusted 3 h at  $450^{\circ}\text{C}$ ) for the determination of dry weight (dry wt) and total particulate carbon (TPC) fluxes. Filters were dried for 24 h at  $60^{\circ}\text{C}$ , weighed again for dry wt, and analyzed on a Perkin Elmer carbon–hydrogen–nitrogen–sulfur (CHNS) 2400 Series II to measure TPC. The second set of subsamples was filtered through identically pretreated GF/F filters for the deter-

Table 1. Numerical fluxes (individuals  $\text{m}^{-2} \text{d}^{-1}$ ) of dominant metazoans in the sediment trap moored at 112 m in southeastern Beaufort Sea from October 2007 to July 2008. All developmental stages of copepods are included.

Sampling period	<i>Metridia longa</i>	<i>Pareuchaeta glacialis</i>	<i>Calanus glacialis</i>	<i>C. hyperboreus</i>	Other copepods	Copepod nauplii	Other metazoans
21–31 Oct 07	112	78	21	23	47	0	227
01–15 Nov 07	120	44	11	19	128	0	521
16–30 Nov 07	35	20	8	2	119	0	574
01–31 Dec 07	109	1	4	1	138	1	63
01–31 Jan 08	84	2	8	5	177	1	31
01–29 Feb 08	155	21	11	29	57	9	65
01–15 Mar 08	265	21	20	29	108	171	17
16–31 Mar 08	455	23	32	35	185	125	12
01–15 Apr 08	779	47	42	13	54	0	23
16–22 Apr 08	757	48	25	14	85	5	46
23–30 Apr 08	330	20	19	16	216	76	73
01–07 May 08	179	11	1	8	75	23	65
08–15 May 08	121	18	1	6	56	58	36
16–22 May 08	216	11	0	1	59	9	32
23–31 May 08	239	51	6	4	25	7	24
01–07 Jun 08	417	29	1	5	183	19	55
08–15 Jun 08	277	49	5	12	116	9	48
16–22 Jun 08	286	42	6	9	112	40	141
23–30 Jun 08	437	23	5	1	16	0	233
01–07 Jul 08	195	17	0	3	119	19	110
08–15 Jul 08	786	87	7	5	138	9	135
16–22 Jul 08	514	105	23	16	183	0	734

mination of dry wt and POC fluxes. Those filters were dried as above and weighed again for dry wt. The samples were then fumed for 12 h with concentrated HCL to remove carbonates prior to the determination of POC, and were analyzed on a Leeman Lab CEC 440 carbon-hydrogen-nitrogen (CHN) elemental analyzer to measure POC flux. Results of dry wt measurements from both series of analyses were averaged to estimate the dry wt flux. Then, the percentages of TPC and POC in dry wt from each of the subsample series and averaged dry wt flux were used to calculate TPC and POC fluxes. POC fluxes were expressed as daily fluxes ( $\text{mg m}^{-2} \text{d}^{-1}$ ).

**PSC flux measurements**—The large undecomposed copepods (*C. hyperboreus* CVI, *C. glacialis* CVI, and *P. glacialis* CIV–CVI) were counted, identified, and sorted following the methodology of Sampei et al. (2009b) in order to estimate the PSC fluxes. All samples (i.e., 100%, not only a subsample for each sample) were processed following this method to increase the accuracy of the PSC flux estimation. In brief, this method makes use of the postmortem posture of the antennules (the first antenna) or swimming legs, so copepods could be classified into two postural groups (G1 and G2). Then, G1 copepods (representatives of the PSCs) were dried for 24 h at 60°C and analyzed on a Perkin Elmer CHNS 2400 Series II to measure their POC content. The methodology of Sampei et al. (2009b) makes further use of two correction factors that compensate for the underestimation of PSCs based on the sole abundance of G1 copepods. These correction factors were developed following the demonstration that 56% of *P. glacialis* and 36% of *Calanus* spp. in naturally dead copepods without formalin (i.e., PSCs) were misclassified

by the simple postmortem posture criteria (Sampei et al. 2009b). Thus, PSC fluxes in terms of POC and individual numbers were estimated as (G1 copepods)/0.64 for *Calanus* spp. and (G1 copepods)/0.44 for *P. glacialis* following Sampei et al. (2009b).

