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Non-consumptive mortality in copepods: occurrence of *Calanus* spp. carcasses in the Arctic Ocean during winter

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During a research cruise to the Arctic Ocean in January 2012, we observed high occurrence of carcasses of *Calanus* spp. We analysed live samples to separate living from dead individuals. In Rijpfjorden, an Arctic fjord in north-eastern Svalbard, 9–14% of the *Calanus* population were observed to be dead. At Sofiadjupet, an oceanic basin located at 81.4°N at the southern edge of the Arctic Ocean, 94% of the *Calanus* at depth (between 300 and 2000 m) were dead. This is the first estimation of the contribution of carcasses to high Arctic copepod populations. Lipid sacs were preserved in part of the observed carcasses and the lipid sac area was significantly smaller in dead *Calanus* than in living individuals. We discuss possible causes for the observed mortality, its implication for population dynamics and energy transfer and review previous accounts of non-predatory mortality of marine copepods. In our case, partial consumption by predators and death after reproduction are unlikely causes of mortality, thus other stressors (starvation, environmental conditions, parasitic or viral infection) may be responsible. Our analysis shows that we have a poor understanding of factors other than predation causing mortality in copepod populations.

KEYWORDS: carcasses; life history; marine copepods; non-predatory mortality; population dynamics; review

INTRODUCTION

The dynamics of populations are about births and deaths, and the evolution of life history strategies and diversity are a response to age (and state)-dependent rates of these fundamental processes (Stearns, 1992). Mortality comes in several forms. There is mortality generated by predation, grazing, parasitism, disease and infection. Furthermore, there is mortality through starvation caused by a lack of resources and nutrients, and finally senescence contributes to mortality, although usually in the form of one of the above. Mortality is difficult to observe and estimate, partly because many populations are open, i.e. they are subjected to immigration and emigration and, therefore, changes in population densities do not only result from birth and death only. This is particularly so in advective marine systems (e.g. Aksnes *et al.*, 1997; Speirs *et al.*, 2004). Furthermore, dead individuals are usually soon eaten or degraded, limiting the time window for observations. Nevertheless, we need estimates of *in situ* mortality for reliable predictions of population dynamics and responses of populations to environmental change (Ohman, 2012).

Zooplankton plays a key role in the marine environment being an important link between primary producers and higher trophic levels (e.g. Sims and Quayle, 1998; Varpe *et al.*, 2005; Falk-Petersen *et al.*, 2007). Spatial and temporal variability in zooplankton abundance are determined by rates of growth and mortality as well as behavioural adaptations (e.g. vertical migration) and advection. Not all zooplankton are alive in the natural environment and the contribution of dead organisms to the total zooplankton population can be high (Table I). Traditionally, zooplankton is preserved immediately after collection without estimating the proportion of dead and living organisms although staining methods have become available to solve this problem (Fleming and Coughlan, 1978; Elliott and Tang, 2009). By the time samples are enumerated, it is often not possible to assess which individuals were caught dead and which died during fixation although a number of studies have based their estimates of carcasses abundance on the analysis of preserved samples (Table I). Depending on how samples are processed the contribution of non-viable individuals to zooplankton populations may be either under- or overestimated. Neglecting the contribution of dead organisms can lead to errors when estimating mortality rates and consequently create bias in understanding population dynamics (Ohman and Wood, 1995; Elliott and Tang, 2011a; Ohman, 2012) and life history strategies (Fiksen and Carlotti, 1998; Varpe *et al.*, 2007).

The arctic marine environment is characterized by extreme seasonal variability in light and food availability. A number of adaptations have evolved in arctic zooplankton species to deal with long periods of limited food resources, such as prolonged generation times, seasonal vertical migration and accumulation of energy storages (Hagen and Auel, 2001; Falk-Petersen *et al.*, 2009; Varpe, 2012). Copepods of the genus *Calanus* dominate the arctic mesozooplankton community in terms of biomass (Conover, 1988; Hirche and Mumm, 1992; Falk-Petersen *et al.*, 2009). The general conception of the *Calanus* life cycle is that it includes an overwintering period during which certain developmental stages migrate to deeper water layers where they spend the winter in a state of diapause before ascending again to surface layers in spring to continue development and to reproduce (Conover, 1988; Varpe, 2012). This behaviour is regarded as an energy saving mechanism to reduce metabolic cost during periods of food limitation (Hirche, 1991) and as an adaptation to minimize predation risk (Aksnes and Giske, 1990; Kaartvedt, 1996). Seasonal studies from the Arctic suggest that winter mortality may be considerable as *Calanus* abundance usually peaks in autumn but is rather low in spring (Madsen *et al.*, 2001; Arnkværn *et al.*, 2005; Leu *et al.*, 2011; Daase *et al.*, 2013). However, due to logistical constraints, sampling activity at high latitudes is low during winter, and little is known about mortality during the overwintering period.

We here report on the occurrence of carcasses of *Calanus* spp. from two high Arctic locations observed during a research cruise to the Arctic Ocean during the polar night in January 2012. Stratified zooplankton sampling has not been carried out previously in this area during the polar night and the only other estimations of the population level contribution of copepod carcasses from the Arctic are based on numbers of passively sinking copepods in sediment traps from the Canadian Arctic (Sampei *et al.*, 2009, 2012). As a potential aid in understanding the cause and relevance of the mortality, we also report on the distribution and abundance of the living proportion of the population of the three *Calanus* species, including the difference in the lipid content of dead and living individuals. We discuss possible causes for the observed mortality, its implications for population dynamics and energy transfer, and review previous accounts of non-predatory mortality of marine copepods.

METHOD

Samples were taken on 12–14 January 2012 during a cruise with RV Helmer Hanssen in the high Arctic Rijpfjorden (80° 18.5′N, 22°15.7′E, depth 280 m) and at the ice edge at Sofiadjupet, a deep basin in the southern

Table I: Reported occurrences of copepod carcasses and exoskeletons (i.e. molts) in marine habitats (% dead of total copepod abundance in samples) and likely cause of death

