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Potential misidentifications of two climate indicator species of the marine arctic ecosystem: *Calanus glacialis* and *C. finmarchicus*

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Abstract Calanoid copepods of the genus *Calanus* represent an important, nutrient-rich food source for a multitude of Arctic marine organisms. Although morphologically very similar, their life histories and ecological roles differ. Because the distribution of *Calanus glacialis* and *C. finmarchicus* corresponds to Arctic and Atlantic water masses, respectively, they are regularly used as climate indicators. A correct identification of these species is therefore necessary in many ecological, environmental and climatological studies. In this study, we aimed at validating the traditionally used morphological characteristics (combining prosome length and copepodite stage) for separation of species of *Calanus* by using molecular tools (PCR–RFLP of the 16S mtDNA). A total of 418 specimens of copepodite stages CIV, CV and CVI(af) from three Arctic fjords have been identified both morphologically and genetically. We find that the morphological identification systematically overestimates the abundance of *C. finmarchicus* at the expense of *C. glacialis*. Hence, parts of the *C. glacialis* populations are found to be structurally smaller and the within population size range thus larger than previously assumed. Consequently, using the traditional morphological species delimitation poses a serious problem in the use of these two species as indicators of Atlantic versus Arctic water masses and thus as climatic indicators. Furthermore, it obscures our understanding of the life history differences between the two species and of their relative importance as food for a number of ecologically and economically important species in the Arctic.

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Introduction

Calanus spp. dominate the biomass of the mesozooplankton community by up to 75–90 % in Arctic and sub-Arctic seas (Mumm et al. 1999; Hays et al. 2005; Wassmann et al. 2006; Blachowiak-Samolyk et al. 2008), and these herbivores represent an energy-rich food source of fundamental importance for a number of ecologically and commercially important species such as polar cod (e.g. Lønne and Gulliksen 1989; Renaud et al. 2012), little auk (Steen et al. 2007; Karnovsky et al. 2008), bowhead whales (Weslawski et al. 2000) and for large pelagic fish stocks of the sub-Arctic North Atlantic (Varpe et al. 2005). The difference in size and energy content of *Calanus glacialis* and *C. finmarchicus* suggests that the two species support different arctic food webs (Weslawski et al. 2000; Falk-Petersen et al. 2009).

In the European Arctic, *Calanus* spp. are regarded as biological indicators of Arctic (*Calanus glacialis* and *C. hyperboreus*) and Atlantic (*C. finmarchicus*) water masses, respectively (Kwasniewski et al. 2003; Wassmann et al. 2006; Daase et al. 2007). *Calanus hyperboreus* Krøyer is an Arctic deep-water species with the Greenland Sea and the Arctic Ocean as its core distribution areas

(Hirche 1991; Mumm et al. 1999). The smaller *C. glacialis* Jaschnov is an Arctic shelf species, whereas the smallest *C. finmarchicus* Gunnerus is an Atlantic species that occurs in the Arctic closely associated with the distribution of Atlantic water (Jaschnov 1970; Daase et al. 2007; Søreide et al. 2008).

Biological indicator species play a prominent role in understanding the effects of climate fluctuations on ecosystems. The Arctic region experiences substantial climatic oscillations on annual and decadal scales, and is predicted to experience large and rapid future climate changes (Post et al. 2009). A common prediction of the impact of climate change on biology is changes in species distributions, such as northward shifts of species as temperature increases (Wassmann et al. 2011). In the marine system, significant indicator species are of particular interest for tracing a potential Atlantification of the arctic water masses due to climate warming and sea ice loss (Wassmann et al. 2006). It has been postulated that a warmer climate would expand the distribution of *C. finmarchicus* northwards into waters traditionally dominated by *C. glacialis* and *C. hyperboreus* (Reygondeau and Beaugrand 2011; Slagstad et al. 2011; Wassmann et al. 2011), leading to a potential ecosystem shift in the arctic food web (Falk-Petersen et al. 2007). In the light of their importance as climate indicators and their key role in the arctic marine food web, it is imperative that the *Calanus* species can be identified correctly and that their species ranges and life histories are well understood.

