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Copepod herbivory rate in a large arctic polynya and its relationship to seasonal and spatial variation in copepod and phytoplankton biomass

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ABSTRACT: Large copepod species (*Calanus* spp.) overwinter in the North Water Polynya (NOW; ~75 to 79° N, ~68 to 78° W) and, via upward migration, can potentially exert a rapid and important grazing impact on the spring phytoplankton bloom. This study investigated the pattern and factors controlling copepod herbivory in the NOW from April through July 1998. Typically, there was a chlorophyll maximum between 50 m and the surface. We used incubation experiments to measure weight-specific herbivory rates (0 to 0.24 µg C µg C^{-1} d^{-1}) representing the average for surface-layer copepod assemblages at each station, and we quantified 0 to 50 m *in situ* copepod biomass (20 to 3200 mg C m^{-2}). Weight-specific herbivory rate was positively related to initial chlorophyll *a* concentration in experiments (r^2 = 0.54). Maximum *in situ* copepod herbivory rate and *in situ* copepod biomass were larger and peaked earlier at stations dominated by Baffin Bay water in the southern and eastern NOW versus stations dominated by silica-rich arctic water in the northern and western NOW. We used a standard scaling model ($I = aW^b$), where I = maximum daily ingestion rate and W = individual weight, to test the potential effect of size bias on our estimates of total *in situ* copepod herbivory, because the size structures of experimental and *in situ* copepod assemblages were often statistically different. Although these calculations found up to ±40% difference in our estimate of total *in situ* copepod herbivory, this had very little effect on the estimates of copepod impact on daily primary production (±1% PP), because copepod biomass was usually low relative to NOW phytoplankton biomass and productivity. During pre-bloom and spring-bloom conditions, total *in situ* copepod herbivory was low (<10% of PP). After the spring diatom bloom, we measured higher removal rates (~15 and 55% of PP) at 2 southern stations, where copepod biomass was high and PP was relatively low.

KEY WORDS: Arctic · Polynya · Copepod · Herbivory · Size structure · Plankton food web · Seasonal variation · Spatial variation

INTRODUCTION

The North Water Polynya (NOW; ~75 to 79° N, ~68 to 78° W) is one of the largest of arctic polynyas and is a productive region with abundant bird and mammal populations (Stirling 1997). The NOW is dynamic and the seasonal extent of its open water (max. ~90 000 km^2) is bounded by Canada, Greenland, and regions of thick pack ice (>2 m). The extensive ice-free periods of polynyas are associated with increased annual primary productivity (Rysgaard et al. 1999). Dominant zooplankton (e.g. pelagic tunicates, copepods) determine the amount of primary production transfered to vertebrate planktivores, contribute to seasonal shifts in plankton food-web structure, and may alter carbon export to the benthos. This study was part of a project investigating zooplankton links between the physical processes that form and maintain the polynya and planktonic food-web processes in the NOW. Specifically, this study quantified seasonal and

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water-mass-associated variation in total *in situ* copepod herbivory rate.

In arctic waters, *Calanus* spp. often dominate copepod biomass, and their large (~3 to 7 mm), late-copepodite stages overwinter at intermediate depths (e.g. Dale et al. 1999). A previous study of NOW copepods confirmed the overwintering habit of *Calanus* spp. populations (Tidmarsh 1973). Variability in total grazing flux is most commonly identified where there are large temporal or spatial differences in predator biomass or size structure (e.g. Hirche et al. 1991, 1994, Bautista et al. 1992). Consequently, arctic copepod populations have the potential for a rapid trophic response to spring diatom production via upward migration and may be relatively efficient consumers of large-celled spring phytoplankton (Krause & Trahms 1983, Eilertsen et al. 1989, Bathmann et al. 1990). In contrast, copepods increase to a seasonal maximum sometime after the spring diatom bloom, where cold seas are dominated by smaller coastal species (Nielsen & Richardson 1989, Gowen et al. 1999).

Our primary objective was to describe the seasonal and spatial pattern of herbivory by surface-layer copepod assemblages, estimated from (1) chlorophyll *a* removal rates quantified in shipboard incubation experiments and (2) measurements of *in situ* copepod biomass. We hypothesized that weight-specific herbivory rates of copepods would correspond primarily to food availability, as temperature varies relatively little in polar regions (cf. Huntley & Lopez 1992, Hansen et al. 1997). We also expected total *in situ* herbivory rates to vary seasonally and spatially with composition and biomass of the copepod assemblage. Our secondary objective was to test the effect of copepod size versus specific-rate relationships on our estimates of total *in situ* copepod herbivory rate. We used model-sensitivity analysis to quantify potential estimation error due to size structure differences between experimental and *in situ* copepod assemblages. We discuss the grazing impact of copepods on the NOW spring diatom bloom, evaluate the relationship of herbivory rates and the dominant surface-water masses, and summarize our inferences from these results with regard to carbon export to higher trophic levels and the benthos.

MATERIALS AND METHODS

***In situ* characteristics of surface layer.** We organized experiments by dominant surface-water masses. Tremblay et al. (2002) used silicate–salinity relationships in the upper 50 m to distinguish silica-rich arctic water (SRAW) and Baffin Bay water (BBW); transitional water (MIX) occurred where there was mixing of SRAW and BBW. For each experimental station, we calculated mean water-column temperature from 0 to 50 m profile data (values interpolated at 1 m intervals). We estimated phytoplankton biomass (mg C m^{-2}; 0 to 50 m water column) by integration of chlorophyll *a* profiles generated by Klein et al. (2002), who used a modification of the method of Knap et al. (1996), and a carbon:chlorophyll *a* ratio of 50 (consistent with NOW field data, April to June 1998; Z. P. Mei pers. comm.)

Zooplankton samples were collected by vertical tows of a 6 m long, Nitex-mesh plankton net (200 µm mesh, 1 m^2, square-mouth; or 300 µm mesh, 0.785 m^2, 1 m diameter). Net tows represented surface or middle strata, whose depth varied according to the local fluorescence profile (see third subsection of 'Results'). We retrieved nets at 0.3 to 0.5 m s^{-1}. Samples for quantification of *in situ* copepod assemblages were rinsed into the codend, concentrated, and preserved in 4% formalin. We used a Motoda box splitter or Hensen-Stemple pipette to make fractions of the original sample, and we enumerated copepods by species and stage. *In situ* abundance was calculated using tow-volume estimates determined from net dimensions, flow-meter values, and tow depths. We also categorized each species/stage group as 'large' or 'small,' using data from 6 experiments, for which we divided the copepod treatment using a coarse sieve (see following subsection).

We subsampled 'live' tows (see following subsection) for copepod CHN analysis; the copepods were incubated in filtered seawater for up to 24 h, filtered at <5000 Pa, and stored at −80°C. Using several samples from April and July, we sorted individuals from dominant species/stage groups, measured carapace length, and quantified carbon with a Perkin Elmer 2400 elemental analyzer. We used the following model (Model 1 regression: SAS Institute 1990) to estimate each individual's biomass (C = µg C $ind.^{-1}$, length = mm, $r^2 = 0.76$, n = 63; 11 species/stage groups, 1.9 to 7.2 mm):

$$\ln C = 1.19\,(\pm 0.68) + 4.99\,(\pm 1.04) \times [\ln(\text{length})] - 1.07\,(\pm 0.38) \times [(\ln[\text{length}])^2] \quad (1)$$

Herbivory rates. To determine weight-specific herbivory rates for copepod assemblages, we did shipboard incubation experiments using water and copepods from 6 to 14 stations each month (April, May, June and July 1998). Experiments represented stations extending along the eastern and western edges of the polynya, and additional central stations in the broader southern region of the polynya (see Fig. 1). All experiments were done at stations that were a sub-set of the 84-station NOW sampling grid (Bâcle et al. 2002).

We collected water for incubations from 1 or 2 discrete depths using a rosette fitted with 10 l Brookes Ocean Technology bottles, a Falmouth Scientific Instruments ICTD profiler (integrated conductivity, temperature, and depth), and a Seatech fluorometer. We chose

prey-water sampling depth(s) using the *in situ*, relative-fluorescence profile. One depth represented the chlorophyll maximum, if detectable (Table 1). At 14 stations, we sampled a second depth to represent conditions below the high-chlorophyll layer (results of these 14 experiments are summarized in 'Results', but the data are not included in the tables). Each 10 l sample was transferred gently via silicone tubing into a polyethylene cubitainer, and transported to a dark, ~0°C container laboratory. 'Live' net tows were collected in replicate with the quantitative samples, except in April (see Tables 1 & 2). 'Live' nets were not rinsed; codend contents were immediately and gently diluted in 20 l of surface water. Copepods were transferred into 20 l of rosette-collected incubation water using a 300 µm-mesh sieve cup. We allowed copepods to acclimate for 2 to 24 h in the cold laboratory.

With minimum light, we set up experiments with 2 control (no copepods added) and 3 treatment (copepods added) bottles per prey-water depth. Water was mixed by inversion, then distributed by silicone tubing to 4 l polycarbonate bottles and 5 sets of corresponding time-zero (t_0) samples. Control bottles were filled, sealed with parafilm, and capped. Treatment bottles were filled to within 100 to 200 ml of the top before we added copepods (usually 4 to 10 individuals l^{-1}) and finished as for controls. We harvested copepods with a 300 µm-mesh sieve and a wide-bore pipette, in which we inspected them and did preliminary counts against a low-intensity back-light; 6 experiments measured rates for 'large' and 'small' fractions of the copepod assemblage, defined by a second sieve (nylon window screen, 1300 × 1050 µm-mesh).

