

## Elemental stoichiometry of lower food web components in arctic and temperate lakes

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**Abstract.** Lakes were surveyed to assess the potential patterns of latitudinal variation in carbon:nitrogen:phosphorus (C:N:P) stoichiometry of lower food web components. Thirty-four lakes were surveyed at an arctic latitude (68°38'N, 149°38'W) and 10 lakes at a temperate latitude (46°13'N, 89°32'W) during 1997. The temperate data set was augmented with earlier survey results employing similar methods. It was hypothesized that differences in environmental variables across latitude would cause differences in community C:N:P ratios, leading to differences in trophic interactions. Physical measurements (light, temperature), seston and zooplankton were collected from each lake. Seston and zooplankton were analyzed for C, N and P content, and zooplankton were counted and measured for biomass estimates. The degree of trophic interaction between seston and zooplankton was assessed by (i) measuring elemental imbalances between seston and zooplankton and (ii) calculating the potential recycling ratio by the zooplankton community available for seston. Seston C:nutrient, but not N:P, ratios were higher in temperate than arctic lakes. Conversely, arctic zooplankton had higher C:nutrient, but not N:P, ratios than zooplankton in temperate lakes. Elemental imbalances were greater in temperate than in arctic lakes, but N:P stoichiometry of potential zooplankton recycling was nearly identical between the two latitudes. Zooplankton community C:N:P ratios were not related to either latitude or seston C:N:P. In accordance with stoichiometric theory, relative abundances of calanoid copepods were positively correlated with seston C:N in temperate lakes. Additionally, relative abundances of *Daphnia* were negatively correlated with seston C:N ratios in temperate and arctic lakes, and positively correlated with N:P ratios in the arctic. In general, these results suggest that seston and zooplankton community stoichiometry differ across latitude, and these differences have the potential to affect trophic interactions.

## Introduction

There are a growing number of comparative studies of aquatic ecosystems highlighting differences and similarities between ecosystem components (Nixon, 1988; Cole *et al.*, 1991; Elser and Hassett, 1994; Hassett *et al.*, 1997). These studies have identified many differences between freshwater and marine ecosystems, including nutrient ratios at the zooplankton–phytoplankton interface. For example, Elser and Hassett found large differences in the nitrogen:phosphorus (N:P) imbalance of the producer–consumer interaction (defined as  $N:P_{\text{resource}} - N:P_{\text{consumer}}$ ) as well as in the potential severity of phytoplankton P limitation between freshwater and marine ecosystems (Elser and Hassett, 1994). Additionally, Hassett *et al.* documented large differences in the apportioning of N and P in dissolved, seston and zooplankton pools in freshwater and marine ecosystems (Hassett *et al.*, 1997). These comparative studies demonstrate that different types of aquatic ecosystems may vary with respect to the elemental composition of major ecosystem components.

One potential shortfall of these and many other comparative studies involving lake ecosystems is that they were conducted in temperate environments and, thus, it may be problematic to generalize to other ecosystems. For example, aquatic

ecosystems at arctic latitudes experience different seasonal patterns than temperate lakes and environmental factors that change across latitudes could alter C:N:P ratios and trophic interactions. One important difference is seasonal nutrient loading patterns. In lakes near the Toolik Lake Long Term Ecological Research (LTER) field site in northern Alaska, external nutrient loading occurs primarily at ice-out (Cornwell, 1992), and during the rest of the growing season nutrients are supplied by internal recycling. Another important difference between arctic and temperate lakes is the relative importance of severe, stochastic weather patterns that decrease the growing season for organisms at high latitudes. Finally, total incident solar radiation during the growing season is lower in arctic latitudes. Differences in these environmental variables across latitude have the potential to alter the physiological condition of primary producers and these changes may propagate through the food web and affect consumers.

One hypothesis proposed to explain how environmental variables affect producer elemental content focuses on the balance of light and nutrients (i.e. the light:nutrient ratio) in the mixed layer (Sternner *et al.*, 1997). Greater available light increases carbon (C) fixation, raising C:nutrient ratios, while greater nutrient availability increases uptake, lowering C:nutrient ratios. Since we know that in arctic lakes nutrient loading generally occurs at one discrete time, mixed-layer depth may be dynamic due to widely fluctuating weather conditions, and solar input is reduced (all variables potentially affecting light:nutrient ratios and thus the stoichiometry of primary producers), it is reasonable to expect that arctic producers may have different elemental ratios than temperate communities. Lower intensities of solar radiation would reduce the light for C fixation, possibly resulting in lower algal C:P and C:N ratios. Alternatively, a single nutrient pulse in the beginning of the growing season, followed by little or no nutrient input, may result in high C:P and C:N ratios for much of the growing season. A broad survey of seston stoichiometry across a latitudinal gradient would yield valuable information regarding which variables have a dominant effect on seston stoichiometry at different latitudes.

Latitude-influenced differences in seston elemental content could dramatically affect ecosystem processes such as grazing rates, trophic transfer efficiency and secondary production. Producers and consumers generally have widely divergent elemental contents (Sternner and Hessen, 1994). In particular, primary producers have much higher C:nutrient ratios than do consumers (i.e. high C:N and C:P). This results in nutritional imbalances where N and/or P limits consumers (Hessen, 1992; Urabe and Watanabe, 1992; Sternner *et al.*, 1993; Andersen and Hessen, 1995). As producer C:N and C:P ratios diverge from those of consumers, animal growth and reproduction decrease (Sternner and Hessen, 1994; Sternner and Schulz, 1999). However, since little is known regarding the stoichiometry of arctic seston in relation to better studied temperate communities, measurements need to assess potential differences in latitudinal food quality in arctic systems compared to temperate systems.

