



<http://www.diva-portal.org>

This is the published version of a paper published in *Ecosphere*.

Citation for the original published paper (version of record):

Bergström, A., Karlsson, D., Karlsson, J., Vrede, T. (2015)

N-limited consumer growth and low nutrient regeneration N:P ratios in lakes with low N deposition.

*Ecosphere*, 6(1)

<http://dx.doi.org/10.1890/ES14-00333.1>

Access to the published version may require subscription.

N.B. When citing this work, cite the original published paper.

Permanent link to this version:

<http://urn.kb.se/resolve?urn=urn:nbn:se:umu:diva-102480>

## N-limited consumer growth and low nutrient regeneration N:P ratios in lakes with low N deposition

ANN-KRISTIN BERGSTRÖM,<sup>1,†</sup> DANIEL KARLSSON,<sup>1</sup> JAN KARLSSON,<sup>1,2</sup> AND TOBIAS VREDE<sup>3</sup>

<sup>1</sup>*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden*

<sup>2</sup>*Climate Impacts Research Centre (CIRC), Department of Ecology and Environmental Science, Umeå University, SE-981 07 Abisko, Sweden*

<sup>3</sup>*Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Box 7050, SE-750 07 Uppsala, Sweden*

**Citation:** Bergström, A.-K., D. Karlsson, J. Karlsson, and T. Vrede. 2015. N-limited consumer growth and low nutrient regeneration N:P ratios in lakes with low N deposition. *Ecosphere* 6(1):9. <http://dx.doi.org/10.1890/ES14-00333.1>

**Abstract.** Nutrient limitation of primary producers and their consumers can have a large influence on ecosystem productivity. The nature and strength of nutrient limitation is driven both by external factors (e.g., nutrient loading) and internal processes (e.g., consumer-driven nutrient regeneration). Here we present results from a field study in 10 low productive headwater lakes in northern subarctic Sweden, where nitrogen (N) deposition is low and phytoplankton is primarily N-limited. We assessed the carbon:nitrogen:phosphorus (C:N:P) stoichiometry of seston and zooplankton and estimated the N:P ratio of consumer-driven nutrient regeneration. Based on stoichiometric models, the estimated elemental imbalances between seston and zooplankton suggest that zooplankton were mainly N-limited and regenerated nutrients with low N:P ratios (median 11.9, atomic ratio). The predicted N:P regeneration ratios were consistent with results from phytoplankton nutrient limitation bioassays in mid-summer, i.e., the N:P regeneration was predicted to be low when phytoplankton were N-limited, and high when phytoplankton were P-limited. During other seasons, when water discharge was high, nutrient loading from the surrounding catchments apparently had the strongest effect on phytoplankton nutrient limitation. We propose that lakes with higher N:P ratios than the open ocean is an effect of N deposition, that N-limitation of consumers and phytoplankton is further enhanced by low nutrient regeneration N:P ratios, and that in the absence of N deposition, lake and ocean N:P stoichiometry are similar.

**Key words:** consumer driven nutrient cycling; ecological stoichiometry; nitrogen; nutrient limitation; phosphorus; phytoplankton; zooplankton.

**Received** 7 October 2014; accepted 9 October 2014; final version received 11 December 2014; **published** 21 January 2015.  
Corresponding Editor: D. P. C. Peters.

**Copyright:** © 2015 Bergström et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. <http://creativecommons.org/licenses/by/3.0/>

† **E-mail:** ann-kristin.bergstrom@emg.umu.se

### INTRODUCTION

Primary consumers perform important functions in ecosystems such as transfer of energy and nutrients from primary producers to higher trophic levels and recycling of nutrients. Hence, factors affecting the consumers and their trophic transfer or nutrient recycling may have large repercussions on other components of food webs

and ecosystem functions. Metazoan consumers have limited intraspecific variation in their carbon:nitrogen:phosphorus (C:N:P) stoichiometry (Andersen and Hessen 1991), and the stoichiometry of their prey does not necessarily match their nutritional requirements (Urabe and Sterner 1996, Hessen and Andersen 2008). Consequently, according to ecological stoichiometry theory, consumers are predicted to selectively

retain the limiting element while excreting or egesting excess elements in order to maintain their C:N:P stoichiometry (Sterner and Hessen 1994, Sterner and Elser 2002).

Conventional wisdom and most published literature state that the N:P ratio of phytoplankton (or rather of seston which also includes bacteria, protozoans and detritus, *c.f.* Hessen 2006) is higher in lakes than in marine systems, and that zooplankton N:P ratios are higher in marine systems than in lakes (Elser and Hassett 1994, Hassett et al. 1997). These observations subsequently imply that the nutrient N:P imbalances between prey (seston) and consumers (zooplankton), are generally positive (i.e.,  $N:P_{\text{seston}} - N:P_{\text{consumers}} > 0$ ) in lakes, and negative (i.e.,  $N:P_{\text{seston}} - N:P_{\text{consumers}} < 0$ ) in marine systems. As a result, zooplankton growth is predicted to be P-limited in many lakes but N-limited in marine systems. This in turn has implications for consumer-driven nutrient regeneration, i.e., feeding on phytoplankton with suboptimal P (in lakes) or N (in marine systems) content is predicted to result in high consumer-driven N:P regeneration in lakes and low N:P regeneration in marine systems, which in turn underpins phytoplankton P-limitation in lakes and N-limitation in marine systems (Hassett et al. 1997, Elser et al. 2007).

Although P-limitation has long been the dominating paradigm for lake ecosystems (*cf.* Schindler 1978, Lewis and Wurtsbaugh 2008), it may not be applicable to all lakes, particularly not for the most common lake type worldwide; i.e., low productive lakes, with naturally low levels of available nutrients (Elser et al. 2009a, Karlsson et al. 2009). Recent research has shown that phytoplankton production is naturally N-limited in lakes subject to low rates of N deposition (Bergström et al. 2008, Elser et al. 2009a). Furthermore, enhanced anthropogenic N deposition has resulted in elevated TN:TP ratios in many lakes in the northern hemisphere, and a corresponding shift from N- to P-limitation (Bergström et al. 2005, Elser et al. 2009a), which in turn has increased phytoplankton biomass (Bergström and Jansson 2006) and elevated sestonic N:P ratios (Elser et al. 2009b). It has also been shown that phytoplankton P-limitation induced by high N deposition impairs the growth of consumers with high P demand due

to food quality constraints and low P content in phytoplankton (Elser et al. 2010).

Here we present a study on the elemental stoichiometry of seston and crustacean zooplankton in a series of subarctic headwater lakes in northern Sweden with low N deposition where phytoplankton are primarily N- and NP-limited (Bergström et al. 2008, 2013). By using stoichiometric models (Sterner 1990, Hassett et al. 1997), we estimated the N:P imbalances between prey (seston) and consumers (zooplankton) and the consumer driven N:P regeneration ratios. We also tested if consumer driven N:P regeneration was related to patterns in N- or P-limitation of phytoplankton (Bergström et al. 2013) and compared our results with previous studies from subarctic and boreal lakes with low and high N deposition (Hassett et al. 1997, Dobberfuhl and Elser 2000), and marine ocean sites where zooplankton-phytoplankton interactions have been assessed (Elser and Hassett 1994, Hassett et al. 1997). We hypothesize that (1) N:P imbalances between seston and zooplankton are negative (i.e., similar to ocean sites with N-limited phytoplankton), which results in low consumer-driven N:P regeneration, and (2) the N:P regeneration ratio of the consumers is negatively related to the strength of phytoplankton N-limitation relative to P-limitation, i.e., consumer-driven nutrient recycling in these systems further enhances N-limitation particularly in systems with large negative N:P imbalance.

## MATERIAL AND METHODS

### Study area

The 10 study systems are clear-water, nutrient poor, headwater lakes in subarctic Sweden, with short growing seasons and low water temperature. The lakes are situated along an altitudinal and climate gradient from sub-alpine (300–650 mean catchment altitude above sea level [mca<sub>sl</sub>]; three lakes) to low-mid alpine (600–1000 mca<sub>sl</sub>; four lakes) to high-alpine (>1000 mca<sub>sl</sub>; four lakes) vegetation zones (Table 1) (*cf.* Bergström et al. 2013). This altitude gradient corresponds to a difference in mean annual air temperature range of ca. 6.3°C assuming a lapse rate of 0.57°C per 100 m elevation (Laaksonen 1976). The length of the ice-free season varies from ca. 4 months in

Table 1. Location, catchment characteristics, morphometry and fish species of the 10 study lakes in N. Sweden.