The bottles were rotated continuously on a plankton wheel at ~1.5 rpm for 24 or 48 h in the dark. Our goal was 20 to 80% removal of chlorophyll *a* during each incubation. Time-final (t_f) water samples were collected by gravity, with 300 µm Nitex mesh attached to the inflow of the silicone siphon in order to retain treatment copepods for quantification. The copepods were rinsed onto a

Table 1. Specifications of copepod grazing experiments in North Water Polynya (April to July 1998). Dominant water-mass abbreviations defined as in Tremblay et al. (2002): SRAW: silica-rich arctic water; BBW: Baffin Bay water; Mix: transitional water (mixing of SRAW and BBW); SRAW + MIX: combined data for SRAW and MIX stations; BBW_{cold}: Baffin Bay water, <1°C; Prey depth: prey water depth (m); t_0[chl*a*]: average and CV initial chlorophyll *a* concentration (µg chl *a* l^{-1}); Net tow depth: net tow depth (range in m) for experimental copepods; Cop. biomass: average and CV copepod biomass during experiments (mg C l^{-1}); L, S: large-copepod and small-copepod fractions, respectively

Water mass Stn	Date (1998)	Prey depth	t_0[chl*a*] avg.	CV	Net tow depth	Cop. biomass avg.	CV
SRAW + MIX							
2	14 Apr	75	0.031	23	600–150	24 (L)	17
						21 (S)	27
22	17 Apr	50	0.046	19	400–0	5.1 (L)	7
						3.7 (S)	1
44	21 Apr	50	0.049	27	385–0	3.7 (L)	11
						3.0 (S)	12
BBW							
49	23 Apr	26	0.11	6	460–0	3.5 (L)	38
						5.9 (S)	20
27	27 Apr	35	0.39	7	75–0	4.8	36
40	02 May	20	1.4	32	50–0	0.75	18
SRAW + MIX							
2	09 May	20	0.53	5	50–0	1.2	45
27	17 May	40	0.58	6	150–0	3.0 (L)	2
						0.81(S)	20
22	18 May	100	0.12	18	150–0	0.26	85
44	28 May	30	4.4	2	75–0	0.47	43
31	29 May	20	2.6	9	50–0	0.65	62
BBW							
40	25 May	25	3.2	18	50–0	1.6	23
54	26 May	15	14	12	50–0	5.2	7
SRAW + MIX							
2	07 Jun	37	0.31	15	50–0	2.1 (L)	18
						0.06 (S)	48
14	10 Jun	15	7.6	8	55–0	0.30	32
27	12 Jun	15	7.8	3	30–0	0.11	26
22	14 Jun	15	2.9	7	50–0	0.16	64
31	15 Jun	15	4.6	38	50–0	0.24	27
60	25 Jun	4	3.5	8	25–0	0.86	8
BBW							
54	05 Jun	11	4.2	9	50–0	3.5	19
49	05 Jun	20	10	10	50–0	1.9	40
40	19 Jun	15	10	6	20–0	0.73	16
54	22 Jun	35	1.9	7	75–0	2.0	34
50	22 Jun	20	7.5	4	75–0	0.44	11
44	24 Jun	21	5.3	14	25–0	1.2	37
BBW_{cold}							
68	26 Jun	41	0.46	5	75–0	1.2	52
82	27 Jun	31	0.49	5	75–0	2.6	6
SRAW + MIX							
2	13 Jul	15	4.2	12	75–0	0.54	30
BBW							
68	01 Jul	50	0.66	6	75–0	2.2	14
50	05 Jul	40	2.9	7	75–0	0.80	39
44	09 Jul	33	1.5	11	60–0	0.62	69
1	16 Jul	11	4.8	8	40–0	0.32	27
40	17 Jul	13	0.99	15	50–0	0.79	1
35	19 Jul	8	2.6	14	100–0	0.58	47
54	21 Jul	20	1.5	24	80–0	0.68	41

300 µm Nitex sieve, collected on a 45 mm GF/C filter under low (<5000 Pa) vacuum, quick-frozen on an aluminum block (ca. –80°C), and stored at –80°C.

Quantification: We collected samples (200 to 510 ml) for analyses of chlorophyll *a* and pheopigments on 25 mm GF/F filters and stored them at –80°C until post-cruise processing. We used 90% acetone to extract pigments overnight at –20°C, and determined fluorescence values using a Turner Designs Model 10 fluorometer.

We processed experimental copepod samples in a stratified (month, location) sequence, to avoid seasonal or spatial bias in fecal pellet observations. We thawed samples in a few milliliters of water and enumerated all copepods to species and stage. We measured carapace length, usually to the nearest 40 µm. In a few cases we stopped measuring abundant groups (n > 40) and applied the sample-average length to counted individuals. We estimated treatment biomass using the same empirical model applied to *in situ* samples (see first subsection).

We noted the presence (n ≥ 10) or absence of fecal pellets in treatment samples and noted pellet color(s). After sorting copepods by carapace length into 0.5 mm bins, we used the Kolmogorov-Smirnov 2-sample test to determine similarity of the copepod size-frequency distribution among treatment replicates (Sokal & Rohlf 1995, p. 434).

Analysis: We assessed treatment effects with a general linear model that compared daily chlorophyll *a* change ($t_f - t_0$) in control versus copepod-addition bottles ($\alpha = 0.1$, due to low power of design). With these data we calculated clearance rate for each bottle (Frost 1972). Chlorophyll *a* was converted to carbon units (C:chl *a* = 50), and clearance rates were normalized by the respective bottle's treatment biomass to calculate weight-specific herbivory rate. We calculated the average rate for each experiment, but only if 2 or 3 replicate treatment bottles showed net removal of chlorophyll *a*; otherwise, we report the weight-specific herbivory rate as zero (see Table 3). We also deleted a single replicate with no net chlorophyll removal from 6 experiments, each with positive removal in the remaining 2 replicates (see Table 3: April: Stns 2S and 22L; June: Stns 31 and 82; July: Stns 2 and 50).

Extrapolation of experimental to* in situ *rate: We estimated total *in situ* copepod herbivory rate (d^{-1}) for the 50-to-0 m water column as the product of *in situ* copepod biomass (m^{-2}) and average weight-specific herbivory rate. For experiments with 'Large' and 'Small' copepod assemblages, we summed separate calculations for each treatment.

We used the Kolmogorov-Smirnov 2-sample test to compare the size distributions of copepods in experimental bottles with corresponding *in situ* samples. Other studies have sometimes reported a relationship between copepod body size and specific ingestion rate (see 'Introduction'); we applied a scaling model to assess potential differences in our estimate of total copepod herbivory due to size structure changes between experiments and *in situ* assemblages. Each size-weighted specific rate depends on (1) the exponential coefficient of the scaling model, (2) the size structure of the experimental copepod assemblage, and (3) the total chlorophyll removal rate. We parameterized a scaling model $I = W^b$, where I = maximum daily ingestion rate (µg C µg C^{-1} d^{-1}), W = individual weight (µg C) and b = constant (µg C^{-1} d^{-1} = 0, –0.1, –0.2, or –0.3) (the empirical model of Hansen et al. 1997 showed b as –0.23) to calculate a weighting coefficient (WC_i) for each size of copepod in a treatment:

$$WC_i = I_i/(I_1 + I_2 + ... + I_n) \quad (2)$$

where i = size of each copepod in the bottle, n = total number of size-groups in the bottle, and I_i = predicted daily herbivory rate for each size group ($I_i = W_i^b$). Next, we used WC_i values to calculate a scaling factor ($SF_{size\text{-}group}$) to represent the proportional ingestion by each size-group:

$$SF_{size\text{-}group} = \frac{(WC_i \times W_i \times \#\text{ ind. size-group}^{-1})}{\sum(WC_i \times W_i \times \#\text{ ind. size-group}^{-1})} \quad (3)$$

Finally, we calculated a size-weighted estimate of specific rate ($SHR_{scaled\ estimate}$) for each size-group in a treatment bottle:

$$SHR_{scaled\ estimate} = \frac{\text{total phytoplankton-carbon removal (mg C l}^{-1}\text{ d}^{-1}) \times SF_{size\text{-}group}}{W_i \times \#\text{ ind. size-group}^{-1}\text{ l}^{-1}} \quad (4)$$

We estimated linear regression parameters (Model I) for each treatment assemblage [$\ln(SHR_{scaled\ estimate}) = Y\text{-int} + \text{slope} \times \ln(W)$]. The slope was constant (b), because it was derived from the original scaling model (0, –0.1, –0.2, or –0.3). The Y-intercept was variable. We used the mean parameter values for each experiment to predict specific rates for 1, 3, and 5 mm 'standard-length' copepods. We calculated size-scaled estimates of total *in situ* copepod herbivory rate using the specific rate for each *in situ* size group and *in situ* size-frequency data.

RESULTS

In situ characteristics of surface layer

SRAW was dominant in May, BBW was dominant in July, and the 2 water masses had a more intermediate influence in April and June (Fig. 1). Comparison of 50 versus 100 m integrations showed that BBW spread as

a shallow layer over depths more influenced by SRAW at southwestern stations (Stns 44 and 50).