In addition to environmental factors influencing nutrient ratios in the major ecosystem compartments, a short growing season and stochastic weather patterns present unique constraints impinging on zooplankton species (Taylor and

Gabriel, 1993) and communities, potentially affecting elemental patterns at the community level. The short growing season in the arctic is potentially one of the most important constraints influencing zooplankton community structure. In response to this constraint, animals with rapid growth rates may have increased fitness during the brief, stochastic growing season. Rapidly growing animals possess cellular investments characterized by increased allocation to RNA, raising P contents in zooplankton (Elser *et al.*, 1996; Dobberfuhl, 1999). Maximizing growth rate may also be associated with reductions in body protein, lowering body N contents (Dobberfuhl, 1999). Thus, arctic zooplankton communities might be dominated by rapidly growing species, resulting in lower bulk community N:P ratios than in temperate communities. A lower zooplankton community N:P ratio would have important consequences for food quality constraints for the zooplankton themselves and for the internal nutrient recycling regime generated by the zooplankton assemblage.

In this study, our primary goal was to characterize the ecological stoichiometry of the zooplankton–phytoplankton interface in arctic and temperate lakes. In addition to examining the separate C:N:P ratios of seston and zooplankton, we also wanted to calculate the elemental imbalance and potential recycling ratio at the seston–zooplankton interface. Elemental imbalance between seston and zooplankton provides an indication of the magnitude of potential food quality constraints and the corresponding reductions in zooplankton production. N:P recycling ratios provide insight into how the zooplankton community may be qualitatively affecting the relative internal resupply of N and P to the phytoplankton. Many environmental variables differ between temperate and arctic latitudes, and we wanted to ascertain how the environment affects the elemental composition of phytoplankton and zooplankton. Given that we have an *a priori* expectation for differences in the elemental composition of phytoplankton and zooplankton, we further wanted to test whether these elemental differences had any effect on ecosystem processes.

In this paper, we use the terms seston and zooplankton to describe our operational size fractions. We recognize that these terms generally refer to taxonomic groups rather than size-fractionated bulk samples. Clearly, separation of bulk field samples by taxonomic group is currently impossible for large numbers of samples. Our intention was to employ size fractions that would be likely to include the major components of both resource and the consumer (e.g. ‘seston’ and ‘zooplankton’). Undoubtedly, there is taxonomic overlap (i.e. small *Tropocyclops* and rotifers in the seston fraction). However, in lieu of a more elegant separation technique, we assume that the majority of the biomass in each of our size fractions represents different trophic levels.

## Method

### *Study sites*

Lakes in Alaska, Wisconsin and Michigan were surveyed at two different latitudes during the summer of 1997. In the arctic, 34 lakes were sampled during a 1 month period in the vicinity of the Toolik Lake LTER field station (68°38'N,

149°38'W). July sampling at Toolik Lake corresponds to the post-ice-out period dominated by internal nutrient cycling. Temperate latitude lakes in our 1997 sampling were represented by 10 lakes in the vicinity of the University of Notre Dame Environmental Research Center (UNDERC; 46°13'N, 89°32'W) and the nearby Trout Lake LTER research station (Table I). The number of temperate lakes surveyed during the 1997 season was limited, so the data set was augmented with survey data of temperate lakes from Elser and Hassett (Elser and Hassett, 1994), who used similar sampling and analytical techniques. Comparisons between the two temperate data sets revealed no significant differences in seston or zooplankton elemental ratios. This earlier survey included 26 lakes in the UNDERC and Trout Lake area as well as nine lakes from the Experimental Lakes Area in northwest Ontario, Canada (49°40'N, 93°45'W).

### *Sampling regime*

Physical parameters measured in each lake during the 1997 survey [but not in the Hassett *et al.* (Hassett *et al.*, 1997) survey] included vertical profiles of light, temperature and dissolved oxygen (DO). Light was measured using a Licor submersible quantum sensor, and temperature and DO were measured using a YSI meter. Secchi depth was also recorded for each lake. Using the light profile, the extinction coefficient and the mean light intensity (dimensionless) in the mixed layer were calculated using the equation:

$$I_m = \frac{1 - e^{-Kz_m}}{Kz_m} \quad (1)$$

where  $K$  is the light extinction coefficient in  $\text{m}^{-1}$  and  $z_m$  is the mixed-layer depth in meters (Riley, 1957).

Surface water (0 m) was collected from each lake and macrozooplankton were removed by passing the water through 153  $\mu\text{m}$  Nitex mesh. The screened water was then filtered through pre-combusted GF/F filters. In arctic lakes, water was filtered on site using a syringe filter at each lake. Duplicate filters were prepared for both P and CHN analysis. Filters were dried in a drying oven and frozen until analysis. Phosphorus filters were digested in persulfate followed by the molybdate–ascorbic acid colorimetric reaction (American Public Health Association, 1992). CHN filters were analyzed using a Perkin Elmer CHN/SO Model 2400 elemental analyzer.

Zooplankton were collected using a calibrated 153 mm plankton net. Repeated tows (2–4 tows depending on zooplankton density) were made from the bottom to the surface. Zooplankton were returned to the laboratory and split using a plankton splitter. One fraction was preserved with Lugol's iodine for later enumeration and measurement using a dissecting microscope. The remaining fraction was collected on a 35 mm Nitex mesh screen, transferred to an Eppendorf tube, and placed in a drying oven. After 24–36 h, tubes were placed in the freezer for later elemental analysis. Zooplankton community samples were homogenized and analyzed for C, N and P in the same manner as seston samples (see above).