The delimitation of the North Atlantic *Calanus* species relies mainly on few and subtle morphological characteristics. The largest of the three arctic species, *C. hyperboreus*, can be separated from the two others by an acute process on the 5th metasome segment in copepodite stages CIV, CV and CVI. There are also a few diagnostic taxonomical characters on the fifth pair of swimming legs that can be used to separate the adults of *Calanus glacialis* and *C. finmarchicus* (Frost 1974), although these two species are traditionally more difficult to distinguish compared to the much larger *C. hyperboreus*. The diagnostic taxonomical characters are time-consuming to use, and the Arctic *Calanus* spp. of all stages are therefore traditionally separated based on prosome length, with the separation of the species being based on the frequency distribution of prosome size within each copepodite stage. (e.g. Unstad and Tande 1991; Kwasniewski et al. 2003; Arnkvaern et al. 2005; Forest et al. 2011).

The Barents Sea—Svalbard region is a transition zone between warm and saline Atlantic water and cold and less saline Arctic water and represents a region of sympatry for *C. glacialis* and *C. finmarchicus*. The two species were recently shown to overlap in size in areas of sympatric distribution in the Canadian Arctic (Parent et al. 2011) and in the Irminger Sea (Lindeque et al. 2006), thus pointing at a potential challenge to correctly identify the species using the traditional method of prosome length. In this study, we use the molecular tools developed by Lindeque et al. (1999) to test for the reliability of morphometric species identification of stages CIV, CV and adult females of *C. finmarchicus* and *C. glacialis* in the European Arctic. In this region, many past and ongoing studies have relied on *C. finmarchicus* and *C. glacialis* as climate change indicator species (e.g. Wassmann et al. 2006; Slagstad et al. 2011). Hence, we also test the reliability of using the two species as endpoints in studies of effects of climate change (e.g. Beaugrand et al. 2002; Slagstad et al. 2011).

Materials and methods

Calanus copepods were collected from Rijpfjorden (N 80° 17.034 E 22° 18.149), Kongsfjorden (N 78° 57.754 E 11° 45.556) and Billefjorden (N 78° 35.7 E 16° 30.36; Fig. 1) in Svalbard using WP2 nets with 0.25 m² opening and 200 μm mesh size. A total of 419 individuals were picked, rinsed in distilled water and photographed using a digital video camera (Sony HDR-HC7E) mounted to a stereomicroscope (Leica MZ16) before they were fixed in 80–96 % Ethanol and stored in 80 % Ethanol until analysis. The copepodite stage and prosome length (from the tip of the cephalosome to the distal lateral end of the last thoracic segment) of each individual was identified from the digital photos and measured using the free image analysis software ImageJ (V 1.42q) (http://rsbweb.nih.gov/ij) as described in Vogedes et al. (2010).
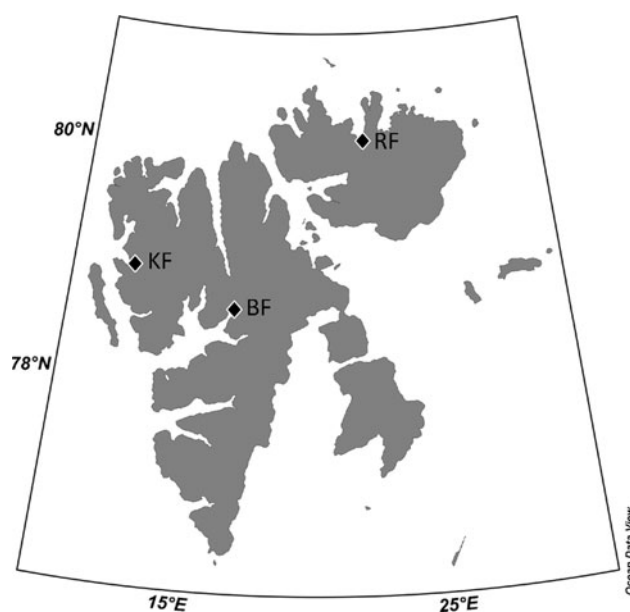

