Seasonal vertical strategies in a high-Arctic coastal zooplankton community

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ABSTRACT: We studied the larger (>1000 µm) size fraction of zooplankton in an Arctic coastal water community in Billefjorden, Svalbard (78° 40′ N), Norway, in order to describe seasonal vertical distributions of the dominant taxa in relation to environmental variability. *Calanus* spp. numerically dominated the herbivores; *Aglantha digitale*, *Mertensia ovum*, *Beroë cucumis*, and *Parasagitta elegans* were the dominant carnivores. Omnivores and detritivores were numerically less important. Descent to deeper regions of the water column (>100 m) between August and October, and ascent to the shallower region (<100 m) between November and May was the overall seasonal pattern in this zooplankton community. In contrast to other groups, *P. elegans* did not exhibit pronounced vertical migrations. Seasonal vertical distributions of most species showed statistical associations with the availability of their main food source. The vertical distribution of later developmental stages of *Calanus* spp. was inversely associated with fluorescence, indicating that they descended from the shallower region while it was still relatively productive, and ascended before the primary production had started to increase. Strong associations between the vertical distributions of secondary consumer *M. ovum* and *Calanus* spp., and tertiary consumer *B. cucumis* and *M. ovum* indicated that these carnivores seasonally followed their prey through the water column. We conclude that seasonal vertical migrations are a widespread trait in the high Arctic community studied, and predator–prey interactions seem particularly central in shaping the associations between the seasonal vertical strategies of adjacent trophic levels.

KEY WORDS: Seasonal vertical migration · Food availability · Trophic interactions · Pelagic environments · Predator–prey interactions

INTRODUCTION

Pronounced seasonal oscillations in abiotic (e.g. solar radiation, temperature, sea ice) and biotic (e.g. food availability, predation pressure) environments offer challenges to zooplankton in high latitudes. In particular, seasonality in food availability is believed to be a significant challenge (Clarke & Peck 1991, Conover & Huntley 1991, Hagen 1999, Varpe 2012). Arctic zooplankton possess adaptations to counter a seasonally variable food supply, such as energy stor-

age (Lee et al. 2006, Varpe et al. 2009), diapause (Carlisle 1961, Hirche 1996), and seasonal vertical migrations (Conover 1988). Zooplankton seasonal vertical migrations are understood as an adaptive behavior that optimizes their position in the water column in response to seasonal variability in the environment (Werner & Gilliam 1984). We refer to this behavior as their 'seasonal vertical strategy'. Seasonal vertical strategies of some high-latitude herbivorous zooplankton are well-documented (e.g. Conover 1988, Falk-Petersen et al. 2009), and their adap-

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tive value has also been analyzed in modeling studies (e.g. Fiksen 2000, Varpe et al. 2007).

The underlying regulation of zooplankton seasonal vertical strategies has been a subject of interest since early 1900s (Russell 1927, Banse 1964). Seasonal variability in hydrography (Hirche 1991), photoperiod (Sømme 1934, Miller et al. 1991), and visual predation (Kaartvedt 1996, Dale et al. 1999, Kaartvedt 2000) are some external environmental cues that are thought to regulate seasonal vertical strategies. Internal (endogenous) regulation through seasonal changes in gonad development (Østvedt 1955), lipids and buoyancy (Visser & Jónasdóttir 1999), and long-term endogenous timers (Miller et al. 1991, Hirche 1996) have also been suggested.

Many components of zooplankton life strategies are viewed as adaptations to seasonal variations in food supply (Ji et al. 2010, Varpe 2012), but the influence of food availability on seasonal vertical strategies remains poorly understood, particularly for carnivorous species. As the seasonal food supply is more pronounced for Arctic herbivorous zooplankton (Conover & Huntley 1991, Hagen 1999), whose energetic demands mainly depend on a short period of annual primary production (Falk-Petersen et al. 2009), it can be argued that their seasonal vertical strategies are tightly coupled with food availability. Although vertical distributions of *Calanus* spp. appear to be associated with food availability (chlorophyll *a* distributions) in spring (Herman 1983, Søreide et al. 2008, Basedow et al. 2010), it is less well-studied for the rest of the year. Compared to herbivores, Arctic carnivorous and omnivorous zooplankton rely to a greater extent on a year-round food supply (Hagen 1999). Therefore, it has been suggested that their seasonal adaptations are less pronounced compared to herbivores (Ji et al. 2010, Varpe 2012). As vertical distributions vary seasonally in a number of carnivorous hydromedusae (e.g. Pertsova et al. 2006), ctenophores (e.g. Siferd & Conover 1992), chaetognaths (e.g. Grigor et al. 2014), euphausiids (e.g. Lass et al. 2001), and copepods (e.g. Vestheim et al. 2005), it appears that seasonal vertical strategies of Arctic carnivorous zooplankton are more diverse than previously thought. Since many carnivores rely on herbivores as their main food source, the potential influence of the vertical strategies of herbivorous zooplankton on their predators may be ecologically significant. This is portrayed in the findings of Nelson et al. (1997) and Sims et al. (2005), where a close resemblance between the vertical behavior of planktivorous sharks and the diel vertical migration (DVM) of herbivorous zooplankton were reported. Whether such relation-
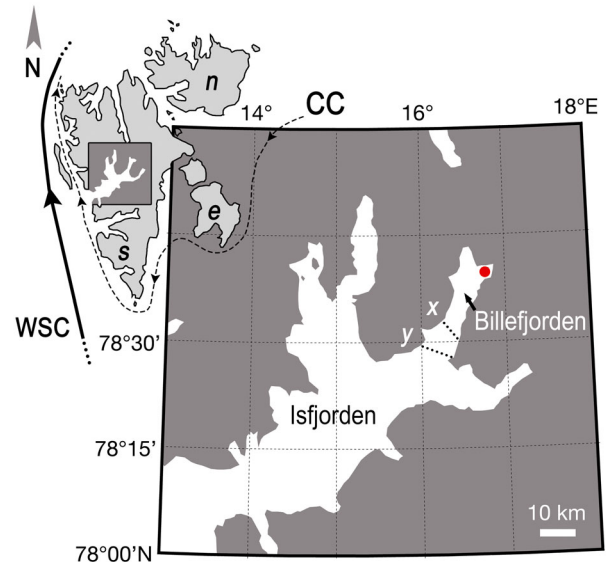

Fig. 1. Study area; sampling site is indicated by the red dot. *x* and *y* indicate coarse locations of the inner and outer sills of Billefjorden respectively. Positions of the west Spitsbergen current (WSC) and the coastal current (CC) were adopted from Svendsen et al. (2002). *s*: Spitsbergen, *n*: Nordaustlandet, *e*: Edgeøya

ships exist on seasonal timescales is not known, and open for investigation.

Investigating the seasonality of zooplankton strategies and interactions requires studying pelagic communities over the course of an annual cycle. Apart from a few studies (e.g. Hop et al. 2006), year-round zooplankton community investigations are rare in the Arctic. Here, we investigated seasonal vertical distributions of the dominant herbivore and carnivore zooplankton in a high-latitude coastal zooplankton community during a 10-month period in 2008 and 2009. We studied the extent to which the seasonal vertical distributions of the above zooplankton could be explained by the seasonal dynamics of their primary food source, or physical environmental variables such as temperature, salinity, and irradiance.

MATERIALS AND METHODS

Study site

Environmental variables and zooplankton samples were collected monthly between August 2008 and May 2009 at a 189 m deep station (78° 39.72' N, 16° 44.34' E) within the inner basin of Billefjorden, located at the west coast of Spitsbergen, the largest island in the Svalbard archipelago (Fig. 1). The inner basin of Billefjorden remains ice-covered from ca.

December to June (Arnkværn et al. 2005). Two 50 to 70 m deep sills located near the mouth of the fjord (Fig. 1) act as a topographical barrier that hinders the advection of the Atlantic water masses into Billefjorden (Cottier et al. 2005, Nilsen et al. 2008). Because of this, Arnkværn et al. (2005) argued that zooplankton population dynamics in Billefjorden are influenced more by internal processes than by advection.