**Table I.** List of lakes sampled during the 1997 field season in Alaska and Wisconsin. Sample date, mean light intensity in the mixed layer ( $I_m$ ) and net haul depth are provided. Also shown are the biomass estimates for the zooplankton community in each lake separated into broad taxonomic groups. Mean C:N:P ratios are shown for both bulk seston and zooplankton community samples. In many cases, data are missing due to loss during analysis or inadequate material. Values are means of multiple replicates (see the text)

Lake	Sample date	<i>I<sub>m</sub></i>	Net haul depth	Zooplankton proportions (% DW)							Zooplankton			Seston			
				<i>Bosmina</i>	<i>Daphnia</i>	<i>Holopedium</i>	Calanoid	Cyclopoid	Nauplii	Rotifers	C:N	C:P	N:P	C (µg l <sup>-1</sup> )	C:N	C:P	N:P
Toolik Lake LTER																	
Toolik	7/5/1997	0.20	13	0.7	0.0	0.0	75.1	24.0	0.0	0.2							
35	7/6/1997	0.26	2											256.3	8.5	102.0	12.1
36	7/6/1997	0.47	4	0.0	84.3	0.0	13.6	1.1	0.0	1.0	5.1	99.0	19.3	489.1	4.1	339.3	83.7
37	7/6/1997	0.21	4	0.2	87.1	0.0	0.0	12.2	0.1	0.4	6.3	91.7	14.6	374.4	4.1	245.9	59.8
38	7/6/1997	0.19	2	0.0	14.0	0.0	73.3	11.9	0.2	0.6	5.6	123.3	21.9				
39	7/6/1997	0.19	7	0.0	0.0	51.2	13.8	33.4	0.1	1.6	6.0	126.2	21.2				
40	7/8/1997	0.36	1.5	0.0	0.8	98.8	0.0	0.5	0.0	0.0	6.3	108.8	17.4	371.9	10.3	178.2	17.3
41	7/8/1997	0.18	3	0.0	29.0	0.0	40.9	30.1	0.1	0.0	6.1	96.6	15.9				
42	7/8/1997	0.12	14	15.2	0.9	71.9	4.8	7.1	0.0	0.0	6.9	123.9	17.9				
44	7/10/1997	0.44	2	0.0	0.0	0.0	99.2	0.0	0.1	0.8	5.9	96.5	16.4	383.9	10.1	99.9	9.9
45	7/10/1997	0.25	5	0.0	23.7	9.0	63.5	3.1	0.0	0.7	5.9	102.5	17.3	836.7	5.2	312.0	59.4
46	7/10/1997	0.34	8	0.0	0.6	95.7	3.2	0.6	0.0	0.0	5.7	103.4	18.2	426.4	7.4	285.1	38.5
47	7/15/1997	0.10	8								6.4	128.1	19.9	648.0	7.4		
48	7/15/1997	0.08	9														
49	7/15/1997	0.22	3	0.0	9.9	50.8	32.8	6.1	0.0	0.4							
51	7/17/1997	0.13	8														
52	7/17/1997	0.06										164.9	3.0	220.7	72.7		
53	7/17/1997	0.05	7	4.4	18.0	0.0	40.3	34.7	0.1	2.6	7.3	142.0	19.4	185.1	10.2	272.7	26.7
55	7/17/1997	0.14	6	0.0	0.0	0.0	98.6	0.0	1.4	0.0	6.5	143.5	22.2	177.0	8.5	55.0	6.4
61	7/24/1997	0.07	8	0.0	0.0	43.5	40.4	15.1	0.4	0.6	5.8	200.2	34.5	304.9	8.1	157.2	19.4
62	7/24/1997	0.26	5	0.0	0.0	96.1	2.8	1.1	0.0	0.0	5.4	161.7	29.9	292.9	8.9	149.1	16.8
65	7/29/1997	0.16	10	2.6	3.9	89.0	1.9	2.5	0.0	0.0	6.6	137.3	20.8	406.4	7.7	358.6	46.8
66	7/29/1997	0.20	10	0.1	0.0	97.0	2.3	0.6	0.0	0.1	6.1	127.6	21.1	571.0	9.3	335.5	36.1
67	7/29/1997	0.19	6	0.0	0.1	84.9	12.0	2.4	0.0	0.5	6.4	137.8	21.7	427.0	9.2	457.6	49.8
68	7/29/1997	0.05	10	0.0	10.3	29.9	46.2	11.9	0.1	1.6	6.4	158.8	24.9	271.7	8.0	400.4	50.0
69	7/29/1997	0.10	10	1.6	53.3	0.0	18.5	19.4	0.3	6.8	7.7	122.7	15.9	336.3	9.4	244.8	26.0
70	7/29/1997	0.20	4	8.3	30.7	45.1	7.2	8.7	0.0	0.1	7.2	135.7	18.8				
North Temperate Lakes LTER																	
Big Musky	6/23/1997	0.05	14	0.0	80.3	0.1	9.6	10.0	0.1	0.0	9.1	176.1	19.4	497.9	9.1	176.1	19.4
Nebish	6/23/1997	0.09	6	0.0	0.3	99.5	0.1	0.0	0.0	0.0							
South Trout	6/23/1997	0.06	14	1.5	26.7	63.9	4.7	3.2	0.0	0.0	9.0	210.4	23.3	444.3	9.0	210.4	23.3
Sparkling	6/23/1997	0.06	13	0.0	1.3	97.3	0.5	0.8	0.0	0.0	8.8	122.7	13.9	364.5	8.8	122.7	13.9
University of Notre Dame Environmental Research Center																	
North Gate Bog	6/9/1997	0.90	7	3.2	24.6	60.4	0.0	5.1	0.2	6.5							
Paul											10.1	140.1	13.8	305.6	10.1	140.1	13.8
Peter	6/9/1997	0.41	15	6.9	75.7	0.0	0.0	16.8	0.1	0.6	9.0	236.0	26.3	1137.0	9.0	236.0	26.3
Plu	6/11/1997	0.19	6.5	1.8	63.5	30.2	0.9	3.5	0.0	0.0	10.1	224.3	22.3	663.4	10.1	224.3	22.3
Roach	6/12/1997	0.14	8	0.6	0.2	88.1	8.1	2.5	0.1	0.3	8.4	176.8	21.1	398.0	8.4	176.8	21.1
Tender Bog	6/5/1997	0.90	9								8.5	309.9	36.3	1019.3	8.5	309.9	36.3
West Long	6/5/1997	0.46	10	2.1	92.3	0.0	0.0	5.5	0.1	0.0							

