

## Significant contribution of passively sinking copepods to the downward export flux in Arctic waters

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### Abstract

Typically, all undecomposed metazoans found in formalin-poisoned cups of sediment traps are considered to be active intruders (or “swimmers”) and are removed to prevent an overestimation of the downward particle flux. However, intact metazoans dead before entering the trap should be included in the estimation of downward flux of carbon. Arctic copepods collected in the field were killed either by formalin to mimic death by actively swimming into the formalin-poisoned cups, or by crowding or high temperature and then preserved in formalin to simulate death before entering the trap. In the crowding and heat treatments, 64% of *Calanus hyperboreus* and *C. glacialis* and 44% of *Pareuchaeta glacialis* differed from copepods killed by formalin in the postmortem posture of the antennules or swimming legs. These frequencies were used to estimate the contribution of passively sinking copepods (PSCs) to the particulate organic carbon (POC) flux measured by a sediment trap moored at 70 m in the Beaufort Sea (Canadian sector of the Arctic Ocean). PSCs represented only a small fraction (<5%) of the copepods collected in the trap, thus justifying the removal of swimmers from samples to avoid a massive overestimation of fluxes. Nevertheless, PSCs contributed 36% of the overall POC flux of 6.8 g C m<sup>-2</sup> yr<sup>-1</sup>, and discarding them along with the swimmers would have resulted in a significant underestimation of downward export. Given their rich carbon content (up to 50%), PSCs could be an important food resource for pelagic and benthic scavengers.

Sinking particles represent the main pathway of transport of organic matter from the surface ocean to the interior ocean and to the bottom. The quantity and quality of sinking particles vary widely depending on the autotrophic (e.g., phytoplankton in different sizes and species) and heterotrophic (e.g., feeding, egestion, and decomposition) processes prevailing in different areas and seasons. Knowledge of the magnitude and nature of the vertical flux of particles can help understand the production and distribution of organisms, food-web structures, and the processes that supply food resources to mesopelagic and benthic heterotrophs (Wassmann 1998).

However, the accuracy of measurements of particle fluxes by sediment traps can be affected by “swimmers,” i.e., live organisms that actively swim into the traps as compared to passively sinking particles (Michaels et al. 1990; Buesseler et al. 2007). Most swimmers are metazoans such as copepods, amphipods, and euphausiids (Steinberg et al. 1998) that are generally much larger in size than passively sinking particles. Contamination by swimmers results in the overestimation of the downward flux of organic particles (Silver and Gowing 1991; Buesseler et al. 2007). Hence, while carcasses showing signs of decay are included inasmuch as possible in the flux, intact metazoans have traditionally been sorted out from trap samples before

analysis to prevent overestimation of the downward biogenic particle flux.

Undecomposed copepods in trap samples can either be actively intruding copepods (AICs) that swam into the preservative or passively sinking copepods (PSCs) that died recently in the water column before sinking into the trap. Contrary to AICs, PSCs should be included in the estimation of the downward flux as sinking particles that would eventually end up in the deep ocean or on the bottom. However, little attention has been paid to the potential contribution of PSCs to the downward flux because of the difficulty of distinguishing PSCs from AICs. The art of swimmer differentiation and removal remains a complicated issue in studies of particle fluxes based on sediment traps (Buesseler et al. 2007).

Our objective was to estimate the in situ flux of PSCs in formalin-poisoned sediment-trap samples, using experimentally determined criteria to distinguish live copepods killed by the formalin preservative and copepods dead before entering the formalin preservative. In the laboratory, live specimens of the large calanoids *Calanus hyperboreus*, *C. glacialis*, and *Pareuchaeta glacialis* that dominate zooplankton biomass in trap samples from the Arctic Ocean were killed directly by formalin (to mimic AICs) and killed by crowding or high temperature prior to preservation in formalin (to mimic PSCs). Based on differences in the postmortem posture of appendages between the two treatments, the PSC flux of the three species was estimated in sequential samples from a sediment trap deployed over an annual cycle in the southeastern Beaufort Sea (Canadian Arctic Ocean).