## Results

**Average current velocity around the sediment trap**—Monthly averaged current velocities at 90 m ( $\sim 20$  m above the sediment trap) during 2007–2008 oscillated between  $\sim 6 \text{ cm s}^{-1}$  and  $\sim 18 \text{ cm s}^{-1}$  (not shown). Highest values were reached in October 2007 ( $14 \pm 5 \text{ cm s}^{-1}$ ), November 2007 ( $18 \pm 7 \text{ cm s}^{-1}$ ), and February 2008 ( $14 \pm 10 \text{ cm s}^{-1}$ ). The relatively high variability in current speed recorded in February was linked to episodically high velocity values (25–40  $\text{cm s}^{-1}$ ) detected from 11 to 14 February. Averaged current speed in other months was less variable and remained  $\leq 12 \text{ cm s}^{-1}$  with a standard deviation of  $\pm 5 \text{ cm s}^{-1}$ .

**Seasonal variations in the PSC and traditional sinking-POC fluxes**—Traditional sinking-particle fluxes and PSC fluxes ranged from 1.5  $\text{mg C m}^{-2} \text{d}^{-1}$  to 72.0  $\text{mg C m}^{-2} \text{d}^{-1}$  and from 0  $\text{mg C m}^{-2} \text{d}^{-1}$  to 14.6  $\text{mg C m}^{-2} \text{d}^{-1}$ , respectively (Fig. 2). The highest traditional sinking-particle flux was observed at the end of July (72.0  $\text{mg C m}^{-2} \text{d}^{-1}$ ). The highest PSC flux (14.6  $\text{mg C m}^{-2} \text{d}^{-1}$ ) occurred in February when the lowest traditional sinking-particle flux (1.5  $\text{mg C m}^{-2} \text{d}^{-1}$ ) was recorded. The total POC flux in February (as cumulated from PSC and traditional fluxes; 16.0  $\text{mg C m}^{-2} \text{d}^{-1}$ ) was one order of magnitude higher than the traditional sinking-particle flux alone.

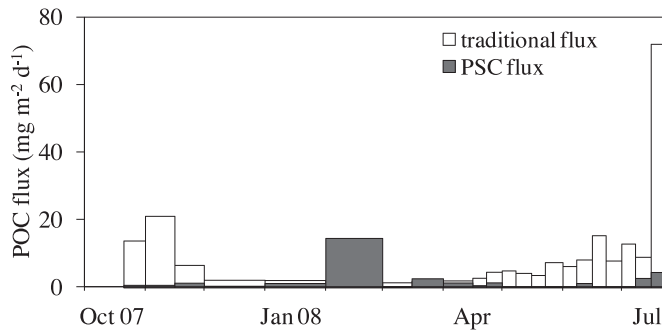


Fig. 2. Time-series of total particulate organic carbon (POC) flux (i.e., traditional flux + passively sinking copepods [PSC] flux) from 21 October 2007 to 22 July 2008, measured by a sequential sediment trap moored at 112 m (station depth of 309 m) in the Beaufort Sea (Arctic Ocean). The traditional POC flux excludes all undecomposed metazoans. The PSC flux corresponds to the estimated contribution of the undecomposed, passively sinking copepods that dominated the zooplankton biomass in the sediment trap samples (*Calanus hyperboreus* CVI, *C. glacialis* CVI, and *Pareuchaeta glacialis* CIV–CVI).

For each month of the year, daily total POC fluxes were integrated to provide monthly POC flux estimates (Fig. 3). The total flux in February ( $466 \text{ mg C m}^{-2}$ ) was higher than the fluxes of productive spring periods (in May [ $162 \text{ mg C m}^{-2}$ ] and June [ $291 \text{ mg C m}^{-2}$ ]). Although the flux in February did not reach a value equivalent to the highest flux of July ( $1015 \text{ mg C m}^{-2}$ ), the second highest total POC flux of February ( $466 \text{ mg m}^{-2}$ ) was equivalent to 18% of the quasi-annual traditional POC flux ( $2543 \text{ mg m}^{-2}$ ).