Fig. 1 Map of Svalbard and the sampled populations in Billefjorden (*BAB*), Kongsfjorden (*KF*) and Rijpfjorden (*RF*)

The analysed individuals were selected to cover the prosome lengths known to overlap among the different copepodite stages of *Calanus glacialis* and *C. finmarchicus* (Kwasniewski et al. 2003 [Kongsfjorden]; Arnkvaern et al. 2005 [Billefjorden]). Samples were collected in the autumn of 2009 (all three fjords) as well as in Billefjorden in the spring of 2009 and 2010. In the spring of 2010, sampling was done at two different dates in Billefjorden. The analysed individuals represented the copepodite stages CIV (127 specimens), CV (177 specimens) and CVI (af; 113 specimens) with the most individuals analysed from Billefjorden (329 specimens). During the 2010 field work in Billefjorden, the prosome length distribution of the whole population was estimated at each date separately, in addition to the sampling of individuals for genetic analyses.

Prior to DNA extraction, single individuals were rinsed well and hydrated in distilled water over night. DNA was extracted using the EZNA kit (Omega Bio-Tek Inc.) according to the manufacturer's recommendation. PCR reactions were performed in volumes of 25 μl containing 200 μM dNTPs, 0.4 μM of each primer (16SAR; Palumbi and Benzie 1991 and 16SB2R; Lindeque et al. 1999), 1× PCR buffer, 0.5U DreamTaq polymerase (Fermentas Life Sciences) and 2 μl extracted DNA. The cycling conditions included an initial denaturation step at 95 °C for 3 min followed by 35 cycles of 94 °C for 30 s, 54 °C for 30 s and 72 °C for 60 s. A final extension phase of 10 min at 72 °C was allowed, and the samples were then stored at 4 °C until use. The PCR products were cut using the restriction enzymes VspI and DdeI according to the manufacturer's recommendation (Fermentas Life Sciences), and the products were separated on 2 % agarose gels and identified to *C. glacialis* or *C. finmarchicus* according to the restriction patterns (Lindeque et al. 1999).

Results

Our analyses show that *C. glacialis* is frequently misidentified as *C. finmarchicus* when the species delimitation is based solely on prosome length (Table 1; Fig. 2). Genetic species delimitation based on the PCR–RFLP pattern identified 329 individuals to *C. glacialis* and 88 individuals to *C. finmarchicus*, whereas size-morphological species delimitation identified 234 individuals to *C. glacialis* and 183 individuals to *C. finmarchicus*. Overall, 25.7 % of the analysed individuals were wrongly identified, and only 5.6 % of the wrongly identified individuals were *C. finmarchicus* misidentified as *C. glacialis*. The misidentification was greatest for adult females, followed by CV and CIV.

Copepodite stage IV

A total of 127 individuals of copepodite stage CIV (1.5–2.7 mm PL; Fig. 2) were analysed, of which 95 were

Table 1 A comparison of morphological (prosome length) and genetic (PCR–RFLP) species delimitation of *C. finmarchicus* and *C. glacialis* with a calculation of the percentage of wrongly identified specimens in each copepodite stage as well as a calculation of the percentage overestimation of *C. finmarchicus* (C fin (morph)—C fin (gen))/C fin (gen))