Lake†	Latitude (°N)	Longitude (°E)	Mean catchment altitude (m)	Catchment area (ha)	Unvegetated area (%)	Lake area (ha)	Max. depth (m)	Fish species
SA2	68°20.0566'	18°58.0968'	400	57	0	5.7	5	Arctic char
SA3	68°26.0631'	18°25.8088'	460	58	0	3.5	11	Arctic char
SA4	68°26.3886'	18°26.3295'	480	17	0	2.0	14	Arctic char
LMA5	68°12.2633'	19°33.9857'	734	25	0	3.5	8	Arctic char, Ninespine stickleback
LMA7	68°17.8734'	19°7.2586'	874	21	18	1.9	8	Arctic char
LMA8	68°17.6215'	19°6.6546'	966	156	10	10.9	8	Arctic char
HA9	68°16.7145'	19°5.6800'	1100	124	30	17.4	16	Arctic char
HA10	68°21.8690'	18°41.8095'	1129	60	96	1.4	5	no fish
HA11	68°16.3396'	18°41.4872'	1314	249	96	17.4	12	no fish
HA12	68°14.1792'	18°49.4410'	1478	532	99	26.6	24	no fish

† Lake names indicate the vegetation zone in which the catchments are mainly situated: SA, sub-alpine; LMA, low- to mid-alpine; HA, high-alpine.

sub-alpine areas to ca. 3 months in high-alpine areas. Lake area and maximum lake depth range between 2 and 27 ha, and 5 and 24 m, respectively. Seven of the lakes have fish, mostly Arctic char (*Salvelinus alpinus*), and three lakes (high-alpine) are fishless (Table 1). The lakes are located on weathering resistant bedrock (granite, gneiss and amphibolites) (Karlsson et al. 2005, Jansson et al. 2010). The terrestrial net primary production, which is correlated with air temperature, ranges from 2 g C m<sup>-2</sup> yr<sup>-1</sup> (high-alpine) to 250 g C m<sup>-2</sup> yr<sup>-1</sup> (sub-alpine) (Jansson et al. 2008). Precipitation (Karlsson et al. 2005) and N deposition varies little with altitude; wet dissolved inorganic nitrogen (DIN) deposition < 0.3 kg N ha<sup>-1</sup> yr<sup>-1</sup> (Bergström et al. 2013). Anthropogenic influences via land use are negligible.

### Sampling and analyses

Sampling was conducted three times in each lake during the open water season (mid-June to early September) 2011, i.e., covering the whole ice-free season (depending on altitude and year, ice out and beginning of ice cover takes place in June/early July and late September/October, respectively). On each occasion, vertical profiles of temperature (WTW multiline P4 Sensor, WTW, GmbH, Weilheim, Germany) and photosynthetically active radiation (PAR) light intensity (LI-193 Spherical Quantum Sensor, LI-COR Biosciences, Lincoln, Nebraska, USA) were measured. The mean PAR irradiance for the mixed water layer ( $I_m$ ), which is a dimensionless estimate that express the variation in light climate between lakes, was calculated according to Karlsson et al. (2009). Water samples for

analysis of lake water chemistry and chlorophyll a (Chl a) were collected on each occasion at a depth of 1.5 m, within the mixed layer. Lake water samples were analyzed for dissolved organic carbon (DOC), total nitrogen (TN), ammonium (NH<sub>4</sub><sup>+</sup>-N), nitrite plus nitrate (NO<sub>2</sub><sup>-</sup>+NO<sub>3</sub><sup>-</sup>-N), total phosphorus (TP) and Chl a as described in Bergström et al. (2013). Water was also collected, prescreened through a 50-µm net, and the filtered water was later used for sestonic particulate C, N, and P analysis (see below). Sampling for zooplankton biomass and composition were obtained by vertically hauling a plankton net (25 cm diameter; mesh size 100 µm) one meter from the bottom to the surface at the deepest point in the lake. Samples were preserved with Lugol's solution and stored dark and cold until counting. Zooplankton samples for stoichiometric analyses (C:N:P) were taken following the same procedure as for biomass, with the exception that several net hauls were used to make sure that sufficient plankton were collected. Samples from the hauls were transferred to plastic bottles in the field and brought to the lab. In the lab, zooplankton were collected on a 200-µm net, which was wrapped in aluminum foil, and stored frozen until analysis (see below).

For analysis of sestonic particulate C, N, and P, prescreened (50 µm) lake water was passed through a pre-combusted (550°C, 4h) and acid-washed (1.2M HCl) 25mm GF/F glass fiber filter (Whatman Arbor Technologies, Ann Arbor, MI, USA), until the filter was clogged. This procedure was repeated twice, i.e., two filters, one for analyses of C and N, and one for P. The filters

were stored frozen until analyses, and then analyzed using a Costech ECS 4010 elemental analyzer (Costech International). Analyses for P were made according to Swedish standard (ISO 15681-1, rev 4) using a FIAstar 5000 (FOSS).

Crustacean zooplankton taxa were identified and counted using inverted microscopy, and the dry weight (DW) was estimated from length measurements and length-dry weight regressions (Bottrell et al. 1976). Zooplankton were grouped into cladocerans (comprising *Holopedium gibberum*, *Bosmina* spp. and *Daphnia* spp.) and copepods (comprising nauplii, cyclopoid and calanoid copepodites and adults). For C, N and P determination, zooplankton were also pooled into groups of cladocerans and copepods, but when abundances were high *Bosmina* spp., *Daphnia* spp. and *Holopedium gibberum* were also analyzed separately for C, N, and P content. For analyses of C and N, each group was picked and placed onto pre-weighed combusted (550°C, 4h) GF/C filter (Whatman Arbor Technologies). The same procedure was repeated for P, but using burned, pre-weighed and acid-washed (1, 2M HCl) GF/C filters. Filters were dried (60°C) overnight, and then weighed to determine dry weight of copepods and cladocerans, respectively. Analyses for C, N and P were then the same as for seston (see above). The zooplankton DW ranged between 200–400 µg DW for C and N analyses and 100–200 µg DW for P analyses.

Elemental imbalances between resources (seston) and consumers (zooplankton) and the stoichiometry of the nutrients recycled by the zooplankton were predicted based on stoichiometric models according to Sterner (1990) and Hassett et al. (1997):

$$N : P_{\text{imbalance}} = N : P_{\text{seston}} - N : P_{\text{consumer}} \quad (1)$$

If  $N : P_{\text{imbalance}} > 0$ ,

then

$$N : P_{\text{recycled}} = \frac{(N : P_{\text{seston}} - N : P_{\text{consumer}})AE}{1 - AE} \quad (2)$$

If  $N : P_{\text{imbalance}} \leq 0$ ,

then

$$N : P_{\text{recycled}} = \frac{N : P_{\text{seston}}(1 - AE)}{1 - \frac{AE N : P_{\text{seston}}}{N : P_{\text{consumer}}}} \quad (3)$$

where AE is the maximum accumulation effi-

ciency of the limiting element. For P the AE has been reported to range from 0.5 to 0.9, with the most common AEs being in the upper range of 0.7–0.9 (DeMott 1998, DeMott et al. 1998), whereas values of AE for N are less known. Hence, AE was assumed to be the same for both elements (cf. Sterner 1990). Similar to Hassett et al. (1997) we used an AE of 0.75, but also calculated  $N:P_{\text{recycled}}$  using AE equal to 0.5 and 0.9. The predicted  $N:P$  recycling ratios were calculated for copepods and cladocerans separately, as well as for all zooplankton using weighted means based on the relative proportion of copepods and cladocerans of the total zooplankton biomass.

We compared our results in seston and zooplankton stoichiometry, as well as predicted nutrient imbalances, to those reported from the Canadian shield experimental lake area (ELA), Ontario, Canada (Hassett et al. 1997), the Toolik Lake Area in Alaska, US (Dobberfuhl and Elser 2000), and from marine ocean sites (Hassett et al. 1997). Hence, these stoichiometric assessments of the zooplankton-phytoplankton interactions were performed without considering the possible impacts of N deposition on lake water  $N:P$  ratios and phytoplankton nutrient limitation. For the ELA and Alaska sites, the wet DIN deposition has been reported to be around 3–4 kg N ha<sup>-1</sup> yr<sup>-1</sup> (Canadian National Atmospheric Chemistry Particulate Matter Database 2014), and <0.5 kg N ha<sup>-1</sup> yr<sup>-1</sup> (Shaver et al. 1991), respectively. In the ELA lakes, phytoplankton has been shown to be mainly P-limited (Schindler 1977), whereas the phytoplankton in the Alaskan lakes have been reported to be both N- and P-limited (Levine and Whalen 2001). The marine ocean sites were chosen for comparison primarily based on earlier studies showing negative consumer  $N:P$  imbalances (Elser and Hassett 1994, Hassett et al. 1997), and phytoplankton N-limitation in these systems (Elser and Hassett 1994).