The contributions of PSCs to the total POC flux varied considerably over the quasi-annual cycle (Fig. 3). The contributions were generally high in winter to early spring (16–91%) and low in other periods (1–30%). During the peak downward POC export of July, PSCs represented only 7% of the total POC flux. By contrast, the contribution of PSCs in February was high (91%).

**Numerical flux of metazoans**—The total flux of *C. hyperboreus*, *C. glacialis*, and *P. glacialis* was highest from 16 to 22 July 2008 ( $144 \text{ individual [ind.] m}^{-2} \text{ d}^{-1}$ ; Table 1). The total flux of the three target copepod species in February was moderate ( $61 \text{ ind. m}^{-2} \text{ d}^{-1}$ ). Other than the three target copepod species, a substantial amount of copepods and other metazoans was found in the sediment trap samples. The flux of other copepods was dominated by *M. longa*, *Microcalanus* spp., copepod nauplii, and *Pseudocalanus* spp. in decreasing order of numerical importance. A peak flux of copepod nauplii was detected in March 2008 (Table 1). Quasi-annual averaged fluxes (275 d) of *M. longa*, *Microcalanus* spp., copepod nauplii, and *Pseudocalanus* spp. were  $312 \text{ ind. m}^{-2} \text{ d}^{-1}$ ,  $28 \text{ ind. m}^{-2} \text{ d}^{-1}$ ,  $26 \text{ ind. m}^{-2} \text{ d}^{-1}$ , and  $22 \text{ ind. m}^{-2} \text{ d}^{-1}$ , respectively. Other metazoans included *Limacina helicina*, *Oikopleura* spp., Chaetognaths, and *Themisto* spp. in decreasing order of numerical importance. Quasi-annual averaged fluxes of *Limacina helicina*, *Oikopleura* spp., Chaetognaths, and *Themisto* spp. were  $65 \text{ ind. m}^{-2} \text{ d}^{-1}$ ,

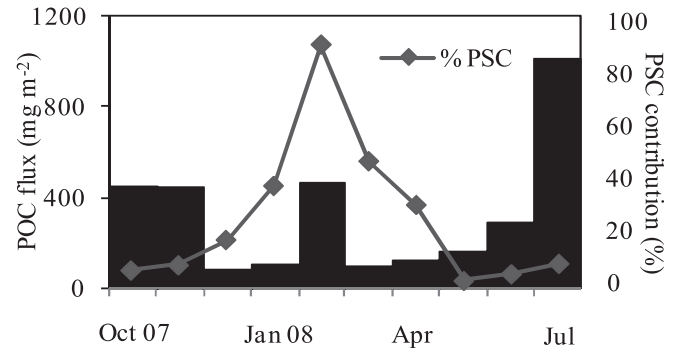


Fig. 3. Quasi-annual cycle (Oct 2007 to Jul 2008) of monthly total particulate organic carbon (POC) flux (i.e., traditional flux + passively sinking copepods [PSC] flux). The traditional flux excludes all undecomposed metazoans. The PSC flux corresponds to the estimated contribution of the undecomposed, passively sinking copepods that dominated the zooplankton biomass in the sediment trap samples (*Calanus hyperboreus* CVI, *C. glacialis* CVI, and *Pareuchaeta glacialis* CIV–CVI). Contribution of the PSC to total POC flux is also given in %.

$25 \text{ ind. m}^{-2} \text{ d}^{-1}$ ,  $14 \text{ ind. m}^{-2} \text{ d}^{-1}$ , and  $6 \text{ ind. m}^{-2} \text{ d}^{-1}$ , respectively.

In February, PSCs were identified in all three target copepod species (Table 2). This did not occur in other months than February. The number of PSCs identified in the collection of sediment trap samples varied from 0 to 22 (maximum number was in Feb 2008). These numbers might appear low, but we are confident that they were sufficient to provide reliable estimates of the proportion of PSCs within the total POC flux sampled by the trap. The number and carbon content of PSCs were expressed as daily fluxes in order to assess their variability between seasons and to compare their magnitude to total POC fluxes. Accordingly, the total PSC flux was highest from 16 to 31 March 2008 ( $7.0 \text{ ind. m}^{-2} \text{ d}^{-1}$ ), whereas the highest PSC flux in terms of carbon was observed in February (Fig. 1). This difference was due to the difference of species composition of PSCs between these periods. From 16 to 31 March 2008, all of PSCs were *C. glacialis*, which contained less carbon ( $\sim 0.4 \text{ mg C ind.}^{-1}$ ) when compared to *C. hyperboreus* ( $\sim 2.0 \text{ mg C ind.}^{-1}$ ) and *P. glacialis* ( $\sim 2.3 \text{ mg C ind.}^{-1}$ ) in our PSC specimens.

