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Title: Benthic mats offer a potential subsidy to pelagic consumers in tundra pond food webs

Year: 2014

Version:

Please cite the original version:

Mariash, H., Devlin, S., Forsström, L., Jones, R., & Rautio, M. (2014). Benthic mats offer a potential subsidy to pelagic consumers in tundra pond food webs. *Limnology and Oceanography*, 59(3), 733-744. <https://doi.org/10.4319/lo.2014.59.3.0733>

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Benthic mats offer a potential subsidy to pelagic consumers in tundra pond food webs

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Abstract

We quantified the potential nutritional contribution of benthic mats to pelagic consumers in tundra ponds using three approaches. (1) We compared benthic and pelagic habitats based on their algal biomass and community composition and assessed the dietary quality in terms of fatty acid (FA) concentrations in both habitats. The algal community compositions differed significantly between habitats. Both benthic and pelagic habitats contained saturated and unsaturated FAs, but on average there were more FAs relative to carbon in the pelagic habitat ($44 \pm 29 \mu\text{g mg C}^{-1}$) than the benthic habitat ($23 \pm 18 \mu\text{g mg C}^{-1}$) across all studied ponds. (2) We quantified the contribution of benthic mats to the whole-lake FA pool and found that benthic mats dominate (on average > 90%) the basal FA resource within tundra ponds. (3) Using a series of feeding experiments, we found that *Daphnia* survival and FA concentrations increased when a benthic mat slurry supplemented low concentrations of phytoplankton. However, *Daphnia* could not survive solely on benthic mats, and nor did benthic mats increase adult *Daphnia* survival when mats were offered as coherent pieces. The extent to which pelagic consumers could be supported by benthic production challenges the view that benthic habitats are functionally separate from the pelagic food webs within northern lake ecosystems.

A key concept in ecosystem and food web ecology is the role of resource subsidies (Marecchi et al. 2011). In spatially heterogeneous systems, both the quality and quantity of resources are important factors for consumer–resource dynamics (Polis et al. 1997; Marecchi et al. 2011). Often it is a lower quality but more productive resource that subsidizes consumers when the primary resource does not meet a threshold for survival (Polis et al. 1997). In northern latitudes, where small, flat-bottomed ponds are a predominant feature of the landscape, high irradiance, an oligotrophic water column but nutrient-rich sediment, and microbial recycling of allochthonous carbon promote high benthic productivity (Quesada et al. 2008; Ask et al. 2009). This combination, along with slow decomposition, often creates a thick cohesive heterogeneous microbial biofilm (hereafter referred to as a benthic mat) attached to sediment or rock surfaces. Whereas the suspended phytoplankton is assumed to be the primary resource for pelagic consumers, these oligotrophic ponds tend to be nutrient-limited, with very low rates of pelagic primary production (Rautio et al. 2011). Hence, in these ecosystems the more productive benthic mats, often accounting for > 90% of the total primary production (Ask et al. 2009; Rautio et al. 2011), might serve as a resource subsidy for pelagic consumers.

Benthic mats are rarely considered in pelagic food web studies (Vadeboncoeur et al. 2002; Karlsson and Sävström 2009). In terms of food quality, preferred species availability, and the feeding habits of zooplankton, benthic mats alone are unlikely to sustain pelagic consumers (Rautio and

Vincent 2006); but, when forming part of a mixed diet, there is evidence that benthic mats can enhance *Daphnia* biomass (Siehoff et al. 2009). The high benthic primary production has the potential to fill a nutritional gap in zooplankton diets, especially in highly oligotrophic systems, in which phytoplankton quantities are insufficient to support planktivorous food webs (Sierszen et al. 2003; Cazzanelli et al. 2012). More specifically, it is the abundant matrix of algae, bacteria, associated protists, and nutrients at the biofilm boundary layer that makes benthic mats an attractive alternative to the limited primary pelagic food source, phytoplankton.

Tundra ponds are shallow, oligotrophic water bodies with short open-water seasons, favoring pelagic populations that have short life histories (Rautio et al. 2011). Viable populations of these consumers depend on the availability and quality of food sources within the short summers. Aquatic basal food quality has been examined for its digestibility, shape, or size of taxa (Rautio and Vincent 2006), by a comparison of its stoichiometry (Sterner and Hessen 1994), or, more recently, for its fatty acid (FA) content (Mariash et al. 2011). Competition for high quality but limited phytoplankton may force pelagic consumers to feed on a secondary food source. Various alternative carbon sources such as heterotrophic bacteria (Sävström et al. 2009), methanotrophic bacteria (Taipale et al. 2008), and terrestrial carbon sources, albeit with variable production efficiencies (Brett et al. 2009a; Cole et al. 2011), have been reported to make important contributions to zooplankton diets under certain conditions. Grazers accessing benthic mats as an alternative to pelagic phytoplankton could act as important habitat integrators, influencing both abiotic and biotic communities and subsequent trophic cascades (Sävström et al. 2009). Often it is such movements of nutrients, detritus, and

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Table 1. Background limnological data for the studied circumpolar ponds. max.z, maximum depth; chl.pel and chl.ben, chlorophyll *a* pelagic and benthic, respectively; DOC, dissolved organic carbon; phytoplankton biomass calculated from (a) biovolumes and (b) chlorophyll *a*; the presence or absence of *Daphnia*; indicated with +/-; and ponds included in the comparison of fatty acid composition analysis indicated with “+” in the last column.

Pond	Area (m ²)	max.z (m)	Volume (m ³)	chl.pel (μg L ⁻¹)	chl.ben (μg m ⁻²)	DOC (mg L ⁻¹)	Phytoplankton biomass (mg C L ⁻¹)		<i>Daphnia</i>	Analysis FA
							a	b		
Kilpisjärvi, Finland										
Boat	471	1.7	471	1.88	4.18	1.7	0.06	0.08	+	
Big Rock	47	0.7	33	1.76	0.18	6.0	0.04	0.07	+	+
Rock Fall	45	0.3	470	—	0.56	—	0.03	0.08	—	+
Tibors	471	1.1	330	—	6.18	5.9	0.07	0.07	+	+
Malla North	11,775	3.3	23,550	0.54	0.79	3.2	0.02	0.02	+	+
Reindeer	1178	1.5	1060	0.77	0.88	3.4	0.02	0.03	—	+
Tsahkal	350	1.5	2000	1.37	7.13	5.4	0.08	0.09	+	+
Lampo	550	7.6	2750	0.31	0.28	1.7	0.02	0.01	—	+
Tuono	79	0.8	40	1.00	0.36	2.8	0.01	0.04	—	+
Straca	47	0.5	12	0.58	0.07	1.2	—	0.02	—	
Kangerlussuaq, Greenland										
1	5024	2.0	7536	0.76	18.84	43.4	—	0.28		+
2	2826	2.5	4239	0.48	5.03	15.3	—	0.10		+
3	2355	2.0	4710	0.53	5.42	11.8	—	0.07		+
4	54,950	1.0	54,950	0.20	6.93	13.8	—	0.09		+
5	3533	0.8	2649	0.56	1.27	60.1	—	0.39		+
6	2747	1.0	5495	0.34	0.18	30.7	—	0.20		+
7	2826	1.5	7065	0.45	22.51	23.3	—	0.15		+
8	7536	1.5	7536	0.53	11.68	7.3	—	0.04		+
9	23,550	1.5	35,325	0.72	13.64	6.6	—	0.04		+

consumers across habitats that control community dynamics and the local food web structure (Polis et al. 1997; Schindler and Scheuerell 2002).