Environmental variables

Temperature and salinity were profiled *in situ* using either a CTD/STD model DS 204 (SAIV) or a Seabird™ CTD (Sea-Bird Electronics). Since no CTDs were deployed on 27 August and 07 September 2008, and 23 March 2009 (Table 1), we obtained temperature and salinity data for these dates from a moored instrument series (www.sams.ac.uk/oceans-2025/arctic-mooring) deployed <0.5 nautical miles away (78° 39.76′ N, 16° 11.24′ E) from the sampling site (see Supplement 1 at .int-res.com/articles/suppl/m555p049_supp.pdf). We measured photosynthetically active radiation (PAR) from a QSP 2300 log quantum scalar irradiance sensor (Biospherical Instruments), and fluorescence from a Seapoint™ chlorophyll fluorometer (Seapoint Sensors) affixed to the above mooring at 29 m. Fluorescence could not be accurately estimated due to the lack of fluorometer calibration coefficients for most

Table 1. Zooplankton samples and CTD casts collected during the study. A sample is a depth-stratified 0–180 m net haul. Day samples (D) were collected between 11:00 and 17:00 h; night samples (N), between 23:00 and 04:00 h local time (UTC + 1). Note that the lack of CTD data in August, September, and March (dashes in the rightmost column) were compensated by the data of the mooring (see Supplement 1 at www.int-res.com/articles/suppl/m555 p049_supp.pdf)

Date (dd/mm/yyyy)	No. of Samples	Time of collection	CTD casts
27/08/2008	1	N	–
07/09/2008	2	D + N	–
23/09/2008	2	D + N	x
17/10/2008	3	D + N	x
04/11/2008	2	D + N	x
03/12/2008	2	D + N	x
14/01/2009	1	D + N	x
26/02/2009	3	D + N	x
23/03/2009	1	N	–
30/03/2009	1	D	x
20/04/2009	1	D	x
27/04/2009	1	D	x
04/05/2009	1	D	x

of the year. Therefore, raw voltage outputs of the fluorometer were presented as normalized values between 0 and 1 after removing some extreme readings (sensor noise). This provided an approximate variation of the fluorescence during the study, because according to the calibration equation (Seapoint Sensors; data not shown), fluorescence is estimated as a linear function of the voltage outputs.

Raw voltage outputs (O_i) of the irradiance sensor were converted to PAR by applying a wet calibration factor ($C = 5.05 \times 10^{12}$), and a dark voltage of 0.0130 V (Biospherical Instruments) as:

$$PAR = C(10^{O_i} - 10^{0.0130}) \qquad (1)$$

Temperature and salinity measurements were visualized using the Spatial Analyst™ extension of ArcGIS™ version 9.3 (ESRI). Here, the data were interpolated temporally over the depth range using the natural neighbor method (Sibson 1981). Fluorescence and PAR data are presented as daily means. Sea ice charts developed by the Ice Information Portal of the Norwegian Metrological Institute (http://polarview.met.no/) were used to describe the sea ice extent in Billefjorden during the study period.

Zooplankton

Zooplankton were sampled by vertical hauls using a WP-3 net (area of the opening: 1 m²; mesh size: 1 mm) fitted with a Nansen-type messenger-operated closing device. Samples were taken from the vessel, or with a tetrapod-mounted cable towed by a snowmobile at ca. 1 m s⁻¹ when sampling from sea ice. Three depth strata were sampled (0–50, 50–100, and 100–180 m), excluding the bottommost 10 m. Larger (>10 mm) gelatinous zooplankton that could dissolve upon formaldehyde preservation were identified, and their body lengths were measured immediately after collection. The rest of the samples were preserved in a borax-buffered 4 % formaldehyde-in-seawater solution.

In the laboratory, the larger specimens were counted from the entire samples. The smaller and more numerous individuals (predominantly copepods) were counted in subsamples obtained using a box splitter (Motoda 1985) until a minimum of 100 individuals were counted per sample. On average, ~24 % (range: 0.15 to 100 %) of the total sample volume was used. Zooplankton were identified to the lowest possible taxonomic level, and classified into trophic groups according to the literature (see Table 2).

Prosome lengths (PL) of copepods were measured to the nearest 0.1 mm using a stereomicroscope (Leica Microsystems). We measured bell heights (BH) of hydromedusae and total lengths (TL) of other zooplankton. The copepodite stage 4 (CIV) and older developmental stages of *Calanus hyperboreus* (which were the only stages captured in this species) were identified by the presence of an acute spine on their fifth thoracic segment (e.g. Parent et al. 2011). The rest of the *Calanus* spp. were identified by a length frequency analysis following Arnkværn et al. (2005) using the R (R Core Team 2013) package 'mixdist' v.0.5-4 (Macdonald & Du 2012). We used the PLs of 3908 CVs, 1409 adult females, and 387 adult males of *Calanus* spp. pooled over the study period for the analysis. PL boundaries derived by the length frequency analysis were evaluated against those published in relevant literature to distinguish species. We also used this method on monthly pooled length measurements (BH or TL) of other taxa to identify any size groups.

Zooplankton abundances (ind. m^{-3}) were estimated assuming 100% filtration efficiency of the WP-3 net. Monthly mean abundances were used in data presentation and analyses. This was estimated by averaging the total abundance of a given taxon in a given month over the number of samples (i.e. net hauls) collected in that month (Table 1).

Seasonal vertical distributions of the dominant zooplankton species (i.e. those that contributed >0.1% of the total numerical abundance [corresponding to 5 ind. m^{-3}], and were captured more or less throughout the investigation) were presented as monthly mean abundances in each depth stratum. Since the relative abundance of dominant taxa in each depth stratum in day and night replicate samples (Table 1) varied <9%, the mean abundances of the replicates were used in the presentation and analyses of seasonal vertical distributions.

Seasonal vertical strategies

In order to describe zooplankton seasonal vertical distributions as seasonal vertical strategies, we described the water column in 2 regions: a shallower region (0 to 100 m), and a deeper region (100 to 180 m). We considered the maximum sill depth of the fjord (~70 m), maximum thermohaline stratification depth (~80 m) recorded in the study, and the vertical resolution of our sampling design (minimum 50 m) in making the above discrimination. We estimated a vertical distribution index (*V*) for each spe-

cies by taking the difference between the population proportions of the 2 vertical regions in each month as:

$$V = \frac{(N_{0-100} - N_{100-180})}{(N_{0-100} + N_{100-180})} \quad (2)$$

where N_{0-100} and $N_{100-180}$ represent the monthly mean abundance of the shallow and deeper regions of the water columns, respectively. *V* ranges between −1 and 1, in which the upper limit represents the entire population distributed in the shallower region of the water column, and the lower limit represents the opposite scenario. Here we assumed the influences of zooplankton advection in and out of this community to be negligible (see Supplement 2 at www.int-res.com/articles/suppl/m555p049_supp.pdf), and therefore, the dynamics of *V* over the time series is primarily due to the vertical migration of zooplankton across the 2 vertical regions.

We used correlation analyses to describe the association between the monthly vertical distribution indices of the dominant taxa and physical (i.e. mean temperature, salinity, and PAR) and biological (availability of the main food source) environmental variables, assuming a linear association between the above. We tested the above variables for normality (Shapiro-Wilk test; Shapiro & Wilk 1965), and homoscedasticity (2-sample Levene's test; Levene 1960), and found that most variables violated the assumptions of parametric correlation tests. Therefore, we used the nonparametric Kendall's rank correlation test with adjustment to tied ranks (coefficient = τ_b) (Kendall 1938, 1945) in the analyses.