The overall estimated frequency of PSCs ( $\%_{\text{PSC}}$ ) in *C. hyperboreus* (2%) and *P. glacialis* (2%) was low (Table 2). These two species, nonetheless, represented  $\sim 80\%$  of the quasi-annual PSC flux in terms of carbon.

## Discussion

**An unusual peak of POC export flux in the Amundsen Gulf in February 2008**—The present traditional sinking-particle flux was comparable with those observed in previous studies in the same area, at  $\sim 100\text{-m}$  depth in the central Amundsen Gulf ( $1.7\text{--}71.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ , Forest et al. 2010; Sampei et al. 2011). This suggests that the traditional sinking-particle flux observed in 2007–2008 was similar to fluxes recorded in other years in the Amundsen Gulf. Average current velocity at 90 m re-

Table 2. Numerical fluxes (individuals [ind.]  $\text{m}^{-2} \text{d}^{-1}$ ) of actively intruding copepods (AICs) and passively sinking copepods (PSCs) in the sediment trap moored at 112 m in southeastern Beaufort Sea.  $\%_{\text{PSC}}$  is the percent contribution of PSCs to the overall copepod flux [ $\text{PSC} / (\text{PSC} + \text{AIC}) \times 100$ ]. The fluxes integrated over the quasi-annual sampling period (sum of every daily flux multiplied by its sampling duration, in ind.  $\text{m}^{-2}$ ) and corresponding percent contributions are also given. na shows nonapplicable.

Sampling period	<i>Pareuchaeta glacialis</i>			<i>Calanus hyperboreus</i>			<i>C. glacialis</i>			Total		
	AICs	PSCs	$\%_{\text{PSC}}$	AICs	PSCs	$\%_{\text{PSC}}$	AICs	PSCs	$\%_{\text{PSC}}$	AICs	PSCs	$\%_{\text{PSC}}$
21–31 Oct 07	68.7	3.3	5	21.1	0.0	0	4.4	0.0	0	94.2	3.3	3
01–15 Nov 07	43.0	1.2	3	13.0	0.0	0	6.4	0.0	0	62.4	1.2	2
16–30 Nov 07	20.3	0.0	0	0.5	0.0	0	0.0	2.1	100	20.8	2.1	9
01–31 Dec 07	1.0	0.0	0	0.8	0.0	0	0.0	0.8	100	1.8	0.8	31
01–31 Jan 08	1.8	0.0	0	4.7	0.4	8	0.4	0.4	50	6.9	0.8	10
01–29 Feb 08	18.5	2.5	12	27.7	1.3	5	3.9	2.2	36	50.1	6.0	11
01–15 Mar 08	18.7	0.0	0	27.2	0.0	0	5.5	0.9	14	51.4	0.9	2
16–31 Mar 08	12.5	0.0	0	33.5	0.0	0	1.5	7.0	82	47.5	7.0	13
01–15 Apr 08	34.1	0.0	0	10.7	0.0	0	8.9	3.4	28	53.7	3.4	6
16–22 Apr 08	36.6	0.0	0	13.7	0.0	0	2.7	1.8	40	53.0	1.8	3
23–30 Apr 08	16.0	0.0	0	16.0	0.0	0	0.0	3.0	100	32.0	3.0	9
01–07 May 08	10.3	0.0	0	8.0	0.0	0	0.0	0.0	na	18.3	0.0	0
08–15 May 08	12.0	0.0	0	2.0	0.0	0	1.0	0.0	0	15.0	0.0	0
16–22 May 08	10.3	0.0	0	1.1	0.0	0	0.0	0.0	na	11.4	0.0	0
23–31 May 08	45.3	0.0	0	4.4	0.0	0	3.0	1.4	32	52.7	1.4	3
01–07 Jun 08	19.4	0.0	0	3.4	0.0	0	1.1	0.0	0	23.9	0.0	0
08–15 Jun 08	41.0	0.0	0	4.4	1.6	27	2.0	0.0	0	47.4	1.6	3
16–22 Jun 08	42.3	0.0	0	9.1	0.0	0	1.1	0.0	0	52.5	0.0	0
23–30 Jun 08	23.0	0.0	0	1.0	0.0	0	4.0	0.0	0	28.0	0.0	0
01–07 Jul 08	17.1	0.0	0	3.4	0.0	0	0.0	0.0	na	20.5	0.0	0
08–15 Jul 08	66.7	2.3	3	2.0	0.0	0	1.0	0.0	0	69.7	2.3	3
16–22 Jul 08	61.4	2.6	4	8.0	0.0	0	3.4	0.0	0	72.8	2.6	3
Integrated	6372.8	163.2	2	3088.8	63.2	2	660	356	35	10,122	582.4	5