In this paper we examine the potential of benthic mats to serve as an additional food source to phytoplankton for pelagic zooplankton in tundra ponds. We took three approaches to investigate the contribution of benthic mats to primary and secondary production. (1) We sought to characterize the potential food source availability and quality in terms of algal community composition, biomass, and FA composition from both benthic and pelagic habitats. (2) We took an ecosystem approach to calculate the potential contribution of benthic mats to the whole-lake FA pool. We predicted that in these small, shallow oligotrophic ponds, the higher primary production in benthic habitats could yield more FAs than the pelagic phytoplankton. If this were true, benthic mats would have the potential both in quality and quantity to support primary consumers. (3) We ran a series of feeding experiments to measure the potential dietary value of benthic mats by evaluating *Daphnia* survival and their FA concentrations when fed different proportions of pelagic and benthic diets.

Methods

Community composition characteristics—We sampled ponds from two different tundra regions. Ten subarctic ponds (500–1000 m above sea level [asl]) were located in the

Scandinavian mountain birch forest zone of northwestern Finland, near Kilpisjärvi (69°04'N, 22°45'E). Nine arctic ponds (100–630 m asl) were located in the shrub tundra of southwest Greenland at the head of the Søndre Strømfjord, near Kangerlussuaq (67°00'N, 50°60'W). In both regions, the majority of the water bodies are small (< 0.20 km²), shallow (< 3 m), fishless (with the single exception of Malla North in Kilpisjärvi), and oligotrophic (5–20 total phosphorus μg L⁻¹). *Betula* spp. (*B. pubescens* subsp. *czerepanovii* in Kilpisjärvi, *B. nana* L. in Kangerlussuaq) and *Salix* spp. make up the dominant vegetation in both regions. Basic limnological data for each pond are presented in Table 1. In the Kilpisjärvi ponds, *Daphnia* (*D. longispina*, *D. pulex*, and *D. umbra*), *Eudiaptomus graciloides*, and *Branchinecta paludosa* were the predominant zooplankton, whereas *Eurycercus glacialis*, *Leptodiaptomus minutus*, *D. pulex*, *D. middendorffiana*, and *Branchinecta paludosa* dominated the Kangerlussuaq ponds. The Kilpisjärvi ponds were sampled the first week of July and second week of August 2010, specifically for algal community composition characteristics, FA data, and presence of *Daphnia*. The Kangerlussuaq area ponds were sampled in mid-July 2010 using the same procedures as for Kilpisjärvi.

Benthic and pelagic habitats were sampled from each pond for algae biomass and FA analysis. The pelagic food source was obtained from integrated bulk water samples taken from three points around the pond at 0.5 m depth. The water was first sieved through a 50 μm mesh in order to remove zooplankton. Approximately 1–4 liters, depending

on the particulate organic matter (POM) content of the pond, was then filtered on preweighed glass-fiber filters (Whatman GF/F) for chlorophyll *a* (Chl *a*) and FA analysis. Dissolved organic carbon (DOC) was determined from the bulk water sample after filtration through a prerinsed 0.22 μm cellulose acetate filter and was measured as nonpurgeable organic carbon with a Shimadzu Total Organic Carbon analyzer. Benthic and pelagic Chl *a* was extracted with 95% ethanol and was determined fluorometrically. From Kilpisjärvi, benthic Chl *a* was measured from Rock Fall, Tibors, and Tsahkal in this study; but, for the other ponds, values were taken from Mariash et al. (2011). Benthic mats were sampled using a brush sampler (Peters et al. 2005; sampling area 3.14 cm^2) to brush littoral rocks (taking only the upper 1 mm of benthic mats, which is potentially accessible to *Daphnia*). Samples from seven locations around the perimeter (20–60 cm depth) were collected: three were examined for algal community composition, one sample was filtered onto a glass-fiber filter for benthic Chl *a*, and three were freeze-dried for FA analysis. Both benthic and pelagic samples represent the available food source in each habitat and are a mixture of algal and nonalgal particles. However, as bacteria and detritus lack essential FAs, the reported polyunsaturated FA (PUFA) results give a good estimate of the algal difference between the benthic and pelagic habitats. Triplicate samples of seston filters and benthic algae were freeze-dried for subsequent FA analysis.

FAs were analyzed using a three-step extraction–methylation protocol. (1) Freeze-dried and weighed samples (pelagic: 0.5–5 mg dry weight [dry wt], benthic: 5–30 mg dry wt) were extracted using chloroform at -80°C . (2) A chloroform–methanol wash cycle separated the extracted lipids, and gravimetric analysis of the extraction was made for each sample to determine the μg lipid mg^{-1} dry wt. (3) The extracted lipids were methylated using toluene and sulfuric acid–methanol and then were solubilized in hexane. FAs (C14–C24) were identified as FA methyl esters (FAMES), using a gas chromatograph equipped with a Supelco™ SP-2560 column (100 m, 25 mm inner diameter, 0.2 μm film thickness) and a gas chromatograph flame ionization detector (TRACE GC-FID THERMO™). FA concentrations were calculated using calibration curves based on known standard concentrations. For the quantified FA data, only concentrations $> 1.0 \mu\text{g mg C}^{-1}$ were included. FAs were quantified to mg C based on the measured average of 43% carbon content per mg dry wt for pelagic seston, but for benthic mats the individual carbon content was used for each pond, respectively. The heterogeneity of the benthic mats can be seen in the difference in carbon content within and between regions (mean \pm standard deviation [SD]; 22% \pm 0.04% for Kilpisjärvi and 10% \pm 10% for Kangerlussuaq). FA composition and concentrations were analyzed from total lipids. Individual FAs are summarized in the results into general lipid classes: saturated (SAFAs), monounsaturated (MUFAs), polyunsaturated (PUFAs), and iso and anti-iso bacterial (BACT; Table 2). The latter group contains typical FAs found in bacteria (Taipale et al. 2009).

Nine of 10 Kilpisjärvi ponds were further analyzed for algal community composition from benthic mats and pelagic phytoplankton. The samples were preserved with acid Lugol's solution, and species composition and phytoplankton biovolumes (pelagic only) were determined using an inverted microscope (Utermöhl 1958). Taxa were identified to species when possible but later were grouped into class level for comparison. Phytoplankton carbon biomass was calculated from Chl *a* values using a factor of 40:1 (Mariash et al. 2011). To verify that this conversion factor was appropriate, biovolumes from actual phytoplankton community data from a subset of the ponds were calculated from cell densities based on measurements of the size of the species and the approximation of the shapes to geometrical figures; for rare species, biovolumes were taken from the literature (Hillebrand et al. 2006; Olenina et al. 2006). Biomass was calculated from measured algal volumes, assuming a density of 1. Phytoplankton biomass was converted to carbon using taxa-appropriate carbon conversion factors (Ahlgren 1983). Chl *a*-derived biomass values were similar to or slightly higher than phytoplankton biovolume–derived values (Table 1), but they were used in the analysis because they were available for all ponds.