|	N	Morphological delimitation				Genetic delimitation				% Wrongly identified	% Overestimation of *C. finmarchicus*
		finm no	finm %	glac no	glac %	finm no	finm %	glac no	glac %		
Billefjorden											
CIV	103	35	34.0	68	66.0	20	19.4	83	80.6	20.4	75.0
CV	120	75	62.5	45	37.5	42	35.0	78	65.0	29.2	78.6
CVI(af)	106	38	35.8	68	64.2	2	1.9	104	98.1	34.0	1,800.0
Kongsfjorden											
CIV	17	13	76.5	4	23.5	11	64.7	6	35.3	11.8	18.2
CV	21	11	52.4	10	47.6	6	28.6	15	71.4	23.8	83.3
CVI(af)	5	4	80.0	1	20.0	4	80.0	1	20.0	n/a	n/a
Rijpfjorden											
CIV	7	0	0.0	7	100.0	1	14.3	6	85.7	n/a	n/a
CV	36	7	19.4	29	80.6	2	5.6	34	94.4	13.9	250.0
CVI(af)	2	0	0.0	2	100.0	0	0.0	2	100.0	n/a	n/a
All populations											
CIV	127	48	37.8	79	62.2	32	25.2	95	74.8	18.9	50.0
CV	177	93	52.5	84	47.5	50	28.2	127	71.8	25.4	86.0
CVI(af)	113	42	37.2	71	62.8	6	5.3	107	94.7	33.6	600.0
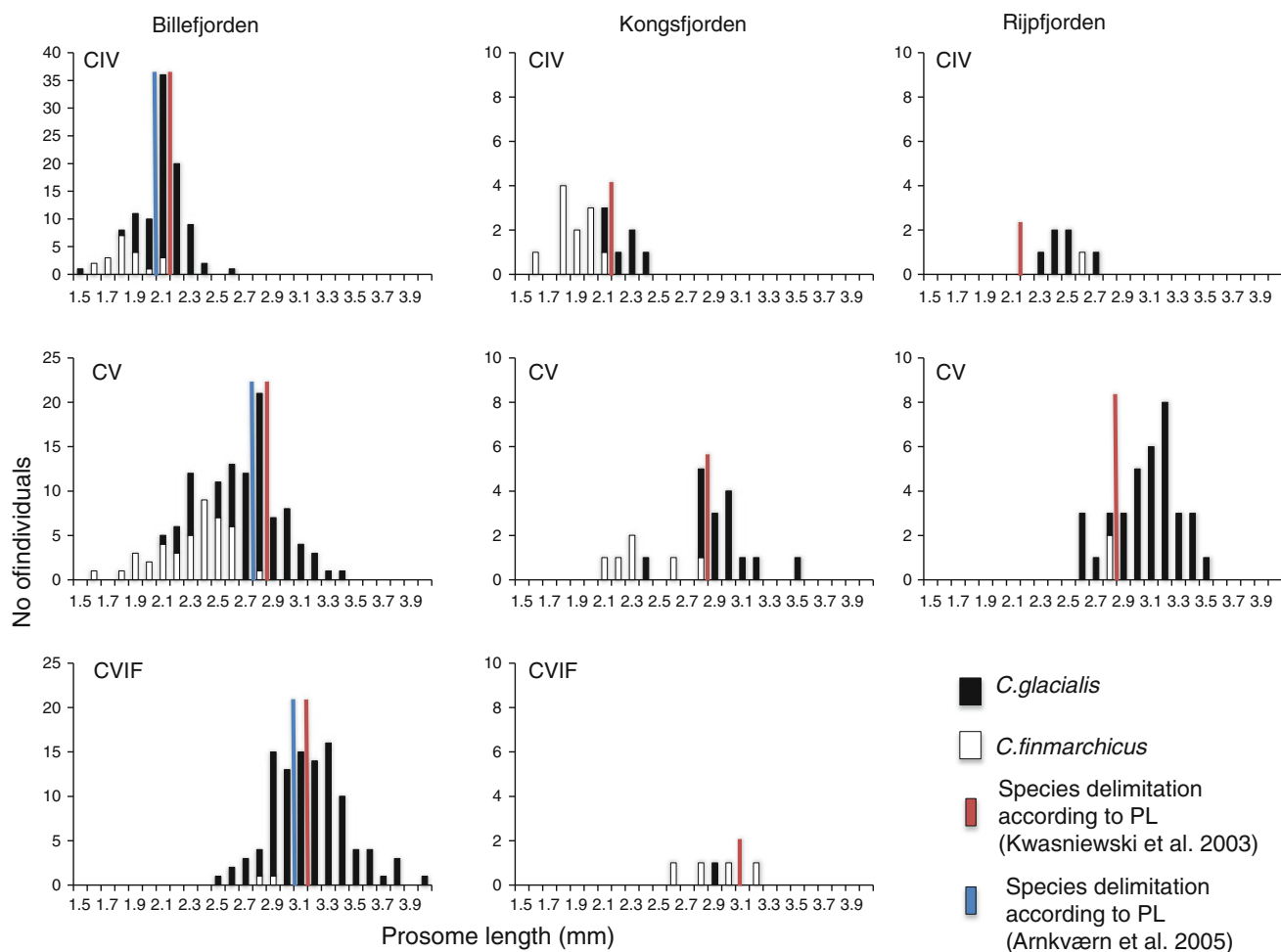
Fig. 2 Prosome length (*PL*) distribution of the *Calanus* spp. specimens of copepodite stages CIV, CV and CVI (af) analysed using PCR–RFLP of the 16S mtDNA gene. The *coloured lines* represent the prosome lengths utilized to distinguish the two species according to Arnkværn et al. (2005; *blue line*) and Kwasniewski et al. (2003; *red line*)