### Data analyses

Seston and zooplankton C:N, C:P and N:P ratios were calculated for both the arctic and temperate latitudes. These values were then used to calculate the elemental imbalance in each lake as:

$$X:Y_I = X:Y_{\text{resource}} - X:Y_{\text{consumer}} \quad (2)$$

where  $X:Y_I$  is the elemental imbalance and  $X:Y$  is the ratio of two different elements. In addition, we also used the measured resource and consumer N:P ratios to calculate the potential recycling ratio of the zooplankton community using the equations of Sterner (Sterner, 1990).

$$\text{When } f > b \quad s = \frac{f \left( \frac{1 - bL}{f} \right)}{(1 - L)} \quad (3)$$

$$\text{When } f < b \quad s = \frac{f(1 - L)}{\frac{1 - Lf}{b}} \quad (4)$$

where  $s$  is the N:P recycling ratio,  $f$  is the seston N:P ratio in each lake,  $b$  is the zooplankton community N:P ratio in each lake, and  $L$  is the accumulation efficiency for N and P. We assumed a maximum accumulation efficiency of 0.8 for all calculations. Elemental ratios, elemental imbalance and potential recycling ratios for arctic and temperate lakes were compared using a Student's  $t$ -test of means.

To ascertain the association of zooplankton community structure with seston C:N:P ratio, least squares regressions of seston C:N:P ratio versus the proportion of dominant zooplankton taxa were performed using mean values of each parameter for each site. We used this regression to examine the possibility of indirect effects of zooplankton recycling ratios on the seston elemental ratios.

Statistical comparisons were also subjected to a table-wide sequential Bonferroni test (Rice, 1989). In this test,  $\alpha$  is weighted by the number of possible comparisons. For example, in comparing seston and zooplankton elemental ratios by latitude, there are six independent  $t$ -tests and the critical  $\alpha$  would be 0.008. There are also eight regression analyses in Table II (2 taxa  $\times$  2 ratios  $\times$  2 latitudes) and the critical  $\alpha$  would be 0.006. This test was performed to control the type-I error rate.

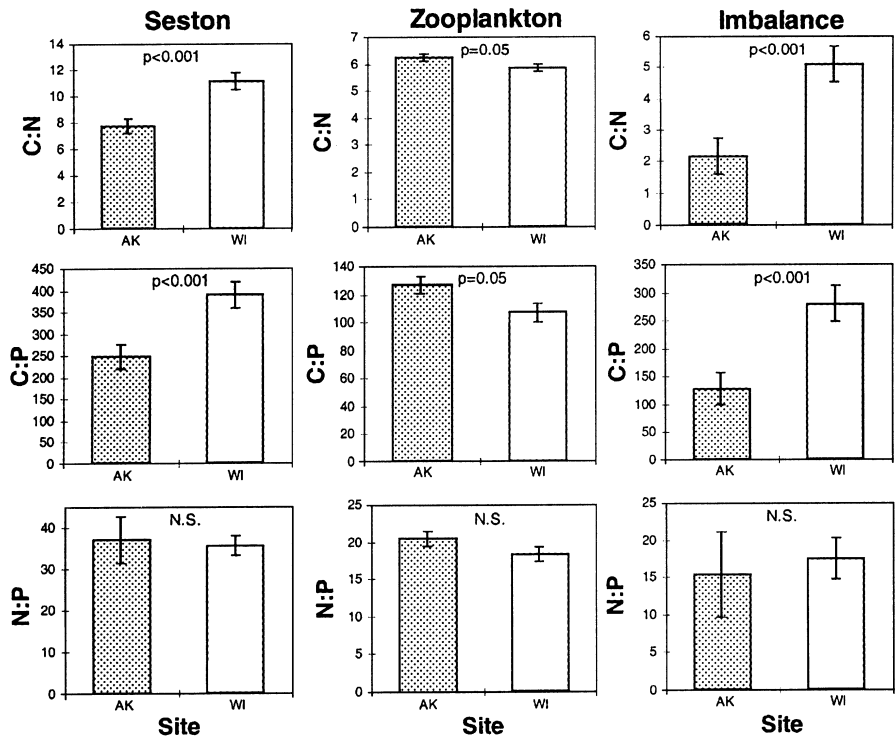
### Results and discussion

Elemental stoichiometry of lower food web components differed between arctic and temperate lakes. Seston C:N and C:P ratios were significantly higher in Wisconsin than in Alaska (Figure 1). In fact, mean C:P ratios in temperate lakes exceeded the threshold level (300) thought to begin to limit *Daphnia* growth (Urabe and Watanabe, 1992; Sterner *et al.*, 1993). However, the seston N:P ratio was not significantly different between latitudes (Figure 1). This indicates that there was a fundamental difference in producer C allocation across the latitudinal gradient.

