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PRIMARY RESEARCH PAPER

Impacts of atmospheric nitrogen deposition and lake browning on planktonic biomass ratios and nutrient accumulation in northern lakes

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Abstract Nitrogen (N) deposition and dissolved organic carbon (DOC) levels in northern lakes are shifting due to climate change and atmospheric deposition declines, altering the availability of light and nutrients in these ecosystems. Yet their impacts on the biomass, stoichiometry, and the structure of planktonic food chains remain uncertain. We therefore investigated zooplankton-to-seston biomass ratios (Z:S in C, N, and P) across 34 Swedish lakes with varying N deposition, DOC concentration, and fish predation control. Mean Z:S values were 2.9% for C, 7.5% for N, and 7.7% for P, with substantial regional variation. Z:S ratios were higher in lakes with lower atmospheric N deposition, improved seston quality, and greater calanoid copepod dominance in zooplankton. The strong link between zooplankton stoichiometry and community composition underscores the role of calanoids in regulating nutrient dynamics in northern lakes. Fish predation reduced zooplankton biomass but did not significantly alter Z:S ratios or zooplankton community composition. Meanwhile, increasing DOC dampened the higher Z:S in low N deposition lakes by reducing calanoid dominance and promoting more uniform zooplankton assemblages. Our findings suggest that lake browning counteracts the expected increase in Z:S ratios associated with recovery from atmospheric N deposition, potentially altering nutrient transfer in lake food webs.

Keywords Zooplankton · Seston · Stoichiometry · Lake browning · Nitrogen deposition · Calanoids · Fish predation · Food web dynamics

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Introduction

The northern high-latitude landscape is undergoing profound changes driven by global forces such as climate change, recovery from atmospheric acid deposition, and land cover modifications. These drivers have been linked to declines in essential nutrients, including nitrogen (N) and phosphorus (P) (Eimers et al., 2009; Canham et al., 2012; Isles et al., 2018, 2023), alongside increasing concentrations of colored dissolved organic carbon (DOC; also called lake browning) in many northern lakes (Monteith et al., 2007; de Wit et al., 2016; Finstad et al., 2016. These environmental shifts are expected to alter the food web structures (Hessen et al., 2006; Karlsson et al., 2009; Bergström et al., 2022) and the relative influence of resource supply and consumer predation on the planktonic biomass in northern high-latitude lakes (Jeppesen et al., 2003; Hessen et al., 2006).

To assess the relative importance of resource supply and consumer control on pelagic food web structure, the biomass ratios between herbivorous zooplankton and phytoplankton can be used (Hessen et al., 2003, 2006; Jeppesen et al., 2003). Here the biomass ratios of specific elements can provide further clues as to elemental imbalances that can limit trophic transfer efficiencies (Hessen, 2008). Previous studies have shown that the zooplankton/phytoplankton biomass ratio tends to decline with increasing P concentrations and lake productivity (Jeppesen et al., 2003; Hessen et al., 2006). This decline has been attributed to both bottom-up forces, such as changes in nutrient-driven phytoplankton quantity and quality (Hessen et al., 2006; Hessen, 2008; Filstrup et al., 2014), and top-down forces, such as increased predation pressure on zooplankton by planktivorous fish in more productive lakes (Carpenter et al., 1985; Gulati et al., 1990; Jeppesen et al., 2003; Hessen et al., 2006). Yet, most research has focused on gradients of lake productivity, leaving the drivers of zooplankton/phytoplankton biomass ratio changes in oligotrophic lakes—dominant in northern high-latitude regions—relatively unexplored.

Oligotrophic lakes differ fundamentally from eutrophic ones, as their productivity is more influenced by colored terrestrial organic matter (i.e., DOC) that impacts both light availability and nutrient concentrations simultaneously, in contrast to the pure nutrient effects common in more eutrophic lakes (Karlsson et al., 2009; Bergström & Karlsson, 2019; Isles et al., 2021). Consequently, changes in nutrient concentrations in oligotrophic lakes do not induce the same changes in phytoplankton and zooplankton biomass, community composition, zooplankton/phytoplankton biomass ratios, or fish communities as observed in eutrophic lakes (Gulati et al., 1990; Hessen et al., 2003; Jeppesen et al., 2003; Deininger et al., 2017a; Bergström et al., 2021; Norman et al., 2022). Previous studies of oligotrophic lakes have also shown large variabilities in zooplankton/phytoplankton biomass ratios at given P-levels and fish predation pressure (Jeppesen et al., 2003; Hessen et al., 2006). This suggests that other factors, such as the mineral food quality of phytoplankton, might play a more dominant role in determining zooplankton/phytoplankton biomass ratios (Persson et al., 2007; Hessen, 2008). However, distinguishing food quality from predation control on zooplankton/phytoplankton biomass ratios in oligotrophic lakes is difficult since they both can reduce the ratio (Hessen et al., 2006).

Previously, we assessed how changes in food quantity–quality affects zooplankton biomass and community composition, and their N:P recycling ratios, in a set of oligotrophic Swedish lakes with contrasting levels of atmospheric N deposition and DOC concentration (Bergström et al., 2020, 2022; Isles et al., 2020). Seston of particle size < 50 μm—representing the edible fraction for herbivorous zooplankton that comprises of phytoplankton, bacteria, and detritus (cf. Burns, 1968; Hessen, 2006)—was used as a measure of food quantity and quality. These studies found that atmospheric N deposition and DOC influence the ratio between dissolved inorganic N and total P concentrations (DIN:TP) in lake water, and the nutrient limitation regimes for phytoplankton growth (Bergström, 2010) that are reflected by the seston C, N, and P concentrations (food quantity) and seston C:N:P stoichiometry (food mineral quality) (Bergström et al., 2020, 2022). Typically, there are large gradients from low lake DIN and low DIN:TP in northern Sweden with low atmospheric N deposition, to high lake DIN and high DIN:TP in southern Sweden with higher atmospheric N deposition (Bergström et al., 2022). Lower lake DIN and DIN:TP in the north is further associated with N-limitation and higher food mineral quality (lower seston C:P and N:P) (Bergström et al., 2020; Isles et al., 2020) and with higher zooplankton biomass (Bergström et al., 2022). Lake DIN:TP also declines with increasing lake DOC regardless of the level of N deposition (Bergström et al., 2020, 2022) as an effect of increasing TP with increasing DOC (Isles et al., 2020).

Changes in lake environmental conditions (e.g., increasing DOC and TP and decreasing DIN:TP) related to browning and declines in atmospheric acid deposition (Isles et al., 2018) also affect the community composition of zooplankton (Bergström et al., 2022). Zooplankton are generally dominated by calanoid copepods with high body N:P in N-limited lakes with low atmospheric N deposition (low DIN:TP, northern Sweden), but by cladocerans with high P requirements and low body N:P in relatively more P-limited lakes with higher atmospheric N deposition (high DIN:TP, southern Sweden) (Bergström et al., 2022). However, there is low intraspecific variation in zooplankton C:N:P stoichiometry among lakes with contrasting levels of atmospheric N deposition and lake DOC (Bergström et al., 2022). Consequently, shifts in zooplankton community composition, driven by changes in lake environmental conditions due to reduced atmospheric N deposition and lake browning, are expected to have large impacts on not only zooplankton biomass (i.e., zooplankton C) but also their nutrient content (zooplankton N and P) in ways that do not always align with stoichiometry changes.