identified as *C. glacialis* and 32 were identified as *C. finmarchicus* based on the PCR–RFLP pattern. Overall, 18.9 % of the individuals were wrongly identified using species delimitation based on the prosome length. The overestimation of *C. finmarchicus* was most pronounced in Billefjorden with 75 % of the investigated specimens wrongly identified as *C. finmarchicus* (Table 1).

Copepodite stage V

A total of 177 specimens of copepodite stage CV (1.6–3.5 mm PL; Fig. 2) were analysed. Of these, 127 were identified as *C. glacialis* and 50 were identified as *C. finmarchicus* based on the PCR–RFLP pattern. Overall, 25.4 % of the individuals were wrongly identified based on morphological species delimitation (Table 1), most severely so in our Rijpfjorden case.

Adult females

A total of 113 adult females (2.4–4.0 mm PL; Fig. 2) were analysed. Of these, 107 individuals were identified as *C. glacialis* and only 6 were identified as *C. finmarchicus* based on the PCR–RFLP pattern. Overall, 33.6 % of the individuals were misidentified using morphological species delimitation, and there was a distinct overestimation of *C. finmarchicus* over *C. glacialis* (Table 1). The overestimation of *C. finmarchicus* was most pronounced among the adult females collected in Billefjorden where the presence of *C. finmarchicus* was overestimated by 1,800 % (Table 1).

