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Variations in contributions of dead copepods to vertical fluxes of particulate organic carbon in the Beaufort Sea

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Running title: Temporal and regional PSC flux variabilities

Abstract

Dead zooplankton, including crustaceans, are increasingly recognized as important agents of vertical carbon export from surface waters and in marine food webs. Quantifying contribution of passively sinking copepods (PSCs) to total particulate organic carbon (POC) vertical flux is important to understanding marine ecosystem carbon budgets. Information on this is limited because identifying PSC in sediment trap samples is difficult. Generally, swimmers (undecomposed metazoa caught in sediment traps including PSCs) are removed from a trap sample before the POC content is measured, although ignoring PSCs causes the total POC flux to be significantly underestimated. We quantified temporal and regional variability in PSC flux and contribution of PSCs to total POC flux (PSCs + detrital sinking particles, generally analyzed to estimate detrital POC flux) at the Mackenzie Shelf margins in the Beaufort Sea. Six datasets were used to examine PSC flux variability at ~100 m depth, which is deeper than the winter pycnocline depth (30–50 m), at the continental margin. The average annual PSC flux ($1378 \pm 662 \text{ mg C m}^{-2} \text{ y}^{-1}$, $n = 6$) and PSC contribution to the total POC flux ($21\% \pm 10\%$, $n = 6$) suggested that PSCs, especially *Pareuchaeta glacialis*, were important agents of POC export from the surface layer (~100 m) to deeper water at the inter-regional and multiyear scales. We also proposed hypothesis that processes controlling PSC flux variability may vary seasonally, perhaps relating to life cycle (reproduction) in winter (February) and osmotic stress in July–October when the PSC flux is relatively high.

1. INTRODUCTION

Estimating vertical flux of particles, especially the export flux from the base of the epipelagic zone (~100–200 m), is important to understanding the efficiency and strength of the biological carbon pump (Wassmann 1998, Buesseler et al. 2007). Understanding the export flux is also important to understanding biological production and distribution, food web structures in the water column, and the processes involved in food resource supply to heterotrophs in deeper water (Wassmann 1998). Many sediment trap studies have been carried out to estimate the downward flux of particles in the ocean (e.g., Sasaki & Nishizawa 1981, Sampei et al. 2002, Forest et al. 2015). Estimation accuracy may be affected by the relative amounts of swimmers—live metazoans that actively swim into the trap—and passively sinking particles (Michaels et al. 1990, Buesseler et al. 2007). Contamination by swimmers causes the downward flux of organic particles to be overestimated (Silver & Gowing 1991, Buesseler et al. 2007). Hence, while partly and/or totally decomposed metazoans are included in flux estimates as much as possible, intact metazoans (i.e., showing no signs of decay, such as cracking or bursting, and filled with intact tissue) have traditionally been sorted out from trap samples before analysis to prevent the downward biogenic particle flux being overestimated. However, removing all undecomposed metazoans causes the downward flux to be underestimated because PSCs that died recently in the water column before sinking into the trap are themselves undecomposed metazoans (Sampei et al. 2009). Zooplankton carcasses, including those of copepods, have been observed in the water column in previous studies (e.g., Terazaki & Wada 1988, Haury et al. 1995, Genin et al. 1995, Yamaguchi & Ikeda 2001) and

are recognized as important agents of carbon export (Steinberg & Landry 2017).

Research has identified the vertical PSC flux (at ~100 m) and quantitative importance of PSC flux (i.e., fresh copepod carcasses) to the export flux in terms of particulate organic carbon (POC) in the Beaufort Sea (Sampei et al. 2009, 2012), although the importance of the PSC was discussed in relation to only one case study. Those studies also suggested that PSCs were a potential food source to meet the energy requirements of heterotrophs, especially when primary production was low in Arctic water, since the PSCs are more nutritive particles than refractory and/or diluted detrital particles in the water column. Copepods are widely distributed over spatial and temporal scales, and their carcasses can represent 10% or more of copepod biomass in the water column (Yamaguchi et al., 2002, Elliot & Tang 2009). Quantification of the vertical PSC flux is crucial to understanding the food web structure and the biological carbon pump. Our knowledge is, however, extremely limited because it is difficult to identify PSCs in long-term (year-long) sediment trap samples. Hence, improving our understanding by knowledge accumulation of vertical PSC fluxes is therefore important to understanding the biological carbon pump and food web structures.

It is essential to understand downward POC fluxes in water at continental shelves and margins because these areas may act as important sinks for atmospheric CO₂ (Walsh et al. 1981, Antia et al. 1999). The Arctic Ocean accounts for 20% of global continental shelves (Macdonald et al. 1998) and is thus expected to play an important role in regulating atmospheric CO₂ despite its small area (4% of the global ocean (Jakobsson 2002)). As a source of organic carbon (i.e., a food source for heterotrophs), Arctic continental margins may have a major impact on marine food webs in adjacent deep waters (i.e., the Arctic Basin). Higher primary productivity occurs on the shelf and

its margins than in the Arctic Basin (Sakshaug 2004) and organic matter may be transported horizontally to the Arctic Basin (Forest et al. 2007). Moreover, the continental shelf break and margins will experience the greatest biogeochemical impact (e.g. light, nutrients, and productivity) because of ongoing climate change in Arctic waters (Carmack et al. 2006).

We quantified temporal and spatial variability in PSC fluxes and the contributions of PSC fluxes to the total (i.e., PSCs + other detritus) POC fluxes in waters at the Mackenzie Shelf margins in the southeastern Beaufort Sea. The aim was to quantitatively confirm the importance of PSCs to the export POC flux based on multiple PSC flux data over inter-regional and multiyear scales at the Mackenzie Shelf margins in the Beaufort Sea. The study was performed because inter-regional and multiyear studies are needed to allow the effects of vertical PSC fluxes on carbon cycling processes to be assessed (Sampei et al. 2012). The results allowed us to suggest possible factors that control the PSC flux.

2. MATERIALS AND METHODS

2.1. Study area

The Mackenzie Shelf is the largest shelf on the North American side of the Arctic Ocean (100 km wide, 60,000 km² (Macdonald et al. 1998)). It receives a massive inflow of particle-rich freshwater (~330 km³ y⁻¹ of freshwater with ~124 × 10⁶ t y⁻¹ of suspended particles) from the Mackenzie River (Macdonald et al. 1998; Holmes et al. 2002). Most (~70%) of the annual

1 freshwater inflow occurs between May and September (Macdonald et al. 1998). The freshwater
2 disperses north through the Mackenzie Trough and then eastward along the shelf break (Forest et al.
3 2007). The particles move across the shelf via cycles of deposition, resuspension, and transport in
4 the nepheloid layer (O'Brien et al. 2006). The shelf is bordered by the Mackenzie Trough near the
5 mouth of the river in the west and the Amundsen Gulf in the east (Fig. 1). Diatomaceous new
6 production ($14.5 \text{ g C m}^{-2} \text{ y}^{-1}$) and the annual detrital POC flux ($4.6 - 6.9 \text{ g C m}^{-2} \text{ y}^{-1}$ at $\sim 100 \text{ m}$) are
7 moderate to high in the Mackenzie Trough over the Mackenzie Shelf break area (Sampei et al.
8 2011). In water close to the Mackenzie Trough, particle transport from the shelf to the deep basin
9 down the shelf slope occurs mostly ($\sim 68\%$) in the winter months when sea ice coverage is $>80\%$
10 (Forest et al. 2015).

11 12 2.2. Sediment trap deployment and sample treatment

13 Long-term moorings with time-programmed sediment traps were deployed at two stations
14 (A and G) in waters off the Mackenzie Trough in the Beaufort Sea from July 2009 to August 2012
15 (Table 1, Fig. 1). At Stn. A (ca. $70^{\circ}45' \text{ N}$, $136^{\circ}00' \text{ W}$, ca. 680 m bottom depth), a cylindrical
16 sediment trap (PPS 3/3-24S (Technicap, La Turbie, France) with a 40 cm diameter mouth) was set
17 at $\sim 100 \text{ m}$ deep, which is deeper than the winter pycnocline depth (30–50 m) in the study area
18 (Carmack & Macdonald 2002). The trap was recovered and redeployed in September 2009, 2010
19 and 2011. At Stn. G (ca $71^{\circ}00' \text{ N}$, $135^{\circ}30' \text{ W}$: ca 700 m bottom depth), a cylindrical trap was
20 deployed over the period 2009–2011, although a conical sediment trap (PPS 5/2 (Technicap, La
21 Turbie, France) with an 80 cm diameter mouth) was deployed in the period 2011–2012. The

collection cups of the sediment traps were filled with GF/F filtered seawater (~36‰ final concentration) treated with buffered formalin (~5 % v/v). No samples were available for analyses from Stn. G for the period 2010–2011 because the sediment trap could not be recovered. The sampling intervals for each sediment trap cup were 7 d in spring to 31 d in winter.