Changes in lake DOC and DIN:TP potentially impact pelagic food web structure by altering the zooplankton-to-seston biomass ratios (Z:S) in terms of carbon (i.e., Z:S-C) and essential nutrients (i.e., Z:S-N and Z:S-P). The Z:S ratios have often focused on C (or energy) (see Hessen et al., 2006), whereas Z:S ratios in terms of nutrients are rarely assessed, possibly due to the time-consuming effort in measuring N and P content in zooplankton. Yet, our previous findings suggest both direct (via seston) and indirect (via zooplankton community composition) influences of lake environmental alterations on the Z:S ratios of C, N and P.

Here, we ask four questions: (Q1) Do Z:S ratios of C, N, and P vary among lakes with contrasting atmospheric N deposition?; (Q2) Do zooplankton taxa differentially contribute to Z:S ratios in these lakes?; (Q3) Does fish predation override the effects of atmospheric N deposition on Z:S ratios in these lakes? And (Q4) Does DOC counteract the effects of atmospheric N deposition on Z:S ratios in these lakes?

We predicted that:

In lakes with low atmospheric N deposition associated with low lake DIN:TP, the Z:S ratios for C, N, and P are higher because zooplankton biomass and seston mineral quality are higher, compared to lakes with higher atmospheric N deposition and higher lake DIN:TP;

In lakes with low atmospheric N deposition associated with low DIN:TP where phytoplankton is predominantly N-limited, increased proportions of calanoid copepods of higher body N:P than cyclopoid copepods and cladocerans promote higher Z:S ratios for C, N, and P;

The relationship between decreasing DIN:TP and increasing Z:S ratios is stronger than the relationship between decreasing fish predation and increasing Z:S ratios.

Lake DOC counteracts the effects of reduced atmospheric N deposition and lower lake DIN:TP on Z:S ratios of C, N and P by increasing seston mineral quality and promoting more similar zooplankton community composition.

Material and methods

Lake sampling and analysis for physicochemical and biological parameters

A total of 34 headwater lakes were studied across Swedish subarctic (16 lakes) and boreal regions (18 lakes), encompassing areas with both low and high atmospheric N deposition (Table S1; Fig. 1a). Subarctic regions included Abisko (low N deposition; nine lakes) and Jämtland (high N deposition; seven lakes), while boreal regions included Västerbotten (low N deposition; nine lakes) and Värmland (high N deposition; nine lakes). These lakes are located at elevations ranging from 348 to 622 m a.s.l. in the subarctic and 227–440 m a.s.l. in the boreal regions, with no or little development in their catchments. Detailed descriptions of these regions and lakes are provided in Lau et al. (2021).

Lakes were sampled three times between mid-June and mid-September in 2016 (Abisko, Värmland, and Västerbotten) or 2017 (Jämtland). Sampling occurred early in the open-water season following stratification, in mid-summer, and in late summer prior to circulation. Sampling dates varied by region due to differences in ice-out, stratification, and circulation periods. The lakes spanned gradients in concentrations of DOC, DIN, TP, molar DIN:TP ratios, and surface water temperature, both within and across regions. The DIN:TP ratio has been shown to be a better proxy than the ratio between total N (TN) and TP for indicating nutrient limitation regimes especially in oligotrophic lakes (Morris & Lewis, 1988; Axler et al., 1993; Ptacnik

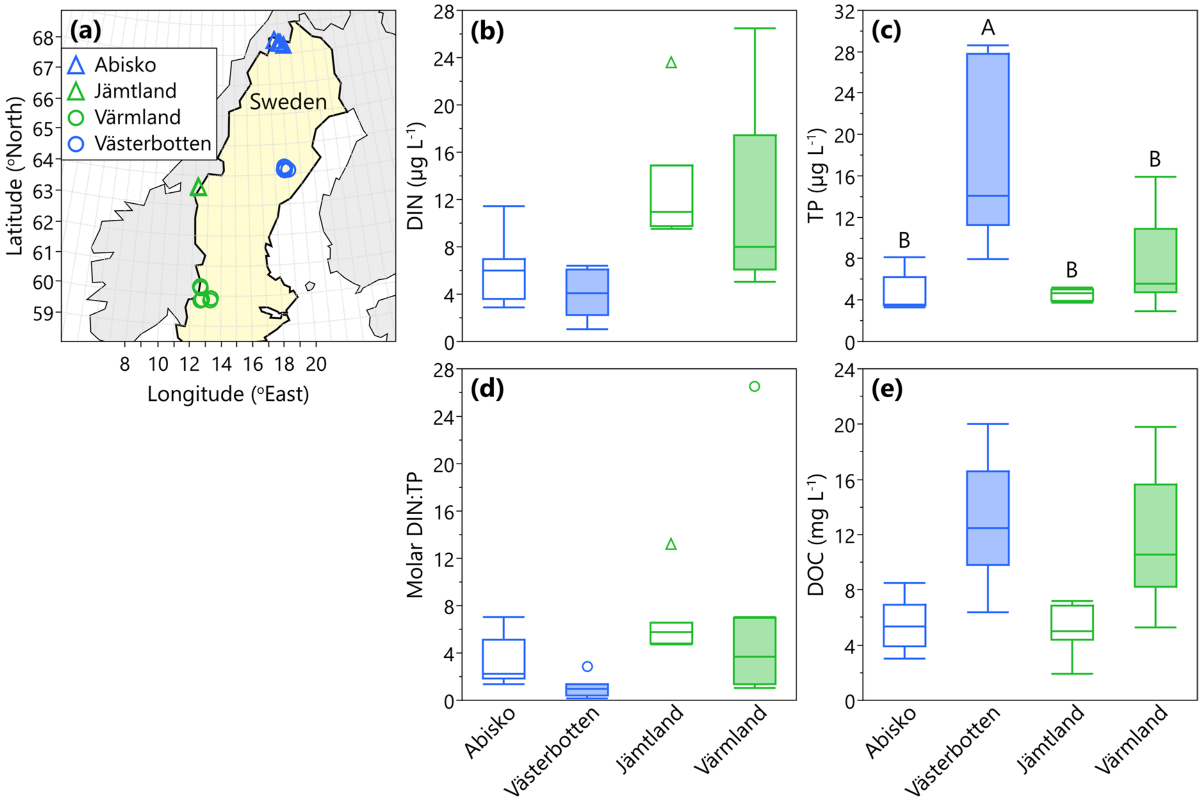

Fig. 1 **a** The location of the subarctic (triangles) and boreal lakes (circles). b Dissolved inorganic nitrogen (DIN), **c** total phosphorus (TP), **d** molar DIN:TP ratios, and **e** dissolved organic carbon (DOC) concentrations in the subarctic and boreal lakes. Blue and green symbols indicate lakes in regions with low and high atmospheric N deposition, respectively. Unfilled and filled boxes indicate subarctic lakes with low DOC and boreal lakes with high DOC, respectively. In **b–e**, the line within the box shows median, the box ends are the 1st and 3rd quartiles, and the whiskers indicate (1st quartile – 1.5(interquartile range)) and (3rd quartile + 1.5(interquartile range)). If the data points do not reach the calculated whisker ranges, then the whiskers are determined by the upper and lower data point values (excluding outliers). Points outside whiskers are outliers. Letters on boxes reflect significant interaction between N deposition and DOC levels in two-way ANOVA (Table 1). Boxes with the same letter indicate no significant differences in post hoc Tukey's comparisons. Post hoc comparisons for separate effects of N deposition and DOC levels are given in Table 1