Overall, the mean surface-layer temperature of BBW stations (mean ± SD = −0.88 ± 0.63°C) was higher than that of SRAW + MIX stations (−1.45 ± 0.31°C; Student's *t*-test, unequal variance: p = 0.003, df = 17,14) (Fig. 2a,b); monthly differences varied: April, p = 0.14; May, p = 0.02; June, p = 0.04; July, not testable. Earliest warming was at eastern stations (Stns 40 and 27); greatest warming was at central and southwestern stations, all of which were usually BBW stations (~1 to 2°C increase at Stns 35, 40, 44, 49 and 50, in April to July; data not shown). Maximum *in situ* temperature at the depth of prey-water sampling was 1.4°C.

Overall, phytoplankton biomass (Fig. 2c,d) was not significantly different between BBW (mean ± SD = 9439 ± 8446 mg C m^{-2}) and SRAW + MIX stations (5830 ± 6555 mg C m^{-2}). However, the pattern of integrated chlorophyll *a* concentration demonstrates a phytoplankton bloom that developed during May in the southeast, June at central stations, and July in the north. In April, there was low phytoplankton biomass (<1000 mg C m^{-2}), except in the eastern polynya (1000 to 5000 mg C m^{-2}; Stns 40 and 27). In May, southern stations showed high concentrations (5000 to 26 000 mg C m^{-2}; Stns 40, 44 and 54), but all other stations had moderate biomass (1000 to 5000 mg C m^{-2}). In June, most stations showed high phytoplankton concentration, but biomass remained moderate in the northwest (Stn 2) and declined to moderate levels at open-water stations in the south (Stn 44, 54). In July, Stn 2 showed high biomass (7855 mg C m^{-2}), most stations had decreased to moderate values, and southern stations remained similar to June values (Stns 44 and 54).

Once phytoplankton biomass increased in an area of the polynya, copepod biomass was often more concentrated in the surface than the middle water column, including 80% of BBW stations (Table 2). Median biomass ratios for surface versus middle strata were 0.4 (April, n = 5), 1.5 (May, n = 5), 2.0 (June, n = 9), and 2.5 (July, n = 7). BBW stations had higher copepod biomass (0 to 50 m water column; mean ± SD = 1212 ± 905 mg C m^{-2}) than SRAW + MIX stations (261 ± 359 mg C m^{-2}; Fig. 2e,f; Student's *t*-test, unequal variance: p = 0.002, df = 17,13), but monthly differences were not strong: April, p = 0.29; May p = 0.29; June p = 0.09; July not testable. In May (Table 2), surface-layer copepod biomass increased by an order of magnitude in the southeast (>500 to 3200 mg C m^{-2}; Stns 40 and 54). In June, similarly high concentrations of copepod biomass extended to east-central and southern stations (Stns 27, 40, 44, 49, 50, 54a, 54b, 68 and 82) as well as 1 northern station (2). In July, copepod biomass remained high in those regions (Stns 1, 35, 44, 50 and 68), except for a decrease in the southeast (Stns 40 and 54); we have no July data for west-central stations.

Maximum 'large' copepod biomass occurred in May (SRAW + MIX and BBW stations), reflecting general seasonal changes in the composition of surface-layer copepod assemblages (Fig. 3). 'Large' copepods included *Calanus hyperboreus* IV to VI, *C. glacialis* V and VI, *C. finmarchicus* V and VI, and *Metridia* spp. $VI_{females}$; 'small' copepods included *C. hyperboreus* I to III, *C. glacialis* I to IV, *C. finmarchicus* I to IV, and *Metridia* I to VI_{males}. The absolute biomass of later-stage *C. glacialis* and *C. finmarchicus* (IV–VI) was approximately constant (monthly median 1.7 to 3.5 mg C m^{-2}), except that their abundance was lower at some SRAW-dominated stations. However, in May and June we did observe an increase in the absolute and relative biomass of late-stage *C. hyperboreus* (IV–VI; Fig. 4) in the southern polynya (Stns 40, 44, 49 and 54), at ice-covered stations (Stns 68 and 82), and in the northwest (Stn 2); both biomass measures decreased in July. Further, during June and July there was a strong increase in absolute and relative bio-

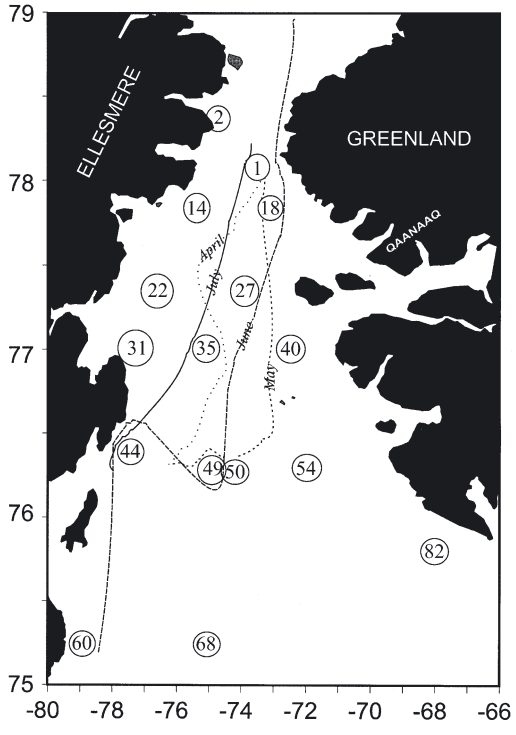

Fig. 1. Sampling stations in North Water Polynya, where we conducted copepod incubation experiments to determine weight-specific herbivory rate. Variable extent of Baffin Bay water (BBW) in upper 50 m is indicated by 4 differently patterned lines drawn through sampling grid. These isolines delimit surface-layer water masses (redrawn from Tremblay et al. 2002). For each month (April to July), stations located east and south of a line were predominantly influenced by BBW, whereas stations west and north of a line were dominated by silica-rich arctic water or a mixture with BBW (see 'Results')

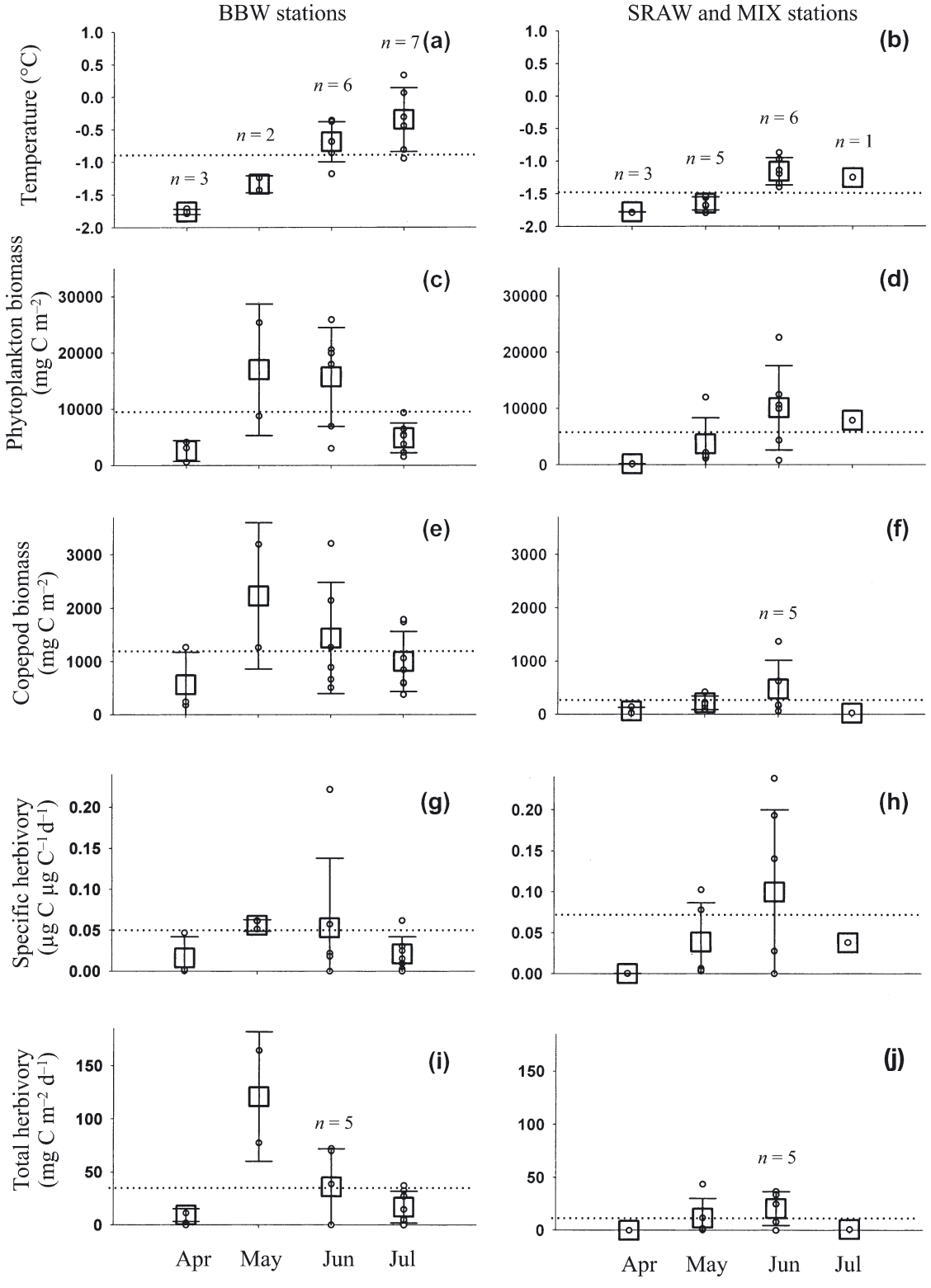

Fig. 2. Summary of 0 to 50 m data for (a), (b) average temperature; (c), (d) phytoplankton biomass; (e), (f) copepod biomass; (g), (h) weight-specific herbivory rate for experimental copepods; and (i), (j) total herbivory rate calculated for *in situ* copepods, 0 to 50 m (BBW_{cold} stations excluded here). (o) individual data-points; large squares and error bars are station averages ± 1 SD. Sample size (n) for each mean is given in (a) and (b) with exceptions indicated. Dotted horizontal lines represent overall mean for each group of stations

mass of early-stage *Calanus* copepodites (I–III; Fig. 4), except in the northwest (Stns 2 and 14) and at ice-covered stations (Stns 68 and 82).