We also used data from previously published bioassay experiments for assessing which nutrient was limiting phytoplankton production (Bergström et al. 2013). These full factorial N- and P-amendment experiments were conducted at the same time as the water and zooplankton sampling. Briefly, clear polycarbonate bottles (250 ml) were filled with 50-µm screened lake

Table 2. Temperature, light climate and water chemistry of the 10 study lakes.  $I_m$ , mean photosynthetically active radiation irradiance in the mixed layer (a dimensionless estimate of the light climate in the mixed layer); DOC, dissolved organic carbon; TN, total nitrogen; TP, total phosphorus; DIN, dissolved inorganic nitrogen. All data show mean  $\pm$  SD for the three sampling occasions in June–August/September.

Lake†	Water temperature (°C)	PAR	DOC (mg C L <sup>-1</sup> )	TN (µg N L <sup>-1</sup> )	TP (µg P L <sup>-1</sup> )	DIN (µg N L <sup>-1</sup> )
SA2	14.9 $\pm$ 3.6	0.41 $\pm$ 0.10	6.0 $\pm$ 0.2	337 $\pm$ 55	3.9 $\pm$ 0.3	5 $\pm$ 2
SA3	10.5 $\pm$ 1.6	0.52 $\pm$ 0.11	3.8 $\pm$ 0.6	149 $\pm$ 43	2.9 $\pm$ 0.4	4 $\pm$ 1
SA	9.4 $\pm$ 2.0	0.51 $\pm$ 0.12	4.6 $\pm$ 0.6	207 $\pm$ 104	2.9 $\pm$ 0.7	3 $\pm$ 0
LMA5	11.4 $\pm$ 1.8	0.42 $\pm$ 0.10	3.2 $\pm$ 0.3	143 $\pm$ 39	4.6 $\pm$ 0.2	6 $\pm$ 6
LMA7	11.5 $\pm$ 2.1	0.51 $\pm$ 0.23	3.6 $\pm$ 0.7	149 $\pm$ 58	8.2 $\pm$ 2.2	5 $\pm$ 3
LMA8	10.6 $\pm$ 2.1	0.25 $\pm$ 0.07	3.1 $\pm$ 0.5	159 $\pm$ 32	7.0 $\pm$ 2.2	4 $\pm$ 1
HA9	9.6 $\pm$ 3.0	0.25 $\pm$ 0.07	2.3 $\pm$ 0.6	115 $\pm$ 22	4.2 $\pm$ 0.1	6 $\pm$ 3
HA10	9.6 $\pm$ 1.3	0.74 $\pm$ 0.21	2.1 $\pm$ 0.1	115 $\pm$ 25	3.8 $\pm$ 1.9	32 $\pm$ 18
HA11	9.6 $\pm$ 0.8	0.41 $\pm$ 0.11	1.3 $\pm$ 0.1	92 $\pm$ 27	2.2 $\pm$ 0.4	12 $\pm$ 7
HA12	7.7 $\pm$ 1.2	0.24 $\pm$ 0.08	1.0 $\pm$ 0.0	77 $\pm$ 21	2.1 $\pm$ 1.4	34 $\pm$ 19

† Lake names indicate the vegetation zone in which the catchments are mainly situated: SA, sub-alpine; LMA, low- to mid-alpine; HA, high-alpine.

water. Four treatments in triplicates were prepared: untreated controls (C), nitrogen addition (N), phosphorus addition (P), and combined nitrogen and phosphorus addition (NP). Nutrients were added to the bottles to increase N concentrations by 100 µg L<sup>-1</sup> (7.2 µmol L<sup>-1</sup>) and/or P concentrations by 10 µg L<sup>-1</sup> (0.3 µmol L<sup>-1</sup>). N was added as NH<sub>4</sub>NO<sub>3</sub> and P as KH<sub>2</sub>PO<sub>4</sub>. Bottles were incubated in a cabinet at temperatures and light levels similar to those measured in each lake at 1.5 m depth at each sampling occasion. After 48 hours, water was filtered onto GF/F filters which were then frozen and later processed for chlorophyll measurements as described above. Analysis of the bioassay results was carried out by calculating the relative response in final chlorophyll concentrations to N (RR-N), P (RR-P) or NP (RR-NP) additions relative to the control. The relative response to N and P amendment were subsequently calculated as RR-N/RR-P, where values >1 indicate stronger response to N- than to P-amendment. See detailed descriptions in Bergström et al. (2013).

Changes in nutrient concentrations, environmental factors, and stoichiometry of seston and zooplankton along the altitudinal gradient were analyzed using Pearson's product-moment correlation (SPSS Statistics 20). Zooplankton elemental content was analyzed with ANOVA followed by post hoc Tukey least significant difference tests (JMP 10.0). Differences in seston and zooplankton N:P stoichiometry and estimated N:P imbalances between our Swedish lakes and the ELA, Alaskan lakes and the marine ocean sites were

analyzed using one-way ANOVA followed by Holm-Sidak test (SigmaStat 12.0). Seasonal changes in zooplankton stoichiometry, elemental imbalance and N:P<sub>recycled</sub> as well as seasonal relationships between RR-N/RR-P and predicted N:P<sub>recycled</sub> were analyzed using ANCOVA (JMP 10.0).

## RESULTS

All lakes had nutrient poor low DOC water. Seasonal means for TP, TN, and DOC concentrations were 2–8 µg P L<sup>-1</sup>, 77–337 µg N L<sup>-1</sup>, and 1–6 mg C L<sup>-1</sup>, respectively (Table 2). The highest TP concentrations were found in two of the low- to mid-alpine lakes. TN concentrations were highest in the sub-alpine lakes, and decreased with increasing altitude ( $R = -0.503$ ,  $p = 0.000$ ). DIN concentrations were approximately four times higher in the high-alpine lakes than in the lakes at lower altitudes (Table 2). DOC decreased with increasing altitude ( $R = -0.881$ ,  $p = 0.000$ ). The mean PAR in the mixed layer ( $I_m$ ) ranged between 0.146 and 0.893 and was not significantly related with increasing altitude ( $R = -0.321$ ,  $p = 0.09$ ). Water temperature ranged from 7° to 19°C at 1.5 m depth, with highest temperatures in July/early August, and decreased with increasing altitude ( $R = -0.503$ ,  $p = 0.005$ ) (Table 2). Chlorophyll a concentrations ranged between 0.5 and 2.8 µg L<sup>-1</sup>, and was not significantly related with increasing altitude ( $R = -0.181$ ,  $p = 0.338$ ), but with the lowest concentrations found in two of the high-alpine lakes (Table 3). Sestonic

Table 3. Chlorophyll a (Chl a), seston C-, seston N-, and seston P-concentrations, and C:N, C:P and N:P ratios (atomic ratios) of the 10 study lakes. All data show mean  $\pm$  standard deviation for the three sampling occasions in June–August/September.