et al., 2010), where the large part of TN is organic N that is less bioavailable for phytoplankton (Bergström, 2010; Ptacnik et al., 2010). Seasonal means in lake DIN, TP concentrations and molar DIN:TP ratios ranged from 1.1 to 11.5 $\mu g\ L^{-1}$, 3.3–28.6 $\mu g\ L^{-1}$, and < 1–7, respectively, in the low N deposition regions (Abisko and Västerbotten), and from 5.0 to 26.5 $\mu g\ L^{-1}$, 2.9–15.9 $\mu g\ L^{-1}$, and 1–27, respectively, in the high N deposition regions (Jämtland and Värmland) (Fig. 1b–d; Tables 1 and S1). Seasonal means in lake surface water temperature ranged from 10.2 to 14.7 °C in the subarctic lakes and 14.9–20.2 °C in the boreal lakes (Table S1). Seasonal means in lake DOC concentrations ranged from 1.9 to 7.2 $mg\ L^{-1}$ in the subarctic lakes and 5.3–20.0 $mg\ L^{-1}$ in the boreal lakes (Fig. 1e; Tables 1 and S1). Between 1997 and 2017, the atmospheric N deposition has showed a declining trend at all regions (– 8.4 $mg\ N\ m^{-2}\ year^{-1}$ (Abisko), – 7 $mg\ N\ m^{-2}\ year^{-1}$ (Jämtland), – 10.6 $mg\ N\ m^{-2}\ year^{-1}$ (Västerbotten), – 16.2 $mg\ N\ m^{-2}\ year^{-1}$ (Värmland); see Bergström et al., 2022) and was 123 $mg\ N\ m^{-2}\ year^{-1}$ in Abisko (subarctic north), 147 $mg\ N\ m^{-2}\ year^{-1}$ in Jämtland (subarctic south), 223 $mg\ N\ m^{-2}\ year^{-1}$ in Västerbotten (boral north), and 433 $mg\ N\ m^{-2}\ year^{-1}$ in Värmland (boreal south) during the sampling year (Bergström et al., 2022).

Table 1 Results of two-way ANOVA on comparisons of lake data between regions with low atmospheric N deposition in the north (Abisko and Västerbotten) and regions with high N deposition in the south (Jämtland and Värmland), and between subarctic regions with low DOC (Abisko and Jämtland) and regions with high DOC (Västerbotten and Värmland)

Variable	Factor	*DF*	DF_{Error}	*F*	*p*	Student's *t*-test
Log_{10}(DIN)	Model	3	30	12.727	**< 0.001**	
	N dep region	1	30	27.125	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	13.232	**0.001**	Low DOC > High DOC
	DOC region*N dep region	1	30	0.017	0.899	
Log_{10}(TP)	Model	3	30	14.611	**< 0.001**	
	N dep region	1	30	7.864	**0.009**	Low N dep > High N dep
	DOC region	1	30	25.548	**< 0.001**	High DOC > Low DOC
	DOC region*N dep region	1	30	8.899	**0.006**	
Log_{10}(DIN:TP)	Model	3	30	18.788	**< 0.001**	
	N dep region	1	30	26.348	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	28.360	**< 0.001**	Low DOC > High DOC
	DOC region*N dep region	1	30	2.526	0.123	
DOC	Model	3	30	10.544	**< 0.001**	
	N dep region	1	30	0.439	0.513	
	DOC region	1	30	30.976	**< 0.001**	High DOC > Low DOC
	DOC region*N dep region	1	30	0.132	0.719	
Seston C	Model	3	30	1.082	0.372	
	N dep region	1	30	0.769	0.388	
	DOC region	1	30	2.290	0.141	
	DOC region*N dep region	1	30	0.194	0.663	
Seston N	Model	3	30	0.828	0.489	
	N dep region	1	30	0.715	0.404	
	DOC region	1	30	0.819	0.373	
	DOC region*N dep region	1	30	0.826	0.371	
Seston P	Model	3	30	9.289	**< 0.001**	
	N dep region	1	30	13.238	**0.001**	Low N dep > High N dep
	DOC region	1	30	9.047	**0.005**	High DOC > Low DOC
	DOC region*N dep region	1	30	4.882	**0.035**	
Zooplankton biomass	Model	3	30	27.705	**< 0.001**	
	N dep region	1	30	68.714	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.212	0.649	
	DOC region*N dep region	1	30	18.703	**< 0.001**	
%Calanoids	Model	3	30	8.996	**< 0.001**	
	N dep region	1	30	21.238	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.359	0.553	
	DOC region*N dep region	1	30	6.053	**0.020**	
%Cyclopoids	Model	3	30	12.867	**< 0.001**	
	N dep region	1	30	19.514	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	2.230	0.146	
	DOC region*N dep region	1	30	20.723	**< 0.001**	
%Cladocerans	Model	3	30	2.059	0.127	
	N dep region	1	30	5.810	**0.022**	High N dep > Low N dep
	DOC region	1	30	0.037	0.848	
	DOC region*N dep region	1	30	0.122	0.729	

Table 1 (continued)