**Table II.** Regression coefficients for relationships between relative zooplankton abundance (as % dry weight) and seston elemental ratios

Relationship	Temperate					Arctic				
	Intercept	Slope	P	r <sup>2</sup>	Bonferroni	Intercept	Slope	P	r <sup>2</sup>	Bonferroni
Calanoid versus C:N	9.25	0.076	**	0.19	*	7.76	0.009	n.s.	0.02	n.s.
<i>Daphnia</i> versus C:N	12.52	−0.045	*	0.12	n.s.	8.93	−0.048	**	0.51	*
<i>Daphnia</i> versus N:P	33.44	0.104	n.s.	0.05	n.s.	27.92	0.453	**	0.41	n.s.

Both temperate and arctic relationships are shown for comparison if either was significant. \**P* < 0.05; \*\**P* < 0.01. Also shown are results of a table-wide sequential Bonferroni test. \**P* < 0.006.



**Fig. 1.** C:N, C:P and N:P ratios of bulk seston and bulk zooplankton community. Also shown is the mean calculated elemental imbalance for C:N, C:P and N:P ratios between seston and zooplankton in all lakes. Bars indicate  $\pm 1$  SE. Results of Student's *t*-test are shown for significant differences and N.S. indicates that the means were not significantly different. Although not shown, a sequential Bonferroni test showed seston C:P and C:N to be significantly different between latitudes.

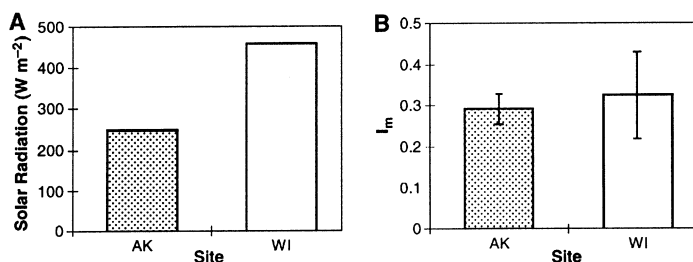
We examined relative light intensities to assess why seston C:P might be higher in arctic than in temperate lakes. During the time of the study, incident solar radiation at the temperate latitude was almost double that of arctic levels (Figure 2A). Lower levels of solar radiation were not reflected in  $I_m$  measurements (Figure 2B). Similar  $I_m$  measurements across latitude may indicate that lower incident

solar radiation in Alaska may have been offset by shallower mixed depths, raising the ambient light availability in the mixed layer. This comparison is somewhat uncertain as we have light profile data for only a small portion of the temperate lakes. However, it appeared that the light gradient across latitude was a potential causal factor driving latitudinal patterns in seston stoichiometry.

Like seston, zooplankton C:N:P stoichiometry differed across latitude as well. Zooplankton C:N and C:P ratios were significantly higher in the arctic lakes relative to temperate lakes (Figure 1). However, these differences were relatively small. As with seston stoichiometry, zooplankton community N:P ratio was not significantly different between latitudes (Figure 1). The lack of difference in the N:P ratios may indicate that, within species, allocations to various biochemical pools containing N and P (e.g. protein, nucleic acids) was similar between latitudes. The similarity in zooplankton N:P may also indicate that overall species composition was likely to be similar between latitudes. For example, if arctic communities had been consistently biased towards more rapidly growing species, or clones with low species N:P, then we would have observed lower community N:P ratios. Similarity in zooplankton community N:P ratios indicates that neither zooplankton physiology nor species composition was substantially different between latitudes.

Because C:P and C:N ratios were higher in arctic zooplankton communities, an important latitudinal effect appeared to center around zooplankton C allocation. Variations in total lipid content have previously been demonstrated between conspecific populations across latitudinal gradients (Sargent and Falk-Petersen, 1988). Increased lipid contents may have an adaptive advantage in energetically buffering zooplankton against reduced food supplies due to extreme weather patterns (Reinhardt and Van Vleet, 1986; Sargent and Falk-Petersen, 1988). Increasing lipid contents would raise C contents without affecting N or P contents, resulting in higher C:P and C:N ratios, as seen in these data.

Knowing the seston and zooplankton C:N:P ratios, elemental imbalances between these two trophic levels can be calculated. Elemental imbalance between trophic levels is important because as the elemental ratio of seston deviates from that of the zooplankton, growth gross efficiency and fecundity should decrease (Sterner and Hessen, 1994). The elemental imbalance data indicated that

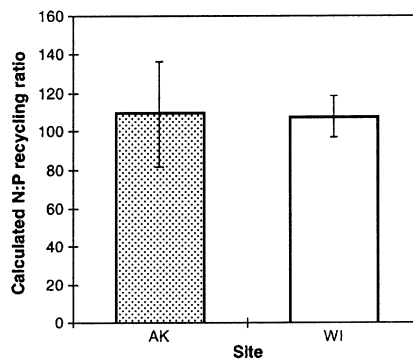


**Fig. 2.** (A) Total daily solar radiation in 1997 averaged over the month of June for arctic and temperate latitudes. (B) Average of mean light intensity in the mixed layer, using equation (1), for lakes in the 1997 survey for which I have data. Bars indicate  $\pm 1$  SE.

zooplankton production at temperate latitudes was more likely to be nutrient limited than in the arctic since imbalances for both C:N and C:P were significantly higher for Wisconsin relative to Alaska (Figure 1). However, N:P imbalance did not differ for the two latitudes, as seston N:P and zooplankton N:P did not differ (Figure 1). Thus, these data suggest that nutrients, especially P, were potentially more limiting to zooplankton production in lakes at temperate latitudes during our study.