Lake†	Chl a ( $\mu\text{g L}^{-1}$ )	Seston C ( $\mu\text{g L}^{-1}$ )	Seston N ( $\mu\text{g L}^{-1}$ )	Seston P ( $\mu\text{g L}^{-1}$ )	C:N	C:P	N:P
SA2	1.9 $\pm$ 0.4	391 $\pm$ 88	49.0 $\pm$ 4.2	3.3 $\pm$ 1.5	9.3 $\pm$ 1.5	322 $\pm$ 73	36 $\pm$ 11
SA3	1.1 $\pm$ 0.4	241 $\pm$ 88	32.0 $\pm$ 9.1	2.4 $\pm$ 0.5	8.6 $\pm$ 0.9	251 $\pm$ 77	29 $\pm$ 6
SA	1.3 $\pm$ 0.2	242 $\pm$ 72	31.2 $\pm$ 11.0	1.9 $\pm$ 0.4	9.2 $\pm$ 0.7	317 $\pm$ 45	35 $\pm$ 7
LMA5	2.2 $\pm$ 0.7	349 $\pm$ 57	45.7 $\pm$ 5.5	3.5 $\pm$ 0.6	8.9 $\pm$ 0.6	258 $\pm$ 40	29 $\pm$ 3
LMA7	1.9 $\pm$ 0.1	295 $\pm$ 77	38.8 $\pm$ 7.1	3.9 $\pm$ 0.4	8.8 $\pm$ 1.1	197 $\pm$ 48	22 $\pm$ 3
LMA8	1.7 $\pm$ 0.4	244 $\pm$ 23	35.9 $\pm$ 0.8	3.1 $\pm$ 0.1	7.9 $\pm$ 0.9	204 $\pm$ 19	26 $\pm$ 1
HA9	2.3 $\pm$ 0.1	216 $\pm$ 15	32.8 $\pm$ 2.1	2.9 $\pm$ 0.2	7.3 $\pm$ 1.3	191 $\pm$ 18	27 $\pm$ 4
HA10	0.4 $\pm$ 0.1	187 $\pm$ 23	23.9 $\pm$ 6.5	1.8 $\pm$ 0.1	9.6 $\pm$ 2.7	261 $\pm$ 26	29 $\pm$ 7
HA11	1.9 $\pm$ 1.1	286 $\pm$ 72	39.3 $\pm$ 8.4	2.5 $\pm$ 0.8	8.4 $\pm$ 0.5	308 $\pm$ 53	37 $\pm$ 6
HA12	0.6 $\pm$ 0.1	110 $\pm$ 26	13.4 $\pm$ 3.4	1.1 $\pm$ 0.1	9.8 $\pm$ 2.4	265 $\pm$ 77	27 $\pm$ 4

† Lake names indicate the vegetation zone in which the catchments are mainly situated: SA, sub-alpine; LMA, low- to mid-alpine; HA, high-alpine.

C concentrations were also low (means for all lakes  $< 400 \mu\text{g C L}^{-1}$ ; Table 3), and decreased with increasing altitude ( $R = -0.483$ ,  $p = 0.007$ ). This was also the case for sestonic N concentrations which were negatively related with altitude ( $R = -0.449$ ,  $p = 0.013$ ). Seston P concentrations were not related to altitude ( $R = -0.312$ ,  $p = 0.09$ ). Across all lakes (Table 3), seston C:N, C:P and N:P ratios were  $8.8 \pm 1.4$ ,  $257.8 \pm 65.4$  and  $29.6 \pm 4.3$  (mean  $\pm$  SD, atomic ratios), respectively, and varied little among lakes (CV for C:N, C:P and N:P = 9%, 11% and 11%, respectively) and seasons (CV within each lakes for C:N, C:P and N:P varied between 6% and 11%, 13% and 36%, and 10% and 30%, respectively). Seston C:N, C:P and N:P ratios were not related to mean PAR in the mixed layer ( $I_m$ ) ( $R = -0.288$ ,  $p = 0.129$ ;  $R =$

$-0.194$ ,  $p = 0.313$ ;  $R = -0.042$ ,  $p = 0.828$ ).

Crustacean zooplankton biomass ranged between 9 and  $115 \mu\text{g DW L}^{-1}$ , and the lowest biomasses were observed in the high-alpine fishless lakes (Table 4). Zooplankton DW was not related with sestonic C, N, or P concentrations ( $R = 0.239$ ,  $p = 0.202$ ;  $R = 0.170$ ,  $p = 0.369$ ;  $R = 0.243$ ,  $p = 0.195$ ; respectively). Copepods (mainly calanoid copepods) dominated in biomass ( $80 \pm 24\%$ ) in all lakes except in two of the high-alpine lakes (Table 4). Cladocerans consisted mainly of *Bosmina* spp., *Daphnia* spp. and *Holopedium gibberum*.

The C content (% of DW, mean  $\pm$  SD) did not differ between copepods ( $53.2\% \pm 4.7\%$ ), mixed cladocerans ( $49.1\% \pm 3.0\%$ ), *Bosmina* ( $50.1\% \pm 4.8\%$ ) and *Daphnia* ( $49.4\% \pm 2.6\%$ ) (ANOVA,  $R^2_{\text{adj}} = 0.08$ ,  $p = 0.10$ ,  $F_{3,39} = 2.24$ ). The N content did not differ between copepods ( $8.4\% \pm 1.5\%$ ), mixed cladocerans ( $9.2\% \pm 0.6\%$ ) and *Bosmina* ( $9.0\% \pm 0.3\%$ ), but was significantly lower in *Daphnia* ( $5.9\% \pm 1.2\%$ ) in comparison with the other taxon (ANOVA followed by Tukey test,  $R^2_{\text{adj}} = 0.24$ ,  $p = 0.0035$ ,  $F_{3,39} = 5.34$ ) (Fig. 1 and Table 5). The P content was significantly lower in copepods ( $0.37\% \pm 0.22\%$ ) than in mixed cladocerans ( $0.64\% \pm 0.33\%$ ) and *Daphnia* ( $0.77\% \pm 0.13\%$ ), but *Bosmina* ( $0.46\% \pm 0.13\%$ ) did not differ significantly from any other taxon (ANOVA followed by Tukey test,  $R^2_{\text{adj}} = 0.21$ ,  $p = 0.0069$ ,  $F_{3,39} = 4.68$ ) (Fig. 1 and Table 5). The single *Holopedium* sample (not included in the statistical analyses above) contained 50.7% C, 9.6% N and 0.50% P.

Sestonic N:P ratios were significantly lower

Table 4. Zooplankton dry weight (DW) and proportions of copepods and cladocerans of the 10 study lakes. All data show mean  $\pm$  SD for the three sampling occasions in June–August/September.

Lake†	Zooplankton ( $\mu\text{g DW L}^{-1}$ )	Copepods (% DW)	Cladocerans (% DW)
SA2	63 $\pm$ 11	99.5 $\pm$ 0.4	0.5 $\pm$ 0.4
SA3	59 $\pm$ 49	86.5 $\pm$ 16.2	13.5 $\pm$ 16.2
SA4	54 $\pm$ 21	86.6 $\pm$ 12.4	13.4 $\pm$ 12.4
LMA5	83 $\pm$ 38	88.3 $\pm$ 7.6	11.7 $\pm$ 7.6
LMA7	87 $\pm$ 58	85.4 $\pm$ 5.1	14.6 $\pm$ 5.1
LMA8	47 $\pm$ 19	86.2 $\pm$ 8	13.8 $\pm$ 8
HA9	56 $\pm$ 53	88.1 $\pm$ 6.1	11.9 $\pm$ 6.1
HA10	35 $\pm$ 30	44.4 $\pm$ 32.1	55.6 $\pm$ 32.1
HA11	17 $\pm$ 6	99.8 $\pm$ 0.4	0.2 $\pm$ 0.4
HA12	25 $\pm$ 9	39.5 $\pm$ 29.8	60.5 $\pm$ 29.8

† Lake names indicate the vegetation zone in which the catchments are mainly situated: SA, sub-alpine; LMA, low- to mid-alpine; HA, high-alpine.

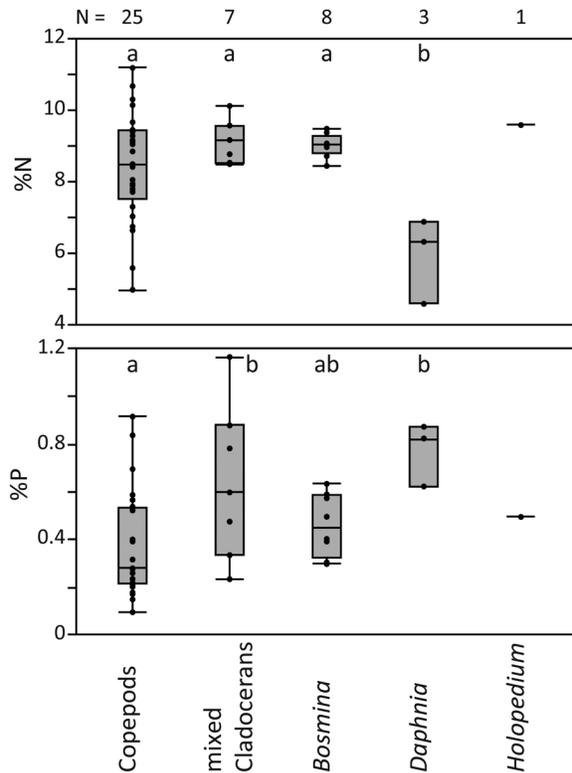


Fig. 1. Nitrogen (N) and phosphorus (P) content (% of DW) in zooplankton in the 10 studied subarctic lakes. The line within the box show median, the box 25% and 75% percentiles and the whiskers 10% and 90% percentiles. Significantly different N and P contents are shown by different letters (Tukey post hoc test,  $\alpha = 0.05$ ).