Variable	Factor	*DF*	DF_{Error}	*F*	*p*	Student's *t*-test
Log_{10}(Zooplankton C)	Model	3	30	24.330	**< 0.001**	
	N dep region	1	30	60.154	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	3.222	0.083	
	DOC region*N dep region	1	30	15.437	**< 0.001**	
Zooplankton N	3	30	22.057	**< 0.001**		
	N dep region	1	30	52.261	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.218	0.644	
	DOC region*N dep region	1	30	16.110	**< 0.001**	
Zooplankton P	Model	3	30	13.723	**< 0.001**	
	N dep region	1	30	30.523	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	2.131	0.155	
	DOC region*N dep region	1	30	12.233	**0.001**	
Log_{10}(Seston C:P)	Model	3	30	4.759	**0.008**	
	N dep region	1	30	10.331	**0.003**	High N dep > Low N dep
	DOC region	1	30	1.539	0.224	
	DOC region*N dep region	1	30	1.999	0.168	
Log_{10}(Seston N:P)	Model	3	30	8.353	**< 0.001**	
	N dep region	1	30	17.697	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	6.689	**0.015**	Low DOC > High DOC
	DOC region*N dep region	1	30	0.983	0.329	
Log_{10}(Zooplankton C:P)	Model	3	30	4.771	**0.008**	
	N dep region	1	30	13.823	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.169	0.684	
	DOC region*N dep region	1	30	0.195	0.662	
Log_{10}(Zooplankton N:P)	Model	3	30	9.353	**< 0.001**	
	N dep region	1	30	24.548	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.135	0.716	
	DOC region*N dep region	1	30	4.833	**0.036**	
Log_{10}(Imbalance C:P)	Model	3	30	11.795	**< 0.001**	
	N dep region	1	30	34.386	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	1.569	0.220	
	DOC region*N dep region	1	30	0.892	0.352	
Log_{10}(Imbalance N:P)	Model	3	30	14.981	**< 0.001**	
	N dep region	1	30	42.526	**< 0.001**	High N dep > Low N dep
	DOC region	1	30	3.360	0.077	
	DOC region*N dep region	1	30	1.419	0.243	
Log_{10}(Z:S-C)	Model	3	30	14.113	**< 0.001**	
	N dep region	1	30	35.345	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	0.318	0.577	
	DOC region*N dep region	1	30	9.213	**0.005**	
Log_{10}(Z:S–N)	Model	3	30	27.261	**< 0.001**	
	N dep region	1	30	53.134	**< 0.001**	Low N dep > High N dep
	DOC region	1	30	4.339	**0.046**	High DOC > Low DOC
	DOC region*N dep region	1	30	32.171	**< 0.001**	

Table 1 (continued)

Variable	Factor	*DF*	DF_{Error}	*F*	*p*	Student's *t*-test
Log_{10}(Z:S-P)	Model	3	30	6.961	**0.001**	
	N dep region	1	30	4.503	**0.042**	Low N dep > High N dep
	DOC region	1	30	0.418	0.523	
	DOC region*N dep region	1	30	17.402	**< 0.001**	

P values ≤ 0.05 are boldfaced

Sampling procedure and analytical methods for lake water temperature and chemistry (including DOC, DIN, and TP) are presented in detail in Bergström et al. (2018, 2022). The biological sampling is briefly presented below but also previously described in Bergström et al. (2022). For Chl-a analysis, lake water (100 mL) was filtered onto 0.7 µm GF/F filters, which were wrapped in aluminum foil and frozen. Chl-a was extracted with 95% ethanol over 24 h with agitation, then measured using a Perkin-Elmer LS-55 fluorescence spectrometer (excitation: 433 nm, emission: 673 nm).

For zooplankton biomass, mesozooplankton were sampled by vertical net hauling (100-µm mesh) from the deepest point of the lake (starting 1 m above the lake bottom with hauling depths ranging between 2 and 10 m, with an overall median hauling depth of 5 m), preserved with Lugol's solution, identified to genus level, and counted using inverted microscopy. Zooplankton biomass (dry weight, DW) was calculated using length–weight regressions for individual taxa (Bottrell et al., 1976; Deininger et al., 2017b). Zooplankton C, N, and P content analyses followed the same sampling procedure as for biomass, with the exception that several hauls (100-µm mesh) were performed to collect enough zooplankton for analyses. After collection, zooplankton bulk samples were transferred to plastic bottles and left at 4 °C dark overnight (12–24 h) for gut evacuation. Zooplankton were then sorted and separated by hand under a microscope into three groups: cladocerans (mainly *Bosmina* sp., *Ceriodaphnia* sp., *Diaphanosoma brachyurum* (Liévin, 1848), *Holopedium gibberum* Zaddach, 1855, and *Daphnia* sp.), calanoids (mainly *Eudiaptomus* sp. *Acanthodiaptomus* sp., *Heterocope* sp. and *Mixodiaptomus* sp.) and cyclopoids (*Cyclops* spp.). Primarily adults were sorted and nauplius were not included in the analyses. For analyses of C and N contents, zooplankton samples from each group, or when abundances were high samples of *Bosmina* sp., *Dahpnia* sp. and *Holopedium gibberum* were analyzed separately, were freeze dried, homogenized, and weighed into tin capsules. Samples were then analyzed using a continuous-flow isotope ratio mass spectrometer. For P content, zooplankton samples from each group, or for *Bosmina* sp., *Dahpnia* sp., and *Holopedium gibberum* separately, were transferred onto pre-weighed and acid-washed (1.2 M HCl) Whatman GF/C filters, dried overnight (60 °C), and then weighed again to determine dry mass. The P content was analyzed as molybdate reactive phosphate after an acid digestion with persulfate (120 °C/1 h) according to the Swedish standard using a FIAstar 5000. The cladocerans, calanoids, and cyclopoids, as well as the zooplankton C, N, and P contents, were reported as percent DW (for example % C per DW = µg C $µg^{-1}$ DW in zooplankton).

For seston C:N:P stoichiometry, known volumes of pre-screened composite water samples (filtered through a 50-µm net) were filtered onto pre-combusted (550 °C, 4 h) and acid-washed (1.2 M HCl) Whatman GF/F filters. Seston C and N contents were measured using a Costech ECS 4010 elemental analyser. Seston P content was measured using the molybdate blue method after an acid digestion with persulphate (120 °C/1 h) using a FIAstar 5000.

Zooplankton/seston biomass ratios of C, N, and P (Z:S-C, Z:S–N and Z:S-P)

Zooplankton C, N, and P contents were estimated by multiplying measured percent C, N, and P per DW by the biomass for each zooplankton group (i.e., cladocerans, calanoids, and cyclopoids). Total C, N, and P in zooplankton were calculated by summing the values for each zooplankton group. The Z:S-C, Z:S-N, and Z:S-P ratios were then calculated by dividing the C, N, and P concentrations for each group of zooplankton and for all zooplankton by the C, N, and P concentrations in seston. The Z:S of each element was then expressed as percentage (%) of C, N, and P, i.e., the amounts of seston C, N, and P that were accumulated in zooplankton.

Fish data

Fish presence or absence was determined from previous studies (Deininger et al., 2017a, b; Norman et al. 2022) and visual observations during sampling. Fish biomass (catch per unit effort, CPUE; g wet weight per net) was available for a subset of lakes (Norman et al., 2022; Pär Byström, unpublished data). Fish CPUE data were available mainly from the subarctic lakes (Table S2). Arctic char [*Salvelinus alpinus* (Linnaeus, 1758)] and trout (*Salmo trutta* Linnaeus, 1758) dominated subarctic lakes, while perch (*Perca fluviatilis* Linnaeus, 1758) predominated boreal lakes (Karlsson et al., 2015; Norman et al., 2022). These fish species represent low to medium zooplankton predation pressure according to Hessen et al. (2003).