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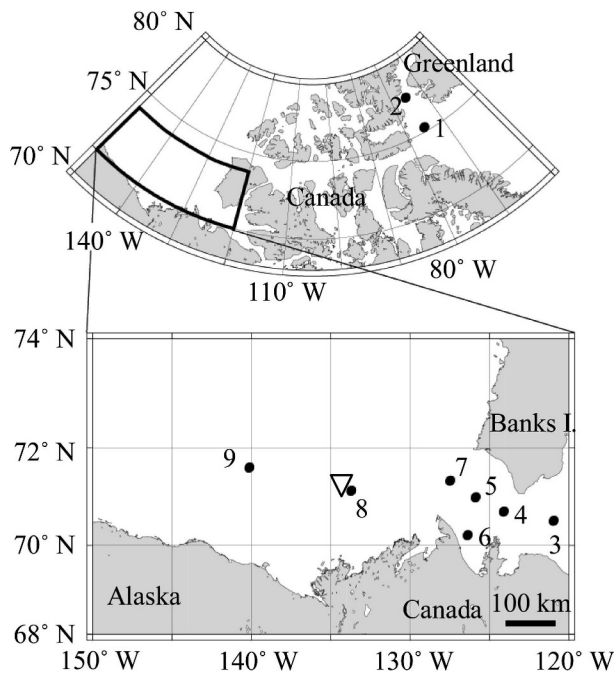


Fig. 1. Map of the Canadian Arctic with sampling stations (1–9) where zooplankton was collected for experimental treatments on board the ship, and mooring position of the sediment trap (inverted triangle).

## Methods

**Distinguishing copepods killed by formalin and non-formalin treatments**—Zooplankton samples were collected with a 200- $\mu\text{m}$  mesh, conical-square net with a 1-m<sup>2</sup> mouth aperture equipped with a rigid live-capture cod-end at nine stations in the Beaufort Sea during the Canadian Arctic Shelf Exchange Study (CASES) in 2003–2004 and in the North Water (northern Baffin Bay) during the ArcticNet annual expedition of 2005 (Fig. 1). Except at Station 4, the sampler was hauled vertically from the bottom to the surface at a towing speed of 0.5 m s<sup>-1</sup>. Live specimens of *C. hyperboreus*, *C. glacialis*, *P. glacialis*, and *Metridia longa* were kept in an undisturbed chamber for at least 3 h at a temperature of  $-1^{\circ}\text{C}$  prior to the experiments.

To determine differences in the morphology or post-mortem posture of copepods killed with and without formalin, live specimens of the four species were exposed to solutions of 1% v/v and 5% v/v buffered formalin in glass-microfiber filter (grade GF/F, Whatman) seawater with final salinity of  $\sim 36$ . Other live specimens were killed by crowding ( $>1000$  individuals in 300 mL at  $-1^{\circ}\text{C}$ ) for 48 h or by high temperature (in seawater at  $20^{\circ}\text{C}$ ) for 48 h. After death, the copepods killed by the two processes without formalin were preserved in formalin (1% v/v) seawater solutions. Copepods killed directly by formalin were assumed to be representative of copepods that actively intruded into the sediment trap (AICs), and copepods killed in treatments without formalin were assumed to be representative of dead copepods that passively sank into the poisoned trap (PSCs). The morphology and postmor-

tem posture of appendages of copepods killed by the different treatments were examined under a Leica MZ16 stereomicroscope ( $<40\times$  magnification). Only copepods with intact antennules (or lacking only the last antennule segment) and intact swimming legs were used for observations.

**Sediment trap deployment and sample analysis**—A long-term mooring carrying a time-programmed sediment trap was deployed for 345 d at  $71^{\circ}10'\text{N}$ ,  $133^{\circ}53'\text{W}$  (505-m depth) in the Beaufort Sea from 21 Sep 2002 to 31 Aug 2003 (Fig. 1). The cylindrical sediment trap with a 16-cm-diameter mouth (Nichiyu SMD12S) was set at a depth of 70 m. Collection cups were filled with a solution of  $\sim 5\%$  v/v buffered formalin in GF/F-filtered seawater with final salinity of  $\sim 36$ , so that the density of the solution exceeded that of seawater. Upon recovery, we confirmed that formalin remained in the cups. Sampling intervals varied from 15 d in spring to 61 d in winter.

After recovery of the trap, samples were left undisturbed for 24 h to allow particles to settle at  $\sim 5^{\circ}\text{C}$  in the dark. Large zooplankton were removed by sieving the entire sample through a 1-mm mesh net. Decomposed animals were returned to the sample, and undecomposed copepods were kept for later microscopic analyses. The entire sample was then quantitatively split into several fractions for later analyses. Zooplankton  $<1$  mm were manually removed from the subsamples intended for chemical analyses under a stereomicroscope.