Prosome length distribution of the Billefjorden population

The prosome length distributions of the Billefjorden *Calanus* population collected at two sampling dates in 2010
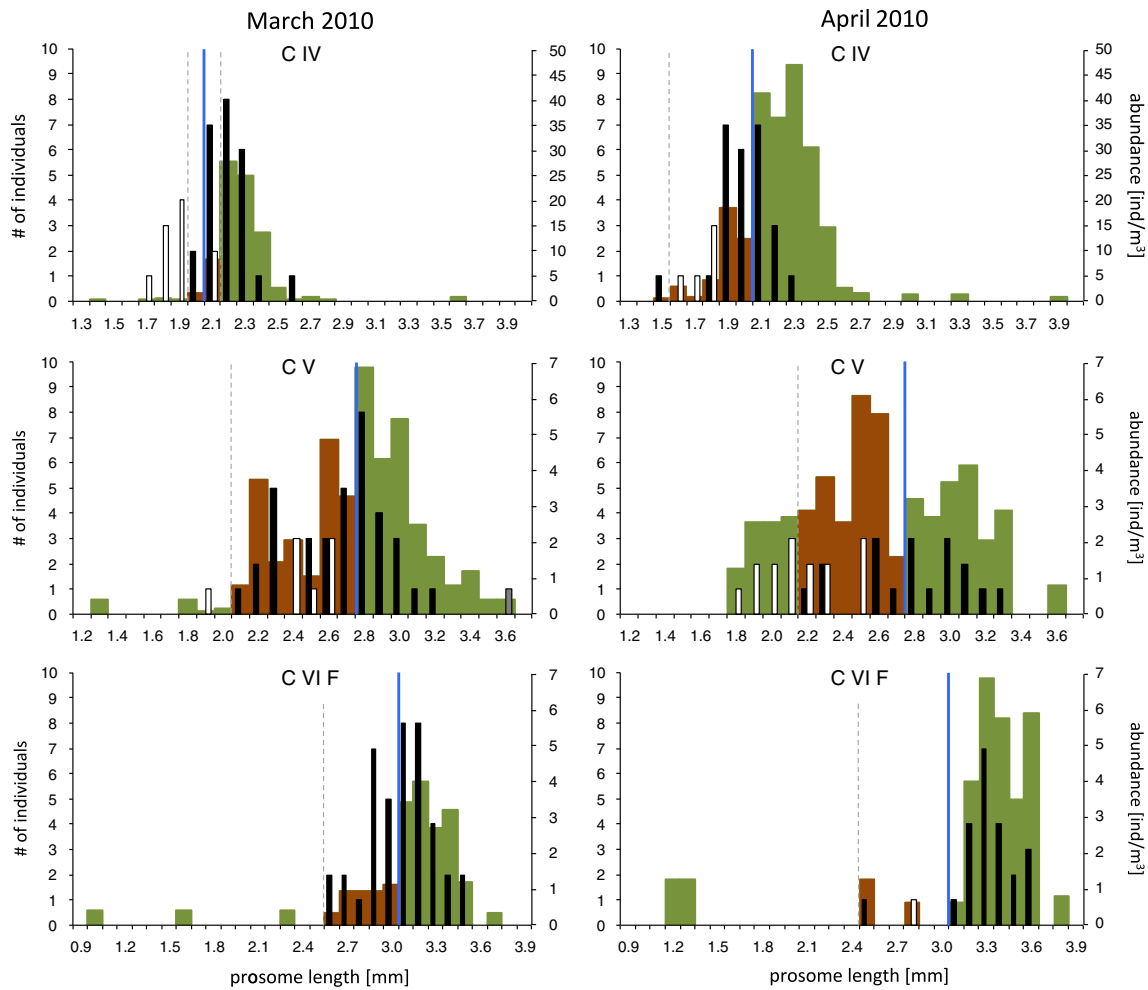
Fig. 3 Prosome length (*PL*) distribution of the two Billefjorden samples of *Calanus* spp. copepodite stages CIV, CV and CVI (af) for which the PL of the whole sample was analysed. The samples were collected in March of 2010 (*left three panels*) and in April of 2010 (*right three panels*), and included samples from both deep and surface waters (cf. Fig. 1). The blue line represents the prosome length utilized to distinguish the two species according to Arnkvaern et al. (2005), the *green bars* are the total amount of specimens collected (scale on the *right*), the *white bars* are the number of genetically identified *C. finmarchicus* specimens (scale on the *left*) and the *black bars* are the number of genetically identified *C. glacialis* specimens (scale on the *left*). *Brown background* individuals of PL where the species id was uncertain based solely on prosome size. The *dotted lines* show the overlap region based on genetic identification of species

show that a large part of the population is within the size range where identification based solely on size morphology is difficult (Fig. 3). Based on the minimum and maximum of misidentified PL as shown in Fig. 3, an average of 14 % of the total population of CIV, 42 % of the total population of CV and 13 % of the total population of CVI (af) in March and April of 2010 were within the prosome length size range where morphological identification was uncertain (Table 2).