Mean copepod biomass was loosely coupled to mean phytoplankton biomass, with stations grouped by watermass and month (Figs. 2c–f & 5). One exception was that phytoplankton biomass at BBW stations decreased significantly between June and July (mean = 15 687 vs 4850 mg C m^{-2}; Tukey's HSD test: $p < 0.05$), whereas copepod biomass did not (mean = 1445 vs 999 mg C m^{-2}; $p > 0.05$). There were also differences between the 2 water masses. BBW stations showed an earlier peak and larger accumulation of phytoplankton and copepod biomass than did SRAW + MIX stations. BBW stations also had a larger copepod stock per unit phytoplankton (median ratio = 0.15) than did SRAW + MIX stations (0.075: Fig. 5).

Herbivory rates

Weight-specific herbivory rates were <0.01 to 0.24 µg C µg C^{-1} d^{-1} for copepod assemblages incubated with prey from the fluorescence maximum (Table 3). Chlorophyll removal in treatment bottles was statistically significant ($p < 0.1$) in 14 of 35 experiments (40%). Another 14 experiments (40%) suggested net removal of chlorophyll-containing prey cells, but higher replicate variance and/or lower removal rate may have occluded statistical significance in some cases (Table 3). These non-significant experiments included 7 in July with copepod fecal pellets in treatment bottles, an indication of active feeding. However, of those experiments with no net removal of chlorophyll *a* (20%), 4 also had fecal pellets.

There were copepod fecal pellets in 21 of 23 experiments with phytoplankton biomass >50 µg C l^{-1} (= 1 µg chl *a* l^{-1}; Tables 1 & 3). We did not observe fecal pellets in the 12 experiments with phytoplankton biomass <50 µg C l^{-1}. Fecal pellets were abundant in July experiments, when we did not measure any statistically significant chlorophyll re-

Table 2. *In situ* copepod data for stations where copepod herbivory experiments were conducted. *In situ* copepod biomass (mg C m^{-2}) standardized to a 50 to 0 m water column. Cop:Phyto biomass ratio compares *in situ* copepod biomass with 0 to 50 m phytoplankton biomass (copepod carbon/chlorophyll *a* × 50, where 50 = carbon:chl *a* conversion factor). Depth strata: original net-tow depths; Relative biomass: relative biomass of copepods in net tows from surface versus middle depth strata. nd: no data

Water mass Stn	Copepod[a] biomass *in situ*	Cop:Phyto[b] biomass ratio	Depth strata (m) surface	middle	Relative biomass
April, SRAW + MIX					
2	27	0.16	100–0[c]	600–100	0.1
22	143	0.98	150–0[c]	300–150	1.1
44	18	0.14	100–0[c]	200–100	0.3
April, BBW					
49	178	0.32	460–0[c]	nd	nd
27	1268	0.42	100–0[c]	200–100	5.8
40	242	0.06	150–0[c]	300–100	0.4
May, SRAW + MIX					
2	226	0.14	50–0	100–50	9.0
27	195	0.12	150–0	nd	nd
22	87	0.08	150–0	nd	nd
44	423	0.04	75–0	340–75	0.7
31	371	0.07	50–0	nd	nd
May, BBW					
40	1262	0.14	50–0	100–0	1.4
54	3194	0.13	50–0	150–50	2.1
June, SRAW + MIX					
2	1366	1.71	50–0	nd	nd
14	56	0.00	55–0	220–75	0.2
27	622	0.06	30–0	160–30	2.2
22	154	0.02	50–0	180–50	0.3
31	173	0.01	50–0	150–50	0.5
60	–	nd	–	nd	nd
June, BBW					
54a	3207	0.16	50–0	nd	nd
49	661	0.03	50–0	150–50	69.5
40	887	0.05	120–0[c]	nd	nd
54b	2143	0.71	75–0	475–75	2.1
50	508	0.03	70–0	270–75	2.0
44	1265	0.18	25–0	250–25	0.2
June, BBW_{cold}					
68	1113	0.58	80–0	250–80	11.3
82	511	0.34	75–0	nd	nd
July, SRAW + MIX					
2	20	0.00	75–0	425–75	0.1
July, BBW					
68	1739	1.14	75–0	125–75	25.5
50	1789	0.28	75–0	250–75	2.5
44	1062	0.20	60–0	140–60	12.3
1	839	0.09	40–0	nd	nd
40	373	0.10	50–0	175–50	2.0
35	588	0.11	100–0	350–100	0.9
54	602	0.26	80–0	200–80	6.6

[a]Integrated copepod carbon (50 to 0 m, mg m^{-2}) calculated using data of L. Fortier et al., Université Laval, and D. Deibel et al.

[b]Phytoplankton biomass estimated from chlorophyll a data provided by L. Legendre et al., Université Laval (for method see Klein et al. 2002)

[c]Depths of net tow used to quantify *in situ* biomass did not correspond to depths of 'live' tow used for experiments (see text)

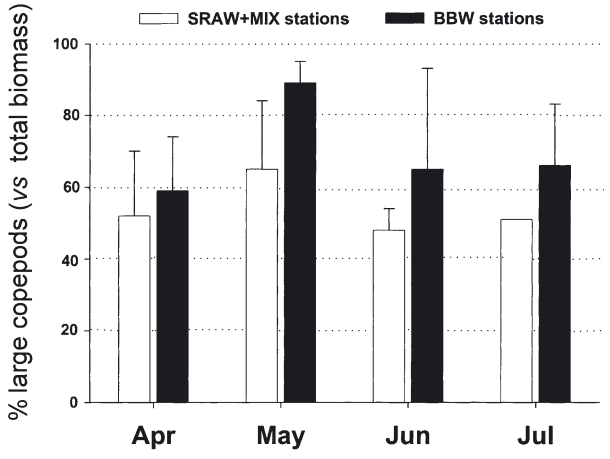

Fig. 3. Copepod biomass. Relative biomass (% total) of 'large' copepods *in situ* (monthly station avg. ± 1 SD); total: biomass of large and small copepods

moval. There was a general monthly change in pellet color from brown-green in May to light or grey-green in June, then grey-green or white in July (Table 3).

We measured no overall difference in weight specific herbivory rates of SRAW + MIX versus BBW copepod assemblages (Table 3, Fig. 2g,h). Highest specific rates were measured in late May and June, when we often observed high chlorophyll *a* concentrations (Table 1). Initial food concentration explained 54% of the variance in weight-specific herbivory rate (Fig. 6: $r^2 = 0.54$, $p = 0.0001$, $n = 30$; rate [d^{-1}] = 0.0044 (±0.011) + 0.020 (±0.0035) × t_0 chl *a*[µg l^{-1}]; we excluded 1 outlier from final regression analysis: Stn 54 in May).

Depths below the chlorophyll maximum were represented at 13 stations where we did a second experiment (data not shown; prey water from 60 to 125 m, median = 95 m). Only 2 of 13 showed statistically significant herbivory by copepods (Stns 27 and 31 in June); these had initial phytoplankton concentrations of 38 and 105 µg C l^{-1}. Fecal pellets were observed in these and in 2 other 'deep' experiments (initial phytoplankton = 60 and 74 µg C l^{-1}).

Copepod size-frequency distributions in experimental replicates were usually statistically equivalent. Because of statistical differences between a few samples, we excluded 1 'deep' experiment (April, Stn 40, 100 m) and 2 bottles (1 each for June [Stn 14, 15 m] and July [Stn 44, 33 m]).

Extrapolation of experimental to *in situ* herbivory rates

Experiments were designed to represent the surface layer, which we define as the upper 50 m of the water column (except where we discuss the original zooplankton net tows). In fact, the average initial concentration of chlorophyll *a* in experiments was a good predictor ($r^2 = 0.76$, $p < 0.0001$) of the *in situ* phytoplankton carbon concentration estimated independently using chlorophyll *a* profiles for the 0 to 50 m water column (Fig. 7). The 0 to 50 m water column usually incorporated the mixed-layer depth (32 of 35 stations: Y. Gratton et al. unpubl. data), and the 1% light depth (30 of 35 stations; Mei et al. 2002).