RESULTS

Environmental variables

The inner basin of Billefjorden was covered with land-fast sea ice from late December 2008 until the end of the investigation in May 2009 (Fig. 2a). Maximum PAR and fluorescence values were recorded between August and September, and decreased to 0.2 µmol m^{-2} s^{-1} and 0.10 units respectively after November (Fig. 2a,b). Pronounced thermo-haline stratifications observed in the early part of the study broke down between November and January, and resulted in a well-mixed, cold (<−1.0°C), and relatively high saline (>34 PSU) water column (Fig. 2c,d). This lack of stratification persisted until the end of sampling.
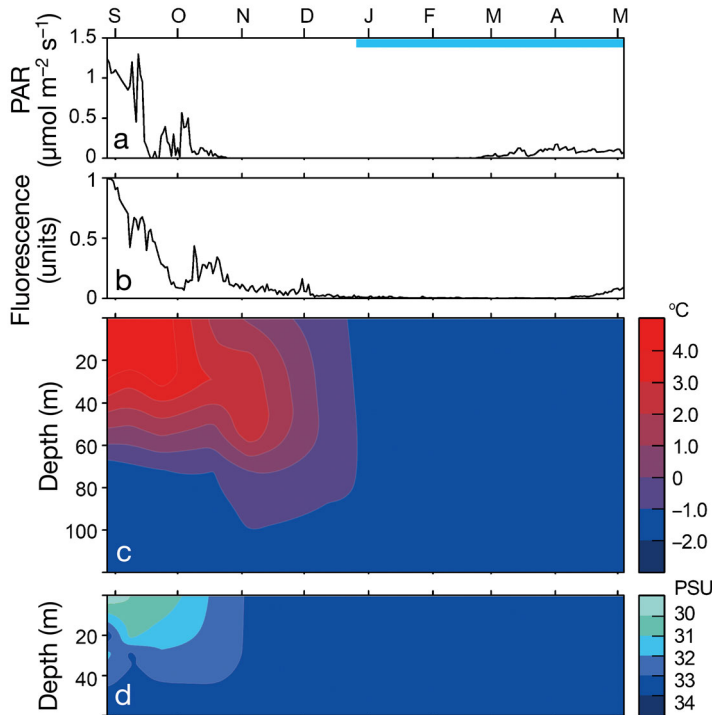
Fig. 2. Seasonal variability in (a) photosynthetically active radiation (PAR), (b) fluorescence (normalized between 0 and 1 unit), (c) temperature, and (d) salinity during the study. The blue bar in (a) indicates the period of land-fast sea ice cover. The ordinates of (c) and (d) are cropped at 120 and 60 m respectively due to the prevailing homogeneity of those parameters. Note that the abscissa extends from 27 August 2008 to 04 May 2009

Zooplankton community composition and trophic relationships

A total of 8 herbivores, 8 omnivores, 4 detritivores, and 17 carnivores comprised the 37 zooplankton taxa captured in this study (Table 2). The PL boundaries derived from the length–frequency analysis of *Calanus* spp. (Table 3) were in accordance with those published for *C. finmarchicus* and *C. glacialis* (see Supplement 3 at www.int-res.com/articles/suppl/m555p049_supp.pdf). Numerically, *C. glacialis* dominated the herbivore community (relative abundance ~77.6%; Table 2) alongside *C. finmarchicus* (~17%) and *C. hyperboreus* (~2%). Carnivores accounted for ~2.5% of the total numerical abundance (Table 2), and were dominated by the chaetognath *Parasagitta elegans* (~1.2%), the ctenophores *Mertensia ovum* (~0.5%) and *Beroë cucumis* (~0.4%), and the hydromedusa *Aglantha digitale* (~0.2%). Omnivorous and detritivorous zooplankton only contributed to ~1% of the total numerical abundance (Table 2).

Table 2. Zooplankton taxa captured in this study, their relative abundances, and feeding modes (references given as numbers in superscript). Indet.: indeterminate

Taxon	Feeding mode	Relative abundance (%)
Bougainvillia spp.	Carnivore[02, 42]	0.02
Halitholus spp.	Carnivore[18]	0.01
Sarsia spp.	Carnivore[42]	<0.01
Aglantha digitale	Carnivore[05, 27, 42]	0.21
Mertensia ovum	Carnivore[35, 39]	0.45
Beroë cucumis	Carnivore[22, 31]	0.36
Clione limacina	Carnivore[04, 23]	0.02
Limacina helicina	Omnivore[17, 21]	0.03
L. retroversa	Herbivore[40], omnivore[17]	<0.01
Gastropoda indet.	–	0.01
Parasagitta elegans	Carnivore[16, 24]	1.18
Eukrohnia hamata	Carnivore[07, 20]	0.08
Anonyx nugax	Scavenger[14, 19]	<0.01
Themisto abyssorum	Carnivore[16]	<0.01
T. libellula	Carnivore[32]	<0.01
Amphipoda indet.	–	<0.01
Munnopsis spp.	Herbivore/detritivore[28]	<0.01
Isopoda indet.	–	<0.01
Mysidae indet.	–	0.03
Meganyctiphanes norvegica	Carnivore[03, 10]	<0.01
Thysanoessa inermis	Herbivore[03, 19]	0.11
T. longicaudata	Omnivore[11, 36]	<0.01
T. raschii	Omnivore[09, 10]	<0.01
Eualus gaimardii	Carnivores[29, 37]	<0.01
Pandalus borealis	Omnivore[15]	<0.01
Necora puber	Carnivore[26, 41]	<0.01
Hyas spp.	Carnivore/scavenger[43]	<0.01
Calanus sp.	–	0.11
Calanus finmarchicus	Herbivore[25, 38]	16.92
C. glacialis	Herbivore[25, 38]	77.56
C. hyperboreus	Herbivore[25, 38]	2.02
Microcalanus spp.	Herbivore/detritivore[13]	<0.01
Pseudocalanus spp.	Herbivore[34]	<0.01
Paraeuchaeta norvegica	Carnivore[30, 33]	<0.01
Metridia longa	Omnivore[01]	0.86
Oikopleura spp.	Particle feeder/omnivore[06]	<0.01
Leptoclinus spp. (larvae)	Carnivore[12]	<0.01

References (in chronological order): [01]Haq (1967); [02]Fraser (1969); [03]Ackman et al. (1970); [04]Conover & Lalli (1972); [05]Smedstad (1972); [06]Alldredge (1976); [07]Sullivan (1980); [08]Falk-Petersen et al. (1981); [09]Sargent & Falk-Petersen (1981); [10]Falk-Petersen et al. (1982); [11]: Williams & Lindley (1982); [12]Eschmeyer et al. (1983); [13]Hopkins (1985); [14]Sainte-Marie & Lamarche (1985); [15]Shumway et al. (1985); [16]Falk-Petersen et al. (1987); [17]Lalli & Gilmer (1989); [18]Larson & Harbison (1989); [19]Sainte-Marie et al. (1989); [20]Øresland (1990); [21]Gilmer & Harbison (1991); [22]Purcell (1991); [23]Hermans & Satterlie (1992); [24]Alvarez-Cadena (1993); [25]Graeve et al. (1994); [26]Freire & Gonzalez-Gurriaran (1995); [27]Pagès et al. (1996); [28]Brusca (1997); [29]Graeve et al. (1997); [30]Olsen et al. (2000); [31]Falk-Petersen et al. (2002); [32]Auel & Werner (2003); [33]Skarra & Kaartvedt (2003); [34]Lischka & Hagen (2005); [35]Lundberg et al. (2006); [36]Blachowiak-Samolyk et al. (2007); [37]Nygård et al. (2007); [38]Falk-Petersen et al. (2009); [39]Graeve et al. (2008); [40]Bernard & Froneman (2009); [41]Silva et al. (2010); [42]Prudkovsky (2013); [43]Boxshall et al. (2015)

Table 3. Prosome length boundaries (mm) used to separate the 2 *Calanus* taxa, with their % composition within each developmental stage in parentheses. The rightmost column presents chi-squared statistic of the fitted model with the degrees of freedom in parentheses. *p < 0.05; **p < 0.01; ***p < 0.001

Developmental stage	Prosome length (% composition)		χ^2 (df)
	C. finmarchicus	*C. glacialis*	
CV	2.45–2.98 (38.96)	≥2.98 (59.74)	187.97** (11)
Adult females	2.38–2.92 (16.64)	≥2.92 (83.24)	54.47** (13)
Adult males	≤3.04 (7.20)	>3.04 (92.08)	19.55* (10)

Based on the literature, we considered fluorescence as an indicator of the primary food source for herbivorous zooplankton, and identified *Calanus* spp. as the main prey of the secondary consumers *A. digitale*, *M. ovum*, and *P. elegans*, and *M. ovum* as that of the tertiary consumer *B. cucumis* (see references in Table 2).