mained in the range of 5–18  $\text{cm s}^{-1}$ , an envelope that does not affect the collection efficiency of Technicap traps (Forest et al. 2010).

The monthly total flux in February was lower than the highest flux of July. However, the total flux in February was second highest and was even higher than in May and June, when phytoplankton blooms in the Amundsen Gulf (Tremblay et al. 2008). Indeed, the substantial total POC flux in February—which was equivalent to 18% of the quasi-annual traditional POC flux—was comparable to the traditional POC fluxes recorded during the spring–summer periods in Arctic waters. For example, the total POC flux in February was equivalent to the monthly averaged POC flux for spring–summer in the eastern North Water polynya ( $495 \pm 300 \text{ mg m}^{-2}$ ,  $n = 6$ ; Sampei et al. 2004), a highly productive area in the Arctic Ocean (Klein et al. 2002). Moreover, the total POC flux in February was up to two orders of magnitude higher than previously observed traditional POC fluxes at  $\sim 100\text{-m}$  depth in ice-covered waters during Arctic winter (Hargrave et al. 1994; Forest et al. 2010).

At 91% of the total POC flux in February, the PSC flux reported here is probably a conservative estimate because the small but abundant copepod *M. longa* ( $4495 \text{ ind. m}^{-2}$  in Feb), and other less abundant but large metazoans (e.g., the amphipod *Themisto libellula* [ $32 \text{ ind. m}^{-2}$  in Feb], which may be killed by parasitic infection in the water column before entering sediment traps [Prokopowicz et al. 2010]), were not included in the estimation of the PSC flux. Therefore, our results suggest that events of relatively high

total export POC flux could occur during the dark Arctic winter despite the lack of primary production.

*Possible explanations for the high vertical flux of copepod carcasses during winter*—There are two possible explanations for the high PSC flux in February: (1) lateral transport of allochthonous PSCs over the sediment trap via mesoscale processes such as an eddy; and/or (2) increased local mortality by natural death (e.g., death due to ageing) and subsequent enhanced flux of carcasses. Eddy-like features filled with suspended matter could increase vertical POC fluxes when particles rainout during its propagation (O'Brien et al. 2011). Within their core, eddies can also accumulate zooplankton (Linàs et al. 2009), which would likely comprise a variable proportion of carcasses that could sink to depth. In fact, the passage of an anticyclonic eddy centered at  $\sim 120\text{-m}$  depth (diameter  $\sim 15 \text{ km}$ , maximal vertical extent  $\sim 150 \text{ m}$ ) was detected from 09 to 17 February 2008 at 5 km southwest of the sediment trap site (J. Barrette, INRS-ETE, Québec, Canada, pers. comm.). The episodic increase in current velocity detected above the sediment trap during this period appears to be linked to this eddy. However, no specific peak in the traditional POC flux or in the AIC flux (i.e., particles other than PSCs) was recorded in February. Hence, it is unlikely that the anticyclonic eddy observed close to the sediment trap site was the prime cause for the high PSC flux detected in February.