We also calculated the potential N:P recycling ratio by the zooplankton community based on seston and zooplankton community N:P ratios. Because the N:P ratios of both the seston and the zooplankton were similar at each latitude (Figure 1), there was little difference in the calculated recycling ratios for the two latitudes (Figure 3). The zooplankton N:P release ratio was calculated to be ~110 for both latitudes (Figure 3), indicating that zooplankton communities at both latitudes would have similar effects on nutrient availability for the producers. Moreover, these high recycling ratios suggest that zooplankton at both latitudes have the potential to sequester P disproportionately and skew N:P recycling ratios towards higher values, potentially leading to P limitation in the phytoplankton.

Another interesting facet of zooplankton community stoichiometry was the relative lack of variation across a broad range of lake types, environmental clines and seston food quality conditions encountered in our survey. Based on zooplankton growth rate and fecundity responses to variations in mineral food quality in laboratory and field experiments (Urabe and Watanabe, 1992; Sterner *et al.*, 1993; DeMott, 1998), it has been suggested that species replacements in the zooplankton community should be common across a food quality gradient. For example, low-C:P species suffer greater growth rate reductions than high-C:P species when fed high-C:P food (Sterner and Schulz, in press). Therefore, Sterner *et al.* predicted that high-C:P seston should preclude low-C:P animals and result in positive correlations between zooplankton community C:P and seston C:P (Sterner *et al.*, 1999). However, data from five temperate zone lakes representing a broad range of food quality conditions failed to support this prediction (Sterner



**Fig. 3.** Mean recycling ratios for zooplankton communities in arctic and temperate lakes. Recycling ratios were calculated using equations (3) and (4) for each lake. Bars indicate  $\pm 1$  SE.

*et al.*, 1999). In contrast, a survey of European lakes found that zooplankton community C:P was positively correlated to seston C:P (Gulati *et al.*, 1991). In addition, abundance of *Daphnia*, a high-P/low-C:P genus, was negatively correlated with seston C:P in three Dutch lakes (DeMott and Gulati, 1999). Our data agree with those of Sterner *et al.* (Sterner *et al.*, 1999), but contradict those of Gulati *et al.* (Gulati *et al.*, 1991) and DeMott and Gulati (DeMott and Gulati, 1999).

Our survey included a larger number of lakes than earlier studies and encompassed a broad range of seston elemental ratios (C:P 55–963, N:P 6–86). Yet there was no discernible change in zooplankton community C:P or N:P across this range of seston elemental ratios, despite relatively large changes in zooplankton species composition (Table I). In spite of the fact that we encountered zooplankton communities dominated by calanoid copepods (high N:P) or by *Daphnia* (low N:P), at the community level (Table I) there was only a narrow range in measured zooplankton elemental ratios. The lack of concordance between species composition patterns and bulk elemental composition may be related to a lack of observational resolution. Shifts in population age structure or species replacements within guilds may be occurring on spatial and temporal scales finer than those commonly measured in this and other studies. Alternatively, there may be higher order constraints such as life history/food quality trade-offs.

The congruence between our findings and those of Sterner *et al.* (Sterner *et al.*, 1999) reinforce their suggestion that there may be some type of community homeostatic set point. This set point may be related to a set of species where the integrated community C:N:P represents an optimal state in the trade-off between competitive abilities of low-C:nutrient species and food quality constraints on those species. For example, low-C:P species are associated with rapid growth rates (Main *et al.*, 1997; DeMott, 1998), but also appear to become limited by food C:P ratios at lower values than higher C:P zooplankton species (DeMott, 1998; Sterner and Schulz, 1999). These trade-offs could result in different species abundance distributions leading to similar mean community N:P ratios. In a diverse community, low-C:P species may be present, but may be subject to food quality limitation and relatively low production. High-C:P species may then have a slight competitive advantage and be present in the community. Alternatively, the zooplankton community could be dominated by intermediate-C:P species that are well matched to their food resources. An additional possibility is that species that have not been measured for body elemental content may have more intermediate C:P ratios than a priori expectations. In other words, *Daphnia*-dominated communities may have higher C:P ratios than expected based on prior measurements of different species. The net result in any of these scenarios is that we would observe intermediate C:P and N:P ratios unrelated to community composition. We are only beginning to understand the role of environmental constraints on the competitive interactions of zooplankton taxa possessing different life history strategies, C:N:P composition, and subsequent effects on community-level patterns in stoichiometry. Effects of food quality constraints on zooplankton competition and species composition need to be investigated further across lake types.

As an alternative to examining the effects of seston food quality on zooplankton species composition, we can examine the 'flip side' of the trophic interaction and look at the indirect effects of zooplankton on seston nutritional status. Zooplankton community structure has previously been shown to influence relative nutrient availability and seston stoichiometry in a number of systems (Elser *et al.*, 1988, 1995; Urabe *et al.*, 1995; Hassett *et al.*, 1997; Rothaupt, 1997), presumably through differential recycling of N and P (Sterner, 1990). Stoichiometric theory predicts that low N:P consumers recycle at relatively high N:P, while high N:P consumers recycle at relatively low N:P ratios (Sterner, 1990). Therefore, if zooplankton are affecting seston through differential recycling of N and P, then we would expect that zooplankton species would correlate differently with seston C:N:P. Specifically, we would expect low-N:P taxa like *Daphnia* to correlate positively with seston C:N and negatively with seston C:P and N:P. Similarly, we would expect high-N:P taxa like calanoids to correlate negatively with seston C:N and positively with seston C:P and N:P.