Whole-lake production of FAs—We calculated the total mass of FAs available for consumers in each habitat. To calculate the total FAs produced in each habitat, we first determined the FA content of each sample relative to the carbon content; this yields $\mu\text{g FAME mg C}^{-1}$. Then this was multiplied by the total mg C m^{-2} (benthic mat) and mg C L^{-1} (pelagic) to determine the FAs per respective unit area or volume. Finally, these values were multiplied by the pond area or volume, respectively, for each pond (Table 1). The omega 3 to omega 6 ratio ($\omega 3:\omega 6$) was used as a biomarker to distinguish where the FAs were produced; the higher the ratio, the more pelagic the FA pool (Desvillettes et al. 1997; Ahlgren et al. 2009). For instance, typical pelagic taxa (Chrysophyceae, Chlorophyceae, Cryptophyceae, and Bacillariophyceae) are characterized by high levels of long-chain $\omega 3$ FAs (Desvillettes and Bourdier 1997; Ahlgren et al. 2009).

Feeding experiment—We ran two survival experiments with a similar setup and operation. The experiments included feeding *Daphnia longispina* with different proportions of phytoplankton (represented by a culture of *Scenedesmus obliquus*) and benthic mats (from Malla North). One treatment was fed only *Scenedesmus* (P), whereas the other had both *Scenedesmus* and benthic mat (P + B) added. Our experimental setup included three *Scenedesmus* concentrations (0, 0.2, 0.5 mg C L^{-1}), crossed with the absence or presence of benthic mat (P or P + B), with three to five replicates, depending on the experiment. *D. longispina* was chosen for the experiments as a model species because it was common in Kilpisjärvi and can be easily cultured in the lab. Several other zooplankton species have been associated with benthic mats as well: the copepod *Boeckella michaelsoni* and the cladocerans *Alona weinekii* (Hansson and Tranvik 2003), *Branchinecta paludosa*, *Ceriodaphnia quadrangula*, *D. magna*, *D. pulex*

Table 2. Summary of benthic and pelagic fatty acid methyl ester concentrations (mean \pm SD) from ponds in Kilpisjärvi ($n = 8$) and Kangerlussuaq ($n = 9$). All summed values are in bold for saturated fatty acids (SAFAs), monounsaturated fatty acids (MUFAs), polyunsaturated fatty acids (PUFAs), and bacterial fatty acids (BACTs) and for the ratio of omega 3 to omega 6 fatty acids ($\omega 3:\omega 6$).

	Benthic ($\mu\text{g mg C}^{-1}$)		Pelagic ($\mu\text{g mg C}^{-1}$)	
	Kilpisjärvi ($n = 33$)	Kangerlussuaq ($n = 27$)	Kilpisjärvi ($n = 45$)	Kangerlussuaq ($n = 26$)
Σ SAFAs	10.4\pm7.5	6.5\pm4.1	28.9\pm21.2	18.1\pm10.4
14:0	0.8 \pm 0.6	0.6 \pm 0.4	4.0 \pm 3.5	1.7 \pm 1.2
15:0	0.1 \pm 0.1	0.1 \pm 0.1	1 \pm 0.8	0.8 \pm 0.6
16:0	6.2 \pm 5.3	3.6 \pm 2.7	14.1 \pm 10	10.3 \pm 5.5
17:0	0.5 \pm 1.7	0 \pm 0	0.2 \pm 0.2	0.2 \pm 0.2
18:0	0.9 \pm 0.7	1.1 \pm 1.0	7.9 \pm 6	4.3 \pm 3
20:0	0.2 \pm 0.2	0.1 \pm 0.1	0.4 \pm 0.4	0.2 \pm 0.2
21:0	0.0 \pm 0.04	0 \pm 0	0 \pm 0	0.1 \pm 0.3
22:0	0.6 \pm 0.5	0.3 \pm 0.3	0.5 \pm 0.6	0.4 \pm 0.5
23:0	0.2 \pm 0.2	0.1 \pm 0.1	0.2 \pm 0.4	0 \pm 0
24:0	0.8 \pm 0.7	0.7 \pm 0.7	0.6 \pm 0.5	0.2 \pm 0.2
Σ MUFAs	10.3\pm7.5	5.3\pm4	14.1\pm10.6	7.9\pm3.7
16:1.7c	4.9 \pm 4.8	2.4 \pm 2.0	5.1 \pm 4.5	2.0 \pm 0.82
16:1.9c	0.2 \pm 0.3	0.1 \pm 0.2	2 \pm 0.8	1.2 \pm 0.8
18:1.7c	1.3 \pm 1.0	0.7 \pm 0.5	2.1 \pm 1.6	1.0 \pm 0.4
22:1.9	3.8 \pm 3.5	2 \pm 1.8	4.6 \pm 4.4	3.6 \pm 2.1
Σ PUFAs	9.9\pm12.2	3.7\pm3.4	10.3\pm8.3	6.7\pm3.7
18.2.6	3.1 \pm 3.8	1.4 \pm 1.4	1.7 \pm 1.1	1.5 \pm 0.9
18.3.6	0.2 \pm 0.2	0.1 \pm 0.1	0.3 \pm 0.4	0.0 \pm 0.1
18.3.3	3.3 \pm 4.4	1.3 \pm 1.4	1.7 \pm 1.4	2.7 \pm 1.5
18.4.3	1.1 \pm 1.7	0.4 \pm 0.6	2.5 \pm 2.4	1.8 \pm 1
20:04.6	0.4 \pm 0.6	0.1 \pm 0.1	0.5 \pm 0.5	0.1 \pm 0.15
20:5.3c	1.5 \pm 1.8	0.4 \pm 0.3	2.3 \pm 3.7	0.8 \pm 0.5
22:6.3c	0.4 \pm 0.6	0.1 \pm 0.09	1.2 \pm 1.4	0.3 \pm 0.3
$\Sigma\omega 3:\omega 6$	1.8\pm0.5	1.2\pm0.3	2.9\pm1.1	2.2\pm0.8
Σ BACTs	0.2\pm0.1	0.3\pm0.3	1.4\pm1.1	0.8\pm0.5
14.Me13	0.1 \pm 0.07	0.1 \pm 0.1	0.6 \pm 0.4	0.3 \pm 0.3
14.Me12	0.1 \pm 0.04	0.13 \pm 0.1	0.8 \pm 0.6	0.5 \pm 0.3
15.Me14	0 \pm 0.01	0.01 \pm 0.02	0 \pm 0.1	0.02 \pm 0.05
Total	30.8\pm25	15.7\pm10.4	54.7\pm38.9	33.5\pm17.3

(Rautio and Vincent 2006), and *D. middendorffiana* (Rautio and Vincent 2006; Cazzanelli et al. 2012).

We first determined if the pelagic food source in the ponds might be at a level that would limit zooplankton growth. The range of total pelagic algal biomass for the ponds was 0.01–0.39 mg C L⁻¹ (Table 1). In 16 of 19 ponds, phytoplankton concentrations were lower than the 0.18 mg C L⁻¹ threshold for adult *Daphnia* (size range: 1.7 mm [*D. galeata*] to 5 mm [*D. magna*]), at which they survive but cannot maintain reproduction (Müller-Navarra and Lampert 1996; Siehoff et al. 2009). Based on the low rates of pelagic production (8 mg C m⁻² h⁻¹; Rautio et al. 2011), the calculated standing stock of the study sites, and the threshold food concentration of *Daphnia* set by Müller-Navarra and Lampert (1996) and Siehoff et al. (2009), we conclude that the natural density of phytoplankton in these ponds is insufficient to sustain a reproductive population of *Daphnia* (size range: 2.5–5.5 mm). Thus, the zooplankton in these tundra ponds are exposed to persistent limiting food conditions. Similar food limitation was found in a comparable tundra pond, with pelagic primary production providing only half of the daily energy requirements of *Daphnia* (Cazzanelli et al. 2012). Because we used native

Daphnia from a tundra pond, we were specifically aiming for natural minimum food concentration limits. Although food thresholds are dependent on species, ontogenetic stage, body length, filtering rates, and/or additional food sources not included in the phytoplankton concentration (i.e., bacteria, protozoans, detritus), several references give a similar lower food range, which we used as a starvation threshold for these tundra ponds (Müller-Navarra and Lampert 1996; Siehoff et al. 2009). Survival was measured in all cases. The first experiment used a natural pond population of *Daphnia* and filtered pond water, whereas the subsequent experiment used laboratory cultures of *Daphnia* raised in *Daphnia* medium (AdaM, Klüttgen et al. 1994).