A simple alternative to a possible eddy-induced transport is an enhanced vertical flux of copepod carcasses that

would have been caused by the natural death of copepods following reproduction (Terazaki and Wada 1988). Actually, all PSCs identified in the sediment trap sample of February 2008 were adult stages. Ninety-four percent of PSC flux in terms of POC was induced by the large *C. hyperboreus* and *P. glacialis* in February. Breeding of *C. hyperboreus* in the Amundsen Gulf appears to begin in November–December, continuing through January–March and completed by April (Ota et al. 2008). The spawning of *C. hyperboreus* should, thus, peak at some point over February, resulting in the senescence and mortality of most of adult stages during this period. Similarly, egg production in *Pareuchaeta* spp. peaks during winter, supported primarily by the lipid reserves of the females and relying partly on predatory feeding (Båmstedt 1979; Alonzo et al. 2000). The reproduction cycle of *P. glacialis* in the Beaufort Sea is unknown, but it is likely that this large carnivore would have benefited from better feeding and reproduction conditions from January to March 2008, when mesozooplankton (> 1 mm) overwinter below 70 m in the region (Geoffroy et al. in press).

Our hypothesis that the substantial PSC flux of February was the result of ageing copepods is supported by the relatively high abundance of copepod nauplii collected by the sediment trap in March 2008 (Table 1). The copepod nauplii in March were certainly the result of eggs laid between December 2007 and March 2008, because the development time from egg to hatching (i.e., beginning of nauplius stages) or CI (i.e., end of nauplius stages) is 8–74 d for *C. hyperboreus* (calculated with eqs. of table 48 in Mauchline [1998]) for water temperature of  $\sim -1^{\circ}\text{C}$ , as prevailing at  $\sim 100$  m in the Amundsen Gulf throughout the year (Geoffroy et al. in press). The development time of *P. glacialis* is probably similar to the one of *C. hyperboreus*, because growth depends on body size and environmental conditions (e.g., temperature: Mauchline 1998). Maximum prosome length of *P. glacialis* females ( $\sim 7.8$  mm) and *C. hyperboreus* females ( $\sim 6.2$  mm) are similar in the southeastern Beaufort Sea (Sampei et al. 2009a). Thus, the high PSC flux in February 2008 was most likely induced by the senescence and natural death following the reproduction of large copepods. Such a conclusion supports the early work of Sampei et al. (2009b), who recorded high winter monthly flux ( $\sim 300$  mg C m $^{-2}$  in Jan and in Feb) due to a large contribution by PSCs (87%), which is comparable to what we recorded in the Amundsen Gulf in February 2008.

*Implications for the food web and biological carbon pump during the Arctic winter*—In the absence of primary production, zooplankton carcasses are likely to be very nutritive particles when compared to refractory and/or diluted detrital particles remaining in the water column (Sampei et al. 2009b). PSCs could be a potential food source to meet the energy requirements of omnivores, carnivores, and necrophages in winter when the under-ice ecosystem shifts to a detrital mode. (Sampei et al. 2009b). In particular, dense aggregations of polar cod (up to 0.732 kg m $^{-2}$ )—which prey primarily on late stages of large calanoid copepods—were detected below 100 m in the

Amundsen Gulf during winter 2008 (Geoffroy et al. in press). Copepod carcasses could also represent a significant but neglected carbon source for the active microbial community that prevails in the dark waters of the Arctic Ocean during winter (Garneau et al. 2008). Thus, PSCs might contribute to POC exportation from the surface mixed layer, because our time-series was recorded below the pycnocline, but uncertainties remain regarding the ultimate fate of the POC exported at depth.

Nevertheless, while they may not be numerically abundant, each PSC is indeed a package of concentrated organic matter and, therefore, zooplankton carcasses can be an important but grossly ignored and poorly sampled component of the biological pump, especially in low-productive periods and areas, such as in the Arctic Ocean during winter. Hence, further inter-regional and multiyear studies are needed to examine how vertical POC fluxes of copepod carcasses, and especially their apparent winter maximum, may affect carbon cycling processes on a regional scale.

#### Acknowledgments

We are grateful to D. G. Barber, G. Stern, and M. Fortier for their contribution to the planning and realization of this study. We thank the officers and crew of the Canadian Coast Guard icebreaker *Amundsen* for their help at sea. L. Michaud, A.-M. Busque-Aubois, M.-C. Perreault, L. Létourneau, P. Massot, and S. Blondeau contributed to field works and/or laboratory analyses. We are grateful to two anonymous reviewers for valuable comments and suggestions on an earlier version of this paper. Part of this study was supported by grants from the Natural Science and Engineering Research Council of Canada to L. Fortier. This is a contribution to the program of Québec-Océan, ArcticNet, Circumpolar Flaw Lead system study, and the Canada Research Chair on the response of Arctic marine ecosystems to climate warming.