When these predictions were tested using these data, relationships between zooplankton community composition and seston stoichiometry in Alaskan and Wisconsin lakes generally agreed with our predictions. However, relationships between seston and zooplankton stoichiometry differed qualitatively across latitude. Calanoid proportion was positively correlated with seston C:N in temperate lakes ( $P = 0.006$ ,  $r^2 = 0.19$ ), but not in arctic lakes (Table II). However, *Daphnia* proportion was negatively correlated with seston C:N in both temperate ( $P = 0.03$ ,  $r^2 = 0.12$ ) and arctic ( $P = 0.003$ ,  $r^2 = 0.51$ ) lakes (Table II). Finally, *Daphnia* proportion correlated positively with seston N:P in arctic lakes ( $P = 0.01$ ,  $r^2 = 0.41$ ), but not in temperate lakes (Table II). These data suggest that *Daphnia* may have a disproportionately greater effect on the nutrient status of the seston in arctic lakes, relative to temperate lakes. While relationships between zooplankton community composition and seston stoichiometry largely coincided with our expectations, these relationships were not very strong, particularly in temperate lakes. Low correlation coefficients suggest that other parameters, in combination with zooplankton species composition, were important in controlling seston stoichiometry. It should be noted that if a table-wide sequential Bon Feroni test is applied some of the relationships are no longer significant.

Relationships mentioned above were largely consistent with our predictions of the effects of differential nutrient recycling on seston stoichiometry. Calanoids have relatively high N contents (Andersen and Hessen, 1991) and thus are more likely to serve as short-term N sinks. Calanoid-dominated communities grazing on seston would thus release relatively little N, resulting in higher seston C:N ratios, as seen at the temperate latitude. However, a large proportion of calanoids in arctic lakes consists of *Heterocope*, a large carnivorous species. Since *Heterocope* consumes animals, it does not face the nutritional imbalances that herbivores do and probably releases N in larger quantities than herbivorous calanoids. Therefore, the presence of *Heterocope* in arctic lakes may contribute to the weak correlation between calanoid biomass and seston C:N in the arctic lakes.

A potentially more interesting relationship is between the proportion of *Daphnia* biomass and seston stoichiometry. There was a negative relationship

between the proportion of *Daphnia* and seston C:N at both latitudes and a positive relationship with seston N:P in the arctic. The strong correlations between C:N, N:P and the proportion of *Daphnia* biomass in the arctic lakes, relative to the temperate lakes, are particularly important. Because of the nature of nutrient dynamics in the arctic (Cornwell, 1992), consumers in general, and *Daphnia* in particular, may play a particularly important role in influencing nutrient availability for primary production. Arctic lakes are characterized by a nutrient pulse at ice-out and nutrients for the remainder of the growing season are primarily resupplied by consumers. *Daphnia*, an abundant and efficient consumer in many arctic lakes, releases nutrients at high N:P ratios because of its relatively high P and low N demand for biomass production. As a result, when *Daphnia* supplies a large proportion of available nutrients, seston C:N ratios would be expected to be lower (due to reduced N limitation) and seston N:P ratios would be expected to be higher (due to enhanced P limitation). Thus, we can understand how *Daphnia*, as a result of nutrient loading patterns in the arctic and its characteristic body stoichiometry, may be able to modify seston stoichiometry more extensively than at temperate latitudes.

## Conclusion

Our data indicated that there were significant differences in the stoichiometry of ecological interactions at the base of the food web across a latitudinal gradient. C:nutrient ratios of seston were higher in temperate lakes than in the arctic. Conversely, C:nutrient ratios of zooplankton were somewhat lower in temperate lakes than in the arctic. Zooplankton recycled N:P was calculated to be nearly identical at both latitudes, indicating that the zooplankton community would affect the nutrient environment of the seston at each latitude similarly. Likewise, elemental imbalances, while different between latitudes, did not indicate acute nutritional constraints at either latitude, although the potential for elemental limitation appeared to be greater in temperate lakes. It is important to note that our data represent an ecological snapshot—both seston and zooplankton elemental ratios change over the course of the growing season, and there may be strong trophic effects from zooplankton recycling and seston elemental limitation at other times of the year.

Finally, our data indicated that seston C:N:P correlated with zooplankton community structure differently across latitude. The relative abundance of calanoids and *Daphnia* and seston stoichiometry appeared to be related, and were consistent with stoichiometric predictions that calanoids and *Daphnia* release N and P at different rates and influence relative nutrient availability and seston elemental content accordingly. *Daphnia*, a keystone herbivore, appeared to be particularly effective in influencing seston stoichiometry. Thus, we can see how changes in zooplankton species composition, and accompanying changes in potential recycling ratios, may have the potential to affect seston stoichiometry and, conversely, how changes in seston stoichiometry might differently affect zooplankton nutrient limitation at each latitude.