Location	Latitude	Habitat	Group/species	Year	Season/ month	Sampling depth (m)	% dead (of total)	Suggested cause of death	Observed condition	Method	Reference
Atlantic											
Southern Arctic Ocean (Sofiadjupet)	82°N	Oceanic	*Calanus finmarchicus*	2012	January	300–2000	98	n.s.	Carcasses	Visual discrimination, live samples	Present study
	82°N		*Calanus hyperboreus*				81	n.s.	Carcasses	Visual discrimination, live samples	
Svalbard (Rijpfjorden)	80°N	Fjord	*Calanus finmarchicus* and *glacialis*	2012	January	0–256	9–14	n.s.	Carcasses	Visual discrimination, live samples	Present study
	80°N		*Calanus hyperboreus*				0–3	n.s.	Carcasses	Visual discrimination, live samples	
NE Atlantic	56°N	Oceanic	Copepods	1975	July–August	2600–3200^a	71–86	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Wishner, 1980)
NE Atlantic	47°N	Oceanic	Calanoid copepods	1985	September	3400–4700	28–89	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Beckmann, 1988)
Bay of Biscay	46–47°N	Oceanic	Copepods	1900	July	914–3658	50–90	n.s.	Carcasses	Visual discrimination^b	(Farran, 1926)
Chesapeake Bay	37°N	Estuaries	Copepods (70–100% *Acartia tonsa*)	2005	June–July	5	29–34	n.s.	Carcasses	Neutral red staining	(Tang *et al.*, 2006)
Chesapeake Bay	37°N	Estuaries	*Acartia tonsa*	2007–2009	All seasons	7–20	14	n.s.	Carcasses	Neutral red staining	(Elliott and Tang, 2011b)
Chesapeake Bay	37°N	Estuaries	*Eurytemora affinis*	2007–2009	All seasons	7–20	4–8	n.s.	Carcasses	Neutral red staining	(Elliott and Tang, 2011b)
Chesapeake Bay	37°N	Estuaries	*Acartia tonsa* copepodites	2010–2011	May–September	2–20	1–14	ns	Carcasses	Neutral red staining	(Elliott *et al.*, 2013)
			Acartia tonsa nauplii				0.5–38	Hypoxia			
Sargasso Sea	32°N	Oceanic	Copepods	1968–69	All seasons	0–500	15	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Deevey and Brooks, 1971)
	32°N					500–100	12	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Deevey and Brooks, 1971)
	32°N					1000–1500	18	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Deevey and Brooks, 1971)
	32°N					1500–2000	21	n.s.	Exoskeletons and carcasses	Visual discrimination^b	(Deevey and Brooks, 1971)
North Atlantic (Madeira Abyssal Plain)	31°N	Oceanic	Copepods	1985	June–July	1500–5300	25–70	n.s.	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Roe, 1988)
NW Atlantic	20–38°N	Oceanic	Calanoid copepods	1966	October	2200–4100	50–69	n.s.	Carcasses	Visual discrimination, preserved samples	(Wheeler, 1967)
NW Africa	19°N	Oceanic (upwelling system)	Copepods (mainly *Temora* spp.)	1972	February–March	0–30	16–28	Environmental stress	Carcasses	Visual discrimination, preserved samples	(Weikert, 1977)

Continued

Table I: Continued

Location	Latitude	Habitat	Group/species	Year	Season/month	Sampling depth (m)	% dead (of total)	Suggested cause of death	Observed condition	Method	Reference
Pacific											
Bering Sea	53°N	Oceanic	Copepods	2006	June	0–750	<10	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Homma and Yamaguchi, 2010)
	53°N					750–1000	~70	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Homma and Yamaguchi, 2010)
	53°N					1000–2000	16–33	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Homma and Yamaguchi, 2010)
	53°N					2000–3000	~50	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Homma and Yamaguchi, 2010)
Western subarctic Pacific (Oyashio)	44°N	Oceanic	Copepods	1998	August	0–1500	1–50	n.s.	Carcasses	Visual discrimination, preserved samples	(Yamaguchi *et al.*, 2002)
	44°N					1500–4000	50–90	n.s.	Carcasses	Visual discrimination, preserved samples	
Western subarctic Pacific (Oyashio)	41–42°N	Oceanic	*Pareuchaeta elongata*	1996–1997	All seasons	0–2000	7–12	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Yamaguchi and Ikeda, 2001)
	41–42°N		*Pareuchaeta birostrata*	1996–1997	All seasons	0–2000	1–21	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	
	41–42°N		*Pareuchaeta rubra*	1996–1997	All seasons	0–2000	4–19	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	
Japan Sea	38–43°N	Oceanic	*Calanus cristatus*	1970, 1984, 1985	All seasons	0–3850	~30	Environmental stress; starvation	Carcasses	Visual discrimination, preserved samples	(Terazaki and Wada, 1988)
Eastern Pacific (Fieberling Guyot)	32°N	Seamount	Copepods	1989	September	0–600	10–40	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Haury *et al.*, 1995)
	32°N			1990	September	95–105	22–58	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	
	32°N			1991	September	60–85	15–20	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	
Eastern Pacific (North-east Bank)	32°N	Seamount	Copepods	1990	September	55–65	~25	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Haury *et al.*, 1995)
Eastern Pacific (Sixtymile Bank)	32°N	Seamount	Copepods	1991	September	30–55	25–55	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Haury *et al.*, 1995)
Pacific (San Diego Trough)	32°N	Oceanic	Copepods	1976	April	1100–1200[a]	62–80	n.s.	Exoskeletons and carcasses	Visual discrimination[b]	(Wishner, 1980)
Eastern Pacific (Jasper Seamount)	30°N	Seamount	Copepods	1984	September	550–1080	75–95	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Haury *et al.*, 1995)
Eastern tropical Pacific	7–9°N	Oceanic; oxygen minimum layer	Copepods	1981	March–April	0–1000	0.5–48	n.s.	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Sameoto, 1986)

Eastern tropical Pacific	0°	Oceanic	Copepods	1974	October	2700–2900[a]	88	n.s.	Exoskeletons and carcasses	Visual discrimination[b]	(Wishner, 1980)
Eastern tropical Pacific	0°	Oceanic	Copepods	1974	November	2400–3000[a]	80	n.s.	Exoskeletons and carcasses	Visual discrimination	(Wishner, 1980)
Pacific (Chilean coast)	23°S, 36°S	Coastal upwelling sites	*Paracalanus indicus*	2009–2010	All seasons	0–80	0.5–60	Environmental stress	Carcasses	Neutral red staining	(Yanez *et al.*, 2012)
Indian Ocean											
Gulf of Eilat, Israel	29°N	Coral reef	Copepods	1990–1991	July–September	5–40	22–65	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Genin *et al.*, 1995)
Gulf of Eilat, Israel	29°N	Sandy shore	Copepods	1990–1991	July–September	5–40	10–22	Incomplete consumption	Carcasses	Visual discrimination, preserved samples	(Genin *et al.*, 1995)
Central Red Sea (Atlantis II Deep)	21°N	Oceanic	Copepods	1977	November	0–450	5	Environmental stress	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Weikert, 1982)
	21°N					450–1850	13	Environmental stress	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Weikert, 1982)
	21°N					1050–1850	32–34	Environmental stress	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Weikert, 1982)
Arabian Sea	18°N	Oceanic	Copepods	1987	April–May	0–1850	1–75	n.s.	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Böttger-Schnack, R, 1996)
Arabian Sea	14–16°N	Oceanic	Zooplankton (>80% copepods)	1995	October	1050–4000	55–93	n.s.	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Koppelmann, 2000)
	14–16°N	Oceanic	Zooplankton (>80% copepods)	1997	April	1050–4000	50–60	n.s.	Exoskeletons and carcasses	Visual discrimination, preserved samples	(Koppelmann, 2000)

[a] Epibenthic sampling (10–100 m above seafloor).