#### References

- ALONZO, F., P. MAYZAUD, AND S. RAZOULS. 2000. Egg production, population structure and biochemical composition of the subAntarctic copepod *Paraeuchaeta antarctica* in the Kerguelen Archipelago. *Mar. Ecol. Prog. Ser.* **205**: 207–217, doi:10.3354/meps205207
- BÅMSTEDT, U. 1979. Reproductive bioenergetics within the summer and winter generations of *Euchaeta norvegica* (Copepoda). *Mar. Biol.* **54**: 135–142, doi:10.1007/BF00386592
- BARBER, D., M. ASPLIN, Y. GRATTON, J. LUKOVICH, R. J. GALLEY, R. L. RADDATZ, AND D. LEITCH. 2010. The International Polar Year (IPY) Circumpolar Flaw Lead (CFL) system study: Overview and the physical system. *Atmos.-Ocean* **48**: 225–243.
- BROWN, T. A., S. T. BELT, B. PHILIPPE, C. J. MUNDY, G. MASSÉ, M. POULIN, AND M. GOSSELIN. In press. Temporal and vertical variations of lipid biomarkers during a bottom ice diatom bloom in the Canadian Beaufort Sea: Further evidence for the use of the IP<sub>25</sub> biomarker as a proxy for spring Arctic sea ice. *Polar Biol.* doi:10.1007/s00300-010-0942-5
- BRUGEL, S., AND OTHERS. 2009. Phytoplankton biomass and production in the southeastern Beaufort Sea in autumn 2002 and 2003. *Mar. Ecol. Prog. Ser.* **377**: 63–77, doi:10.3354/meps07808
- CARMACK, E. C., AND R. W. MACDONALD. 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: A setting for marine life. *Arctic* **55**: 29–45.