Seasonal variability in abundance of the dominant zooplankton

Herbivores

The highest mean abundances of *C. finmarchicus* (~100 ind. m^{-3}), *C. glacialis* (~430 ind. m^{-3}), and *C. hyperboreus* (~13 ind. m^{-3}) were recorded between August and November (Fig. 3a–c). During this period, CV was the dominant developmental stage of *C. finmarchicus* and *C. glacialis* (>95%: Fig. 3d,e). After November, relative abundance of CV decreased, and adult male and female copepodites increased. In *C. hyperboreus*, CIV was the dominant developmental stage throughout the study (Fig. 3f).

Carnivores

The mean abundances of *A. digitale* and *M. ovum* peaked at ~4 ind. m^{-3} in October (Fig. 4a,b). *B. cucumis* was captured in relatively large numbers (mean abundance: ~2.5 ind. m^{-3}) in October and May (Fig. 4c). We could not identify any size groups of the 3 above species from length–frequency analyses. However, their abundance peaks were dominated by relatively small individuals (mean ± SD body length: 6.6 ± 1.5 mm for *A. digitale*, 6.7 ± 5.3 mm for *M. ovum*, and 2.9 ± 1.6 mm for *B. cucumis*; Fig. 4 e–g). The mean body lengths of *A. digitale* and *M. ovum* increased throughout the study period, while that of *B. cucumis* decreased after reaching a maximum (9.31 ± 6.4 mm) in November. *P. elegans* was captured in higher numbers in September (~5.5 ind. m^{-3}), December (~4.5 ind. m^{-3}), and between April and May
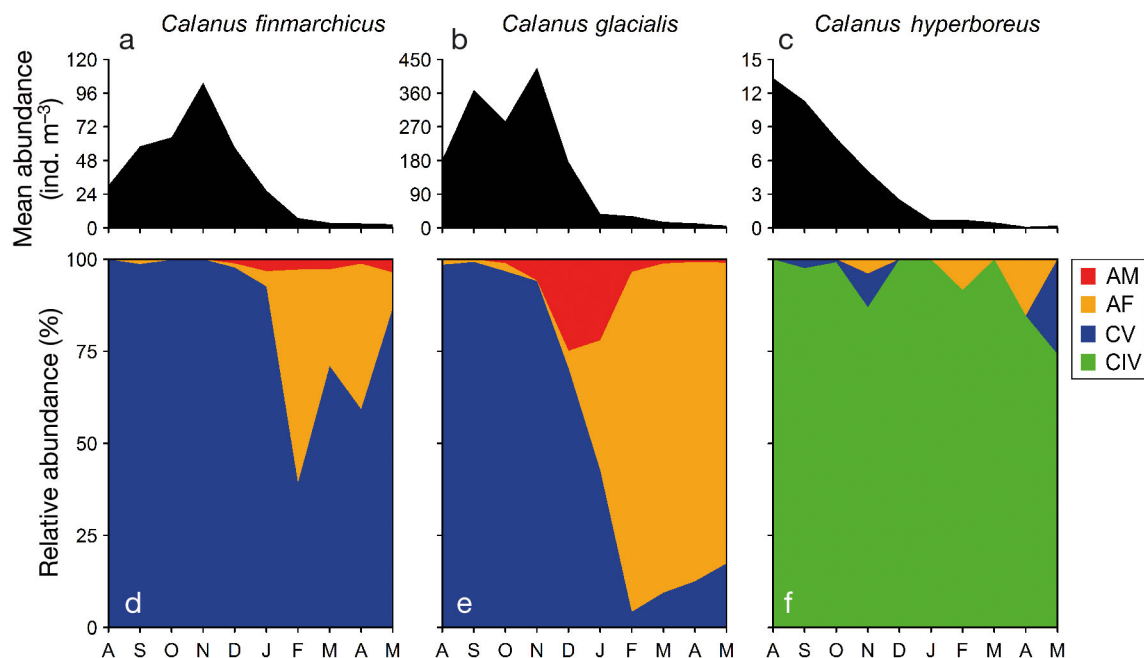

Fig. 3. Seasonal variability in (a–c) mean abundance and (d–f) relative developmental stage composition of dominant herbivores during the study. AM: adult males; AF: adult females; CV and CIV: copepodite stage 5 and 4, respectively
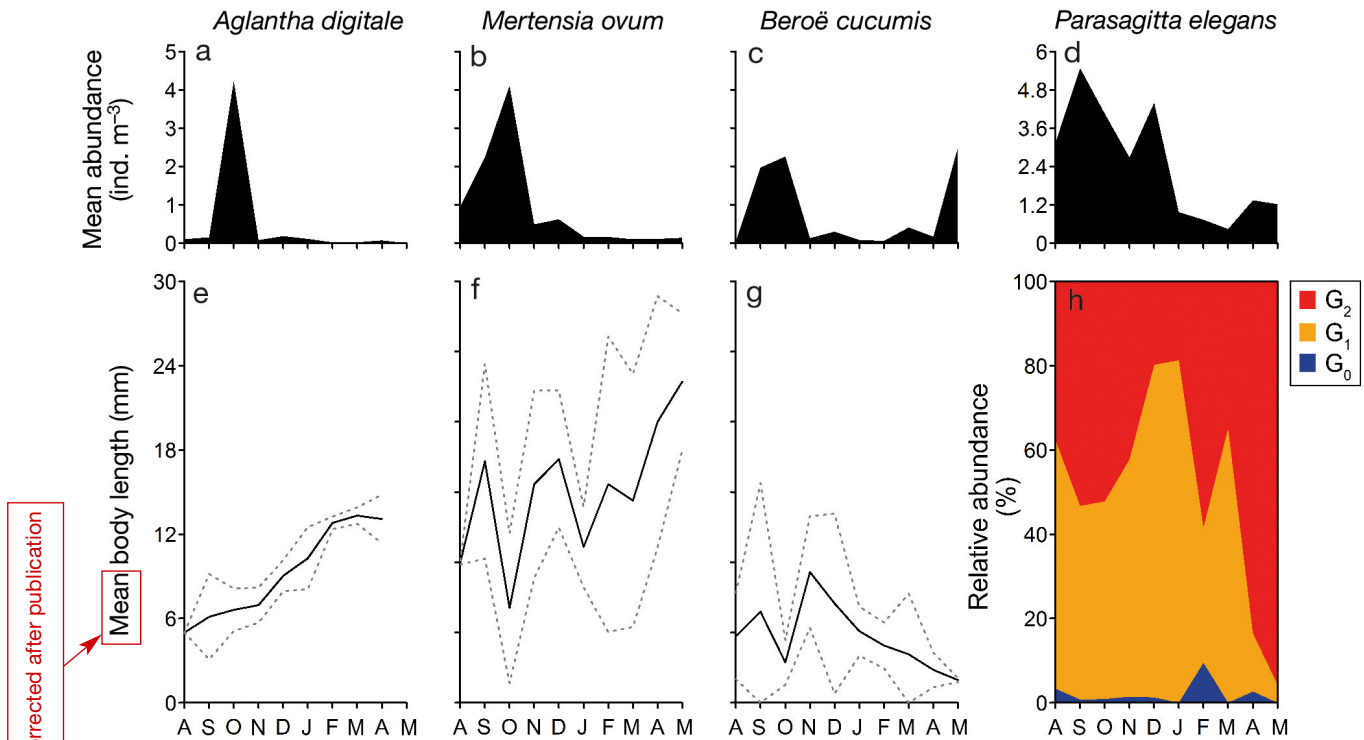
Fig. 4. Seasonal variability in (a–d) mean abundance and (e–h) mean body length of dominant carnivores during the study. Body lengths are presented as bell height for *A. digitale* and total length (TL) for other species. The TL dynamics of *P. elegans* in (h) is presented as variation in relative abundance of the 3 size groups. Dashed lines in (e–g) denote standard deviation of body length (mm)