After removing the zooplankton, sediment-trap samples were filtered on pre-combusted ( $450^{\circ}\text{C}$  for 3 h) GF/F filters (Whatman) which were dried at  $60^{\circ}\text{C}$  for 48 h for the determination of particulate dry weight (dry wt) on a precision scale. The samples were then fumed for 3 h over concentrated (37 percent weight/weight) hydrochloric acid (HCl) to remove carbonates prior to the determination of particulate organic carbon (POC) and particulate organic nitrogen (PON) using a carbon–hydrogen–nitrogen (CHN) elemental analyzer (Yanaco). Dry wt, POC, and PON were measured on copepod specimens from sediment-trap samples. Copepods were dried at  $60^{\circ}\text{C}$  for 48 h for individual dry wt measurement followed by POC and PON determination on a CHN elemental analyzer (2400 Series II, PerkinElmer).

## Results

**Postmortem posture of dead copepods in different experimental treatments**—Based on the postmortem posture of the antennules (the first antenna), the adult stages (copepodite stage IV; CVI) of *C. hyperboreus* and *C. glacialis* were classified into two groups, G1 and G2 (Fig. 2). When the antennules were straight from the eighth segment to the penultimate segment and ran parallel to a line passing from the base of the antennules to the base of swimming leg 1, or were perpendicular to the body axis from a dorsoventral view, the copepods were classified as G1. The orientation of straight antennules characteristic of G1 is also typical of live copepods in culture. *Calanus* with straight or curved antennules presenting a different

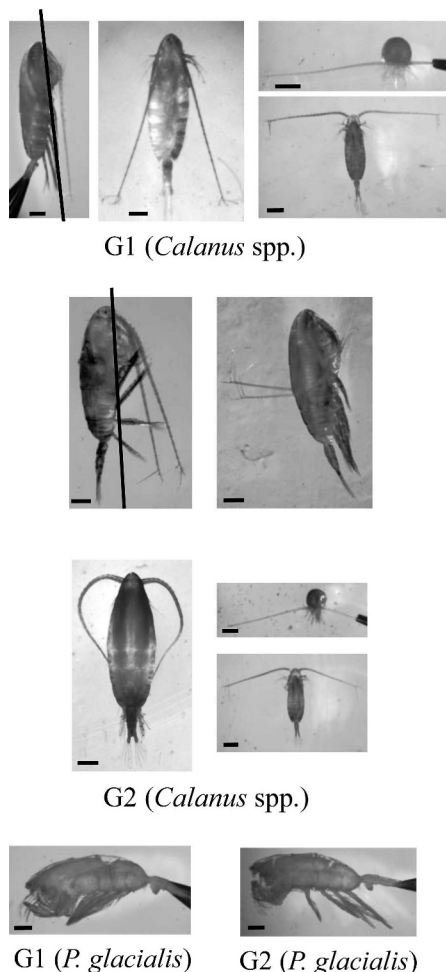


Fig. 2. Microphotographs illustrating typical postmortem postures of appendages in *C. hyperboreus*, *C. glacialis*, and *P. glacialis* killed by different experimental treatments. Added black reference lines indicate the axis between the base of the antennules and the base of the first pair of swimming legs. Scale bars at left bottom of each panels represent 1 mm. G1 postures were unique to copepods killed by crowding or heat to mimic PSCs dead before entering formalin-poisoned sediment-trap cups. G2 postures were invariably seen in copepods killed by formalin to mimic AICs killed upon entering the formalin-poisoned sediment-trap cups.

orientation were classified as G2. All the *C. hyperboreus* and *C. glacialis* killed directly by formalin were classified as G2, while 64% of the copepods killed by crowding and 67% of the copepods killed by high temperature were classified as G1 (Table 1).

Late copepodite (CIV and CV [copepodite stage V]) and CVI (copepodite stage VI) of *P. glacialis* were classified into G1 when presenting forward extending swimming legs, and into G2 when at least one among the first to fourth pairs of swimming legs pointed backward (Fig. 2). All *P. glacialis* killed by formalin were classified as G2, while 43% of *P. glacialis* killed by crowding and 45% of *P. glacialis* killed by high temperature were classified as G1 (Table 1). No differences among treatments were found in the postmortem morphology or posture of *M. longa*, the fourth species tested in our experiments.

Differences in the frequencies of G1 and G2 between the crowding treatment and the high-temperature treatment were not statistically significant ( $\chi^2$  test,  $p > 0.05$ ), and the results of the two treatments were pooled for subsequent analyses. After pooling, 67% of the *C. hyperboreus*, 61% of the *C. glacialis*, and 44% of the *P. glacialis* dead before preservation in formalin were classified as G1. The remainder could not be distinguished from copepods killed by formalin. No change in classification occurred when 85 *Calanus* spp., and 54 *P. glacialis* killed by formalin were examined again one year after the original observations.