Data analysis

Statistical comparisons in lake physicochemical characteristics, zooplankton assemblages, seston and zooplankton stoichiometry, nutrient imbalances between seston and zooplankton, and Z:S in C, N, and P were made among all four regions, i.e., Abisko [subarctic north, $n=9$], Västerbotten [boreal north, $n=9$]), Jämtland [subarctic south, $n=7$], and Värmland [boreal south, $n=9$]), to assess the effects of low atmospheric N deposition (Abisko and Västerbotten) versus high atmospheric N deposition (Jämtland and Värmland) and the effects of low DOC concentrations (subarctic north and south) versus high lake DOC concentrations (boreal north and south). For all lake physical, chemical, and biological variables, the seasonal averages from individual lakes were used for subsequent statistical analyses. Molar ratios were calculated and then $\log_{10}$-transformed before seasonal averaging (Isles, 2020). Nutrient imbalances for assessing differences in mineral food quality between seston and zooplankton (Sterner, 1990; Hassett et al., 1997) in terms of C:P and N:P ratios were estimated as in Bergström et al. (2022) (e.g., $\log_{10}$N:P or $\log_{10}$C:Pseston—$\log_{10}$N:P or $\log_{10}$C:P consumer) and expressed in $\log_{10}$(Imbalance C:P) and $\log_{10}$(Imbalance N:P). Changes in nutrient imbalances with lake DIN:TP and DOC were used to infer food quality impacts on Z:S ratios. We used two-way ANOVA for comparisons of lake physicochemical and biological data between regions with low versus high N deposition (i.e., north versus south) and between regions with low versus high DOC (i.e., subarctic versus boreal). The ANOVA models also included the interaction between N deposition and DOC. When significant effects were detected in ANOVA, we used Student's *t*-test (for N deposition and DOC) and/or Tukey's honest significance test (for interaction) for the post hoc comparisons. Data that were not normally distributed nor homoscedastic were $\log_{10}$-transformed before ANOVA.

We assessed the relation between atmospheric N deposition, lake DIN:TP, and Z:S ratios for C, N, and P (Q1). For this, we first compared the Z:S in C, N, and P among the four regions using one-way ANOVA with post hoc Tukey's tests (or Kruskal–Wallis with Dunn's test for data that were not normally distributed nor homoscedastic after $\log_{10}$-transformation). We then used linear regression to test whether the Z:S in C, N, and P changed with lake DIN:TP in the regions with low N deposition (Abisko and Västerbotten) and high N deposition (Jämtland and Värmland), respectively. We also used ANCOVA to test whether the Z:S ratios differed between the regions with low (Abisko and Västerbotten) and high (Jämtland and Värmland) N deposition. When ANCOVA detected significant effects of region, Student's *t*-test was used for the post hoc comparison between the low and high N deposition regions.

We investigated which zooplankton group was most important for the Z:S ratios (Q2). For this, the dependence of the Z:S for C, N, and P on the relative biomass of individual zooplankton groups was tested using linear regression.

We assessed the possible top-down impacts of fish (presence versus absence) on the biomass of zooplankton and phytoplankton (i.e., Chl-a concentration), as well as the Z:S ratios, in 27 study lakes (Table S2) where fish presence-absence data were available using Student's *t*-test (Q3). Only 14 study lakes had fish biomass CPUE data (Table S2), hindering the use of ANCOVA to test and compare the effects of fish CPUE on the Z:S ratios between regions with high versus low N deposition. We instead used stepwise multiple linear regressions with forward selection to assess whether lake water DIN:TP and DOC were significant determinants on the Z:S ratios after considering the effects of fish CPUE in these 14 lakes. The model with the lowest corrected Akaike information criterion (AICc) was selected as the best model. Except the relative biomass of individual zooplankton groups, the total zooplankton biomass, and the fish CPUE, which were normally distributed and homoscedastic, all other data used for the ANCOVA, *t*-tests, and linear regressions were $\log_{10}$-transformed.

We assessed the interaction of DOC with atmospheric N deposition and DIN:TP on Z:S ratios (Q4). Linear regression was used to test whether the Z:S in C, N, and P changed with DOC in the regions with low N deposition (Abisko and Västerbotten) and high N deposition (Jämtland and Värmland), respectively. We also used ANCOVA to test whether the Z:S ratios differed between the regions with low and high N deposition, and whether the changes in Z:S across the DOC gradient were consistent between regions with low and high N deposition. We used region (low N deposition vs. high N deposition) as the fixed factor, DOC as the covariate, and the interaction between region and DOC in the ANCOVA model. When ANCOVA detected significant effects of region, Student's *t*-test was used for the post hoc comparison between the low and high N deposition regions. Based on the linear regression models we also predicted the change in Z:S in C, N, and P along a stepwise increase in DOC from 3 to 20 mg L^{-1} for the low N deposition regions (Abisko and Västerbotten) and the high N deposition region (Jämtland and Värmland).

All statistical analyses and outputs were conducted using JMP® Pro version 15.0.0.

Results

Seston quantity and quality

The seston C and N concentrations did not differ among regions (Table 1), while seston P concentration was higher in regions with low N deposition than high N deposition and with high DOC than low DOC (Tables 1 and 2; Fig. 2a-c). The seston C:P and N:P in regions with high N deposition (i.e., Jämtland and Värmland) were higher and therefore of lower quality for zooplankton than those in regions with low N deposition (i.e., Västerbotten and Abisko) (Tables 1 and 3; Fig. S1a, b). Seston N:P was also higher in regions with low DOC (i.e., Abisko and Jämtland) than with high DOC (i.e., Västerbotten and Värmland) (Tables 1 and 3; Fig. S1b).

Zooplankton biomass, community composition, and elemental content

Zooplankton biomass was higher in regions with low N deposition than with high N deposition (Tables 1 and 2; Fig. S2a). There was a low to high N deposition separation in zooplankton communities, with a dominance of calanoid copepods in the regions with low N deposition (Abisko and Västerbotten) and a dominance of cyclopoid copepods and cladocerans in the regions with high N deposition (Jämtland and Värmland) (Tables 1 and 2; Fig. S2b-d). There was also significant interaction between N deposition and DOC levels on the relative biomass of calanoids and cyclopoids (Table 1), indicating greater differences in zooplankton composition between subarctic regions with low DOC (Abisko vs. Jämtland) than between boreal regions with high DOC (Västerbotten vs. Värmland), with cyclopoids more abundant in Jämtland (south with high N deposition) and calanoids more abundant in Abisko (north with low N deposition) (Table 2; Fig. S2b, c).