We first conducted an experiment using adult *D. longispina* from a birch forest pond in Kilpisjärvi (Tibors pond) during early July, only a few weeks after ice-off, when the *Daphnia* population was still in its exponential growth phase and was reproducing parthenogenetically. The pond *Daphnia* were collected using a hand net (210 μ m mesh) and were kept overnight in pond water to allow them to acclimatize to laboratory conditions before the large adults were randomly allocated to treatments, 10 individuals per jar of 200 mL filtered (GF/F) lake water. There

were three replicates, totalling 30 individuals per food treatment. In order to maintain a constant food concentration, *Scenedesmus* was added every 12 h and the water was replaced every second day. The concentrations of laboratory cultured *Scenedesmus* were 0, 0.25, and 0.5 mg C L⁻¹; values were determined by cells per volume, using a Burkman slide counter, and were converted to mg C L⁻¹ using a factor of 1.1778×10^{-11} g C cell⁻¹ (Rocha and Duncan 1985). The second treatment paralleled that for *Scenedesmus* (concentrations as above) but included added benthic mats. Benthic mats, collected from one of the sampled Kilpisjärvi ponds (Malla North), were kept intact to represent the natural form, using equal 2 cm² portions of benthic mat for each replicate, and then were transferred to the new container along with the surviving *Daphnia* during water changes. The experiment was run outdoors at ambient temperatures (low, 5°C; high, 23°C) for 14 d. The number of live *Daphnia* was recorded daily.

The second experiment was conducted under laboratory conditions, using juvenile *Daphnia*, at a constant 18°C and with a 16:8 light:dark cycle. A laboratory culture of *D. longispina* (Mekkojärvi, Finland, 2007 population) was reared in AdaM medium and with *Scenedesmus obliquus* under aerated conditions. When enough neonates developed (48–78 h old), they were then randomly sorted into glass containers (10 per 100 mL jar) among the six treatments (P, P + B), with five replicates per treatment. Benthic mats were taken from Malla North pond (Table 1) at the end of summer and were stored for 3 months in the cold and dark. The dormant benthic mats were exposed to light and higher temperatures only during the experiment to trigger algal growth. For the laboratory experiments, the benthic mat material was blended into a slurry in AdaM and was sieved through a 50 µm mesh in order to represent an edible fraction size. The concentration was determined using carbon weight of a known volume (mL). The same concentration of benthic slurry was added equally to all treatments and was refreshed when the medium was changed. *Scenedesmus* cell counts were taken daily, and the respective volume added to treatments varied according to the number of *Daphnia* alive. These counts were converted to concentration of carbon per 100 mL jar, so that the final *Scenedesmus* concentrations for the treatments were 0, 0.2, and 0.5 mg C mL⁻¹. *Daphnia* survival was measured every other day when the water was changed. Each treatment was terminated when roughly half of the original population remained. These remaining individuals were handpicked, freeze-dried, and stored at -80°C until they were analyzed for FAs.

Statistical analysis—Differences in algal community structure among habitats (benthic vs. pelagic), sampling period (June vs. August), lake size (depth ratio), and presence or absence of *Daphnia* in pond were tested using Bray–Curtis similarity (log-transformed abundances) with Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson et al. 2008). Nonmetric multidimensional scaling (nMDS) was used to visualize algal communities and associated FA composition (normalized concentration, Euclidean distances). The contribution of

each algal species to the average Bray–Curtis dissimilarity between habitat (pelagic or benthic) was assessed (similarity percentages [SIMPER] analyses, Primer). The link between algal community assemblages and associated FAs was done using Spearman's rank correlations between the algal and FA resemblance matrices (Bio-Env analysis—a comparison between two separate ordinations, one from species data and the second from environmental data, Primer). For the survival experiment, instead of the classical repeated measures approach, we followed a procedure recommended by K. Robert Clark (Primer-E programmer) that compared the differences in treatment curves by incorporating both time and survival into the treatment effects. They were then analyzed as a bivariate set of responses (survival proportion and time in days), with two treatment factors as well as their interaction (three levels of *Scenedesmus* concentrations and presence or absence of a benthic mat supplement) with PERMANOVA (Anderson et al. 2008), an add-on in the software package Primer 6 (Clarke and Gorley 2006). For the neonate survival experiment, a two-way ANOVA compared the survival between treatments at day 4. Differences in FA concentration (SAFA, MUFA, PUFA, BACT) among FA class and habitat were analyzed using two-way ANOVA with fixed effect. ANOVA assumptions were visually checked with residuals. Multiple comparison tests were carried out when necessary (Tukey's honestly significant difference [HSD] or multiple pairwise in PERMANOVA). A significance level of $\alpha = 0.05$ was used for all statistical tests.

Results

Algal community composition characteristics—Algal community composition was significantly different for benthic vs. pelagic habitats in Kilpisjärvi ponds (Fig. 1A; $pseudo-F_{1,27} = 4.89$, $p < 0.001$; Table 3a). There was no distinction between July and August sampling periods ($pseudo-F_{1,19} = 0.82$, $p = 0.69$) or with the presence or absence of *Daphnia* (pooled habitats: $pseudo-F_{1,27} = 1.03$, $p = 0.4$) among ponds based on PERMANOVA. Because there were no significant differences between these groupings, we pooled the data only by habitat type (benthic, pelagic) for subsequent analysis. In general, ponds had a diverse taxa assemblage in the pelagic community, with Chrysophyceae (CHR), Chlorophyceae (CHL), and Conjugatophyceae (CON) making up 77% of biomass; specifically, *Pseudopedinella* and *Chrysoflafellata* were the genera contributing to 46% of the similarity. Cyanophyceae (CYA) and Bacillariophyceae (BCL) were predominant in the benthic communities, with pennate diatoms and *Nostoc* contributing 65% of the benthic community (Fig. 2A). When CYA dominated the benthic mats (> 60%), *Daphnia* were absent, whereas ponds with *Daphnia* had ≤ 15% CYA and a mix of other taxa in the benthic mats.