*Estimated contribution of PSCs to vertical fluxes*—The numerically dominant metazoans  $>1$  mm collected in the sediment trap were *C. hyperboreus*, *C. glacialis*, *P. glacialis*, and *M. longa* (Table 2). The total of the four species was highest from Mar 2003 to Jun 2003. The abundance of *C. hyperboreus* and *P. glacialis* peaked in early fall 2002 (21 Sep–31 Oct), while maximum numbers of *C. glacialis* and *M. longa* occurred in Mar 2003 and early May 2003, respectively. Over the sampling period, CVI accounted for 53% of *C. hyperboreus* and 84% of *C. glacialis*. CIV–CVI accounted for 91% of *P. glacialis*. When converted into POC, these stages represented, respectively, 74%, 94%, and 98% of the biomass of *C. hyperboreus*, *C. glacialis*, and *P. glacialis* in the sediment-trap samples.

The vast majority of *Calanus* spp. CVI and *P. glacialis* CIV–CVI collected in the trap exhibited the postmortem posture of appendages typical of death by formalin (G2) and were classified as live AICs (Table 3). The relatively few copepods presenting a posture characteristic of death before entering the formalin solution (G1) were interpreted as dead PSCs. *C. hyperboreus* PSCs were infrequent, only a few being detected in only one of the trap cups (mid-Apr). The flux of *C. glacialis* PSCs was relatively strong and variable (0 to 12.1 individuals  $m^{-2} d^{-1}$ ) among cups (Table 3). The flux of *P. glacialis* PSC was weak (0 to 3.6 individuals  $m^{-2} d^{-1}$ ) relative to the strong flux of AIC of this species (84.5 individuals  $m^{-2} d^{-1}$  to 841.1 individuals  $m^{-2} d^{-1}$ ).

The PSC fluxes for each species are minimum estimates since a significant fraction of the copepods killed experimentally without formalin presented the symptoms of death by formalin (36% of *Calanus* spp. and 56% of *P. glacialis*, Table 1). A corrected estimate (PSC<sub>c</sub>) was calculated for each species by transferring this misclassified fraction from the copepods visually classified as AICs to the PSCs (Table 3). The estimated percent contribution of PSC<sub>c</sub> (%PSC) to the total number of *C. glacialis* and *P. glacialis* collected by the trap varied seasonally, being highest from Nov to Feb and increasing again from mid-May to Jun (*P. glacialis*) or Jul (*C. glacialis*) (Table 3). Relatively high %PSC coincided with periods of low abundance of the three species in the traps. Hence, when integrated over the year, the contribution of dead PSCs to the overall fluxes of copepods was low, representing 0.8%, 5.0%, and 0.9% of the total for *C. hyperboreus*, *C. glacialis*, and *P. glacialis*, respectively (Table 3).

On average over the year, the copepods collected in the sediment trap were 3.5 times richer in carbon ( $46\% \pm 7$  SD

Table 1. Percent frequency of postmortem posture G1 and G2 in *C. hyperboreus* CVI, *C. glacialis* CVI and *P. glacialis* CIV–CVI killed directly by formalin (5% v/v and 1% v/v) and killed by crowding or heat.

Treatments	Species	Sample size	Postural group	
			G1 (%)	G2 (%)
5% formalin	<i>C. hyperboreus</i>	84	0	100
	<i>C. glacialis</i>	36	0	100
	<i>P. glacialis</i>	69	0	100
1% formalin	<i>C. hyperboreus</i>	130	0	100
	<i>C. glacialis</i>	34	0	100
	<i>P. glacialis</i>	57	0	100
Crowding	<i>C. hyperboreus</i>	77	68	32
	<i>C. glacialis</i>	47	57	43
	<i>P. glacialis</i>	37	43	57
Heat	<i>C. hyperboreus</i>	17	65	35
	<i>C. glacialis</i>	19	68	32
	<i>P. glacialis</i>	44	45	55

vs.  $13\% \pm 3$  SD) and in nitrogen ( $6.7\% \pm 0.15\%$  SD vs.  $1.9\% \pm 0.4\%$  SD) than the remainder of the particulate flux.