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## References

- American Public Health Association (1992) *Standard Methods for the Examination of Water and Wastewater*, 18th edn. APHA, Washington.
- Andersen,T. and Hessen,D.O. (1991) Carbon, nitrogen and phosphorus content of freshwater zooplankton. *Limnol. Oceanogr.*, **36**, 807–814.
- Andersen,T.R. and Hessen,D.O. (1995) Carbon or nitrogen limitation in marine copepods. *J. Plankton Res.*, **17**, 317–331.
- Cole,J.J., Lovett,G.M. and Findlay,S. (1991) *Comparative Analyses of Ecosystems: Patterns, Mechanisms and Theories*. Springer-Verlag, New York.
- Cornwell,J.C. (1992) Cation export from Alaskan arctic watersheds. *Hydrobiologia*, **240**, 15–22.
- DeMott,W.R. (1998) Utilization of a cyanobacterium and a phosphorus deficient green alga as complementary resources by daphnids. *Ecology*, **79**, 2463–2481.
- DeMott,W.R. and Gulati,R.D. (1999) Phosphorus limitation in *Daphnia*: Evidence from a long term study of three hypereutrophic Dutch lakes. *Limnol. Oceanogr.*, **44**, 1557–1564.
- Dobberfuhr,D.R. (1999) Elemental stoichiometry in crustacean zooplankton: Phylogenetic patterns, physiological mechanisms and ecological consequences. PhD Thesis, Arizona State University.
- Elser,J.J. and Hassett,R.P. (1994) A stoichiometric analysis of the zooplankton–phytoplankton interaction in marine and freshwater ecosystems. *Nature*, **370**, 211–213.
- Elser,J.J., Elser,M.M., MacKay,N.A. and Carpenter,S.R. (1988) Zooplankton-mediated transitions between N- and P-limited algal growth. *Limnol. Oceanogr.*, **33**, 1–14.
- Elser,J.J., Lubnow,F.S., Marzolf,E.R., Brett,M.T., Dion,G. and Goldman,C.R. (1995) Factors associated with interannual and intraannual variation in nutrient limitation of phytoplankton growth in Castle Lake, California. *Can. J. Fish. Aquat. Sci.*, **52**, 93–104.
- Elser,J.J., Dobberfuhr,D.R., MacKay,N.A. and Schampel,J.H. (1996) Organism size, life history and N:P stoichiometry: Towards an evolutionary synthesis of cellular and ecosystem processes. *BioScience*, **46**, 674–684.
- Gulati,R.D., DeMott,W.R. and Van Liere,L. (1991) Carbon and phosphorus relationships of zooplankton and its seston food in Loosdrecht lakes. *Mem. Ist. Ital. Idrobiol.*, **48**, 279–298.
- Hassett,R.P., Cardinale,B., Stabler,L.B. and Elser,J.J. (1997) Ecological stoichiometry of N and P in pelagic ecosystems: Comparison of lakes and oceans with emphasis on the zooplankton–phytoplankton interaction. *Limnol. Oceanogr.*, **42**, 648–662.
- Hessen,D.O. (1992) Nutrient element limitation of zooplankton production. *Am. Nat.*, **140**, 799–814.
- Main,T.M., Dobberfuhr,D.R. and Elser,J.J. (1997) N:P stoichiometry and ontogeny of crustacean zooplankton: A test of the growth rate hypothesis. *Limnol. Oceanogr.*, **42**, 1474–1478.
- Nixon,S.W. (1988) Physical energy inputs and the comparative ecology of lake and marine ecosystems. *Limnol. Oceanogr.*, **33**, 1005–1025.
- Reinhardt,S.B. and Van Vleet,E.S. (1986) Lipid composition of twenty-two species of Antarctic midwater zooplankton and fish. *Mar. Biol.*, **91**, 149–159.
- Riley,G.A. (1957) Phytoplankton of the North Central Sargasso Sea, 1950–52. *Limnol. Oceanogr.*, **2**, 252–270.
- Rice,W.R. (1989) Analyzing tables of statistical tests, *Evol.*, **43**, 223–225.
- Rothhaupt,K.O. (1997) Grazing and nutrient release of *Daphnia* and *Eudiaptomus* on phytoplankton in laboratory microcosms. *J. Plankton Res.*, **19**, 125–139.
- Sargent,J.R. and Falk-Petersen,S. (1988) The lipid biochemistry of calanoid copepods. *Hydrobiologia*, **167/168**, 101–114.
- Sterner,R.W. (1990) The ratio of nitrogen to phosphorus resupplied by herbivores: Zooplankton and the algal competitive arena. *Am. Nat.*, **136**, 209–229.
- Sterner,R.W. and Hessen,D.O. (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu. Rev. Ecol. Syst.*, **25**, 1–29.

- Sterner,R.W. and Schulz,K.L. (1999) Zooplankton nutrition: recent progress and a reality check. *Aquatic Ecol.*, **32**, 261–279.
- Sterner,R.W., Hagemeier,D.D., Smith,W.L. and Smith,R.F. (1993) Phytoplankton nutrient limitation and food quality for *Daphnia*. *Limnol. Oceanogr.*, **38**, 857–871.
- Sterner,R.W., Elser,J.J., Fee,E.J., Guildford,S.J. and Chrzanowski,T.H. (1997) The light:nutrient ratio in lakes: The balance of energy and materials affects ecosystem structure and process. *Am. Nat.*, **150**, 663–684.
- Sterner,R.W., Schampel,J.H., Shulz,K.L., Galford,A.E. and Elser,J.J. (1999) Joint variation of zooplankton and seston stoichiometry in lakes and reservoirs. *Verh. Int. Ver. Limnol.*, in press.
- Taylor,B.E. and Gabriel,W. (1993) Optimal adult growth of *Daphnia* in a seasonal environment. *Func. Ecol.*, **7**, 513–521.
- Urabe,J. and Watanabe,Y. (1992) Possibility of N or P limitation for planktonic cladocerans: An experimental test. *Limnol. Oceanogr.*, **37**, 244–251.
- Urabe,J., Nakanishi,M. and Kawabata,K. (1995) Contribution of metazoan plankton to the cycling of N and P in Lake Biwa. *Limnol. Oceanogr.*, **40**, 232–241.

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