After recovery, the sediment trap samples were left undisturbed for 24 h to allow all particles to settle. Each sample was then quantitatively split into several fractions using a Motoda-type wet sample splitter (Rigo, Saitama, Japan) (Motoda 1959) for later analyses. Large undecomposed copepods showing no signs of decay, such as being cracked or burst, and being filled with intact tissue (i.e., adult stages and copepodite stage V (CV) of *Calanus hyperboreus* and *Calanus glacialis* and adult stages and copepodite stage IV (CIV)+ CV of *Pareuchaeta glacialis*) were manually removed from all the original samples in three sampling campaigns (i.e., Stns. A and G in 2009–2010 and Stn. A in 2010–2011) and from half of the original samples in the other two sampling campaigns (i.e., Stns. A and G in 2011–2012) under a C-DS stereo microscope with <40 times magnification (Nikon, Tokyo, Japan). These copepods were removed from the sediment trap samples and kept to estimate the PSC flux. These large manually removed undecomposed copepods were classified as PSCs (copepods that had died in the water column before sinking into the trap) and sinkers (living copepods that swam into the trap and died there because of the preservative) based on their post-mortem postures following the method described by Sampei et al. (2009). To decrease uncertainties in the PSC flux estimates, we double-checked the post-mortem postures at two different microscopic magnifications ($\times 10$ – $\times 20$ and $\times 20$ – $\times 40$). Because of methodological limitations, only large copepod species and developmental stages were included when estimating

the PSC flux (Sampei et al. 2009). Other undecomposed metazoans were removed manually under a stereo microscope from the sub-samples intended for carbon-hydrogen-nitrogen (CHN) analysis.

2.3.Determination of vertical fluxes of the detrital sinking particles and PSCs

Sediment trap samples (other than undecomposed metazoans) were passed through pre-combusted (at 450 °C for 3 h) GF/F glass fiber filters, and dried at 60 °C for 48 h to allow the particulate mass dry weight (DW) to be determined using an XP6 precision balance (Mettler Toledo, Columbus, OH, USA). These filter samples were exposed to the fumes above concentrated HCl for 12 h to remove carbonates before the detrital POC and particulate organic nitrogen (PON) were determined using a PerkinElmer CHN elemental analyzer 2400 Series II (PerkinElmer, Waltham, MA, USA). The detrital sinking particulate mass (i.e., particles traditionally analyzed to determine the vertical flux of particles) was expressed as daily vertical flux ($\text{mg m}^{-2} \text{d}^{-1}$ calculated from the analytical data; i.e., $\text{POC flux} = \text{POC mass} \times \text{collection area}^{-1} \times \text{collection days}^{-1}$). Vertical fluxes of detrital sinking particles on DW and POC bases were also published by Forest et al. (2015). Annual vertical fluxes ($\text{mg m}^{-2} \text{y}^{-1}$) were calculated by adding together the daily fluxes for 365 d from the start of the sampling period (e.g., from 21 July 2009 to 20 July 2010 for Stn. A in 2009–2010). The missing fluxes at the time the sample changeover at a mooring occurred (when no sinking particle sampling was conducted) were estimated by linear interpolation between the two contiguous values. The two contiguous values for Stn. A in 2009–2010 and 2010–2011, for example, were the last datum for each sampling period (i.e., 22–29 June 2010 or 24–31 August 2011) and the first datum for the next sampling period (i.e., 13–30 September 2010 or 14–30 September 2011).

The two contiguous values for the other three cases (i.e., Stn. A in 2011–2012 and Stn. G in 2009–2010 and 2011–2012) were the first and last data for each sampling period (e.g., 14–30 September 2011 and 24 August–1 September 2012 for Stn. A in 2011–2012).

The PSCs were dried at 60 °C for 48 h and the DWs determined using a Mettler Toledo XP6 precision balance. The PSCs were then subjected to carbon and nitrogen analyses using a PerkinElmer CHN elemental analyzer 2400 Series II. The PSC mass was expressed as a daily PSC flux calculated from the analytical data. The PSC flux data were corrected using the equations shown below because of misclassifications caused by underestimations related to the post-mortem posture criteria (see Sampei et al. (2009) for details). The equations were $\text{PSC flux}/0.64$ for *C. hyperboreus* and *C. glacialis* and $\text{PSC flux}/0.44$ for *P. glacialis* (Sampei et al. 2009). All statistical analyses were performed using JSTAT 20.0J software (Masato Sato, Japan).

2.4. Fresh water discharge from the Mackenzie River

Monthly Mackenzie River discharges at a station of the Mackenzie River (at Arctic Red River) were obtained using with Environmental Canada Data Explorer (version 2.1.8) HYDAT (version 1.0) for May–July in 2003, 2008, 2009, 2011 and 2012. May–July is a period when river flow occurs mostly (Macdonald & Wong 1987) and before the accumulated rubble ice (stamukhi) breaks up (Macdonald & Yu 2006).

3. RESULTS

3.1. Vertical detrital sinking particle flux

The seasonal pattern of vertical flux of the detrital sinking particles in terms of POC in the three deployment years (i.e., 2009–2010, 2010–2011, and 2011–2012) were similar (Fig. 2). Relatively high detrital sinking particle fluxes, up to $117.9 \text{ mg C m}^{-2} \text{ d}^{-1}$, were recorded at both stations in spring–summer (June–September) 2009–2011. The particle flux increased sharply in June–July and remained moderate until September. The particle flux in winter (December–February) remained relatively low ($0.4\text{--}12.4 \text{ mg C m}^{-2} \text{ d}^{-1}$), although it was equivalent to the autumn flux (October–November, $0.7\text{--}19 \text{ mg C m}^{-2} \text{ d}^{-1}$).

Annual detrital sinking particle fluxes in terms of DW, POC, and PON and the C/N ratios are shown in Table 2. The annual fluxes in terms of POC and PON were almost equivalent (slightly higher at Stn. G by 24% for POC and 8% for PON) between Stn. A and G in 2009–2010, although the fluxes were ~3 times higher at Stn. A than G in 2011–2012. The C/N ratio (mol/mol) was slightly higher at Stn. G (9.1 in 2009–2010 and 8.3 in 2011–2012) than at Stn. A (7.9 in 2009–2010 and 7.4 in 2011–2012).

3.2. Vertical PSC flux

The PSC flux in terms of POC varied seasonally (Fig. 2). No remarkable differences were observed in the seasonal patterns for Stns. A and G. The PSC flux was generally high from mid-summer to mid-autumn (July–October), and a small peak appeared in winter (February) and early spring (March). The maximum PSC daily flux at Stn. A ($34.4 \text{ mg C m}^{-2} \text{ d}^{-1}$) was ~3 times

1 higher than at Stn. G ($12.3 \text{ mg C m}^{-2} \text{ d}^{-1}$) in 2009–2010 and ~8 times higher at Stn. A (12.9 mg C
2 $\text{m}^{-2} \text{ d}^{-1}$) than at Stn. G ($1.6 \text{ mg C m}^{-2} \text{ d}^{-1}$) in 2011–2012.

3 Annual PSC fluxes in terms of DW and POC and the C/N ratios are shown in Table 2. The
4 annual PSC fluxes in terms of POC were 1.4–28 times higher at Stn. A than at Stn. G in both
5 available study periods (i.e., 2009–2010 and 2011–2012). Annual variability in the PSC fluxes were
6 one order of magnitude higher at Stn. G (for which the variability factor was 24) than at Stn. A (for
7 which the variability factor was 2.5). The C/N ratio (mol/mol) varied from 6.6 (at Stn. G in
8 2011–2012) to 8.9 (at Stn. A in 2009–2010), and was slightly higher at Stn. A than at Stn. G (8.9 vs.
9 8.3 in 2009–2010 and 8.0 vs. 6.6 in 2011–2012). The C/N ratios were comparable to the C/N ratios
10 for live copepods ~3 to 12 for *C. glacialis* and 5 to 9 for *C. hyperboreus* in the Amundsen Gulf
11 (Forest et al. 2011) and 4 to ~10 for *Pareuchaeta norvegica* (a species related to *P. glacialis*) in
12 Loch Etive, Scotland (Nemoto et al. 1976).

13 14 3.3. Comparison of PSCs and detrital sinking particle fluxes

15 The annual PSC flux was equivalent to 2%–27% ($15\% \pm 9\%$, $n = 5$) of the total flux (i.e.,
16 PSCs + detrital sinking particles) in terms of POC and to 3%–25% ($15\% \pm 8\%$, $n = 5$) in terms of
17 PON (Table 2). In comparison with the detrital sinking particle flux, the PSC flux clearly showed
18 high annual and regional variability (Table 2). The coefficient of variation of annual variability in
19 terms of POC was 0.34 (Stn. A) or 0.93 (Stn. G) for the PSC flux and only 0.13 (Stn. A) or 0.47 (Stn.
20 G) for the detrital sinking particle flux. The coefficient of variation of regional variability was 0.16
21 (in 2009–2010) and 0.93 (in 2011–2012) for the PSC flux and only 0.11 (in 2009–2010) and 0.47

(in 2011–2012) for the detrital sinking particle flux. Higher coefficients at Stn. G than A, and in 2011–2012 than 2009–2010 might be due to a bias of sampling at Stn. G in 2011–2012 (see section 4.1). These variabilities illustrated the instability of the PSC flux in terms of POC at the annual and regional scales.