[b] Not specified if analysis was done on preserved or live samples.

Table is sorted after region (Atlantic, Pacific and Indian Ocean) and after latitude (north to south) within each region. n.s., no suggestion.

part of the Arctic Ocean (81° 42′N, 14°16′E, depth 2290 m). Zooplankton was sampled by vertical hauls (towing speed 0.5 m s^{-1}) from close to the bottom to the surface using a multiple opening/closing net (Multinet, Hydrobios, Kiel, mesh size 200 μm, mouth opening 0.25 m^2). In Rijpfjorden samples were taken from 256−224−192−160−128−0 at noon (14:00 UTC) and from 256−224−192−128−20−0 m at night (2:00 UTC). At Sofiadjupet samples were taken from 2000−1800−1600−1400−1200−900−600−300−50−0 m between 17:00 and 21:00 UTC. On deck nets were carefully hosed down with sea water before cod ends were removed. The cod end content was transferred into 5-L buckets filled with filtered seawater and the cod ends themselves were flushed with a squeeze bottle containing sea water. Samples were kept in a cool room (+2°C) until analysis. Samples were processed within 12 h after catch.

For analysis, surplus water was removed by pouring the sample through a 180-μm sieve submerged in sea water. The sample was then transferred into a measuring beaker and filled with filtered sea water to a known volume (100−1000 mL, depending on density of the sample). Quantitative subsamples were taken with a 5 mL pipette with an enlarged opening and transferred into a petri dish. *Calanus* were picked from quantitative subsamples and digital images were taken of all *Calanus* (living and dead) in each subsample using a Leica stereomicroscope with a camera (Leica DFC420). Subsample size was chosen to contain at least 100 *Calanus* from each sample and subsample size varied from 2 to 100% of the total sample. Copepodite stage and physical state (alive or dead) of each individual was determined while taking the pictures. Organisms were defined as being alive if they were actively moving around in the sample, had moving appendages or reacted when gently poked with a laboratory needle. Organisms were defined as dead if they did not react to physical stimulation. We classified the dead copepods into one of four categories (Table II) depending on their state of decomposition at the time their picture was taken. Category 1: dead *Calanus* with intact carapaces and lipid sacs and often opaque body colour (Fig. 1b). Category 2: carcasses with intact carapaces (no obvious fractures or cracks) but with broken lipid sac and partly dissolved inner tissue (Fig. 1c). Category 3: carcasses with broken carapaces but remnants of lipid sacs (often broken) and inner tissue still visible (Fig. 1d). Category 4: intact or broken carapaces which were largely depleted of all inner tissue apart from occasional lipid droplets

Table II: Percentage of Calanus *carcasses classified into one of four categories describing their physical state at the time their picture was taken (see Methods and Fig. 2).*

		Carcass category					
	Sample depth	1 %	2 %	3 %	4 %	No. carcasses in subsample	Fraction of sample (%)
Rijpfjorden							
Mid-day	128–0 m	0.0	50.0	50.0	0.0	8	20
	160–128 m	12.5	6.3	50.0	31.3	15	37
	192–160 m	0.0	14.3	35.7	50.0	14	20
	224–192 m	0.0	11.8	58.8	29.4	18	22
	256–224 m	9.1	15.2	43.9	31.8	65	30
	256–0 m	6.6	15.7	46.3	31.4	120	
Mid-night	20–0 m	7.7	7.7	23.1	61.5	12	10
	128–20 m	0.0	6.7	20.0	73.3	15	2
	192–128 m	0.0	12.5	62.5	25.0	8	6
	224–192 m	0.0	60.0	40.0	0.0	5	10
	256–224 m	0.0	0.0	100.0	0.0	1	50
	256–0 m	2.4	14.3	33.3	50.0	41	
Sofiadjupet							
	50–0 m	16.7	66.7	0.0	16.7	6	8
	300–50	0.0	0.0	0.0	0.0	0	100
	600–300 m	12.4	28.3	1.8	57.5	113	25
	900–600 m	70.8	11.2	3.7	14.3	160	100
	1200–900 m	16.0	22.3	21.3	40.4	93	4
	1200–1400 m	0.0	0.0	0.0	100.0	3	100
	1400–1600 m	0.0	30.0	10.0	60.0	13	100
	1800–1600 m	0.0	7.7	15.4	76.9	14	100
	2000–1800 m	10.0	25.0	0.0	65.0	19	100
	2000–0 m	33.4	21.7	7.3	37.5	421	

Category 1: intact carapaces and lipid sacs, often opaque body colour (Fig. 1b). Category 2: intact carapaces (no obvious fractures), broken lipid sac and partly dissolved inner tissue (Fig. 1c). Category 3: broken carapaces, remnants of lipid sacs and inner tissue still visible (Fig. 1d). Category 4: ‘empty’ carapaces (intact or broken), largely depleted of inner tissue, occasionally some lipid droplets left (Fig. 1e and f).