(~1.5 ind. m^{-3}) (Fig. 4d). We derived 3 size groups for *P. elegans* from the length–frequency analysis (G_0, G_1, and G_2: see Supplement 4 at www.int-res.com/articles/suppl/m555p049_supp.pdf). The first abundance peak was composed of more or less equal proportions of the 2 relatively large size groups (G_1: mean ± SD TL: 23.4 ± 1.8 mm; G_2: 34.2 ± 1.4 mm), with G_1 dominating ~80% of the second abundance peak (Fig. 4h). The relative abundance of G_2 increased from January to >80% in April and May, while the smallest size group (G_0: 14.7 ± 1.2 mm) remained less prominent (<10%) throughout the investigation.

Seasonal variability in vertical distribution of the dominant zooplankton

Herbivores

Between August and November, the mean abundance of *C. finmarchicus* (CV) and *C. glacialis* (CV and adult females) in the lower 80 m of the water column gradually increased (Fig. 5a,b). Conversely, the mean abundance of these 2 species in the upper 100 m decreased from August, and reached a mini-

mum in October, during which their vertical distribution indices were at the lowest ($V \sim -0.9$; Fig. 6a,b). From November onwards, *C. finmarchicus* and *C. glacialis* CVs had relocated to the upper 100 m along with adult copepodites. By February, the vertical distribution indices of these 2 species reached the maximum ($V \sim 0.6$ for *C. finmarchicus* and $V \sim 0.8$ for *C. glacialis*). Thereafter, the mean abundance of CV and adult copepodites of the above species in the upper 100 m decreased, and by the end of the investigation in May, their vertical distribution indices remained around zero. The mean abundance of CIV *C. hyperboreus* in the lower 80 m progressively decreased from August, and was only distributed in the upper 100 m between November and January (Figs. 5c & 6c). From February onwards, a few *C. hyperboreus* CIV, CV and adult female copepodites (mean abundance <1 ind. m^{-3} mo^{-1}) were relocated in the lower 80 m.

Carnivores

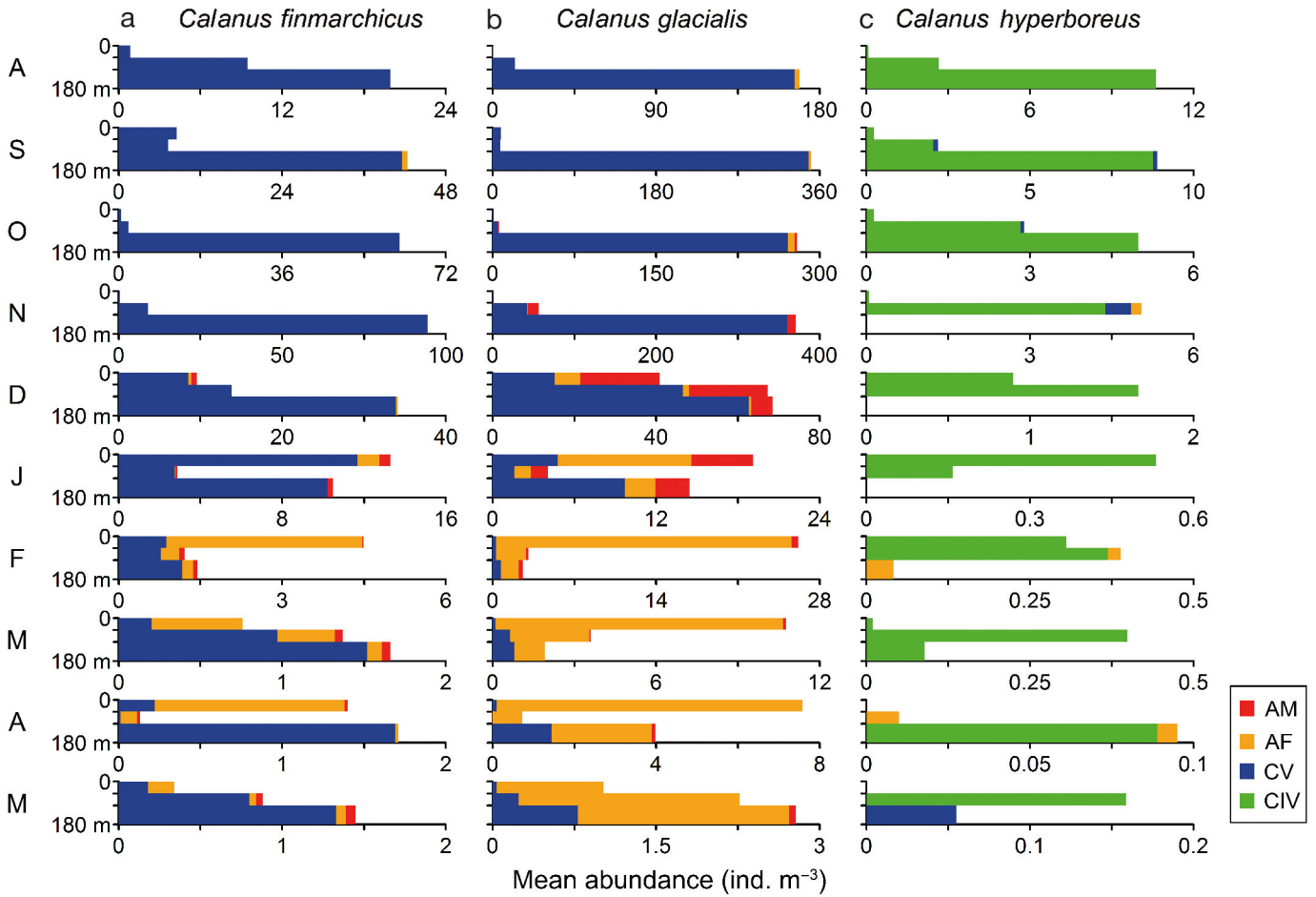The mean abundance of *A. digitale*, *M. ovum*, and *B. cucumis* in the upper 100 m gradually