3.4.PSCs and sinkers

The flux in the numbers of PSC and sinker specimens and the contributions of PSCs and sinkers to the total copepod (i.e., PSCs + sinkers) flux are shown in supplementary Table S1. The results clearly show that the largest PSC, *P. glacialis*, was a major contributor to PSCs throughout the study. *Pareuchaeta glacialis* contributed 89%–98% of the integrated total annual PSC fluxes for the five study cases. The highest numerical PSC fluxes were recorded at Stn. A in 2011–2012 for all three species (*P. glacialis*, *C. hyperboreus*, and *C. glacialis*). The highest numerical PSC flux for *P. glacialis* (70.6 ind. m⁻² d⁻¹) was one order of magnitude higher than highest numerical PSC fluxes for *C. hyperboreus* (3.1 ind. m⁻² d⁻¹) and *C. glacialis* (5.0 ind. m⁻² d⁻¹). The annual integrated PSC fluxes were one–two orders of magnitude higher for *P. glacialis* (2242.3 ± 1271.6 ind. m⁻² y⁻¹, *n* = 5) than *C. hyperboreus* (19.2 ± 19.5 ind. m⁻² y⁻¹, *n* = 5) and *C. glacialis* (121.9 ± 126.3 ind. m⁻² y⁻¹, *n* = 5).

The contributions of PSCs to the numerical fluxes of total copepods (%PSC) varied widely seasonally (supplementary Table S1). The ranges for the daily contributions of *P. glacialis*, *C. hyperboreus*, and *C. glacialis* were 0%–34.5%, 0%–100%, and 0%–100%, respectively. Even

though the daily contributions varied widely, variability in the annual contributions was comparatively low, at 1.0%–5.5% for *P. glacialis*, 0%–2.5% for *C. hyperboreus*, and 0.1%–2.3% for *C. glacialis*. These results show clearly that most copepod specimens collected by the sediment traps were sinkers.

3.5. Dominant contributors to the PSC flux in terms of POC

Seasonal variabilities in the PSC flux by developmental stage (CIV+CV, or adult) for each copepod species (*P. glacialis*, *C. glacialis*, and *C. hyperboreus*) are shown in Fig. 3. The highest PSC flux for *P. glacialis* ($33.9 \text{ mg C m}^{-2} \text{ d}^{-1}$) was one order of magnitude higher than the highest PSC fluxes for *C. hyperboreus* ($1.8 \text{ mg C m}^{-2} \text{ d}^{-1}$) and *C. glacialis* ($2.3 \text{ mg C m}^{-2} \text{ d}^{-1}$) in the five study cases. The average annual PSC fluxes were also one order of magnitude higher for *P. glacialis* ($918 \pm 602 \text{ mg C m}^{-2} \text{ y}^{-1}$, $n = 5$) than *C. hyperboreus* ($18 \pm 12 \text{ mg C m}^{-2} \text{ y}^{-1}$, $n = 5$) and *C. glacialis* ($43 \pm 46 \text{ mg C m}^{-2} \text{ y}^{-1}$, $n = 5$). A positive correlation was observed between the PSC flux for *P. glacialis* and the total PSC flux in terms of POC ($r = 0.998$, $p < 0.01$, $n = 5$). These results and the numerical PSC fluxes (see sub-section 3.4) clearly indicate that *P. glacialis* was the most important copepod species contributing to the total PSC flux.

Although the importance of *P. glacialis* as a PSC to the vertical flux of total POC, large and dominant Arctic copepods *C. hyperboreus* and *C. glacialis* could be still important contributors to the total POC flux due to their large and fast sinking fecal pellets production. In fact, formerly reported annual fecal pellets contribution to the detrital POC flux is comparable or higher (7-31%: Sampei et al. 2002, 2004, Forest et al. 2007) than the annual contribution of PSCs (10-27%: Table

2) in the Arctic waters.

Copepodite stages generally dominated the daily PSC flux over the sampling period, although peaks for the adult stages appeared during the high PSC flux period (i.e., July–October),; for example, the end of July 2009 at Stn. A, mid-August 2011 at Stn. A, the beginning of July 2012 at Stn. A, and the end of July to the beginning of August 2009 at Stn. G (Fig. 3). In the high PSC flux period, the term-averaged contribution of the copepodite stages of PSCs to the total PSC fluxes was as high as $75\% \pm 13\%$ ($n = 5$) and was never below 50% in the five study cases. Even the annual contribution of the copepodite stages to the total PSC flux (60%–84%) was higher than the contribution of the adult stages in terms of POC in all five study cases. The positive correlation between the total PSC (adult + copepodite) flux and copepodite PSC flux was significant ($r = 0.974$, $p < 0.01$, $n = 5$) and was stronger than the correlation between the total PSC flux and adult PSC flux ($r = 0.864$, $p > 0.05$, $n = 5$). The high contributions of the copepodite stages and strong positive correlations indicated that the PSC flux was more strongly affected by the copepodite stages than the adult stage except during winter.

3.6. Mackenzie River water discharge and correlation with PSC flux

Mackenzie River discharge between May–July 2003, 2008, 2009, 2011 and 2012 were 144 km³, 152 km³, 163 km³, 130 km³ and 152 km³, respectively. Those river discharges were correlated with PSC fluxes in July (when the highest PSC flux was observed in the present study), although the correlation was not significant (Spearman's correlation coefficient by rank, $r = 0.949$, $n = 4$, $p > 0.05$). The monthly PSC fluxes in July were 989 mg C m⁻² at Stn. A in 2009, 246 mg C m⁻² at Stn. G

1 in 2009, 8 mg C m⁻² at Stn. A in 2011 and 125 mg C m⁻² at Stn. A in 2012. In case of the monthly
2 PSC fluxes from two previous studies (51 mg C m⁻² at Stn. CA7 in 2003 and 73 mg C m⁻² at Stn.
3 CA16 in 2008: Sampei et al. 2009, 2012) were also included in the statistical analysis, the
4 correlation was significant (Spearman's correlation coefficient by rank, $r = 0.928$, $n = 6$, $p < 0.05$).

7 **4. DISCUSSION**

9 **4.1. Uncertainties and biases in the vertical flux estimates**

10 Logistical limitations meant that two sediment traps of different shapes, cylindrical and
11 conical, were used in this study. The conical sediment trap was used only for Stn. G in 2011–2012
12 and the cylindrical trap was used for the other sampling periods at both station (Table 1). The shape
13 of a sediment trap will affect the particle trapping efficiency and will bias the vertical particle flux
14 estimate (e.g., Butman et al. 1986, Hargrave et al. 2002). A cylindrical trap will perform more
15 efficiently than a conical trap in collecting samples (e.g., Gardner 1985, Ducklow et al. 2015). In
16 fact, the detrital POC flux estimates based on the conical trap collections (i.e., the flux at Stn. G in
17 2011–2012) was only about one-third of the detrital POC flux at Stn. G in 2009–2010 even though
18 there was no obvious difference between the detrital POC fluxes at Stn. A in 2009–2010 and
19 2011–2012 (Table 2). The detrital POC flux at Stn. G in 2011–2012 was also about one-third of the
20 detrital POC flux at Stn. A in 2011–2012 even though there were no obvious differences between
21 the detrital POC fluxes at Stns. A and G in 2009–2010 (Table 2). The detrital POC flux at the two

1 sites may be similar because of the environmental settings, such as similar patterns in the
2 temperature–salinity diagrams of the water columns (Forest et al. 2015), the small distance between
3 the study sites, and similar topographical characteristics (i.e., on the Mackenzie Shelf slope) (Fig. 1).
4 Together, the sediment trap shape issue and our detrital POC flux estimates strongly suggest that the
5 comparatively low detrital POC flux at Stn. G in 2011–2012 was caused by bias caused by the
6 sediment trap shape rather than there being fewer sinking particles in the water column. Hence, we
7 excluded the flux data from Stn. G in 2011–2012 from the discussion below.

8 Even the cylindrical sediment traps may have had decreased sinking particle collection
9 efficiencies because of the surface water currents (Buesseler et al. 2007). The annual average
10 current velocities were $14\text{--}16\text{ cm s}^{-1}$ at 100 m deep at Stns. A and G in the study period (Forest et al.
11 2015). However, our sediment trap had a high aspect ratio (i.e., height/diameter) of 4 and a baffle lid
12 (aspect ratio 5) on top. The high aspect ratio ($>3\text{--}5$) reduced internal turbulence and increased the
13 collection efficiency (e.g., Hargrave et al. 2002, Buesseler et al. 2007). In fact, in previous studies
14 detrital POC fluxes have been successfully estimated using the same type of sediment trap deployed
15 at ~ 100 m in the Mackenzie Shelf margins (e.g., Forest et al. 2010, Sampei et al. 2011). Our
16 estimates of the annual detrital POC fluxes ($4.6\text{--}6.3\text{ g C m}^{-2}\text{ y}^{-1}$) were comparable to detrital POC
17 fluxes of 4.6 and $6.9\text{ g C m}^{-2}\text{ y}^{-1}$ estimated in a previous study in waters around the Mackenzie
18 Trough (Sampei et al. 2011). Thus, our detrital POC fluxes estimated using the cylindrical sediment
19 trap were reasonable.