- DARNIS, G., D. G. BARBER, AND L. FORTIER. 2008. Sea ice and the onshore-offshore gradient in pre-winter zooplankton assemblages in south-eastern Beaufort Sea. *J. Mar. Syst.* **74**: 994–1011, doi:10.1016/j.jmarsys.2007.09.003
- FOREST, A., S. BÉLANGER, M. SAMPEI, H. SASAKI, C. LALANDE, AND L. FORTIER. 2010. Three-year assessment of particulate organic carbon fluxes in Amundsen Gulf (Beaufort Sea): Satellite observations and sediment trap measurements. *Deep-Sea Res. I* **57**: 125–142, doi:10.1016/j.dsr.2009.10.002
- GALLEY, R. J., E. KEY, D. G. BARBER, B. J. HWANG, AND J. K. EHN. 2008. Spatial and temporal variability of sea ice in the southern Beaufort Sea and Amundsen Gulf: 1980–2004. *J. Geophys. Res.* **113**: C05S95, doi:10.1029/2007JC004553
- GARNEAU, M. E., R. S. ROY, C. LOVEJOY, Y. GRATTON, AND W. F. VINCENT. 2008. Seasonal dynamics of bacterial biomass and production in a coastal arctic ecosystem: Franklin Bay, western Canadian Arctic. *J. Geophys. Res.* **113**: C07S91, doi:10.1029/2007JC004281
- GEOFFROY, M., D. ROBERT, G. DARNIS, AND L. FORTIER. In press. The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. *Polar Biol.* doi:10.1007/s00300-011-1019-9
- HARGRAVE, B. T., B. VON BODUNGEN, P. STOFFYN-EGLI, AND P. J. MUDIE. 1994. Seasonal variability in particle sedimentation under permanent ice cover in the Arctic Ocean. *Cont. Shelf Res.* **14**: 279–293, doi:10.1016/0278-4343(94)90017-5
- INGRAM, R. G., W. J. WILLIAMS, B. VAN HARDENBERG, J. T. DAWE, AND E. CARMACK. 2008. Seasonal circulation over the Canadian Beaufort Shelf, p. 13–38. In L. Fortier, D. G. Barber, and J. Michaud [eds.], *On thin ice*. Aboriginal Issues Press.
- KLEIN, B., AND OTHERS. 2002. Phytoplankton biomass, production and potential export in the North Water. *Deep-Sea Res. II* **49**: 4983–5002, doi:10.1016/S0967-0645(02)00174-1
- LLINÁS, L., R. S. PICKART, J. T. MATHIS, AND S. L. SMITH. 2009. Zooplankton inside an Arctic Ocean cold-core eddy: Probable origin and fate. *Deep-Sea Res. II* **56**: 1290–1304, doi:10.1016/j.dsr2.2008.10.020
- MAUCLINE, J. 1998. The biology of calanoid copepods. *Adv. Mar. Biol.* **33**: 1–710, doi:10.1016/S0065-2881(08)60234-5
- O'BRIEN, M. C., H. MELLING, T. PEDERSEN, AND R. MACDONALD. 2011. The role of eddies and energetic ocean phenomena in the transport of sediment from shelf to basin in the Arctic. *J. Geophys. Res.* **116**: C08001, doi:10.1029/2010JC006890
- OTA, Y., H. HATTORI, R. MAKABE, M. SAMPEI, A. TANIMURA, AND H. SASAKI. 2008. Seasonal changes in nauplii and adults of *Calanus hyperboreus* (Copepoda) captured in sediment traps, Amundsen Gulf, Canadian Arctic. *Polar Sci.* **2**: 215–222, doi:10.1016/j.polar.2008.08.002
- PROKOPOWICZ, A. J., S. RUECKERT, B. S. LEANDER, J. MICHAUD, AND L. FORTIER. 2010. Parasitic infection of the hyperiid amphipod *Themisto libellula* in the Canadian Beaufort Sea (Arctic Ocean), with a description of *Ganymedes themistos* sp. n. (Apicomplexa, Eugregarinorida). *Polar Biol.* **33**: 1339–1350, doi:10.1007/s00300-010-0821-0
- SAKSHAUG, E. 2004. Primary and secondary production in the Arctic seas, p. 57–81. In R. Stein and R. W. Macdonald [eds.], *The organic carbon cycle in the Arctic Ocean*. Springer-Verlag.
- SAMPEI, M., A. FOREST, H. SASAKI, H. HATTORI, R. MAKABE, M. FUKUCHI, AND L. FORTIER. 2009a. Attenuation of the vertical flux of copepod fecal pellets under Arctic sea ice: Evidence for an active detrital food web in winter. *Polar Biol.* **32**: 225–232, doi:10.1007/s00300-008-0523-z
- , H. SASAKI, H. HATTORI, A. FOREST, AND L. FORTIER. 2009b. Significant contribution of passively sinking copepods to the downward export flux in Arctic waters. *Limnol. Oceanogr.* **54**: 1894–1900, doi:10.4319/lo.2009.54.6.1894
- , ———, ———, M. FUKUCHI, AND B. T. HARGRAVE. 2004. Fate of sinking particles, especially fecal pellets, within the epipelagic zone in the North Water (NOW) polynya of northern Baffin Bay. *Mar. Ecol. Prog. Ser.* **278**: 17–25, doi:10.3354/meps278017
- , AND OTHERS. 2011. Production and retention of biogenic matter in the southeast Beaufort Sea during 2003–2004: Insights from annual vertical particle fluxes of organic carbon and biogenic silica. *Polar Biol.* **34**: 501–511, doi:10.1007/s00300-010-0904-y
- TERAZAKI, M., AND M. WADA. 1988. Occurrence of large numbers of carcasses of the large, grazing copepod *Calanus cristatus* from the Japan Sea. *Mar. Biol.* **97**: 177–183, doi:10.1007/BF00391300
- TREMBLAY, J.-É., K. SIMPSON, J. MARTIN, L. A. MILLER, Y. GRATTON, AND N. M. PRICE. 2008. Vertical stability and the annual dynamics of nutrients and chlorophyll fluorescence in the coastal, southeast Beaufort Sea. *J. Geophys. Res.* **113**: C07S90, doi:10.1029/2007JC004547

Associate editor: Thomas Kjørboe

Received: 05 May 2011

Accepted: 15 September 2011

Amended: 19 September 2011