The corrected contribution (based on PSC<sub>c</sub>) of the PSCs of the three species to the total fluxes of passively sinking particles (including PSCs and excluding AICs) varied considerably over the annual cycle (Fig. 3). In terms of dry wt, the contribution of PSCs to the particulate flux was relatively small (0% to 53%, Fig. 3a). Given the high carbon (C) and nitrogen (N) content of the three copepods, the contribution of PSCs to the POC flux and to the PON flux was stronger (0% to 86%), particularly in late fall and winter (66% to 86% for C and 56% to 83% for N) when the overall particle fluxes were weak (Fig. 3b, c). During peak downward export from 16 to 30 Jun, PSCs represented 23% and 25% of the overall POC flux and PON flux, respectively (Fig. 3b, c). When integrated over the annual cycle, the dry wt, POC flux, and PON flux of PSCs amounted to  $5.2 \text{ g m}^{-2} \text{ yr}^{-1}$ ,  $2.5 \text{ g m}^{-2} \text{ yr}^{-1}$ , and  $0.32 \text{ g m}^{-2} \text{ yr}^{-1}$ , and represented 12%, 36%, and 34% of the overall dry wt ( $42.7 \text{ g m}^{-2} \text{ yr}^{-1}$ ), POC flux ( $6.8 \text{ g m}^{-2} \text{ yr}^{-1}$ ), and PON flux ( $0.97 \text{ g m}^{-2} \text{ yr}^{-1}$ ), respectively.

## Discussion

*Identifying PSCs in sediment trap samples*—Death by formalin, as experienced by live copepods actively intruding into poisoned sediment trap cups, was relatively straightforward to simulate in the laboratory. Mimicking the natural death of copepods prior to their passive sinking into the formalin solution of the trap proved more challenging. In nature, copepod carcasses likely result primarily from death by starvation or diseases (Tang et al. 2006a), two processes that are difficult to reproduce in vitro (death by predation would leave no carcasses). In the present study we assumed that death by crowding or heat, followed by preservation in formalin, would induce the same postmortem posture of appendages as natural death followed by sinking in the poisoned trap samples. Although admittedly difficult to verify, the validity of this assumption is supported by several observations.

First, the most frequent (64%) G1 posture of antennules in *Calanus* killed by crowding or heat was similar to that observed in live copepods. Second, the frequencies of G1 and G2 characteristics were the same in the crowding and

Table 2. Numerical fluxes (individuals  $\text{m}^{-2} \text{ d}^{-1}$ ) of the dominant metazoans  $>1$  mm in the sediment trap moored at 70 m in southeastern Beaufort Sea by sampling period. All developmental stages of copepods are included. The category “others” includes appendicularians, chaetognaths, ostracods, the amphipod *Themisto* spp., and gastropods in decreasing order of numerical importance.

Sampling period	<i>M. longa</i>	<i>P. glacialis</i>	<i>C. glacialis</i>	<i>C. hyperboreus</i>	Others
21–31 Sep 02	320	904	29	270	107
01 Nov 02–31 Dec 02	245	92	32	9	92
01 Jan 03–28 Feb 03	391	117	106	0	58
01–31 Mar 03	787	326	776	28	32
01–30 Apr 03	705	598	680	50	32
01–15 May 03	1432	380	29	7	79
16–31 May 03	1094	571	87	13	114
01–15 Jun 03	1017	630	57	0	193
16–30 Jun 03	981	659	43	93	308
01–15 Jul 03	451	244	36	43	208
16–31 Jul 03	517	685	20	20	584
01–31 Aug 03	239	742	38	14	222

Table 3. Numerical fluxes (ind.  $m^{-2} d^{-1}$ ) of AICs and PSCs *C. hyperboreus* CVI, *C. glacialis* CVI, and *P. glacialis* CIV–CVI in the sediment trap moored at 70 m in southeastern Beaufort Sea, by sampling period. PSC<sub>c</sub> is the flux corrected for the fraction of copepods misclassified by the postmortem posture criteria (36% of *Calanus* spp. and 56% of *P. glacialis*). Hence PSC<sub>c</sub> = PSC/0.64 for *Calanus* spp. and PSC<sub>c</sub> = PSC/0.44 for *P. glacialis*. %PSC is the percent contribution of PSC to the overall copepod flux (PSC<sub>c</sub>/(PSC + AIC) × 100). Flux values for the period 01–20 Sep 2003 (in italic) not actually sampled by the trap were estimated as the mean of the 01–31 Aug 2003 and 21 Sep to 31 Oct 2002 periods. The fluxes integrated over the year (sum of the products of daily flux by period duration for all periods, in ind.  $m^{-2} yr^{-1}$ ) and corresponding percent contributions are also given.