than those reported from ELA and Alaskan lakes (one-way ANOVA followed by Holm-Sidak test,  $p < 0.001$  and  $p < 0.015$ , respectively) and significantly higher than those reported from ocean sites (one-way ANOVA followed by Holm-Sidak test,  $p < 0.031$ ) (Fig. 2A). The zooplankton N:P ratios (for copepods, cladocerans, and for combined zooplankton) were all significantly higher in this study than those reported from the ELA and Alaskan lakes and from the ocean sites (one-way ANOVA followed by Holm-Sidak test,  $p < 0.05$ ) (Fig. 2B). The predicted N:P nutrient imbalances in zooplankton were negative for the Swedish lakes (Fig. 2C), and differed significantly from the ELA and Alaskan lakes and the ocean sites (one-way ANOVA followed by Holm-Sidak test,  $p < 0.05$ ), except for cladocerans, whose N:P imbalance was similar to ocean sites (one-way ANOVA followed by Holm-Sidak test,  $p < 0.881$ ). For cladocerans, predicted N:P imbalances were negative on 63% of the occasions and positive on 37% of the occasion, whereas for copepods N:P imbalances were mostly negative (85% of the occasions).

The predicted consumer-driven N:P regeneration of cladocerans, copepods and the combined zooplankton community was in most cases below the Redfield ratio (atomic ratio 16), irrespective of varying the AE (i.e., 0.5, 0.75 and 0.9), and the median predicted N:P regeneration declined with increasing AE (Fig. 3). Using an AE of 0.75, the median predicted N:P regeneration ratio was 13.2 for cladocerans, 12.1 for copepods and 12.1 for all zooplankton combined.

The predicted consumer-driven N:P regenera-

Table 5. Zooplankton C, N, and P content per unit DW of pooled samples of copepods and cladocerans of the 10 study lakes. All data show mean  $\pm$  SD for the three sampling occasions in June–August/September.

Lake†	Copepods			Cladocerans		
	(C% DW)	(N% DW)	(P% DW)	(C% DW)	(N% DW)	(P% DW)
SA2	51.4	9.4	0.7	...	...	...
SA3	51.0 ( $\pm 0.4$ )	8.7 ( $\pm 0.8$ )	0.4 ( $\pm 0.1$ )	50.7 ( $\pm 1.5$ )	9.7 ( $\pm 0.6$ )	0.8 ( $\pm 0.2$ )
SA4	50 ( $\pm 7.8$ )	8.6 ( $\pm 0.6$ )	0.5 ( $\pm 0.3$ )	48.5 ( $\pm 3.1$ )	9.6 ( $\pm 0.1$ )	0.7 ( $\pm 0.2$ )
LMA5	47.1 ( $\pm 3.1$ )	10.3 ( $\pm 0.8$ )	0.6 ( $\pm 0.4$ )	45.2 ( $\pm 1.4$ )	9.4 ( $\pm 0.1$ )	0.6 ( $\pm 0.2$ )
LMA7	55.0 ( $\pm 4.2$ )	7.4 ( $\pm 0.6$ )	0.2 ( $\pm 0.1$ )	51.9 ( $\pm 5.1$ )	8.5 ( $\pm 0.1$ )	0.6 ( $\pm 0.5$ )
LMA8	57.8 ( $\pm 1.1$ )	6.5 ( $\pm 0.9$ )	0.3 ( $\pm 0.2$ )	52.2 ( $\pm 1.6$ )	8.9 ( $\pm 0.1$ )	0.4 ( $\pm 0.3$ )
HA9	56.2 ( $\pm 3.7$ )	6.6 ( $\pm 1.5$ )	0.2 ( $\pm 0.0$ )	53.6	9.1	0.3
HA10	52.4 ( $\pm 1.6$ )	9.7 ( $\pm 1.5$ )	0.2 ( $\pm 0.0$ )	49.2 ( $\pm 4.7$ )	8.9 ( $\pm 0.2$ )	0.5 ( $\pm 0.1$ )
HA11	53.6 ( $\pm 2.3$ )	9.4 ( $\pm 0.1$ )	0.3 ( $\pm 0.2$ )	...	...	...
HA12	54.8 ( $\pm 6.4$ )	9.1 ( $\pm 0.0$ )	0.5 ( $\pm 0.1$ )	49.4 ( $\pm 2.6$ )	5.9 ( $\pm 1.2$ )	0.8 ( $\pm 0.2$ )

† Lake names indicate the vegetation zone in which the catchments are mainly situated: SA, sub-alpine; LMA, low- to mid-alpine; HA, high-alpine.

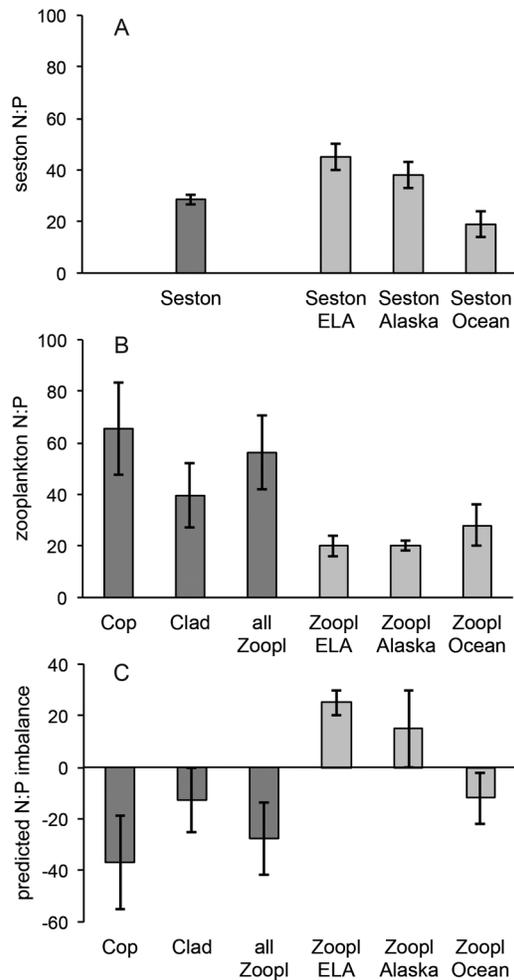


Fig. 2. Atomic N:P ratios of seston, copepods, cladocerans, the whole zooplankton community and predicted N:P imbalances (mean  $\pm$  SD) in the 10 studied subarctic lakes (dark gray bars). For comparison, data from the Canadian Shield experimental lakes area (ELA), Alaska and Oceans sites (from Hassett et al. (1997) and Dobberfuhl and Elser (2000)) is also shown (light gray bars).

tion of zooplankton (using an AE of 0.75) was negatively related to the relative response to N (RR-N) vs. P (RR-P) amendments in the bioassays experiments (i.e., the RR-N/RR-P ratio) with phytoplankton in mid-summer (July; Fig. 4B) but not in early summer (June; Fig. 4A) or in late summer/early autumn (August/September; Fig. 4C). Hence, during mid-summer low predicted N:P regeneration ratios occurred in lakes where phytoplankton were primarily N-limited, and

high predicted N:P regeneration ratios occurred in lakes with primarily P-limited phytoplankton, whereas our estimated N:P regeneration ratios could not predict phytoplankton nutrient limitation during other seasons (Fig. 4).

## DISCUSSION

Our first hypothesis, that there is a negative N:P imbalance (i.e., similar to ocean sites) between seston and zooplankton in lakes with low N deposition where phytoplankton is mainly N-limited, was supported by our results. Furthermore, the hypothesis that consumer-driven nutrient recycling in these systems further enhances N-limitation of phytoplankton was partially supported. Specifically, this negative feedback was observed during the summer period, when internal processes in the lakes rather than external processes on the catchment scale are important determinants of nutrient turnover in these systems.