We collected experimental copepods from surface strata with relatively high fluorescence values (relative fluorescence units, RFU), when present, which we used as a general indicator of elevated food concentration. Net tow depths generally corresponded well with elevated RFU. Net tows often extended below 50 m, especially in May and June, because elevated RFU (and extracted chlorophyll *a* >1 µg l^{-1}) was common below the 1% light depth. Our comparison of size-frequency data for experimental versus *in situ* copepod assemblages showed significant difference in most cases (results not shown). Experimental treatments generally under-represented the smaller copepod groups that were present *in situ*, and we sometimes over-represented intermediate size groups.

If we assume no relationship between copepod size and weight-specific herbivory rate ($b = 0$), estimates of total *in situ* herbivory were 0 to 164 mg C m^{-2} d^{-1} (Method A: Table 4). When we include the maximum size effect tested by our model ($b = -0.3$), which generated reasonable specific rates even for standard 1 mm copepods (Fig. 8), estimates of total *in situ* herbivory were 0 to 176 mg C m^{-2} d^{-1} (Method B: Table 4). The unweighted estimates of total *in situ* copepod herbivory (A) were higher than the size-weighted estimates (B) for 16 stations and lower for 10 stations (max. ± 40%). Median rates were (A) 20 and (B) 17 mg C m^{-2} d^{-1}.

Whether or not a size effect is included in our estimate of total *in situ* herbivory, copepods usually consumed less than ~10% of daily primary production. Larger impacts (15, 55% PP) were observed after the spring bloom at southern stations (Stns 44 and 54, respectively). These were not due to high weight-specific herbivory rates, but to both a relatively high *in situ* biomass of copepods (602 and 2142 mg C m^{-2}, respectively) and relatively low daily primary production (70 and 467 mg C m^{-2} d^{-1}, respectively; Table 4). Rates of total *in situ* herbivory by copepods peaked in May for BBW stations (median = 121 mg C m^{-2} d^{-1}) and in June for SRAW + MIX stations (29 mg C m^{-2} d^{-1}); BBW stations showed generally higher total rates (Table 4 and Fig. 2i,j). Stocks of prey and predator both varied over 3 orders of magnitude; evaluated separately, each explains 50% of the variance in total daily herbivory (Model I regression: $p = 0.0001$, $df = 25$).

Together, these 2 variables explained 66% of variance in total daily herbivory (adjusted $r^2 = 0.66$, p = 0.0001; df = 25; $Y = -4.5\,(\pm 6.2) + [0.019\,(\pm 0.0051) \times$ mg copepod C] + [0.0025 ($\pm$0.00068) $\times$ mg phytoplankton C]; interaction term not significant; Fig. 9).

DISCUSSION

Herbivory rates

Rates for NOW assemblages were comparable to those measured for similar species/stage groups in other cold oceans (Table 5). Although maximum chlorophyll concentrations were observed later at SRAW + MIX than at BBW stations, the overall range of weight-specific herbivory rates was similar in the 2 regions (Fig. 2g,h). Variability of specific herbivory rates for copepod assemblages within both water-mass regions may be attributed to size structure changes in both phytoplankton and copepod assemblages, varying prey concentration, and water temperature.

Booth et al. (2002) found that the general spring-to-summer pattern of phytoplankton species succession in the NOW is typical of arctic waters: in spring the bloom was dominated by ribbon-forming pennate (e.g. *Fragilariopsis* spp.) and chain-forming centric diatoms (e.g. *Thalassiosira* spp.), but by July the bloom was dominated by the small centric diatom *Chaetoceros socialis* (except at southeastern stations). Despite the common use of chlorophyll *a* as a proxy for food concentration, seasonal changes in phytoplankton assemblage size structure can affect actual prey availability. Unfortunately, our chlorophyll data did not include appropriate size fractions for testing this hypothesis. Copepod size also determines the size range of prey particles available to herbivores. The size structure of copepod assemblages increased in May, as late-stage *Calanus hyperboreus* migrated into the surface layer, then decreased in June, when early-stage *Calanus* spp. copepodites emerged in great abundance (Fig. 4). There was some tendency for a smaller average body size of treatment copepods at stations where we measured higher specific herbivory rates, but there was no significant relationship (data not shown). Booth et al. (2002) examined fresh copepod fecal pellets from all of the larger copepod species in July 1998; most pellets at both northern and southern stations included *Chaetoceros* spp. However, these data altogether do not describe how size structure changes affect grazing efficiency or selectivity, and it is not known how these factors interact with intrinsic size-related differences in specific ingestion rate.

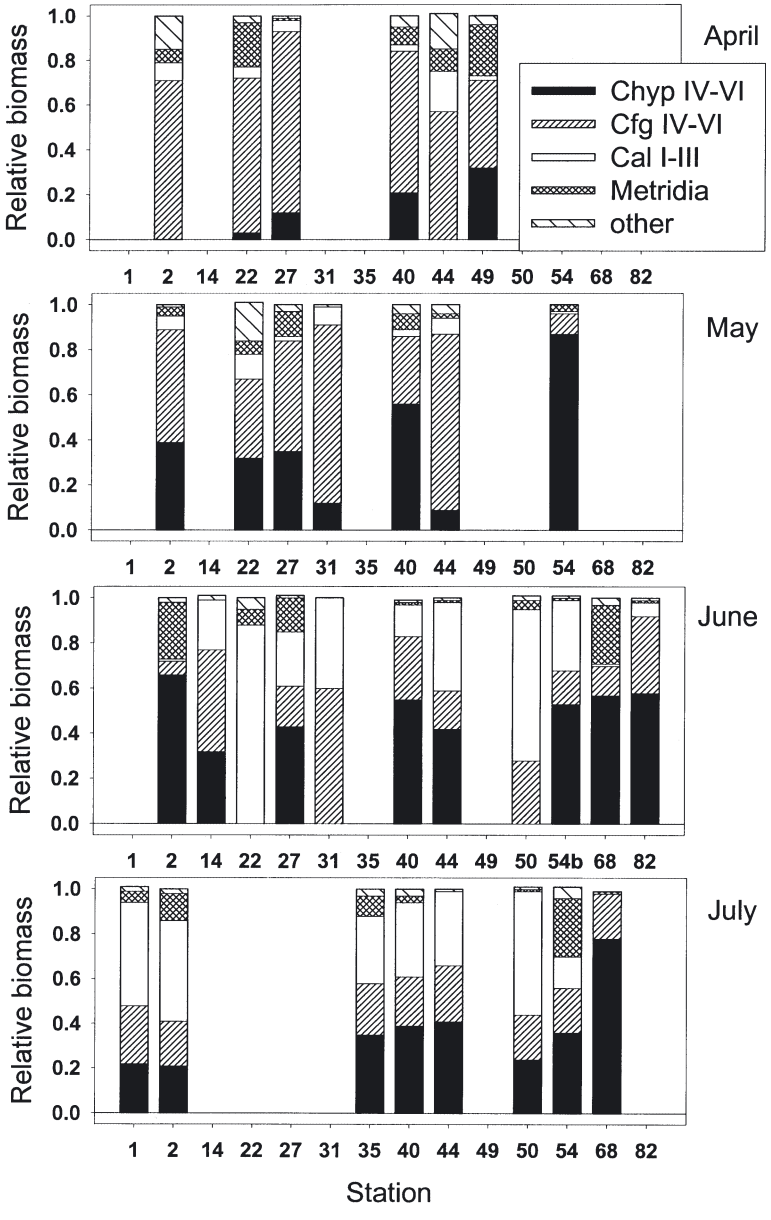

Fig. 4. Relative copepod carbon biomass (% of total) for copepod groups in surface net-tow samples (see Table 2 for depths) at all stations where we conducted incubation experiments to determine specific herbivory rate. For June plot, Stn 54a (5 June) omitted for clarity (data were similar to those for Stn 54 in May). Summary groupings (see key) of copepods are Chyp IV–VI: *Calanus hyperboreus* IV–VI; Cfg IV–VI: *C. finmarchicus* and *C. glacialis* IV–VI; Cal I–III: *Calanus* spp. I–III; Metridia: *Metridia longa*. Other: others (e.g. *Pseudocalanus* sp., *Microcalanus* sp., and *Oithona* sp.)