Sampling period	<i>C. hyperboreus</i>				<i>C. glacialis</i>				<i>P. glacialis</i>			
	AIC	PSC	PSC <sub>c</sub>	%PSC	AIC	PSC	PSC <sub>c</sub>	%PSC	AIC	PSC	PSC <sub>c</sub>	%PSC
21–31 Sep 02	112.7	0.0	0.0	0.0	23.6	0.0	0.0	0.0	841.1	2.6	5.9	0.7
01 Nov 02–31 Dec 02	8.8	0.0	0.0	0.0	14.1	5.3	8.3	42.7	84.5	0.9	2.0	2.4
01 Jan 03–28 Feb 03	0.0	0.0	—	—	89.2	8.2	12.8	13.2	114.7	1.8	4.1	3.5
01–31 Mar 03	24.3	0.0	0.0	0.0	706.9	12.1	18.9	2.6	287.6	1.7	3.9	1.3
01–30 Apr 03	43.0	1.8	2.8	6.3	612.3	3.6	5.6	0.9	490.6	0.0	0.0	0.0
01–15 May 03	0.0	0.0	—	—	14.3	0.0	0.0	0.0	365.3	0.0	0.0	0.0
16–31 May 03	6.7	0.0	0.0	0.0	47.0	6.7	10.5	19.5	503.6	3.4	7.7	1.5
01–15 Jun 03	0.0	0.0	—	—	28.6	3.6	5.6	17.5	565.8	3.6	8.2	1.4
16–30 Jun 03	64.5	0.0	0.0	0.0	14.3	3.6	5.6	31.4	630.2	3.6	8.2	1.3
01–15 Jul 03	28.6	0.0	0.0	0.0	0.0	10.7	—	100.0	200.5	0.0	0.0	0.0
16–31 Jul 03	13.4	0.0	0.0	0.0	13.4	0.0	0.0	0.0	651.3	0.0	0.0	0.0
01–31 Aug 03	3.5	0.0	0.0	0.0	13.9	0.0	0.0	0.0	686.2	1.7	3.9	0.6
<i>01–20 Sep 03</i>	<i>58.1</i>	<i>0.0</i>	<i>0.0</i>	<i>0.0</i>	<i>18.8</i>	<i>0.0</i>	<i>0.0</i>	<i>0.0</i>	<i>763.7</i>	<i>2.2</i>	<i>4.9</i>	<i>0.6</i>
Integrated	10189	54	84	0.8	50004	1666	2603	5.0	151491	579	1315	0.9

heat treatments, suggesting that these frequencies do not vary among causes of death other than by formalin. Third, the G1 postmortem postures that were characteristic of death by crowding or heat were observed in 52 of the 3628 copepods from the trap that were examined under the microscope, confirming the expectation that some copepods died before entering the trap, therefore not showing the telltale symptoms of death by formalin. Together, these first three observations suggest that, contrary to chemical poisoning by formalin that invariably resulted in G2 postmortem postures, slower non-chemical causes of death, such as crowding, heat, and possibly starvation and diseases, induce similar postmortem postures of the appendages (G1) simply by virtue of having little or no effect on the natural posture of these appendages. Fourth, the frequency of passively sinking copepods was not randomly distributed over the annual cycle but corresponded to specific periods (Nov–Feb and mid-May–Jun) that were the same for *C. glacialis* and *P. glacialis*, the two species that contributed most to the PSC flux (Table 3). Finally, based on the postmortem posture criteria, the estimated frequencies of dead PSCs for the three species (0.8%, 0.9%, and 5.0% on average over the annual cycle for *C. hyperboreus*, *P. glacialis*, and *C. glacialis*, respectively) compare well with Hisrt and Kjørboe (2002) estimates of the natural mortality of copepods by causes other than predation (1.9%  $d^{-1}$  to 6.5%  $d^{-1}$ ).

It could be argued that postmortem posture in copepods was affected by the concentration of the formalin solution or by the time elapsed since preservation, thus introducing a bias in the estimation of PSC fluxes. However, death by formalin at either 1% or 5% concentration invariably induced G2 postures and only G2 postures, regardless of concentration. As well, the classification into G1 and G2 of

copepods preserved in formalin remained stable one year after the original observations.