Similar to earlier studies conducted in these lakes we found that basal food resources (sestonic C) decreased with increasing altitude, because of decreasing N concentrations which affect phytoplankton biomass (Karlsson et al. 2005, Bergström et al. 2008, 2013), and decreasing DOC concentrations which affect bacterioplankton biomass and detritus concentrations (Karlsson et al. 2005, Jansson et al. 2008). Zooplankton biomass was, however, not related to food concentrations (sestonic C), although sestonic C concentrations usually were below the threshold for when food quantity become suboptimal and potentially insufficient for somatic growth and reproduction investments ( $<400 \mu\text{g C L}^{-1}$ ) (Müller-Navarra and Lampert 1996, McCauley et al. 1990). In addition, we could not relate zooplankton biomass and/or composition to fish predation (cf. Hessen et al. 1995, Jansson et al. 2010), i.e., zooplankton biomass was not higher in the fishless lakes and neither were cladocerans dominating in all fishless lakes (cf. Johnson et al. 2010). Thus, zooplankton biomass and composition could not be directly coupled to the abundance of food resources or to the presence/absence of fish.

Similar to Hessen (2006), we found the variability in sestonic C:N:P elemental stoichiometry was low both among lakes and over the

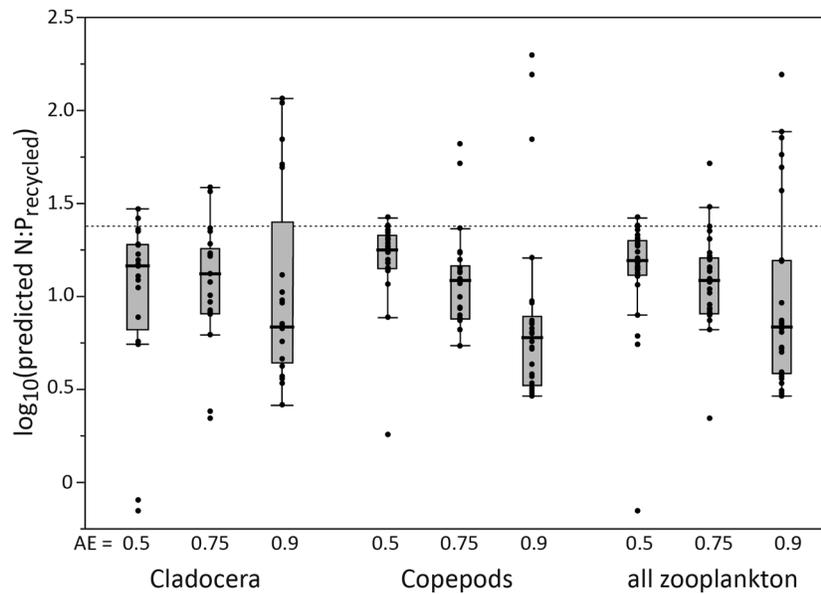


Fig. 3. Predicted nutrient regeneration N:P ratios (molar ratios, calculated with accumulation efficiencies (AE) of 0.5, 0.75 and 0.9, respectively) for cladocerans, copepods and all zooplankton (based on weighted mean biomass) in the 10 studied subarctic lakes. Horizontal hatched line shows N:P = 16 (Redfield ratio).

season. Differences in light availability could potentially increase sestonic C:P and C:N ratios (cf. Dobberfuhl and Elser 2000). However, this was unlikely because the estimated relative light intensities ( $I_m$ ) did not differ among lakes, and were additionally not related to C:P, C:N and N:P ratios. In line with previously reported results, the sestonic N:P ratio was similar in our study (30) to that in lakes of Colorado (28) and Norway (28) where phytoplankton was primarily N-limited, and where N deposition is too low to cause increases in surface water TN:TP or sestonic N:P (e.g., Elser et al. 2009a, b, 2010). Supporting these results on nutrient limitation in phytoplankton, mean sestonic N:P ratios was significantly higher in the ELA lakes (wet DIN deposition 3–4 kg N ha<sup>-1</sup> yr<sup>-1</sup>) where phytoplankton have been reported to be mainly P-limited (Schindler 1977).

However, not only N deposition but also the catchment characteristics and terrestrial N turnover influence the amount of reactive N from deposition that is delivered to lakes and eventually affects DIN concentrations. For that reason, although N deposition levels are much lower, subalpine and arctic catchments with little vegetation can exhibit much higher DIN:TP

ratios than boreal lakes in catchments with well-developed soils and productive forests (Bergström et al. 2008, 2013, Elser et al. 2009a, Hessen 2013). This may therefore be the underlying reason to higher mean sestonic N:P ratios at the Alaskan sites in comparison with the Swedish sites although deposition in Alaska is fairly low (wet DIN deposition < 0.5 kg N ha<sup>-1</sup> yr<sup>-1</sup>). Phytoplankton has also been reported to be N- and/or P-limited in Alaska, and the nature of the limiting nutrient is largely determined by the surrounding catchment characteristics that influence the N:P nutrient delivery to the lakes (Levine and Whalen 2001).

Considering the zooplankton stoichiometry, the C, N, and P contents observed in our study were in the same range as those reported in other studies (e.g., Andersen and Hessen 1991, Sterner et al. 1992) with the exception of the lower N and P contents we observed in *Daphnia*. The N:P ratios of copepods and cladocerans (65 and 50) found in our lakes were similar to or higher than those reported in copepods in lakes in Norway (39 to 52) (Sterner et al. 1992), and higher than the N:P ratios measured on pooled zooplankton samples from ocean sites (ca. 30) (Hassett et al. 1997), ELA lakes (ca. 20) (Hassett et al. 1997), and

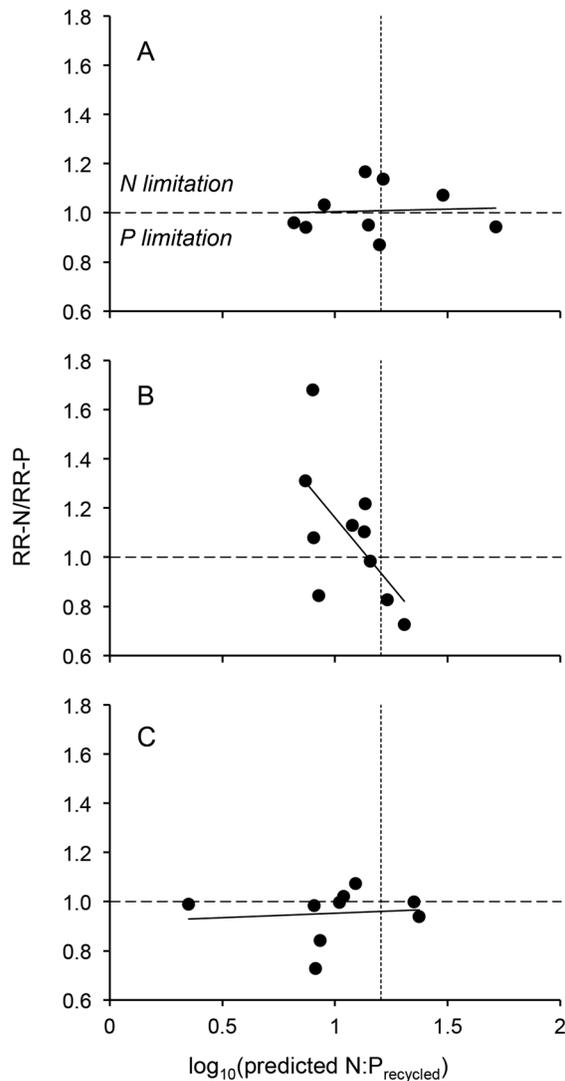


Fig. 4. Relationships between zooplankton molar predicted N:P regeneration ratio ( $\log_{10}$  scale, assuming an assimilation efficiency of 0.75) and phytoplankton response ratio in N (RR-N) and P (RR-P) enrichment bioassay experiments in (A) early summer (June), (B) mid-summer (July), and (C) late summer (late August/early September) in the 10 studied subarctic lakes. Horizontal hatched lines show  $RR-N/RR-P = 1$ , i.e., a value  $> 1$  indicate stronger response to N than to P, and vice versa. Vertical dotted lines show  $N:P = 16$  (Redfield ratio). Regression lines show fitted responses from ANCOVA with the effects  $\log_{10}(\text{predicted } N:P_{\text{recycled}})$ , season and  $\log_{10}(\text{predicted } N:P_{\text{recycled}}) \times \text{season}$ . Whole model:  $R^2 = 0.37$ ,  $F_{5,22} = 2.63$ ,  $p = 0.05$ . Effect tests: season,  $p = 0.31$ ;  $\log_{10}(\text{predicted } N:P_{\text{recycled}})$ ,  $p = 0.03$ ;  $\log_{10}(\text{predicted } N:P_{\text{recycled}}) \times \text{season}$ ,  $p = 0.05$ . The RR-N/RR-P data is from Bergström et al. (2013).