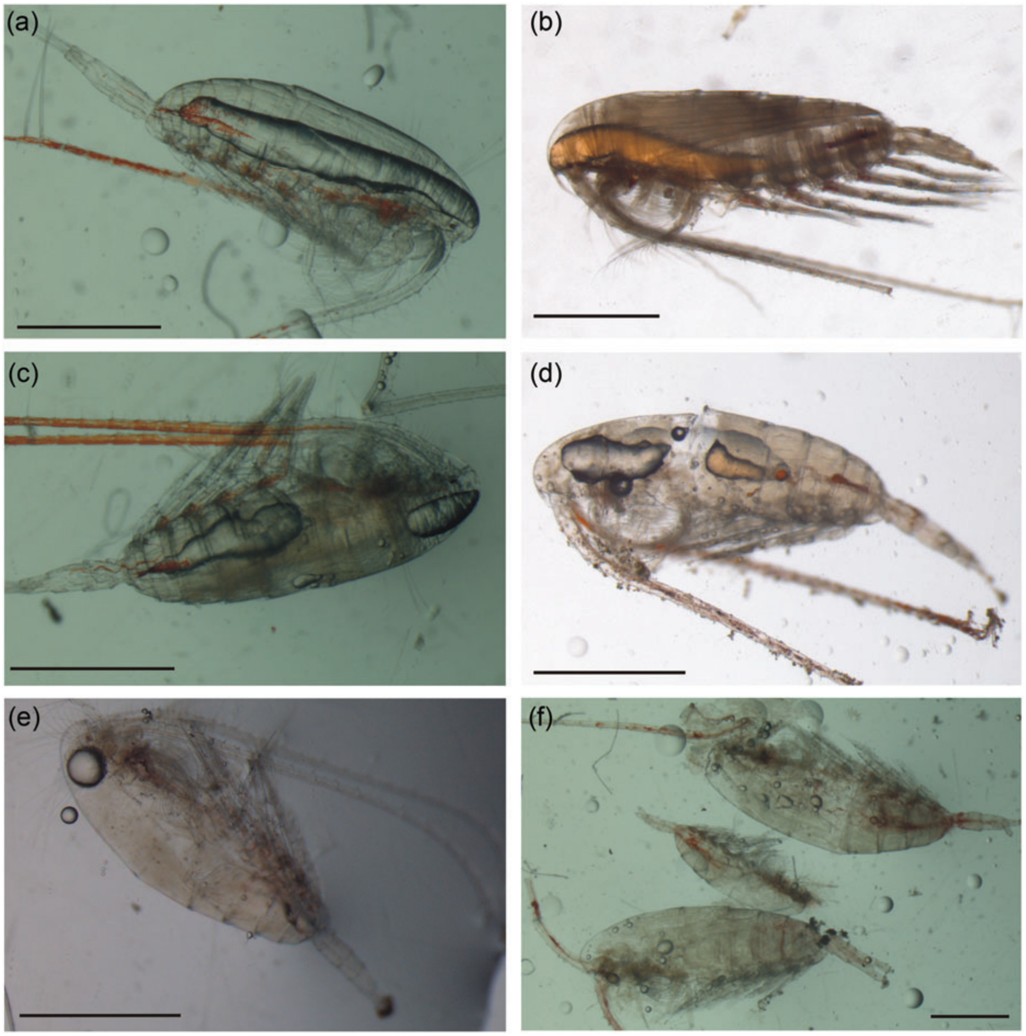

Fig. 1. Living and dead *Calanus* from Rijpfjorden and Sofiadjupet. (**a**) Alive CIV of *C. glacialis* with complete lipid sac, (**b**) carcass of adult female of *C. finmarchicus* with intact carapace and complete lipid sac (category 1), (**c**) carcass of CIV of *C. glacialis* with intact carapace but broken lipid sac (category 2), (**d**) carcass of CIV of *C. hyperboreus* with broken carapace and lipid sac (category 3), (**e**) carcass of CV of *C. finmarchicus* (category 4), (**f**). carcasses of CIV of *C. hyperboreus and C. glacialis* (middle) (category 4). Black scale bar in all pictures is 1 mm long.

(Fig. 1e and f). The classification of the carcasses is based on the analysis of the digital images.

The digital images were also used to measure the prosome length and lipid sac area of individual *Calanus* (Vogedes *et al.*, 2010) using ImageJ, an open source graphics program (Rasband, 1997–2009). Copepodite stages of the morphologicaly similar *Calanus glacialis* and *Calanus finmarchicus* were distinguished based on prosome length using previously established size classes (Daase and Eiane, 2007) but see Gabrielsen *et al*. (Gabrielsen *et al*., 2012). Owing to problems with the calibration of the digital images, length measurement could not be performed on some of the samples from Sofiadjupet and we could therefore not distinguish between *C. finmarchicus* and *C. glacialis* at this station, i.e. species here were only determined as being *C. hyperboreus* or *C. finmarchicus/glacialis*. Analysis of formalin fixed samples from the same location showed that *C. finmarchicus* dominated at Sofiadjupet (85–97% of the *C. finmarchicus* and *C. glacialis* population, unpublished data). Therefore *C. finmarchicus/glacialis* from Sofiadjupet are referred to as *C. finmarchicus* throughout this study. Temperature and salinity from surface to bottom was measured with a ship-board conductivity, temperature and depth profiler (CTD, Sea-Bird Electronics, Bellevue, WA, USA).

RESULTS

Calanus finmarchicus and *C. glacialis* were the abundant *Calanus* species (Fig. 2). In Rijpfjorden, the *Calanus* population (integrated over the entire water column) consisted of

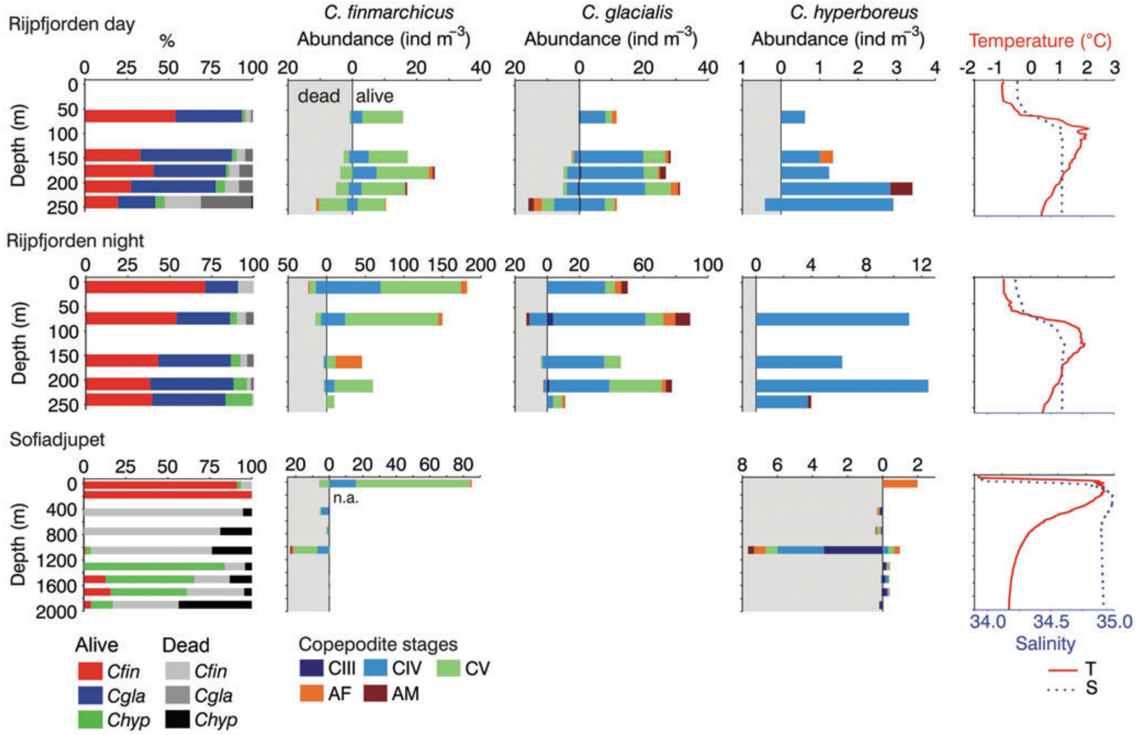

Fig. 2. Proportion *C. finmarchicus* (Cfin), *C. glacialis* (Cgla) and *C. hyperboreus* (Chyp) caught alive (coloured scale) and dead (grey scale) at each station and in each depth; abundance of copepodite stages III –V (CIII-CV), adult female (AF) and adult males (AM) of each species caught alive (white background) or dead (grey background) and temperature (T) and salinity (S) profiles at all stations. *Calanus finmarchicus* and *C. glacialis* were not distinguished at Sofiadjupet but presented as *C. finmarchicus* (see also Section 'Material and Methods'). Note different *x*-axis scales for abundance. No abundance estimate available for Sofiadjupet 300–50 m (n.a.).