20 A lower current velocity may cause a higher detrital POC flux because of the sediment trap
21 collection efficiency being higher (e.g., Buesseler et al. 2007). Also, higher primary production in

1 the surface water could cause a higher detrital POC flux (e.g., Martin et al. 1987). Primary
2 production and the current velocity are two–three times higher (Brugel et al. 2008, Sampei et al.
3 2011) and two–three times lower (Forest et al. 2010, 2015), respectively, in the Amundsen Gulf than
4 in the Mackenzie Trough. Despite regional differences, the detrital POC fluxes at the Amundsen
5 Gulf site (CA16) and Mackenzie Trough sites (A and G) were similar (Table 2). The effect of the
6 current velocity may therefore have been less than the effect of regional variability.

7 The annual flux estimates were based partly on interpolated fluxes for the missing
8 sampling period (see Materials and Methods). The estimated annual fluxes may have been biased
9 because the missing periods (part of July and all of August and September) generally have high
10 vertical detrital POC fluxes in the southeastern Beaufort Sea (e.g., O'Brien et al. 2006, Forest et al.
11 2007, 2010). Evaluating the bias is challenging, but the bias should have been smaller than the
12 interannual variability in the detrital POC flux. At Stn. A, our interpolated detrital POC flux for July
13 2010 was higher than the interpolated detrital POC fluxes in September 2011 (by a factor of 2.4)
14 and September 2012 (by a factor of 9.3). However, our integrated annual detrital POC flux based on
15 the interpolated flux was higher for 2009–2010 (including the relatively low interpolated detrital
16 POC flux for July) than for 2010–2011 and 2011–2012 (both including the relatively high
17 interpolated detrital POC flux for September). This clearly shows that the higher interpolated
18 detrital POC flux did not affect the general size of interannual variability in the annual detrital POC
19 flux.

20 Although the methodology for estimating PSC flux (*see* Sampei et al. 2009) is not within
21 the scope of this paper, we suggest here a possible extra process to avoid increasing uncertainty in

1 the estimate: observing the post-mortem postures after isolating copepods from other sinking
2 particle samples (i.e., not when the copepods are first collected). This process is important because
3 of the difficulty in adequately observing the post-mortem postures when visibility is impeded by
4 large sinking particles. Observations of the post-mortem postures under such conditions may result
5 in the PSC flux being underestimated or overestimated. The extra process is highly recommended
6 even though it is time-consuming compared with the usual process of removing swimmers from
7 sediment trap samples (Knap et al. 1996).

8 The PSC flux may also be underestimated because of the presence of the small but
9 frequently found copepod *Metridia longa* (45583 ± 12795 ind. $\text{m}^{-2} \text{y}^{-1}$, $n = 4$), which was not
10 included in the PSC estimate (Sampei et al. 2009). Furthermore, the PSC estimate did not include
11 lower copepodite stages (CI–CIII) of the three large dominant species (*P. glacialis*, *C. glacialis*, and
12 *C. hyperboreus*) and other small copepod species (e.g., *Pseudocalanus* spp., *Microcalanus* spp., and
13 *Oithona similis*) because of methodological limitations despite these being present in the sediment
14 trap samples. The younger stages also could contribute to PSC flux, since younger stages show
15 higher %dead in the water column (Ohman & Wood 1996). The PSC fluxes and PSC contributions
16 to the total downward POC fluxes were therefore minimum estimates for the four study cases (i.e.,
17 excluding Stn. G in 2011–2012).

18 19 20 4.2. Variability of the PSC flux and the PSC contribution to the total POC flux

21 We made an extended comparison of the PSC fluxes in six study cases, four from this

study and two from previous studies (Sampei et al. 2009, 2012), on the margins of the Mackenzie Shelf in the Beaufort Sea. The range of annual PSC fluxes ($680\text{--}1695\text{ mg C m}^{-2}\text{ y}^{-1}$) in the present study was comparable to the annual PSC fluxes ($891\text{--}2528\text{ mg C m}^{-2}\text{ y}^{-1}$) found in the previous studies (Sampei et al. 2009, 2012). The contributions of the PSC fluxes to the total (i.e., PSC + detrital sinking particle) annual POC fluxes found in the previous studies (13% and 37% (Sampei et al. 2009, 2012)) and present study ($10\%\text{--}27\%$, average $19\% \pm 7\%$, $n = 4$) were also comparable. The average annual PSC flux in the six study cases was $1378 \pm 662\text{ mg C m}^{-2}\text{ y}^{-1}$ ($n = 6$), and the average contribution of PSCs to the total POC flux was $21\% \pm 9\%$ ($n = 6$). These comparisons clearly suggest that PSCs are a substantial agent of POC export from the surface layer ($\sim 100\text{ m}$ deep) to deeper water at the inter-regional and multiyear scales in the southeastern Beaufort Sea even though the PSC fluxes and contributions are variable.

Hirst and Kiørboe (2002) estimated the natural mortality of copepods by causes other than predation in vitro ($1.9\%\text{ d}^{-1}$ to $6.5\%\text{ d}^{-1}$). Daase et al. (2014) identified the natural abundances of copepod carcasses using five degradation levels (category 1 being visual characteristics of undecomposed copepods) in the Arctic Ocean in January and found category 1 abundances of $0\%\text{--}1.1\%$ in water shallower than 128 m . The contributions of PSCs to undecomposed copepod (i.e., PSCs + sinkers) fluxes in this study were $2.4\%\text{--}4.1\%$ for the annually integrated values for all three copepod species and $0\%\text{--}6\%$ for all three copepod species in January (supplementary Table S1). The natural mortality rate in vitro and the natural abundances of carcasses in the water column were comparable to the contribution of PSCs to the total (PSCs + sinkers) undecomposed copepod flux even though the total flux is influenced not only by the copepod abundance in the water column but

also by copepod behavior in relation to entrapment (Makabe et al. 2016). These results and the comparable ranges of PSC fluxes in this study and previous studies may indicate that our PSC flux estimates are reasonable.

4.3. Possible explanations for temporal and/or spatial variability in the PSC flux and dominant contributors to the flux

In two earlier studies (Sampei et al. 2009, 2012) moderately high PSC fluxes in terms of POC were found ($<7.9 \text{ mg C m}^{-2} \text{ d}^{-1}$) at the same time of year as relatively high PSC fluxes were found in this study (i.e., July–October). The contributions of copepodite PSCs to the total PSC fluxes were high ($73\% \pm 27\%$; $n = 6$) for all of the available data sets (i.e., four from the present study and two from the earlier studies) for the southeastern Beaufort Sea in the four month period with a high PSC flux. A positive correlation was found between the total PSC (adult + copepodite) flux and copepodite PSC flux ($r = 0.925$, $p < 0.01$, $n = 6$), and this was stronger than the correlation between the total PSC flux and adult PSC flux ($r = 0.670$, $p > 0.05$, $n = 6$) (Fig. 4A). These comparisons (i.e., of data from the present and previous studies) confirm that the PSC flux is more strongly impacted by copepodite stages than by adult stages in the high PSC flux period.

Intact copepod carcasses (a source of PSCs) may be found because of non-predatory mortality, such as natural death following reproduction, environmental stress, chemical contaminants, disease, and food-related factors (Terazaki & Wada 1988, Tang & Elliot 2014). Natural death following reproduction can occur only in adults because copepodites do not reproduce. Reproduction of *C. hyperboreus* in the Amundsen Gulf appears November–March and completed in

1 April (Ota et al. 2008). Similarly, egg production in *Pareuchaeta* spp. peaks during winter,
2 supported primarily by the lipid reserves of the females and relying partly on predatory feeding
3 (Båmstedt 1979, Alonzo et al. 2000). Thus, the main factor controlling variability in the PSC flux is
4 most likely something other than the copepod life cycle (i.e., reproduction) in July–October when
5 the PSC flux is comparably high in the Beaufort Sea.