Alaska lakes (20) (Dobberfuhl and Elser 2000).

The N:P ratios of copepods, cladocerans, and the combined zooplankton community were on average higher than seston N:P ratios, and the predicted nutrient imbalances were therefore negative. This suggests that zooplankton in these lakes have a food resource with suboptimal N content, which then results in N-limitation of zooplankton production and a high assimilation of N and efficient recycling of P (excess P is excreted or egested). Hence, the predicted nutrient imbalances in our lakes were very similar to those predicted and reported in N-limited marine ocean sites (cf. Hassett et al. 1997). Consequently, feeding on N-limited phytoplankton with low N:P ratio result in low predicted N:P regeneration by zooplankton. This would in turn feedback and sustain N-limitation of phytoplankton in these lakes.

Schindler et al. (2008) proposed that N-limitation can be compensated by increases in abundance of  $N_2$ -fixing cyanobacteria. However, studies of nutrient poor northern lakes show low abundances of  $N_2$ -fixing cyanobacteria in the water column (Holmgren 1983, Jansson et al. 2001), and cyanobacteria do not seem to develop even under extreme N-limited conditions induced by P-enrichment in whole-lake enrichment experiments over the summer (Jansson et al. 2001). Possible explanations (that are not mutually exclusive) for low cyanobacteria abundances in these lakes could be the natural low nutrient levels (of especially P) (Downing et al. 2001), that lakes are too cold (Butterwick et al. 2005), or that ferrous iron concentrations (Molot et al. 2014) are limiting their development.

The median predicted N:P regeneration ratio was  $< 16$  (Redfield ratio) both for copepods and cladocerans, irrespective of which AE we used in our model calculations. Since the zooplankton communities in our lakes were dominated by copepods, the predicted N:P recycling ratio for the zooplankton community as a whole was very similar to the ones for copepods. Our results are in that sense consistent with ecological stoichiometry theory that herbivore assemblages dominated by copepods (high somatic N:P) should result in low N:P regeneration ratios that could potentially lead to N-limitation of phytoplankton (Sterner et al. 1992). However, in our study, this predicted

nutrient recycling pattern could also be attributed to cladocerans. We suggest this pattern in consumer-driven N:P regeneration to be an effect of the composition of cladoceran communities, which in our lakes were dominated by *Bosmina* (with the exception for one of the high-alpine lakes which was dominated by *Daphnia*). *Bosmina* have lower percentage of body P content (cf. Fig. 1, Schulz and Sterner 1999), and lower P:C threshold elemental ratios (Urabe and Watanabe 1992) than that of *Daphnia*, and may also experience N-limitation (Urabe and Watanabe 1992). It has also been shown in mesocosms experiments that, when manipulating zooplankton community composition towards lower biomass and smaller sized herbivore consumers, consumer-driven N:P regeneration can decline and induce N-limitation in phytoplankton (Elser et al. 1988). Thus, low N:P regeneration among cladocerans in our lakes are likely explained by the dominance of small sized *Bosmina*.

Based on our stoichiometric assessment of seston and zooplankton when phytoplankton are N-limited, we predict low rates of N regeneration by zooplankton. Indeed, the predicted N:P recycling ratio by zooplankton was consistent with the pattern in N- and P-limitation in phytoplankton observed in the bioassay experiments but only in mid-summer (Fig. 4B), indicating the importance of the internal nutrient regeneration by the consumers for phytoplankton. This was not the case during other times of the open water season (Fig. 4A, C). We suggest that this seasonal shift is linked to lake and catchment hydrology. Specifically, during early and late parts of the season, lake water N:P stoichiometry and nutrient limitation of phytoplankton growth are mainly determined by external factors, including catchment hydrology and other landscape characteristics (N deposition, character and percentage vegetation cover, etc.) which combined determines the N:P nutrient loading (Downing and McCauley 1992, Bergström et al. 2008, 2013, Bergström 2010, Hessen 2013). The majority of the hydrological loading to these lakes occurs during spring snowmelt and autumn rains, and such inputs are much lower during summer (cf. Bergström et al. 2008, 2013), during which time internal processes, such as nutrient regeneration from

the sediments (cf. Levine and Schindler 1992), or as indicated from our results, nutrient regeneration by zooplankton appears to become an important determinant of nutrient availability to phytoplankton.

The results are therefore in line with those from arctic Alaska lakes where internal consumer-driven nutrient regeneration was shown to be unrelated to patterns of phytoplankton nutrient limitation during periods of high run-off, when the internal nutrient sources were overwhelmed by external loading (Johnson and Luecke 2012). During low-flow periods, however, consumer-driven nutrient regeneration affected patterns in N- and P-limitation in phytoplankton. In addition to the influence of external inputs, periods of high hydrological loading to our studied lakes (especially during the spring and early summer) also correspond to low water temperatures, which may further constrain biological response to nutrient availability during these periods (Bergström et al. 2013).

In conclusion, our results based on stoichiometric models suggest that herbivore zooplankton are N-limited and recycle nutrients with low N:P ratio in low productive lakes with low N deposition. This will, at least during seasons when in-lake processes play an important role in nutrient turn over, contribute to continued or even strengthened N-limitation of phytoplankton production in these systems. The strength of this feedback, however, remains to be empirically tested by direct studies of these ecological processes in low productive lakes along gradients with increasing N deposition and different hydrological and climate regimes. We anticipate that increased N deposition and changes in climate and hydrology may affect this feedback and result in qualitative changes in these ecosystems, changing both autotroph producers and herbivore consumers from being N- to P-limited, eventually affecting important ecosystem characteristics such as productivity, community composition, food web efficiency and turnover of energy and nutrients.

#### ACKNOWLEDGMENTS

We thank Jan Johansson for nutrient analyses, Anders Jonsson for DOC analyses, Erik Geibrink for chlorophyll analyses, and Jakob Hansson for field assistance. The study was funded by grants from Oscar

and Lili Lamm's Foundation and the research council Formas to A. K. Bergström.