Discussion

The prosome length variation identified within *C. glacialis* in this study, with a higher than expected number of small specimens, may compromise our understanding of the ecology and distribution of this species and points to a serious problem in the species delimitation of particularly *C. glacialis* and *C. finmarchicus*. Because structural size is a plastic trait in most organisms and in zooplankton a result of both temperature-dependent developmental time and growth (e.g. McLaren et al. 1988), variability in this characteristic is not unexpected. Also, life history strategies are typically state dependent (McNamara and Houston 1996) and structural size may thus vary between and within populations due to strategic fitness-maximizing processes (cf. Varpe 2012). In fact, analyses of the length–frequency distribution of the arctic *Calanus* spp. in Svalbard waters show slightly different size distributions of the two species in different fjord systems (Kwasniewski et al. 2003;

Table 2 The percentage of the total population of *Calanus* spp. collected in March and April of 2010 that were of a prosome length (PL) where species id was difficult due to overlapping size ranges of *C. glacialis* and *C. finmarchicus*

Individuals	March			April			Average (March–April)		
	CIV	CV	CVI(af)	CIV	CV	CVI(af)	CIV	CV	CVI(af)
Total no	1,639	823	357	3,224	824	448	2,432	824	402
Fraction within total	195	342	69	536	355	26	366	348	47
%	12	42	19	17	43	6	14	42	13
finm no	58	358	93	536	483	59	297	420	76
Fraction within finm	32	342	69	536	355	26	284	348	47
%	55	96	74	100	73	44	78	84	59
glac no	1,581	465	264	2,688	341	389	2,135	403	326
Fraction within gla	163	0	0	0	0	0	82	0	0
%	10	0	0	0	0	0	5	0	0

Individuals	Within total pop	Within finm (morph. delimitation)	Within glac (morph. delimitation)
March			
CIV (%)	12	55	10
CV (%)	42	96	0
CVI(af) (%)	19	74	0
April			
CIV (%)	17	100	0
CV (%)	43	73	0
CVI(af) (%)	6	44	0
Average			
CIV (%)	14	78	5
CV (%)	42	84	0
CVI(af) (%)	13	59	0

Total no—total number of specimens of each stage and sampling date, fraction within total—number of specimens within the PL range where species id was difficult, finm no—number of *C. finmarchicus* specimens identified morphologically for each stage and sampling date, glac no—number of *C. glacialis* specimens identified morphologically for each stage and sampling date, within finm—percentage of the population of *C. finmarchicus* found within the PL size range in which species id was difficult, within glac—percentage of the population of *C. glacialis* found within the PL size range in which species id was difficult

Arnkvaern et al. 2005; Daase et al. 2007; Weydmann and Kwasniewski 2008). The distinct overestimation of the abundance of *C. finmarchicus* over *C. glacialis* in all fjords and copepodite stages investigated around Svalbard was, however, unexpected. This result does support the results by Parent et al. (2011) for *Calanus* spp. off the Canadian coast and Lindeque et al. (2006) for *Calanus* spp. in the Irminger Sea that *C. glacialis* can have a smaller size than is commonly assumed in traditional species delimitation based on prosome length. Thus, wrongly identified material of this sibling species complex may be a problem throughout their distribution area.

The region within which the specimens are unequivocally identified, defined as the size classes where there are no discrepancies between the genetically and morphologically based identification, varies in time, space and among developmental stages (Figs. 2,3). The identification problem is thus not a stable phenomenon (Fig. 3), and the number of misidentifications varied between the two sampling periods in March and April in Billefjorden (Table 2). In March for the CV copepodites, almost half of the population was within the prosome length with a high degree of misidentifications (see also Table 2), whereas only one-third of the population was affected in April. Similarly, for the CIV stages, only very few individuals were within the size range affected by misidentifications in March, whereas almost one-third of the CIV stages could not be unequivocally identified using prosome length in April (Fig. 3; Table 2).