6 It is difficult to suggest a cause of natural death, but we will here suggest possible causes of
7 natural death during the high PSC flux period in July–October. Starvation, which is one cause of
8 natural death (Terazaki & Wada 1988), is not likely to have been a primary reason in our study
9 because the interannual trends in relative contribution of PSC to total POC flux and primary
10 production did not match. Primary production in autumn (September–October) at the Mackenzie
11 Shelf margins was $166 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2010, $108 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2011, $53 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2002,
12 and $28 \text{ mg C m}^{-2} \text{ d}^{-1}$ in 2009 (in decreasing productivity order) (Blais et al. 2017). Relative
13 contribution of PSC to total POC flux in September and October were 72.5% in 2011, 37.7% at Stn.
14 A and 43.1% at Stn. G in 2009, 30.5% in 2002, and 5.6% in 2010 (in decreasing order). There was
15 no statistically significant correlation between primary production and the relative contribution of
16 PSC to total POC flux in autumn (Spearman's correlation coefficient by rank: $r = -0.359$, $n = 5$, $p >$
17 0.05). Another possible explanation for copepod mortality is osmotic stress caused by freshwater
18 inputs (Kaartvedt & Aksnes 1992). Relatively large amounts of freshwater are discharged from the
19 Mackenzie River ($330 \text{ km}^3 \text{ y}^{-1}$, the fourth largest discharge in the Arctic and the 18th worldwide)
20 (Macdonald & Yu 2006). River flow occurs mostly between May and September (Macdonald &
21 Wong 1987). The discharged freshwater forms the seasonal Mackenzie freshwater lake under the

landfast ice cover of the coastal zone (Forest et al. 2007). In late July or early August, flow from the river plume begins to cross the shelf and enter the ocean interior as the accumulated rubble ice (stamukhi) breaks up (MacDonald & Yu 2006). This flow-out period overlaps with the high PSC flux period. Extremely low-saline surface water (as low as 18.5 and range of 18.5-27.9) was found around the mooring sites in July 2009 when the highest PSC flux was recorded, although low-saline surface water was found in August (25.0-26.0) and September (25.9-27.7) 2009 (Amundsen Science Data Collection 2018). We speculate that osmotic stress caused by the input of the large amount of freshwater from the Mackenzie lake/river is a likely cause of natural death in the high PSC flux period, although other causes (i.e. other than osmotic stress) may also contribute to the PSC flux. Moreover, a strong positive correlation between the river discharge and PSC flux (see section 3.6) may suggest that osmotic stress markedly affected interannual variability in the annual PSC flux.

A remarkable difference was found between the PSC flux variabilities for the six study cases in winter. In one study case, the second-highest monthly PSC flux during the study period (October 2007–July 2008) occurred in February ($14.6 \text{ mg C m}^{-2} \text{ d}^{-1}$) (Sampei et al. 2012). The PSC fluxes in the five other study cases were up to one order of magnitude lower, although small peaks were observed in winter ($1.8\text{--}8.9 \text{ mg C m}^{-2} \text{ d}^{-1}$, Fig. 2 and Sampei et al. (2009)). These differences raise a question about how winter PSC fluxes are controlled in the Beaufort Sea.

Sampei et al. (2012) demonstrated that the high PSC flux in winter is induced by senescence and natural death following reproduction by large copepods. They found that adult stages of *P. glacialis* dominated the PSC specimens in the winter peak (in February) with remarkably high PSC fluxes in the Amundsen Gulf (Sampei et al. 2012). However, adult stages of *P.*

1 *glacialis* were not observed among the PSC specimens in the winter peaks of the PSC fluxes in the
2 other five study cases (four from the present study and one by Sampei et al. (2009)) with relatively
3 low PSC fluxes. The correlation between the total PSC (adult + copepodite) flux and adult PSC flux
4 was significant ($r = 0.991$, $p < 0.001$, $n = 6$) and was stronger than the correlation between the total
5 PSC flux and copepodite PSC flux ($r = -0.320$, $p > 0.05$, $n = 6$) in February (Fig. 4B). The sediment
6 trap samples therefore may suggest that the annual and/or spatial variabilities of the PSC fluxes in
7 winter were most likely controlled by senescence and natural death following reproduction by large
8 copepods, although other naturally dead PSCs may also contribute to the PSC flux.

9 Here, we will attempt to explain the large annual and/or spatial variabilities in senescence
10 and natural death following reproduction by large copepods in February. The appearance of
11 copepod nauplii in March may be caused by reproduction (i.e., eggs laid) between December and
12 March (Sampei et al. 2012). The nauplii flux in March was higher at a study site in the Amundsen
13 Gulf (4565 ind. m^{-2}) (Sampei et al. 2012) than at the Mackenzie Trough sites (224–1438 ind. m^{-2}).
14 There was a positive correlation between the adult PSC flux in February and the copepod nauplii
15 numerical flux in March ($r = 0.919$, $p < 0.05$, $n = 5$). Food availability is an important factor for
16 copepod egg production (e.g., Mauchline 1998). Primary production is higher in the Amundsen
17 Gulf than the Mackenzie Trough (Brugel et al. 2009, Sampei et al. 2011). The differences in
18 senescence and natural death following reproduction may therefore have been caused by regional
19 differences favoring reproduction in the Amundsen Gulf rather than the Mackenzie Trough. More
20 detailed studies of copepod reproduction are needed, however, to assess the factors controlling
21 variability in senescence and natural death following reproduction in the Arctic winter.

We drew two conclusions about the importance of the PSC flux from these results. (1) PSCs important contribution to total POC fluxes from the surface layer to the deeper water column varies significantly at the regional, seasonal and annual scales. (2) The copepod life cycle and other processes (including osmotic stress caused by freshwater inputs) are important in controlling PSC fluxes even though the most important processes will vary by season (the life cycle of copepods in winter and other processes in summer–autumn in the southeastern Beaufort Sea).

4.4. Implications of PSCs for marine ecosystems

Quantifying non-predatory copepod carcasses, copepods that have died from causes other than predation, is essential to understanding copepod population dynamics and biogeochemical cycles because non-predatory copepod carcasses may represent substantial copepod stocks in the water column (e.g., 29% in Chesapeake Bay (Tang et al. 2006)). However, non-predatory copepod carcasses are counted rarely because it is difficult to identify carcasses in preserved copepod specimens (Elliott & Tang 2011). This is particularly true with respect to estimating PSC fluxes in the water column, which has been attempted in few studies (Sampei et al. 2009, 2012, Ivory et al. 2014).

Copepod carcasses represent concentrated sources of labile organic matter and a better source of highly nutritious food for heterotrophs than other sinking/suspended particles (Sampei et al. 2009, Bickel & Tang 2010). Fresh copepod carcasses (i.e., PSCs) also have higher sinking rates ($345\text{--}816\text{ m d}^{-1}$ (Sampei unpublished data)) than other sinking particles such as phytoplankton (e.g., $<1\text{--}100\text{ m d}^{-1}$ for single-cell or chain-forming diatoms (Smetacek 1985, Miklasz & Denny 2010)),

1 copepod fecal pellets (e.g., 5–220 m d⁻¹ (Turner 2002, Sampei et al. 2004)), and marine snow (e.g.,
2 16–368 m d⁻¹ (Turner 2002)). These values suggest that PSCs may provide good nutritional support
3 for heterotrophs in water below the surface layer.

4 In the Mackenzie Shelf margin, horizontal advection of resuspended sediments from the
5 shelf is promoted by storms and upwelling events at the shelf break (Carmack & Macdonald 2002,
6 Forest et al. 2007, 2015, Williams & Carmack 2008, Magen et al. 2010). The sediments that supply
7 resuspended particles are dominated by refractory marine and terrestrial end members, which
8 contain less-labile particles (Magen et al. 2010). These less-nutritive refractory resuspended
9 particles may not be favorable sources of food for copepods, other zooplankton and benthos because
10 food quality strongly affects reproductive success (Mauchline 1998). The availability of nutritive
11 food is, therefore, key to successful reproduction (Turner et al. 2001). In fact, an omnivorous
12 copepod, *M. longa* was attracted to dead bodies of *P. glacialis*, *C. hyperboreus*, and *C. glacialis* in
13 laboratory experiments (M. Sampei, unpublished). High C/N ratio of PSCs (Table 2) might indicate
14 high lipid contents, because C/N ratio of dominant copepods changes due to lipid contents in the
15 Amundsen Gulf (Forest et al. 2011). PSCs may therefore be valuable food sources for omnivores
16 and carnivores such as *M. longa* and *P. glacialis*, and benthos in the Mackenzie Shelf margin. We
17 suggest that PSCs (as a highly nutritive food source due to labile carbon and high-quality lipids
18 content) may also affect marine ecosystems at other continental shelf margins because of the large
19 amounts of non-predatory copepod carcasses that have been found (e.g., Weikert 1977, Tang &
20 Elliot 2014) and the occurrence of large amounts of resuspended sediment (i.e., less-labile particles)
21 (e.g., Honjo et al. 1982, Diercks et al. 2018) at continental margins other than the Mackenzie Shelf

margin. The ultimate fate of exported POC as PSCs from the surface layer is still uncertain. How PSCs affect marine ecosystems, especially in the twilight zone (sensu Buesseler et al. 2007) and deeper water, remains to be examined in future studies.

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Table 1. Information on the sediment traps deployed in the Beaufort Sea.