The two habitats had distinct FA compositions ($pseudo-F_{1,30} = 6.84$, $p < 0.001$; Fig. 1B; Table 3b). Benthic mats were characterized by relatively equal proportions of SAFA:MUFA:PUFA contributing 36:36:27% of the total FA concentration, respectively. Pelagic algae was

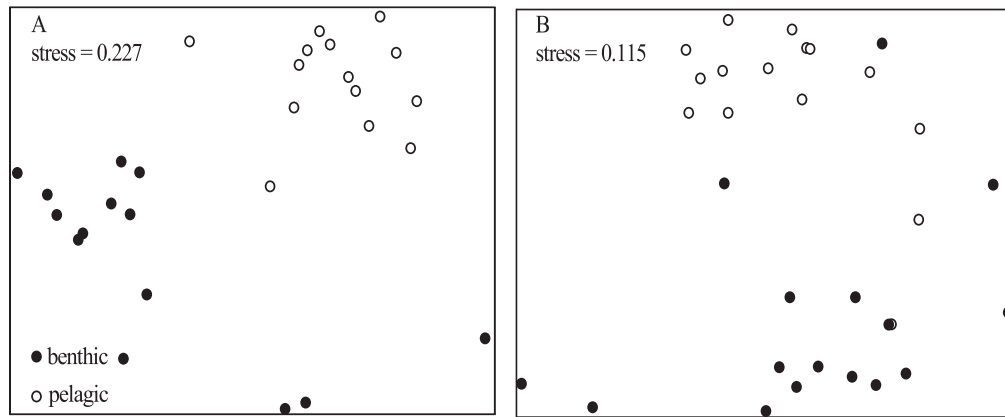


Fig. 1. Nonmetric multidimensional scaling of (A) the algal taxonomic community composition data (proportion of genera) and (B) fatty acid methyl ester concentrations, from benthic (closed symbols) and pelagic (open symbols) habitats from eight Kilpisjärvi ponds (Tibors, Big Rock, Rock Fall, Tsahkal, Malla North, Reindeer, Lampo, and Tuono). Data points represent an individual sampling event in each lake for each benthic and pelagic habitat on two dates (July and August).

dominated by SAFAs, with a respective relative contribution of 53:25:19% of the total FAs (Table 3c). Also, bacterial FAs were found to be significantly higher in the pelagic habitat than in the benthic (Fig. 2B; Table 3c). The FAMES that best explain the similarity among pond algae taxonomic community compositions are 16:0, 16:1 ω 7, 18:0,

18:2 ω 6, and 18:3 ω 3 (Table 4). However, using only palmitoleic acid (16:1 ω 7), stearic acid (18:0), and linoleic acid (18:2 ω 6) is a simpler combination of FAs that similarly describes the pattern separating the ponds and habitats in Fig. 1A. Linoleic acid is an abundant FA in chlorophytes and dinoflagellates (Taipale et al. 2009), both

Table 3. Summary of the ANOVA and PERMANOVA comparing (a) algal structure, (b) FA composition, and (c) the FA classes (SAFA, MUFA, PUFA, BACT) between the benthic and pelagic habitat in Kilpisjärvi area ponds, and the effect of the phytoplankton concentration (P) and benthic mat addition (B) for (d) adult *Daphnia* and (e) neonate survival (at day 4). For (a, b, and d) the *F*-values are *pseudo-F* obtained in PERMANOVA. Bold indicates significant values.

Source	Degrees of freedom	MS	<i>F</i>	<i>p</i> -value	% estimates of components of variation
(a) Algal structure					
Habitat	1	17,835.00	4.89	0.001	25
Residual	22	3646.30			
Total	23				
(b) FA composition					
Habitat	1	133.14	6.84	0.001	31
Residual	24	19.45			
Total	25				
(c) FA classes					
Habitat	1	44.93	69.18	0.001	19
FA types	3	181.65	279.69	0.001	
Habitat \times FA type	3	9.76	15.03	0.001	
Residual	280	0.65			
Total	287				
(d) Adult survival					
P	2	341.72	18.48	0.0004	74
B	1	706.61	8.94	0.0096	50
P \times B	2	154.39	4.04	0.041	
Residual	12	38.22			
Total	17				
(e) Neonate survival					
P	2	104.70	3.05	0.066	
B	1	40.80	1.19	0.286	
P \times B	2	7.43	0.22	0.806	
Residual	24	34.32			
Total	29				

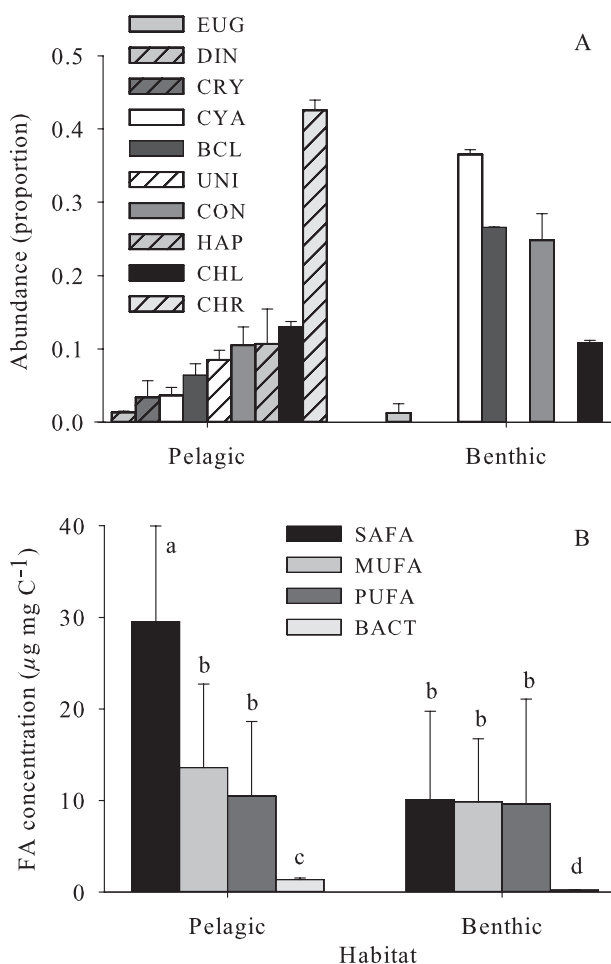


Fig. 2. Pelagic and benthic habitat compositions in terms of (A) proportion of algal class abundance and (B) main type of fatty acid (FA) composition from nine tundra ponds in Kilpisjärvi (mean + standard error [SE]). EUG, Euglenophyceae; DIN, Dinophyceae; CRY, Cryptophyceae; CYA, Cyanophyceae; BCL, Bacillariophyceae; UNI, unidentified cells; CON, Conjugatophyceae; HAP, Haptophyceae; CHL, Chlorophyceae; CHR, Chrysophyceae; SAFA, saturated FA; MUFA, monounsaturated FA; PUFA, polyunsaturated FA; BACT, bacterial FA. Different letters indicate statistically different values.

of which are abundant in the pelagic habitat of the ponds. In terms of quality, the nutritionally important PUFA had similar mean concentrations in both habitats (mean benthic and pelagic concentrations were $9.9 \mu\text{g mg C}^{-1}$ and $10.3 \mu\text{g mg C}^{-1}$, respectively, for Kilpisjärvi, and

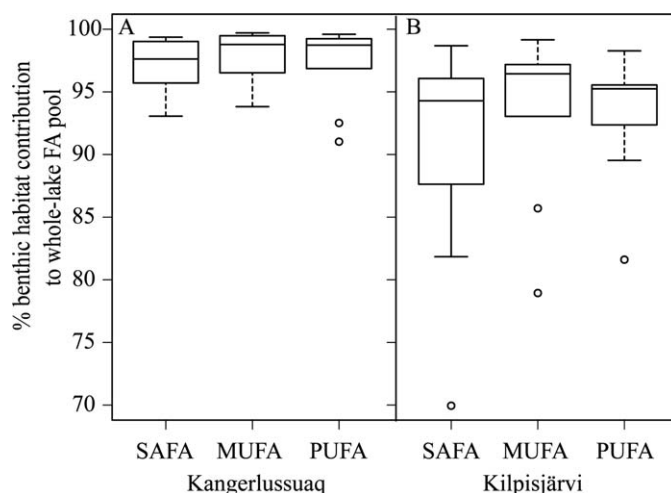


Fig. 3. Box plots of percent benthic habitat contribution to whole-lake FA standing stock from two different Arctic regions (Kangerlussuaq, Greenland, $n = 9$; Kilpisjärvi, Finland, $n = 8$). MUFAs, monounsaturated FAs, PUFAs, polyunsaturated FAs, SAFAs, saturated FAs.