47% of *C. finmarchicus* and 49% of *C. glacialis*, whereas *C. hyperboreus* contributed <2%. At Sofiadjupet *C. finmarchicus* dominated (98% in the upper 50 m, 75% integrated between 300 and 2000 m). At both locations, the *C. finmarchicus* population was mainly composed of overwintering copepodite stage CV and some CIVs (Fig. 2). The *C. glacialis* population in Rijpfjorden consisted mainly of stage CIV. *Calanus hyperboreus* abundance was low and stage CIV dominated in Rijpfjorden, whereas CIII, CV and females were more common in Sofiadjupet (Fig. 2).

Total *Calanus* abundance was higher at night than during day in Rijpfjorden (Table III). The bulk of the *C. finmarchicus* and *C. glacialis* population was found in the upper 128 m at night, while it was more evenly distributed throughout the water column during day (Fig. 2). At Sofiadjupet, the bulk of the *C. finmarchicus* population was found in the upper 50 m (91 ind m^{-3}). In Rijpfjorden, *C. hyperboreus* was mainly observed in the deeper water layers (160–200 m), whereas at Sofiadjupet *C. hyperboreus* abundance was highest at intermediate depth (1200–900 m, 8.7 ind m^{-3}) (Fig. 2). Total *Calanus* abundance was low <1200 m (0.5–0.9 ind m^{-3}) at Sofiadjupet.

In Rijpfjorden, 51% of the *Calanus* population was found to be dead in samples taken from 256 to 224 m during day (Table III). However, only a few dead *Calanus* (1%) were observed in samples taken at the same depth during night. In the other layers, 4–16% of the population was found to be dead both during day and night. The dead part of the *Calanus* population consisted of equal parts of *C. finmarchicus* (mainly CV) and *C. glacialis* (mainly CIV) (Table III, Fig. 2).

At Sofiadjupet, most *Calanus* carcasses were observed between 300 and 1200 m and <1600 m (96–100% of the total *Calanus* population, Table III). Also these carcasses were mainly stages CIV and CV of *C. finmarchicus*/*glacialis*. In the deepest layer ~50% of the dead *Calanus* were *C. hyperboreus* (mainly stage CIII). A higher percentage of older copepodite stages (CV, AF) of *C. hyperboreus* were higher up in the water column and most of these were dead (Fig. 1).

In Rijpfjorden, 33–46% of the carcasses observed were preserved as bodies that showed damage to some part of the prosome (Category 3, Table II, Fig. 1d). The inner tissues were often starting to dissolve or were absent, but lipid sacs, broken lipid sacs or lipid droplets could be observed in most carcasses (Category 3 and 4, Fig. 1d–f). Around 71% of the dead *Calanus* observed at 900–600 m at Sofiadjupet were intact bodies with

Table III: Estimated abundance (individuals m^{-3}) of Calanus *spp. and for each of the three* Calanus *species in each depth layer and integrated (bold) over the entire water column at both stations*

	Total Calanus spp.		*C. finmarchicus*		*C. glacialis*		*C. hyperboreus*	
Depth	ind m^{-3}	% dead	ind m^{-3}	% dead	ind m^{-3}	% dead	ind m^{-3}	% dead
Rijpfjorden day (12 January 2012, 14:00 UTC)								
128–0 m	29.2	4.3	16.7	5.6	11.9	2.6	0.6	0.0
160–128 m	52.0	9.7	19.9	13.6	30.7	7.7	1.4	0.0
192–160 m	62.5	14.0	29.4	12.8	31.9	15.7	1.3	0.0
224–192 m	61.9	16.5	22.2	23.1	36.4	14.1	3.4	0.0
256–224 m	52.5	51.6	21.7	51.9	27.5	57.6	3.3	12.5
256–0 m	43.2	16.4	20.0	16.6	21.7	17.0	1.5	3.5
Rijpfjorden night (13 January 2012, 2:00 UTC)								
20–0 m	256.0	9.4	206.0	11.7	50.0	0.0	0.0	0.0
128–20 m	277.8	10.0	164.8	9.0	101.9	12.7	11.1	0.0
192–128 m	106.3	7.8	50.0	8.3	50.0	8.3	6.3	0.0
224–192 m	156.3	4.0	63.8	5.9	80.0	3.1	12.5	0.0
256–224 m	25.3	1.0	10.3	2.4	11.0	0.0	4.0	0.0
256–0 m	186.4	8.8	107.4	9.0	70.8	9.6	8.3	0.0
Sofiadjupet (14 January 2012, 17–21:00 UTC)								
50–0 m	93.0	6.5	91.0[a]	6.6[a]			2.0	0.0
300–50 m	n.d.	0	n.d.	0[a]			n.d.	0
600–300 m	6.0	100.0	5.7[a]	100.0[a]			0.3	100.0
900–600 m	2.1	100.0	1.7[a]	100.0[a]			0.4	100.0
1200–900 m	32.3	95.9	23.7[a]	98.6[a]			8.7	88.5
1400–1200 m	0.5	76.0	0.1[a]	100.0[a]			0.4	4.5
1400–1600 m	0.9	31.8	0.3[a]	61.5[a]			0.5	20.0
1800–1600 m	0.9	30.2	0.4[a]	68.2[a]			0.4	9.1
2000–1800 m	0.5	11.5	0.2[a]	90.0[a]			0.3	76.9
2000–300 m	7.5	94.2	5.6[a]	98.4[a]			1.8	82.3

[a] *C. finmarchicus* and *C. glacialis* pooled.

Abundance could not be quantified for 300–50 m at Sofiadjupet (not determined n.d.) and integrated abundance has been calculated for 2000–300 m. Also shown are the percentages of dead *Calanus* (total and for each species) in each layer.

complete lipid sacs preserved in the body (Category 1, Table II, Fig. 1b). Many of these carcasses were opaque with orange coloured lipid sacs in contrast to the transparent bodies and lipid sacs of living individuals (Fig. 1a). Carcasses from the other depth at Sofiadjupet fell mostly in category 2 and 4, i.e. the body was found to be intact, but the lipid sac and inner tissues showed signs of decay or were dissolved.

The lipid sac area was larger for living compared with dead individuals of copepodite stage CIV and CV of *C. finmarchicus* and *C. glacialis* in Rijpfjorden (Fig. 3). Differences in the lipid sac area between living and dead individuals were significant for CIV and CV for both species (Student's *t*-test, $P < 0.001$).