*Contribution of PSCs to downward particle fluxes and implications for POC cycling*—After the exclusion of all zooplankton “swimmers” (true swimmers as well as passively sinking carcasses), the supply of sinking POC to the deep ocean as measured by sediment traps (hereafter called the net POC flux) is often less than the estimated POC demand of marine food webs (Boyd et al. 1999; Grant et al. 2002; Steinberg et al. 2008). In the subtropical Pacific for example, a net POC flux of 17.8 mg C  $m^{-2} d^{-1}$  at 150 m was short of the zooplankton demand for POC in the 150–1000 m interval (31.7 mg C  $m^{-2} d^{-1}$ ) by 44% (Steinberg et al. 2008). A similar deficit of 29% between net POC flux at 150 m and zooplankton demand prevailed in the 150–250-m depth interval in the subarctic Pacific (Boyd et al. 1999). In the present study, the annual POC supply by PSCs (2.5 g C  $m^{-2} yr^{-1}$ ) represented 36% of the overall POC flux (net POC flux + PSC flux = 6.8 g C  $m^{-2} yr^{-1}$ ), a fraction commensurate with the deficits reported in the above studies. In the Beaufort Sea, the carbon demand of the benthos at an 86-m deep station, located ~20 km south of the position of our moored trap, was estimated at 24 mg C  $m^{-2} d^{-1}$  for Oct 2003 (Renaud et al. 2007). By comparison, the net POC flux at 70 m was 18.0 mg  $m^{-2} d^{-1}$  from 21 Sep to 31 Oct 2002 (Fig. 3). Assuming that the net POC flux at 70 m on the slope is representative of the flux to the benthos on the nearby shelf break, the carbon requirements of the benthos would exceed supply by 25%. Adding the PSC flux closes this gap by increasing the overall POC flux in Sep–Oct 2002 to 25.9 mg  $m^{-2} d^{-1}$  (Fig. 3). We conclude that the identification of the few dead, passively sinking zooplank-

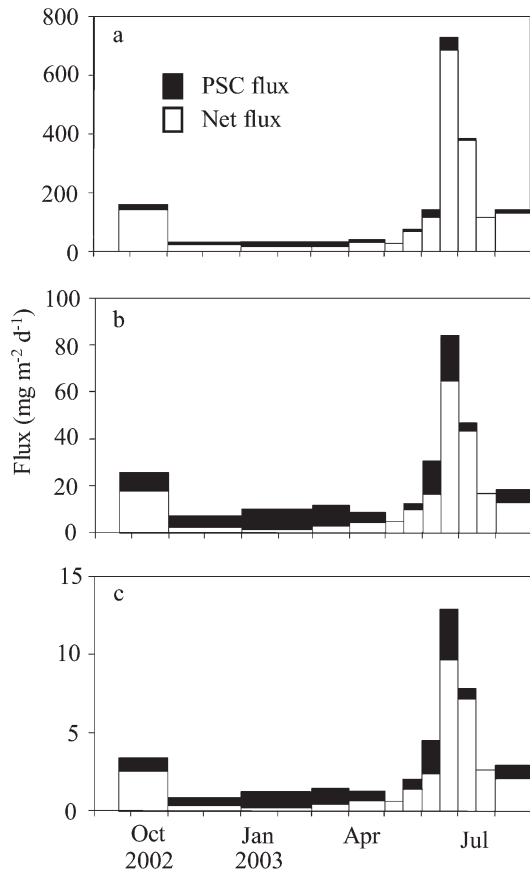


Fig. 3. Quasi-annual cycle (21 Sep 2002–31 Aug 2003) of (a) dry weight, (b) POC flux, and (c) PON flux measured by a sequential sediment trap moored at 70 m from the surface (station depth of 505 m) in the Beaufort Sea (Arctic Ocean). The net flux is the traditional flux including decomposed animals and excluding all undecomposed metazoans. The PSC flux is the estimated contribution of the undecomposed, passively sinking copepods that dominated the zooplankton biomass in the sediment-trap samples (*C. hyperboreus* CVI, *C. glacialis* CVI, and *P. glacialis* CIV–CVI).

ton among the hordes of active swimmers that enter sediment trap samples can help resolve discrepancies between supply and demand of POC in studies of pelagic-bathypelagic and pelagic-benthic coupling.