Mooring Stn. Bottom depth (m)	Cordination (Lat. (N), Long (W))	Sampling period (dd/mm/yy - dd/mm/yy)	Trap depth (m)	Trap type Collector shape	Sampling intervals (days-days)	Data source
A 688	70°46' N, 136°11' W	21/07/09 - 29/06/10	98	Tecnicap PPS3/24 Cyrindrical	3-31	This study
A 684	70°46' N, 136°11' W	13/09/10 - 31/08/11	88	Tecnicap PPS3/24 Cyrindrical	7-31	This study
A 659	70°45' N, 136°11' W	14/09/11 - 01/09/12	72	Tecnicap PPS3/24 Cyrindrical	8-17	This study
G 702	71°00' N, 135°29' W	24/07/09 - 29/06/10	102	Tecnicap PPS3/24 Cyrindrical	7-31	This study
G 705	71°00' N, 135°23' E	20/09/11 - 01/09/12	125	Tecnicap PPS5 Conical	8-15	This study
CA7 505	71°10' N, 133°53' W	21/09/02 - 31/08/03	70	Nichiyu SMD12S Cyrindrical	15-61	Sampei et al. (2009)
CA16 309	71°47' N, 126°30' W	21/10/07 - 22/07/08	112	Tecnicap PPS3/24 Cyrindrical	7-31	Sampei et al. (2012)

Table 2. Regional and temporal variability of annual fluxes of passively sinking copepods (PSCs) and detrital sinking particles in terms of particulate mass dry weight (DW), particulate organic carbon (POC), particulate organic nitrogen (PON), and C/N ratio of the vertical flux.

Sampling Stn.	Sampling year (yyyy-yyyy)	Detrital sinking-particles				PSCs				Data source
		DW flux (mg m ⁻² yr ⁻¹)	POC flux (mg m ⁻² yr ⁻¹)	PON flux (mg m ⁻² yr ⁻¹)	C/N ratio (mol/mol)	DW flux (mg m ⁻² yr ⁻¹)	POC flux (mg m ⁻² yr ⁻¹)	PON flux (mg m ⁻² yr ⁻¹)	C/N ratio (mol/mol)	
Stn. A	2009-2010	34862	4561	675	7.9	3582	1695	222	8.9	This study
	2010-2011	76827	6320	885	8.3	1811	680	111	7.1	This study
	2011-2012	116806	5624	885	7.4	2923	1257	184	8	This study
Stn. G	2009-2010	45260	5672	729	9.1	2886	1217	171	8.3	This study
	2011-2012	51935	2025	283	8.3	105	45	8	6.6	This study
CA7	2002-2003	37464	4307	650	7.7	5408	2528	334	8.8	Sampei et al. (2009)
CA16	2007-2008	52040	5817	892	7.6	1804	891	96	10.8	Sampei et al. (2012)

Figure captions

Fig. 1. Bathymetric map with locations of sediment trap mooring sites at the Mackenzie Shelf margins in the southeastern Beaufort Sea. Closed diamonds and closed circles show the mooring sites used in this study (Stns. A and G) and previous studies (CA7 and 16 (Sampei et al. 2009, 2012)).

Fig. 2. Temporal variabilities in total particulate organic carbon (POC) flux (passively sinking copepods [PSCs] + detrital sinking particles) ($\text{mg C m}^{-2} \text{ d}^{-1}$) at Stns. A and G between July 2009 and August 2012. Dark and light bars show the PSCs and detrital sinking particles, respectively. The total POC flux at Stn. A in July 2011 ($267 \text{ mg C m}^{-2} \text{ d}^{-1}$) exceeded the maximum range of the Y axis. ND, no data.

Fig. 3. Temporal variabilities in the flux of passively sinking copepods (PSCs) by species and developmental stages (CIV + CV or adult stages) at Stns. A and G between July 2009 and August 2012. The dark bar shows CIV + CV of *Pareuchaeta glacialis*. The bar with stripes sloping from left to right shows adult stages of *P. glacialis*. The gray bar shows CIV + CV of *Calanus glacialis*. The bar with stripes sloping from right to left shows adult stages of *C. glacialis*. The white bar shows CIV + CV of *C. hyperboreus*. The bar with dots shows adult stages of *C. hyperboreus*. ND, no data.

Fig. 4. Correlations between the fluxes of total passively sinking copepods (PSCs) and copepodite (CIV + CV) and adult stages. Panels A and B show the correlations in July–October and February, respectively. Closed and open circles are for the copepodite stage and adult stage, respectively. The

- 1 solid and dashed lines are regression lines fitted to the copepodite stage/total PSC and adult
- 2 stage/total PSC data, respectively.