DISCUSSION

True carcasses or sampling artefacts?

This is one of few studies that have estimates the contribution of carcasses based on analyses of live samples. Previous studies have mainly analysed formalin preserved samples while staining methods have recently become more common (Table I). Independent of the method applied, the contribution of carcasses can only be determined after samples have been taken. There is therefore uncertainty as to whether individuals were already dead in the water (i.e. 'true' carcasses) or if they died due to net damage, sample processing and handling (i.e. sampling artefacts). Hosing of nets can lead to mechanical damage, nets may be contaminated with individuals stuck to the net from previous sampling campaigns, and organisms may burst due to changes in salinity or pressure, especially when retrieved from greater depth. However, very little is known about how far sampling and handling actually leads to an increase in zooplankton mortality. Very few studies have tried to quantify the effects or could document a significant effect of handling on zooplankton mortality. Studies on artefact mortality by Elliott and Tang (Elliott and Tang, 2009) and Tang *et al.* (Tang *et al.*, 2006) have shown that the duration of towing plankton nets did not influence the percentage of dead copepods. Tang *et al.* (Tang *et al.*, 2006) also observed no difference in the percentage of dead copepods between two consecutive tows indicating that carryover of dead copepods between tows was negligible if nets were cleaned after each deployment. Elliott and

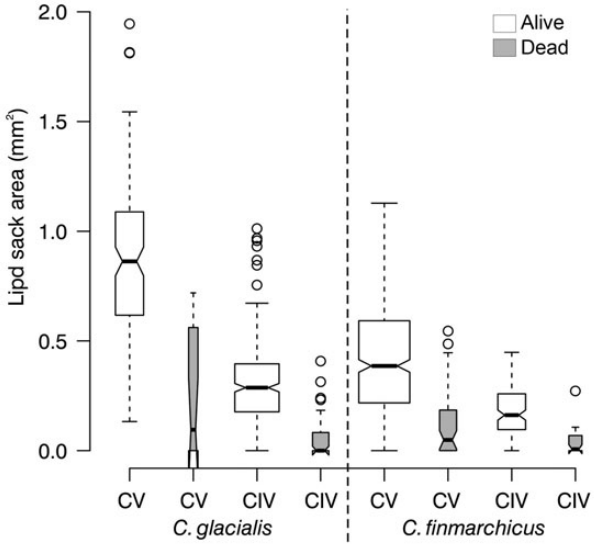

Fig. 3. Boxplot of the lipid sac area (mm^2) of dead and alive copepodites stages IV and V of *C. glacialis* and *C. finmarchicus* in Rijpfjorden (whole water column, day and night pooled). Horizontal line shows the median. The bottom and top of the box show the 25 and 75 percentiles, respectively. Whiskers extend 1.5 times the inter-quartile range of the sample. Values outside this range are marked by circles. The boxes are drawn with widths proportional to the square-roots of the number of observations in the groups. Notches display the variability of the median between samples. The width of a notch is computed so that box plots whose notches do not overlap have different medians (Chambers *et al.*, 1983).

Tang (Elliott and Tang, 2009) did not find a significant difference between the percentage of dead copepods and the use of filtering or non-filtering cod ends.

Some of the methods used in our study may potentially cause artefact mortality. However, the net samples taken in this study were not treated differently from how we usually treat net samples used to analyse living organisms. We applied the exact same method (same net, same towing speed, flushing of net with sea water hose, transferring sample from cod end to bucket, storing samples cool for hours, concentrating samples up and taking digital images) to samples taken at the similar locations on two cruises in July 2012 and observed hardly any dead individuals in those samples (Table IV).

As abundance in most samples was relatively low the copepods were not crowded in the 5-L buckets. In our experience, *Calanus* are quite resilient to handling as organisms caught this way have survived long periods (days to weeks) in a cool room even after being handled with forceps and transferred between beakers and dishes.

The condition of the carcasses observed in the present study varied widely. Some individuals still had lipid sacs and inner organs visible inside them while others were almost empty exoskeletons (Fig. 1, Table II). Individuals with intact carapaces and lipid sacs (category 1) may have more recently deceased. However, we find it unlikely that they died while waiting to be processed since all samples were treated the same way and many individuals appeared unusually inactive when samples were transferred from cod end to buckets, but we cannot with full certainty assess if these are true carcasses or sample artefacts. This possibility mainly affects one sample from Sofiadjupet (900−600 m) in which 70% of the carcasses were classified into this category. Carcasses displaying a fractured carapace (category 3 and 4, Fig. 1, Table II) were particularly common in samples from Rijpfjorden. The fractures may indicate that these organisms suffered mechanical damage. However, fracture of the carapace can also result from bacterial infection during the decomposition process although the carapace proved to be relatively resistant to microbial degradation (Tang *et al.*, 2006). Furthermore, we would expect to find similar percentages of dead copepods in each net if damage by net was the major cause of death. Also, the time from capture to visual inspection of the samples was insufficient to explain the extent of dissolved inner tissue observed in some of the carcasses (in particular category 3 and 4) (Harding, 1973). Wheeler (1967) observed no decomposition in copepods killed by rupturing the exoskeleton with forceps and kept for up to 8 h (at 4 and 24.5°C) concluding that copepods suffering net damage would not be mistaken for carcasses. We, therefore, find it unlikely that these individuals died during sampling or while waiting to be processed. We did not observe copepod skins or exoskeletons left over from moulting processes. Carryover of individuals stuck to the net from previous hauls is also unlikely since the nets were either new or freshly cleaned and we observed high occurrence of carcasses already in the first haul (Rijpfjorden mid-day).

We are therefore confident that the majority of the carcasses observed in this study did not die due to stress during sampling or handling but that these were true carcasses.

Review on copepod carcasses in the oceans

Non-predatory factors can be as important as predation in causing mortality in zooplankton populations (Tang *et al.*, 2006). Hirst and Kiorboe (Hirst and Kiorboe, 2002) estimated that a quarter to a third of the total mortality of marine planktonic copepods may be due to non-predatory mortality. The occurrence of copepod carcasses has been reported from most marine environments (Table I and references within) but most commonly from deep oceanic basins. An increase in the contribution of carcasses with depth is often found (Wishner, 1980; Weikert, 1982; Sameoto, 1986; Roe, 1988; Yamaguchi

Table IV: Abundance of Calanus *spp. and percentages of dead* Calanus *spp. observed in net hauls taken in Rijpfjorden and at off-shelf locations in the pack ice north of Svalbard in July 2012*