At 36% of the overall annual POC flux (net flux + PSC), the PSC flux reported here is probably slightly underestimated because the small but frequent copepod *M. longa* and other infrequent but large metazoans (e.g., the amphipod *Themisto libellula*) could not be classified into actively intruding swimmers or dead passively sinking animals based on their postmortem characteristics. In addition to their carcasses, Arctic copepods also contribute to the POC flux by the production of fecal pellets that were already included in the net POC flux and which accounted for 7–21% of the net annual POC flux at 200 m in the North Water (Sampei et al. 2002; Sampei et al. 2004) and for 24–31% in the Beaufort Sea (Forest et al. 2007). Finally, recent studies suggest that the ontogenetic downward migration of copepods also contribute significantly to vertical POC export (Kobari et al. 2003). Thus, the summed

contributions of copepod carcasses, fecal pellets, and ontogenetic migrations could easily represent >60% of the overall vertical POC flux in Arctic waters. This value is consistent with the estimated fraction (79%) of primary production that transits through zooplankton grazers in spring in the North Water (Tremblay et al. 2006), and confirms that the contribution of copepods to the biological carbon pump in Arctic waters is probably more important than previously believed, as surmised for the Austral Ocean by Bradford-Grieve et al. (2001).

*The trophic role of metazoan carcasses in Arctic waters*—High frequencies of dead copepods, representing up to 30% of the copepod assemblage, have been reported in different aquatic environments (Terazaki and Wada 1988; Yamaguchi et al. 2002; Tang et al. 2006a). At the sub-zero temperatures prevailing most of the year in the Beaufort Sea (Forest et al. 2007), copepod carcasses are expected to resist microbial degradation for several weeks (Terazaki and Wada 1988; Tang et al. 2006b). In addition, on average over the year, copepods were four times richer in carbon (46%) than other particles (13%). Thus, PSCs could represent a source of highly nutritious food for omnivorous and carnivorous heterotrophs such as *Metridia longa* and *Pareuchaeta glacialis*, especially during the winter months when non-metazoan particles along the shelf break comprise mainly recycled and degraded material with low carbon content (Forest et al. 2007). Based on their continuous presence in the trap, *M. longa* and *P. glacialis* remain active throughout the year (Falk-Petersen et al. 1987; Sampei et al. 2009). In laboratory incubations, *M. longa* was attracted to dead bodies of *C. hyperboreus* and *C. glacialis* (M. Sampei, unpubl.). Hence, copepod carcasses could represent an additional food source to meet the energy requirements of omnivorous and carnivorous Arctic copepods in winter when the under-ice ecosystem shifts to a detrital mode (Forest et al. 2008).

*To remove or not to remove metazoans, that is the question*—Based on the postmortem posture of their appendages, the vast majority of *C. hyperboreus* (99.2%), *C. glacialis* (95%), and *P. glacialis* (99.1%) in the sediment-trap samples were classified as AICs or as true swimmers killed at the time of their penetration in the poisoned cups. The inclusion of these swimmers would have inflated the estimated dry wt, POC flux, and PON flux by ~10-fold, 35-fold, and 30-fold, respectively. Alternatively, the exclusion of the few carcasses of the three species identified as dead PSCs would have resulted in an underestimation of the annual POC flux by 36% (varying from 0 to 86% among sampling periods during the annual cycle). Hence, the present study confirms the validity of removing metazoans from trap samples since the resulting underestimation of the fluxes is much less severe than the overestimation that would result from including them. Nevertheless, excluding all metazoans, dead or alive at the time of entering the poisoned cups, may lead to a significant underestimation of the actual vertical biogenic particulate fluxes. Hence, although laborious, developing the experimental criteria to distinguish live and dead metazoans entering sediment

traps, at least for the species that dominate zooplankton biomass in trap samples, should be considered in studies of vertical particulate fluxes in marine ecosystems.

#### Acknowledgments

The authors are grateful to M. Fukuchi, M. Fortier, and H. Melling for their contribution to the planning and realization of this study. The crew of the Canadian Coast Guard icebreakers *Amundsen* and *Sir Wilfrid Laurier* provided first-class service under the extreme conditions of the Arctic Ocean. S. Kudoh, M. O'Brien, B. van Hardenberg, D. Sieberg, L. Létourneau, E. Ayukawa, A. Otsuki, H. Umeda, and M. Furuya helped at sea and in the laboratory. The authors are grateful to J. Raymond and two anonymous reviewers for valuable comments and suggestions on an earlier version of the manuscript.

This study was partially supported by grants from the Japanese Ministry of Education, Culture, Sports, Science and Technology to H. Sasaki (Grant 16510010) and by a grant from the Natural Science and Engineering Research Council of Canada to L. Fortier. This study is a contribution to the Canadian Arctic Shelf Exchange Study, ArcticNet, and the Canada Research Chair on the response of marine arctic ecosystems to climate warming.

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Associate editor: Mary I. Scranton

Received: 07 October 2008

Accepted: 14 June 2009

Amended: 23 June 2009