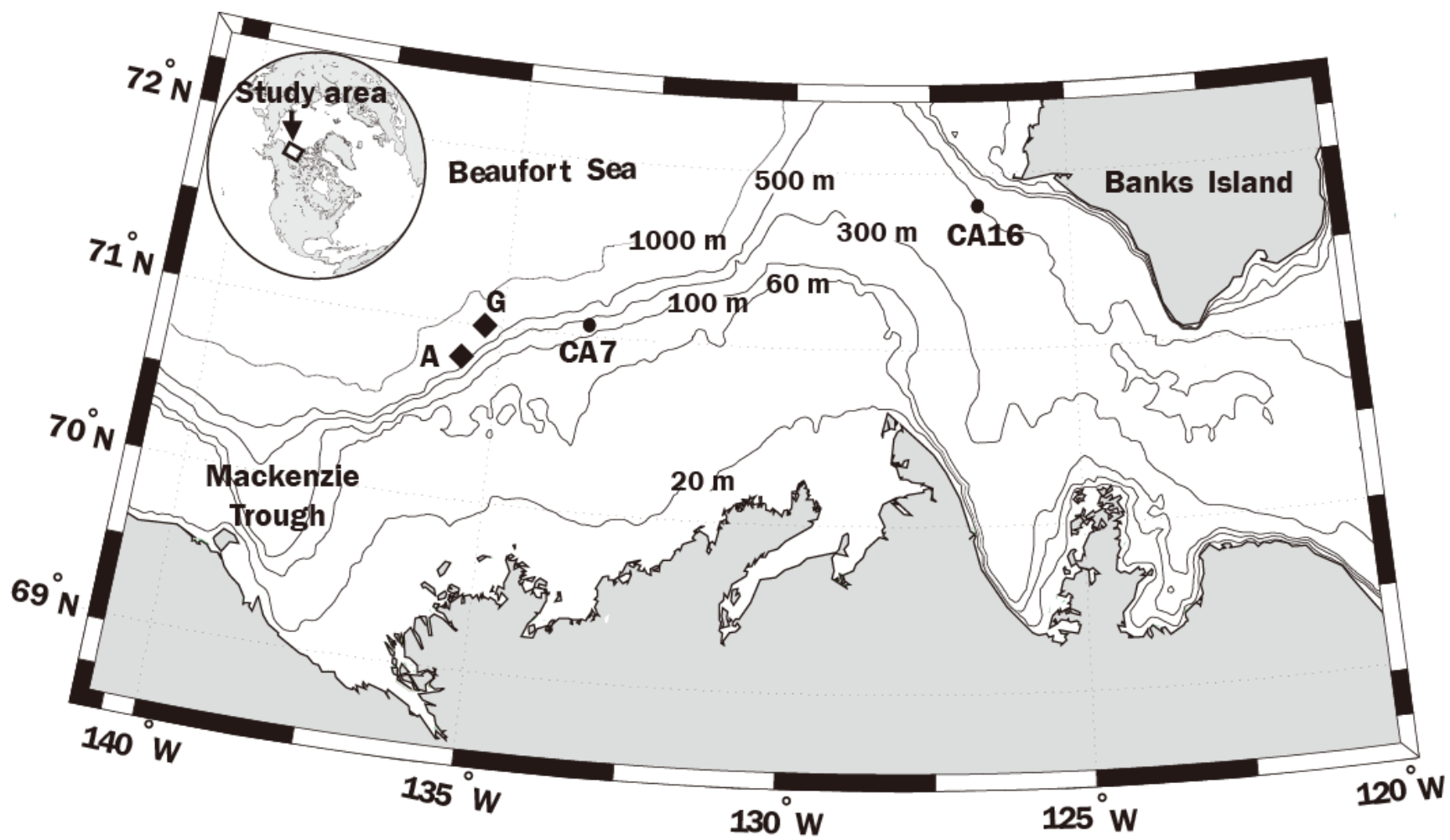


Figure 1

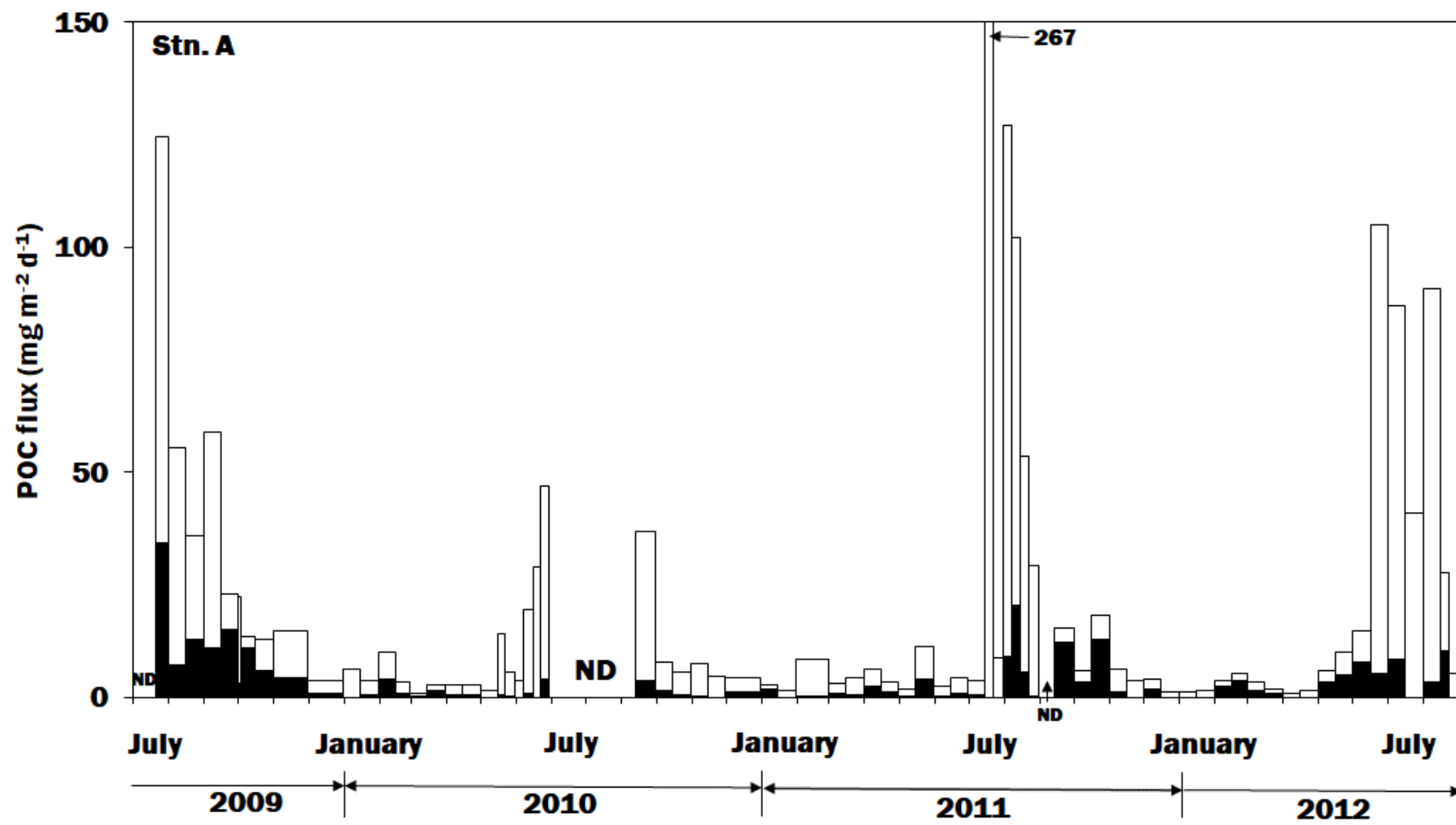


Figure 2

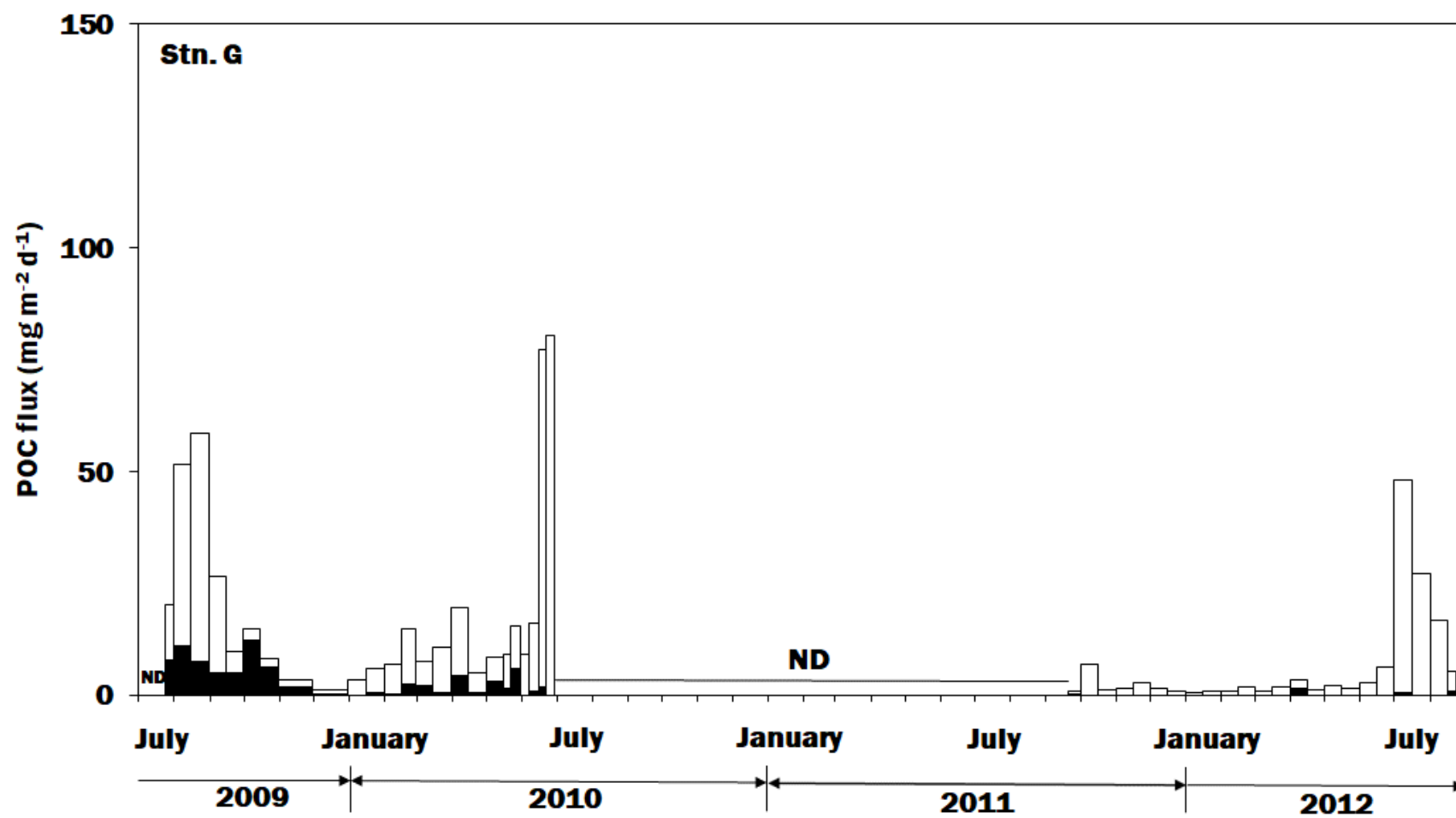


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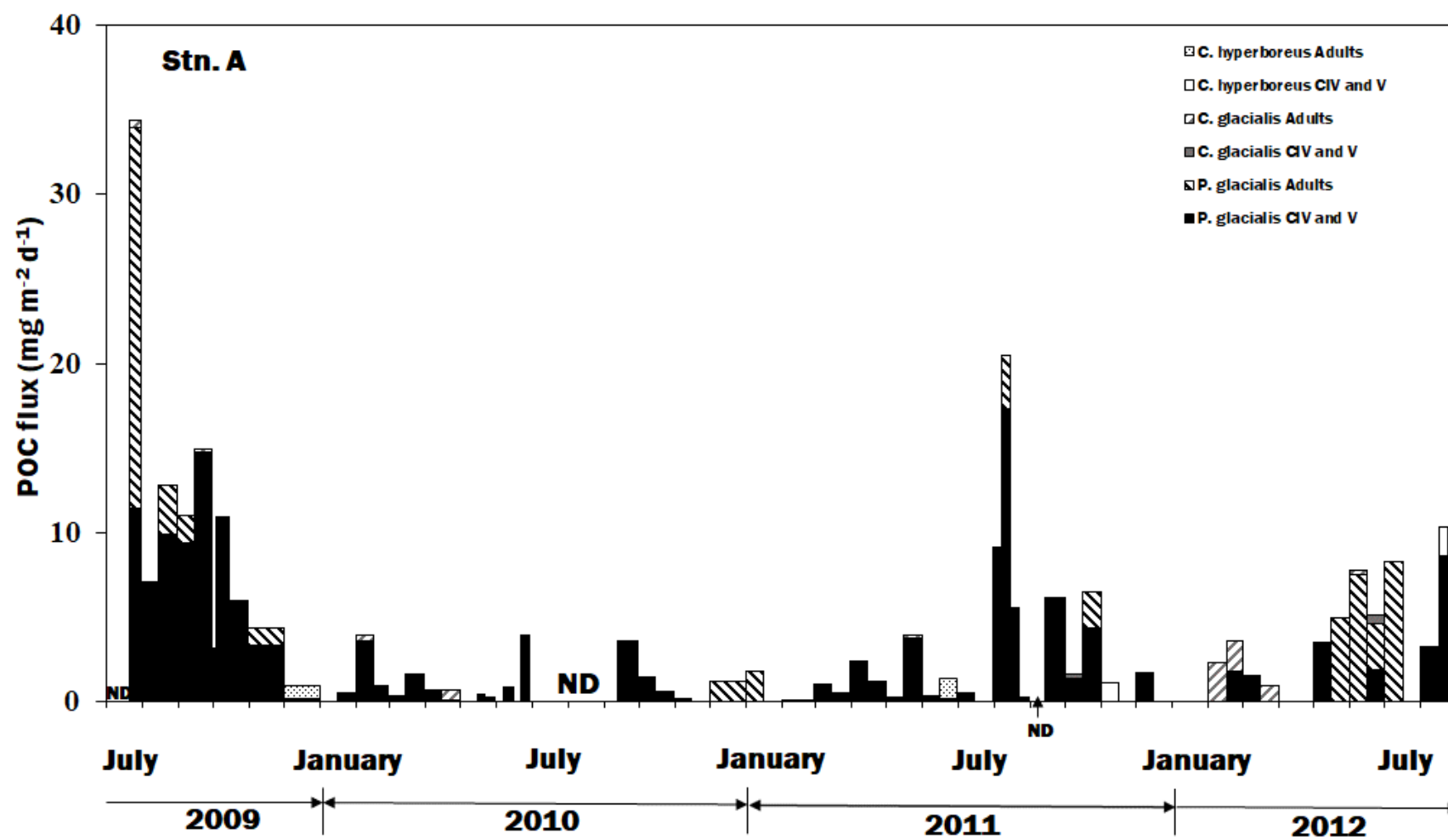