## LITERATURE CITED

- Andersen, T., and D. O. Hessen. 1991. Carbon, nitrogen, and phosphorus content of freshwater zooplankton. *Limnology and Oceanography* 36:807–814.
- Bergström, A.-K. 2010. The use of TN:TP and DIN:TP ratios as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. *Aquatic Sciences* 72:277–281.
- Bergström, A.-K., P. Blomqvist, and M. Jansson. 2005. Effects of nitrogen deposition on nutrient limitation and phytoplankton biomass in unproductive Swedish lakes. *Limnology and Oceanography* 50:987–994.
- Bergström, A.-K., C. Faithfull, D. Karlsson, and J. Karlsson. 2013. Nitrogen deposition and warming: effects on phytoplankton nutrient limitation in subarctic lakes. *Global Change Biology* 19:2557–2568.
- Bergström, A.-K., and M. Jansson. 2006. Atmospheric nitrogen deposition has caused nitrogen enrichment and eutrophication of lakes in the northern hemisphere. *Global Change Biology* 12:635–643.
- Bergström, A.-K., A. Jonsson, and M. Jansson. 2008. Phytoplankton responses to nitrogen and phosphorus enrichment in unproductive Swedish lakes along a gradient of atmospheric nitrogen deposition. *Aquatic Biology* 5:55–64.
- Bottrell, H. H., et al. 1976. A review of some problems in zooplankton production studies. *Norwegian Journal of Zoology* 24:419–456.
- Butterwick, C., S. J. Heaney, and F. F. Talling. 2005. Diversity in the influence of temperature on the growth rates of freshwater algae, and its ecological relevance. *Freshwater Biology* 50:291–300.
- Canadian National Atmospheric Chemistry Particulate Matter Database. 2014. Environment Canada, Science and Technology Branch. Toronto, Ontario, Canada.
- DeMott, W. 1998. Utilization of a cyanobacterium and a phosphorus-deficient green alga as complementary resources by daphnids. *Ecology* 79:2463–2481.
- DeMott, W. R., R. D. Gulati, and K. Siewertsen. 1998. Effects of phosphorus-deficient diets on the carbon and phosphorus balance of *Daphnia magna*. *Limnology and Oceanography* 43:1147–1161.
- Dobberfuhl, D. R., and J. J. Elser. 2000. Elemental stoichiometry of lower food web components in arctic and temperate lakes. *Journal of Plankton Research* 22:1341–1354.
- Downing, J. A., and E. McCauley. 1992. The nitrogen:phosphorus relationship in lakes. *Limnology and Oceanography* 37:936–945.
- Downing, J. A., S. B. Watson, and E. McCauley. 2001. Predicting cyanobacteria dominance in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1905–1908.
- Elser, J. J., T. Andersen, J. S. Baron, A.-K. Bergström, M. Jansson, M. Kyle, K. R. Nydick, L. Steger, and D. O. Hessen. 2009a. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science* 326:835–837.
- Elser, J. J., M. E. S. Bracken, E. E. Cleland, D. S. Gruner, W. S. Harpole, H. Hillebrand, J. T. Ngai, E. W. Seabloom, J. B. Shurin, and J. E. Smith. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwaters, marine and terrestrial ecosystems. *Ecology Letters* 10:1135–1142.
- Elser, J. J., M. M. Elser, N. A. MacKay, and S. R. Carpenter. 1988. Zooplankton-mediated transitions between N- and P-limited algal growth. *Limnology and Oceanography* 33:1–14.
- Elser, J. J., and R. P. Hassett. 1994. A stoichiometric analysis of the zooplankton-phytoplankton interaction in marine and freshwater ecosystems. *Nature* 370:211–213.
- Elser, J. J., M. Kyle, L. Steger, K. R. Nydick, and J. S. Baron. 2009b. Nutrient availability and phytoplankton nutrient limitation across a gradient of atmospheric nitrogen deposition. *Ecology* 90:3062–3073.
- Elser, J. J., A. L. Peace, M. Kyle, M. Wojewodzic, M. L. McCrackin, T. Andersen, and D. O. Hessen. 2010. Atmospheric nitrogen deposition is associated with elevated phosphorus limitation of lake zooplankton. *Ecology Letters* 13:1256–1261.
- Hassett, R. P., B. Cardinale, L. B. Stabler, and J. J. Elser. 1997. Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton-phytoplankton interaction. *Limnology and Oceanography* 42:648–662.
- Hessen, D. O. 2006. Determinants of seston C:P-ratio in lakes. *Freshwater Biology* 51:1560–1569.
- Hessen, D. O. 2013. Inorganic nitrogen deposition and its impacts on N:P ratios and lake productivity. *Water* 5:327–341.
- Hessen, D. O., and T. Andersen. 2008. Excess carbon in aquatic organism and ecosystems: Physiological, ecological and evolutionary implications. *Limnology and Oceanography* 53:1685–1696.
- Hessen, D. O., B. A. Faafeng, and T. Andersen. 1995. Replacement of herbivore zooplankton along gradients of ecosystem production and fish predation pressure. *Canadian Journal of Fisheries and Aquatic Sciences* 52:733–742.
- Holmgren, S. 1983. Phytoplankton biomass and algal composition in natural fertilized and polluted subarctic lakes. Dissertation. University of Uppsala.

- la, Uppsala, Sweden.
- Jansson, M., A.-K. Bergström, S. Drakare, and P. Blomqvist. 2001. Nutrient limitation of bacterioplankton and phytoplankton in humic lakes in northern Sweden. *Freshwater Biology* 46:653–666.
- Jansson, M., T. Hickler, A. Jonsson, and J. Karlsson. 2008. Links between terrestrial primary production and bacterial production and respiration in lakes in a climate gradient in subarctic Sweden. *Ecosystems* 11:367–376.
- Jansson, M., A. Jonsson, A. Andersson, and J. Karlsson. 2010. Biomass and structure of planktonic communities along an air temperature gradient in subarctic Sweden. *Freshwater Biology* 55:691–700.
- Johnson, C. R., and C. Luecke. 2012. Copepod dominance contributes to phytoplankton nutrient deficiency in lakes during periods of low precipitation. *Journal of Plankton Research* 5:345–355.
- Johnson, C. R., C. Luecke, S. C. Whalen, and M. A. Evans. 2010. Direct and indirect effects of fish on pelagic nitrogen and phosphorus availability in oligotrophic Arctic Alaskan lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1635–1648.
- Karlsson, J., P. Byström, J. Ask, P. Ask, L. Persson, and M. Jansson. 2009. Light limitation of nutrient-poor lake ecosystems. *Nature* 460:506–509.
- Karlsson, J., A. Jonsson, and M. Jansson. 2005. Productivity of high-altitude lakes: climate effect inferred from altitude gradient. *Global Change Biology* 11:710–715.
- Laaksonen, K. 1976. The dependence of mean air temperature upon latitude and altitude in Fennoscandia (1921–1950). *Annales Academia Scientiarum Fennicae* 19 (Series A):5–19.
- Levine, S. N., and D. W. Schindler. 1992. Modification of the N:P ratio in lakes by in situ processes. *Limnology and Oceanography* 37:917–935.
- Levine, M. A., and S. C. Whalen. 2001. Nutrient limitation of phytoplankton production in Alaskan Arctic foothill lakes. *Hydrobiologia* 455:189–201.
- Lewis, W. H., and W. A. Wurtsbaugh. 2008. Control of lacustrine phytoplankton by nutrients: erosion of the phosphorus paradigm. *International Review of Hydrobiology* 93:446–465.
- McCauley, E., W. W. Murdoch, and R. M. Nisbet. 1990. Growth, reproduction, and mortality of *Daphnia pulex* Leyding: Life at low food. *Functional Ecology* 4:505–514.
- Molot, L. A., S. B. Watson, I. F. Creed, C. G. Trick, S. K. McCabe, M. J. Verschoor, R. J. Sorichetti, C. Powe, J. J. Venkiteswaran, and S. L. Schiff. 2014. A novel model for cyanobacteria bloom formation: the critical role of anoxia and ferrous iron. *Freshwater Biology* 59:1323–1340.
- Müller-Navarra, D., and W. Lampert. 1996. Seasonal patterns of food limitation in *Daphnia galeata*: separating food quantity and food quality effects. *Journal of Plankton Research* 18:1137–1157.
- Schindler, D. W. 1977. Evolution of phosphorus limitation in lakes. *Science* 195:260–262.
- Schindler, D. W. 1978. Factors regulating phytoplankton production and standing crop in world's freshwaters. *Limnology and Oceanography* 23:478–486.
- Schindler, D. W., R. E. Hecky, D. L. Findlay, M. P. Stainton, B. R. Parker, M. J. Paterson, K. G. Beaty, M. Lyng, and S. E. M. Kasian. 2008. Eutrophication of lakes cannot be controlled by reduced nitrogen input: results of a 37-year whole-ecosystem experiment. *Proceeding of the National Academy of Sciences USA* 105:11254–11258.
- Schulz, K. L., and R. W. Sterner. 1999. Phytoplankton phosphorus limitation and food quality for *Bosmina*. *Limnology and Oceanography* 44:1549–1556.
- Shaver, G. R., K. J. Nadelhoffer, and A. E. Giblin. 1991. Biogeochemical diversity and element transport in a heterogeneous landscape, the north slope of Alaska. Pages 105–125 in M. Turner and R. Gardner, editors. *Quantitative methods in landscape ecology*. Ecological Studies Series Number 82. Springer-Verlag, Berlin, Germany.
- Sterner, R. W. 1990. The ratio of nitrogen to phosphorus resupplied by herbivores: zooplankton and the algal competitive arena. *American Naturalist* 136:209–229.
- Sterner, R. W., and J. J. Elser. 2002. *Ecological stoichiometry*. Princeton University Press, Princeton, New Jersey, USA.
- Sterner, R. W., J. J. Elser, and D. O. Hessen. 1992. Stoichiometric relationships among producers, consumers and nutrient recycling in pelagic systems. *Biogeochemistry* 17:49–67.
- Sterner, R. W., and D. O. Hessen. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology and Systematics* 25:1–29.
- Urabe, J., and R. W. Sterner. 1996. Regulation of herbivore growth by the balance of light and nutrients. *Proceeding of the National Academy of Sciences USA* 93:8465–8469.
- Urabe, J., and Y. Watanabe. 1992. Possibility of N and P limitation for planktonic cladocerans: an experimental test. *Limnology and Oceanography* 37:244–251.