Table 3. Results of copepod grazing experiments in North Water Polynya (April to July 1998). General linear model (GLM) compares 24 h change in chlorophyll *a* in treatment versus control bottles. L, S: large-copepod and small-copepod sieve fractions, respectively. Proportional treatment effect = difference in average chlorophyll *a* concentration [(treatment t_f – control t_f)/control t_f]; Herbivory rate = weight-specific rate (µg C µg C^{-1} d^{-1}); nd = no data

Water mass Stn	Delta [chl *a*], avg. d^{-1} Control	Treatment	Proportional treatment effect	GLM p-value if <0.1	Herbivory rate avg.	CV	n	Fecal pellets at t_f	Fecal pellet color
April, SRAW + MIX									
2 (L)	0.007	0.007	0.01	–	0	–	–	no	–
(S)		0.004	–0.09	–	0.00001	100	2	no	–
22 (L)	–0.002	–0.002	–0.01	–	0.00003	100	2	no	–
(S)		–0.009	–0.15	0.02	0.0001	16	3	no	–
44 (L)	0.011	–0.005	–0.26	–	0.0002	80	2	no	–
(S)		–0.010	–0.44	0.08	0.0004	24	3	no	–
April, BBW									
49 (L)	0.025	0.000	–0.18	–	0.0003	56	2	no	–
(S)		–0.010	–0.31	–	0.0003	32	3	no	–
27	0.014	–0.123	–0.34	0.004	0.0016	48	3	no	–
40	0.392	–0.312	–0.39	0.02	0.0468	6	3	no	–
May, SRAW + MIX									
2	0.006	–0.081	–0.16	–	0.0031	11	2	no	–
27 (L)	–0.006	–0.303	–0.52	–	0.0041	10	3	no	–
(S)		–0.302	–0.51	–	0.0152	4	3	no	–
22	0.006	–0.011	–0.14	–	0.0041	39	3	no	–
44	0.071	–0.859	–0.21	0.04	0.1027	12	3	yes	green-brown
31	0.141	–0.758	–0.33	0.02	0.0779	28	3	yes	green-brown, brown-red
May, BBW									
40	0.827	–1.193	–0.50	0.07	0.0614	1	2	yes	brown, brown-green
54	0.216	–5.128	–0.38	0.0004	0.0514	14	3	yes	green-brown
June, SRAW + MIX									
2 (L)	0.012	–0.097	–0.34	0.06	0.0026	17	3	no	–
(S)		–0.053	–0.21	–	0.0575	58	3	no	–
14	0.597	–0.185	–0.10	0.008	0.1404	33	3	yes	nd
27	–0.173	–0.066	0.01	–	0	–	–	no	–
22	–0.289	–0.806	–0.20	0.1	0.2377	79	3	yes	nd
31	0.249	–0.558	–0.17	–	0.1928	93	2	yes	light olive-green
60	–0.614	–0.701	–0.03	–	0	–	–	yes	brown-green, dark grey
June, BBW									
54a	–0.304	–1.751	–0.37	–	0.0218	74	3	yes	nd
49	–1.521	–0.693	0.10	–	0	–	–	yes	nd
40	–0.343	–3.502	–0.33	0.05	0.2213	21	3	yes	green
54b	0.016	–0.656	–0.35	0.004	0.0180	22	3	yes	grey, grey-green
50	–1.647	–1.266	0.07	–	0	–	–	yes	green
44	0.560	–0.825	–0.24	0.06	0.0571	9	3	yes	green, light green
June, BBW_{cold}									
68	–0.048	–0.034	0.03	–	0	–	–	no	–
82	–0.054	–0.053	0.00	–	0.0004	102	2	no	–
July, SRAW + MIX									
2	–0.235	–0.669	–0.11	–	0.0379	85	2	yes	nd
July, BBW									
68	–0.069	–0.183	–0.19	–	0.0028	71	3	no	–
50	–0.024	–0.267	–0.08	–	0.0152	30	2	yes	green, grey
44	–0.041	–0.163	–0.08	–	0.0306	160	3	yes	green-grey, white
1	–0.100	–0.006	0.02	–	0	–	–	yes	grey, beige, grey-green
40	0.015	–0.133	–0.15	–	0.0095	37	3	yes	light green
35	–0.469	–0.780	–0.15	–	0.0251	68	3	yes	grey, green
54	0.440	–0.507	–0.49	–	0.0619	56	3	yes	grey-green, white

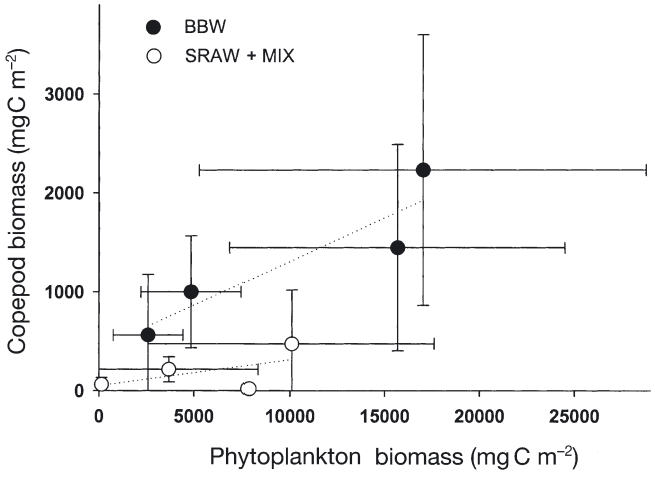

Fig. 5. Relationship between *in situ* copepod biomass and phytoplankton biomass. Mean (±1 SD) values calculated by month and by water-mass assignment of stations

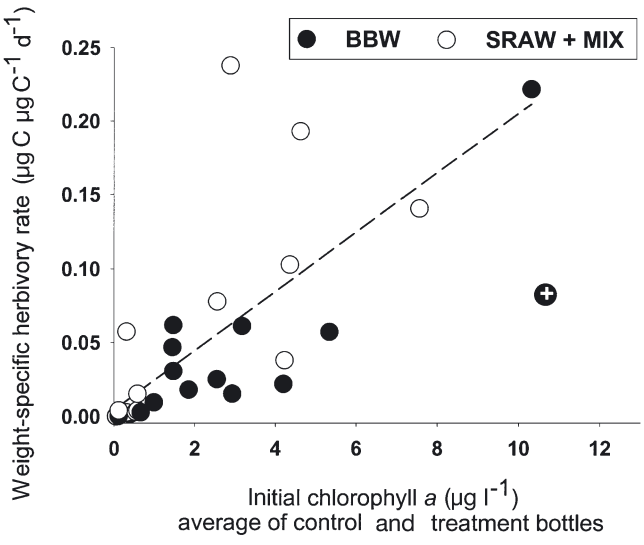

Fig. 6. Copepod herbivory rate. Relationship (r^2 = 0.54, p = 0.0001) between weight-specific herbivory rate and average initial (t_0) chlorophyll *a* concentration in control + treatment bottles: rate (d^{-1}) = 0.0044 (±0.011) + 0.020 (±0.0035) × t_0 chl *a* (µg l^{-1}). (+) statistical outlier from general trend

Despite these uncontrolled sources of variance, there was a significant, positive relationship between chlorophyll *a* concentration and weight-specific herbivory rate (Fig. 6). This relationship represents a broad range of NOW environments, because of the 4 mo sampling period and the large area of the polynya. H. Hattori et al. (unpubl. data) also sampled NOW copepods in June and July 1998, and they found that gut-pigment content (chlorophyll *a* + pheopigments copepod^{-1}, after Baars & Helling 1985) increased with increasing *in situ* chlorophyll *a* concentration (m^{-2}) for most biomass-dominant species/stage groups. Neither our study of assemblages nor the work of H. Hattori et al. (unpubl. data) on species/stage groups gave any evidence that ingestion rate is food-saturated, despite some of the highest *in situ* chlorophyll concentrations observed in arctic systems.

The temperature range observed in this study was relatively small. Herbivory rate patterns could be affected by temperature differences between the cold room and *in situ*, or between months *in situ.* However, we expect that such effects would be small (e.g. a change from –1 to 1°C results in a 25% increase in predicted weight-specific growth rate: Huntley & Lopez 1992). Further, the temperature of the prey-water sampling depth was usually no more than 0.5°C different from the 0 to 50 m mean (30 of 35 stations, data not shown).

Total *in situ* herbivory rate of copepods

The weight-specific herbivory rate explains neither the timing nor the magnitude of total copepod herbivory. Instead, total *in situ* herbivory rate depends on the abundance of predators and prey in combination (Fig. 9). Similar to phytoplankton and copepod biomass, total herbivory rate peaked earlier for BBW stations than for SRAW + MIX stations (Fig. 2). Although estimation methods vary, total *in situ* herbivory rates for the NOW are broadly similar to those determined for 4 other systems (Table 5).

Our test of the copepod size-scaling model does justify one aspect of concern as to how well experimental copepod assemblages represented *in situ* conditions. Each parameterization (b = 0, –0.1, –0.2, –0.3) generated a set

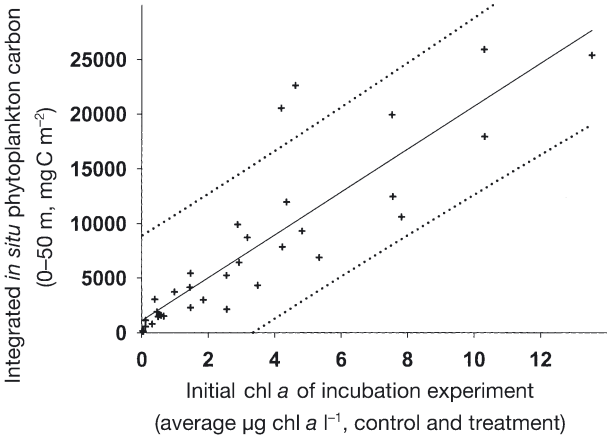

Fig. 7. Chl *a* concentration in experimental prey-water versus water-column concentration of phytoplankton carbon (r^2 = 0.76, p < 0.0001)

of size-weighted specific rates, all of which were biologically reasonable rates for their respective copepod size class (Fig. 8). When we used these to estimate total daily herbivory rate, we did find changes at specific stations (max. ± 40%). However, the overall median rate was about the same for weighted versus unweighted estimates (Table 4). Our estimate of daily grazing impact of copepods on phytoplankton changed little (±1% PP), even when we assumed strong size effects ($b = -0.3$). In the NOW, variation in weight-specific herbivory rate is much less important to copepod impact than the low biomass ratio of copepods versus phytoplankton.