For zooplankton, the C, N, and P contents were higher in regions with low N deposition than with high N deposition (Tables 1 and 2; Fig. 2d–f). Zooplankton C, N, and P contents were consistently the highest in Abisko and the lowest in Jämtland among the regions (Table 2; Fig. 2d–f), attributing to the significant interaction between N deposition and DOC levels (Table 1). The C, N, and P contents in zooplankton were driven by zooplankton biomass, but also modified by the community composition, and the differences in C, N, and P contents among individual zooplankton groups (Table 2; Fig. S2a–d). Results of two-way ANOVA on comparisons of elemental content (C, N and P) and molar stoichiometric ratios (C:P and N:P) within individual zooplankton groups between regions with low atmospheric N deposition in the north (Abisko and Västerbotten) and regions with high N deposition in the south (Jämtland and Värmland), and between

Table 2 Elemental content of seston (μg L^{-1}), individual zooplankton groups (% per dry weight (DW)), and whole zooplankton (% per DW), and zooplankton biomass (μg DW L^{-1}), relative biomass (in percent per dry weight; % per DW) of individual zooplankton groups, and the zooplankton to seston biomass ratios (Z:S; %) in C, N, and P in the study lakes

	Abisko	Västerbotten	Jämtland	Värmland
Seston C (μg L^{-1})	451 ± 222	565 ± 135	425 ± 91	488 ± 189
Seston N (μg L^{-1})	48 ± 21	57 ± 13	48 ± 9	49 ± 15
Seston P (μg L^{-1})	2.7 ± 0.9	4.3 ± 1.2	2.2 ± 0.6	2.5 ± 0.8
Zooplankton (μg DW L^{-1})	54 ± 17	40 ± 7	9 ± 6	26 ± 11
% Cladocerans	25 ± 26	24 ± 17	38 ± 9	42 ± 20
% Calanoids	60 ± 20	40 ± 24	13 ± 8	33 ± 13
%Cyclopoids	8 ± 6	20 ± 12	44 ± 15	20 ± 11
Cladocerans C (% per DW)	54 ± 3.9	55.3 ± 3.3	50.2 ± 3.4	52.6 ± 2.5
Calanoids C (% per DW)	54.6 ± 1.7	54.5 ± 1.4	53.5 ± 0.8	54.8 ± 2.2
Cyclopoids C (%/DW)	56.5 ± 1.4	53.4 ± 1.6	52.8 ± 0.9	54.3 ± 2.3
Cladocerans N (% per DW)	8.6 ± 1.1	9.3 ± 1.7	9.5 ± 1.0	9.6 ± 0.8
Calanoids N (% per DW)	11.4 ± 0.8	11.4 ± 0.9	11.3 ± 0.6	10.9 ± 1.2
Cyclopoids N (% per DW)	10.1 ± 0.6	10.6 ± 0.5	10.8 ± 0.4	10.7 ± 0.9
Cladocerans P (% per DW)	0.60 ± 0.26	0.71 ± 0.33	0.98 ± 0.38	0.99 ± 0.38
Calanoids P (% per DW)	0.44 ± 0.14	0.50 ± 0.18	0.49 ± 0.1	0.41 ± 0.13
Cyclopoids P (% per DW)	0.69 ± 0.28	0.84 ± 0.17	1.17 ± 0.21	0.86 ± 0.24
Zooplankton C (μg L^{-1})	22.1 ± 10.1	13.6 ± 5.1	2.3 ± 1.1	6.9 ± 3.6
Zooplankton N (μg L^{-1})	5.4 ± 1.9	3.6 ± 0.9	0.9 ± 0.6	2.3 ± 0.7
Zooplankton P (μg L^{-1})	0.26 ± 0.07	0.22 ± 0.07	0.08 ± 0.04	0.18 ± 0.05
Z:S-C (%)	5.9 ± 3.3	2.6 ± 1.2	0.6 ± 0.2	2.0 ± 1.6
Z:S–N (%)	13.5 ± 6.0	6.7 ± 2.2	1.9 ± 0.9	6.2 ± 3.4
Z:S-P (%)	11.6 ± 6.3	5.5 ± 2.6	3.6 ± 1.5	8.6 ± 3.4

Values are means ± SD among lakes in each region

subarctic regions with low DOC (Abisko and Jämtland) and boreal regions with high DOC (Västerbotten and Värmland) are reported in Text S1 and Table S2.

The C:P and N:P ratios in zooplankton were higher in regions with low N deposition than with high N deposition (Tables 1 and 3; Fig. S1c, d). Zooplankton C:P and N:P ratios were highest in Abisko and lowest in Jämtland (Table 3; Fig. S1c, d). The variations among regions in zooplankton C:P and N:P ratios (Table 3) were driven by differences in C:P and N:P within individual zooplankton groups (Text S1) and community composition (Table 2). As a result, the C:P and N:P imbalances between seston and zooplankton were generally higher in both subarctic and boreal regions with high N deposition (Jämtland and Värmland) than in the regions with low N deposition (Abisko and Västerbotten) (Tables 1 and 3; Fig. S1 e, f). Zooplankton biomass was also negatively related with $\log_{10}$ (seston molar C:P) and $\log_{10}$(seston molar N:P) (Pearson correlations, $n = 34$, $r = -0.35$ and -0.40, $p = 0.043$ and 0.018, respectively).

Z:S ratios among regions and across gradients in N deposition and lake DIN:TP

The Z:S for C, N, and P ranged between 0.2 and 19%, 0.3 and 38%, and 0.5 and 42%, respectively, and was all higher in regions with low N deposition than with high N deposition (Table 1). There was also significant interaction between N deposition and DOC levels on the Z:S for C, N, and P (Table 1). The Z:S for C and N in Abisko was higher than those in Värmland and Jämtland, while those in Västerbotten were not different from Abisko and Värmland (Table 2; Fig. 2g, h). The Z:S for P was higher in Abisko and Värmland than in Jämtland, whereas the Z:S for P in Västerbotten did not differ from the other regions (Table 2; Fig. 2i).

The Z:S for C and N was overall higher in the low N deposition regions (Abisko and Västerbotten) than in the high N deposition regions (Jämtland and Värmland) based on ANCOVA (Table 4a; Fig. 3a, b). The differences in Z:S for P between the low and high N deposition regions were not significant (Table 4a; Fig. 3c). In the low N deposition regions (Abisko