$3.7 \mu\text{g mg C}^{-1}$ and $6.7 \mu\text{g mg C}^{-1}$, respectively, for Kangerlussuaq; Table 2). On average, per mg C the pelagic habitat provided more FAs ($44 \pm 29 \mu\text{g mg C}^{-1}$) than the benthic habitat ($23 \pm 18 \mu\text{g mg C}^{-1}$) among all the ponds studied. However, due to the larger carbon stock in the benthic habitat, the benthic exceeds the pelagic by 2.5 times in terms of total FA mass.

Whole-lake production of FAs—The benthic habitat was the dominant source of FAs at the whole-lake scale (Fig. 3). In both the Kangerlussuaq and Kilpisjärvi regions, benthic mat FAs contributed an average 91% of the whole-lake FA resource. Benthic mat FAs contributed 75–95% of the FAs produced per unit carbon in the Kilpisjärvi ponds (Fig. 3), significantly higher than pelagic FA production (t -test, $t = 22.4$, degrees of freedom [df] = 1,16, $p < 0.001$). In the Kangerlussuaq ponds, the proportion of benthic-derived FAs was 97.5% on average (range: 93.2–99.4%) and was significantly higher than the pelagic FA pool (t -test, $t = 81.9$, df = 1,16, $p < 0.001$; Fig. 3). Pond morphometry (depth ratio) is clearly a parameter that also affects the proportion of pelagic production; yet, even in the deepest lake (Lampo, Kilpisjärvi), benthic mats contribute 75% of the total standing stock of FAs. A

Table 4. Combinations of fatty acid methyl esters (FAMES = 24), taken k at a time, giving the largest rank correlation ρ_s between habitat similarity matrices; bold type indicates the best combination overall.

k	Best variable combinations (ρ_s)			
3	16:1 ω 7, 18:0, 18:2 ω 6 0.62	16:1 ω 7, 18:0, 18:3 ω 3 0.61		
4	16:1 ω 7, 18:0, 18:2 ω 6, 18:3 ω 3 0.62	16:0, 16:1 ω 7, 18:2 ω 6, 18:3 ω 3 0.62	16:0, 16:1 ω 7, 18:0, 18:2 ω 6 0.61	
5	16:0, 16:1ω7, 18:0, 18:2ω6, 18:3ω3 0.63	16:1 ω 7, 18:0, 18:2 ω 6, 18:3 ω 3, 22:0 0.62	16:1 ω 7, 18:0, 18:2 ω 6, 18:3 ω 3, 24:0 0.61	16:0, 16:1 ω 7, 18:0, 18:2 ω 6, 18:1 ω 7 0.61
				16:0, 16:1 ω 7, 18:0, 18:3 ω 3, 18:1 ω 7 0.61

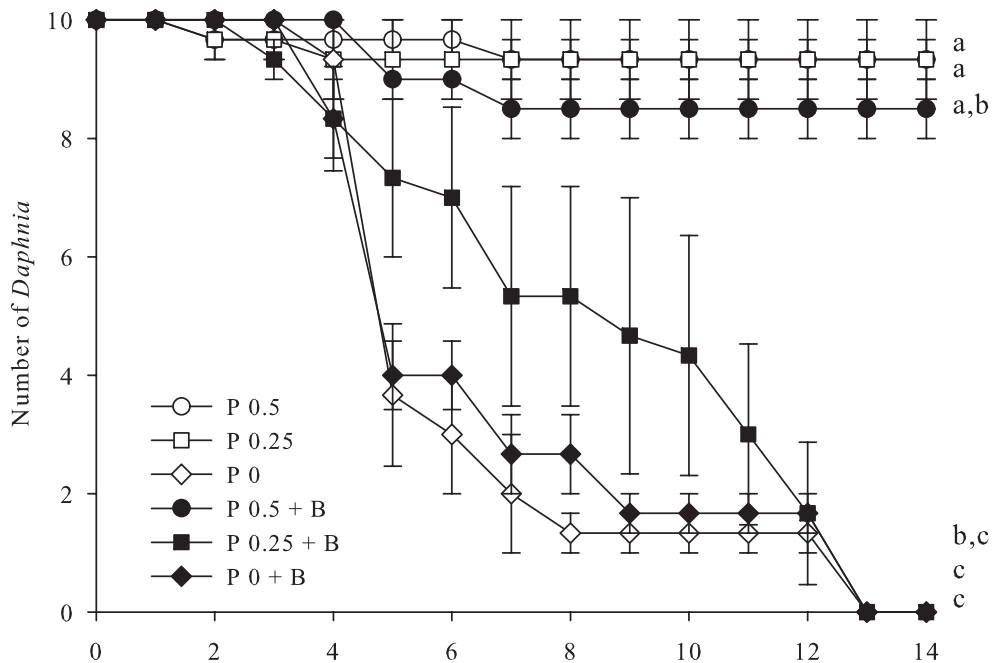


Fig. 4. Adult *Daphnia* survival with *Scenedesmus* provided at three concentrations (0, 0.25, 0.5 mg C L⁻¹) without (P) and with (P + B) a benthic mat supplement. Values are means of three replicates \pm SE. Open symbols represent the *Scenedesmus*-only treatments, whereas the closed symbols are treatments with benthic mat additions. Different letters indicate statistically different survival curves.

paired *t*-test demonstrated significantly different ω 3: ω 6 ratios between the benthic and pelagic FA pools (*t*-test, $t = 17.7$, $df = 1,16$, $p < 0.001$), verifying that the benthic FAs were primarily derived from local benthic production, rather than deposited from phytoplankton (Table 2).

Feeding experiments—When *Scenedesmus* was present, there were few or no deaths of adult *Daphnia*; P0.25, P0.5, and P0.5 + B mg C L⁻¹ had fewer than five deaths, indicating that the *Daphnia* were not exposed to food limitation during the 14 d experiment (Fig. 4). The *Daphnia* survival changed significantly during the experiment and was controlled by both the *Scenedesmus* concentration and the presence of benthic mats (Table 3d). However, at the intermediate concentration, P0.25 vs. P0.25 + B, the benthic mats had a detrimental effect ($p = 0.013$) on *Daphnia* survival. *Scenedesmus* concentration had the largest influence, contributing 74% of the variation (Table 3d). Overall, benthic mats did not increase *Daphnia* survival when available as coherent pieces.

For the second survival experiment using benthic slurry and juvenile *Daphnia* in the laboratory, the treatment with the longest survival was the benthic addition for all respective *Scenedesmus* concentrations (Fig. 5A; Table 3e). Generally, *Daphnia* in the P + B treatments survived better than those in the highest P treatment. However, benthic mat material alone did not prevent complete *Daphnia* mortality. *Daphnia* survived the same number of days with (P0 + B) or without benthic mats (P0; 50% mortality in only 4 d), but the rate of death in the population was slightly lower in benthic mat treatments compared to the P0 group

(Fig. 5). *Daphnia* PUFAs showed a net loss in all but the highest (0.5 mg C L⁻¹) treatments, whereas SAFAs and MUFAs gained proportionally 2:1 (MUFA:SAFA) in all treatments. The daily FA difference was most marked in the P0.5 + B treatment, in which *Daphnia* gained all FAs at twice the rate as did *Daphnia* in P0.5, pointing to the positive effect of benthic mats in this treatment. *Daphnia* FA concentrations were equal in both P0 and P0 + B treatments, indicating that benthic mats alone made no physiological improvements (Fig. 5B).