In the summer environment, herbivory rates based on chlorophyll removal and a carbon:chlorophyll *a* ratio of 50 probably do not represent total carbon ingestion by copepods as well as they do for spring experiments. Seasonal changes in fecal pellet color (Table 3) and cell-count data (P. A. Saunders et al. unpubl. data) both show that copepods were ingesting protozoan prey in late June and July, particularly at southern stations. The relative abundance of fecal pellets in the July experiments (Table 3) is also evidence for feeding activity, despite a statistically insignificant removal of chlorophyll. Copepod herbivory rate can also be underestimated if and when (1) copepods are consuming heterotrophic protists, and (2) heterotrophic protists are also significant herbivores (Nejstgaard et al. 1997, 2001, J. Nejstgaard pers. comm.). These conditions were met to some degree for the post-bloom (~July) experiments. However, copepod biomass was ca. 10-fold the concentration of microzooplankton in those incubations (C. Lovejoy pers. comm.), and such an inequitable ratio would help to minimize food-chain effects in the experiments (Harris et al. 2000). Also, NOW microzooplankton show relatively low specific herbivory rates (max. 0.23 d^{-1} total phytoplankton: H. Bussey unpubl. data). Thus, our calculations for July experiments indicate that small corrections to our estimates of specific copepod herbivory rates are appropriate for some stations (max. increase ca. 20%), but the conclusions of this paper would not change in consequence. Increased prey diversity and lower copepod density in July experiments might accentuate variance in individual feeding behavior (Turner et al. 1993), contributing to a higher variance in specific herbivory rate among experimental replicates (July: median CV = 68%, range = 30 to 160%; April to June: median = 28%, range = 1 to 102%: Table 3).

Table 4. Impact of *in situ* copepod herbivory (mg C m^{-2} d^{-1}) on daily phytoplankton production (PP, mg C m^{-2} d^{-1}). Method A calculates total *in situ* herbivory (mg C m^{-2} d^{-1}) = specific herbivory rate (d^{-1}) × *in situ* copepod biomass (mg C m^{-2}), and B calculates total *in situ* herbivory rate = sum of all (size-scaled specific rate for Group *i* × *in situ* copepod biomass for Group *i*), for Groups 1 to *i*. ±%: percent difference between A and B methods of calculating total *in situ* copepod herbivory (= B/A × 100). %PP: percent PP consumed by copepods; nd = no data

Water mass	Total herbivory			Total daily	% PP
Stn	A	B	A vs B (±%)	PP[a]	consumed
April, SRAW + MIX					
22 (L)	0.002	0.002	0	9	0
22 (S)	0.006	0.006	0	9	0
44 (L)	0.001	0.001	0	92	0
44 (S)	0.005	0.007	40	92	0
April, BBW					
49 (L)	0.026	0.026	0	88	0
49 (S)	0.024	0.025	4	88	0
27	2.0	2.5	23	1026	0
40	11.3	11.9	6	462	2
May, SRAW + MIX					
2	0.70	0.81	16	190	0
27 (L)	0.50	0.48	−5	nd	–
27 (S)	1.1	1.3	14	nd	–
22	0.36	0.36	0	nd	–
44	43.4	51.0	17	674	6
31	28.9	28.5	−1	444	7
May, BBW					
40	77.4	88.0	14	4461	2
54	164.2	176.2	7	4055	4
June, SRAW + MIX					
2 (L)	2.6	2.5	−3	513	1
2 (S)	21.9	13.7	−37	513	4
14	7.9	6.9	−12	4041	0
22	36.6	32.9	−10	796	5
31	33.4	28.7	−14	1435	2
June, BBW					
54 (5 June)	69.9	69.5	−1	nd	–
54 (21 June)	38.6	42.6	11	70	55
44	72.2	67.7	−6	467	15
July, SRAW + MIX					
2	0.77	0.90	17	450	0
July, BBW					
68	4.9	4.9	0	181	3
50	27.2	29.4	8	321	8
44	32.5	26.8	−17	454	7
40	3.5	4.0	14	nd	–
35	14.8	15.4	4	1012	1
54	37.2	39.6	6	402	9

[a]For methods of measuring PP see Klein et al. (2002)

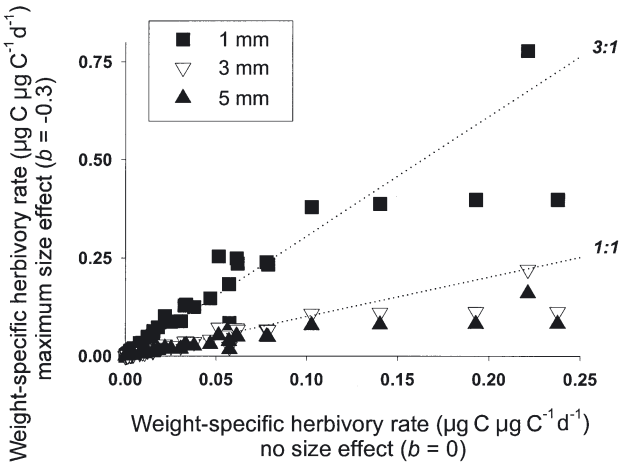

Fig. 8. Relationship between unweighted estimates of specific herbivory rate and size-weighted estimates ($b = -0.3$) for standard-length copepods (1, 3 and 5 mm). Size-weighted estimates were derived using size-scaling model $I = aW^b$. Guidelines (3:1 and 1:1) inserted as a visual aid

Impact of copepod grazing on phytoplankton production

In the arctic, *Calanus* spp. overwinter in relative abundance, suggesting the potential to consume significant portions of spring diatom production (Krause & Trahms 1983). Our data show that copepods respond quickly to initiation of the NOW spring bloom (Fig. 2c–f), and species composition data for surface copepod samples are also consistent with upward migration of large *Calanus* spp. (IV to VI: Ringuette et al. 2002). However, throughout the NOW spring bloom, we found that copepod herbivory had a small impact on daily phytoplankton production, removing <10% PP at most stations (Table 4). Weak coupling of phytoplankton and copepod grazers is also typical of the bloom environment of other cold seas (Table 5: Northeast Water, Davis Station), although not always (Young Sound, Disko Bay). Pre-bloom experiments measured little or no herbivory (where phytoplankton biomass < 50 µg C l^{-1} = 1 µg chl *a* l^{-1}; Table 3). Other studies have observed a similar lower feeding threshold (e.g. Frost 1972, Gamble 1978).

The generally low impact of copepod grazers in the NOW, in comparison with other arctic systems, can be attributed to a very high primary production rate and proportionally low biomass of copepods. High productivity rates are sustained over a relatively long season (Klein et al. 2002), and the NOW spring bloom has a higher maximum biomass than most other described arctic systems (Table 5). Exceptions are the Bering Sea and Bering Strait, where there is strong advection and upwelling. Klein et al. (2002) concluded that the eastern and northern NOW show annual primary productivity higher than predicted by the duration of open-water periods (Rysgaard et al.1999). In the north, polynya circulation may advect nutrient-rich water (Klein et al. 2002), while in the east, Tremblay et al. (2002) showed that moderate wind-mixing after initiation of the spring phytoplankton bloom could resupply nutrients and elevate productivity. In contrast to NOW phytoplankton, maximum NOW copepod biomass was similar to that of other arctic systems (Table 5), and therefore the ratio of copepods versus phytoplankton biomass was relatively small at most stations (Table 2). The weight-specific herbivory rates we measured in experiments were often as high as or higher than predictions of global empirical models for NOW temperatures (e.g. Huntley & Lopez 1992). In this case, a biologically reasonable variation in specific herbivory rate would not affect our conclusion of low copepod impact.