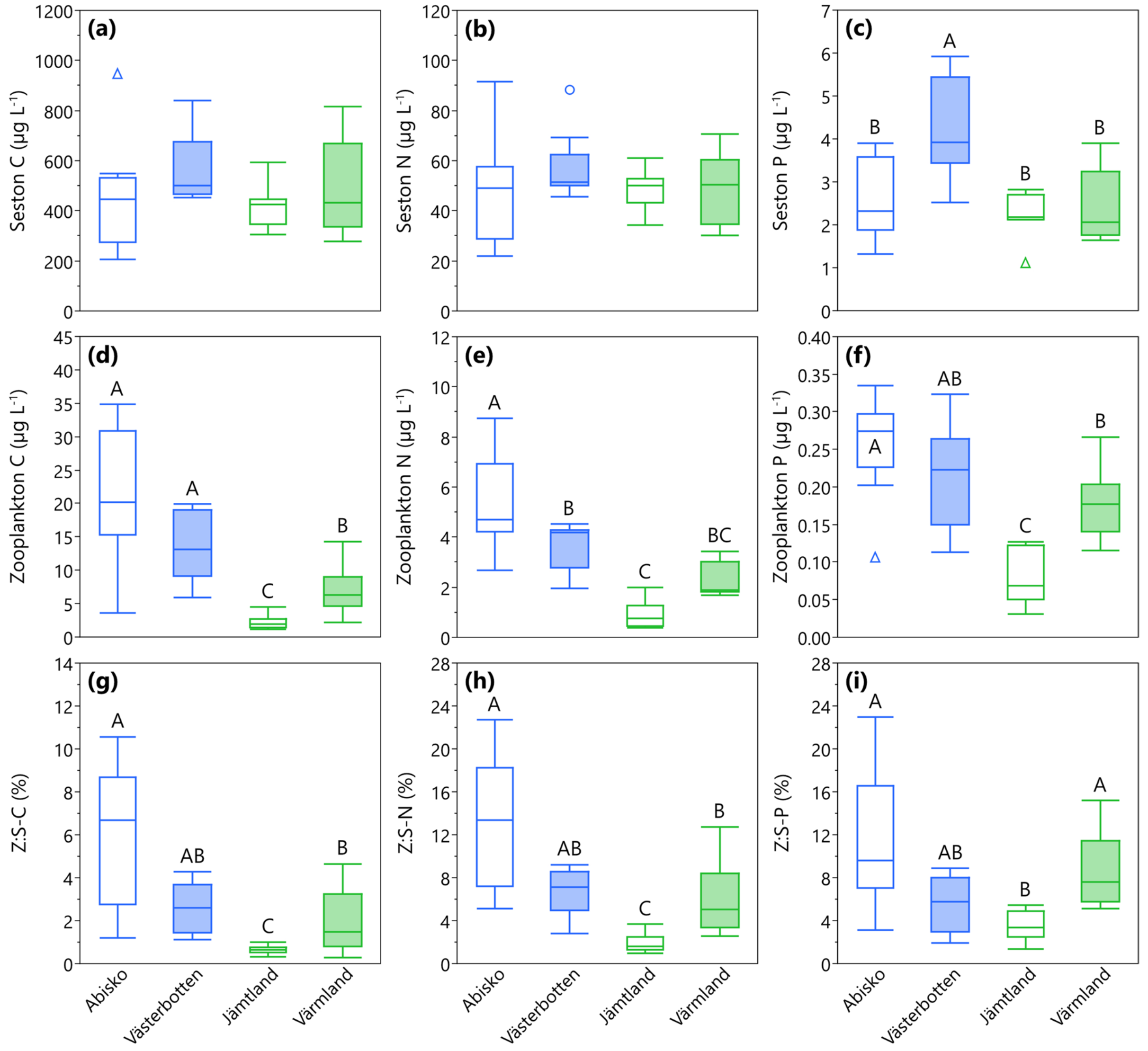

Fig. 2 The C, N, and P concentrations of seston (**a**–**c**) and zooplankton (**d**, **f**), and the lake zooplankton to seston biomass ratios (Z:S) for C, N, and P (**g**–**i**) in the four regions. Data are seasonal means over summer for individual lakes. Blue and green symbols indicate lakes in regions with low and high atmospheric N deposition, respectively. Unfilled and filled boxes indicate subarctic lakes with low DOC and boreal lakes with high DOC, respectively. The line within the box shows median, the box ends are the 1st and 3rd quartiles, and the whiskers indicate (1st quantile − 1.5(interquartile range)) and (3rd quartile + 1.5(interquartile range)). If the data points do not reach the calculated whisker ranges, then the whiskers are determined by the upper and lower data point values (excluding outliers). Points outside whiskers are outliers. Letters on boxes reflect significant interaction between N deposition and DOC levels in two-way ANOVA (Table 1). Boxes with the same letter indicate no significant differences in post hoc Tukey's comparisons. Post hoc comparisons for separate effects of N deposition and DOC levels are given in Table 1

and Västerbotten), the Z:S of C, N, and P tended to increase with increasing lake DIN:TP (Fig. 3a–c). No such trends in Z:S were detected in the high N deposition regions (Jämtland and Värmland) where lake DIN:TP ratios were higher.

Z:S ratio and zooplankton taxa

The Z:S for C, N, and P consistently increased with increasing relative biomass of calanoids in zooplankton (Fig. 3d–f), although these Z:S

Table 3 Elemental stoichiometry of seston, individual zooplankton groups, and in whole zooplankton, as well as nutrient imbalance (IM) in C:P and N:P between seston and zooplankton

	Abisko	Västerbotten	Jämtland	Värmland
$_{\log10}$Seston C:P (molar)	2.63 ± 0.12	2.53 ± 0.11	2.69 ± 0.07	2.70 ± 0.11
$_{\log10}$Seston N:P (molar)	1.59 ± 0.11	1.48 ± 0.10	1.69 ± 0.06	1.64 ± 0.07
$_{\log10}$Cladocerans C:P (mol)	2.42 ± 0.27	2.17 ± 0.21	2.34 ± 0.21	2.17 ± 0.18
$_{\log10}$Calanoids C:P (mol)	2.53 ± 0.14	2.45 ± 0.08	2.47 ± 0.16	2.46 ± 0.11
$_{\log10}$Cyclopoids C:P (mol)	2.37 ± 0.19	2.08 ± 0.11	2.23 ± 0.10	2.23 ± 0.13
$_{\log10}$Cladocerans N:P (mol)	1.55 ± 0.24	1.38 ± 0.21	1.50 ± 0.16	1.36 ± 0.17
$_{\log10}$Calanoids N:P (mol)	1.78 ± 0.15	1.71 ± 0.08	1.73 ± 0.17	1.69 ± 0.12
$_{\log10}$Cyclopoids N:P (mol)	1.55 ± 0.18	1.31 ± 0.10	1.46 ± 0.11	1.47 ± 0.16
$_{\log10}$Zooplankton C:P	2.28 ± 0.34	2.2 ± 0.24	1.89 ± 0.31	1.89 ± 0.31
$_{\log10}$Zooplankton N:P	1.67 ± 0.16	1.59 ± 0.11	1.37 ± 0.08	1.47 ± 0.11
$_{\log10}$IM_C:P	0.18 ± 0.21	0.17 ± 0.10	0.56 ± 0.12	0.44 ± 0.17
$_{\log10}$IM_N:P	− 0.08 ± 0.20	− 0.11 ± 0.11	0.32 ± 0.12	0.16 ± 0.14

Values are means ± SD among lakes in each of the four regions

Table 4 (a) ANCOVA results of the zooplankton to seston biomass ratios (Z:S) for C, N, and P between lakes in regions with low atmospheric N deposition in the north (Abisko and Västerbotten) and regions with high N deposition in the south (Jämtland and Värmland) across the gradient in lake dissolved organic C concentration (DOC; mg L^{-1})