Discussion

Our study evaluated the potential nutritional contribution of benthic mats to pelagic consumers in tundra ponds by three approaches. (1) We demonstrated a nutritional need for an alternative food source by showing that the natural pelagic phytoplankton concentration in these ponds is below the threshold food concentration (0.18 mg C L⁻¹) defined by Müller-Navarra and Lampert (1996). As pelagic consumers are exposed to food limitation, there is a physiological demand to supplement their diets with an alternative food source. (2) We demonstrated that benthic habitats are the dominant source of algal biomass and primary-produced FAs in the study ponds. (3) Through our experiments we showed that benthic mats, when accessible, could supplement *Daphnia* dietary requirements when phytoplankton concentrations are limiting.

Algal community composition characteristics—We assessed the quality of pelagic and benthic habitats in terms of

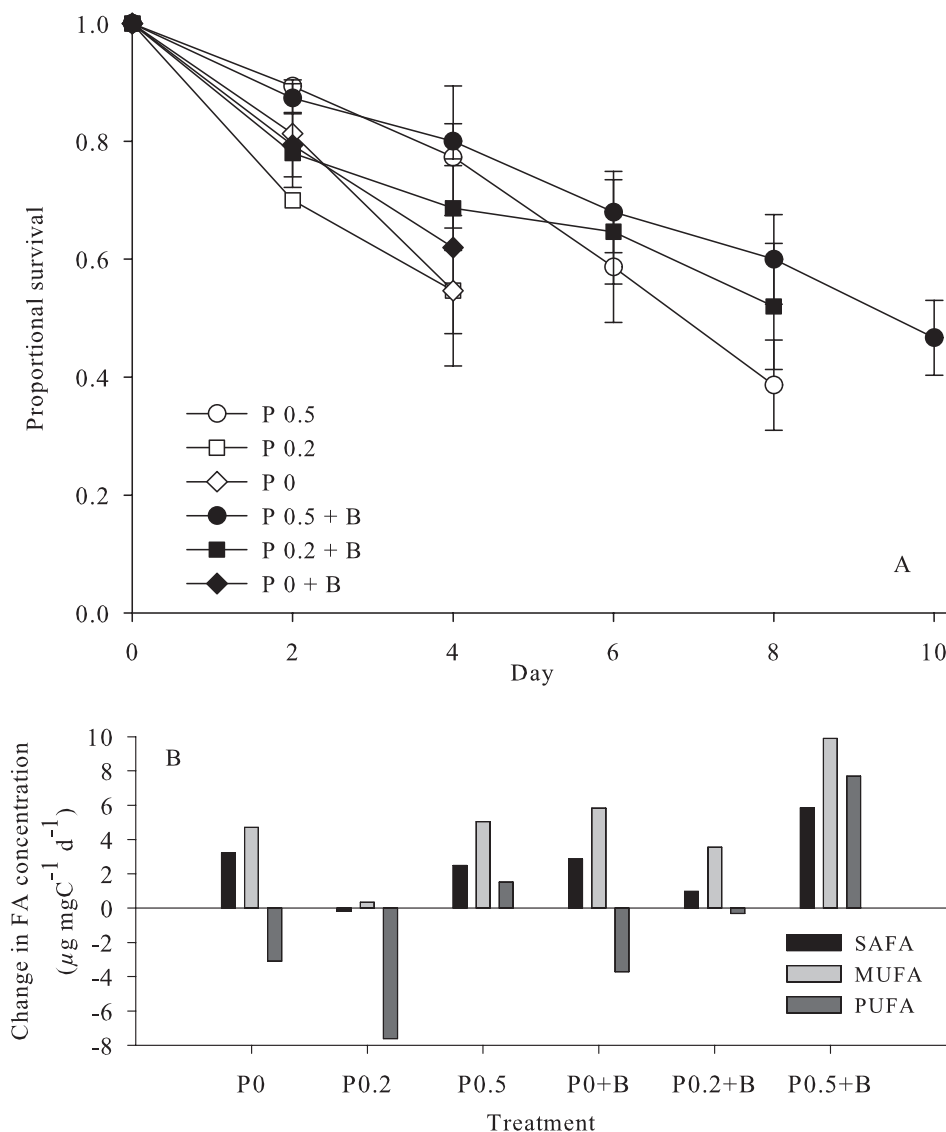


Fig. 5. Juvenile *Daphnia* (48–78 h old) laboratory feeding experiment with *Scenedesmus* provided at three concentrations (0, 0.2, 0.5 mg C L⁻¹) without (P) and with (P + B) a benthic mat slurry supplement. (A) Proportion of *Daphnia* alive (means \pm SE). Open symbols represent the *Scenedesmus*-only treatments, whereas the closed symbols are treatments with benthic mat additions. (B) Changes in *Daphnia* fatty acid concentrations are based on the change from initial (before experiment) concentration and are divided by the day at which the 50% population mark was reached and the treatment was terminated.

algal community composition (only Kilpisjärvi ponds) and FA composition. In general, both habitats had a diverse assemblage of taxa, varying widely among ponds. However, the complexity of algal taxa composition among habitats and ponds could be separated by using only three FAMES (16:1 ω 7, 18:0, and 18:2 ω 6). Cyanobacteria and diatoms dominated the benthic mats. Cyanobacteria, with very low PUFA content and potential toxicity, are not an ideal food source for zooplankton, whereas diatoms are a good source of both PUFAs and MUFAs (Brett et al. 2009b; Sarnelle et al. 2010). Hence, this algal community combination may help to make the benthic mats a nutritious food source for zooplankton and may at least partly explain why *Daphnia*

were not present in ponds when Cyanobacteria alone dominated (> 60%) the benthic mats. The pelagic communities were more dynamic, with chrysophytes, mainly small flagellated species belonging to various genera, making up 40% of the community; chlorophytes and desmids made up the other 60% of the phytoplankton community. Despite the differences in specific algal communities, both habitats provide the FAs essential for zooplankton growth. These essential FAs, mainly PUFAs, are equally distributed among all algal groups (Desvilettes and Bourdier 1997). PUFAs are essential for zooplankton because they can only be acquired from the diet and are specifically important in reproduction and cellular function (Brett et al. 2009a). Our study is the

first to show that benthic mats have similar concentrations of PUFAs to pelagic algae. Further, benthic mats produce all the essential FAs in quantities sufficient to contribute to secondary production. Quantifying the FAME concentrations using the carbon weight of the sample allowed for more accurate comparisons of the two food sources and circumvented differences between lipid content and sample weight. When only dry wt was used to quantify FAMES, benthic mat PUFA concentration was under the detection limit (Mariash et al. 2011).