Increased sea water temperatures have generally been argued to be responsible for prosome size reductions in *Calanus* spp. (Kwasniewski et al. 2003). However, our results identifying smaller than expected *C. glacialis* in all fjords investigated with Kongsfjorden being mostly

influenced by warm Atlantic water masses, Rijpfjorden being mostly influenced by cold Arctic water masses and Billefjorden consisting mostly of winter-cooled water close to freezing temperatures of sea water (Nilsen et al. 2008; Wallace et al. 2010) do not support such an argument. It has previously been shown that *C. glacialis* from the Arctic Ocean also harbour small specimens (adult females with prosome lengths down to 2.81 mm; Frost 1974).

The mitochondrial marker utilized to separate *Calanus* species in the present study cannot be used to properly identify hybridization events between the species because mtDNA in general is uniparentally inherited. If hybridization between *C. glacialis* and *C. finmarchicus* does occur, we could expect to find hybrids with intermediate prosome lengths disturbing the general pattern of prosome length distributions. Hybridization thus offers a possible explanation to the observed pattern of *C. glacialis* specimens that are smaller than expected, although the complete lack of adult females in Billefjorden in our samples indicate that the hybridization pressure is low (at least in the sampled period), and hence that the size distribution represents a biological characteristic of the *Calanus* spp. populations in the examined waters.

An alternative explanation for the larger than expected range in prosome lengths of *C. glacialis* may be size differences resulting from variation in the length of its life cycle. *Calanus glacialis* usually has a 2-year life cycle, spawning in the spring of its third year (Falk-Petersen et al. 2009). Both 1- and 3-year life cycles have been observed, the first is probably more common at the southern fringes of its distribution area (Tande 1991). *Calanus glacialis* thus overwinters as either CIV or CV. The extended prosome length variation that we observed in *C. glacialis* may result from different lengths of life cycles, where populations/specimens with 1-year life cycles would be expected to reach maturity at a smaller size compared to populations/specimens with 2- or 3-year life cycles. The negative shift in prosome length identified in *C. glacialis* may thus result from variation in life history characteristics, with a 1-year life cycle dominating in the populations where we find a shift towards smaller size.

Berge et al. (2012) recently argued that in the presence of strong predation pressure, an adaptation towards shorter life cycles and thus smaller size is an evolutionary advantage enabling *Calanus* to reproduce under high predation pressure. The size variation in *C. glacialis* that we observe in this study may be an adaptation to predation, and one hypothesis to investigate further is if there is size (and thus life history) variation in *C. glacialis* in different regions with different selection pressure based on predation from fish.

Rapid shifts in the distribution of the two northern *Calanus* spp. have been both observed (Beaugrand et al. 2002) and predicted (Slagstad et al. 2011) within the Arctic. These shifts are generally assumed to be directly related to changes in temperature, although the mechanisms are not unequivocal (Kaartvedt 2008). The impact of the herein reported potential misidentification on our understanding of the relationship between climate change and the biology of the two *Calanus* spp., might thus be significant. Based on the common suggestion that the two species support two different food chains (Falk-Petersen et al. 2007) and that at least *C. finmarchicus* is restricted by a northern distribution limit (e.g. Beaugrand et al. 2002), it has become part of our general understanding of the Arctic marine system that *C. finmarchicus* will replace *C. glacialis* as the former expand northwards (see e.g. Slagstad et al. 2011). However, following the herein reported and that of Parent et al. (2011) overestimation of *C. finmarchicus* at the expense of *C. glacialis*, it will be important to map the extent of this problem, both at a spatial and temporal scale, in order to provide insight into potential consequences of the ongoing warming in the Arctic (Comiso et al. 2008).

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