					C. finmarchicus		*C. glacialis*		*C. hyperboreus*	
Location, date	Latitude (N)	Longitude (E)	Bottom depth (m)	Sample depth (m)	ind m^{-3}	% dead	ind m^{-3}	% dead	ind m^{-3}	% dead
Rijpfjorden										
16.07.2013	80° 17′	22° 18′	209	20-0	50.0	0.00	840.0	0.00	20.0	0.00
16.07.2013	80° 17′	22° 18′	209	190-100	15.6	0.00	146.7	1.52	35.6	0.00
Sofiadjupet										
18.07.2013	81° 25′	15° 11′	2317	2000-0	1.1	3.00	0.7	1.99	0.5	1.40
Nansen Basin										
30.07.2013	82° 21′	21° 33′	3775	2000-0	0.4	1.71	0.3	0.00	1.3	2.33

Samples were taken onboard R/V Lance, sampling gear and procedures were the same as described in the ‘Methods’ section apart from sampling intervals (2000–1800–1600–1400–1200–600–200–50–20–0 m in Sofiadjupet and Nansen Basin, 190–100 and 20–0 m in Rijpfjorden).

and Ikeda, 2001; Yamaguchi *et al.*, 2002), but that is not necessarily a common feature of deep stations (Terazaki and Wada, 1988; Homma and Yamaguchi, 2010). Accumulations of carcasses have been associated with stratification in the water column [e.g. oxygen minimum layers (Homma and Yamaguchi, 2010; Yanez *et al.*, 2012)]. If carcasses are determined to species or genus level, incidences of carcasses are more commonly reported for calanoid copepods (e.g. Genin *et al.*, 1995; Table I). This is probably not because calanoids are more prone to occur as carcasses (e.g. Böttger-Schnack, 1996) but rather an artefact caused by the common use of nets with mesh sizes >200 μm which do not sample small copepod orders such as cyclopoids as efficiently as calanoids (Gallienne and Robins, 2001). Potential seasonal patterns in carcass abundance are likely dependent on species and their life history. In general, the occurrence of carcasses does not seem to be more common in any particular season (e.g. Terazaki and Wada, 1988; Yamaguchi and Ikeda, 2001; Table I). On the other hand, Elliott and Tang (Elliott and Tang, 2011b) found higher percentages of dead *Acartia tonsa* in summer and autumn arguing that mortality increases during and after peaks in abundance, whereas Sampei *et al.* (Sampei *et al.*, 2012) found enhanced fluxes of carcasses of adult stages of *C. hyperboreus* and *Pareuchaeta glacialis* in February in the Canadian Arctic following the main reproductive period (see also below). One shortcoming when reporting numbers of carcasses is that many previous studies do not distinguish between exoskeletons or moults (copepod carapaces left over from molting processes) and carcasses. This may lead to an overestimation of the non-viable part of the population.

The reason for non-consumptive mortality is often unknown and as evident from our review, seldom discussed when the occurrence of carcasses is reported (Table I). Zooplankton may suffer non-predatory mortality due to starvation (Tsuda, 1994; Lopez, 1996; Carlotti *et al.*, 2000), injuries (Ohman, 1986), viral and parasite infection (Marshall and Orr, 1955; Kimmerer and Mckinnon, 1990; Skovgaard and Saiz, 2006; Dunlap *et al.*, 2013), harmful algal blooms (Huntley *et al.*, 1986; Landsberg, 2002), pollution and other environmental stressors (e.g. Kaartvedt and Aksnes, 1992; Weslawski and Legezynska, 1998; Bamber and Seaby, 2004; Bickel *et al.*, 2011; Elliott *et al.*, 2013). Some copepods also die after reproduction as a consequence of their semelparous life history strategy (Miller *et al.*, 1984). Finally, carcasses may also be the product of incomplete consumption by planktivorous predators feeding only on the internal tissue of their prey or result from egestion of parts of or whole copepod exoskeletons by predators (Ohman, 1984; Genin *et al.*, 1995; Haury *et al.*, 1995). In the following section, we discuss possible reasons for the occurrence of carcasses in our study.

Potential ecological causes for the mid-winter presence of carcasses in the Arctic

Reproductive strategy and semelparity

Calanus spp. is believed to be mainly semelparous and to die after reproduction although Kosobokova (Kosobokova, 1999) inferred iteroparity in *C. glacialis* from the White Sea. Miller *et al.* (Miller *et al.*, 1984) describe the occurrence of ‘spent’ females (exoskeletons without body tissue) of *Neocalanus* from August to January. Sampei *et al.* (Sampei *et al.*, 2012) found enhanced fluxes of copepod carcasses in February in the Canadian Arctic which were mainly due to dead adult stages of *C. hyperboreus* and *Pareuchaeta glacialis* concluding that death following reproduction may be the most likely cause of death. Similar conclusions were made by Terazaki and Wada (Terazaki and Wada, 1988). The dead carcasses found in our study were mainly composed of copepodite stages

CIV and CV (and not adults) hence they could not have died following reproduction.

Starvation and food limitation

The bulk of the *C. finmarchicus* and *C. glacialis* population was found close to the surface and not at greater depth where they presumably should overwinter. Consequently, they may be more active during winter and energy requirements may be higher than previously assumed (e.g. Marshall and Orr, 1955; Hirche, 1998; Hirche and Kosobokova, 2011). Frangoulis *et al.* (Frangoulis *et al.*, 2011) considered food limitation to be a likely cause of mortality of copepods found dead in the western Mediterranean due to a significant negative correlation between mortality rate and chlorophyll *a* concentration. Chlorophyll concentrations were very low in our study area [0.01–0.02 μg L^{-1} in Rijpfjorden (0-bottom) and 0.02–0.04 μg L^{-1} in Sofiadjupet (0–150 m), E. Nøst Hegseth unpublished data]. However, *Calanus* is assumed to not feed during winter but to sustain themselves on lipid reserves which are accumulated in large amounts during the productive season (Auel *et al.*, 2003; Falk-Petersen *et al.*, 2009). Often, only a small proportion of the lipid reserves of diapausing copepods is actually metabolized during overwintering but rather used to fuel development, maturation and egg production at the end of the overwintering season (Miller *et al.*, 1984; Jonasdottir, 1999; Tarling *et al.*, 2004). In most of the carcasses, we observed broken lipid sacs, lipid sacs reduced in size or lipid droplets (Figs 2 and 3) hence these individuals had lipid reserves remaining before they died (Fig. 3). Direct starvation is therefore an unlikely cause of death. Note, however, that Marshall and Orr (Marshall and Orr, 1952) observed that starved *Calanus* retained their lipid sac until they died, but these observations were made under experimental conditions. Also, other essential substances (proteins, carbohydrates, nutrients etc.) may have been limiting causing mortality during the overwintering period. Future studies should aim to assess the importance of non-lipid compounds for surviving periods of food limitation, a direction also suggested for studies of capital breeding (Varpe *et al.*, 2009).