Fig. 5. Seasonal vertical distributions of dominant herbivores during the study. Ordinates represent depth (0–50, 50–100, and 100–180 m). AM: adult males, AF: adult females; CV and CIV: copepodite stage 5 and 4, respectively
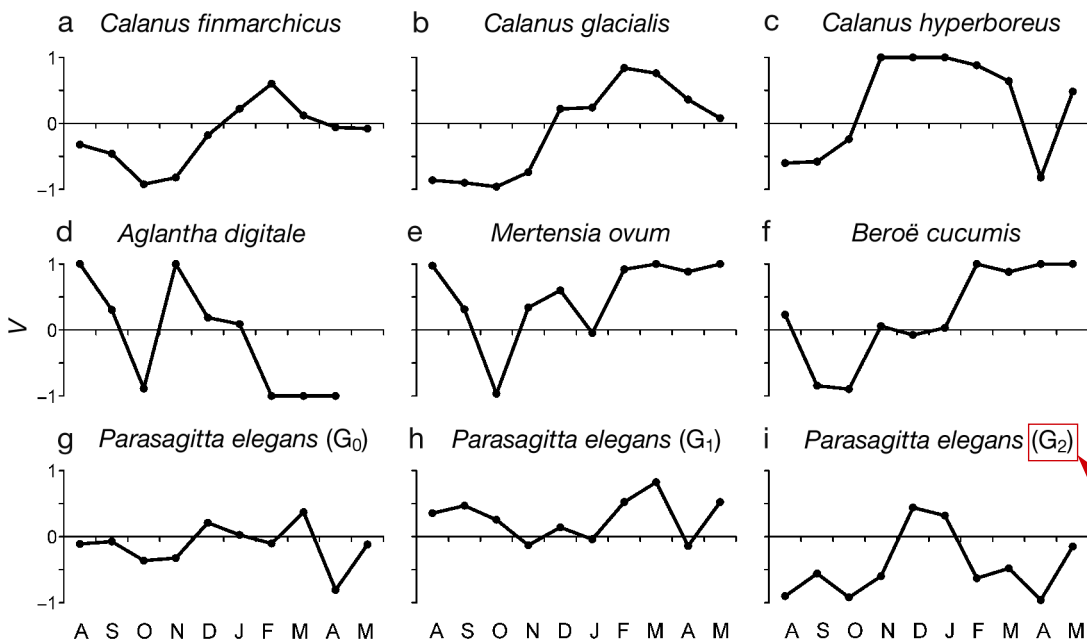

Fig. 6. Seasonal variability in the vertical distribution indices (*V*) of the dominant zooplankton taxa during the study. *V* ranges from −1 to 1, in which the former represents the entire population distributed in the deeper region, and the latter represents the opposite scenario. *A. digitale* was not captured to compute its *V* in May. See Supplement 5 for more information
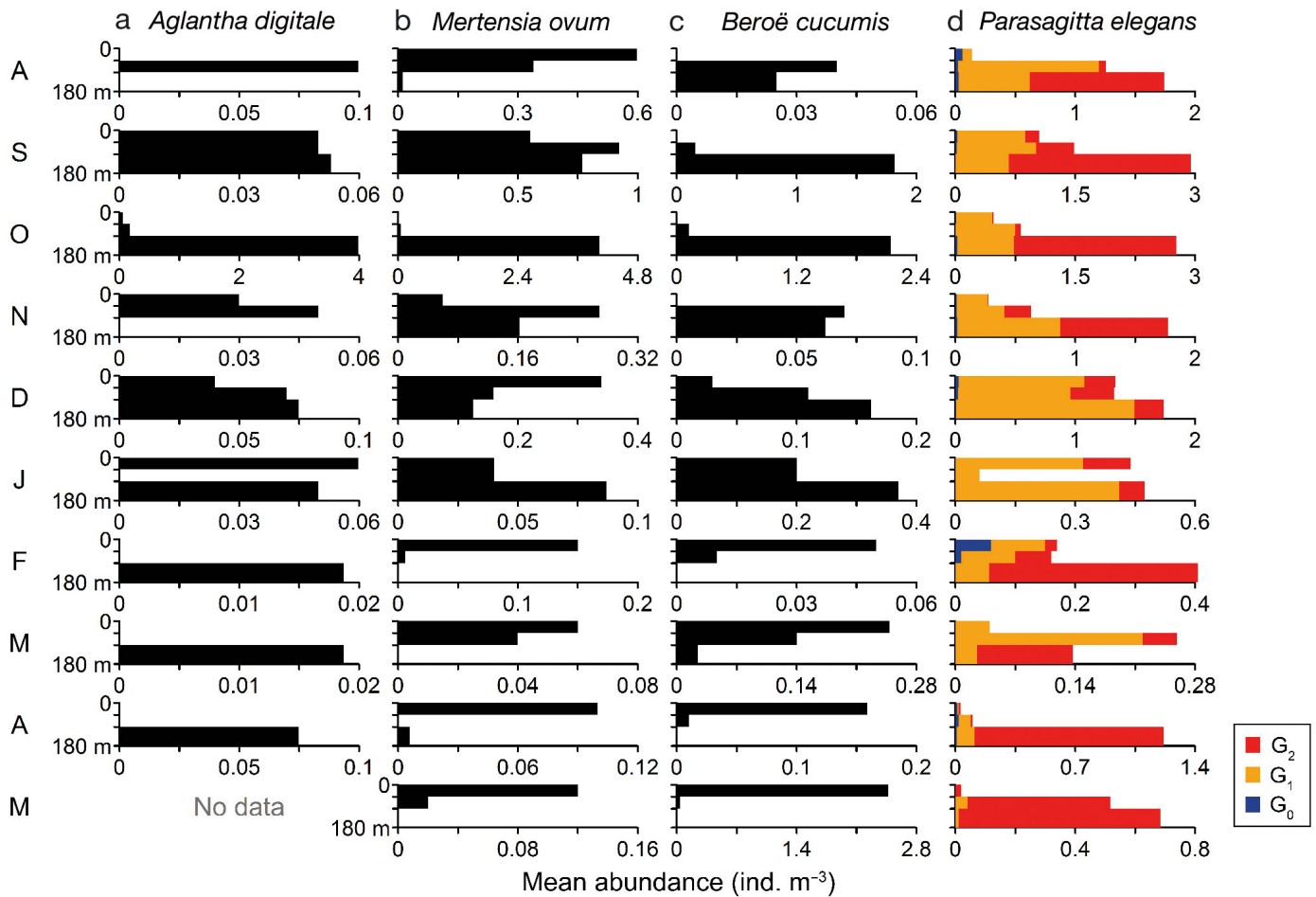
Corrected after publication

Fig. 7. Seasonal vertical distributions of dominant carnivores during the study. Ordinates represent depth (0−50, 50−100, and 100−180 m). Note that *Aglantha digitale* was not captured in May 2009

decreased from August (Fig. 7a−c), and their vertical distribution indices gradually decreased to ~−0.9 in October (Fig. 6d−f). From November onwards, the mean abundance of *M. ovum* and *B. cucumis* in the upper 100 m, and their vertical distribution indices gradually increased, and the latter remained ~1 from February until the end of sampling in May (Fig. 6e, f). Although *A. digitale* had relocated to the upper 100 m between November and January, it was captured in the lower 80 m after February (Fig. 7a). Throughout this study, *P. elegans* was captured in all 3 depth strata (Fig. 7d). The vertical distribution index of the G_2 size group of *P. elegans* remained <−0.5 for most of the time series (Fig. 6i), indicating that >75 % of its population was distributed in the lower 80 m throughout the study. Conversely, the G_0 and G_1 size groups were distributed across the entire depth range (Fig. 6g,h).

Seasonal vertical distributions and environmental variables

The vertical distribution index (*V*) of *Calanus* spp. (all species and developmental stages combined; see Table S5 in Supplement 5 at www.int-res.com/ articles/suppl/m555p049_supp.pdf) showed a strong negative association with mean fluorescence (τ_b = −0.72, p < 0.01, n = 10), and a weak negative association with mean temperature (τ_b = −0.49, p = 0.05, n = 10) (Table 4, Fig. 8a). While the vertical distribution index of *M. ovum* showed a moderate positive association with that of *Calanus* spp. (τ_b = 0.51, p = 0.04, n = 10), we found a strong positive association between the vertical distribution indices of *B. cucumis* and *M. ovum* (τ_b = 0.71, p < 0.01, n = 10) (Table 4, Fig. 8b,c). The vertical distribution index of *A. digitale* showed a moderate negative association with mean temperature (τ_b = −0.57, p = 0.04, n = 9). Vertical distribution indices of *P. elegans* were not significantly associ-
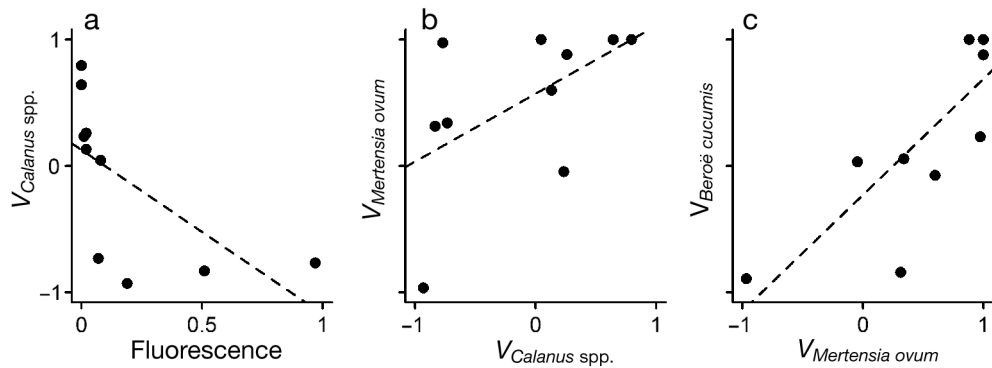
Fig. 8. Representation of statistically significant relationships between the vertical distribution indices (V) of dominant taxa and the availability of their main food source (cf. Table 4). Trend lines (dashed) were estimated by linear regression, and are solely for visualization of patterns in the data