Figure 3

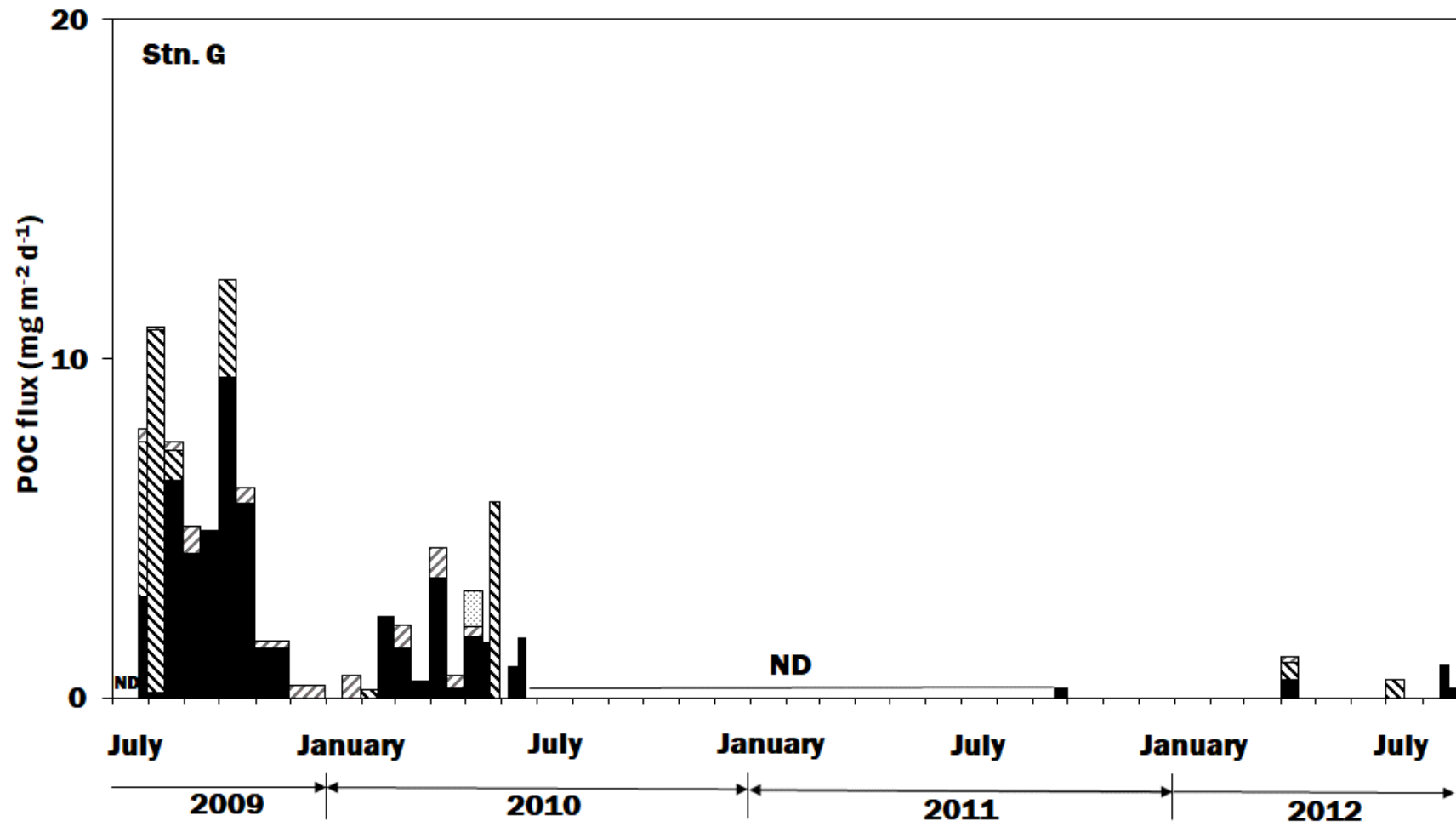


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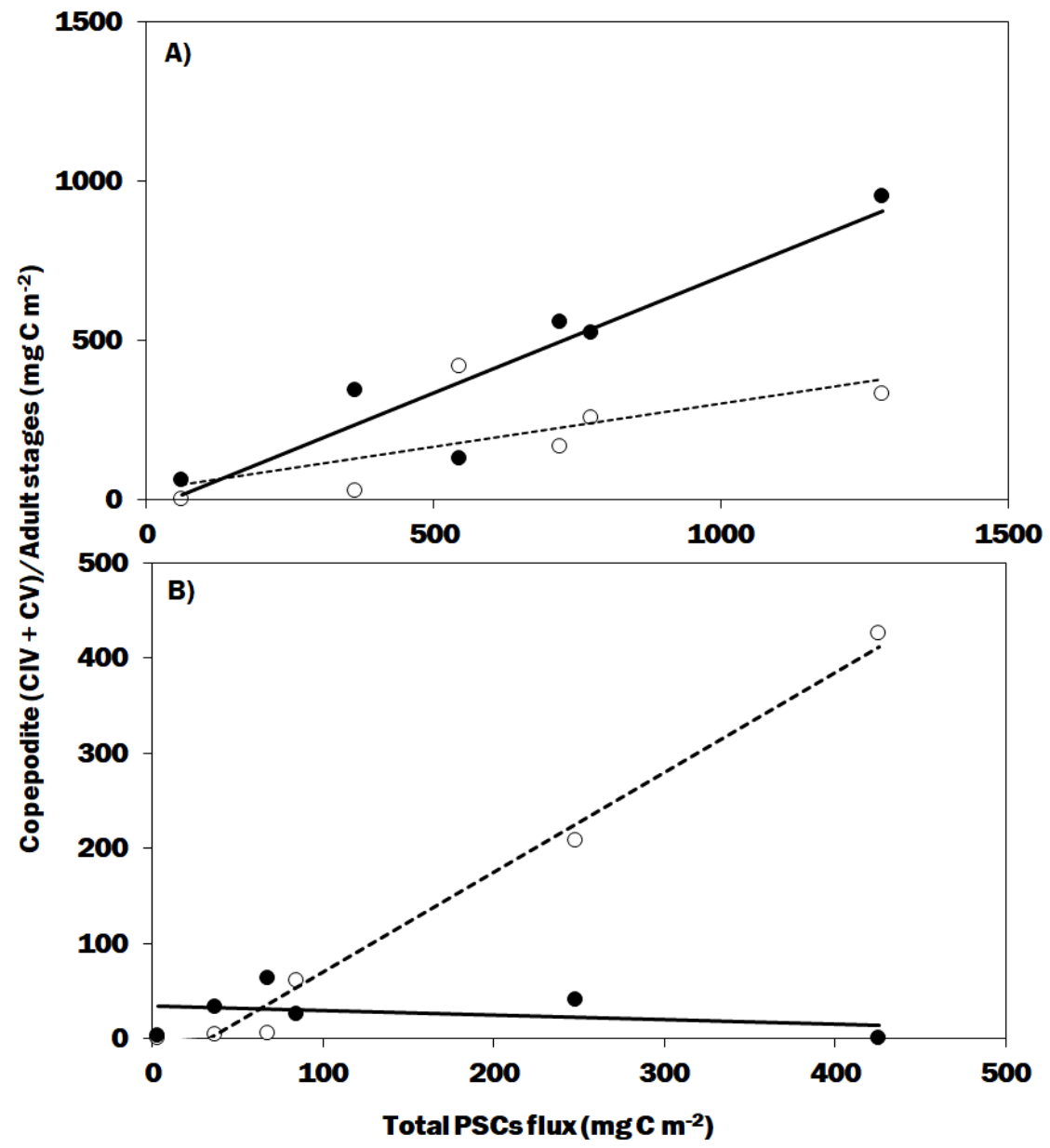


Figure 4