Whole-lake production of FAs—Although there were differences between and within regions, in both Kilpisjärvi and Kangerlussuaq the majority of whole-lake FA production came from benthic mats. Pond morphometry is clearly a parameter that affects the proportion of pelagic vs. benthic production (Vadeboncoeur et al. 2008); yet, by linking lake size and area with FA concentrations, we have demonstrated that the benthic habitat dominates the whole-lake basal standing stock and, likely, the production of FAs. Even in the deepest pond, benthic mats contribute 75% of the total standing stock of FAs, and in both regions the benthic mats produced similar PUFA concentrations as the pelagic habitat. Due to the rapid rate of FA decomposition (Ahlgren et al. 2009) and significantly different $\omega 3:\omega 6$ ratios between benthic and pelagic FA pools, we are confident that the benthic FAs have been produced in the benthic mats rather than through slow accumulation from pelagic sources. Until now, benthic mats have been shown to dominate the algal biomass (Rautio and Vincent 2006), with only little evidence of dietary links to pelagic zooplankton (Rautio and Vincent 2006; Karlsson and Sävström 2009; Cazzanelli et al. 2012). Our results show that the benthic mats have the potential both in quality and quantity to support pelagic primary consumers. The potential FA production in the benthic mats could be substantial, considering that primary production in Arctic benthic habitats is roughly $50 \text{ mg C m}^{-2} \text{ d}^{-1}$ compared to pelagic production of $8 \text{ mg C m}^{-2} \text{ d}^{-1}$ (Rautio et al. 2011). Hence, the more consistent availability of PUFAs in the benthic habitat could buffer the extreme seasonality of pelagic phytoplankton availability.

Feeding experiments—Our results from these experiments indicate that when phytoplankton is scarce or absent, benthic mats cannot completely prevent zooplankton mortality. Therefore, low phytoplankton concentrations would lead to low survival of *Daphnia*. In order to support the abundant zooplankton populations found in these tundra ponds (Rautio and Vincent 2006), zooplankton must be dependent on another food source. In the absence of phytoplankton, benthic mats increased survival of *Daphnia* juveniles, which survived better in the benthic treatments than at the highest phytoplankton-only treatment (P0.5, Fig. 5). When the benthic mats were left in intact mat form, adult *Daphnia* responded more to phytoplankton concentration than to the presence of benthic mats. Mechanistic challenges to feed from the benthic mat crumbs, the loss of the in situ productive surface layer, and high temperature fluctuations may have contributed to the

negative effect of benthic mats. It was difficult to accurately represent the natural complexity of the benthic surface layer or standardize for algal community heterogeneity when this experiment was done under stagnant conditions, as compared to the wind-driven water circulation that naturally occurs in these exposed shallow ponds. Resuspension of benthic particles and bioturbation at the biofilm surface, with associated nutrient and autotrophic and heterotrophic community flux, may facilitate the overall trophic transfer of benthos to pelagic grazers (Rautio and Vincent 2006; Cazzanelli et al. 2012). Converting the benthic mats to a slurry homogenized the mats and made them more ingestible and is likely why the slurry treatment had a clear positive effect on *Daphnia* growth, whereas the coherent benthic mat pieces may have lost their looser surface layer during handling. The continual flux at the surface layer may indicate that the benthic slurry is actually quite representative of the naturally accessible resource for consumers, and the looser surface layer of natural mats may be critical to consumer resource acquisition.

Subarctic zooplankton have adapted to grow on low food concentrations and must respond quickly to changes in phytoplankton availability. If benthic mats are accessible, which is more likely in shallow ponds, with no stratification and an easily mixed water column, then benthic mats may become a functional food source, as seen by the improved survival of juvenile *Daphnia* in the second feeding experiment. When food concentrations of preferred phytoplankton are at a critically low level, the consumers must resort to an alternative food source, such as bacteria, detritus, or benthic mats; but, unlike bacteria and detritus, benthic mats provide all the essential FAs. The FA concentrations increased more than the respective P-only treatment for *Daphnia* supplemented with benthic mats, demonstrating a nutritional improvement from the benthic mat addition (Fig. 5B). At P0 + B and P0 treatments, *Daphnia* gained SAFAs and MUFAs while losing PUFAs, which could mean that PUFAs are preferentially saturated in response to the physiological demands of starvation. SAFAs, MUFAs, and PUFAs were found in net gain, with twice the gain in P0.5 + B vs. the P0.5 treatment, showing that the benthic additions could improve the gain of FAs even at the higher concentrations of phytoplankton.

Based on our experiments, we argue that *Daphnia*, as the primary pelagic grazer in these ponds, may be capable of using benthic mats as a resource to offset limited food in the overlying water. The trophic transfer of benthic-derived primary production is one mechanism by which pelagic consumers can offset the shortages of pelagic resources, thereby stabilizing survival of the population with cross-habitat subsidies. Other examples of alternative food sources subsidizing pelagic consumers have focused on fish populations (Vanni et al. 1996; Vander Zanden et al. 2006) or zooplankton using alternative carbon sources such as methanotrophic bacteria (Taipale et al. 2008) or terrestrial subsidies (Cole et al. 2011; Karlsson et al. 2012). Bacterial biomass in the Kilpisjärvi ponds is low, ranging from 0.02 mg C L^{-1} to 0.05 mg C L^{-1} (Roiha et al. 2012), and is an inadequate source of PUFAs (Kaneda 1991). Even when

bacteria are added to the phytoplankton abundance, the tundra ponds remain below the threshold food concentration. The pelagic food deficit is confirmed by another approach that showed that the daily pelagic production was less than half the required energy demands of pelagic consumers in a tundra pond (Cazzanelli et al. 2012).

Benthic–pelagic coupling provides a relevant example of cross-habitat resource mobilization. Cadenasso et al. (2003) argued that resource heterogeneity at any scale could be a driver of ecological processes. There are two levels of heterogeneity discussed in this study that may contribute to the exploitation of benthic resources. At the lake scale, the benthic and pelagic habitats are spatially and functionally different resources. The pelagic habitat is a free-flowing, spacious media, where grazers can easily filter the phytoplankton through their setae; in contrast, the benthic habitat is a comparatively coagulated matrix that is attached to the pond bottom. Therefore, the feeding strategy of each consumer will drive consumer habitat selection. Within-mat heterogeneity and surface-layer effects may facilitate benthic resource acquisition by pelagic consumers. Although landscape theory is mainly terrestrial based, aquatic ecosystems provide intriguing models of how organisms, material, and energy move across ecological boundaries (Cadenasso et al. 2003). Pond morphometry creates a high potential for physical and chemical interactions between the benthic and pelagic habitats (Vadeboncoeur et al. 2008). Grazers accessing the benthic mats are important habitat couplers, helping to stimulate exchange of nutrients, mix the surface layers, and implement top-down controls on primary producers, all of which, in turn, promote primary and secondary production (Polis et al. 1997). These types of trophic interactions provide a mechanism for how habitat coupling can stabilize and maintain food webs (Marecchelli et al. 2011). Based on the abundance, algal community composition, and nutritional content of benthic mats, our results highlight a more complex function for benthic mats in pond food webs than previously thought. Benthic mats can serve as a key component in aquatic ecosystems and should be regularly incorporated into aquatic food web studies.

Acknowledgments

Thanks to K. Pulkkinen and S. Aalto for providing experimental recommendations, M. Cazzanelli and L. Hamerlik for help collecting Greenland data, J. Watzke for advice regarding fatty acid analysis, and M. Cusson for statistical assistance. We are grateful for in-kind support from the Kilpisjärvi Biological Station and the WasserKluster Lunz Interuniversity Center, Austria. Core funding was provided by Academy of Finland with grants 19205 and 140775 to M.R.

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Associate editor: Alexander D. Huryn

Received: 19 June 2013
 Accepted: 02 January 2014
 Amended: 14 January 2014