Table 4. Associations between the vertical distribution indices (V) of dominant taxa and environmental variables presented as Kendall's rank correlation coefficients (τ_b). See Fig. 8 for additional information. PAR: photosynthetically active radiation; G_0, G_1, G_2: size groups based on length–frequency analysis; *p < 0.05; **p < 0.01

Species	Temperature	Salinity	PAR	Availability of the main food source			n
				Fluorescence	$V_{Calanus\ spp.}$	$V_{M.\ ovum}$	
Calanus spp.	−0.49*	0.31	−0.30	−0.72**	–	–	10
Aglantha digitale	−0.57*	−0.21	0.06	–	−0.53	–	9
Mertensia ovum	−0.30	0.12	0.14	–	0.51*	–	10
Beroë cucumis	−0.44	0.21	0.05	–	–	0.71**	10
Parasagitta elegans (G_0)	−0.13	0.09	−0.26	–	0.24	–	10
P. elegans (G_1)	−0.02	−0.11	0.14	–	0.04	–	10
P. elegans (G_2)	−0.13	0.27	−0.44	–	0.16	–	10

ated with any physical or biological environmental parameters that were used in our analyses (Table 4).

DISCUSSION

Seasonal patterns in vertical distributions and their relation to environmental variability

A gradual decrease in the vertical distribution index from August to October, and an increase from November to May were common to most of the investigated herbivorous (*Calanus* spp.) and carnivorous (*Aglantha digitale*, *Mertensia ovum* and *Beroë cucumis*) zooplankton taxa (Fig. 6a–f). Descent to the deeper region (>100 m) of the water column in early autumn, and ascent to the shallower region (<100 m) from late autumn to early spring was hence the overall seasonal pattern in this high Arctic zooplankton community. During their descent in the autumn, large numbers of zooplankton appeared to migrate from the warmer, sunlit, and productive shallow waters of this fjord (Fig. 2). Zooplankton abundances sharply declined during the winter (Figs. 3 & 4), and during the spring, most of the remaining individuals had ascended to a colder, darker, and unproductive

water mass. As an exception, *Parasagitta elegans* did not show seasonal migrations (Fig. 6g–i).

Seasonal vertical distributions of most zooplankton taxa showed statistical associations with the availability of their main food source (Table 4, Fig. 8). The inverse association between the vertical distribution index of *Calanus* spp. and mean fluorescence indicates that they descended from the shallower region while it was relatively productive, and ascended before the primary production had started to increase (Figs. 2b & 6a–c). Therefore, it seems that the seasonal vertical strategies of the dominant herbivorous zooplankton in this study were not regulated by food (phytoplankton) availability. As vertical distribution indices of the secondary consumer *M. ovum* and *Calanus* spp., and the tertiary consumer *B. cucumis* and *M. ovum* were positively associated, we argue that these predatory zooplankton seasonally followed their prey (e.g. Fraser & David 1959, Torres et al. 1994, Hagen 1999). The seasonal vertical strategies of the above carnivores were likely regulated by seasonality in food availability (i.e. seasonal vertical strategies of their main prey), and further indicates that seasonal vertical strategies of zooplankton in lower trophic levels influence those in higher levels through trophic interactions. Still, we observed con-

siderable variability, and a lack of seasonal migrations in *P. elegans*. Consequently, numerous other factors, such as the timing and trade-offs between feeding and other life cycle events (Heath 1999, Varpe 2012), differences in prey selection (Greene 1986), feeding on alternative food sources (Hirche & Kwasniewski 1997, Søreide et al. 2006, Casanova et al. 2012), and predation risk (Kaartvedt 1996, Dale et al. 1999, Varpe & Fiksen 2010) may also have contributed to the regulation of the observed seasonal vertical strategies.

Seasonal vertical strategies of the dominant zooplankton

Herbivores

The CVs of *Calanus finmarchicus*, CVs and adult females of *C. glacialis*, and CIVs of *C. hyperboreus* likely resided in the deeper region until November (e.g. Conover 1988, Falk-Petersen et al. 2009, our Fig. 5). The gradually decreasing vertical distribution indices of *C. finmarchicus* and *C. glacialis* until October (Fig. 6a,b), and simultaneous increase in their mean abundances in the deeper region (Fig. 5a,b) indicate that a considerable fraction of the CVs of these 2 species descended and recruited to their deep water populations in the autumn. Conversely, the vertical distribution data of *C. hyperboreus* indicate neither a descent (which may have occurred prior to the commencement of sampling), nor recruitment to its deep water population (Figs. 5c & 6c). In order to build up energy reserves, a fraction of the *C. finmarchicus* and *C. glacialis* CVs may have grazed in the shallower region relatively late into the productive season prior to their descent (Fig. 2b). These CVs may have been the *Calanus* spp. reported by Berge et al. (2014) that contributed to the acoustic backscattering detected near a chlorophyll maximum in this fjord in late September. Østvedt (1955), Pedersen et al. (1995) and Hirche (1996) also oberved a part of the summer–autumn *C. finmarchicus* population feeding in surface waters, while the rest resided in deep waters.

The gradually increasing vertical distribution indices indicate an ascent of *Calanus* spp. between November and February (Fig. 6a–c). By February, a maximum of ~80% of the *Calanus* community had ascended to the shallower region (Fig. 5). Similar to our findings, Daase et al. (2014) and Blachowiak-Samolyk et al. (2015) reported shallow vertical distributions (<100 m) of *Calanus* spp. in January from

~81° N in Rijpfjorden, Svalbard. However, the timing of the ascent we report here is earlier than the March to June period reported in most high-latitude investigations (e.g. Heath 1999, Gislason & Astthorsson 2000, Hirche & Kosobokova 2011, Melle et al. 2014).

As the vertical strategy of *Calanus* spp. was inversely related to fluorescence, it is unlikely that food availability served as a primary cue for their descent and ascent. However, a definitive conclusion on this matter cannot be made since vertical fluorescence profiles were not used in our study. We suggest that these herbivores, dominated by *C. glacialis*, ascended early as a part of a capital breeding strategy or to feed on ice algae, which were not detected by our fluorescence measurements (e.g. Varpe et al. 2009, Søreide et al. 2010). *Calanus* spp. use ice algae as an alternative food source to spawn prior to the phytoplankton bloom (Runge & Ingram 1991, Hirche & Kwasniewski 1997, Søreide et al. 2010). A summer–autumn descent while there is still food available near the surface, and ascent to shallow waters during the dark, unproductive winter (Fig. 2a,b) suggest a migration driven by processes other than the availability of food. The negative association between the *Calanus* vertical distribution index and mean temperature (Table 4) reflects the tendency of the seasonal descent and subsequent induction of diapause in *C. glacialis* to occur in relation to the summer–autumn warming of the surface waters (Niehoff & Hirche 2005, Pertsova & Kosobokova 2010). The overwintering depth and timing of the seasonal migration of *Calanus* spp. can also be influenced by planktivorous fish (Kaartvedt 1996, Dale et al. 1999, Kaartvedt 2000, Varpe & Fiksen 2010). Although we did not sample fish populations in this investigation, trawl samples collected in Billefjorden in August 2008 showed that ~60% of the stomach contents of polar cod *Boreogadus saida* consisted of *Calanus* spp. (Renaud et al. 2012). Therefore, the potential influence of visual predation on the seasonal vertical strategies of *Calanus* spp. in this fjord should not be ruled out.