As the spring phytoplankton bloom declined in 1998 (Booth et al. 2002), our estimates of total copepod herbivory showed increased impact on daily PP at 2 southern stations in late June (15 and 55%; Table 4). At these stations (54 and 44), the greater copepod impact was due largely to decreased primary productivity rates. Klein et al. (2002) showed that reduced primary productivity is probably typical of the second half of the NOW growing season, although they cautioned that their productivity data were from 2 sampling years with seasonal differences in surface-layer chlorophyll concentration (see Bélanger et al. unpubl. data). In late August and Sep-

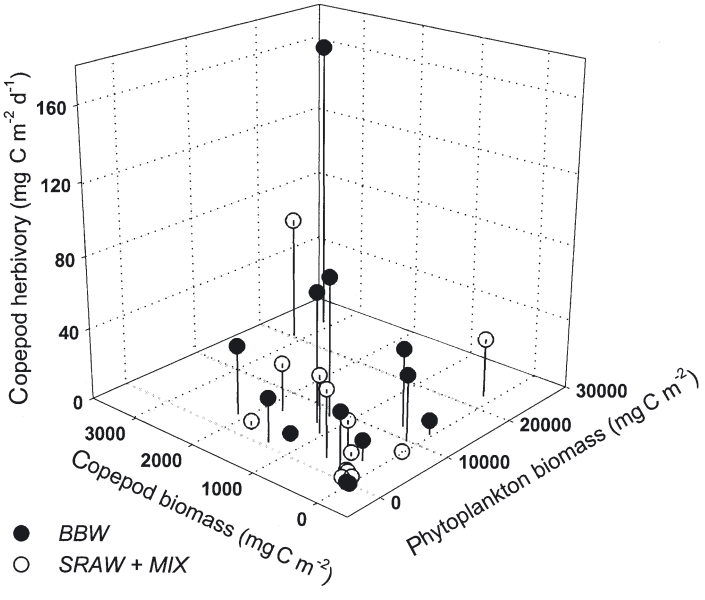

Fig. 9. Total *in situ* herbivory rate of copepods (no size effect) versus total *in situ* biomass of copepods and total *in situ* biomass of phytoplankton (adjusted-r^2 = 0.66, p = 0.0001)

Table 5. Literature data on biomass and copepod herbivory rates in polar-ocean systems (approximately –1 to 5°C). PP: daily primary production; POC: particulate organic carbon stock; APP: annual primary production. Impact (%): daily impact of copepod grazing

Study site	Temp. (°C)	Phytoplankton biomass (mg C m^{-2})	Copepod biomass (mg C m^{-2})	Copepod herbivory (mg C m^{-2} d^{-1})	Weight-specific ingestion rate (mg C mg C^{-1} d^{-1})	Impact (%)	Source
Disko Bay, W Greenland	–0.5–5.5	300–690	1000–4600	150–575[b] 20–230[c]	0.10–0.19	15–85[h] (PP)	Nielsen & Hansen (1995)
	–	–	–	–	~0.02	–	Levinsen et al. (2000)
Barents Sea	–	–	–	–	0.005–0.54	–	Tande & Båmstedt (1985)
Davis Station, E Antarctica	–1	–	–	–	0.05–2.63[g]	1–5	Swadling et al. (1997)
Young Sound, NE Greenland	–	1200–2800	646–2928	80–400[d] 79–389[e]	–	100 (APP)	Rysgaard et al. (1999)
Fram Strait (7/1984, 6/1988)	–1.5–3.0	250–4750[a]	386–4205	5.4–244[c]	–	–	Hirche et al. (1991)
NEW Polynya, NE Greenland (6/1991)	–	–	160–2160	1–445[c]	–	0.2–53[c] (POC, avg. =10)	Hirche et al. (1994)
(5–8/1993)	–1.7–5.2	59–1991	79–647	9–78[d]	–	17–38[d] (PP >5 µm)	Pesant et al. (1998)
Bering Strait	–	<2500–>10 000[a]	–	–	–	–	Sambrotto et al. (1984)
NOW Polynya, NW Greenland–Canada	–1.8–0.3	125–25 880	18–3207	0.4–164[f]	0.0001–0.24	–	This study

[a]Our estimation from reported chlorophyll *a* values, assuming C:chl*a* = 50; [b]Calculated from gut fluorescence and gut turnover data; [c]Calculated from egg-production rate data; [d]Based on empirical model of Huntley & Lopez (1992); [e]Based on empirical model of Hansen et al. (1997); [f]Calculated from chlorophyll removal-rate data; [g]Calculated from radioisotope uptake rate; [h]Range for results by 3 methods

tember 1999, regional primary production rate was 75 and 200% of the July 1998 rate, respectively, but was ca. 50% of the regional rates measured in May and June 1998 (Klein et al. 2002). Other studies of post-bloom conditions have found that daily herbivory can sometimes exceed daily primary production (Longhurst & Head 1989, Hansen et al. 1990), but we do not have experimental data for most of the duration of NOW summer conditions.

During the NOW summer (starting late June to July), copepods face 2 major changes in available prey. One important characteristic of the summer phytoplankton is the abundance of *Chaetoceros socialis* in the form of very small colonies and isolated cells (<10 µm: Booth et al. 2002). Booth et al. (2002) hypothesized that *C. socialis* is especially important to carbon flux in the NOW versus other arctic systems because it blooms through September. A substantial biomass of early-stage *Calanus* spp. copepodites (I to III) appeared in June and July (14 to 88% of the total: Fig. 4), following late-winter and spring egg-production (Ringuette et al. 2002). Booth et al. (2002) observed vegetative cells of *Chaetoceros socialis* in July fecal pellets from dominant NOW copepod species. Huntley (1981) showed that 5 to 10 µm flagellates were consumed by *Calanus finmarchicus*, but not by the 2 larger *Calanus* (*C. hyperboreus* and *C. glacialis*) species, in the Labrador Sea; and Sieracki et al. (1998) found that North Atlantic *C. finmarchicus* females could obtain most of their daily carbon ration from *C. socialis*. Both studies suggest that *C. socialis*, when it dominates the summer diatom assemblage, could be a significant diet component of early-stage *Calanus* spp.

In addition to the change in diatom species and size structure, the summer prey assemblage includes substantial protozoan biomass (July 1998: Booth et al. 2002, Lovejoy et al. 2002). Levinsen et al. (2000) showed a similar increase in the abundance of flagellates, dinoflagellates, and ciliates for Disko Bay, West Greenland. Cell-count data from the NOW experiments show that copepods ingested protozoan prey in late June and July, particularly at southern stations (P. A. Saunders et al. unpubl. data). Thus, for approximately 3 mo of the growing season, both protozoans and *Chaetoceros socialis* contribute to growth and survival of copepods, providing important resources to early copepodites after the decline of the large-cell diatom bloom.

What conditions result in the relatively low biomass of copepods in the NOW? There are clearly intrinsic and temperature-related limits on potential annual population growth. There is also evidence of food-limitation for some NOW copepods: (1) this study showed a general relationship between specific herbivory rate and chlorophyll concentration; (2) Ringuette et al. (2002 and pers. comm.) reported that gonad maturation, and thus egg-production rates, of *Calanus glacialis* and *Pseudocalanus* sp. (although not of other species) are positively related to *in situ* chlorophyll *a* concentration. However, population growth is the sum of potential population increase and extrinsic mortality factors. The outstandingly abundant populations of birds in the NOW include at least 15 million breeding pairs of dovekies in the Thule area (*Alle alle*: Kampp et al. 2000), with 30 to 60 million pairs in the whole NOW region (Karnovsky & Hunt 2002). *A. alle* consumes large *Calanus* spp. for much of their time in the NOW, and our calculations show reasonable agreement between the carbon requirement of the dovekie population (*A. alle*) and approximate production rates of *C. hyperboreus* in May and June 1998 (Karnovksy & Hunt 2002). We speculate that the abundance of large *Calanus* spp. is controlled by predation in the NOW, and that populations therefore do not reach the potential abundance suggested by their large food supply. On the other hand, the egg-production of some smaller copepods in the NOW is controlled by temperature during the spring bloom (Ringuette et al. 2002), and cell size or the availability of non-phytoplankton prey may limit other small species. Vidal & Smith (1986) came to similar conclusions for small copepod species of the middle shelf in the SE Bering Sea.

Our estimates of herbivory by copepods suggest that there is nothing unusually efficient about the coupling of copepods and spring phytoplankton production in the NOW pelagic food web, despite its rich bird and mammal fauna. In the Northeast Water Polynya (Hirche et al. 1994) and the Barents Sea (Eilertsen et al. 1989), most primary production sinks below the upper mixed layer and contributes a significant resource to benthic biota. Sedimentation rates for particulate organic carbon in the NOW were similar (Hargrave et al. 2002). However, we have not accounted for the feeding activity of other herbivores. In the NOW, copepod nauplii may graze an additional fraction of primary production (e.g. Turner et al. 2001); copepods occupying depths below the high-chlorophyll layer (e.g. *Metridia longa*) may use material initially generated in the euphotic layer; and the heterotrophic protozoans consumed by copepods after the spring diatom bloom (e.g. Levinsen et al. 2000) are very probably herbivorous (H. Bussey unpubl. data). Gelatinous mesozooplankton, particularly pelagic tunicates (*Oikopleura* spp., *Fritillaria* spp.) and pteropods (*Limacina* spp.), feed at high specific rates using a mucous 'web.' They can be important grazers, despite low population biomass. For example, *Oikopleura* spp., when abundant during the second half of the NOW growing season, removes more carbon from the surface layer than do copepods (Acuña et al. 2002).

Summary and conclusions

Large, late-stage copepods (*Calanus* spp. IV to adults: Ringuette et al. 2002) are able to respond rapidly to the spring bloom in the NOW via upward migration of overwintering individuals. The weight-specific herbivory rate of copepod assemblages was positively related to phytoplankton concentration. Seasonal peaks in daily rates of total *in situ* copepod herbivory corresponded with increased biomass of prey and predators in the surface layer, and these increases occurred approximately 1 mo earlier at eastern and southern stations (BBW) than at northern and western stations (SRAW + MIX). Although the biomass of copepods in the NOW was comparable to that observed in other arctic polynyas, the dominant diatoms of the bloom accumulated in very high abundance. Copepods were not sufficiently abundant to control phytoplankton biomass during the spring and early summer conditions represented by this study. We speculate that planktivory, especially by small pelagic birds, limits the abundance of large *Calanus* spp. Smaller copepod species may not respond to the high phytoplankton production of the NOW owing to greater limitation by cold temperature, more limited availability of small or non-phytoplankton prey particles, or both.

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