Incomplete consumption

Copepod carcasses observed over sea mounts and coral reefs in subtropical regions were considered to result from incomplete consumption by predators producing empty or partially empty copepod exoskeletons (Genin *et al.*, 1995; Haury *et al.*, 1995). Partly digested crustacean prey have been reported for planktivorous predators such as euphausids (Ohman, 1984; Beyer, 1992; Haury *et al.*, 1995), fish larvae (Checkley, 1982) and adult fish (Redden and Daborn, 1991). Potential planktivorous predators in our study area were amphipods of the genus *Themisto* (Kraft *et al.*, 2013), euphausids, ctenophores and fishes (mainly polar cod (*Boreogadus saida*) but also Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (e.g. Renaud *et al.*, 2012). Stomach content analysis of *B. saida*, *M. aeglefinus* and *G. morhua* showed that *Calanus* were consumed (Varpe unpublished data). Although abundance of the ctenophores *Beroë cucumis* and *Mertensia ovum* can be high in summer in Rijpfjorden (personal observation), we observed only low numbers in January. Stomach content analysis of the amphipods *Themisto libellula* and *T. abyssorum* from Rijpfjorden revealed that these species indeed preyed on *Calanus* (Kraft *et al.*, 2013). *Calanus* was identified from mandibles in the stomachs of *Themisto* spp. The *Calanus* carcasses we observed usually had intact mouth parts indicating that they did not result from partly digestion by *Themisto*. Furthermore, the carcasses did not display injuries as they are described to result from partial consumption by euphausids (Ohman, 1984). Thus, we find it unlikely that the carcasses result from incomplete consumption by predators.

Parasites

We have no data to assess whether parasitic, bacterial or viral infections caused the observed mortality. Skovgaard and Saiz (Skovgaard and Saiz, 2006) estimated mortality rates of adult copepods due to parasitism to be comparable with mortality rates estimated by Hirst and Kiørboe (Hirst and Kiorboe, 2002) and a recent study by Dunlap *et al.* (Dunlap *et al.*, 2013) demonstrated the presence of viral infections in natural copepod populations. More studies are needed to assess the implication of parasitic or viral infection for copepod population dynamics and mortality rates.

Pollution and environmental stress

Finally, other factors such as pollution and environmental stress may increase mortality in natural populations. For example, freezing processes at the surface may cause mortality in copepods (Gradinger and Schnack-Schiel, 1998). Hydrographic conditions in our study area were typical for the time and area. At both locations surface waters were characterized by low temperature (> -1°C) and salinity (<34.2) while relatively warm and saline Atlantic water prevailed (+2°C and 35 psu) <50–100 m at both stations (Fig. 1). In Rijpfjorden, ice had not formed yet, while loose pack ice had formed at Sofiadjupet. The relatively high temperature and salinity (>2°C, >34.9) <70 m and the high abundance of the Atlantic *Calanus* species *C. finmarchicus* in Rijpfjorden indicates that Atlantic water had flushed into the fjord earlier in autumn. However, since the observed carcasses consisted of similar proportions of both *C. glacialis* and

C. finmarchicus this inflow of Atlantic water is unlikely to have caused mortality in Rijpfjorden.

Vertical distribution and advection

At Sofiadjupet dead *Calanus* accumulated in the depth that constitutes the core layer of the Atlantic water flowing north-east into the Arctic Ocean (Rudels *et al.*, 1999; Saloranta and Haugan, 2001), whereas only a few carcasses were observed in the upper 300 m. This is comparable with observations by Yamaguchi *et al.* (Yamaguchi *et al.*, 2002) who observed increased amounts of carcasses with depth in the western subarctic Pacific (50−90% dead copepods <1500 m). Carcasses of copepods exposed to natural seawater are rapidly colonized and decomposed by ambient bacteria (Tang *et al.*, 2006) and decomposition of *C. finmarchicus* was estimated to take 11 days at 4°C (Harding, 1973). However, Terazaki and Wada (Terazaki and Wada, 1988) estimated that carcasses of *Calanus cristatus* could drift for over a year remaining intact in the deep waters of the Japan Sea (<2°C) and Yamaguchi *et al.* (Yamaguchi *et al.*, 2002) speculated that the decomposition of copepod carcasses might take >1 year in the Oyashio region (<5°C). In our study, temperature at the depth where most carcasses were observed was between −1 and 2°C. Thus, *C. finmarchicus* carcasses observed at Sofiadjupet may be allochtonous to the region being advected from the south, i.e. they did not die where they were caught.

Ecological consequences and fate of carcasses

Forest *et al.* (Forest *et al.*, 2007, 2008) suggested that in oligotrophic seas such as the Arctic Ocean zooplankton carcasses may be an important food source for omnivores, carnivores and necrophages in particular during times of the year with low productivity. The *Calanus* carcasses observed during the polar night may potentially be an additional and easily accessible food source. However, visual as well as tactile predators may less successfully encounter passive and dead, compared with moving and living, prey. Pelagic fish in size groups well known to feed on *Calanus*, and caught on the same cruise, had low feeding activity as judged by stomach fullness, but *Calanus* was a frequent prey for those with food in the stomach (Varpe, unpublished data). Dead individuals may also be actively avoided by predators, possibly due to risk of parasites. The bulk of the dead *Calanus* material may therefore accumulate at the sea floor. There is generally a tight pelagic-benthic coupling in the Arctic (Grebmeier and Barry, 1991; Piepenburg, 2005; Tamelander *et al.*, 2006) and a downward flux of carcasses may be an important source of food and nutrients for the benthic community. Sampei *et al.* (Sampei *et al.*, 2009) estimated that passively sinking copepods (i.e. carcasses) contributed 36% of the overall annual POC flux in the Amundsen Gulf (Canadian Arctic). Carcasses may also contribute to nutrient regeneration, elemental recycling and microbial production within the water column. Lipids of dead *Calanus* may be released into the water column and provide a nutritional source to the pelagic community. Fatty acids and fatty alcohols characteristic of calanoid copepods (22:1n-11, 20:1n-9) have been found to be important components of lipid in particulates in water samples from under the ice north of Svalbard and in Greenland (Reuss and Poulsen, 2002; Scott *et al.*, 2002).

We conclude that carcasses of *Calanus* contributed significantly to the *Calanus* population in the high Arctic during the polar night. Partial consumption by predators and death after reproduction are found to be unlikely causes of mortality, thus other stressors (starvation, environmental conditions, parasitic or viral infection) may be responsible. Winter conditions may have had an impact on mortality since we observed a much lower abundance of carcasses during summer (Table IV) in Rijpfjorden and off -shelf north of Svalbard. Our analyses of possible causes for non-consumptive mortality shows that we have a poor understanding of factors other than predation causing mortality in copepod populations. The review also identifies a weakness of several previous studies that are unable to distinguish between carcasses and moults. This distinction is very important from a mortality perspective. Reliable estimates of non-consumptive mortality and a better understanding of factors causing it are relevant, both to understand the life history evolution and population dynamics of these species, as well as their contribution to the bentho-pelagic coupling of the oceans.

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