Carnivores

Vertical distribution data of *A. digitale*, *M. ovum*, and *B. cucumis* indicate that these carnivores descended to the deeper region between August and October (Fig. 6d–f). From November onwards, *M. ovum* and *B. cucumis* gradually ascended and remained in the shallower region from February to the end of this investigation in May. Unlike the 2 cteno-

phore species, the ascent of *A. digitale* is not clearly evident (Fig. 6d). It should be noted that the vertical distribution data of this species after November may not be accurate due to its low numerical abundance (Fig. 4a). Descent to deeper waters in autumn, and ascent to shallower waters between spring and summer has been reported for *A. digitale*, *M. ovum*, and *B. cucumis* from ~59° N in the Northeast Atlantic (Williams & Conway 1981), ~62.5° N in Frobisher Bay (Percy 1989), ~67° N in White Sea (Pertsova et al. 2006), and ~74° N in Resolute Passage (Siferd & Conover 1992). In addition, shallow spring–summer vertical distributions of *M. ovum* and *B. cucumis* have been reported from ~55.5° N in the Bornholm basin of the Baltic Sea (Lehtiniemi et al. 2013), between 68 and 80° N in the Barents Sea and Fram Strait, (Swanberg & Båmstedt 1991a), and between 72 and 75° N in the western Arctic Ocean (Purcell et al. 2010).

Based on the positive association between the vertical distribution indices (Table 4, Fig. 8b), we argue that *M. ovum* seasonally followed *Calanus* spp. *M. ovum* is a secondary consumer that feeds on *Calanus* spp., and specifically on their older developmental stages (Greene 1986, Purcell 1991, Swanberg & Båmstedt 1991b). In the winter, *M. ovum* feeds on overwintering *Calanus* populations (Larson & Harbison 1989, Siferd & Conover 1992) and accumulates lipids (Percy 1989, Lundberg et al. 2006). Therefore, the older developmental stages (CIV, CV, and adult copepodites) of *Calanus* spp. sampled in this study may have served as a main prey source for *M. ovum*, and this predator–prey relationship is reflected by their similar vertical strategies. However, it should be noted that younger developmental stages of *Calanus* spp. which occupy shallower waters between March and May in this fjord (e.g. Arnkværn et al. 2005, Bailey 2010) may also have been a potential source of prey for *M. ovum*. Although *A. digitale* is a secondary consumer that primarily feed on copepods (see references in Table 2), its vertical distribution was not significantly associated with that of *Calanus* spp. (Table 4). Despite the similarities in the vertical strategies of *A. digitale* and *M. ovum* until October (Fig. 6d,e), the low numerical abundances of the former may have inaccurately represented its vertical distribution thereafter, and probably affected the results of the correlation analyses.

The positively associated vertical distribution indices suggest that the predatory ctenophore *B. cucumis* seasonally followed *M. ovum* (Table 4, Fig. 8c). *B. cucumis* is a tertiary consumer that specifically feeds on *M. ovum* (see references in Table 2). Therefore, it

is likely that the strong predator–prey relationship between these 2 ctenophores were reflected in their markedly similar vertical strategies (Fig. 6e,f). Similar spatial associations between these 2 species have been reported from ~74° N in Resolute Passage (Siferd & Conover 1992), and between 75 and 79° N in the Barents Sea (Swanberg & Båmstedt 1991a, Søreide et al. 2003). Although the mean TL of *M. ovum* became substantially larger than that of *B. cucumis* after November (Fig. 4f,g), it may not have affected their predator–prey relationship as *Beroë* can feed on prey larger than itself (Tamm & Tamm 1991), or on body parts of the prey (Swanberg 1974).

The accuracy of interpreting statistical associations between predator and prey zooplankton, as their trophic relationships can be hampered by the coarse vertical resolution of our samples (e.g. Pearre 1979). It is possible for predator and prey zooplankton to coexist in a depth stratum of 50 m (the vertical sampling resolution of this study) without encountering each other. As this bias tends to be pronounced in periods with low predator and/or prey abundances (e.g. Greene 1986), we did not interpret the vertical strategies of *A. digitale* (after November), or the G_0 size group of *P. elegans* in detail (Fig. 4a,d,h). Therefore, further analyses (e.g. gut content analyses and dietary lipid analyses) would be required in order to verify whether the associations between the vertical strategies of predators and prey zooplankton observed in this study truly reflect their trophic interactions.

The 3 size groups of *P. elegans* did not show pronounced seasonal migrations (Fig. 6g–i) irrespective of the seasonal oscillations of the environmental parameters observed in this study (Table 4). However, the largest size group (G_2) occupied the deeper region for most of the study, while the smaller G_0 and G_1 size groups were distributed throughout the water column. Deep water residence of larger individuals of *P. elegans* has been documented from 50° N at 'Ocean Station P' (Sullivan 1980, Terazaki & Miller 1986), ~75° N in Baffin Bay (Samemoto 1987), and ~78° N from our study location in Billefjorden (Grigor et al. 2014). The vertical strategy of the smallest size group (G_0) may not be accurate because our samples did not capture sufficient numbers of those sizes Grigor et al. (2014) reported from this fjord (sampled by nets with finer mesh size and documented as cohort–0 of their study: cf. length data in Table S4 in Supplement 4).

As larger chaetognaths prefer larger prey, such as the older development stages of *Calanus* (Greene 1986, Falkenhaug 1991, Saito & Kiørboe 2001), it is

likely that the G_2 size group of *P. elegans* fed on *Calanus* copepodites occupying the deeper regions of the water column. Despite the ascent of *Calanus* spp. between November and February, a fraction of the *C. finmarchicus* and *C. glacialis* population was observed in the deeper region throughout this study (Fig. 5a,b), and may have served as a year-round prey source for the largest *P. elegans* size group. In support of this view, gut content and lipid analyses of *P. elegans* collected from Billefjorden and other ad-jacent fjords by Grigor et al. (2015) suggests that *P. elegans* primarily feed on *Calanus* spp. It remains unclear why the relatively small size fraction of *P. elegans* population remained in the shallower region throughout this investigation (Fig. 7d). One possibil-ity is that they may have preyed on smaller develop-mental stages of *Calanus* spp. and smaller copepod species, such as *Oithona similis*, *Microcalanus* spp., *Pseudocalanus* spp., and *Metridia longa* (Falkenhaug 1991, Walkusz et al. 2003, Grigor et al. 2015), prey categories which were undersampled by the large mesh width of the WP-3 net used in our investigation.

CONCLUSIONS

This study is one of few that have investigated sea-sonal vertical distributions of multiple members of a zooplankton community in the Arctic over a near-annual, high-resolution time series. Our findings suggest that seasonal vertical migrations are a wide-spread trait in the community, and that seasonality in food availability relates to seasonal vertical strategies of zooplankton in different trophic levels. This rela-tionship was positive and strongest for the associa-tions between herbivores and secondary consumers, and between secondary consumers and tertiary con-sumers. Further year-round field investigations that can combine high-resolution sampling methods with high spatial resolution (e.g. Norrbin et al. 2009), information on individual variability in size and energy reserves (e.g. Vogedes et al. 2010), accurate species determination (e.g. Parent et al. 2011, Gabrielsen et al. 2012), and year-round, mooring-based monitoring of the environment would be nec-essary to test the generality of our findings.

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