Variable	DF	DF_{Error}	SS	F	p	Student's t-test	Model R^2
(a) ANCOVA results							
Z:S-C (%)							0.48
Region	1	30	3.195	29.103	**< 0.001**	Low N dep > High N dep	
DOC	1	30	0.029	0.266	0.610		
Region*DOC	1	30	0.468	4.265	**0.048**		
Z:S–N (%)							0.58
Region	1	30	1.838	29.353	**< 0.001**	Low N dep > High N dep	
DOC	1	30	0.015	0.244	0.625		
Region*DOC	1	30	0.712	11.366	**0.002**		
Z:S-P (%)							0.21
Region	1	30	0.180	2.541	0.121		
DOC	1	30	0.009	0.129	0.722		
Region*DOC	1	30	0.394	5.555	**0.025**		

	DOC (mg L^{-1})				
	3	5	10	15	20
(b) Predicted Z:S ratios					
Predicted Z:S-C (%)					
North	5.4	3.9	2.6	2.0	1.7
South	0.5	0.6	0.8	0.9	1.0
Predicted Z:S-N (%)					
North	13.4	10.3	7.2	5.8	5.0
South	1.4	2.0	3.3	4.4	5.3
Predicted Z:S-P (%)					
North	10.8	8.3	5.8	4.7	4.0
South	3.2	3.9	5.1	6.0	6.7

Data were $\log_{10}$-transformed before ANCOVA. P values ≤ 0.05 are boldfaced. (b) The Z:S ratios for C, N, and P predicted from different DOC concentrations for lakes in the low N atmospheric deposition and the high atmospheric N deposition regions based on the regression models in Fig. 3

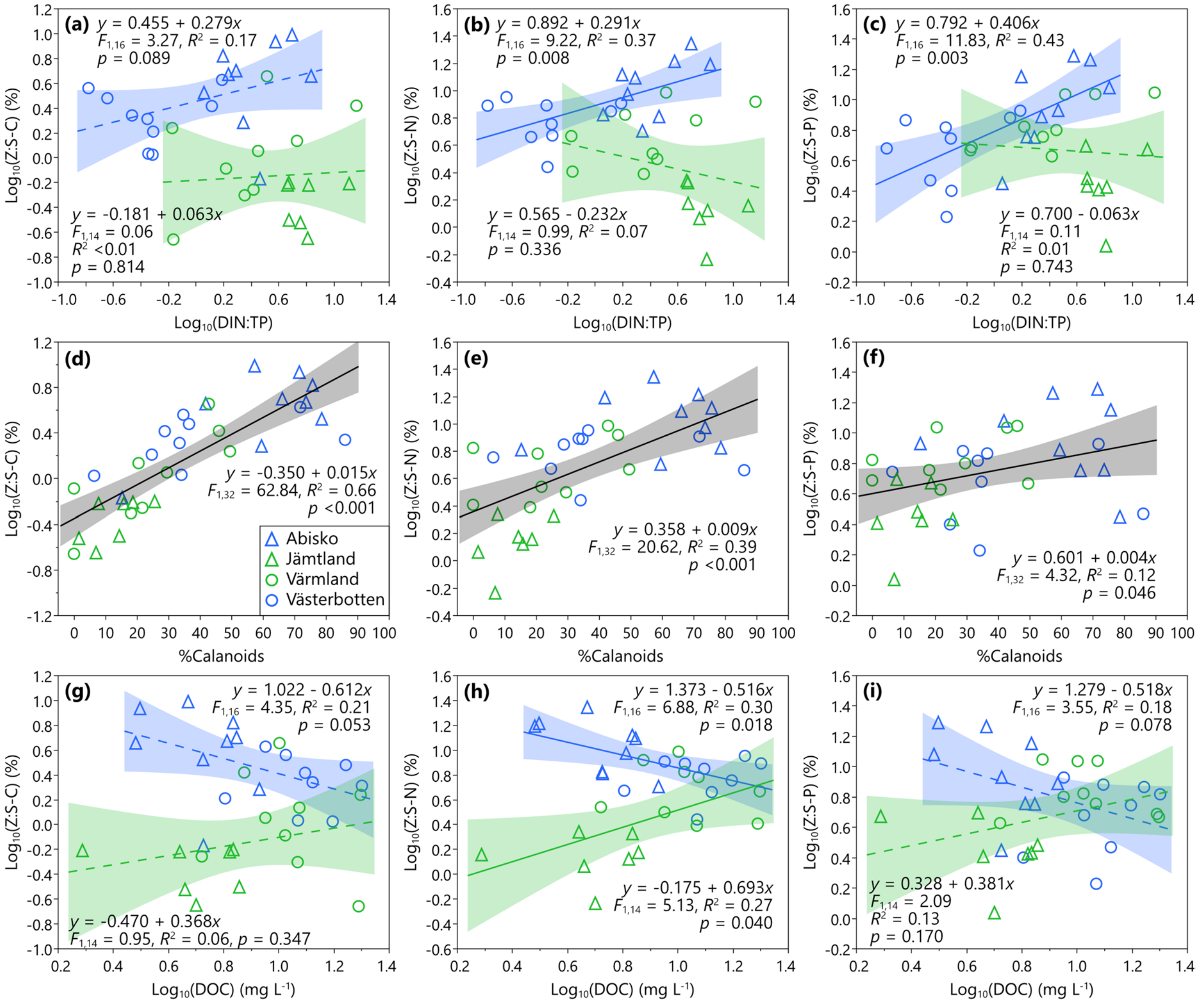

Fig. 3 Trends in the zooplankton to seston biomass ratios (Z:S) for C, N, and P with increasing dissolved inorganic N to total P molar ratio (DIN:TP) (**a**–**c**), relative biomass in dry weight of calanoids in zooplankton (**d**, **f**) and dissolved organic C (DOC) (**g**, **i**) in the study lakes. Data are seasonal means over summer for individual lakes. Solid and broken lines indicate significant and nonsignificant linear regressions (±95% confidence intervals in shades), respectively: blue, lakes with low atmospheric N deposition; green, lakes with high atmospheric N deposition; black, all study lakes

showed contrasting trends with increasing DOC between regions with low versus high N deposition (Fig. 3g–i). The Z:S for C, N, and P decreased with increasing relative biomass of cyclopoids (Fig. S3a, c, e). The Z:S for C was also negatively associated with the relative biomass of cladocerans (Fig. S3b), while the Z:S for N and P was not associated with the relative biomass of cladocerans (Fig. S3d, f). Thus, the Z:S was generally more dependent on the relative biomass of calanoids of higher body N:P (Table 2) which dominated in regions with lower N deposition (Abisko and Västerbotten) than on that of cyclopoids or cladocerans of lower body N:P (Tables 2 and 3) which dominated in regions with higher N deposition (Jämtland and Värmland) (Tables 2 and 3).

Z:S ratio and fish predation

Zooplankton biomass was higher in lakes without fish (mean ± SD = 57.0 ± 22.1 μg L^{-1}) than lakes with fish (30.7 ± 17.2 μg L^{-1}) ($t = -2.72$, $p = 0.012$; Fig. 4a). However, fish presence or absence did not significantly affect the phytoplankton biomass, i.e., Chl-a concentration ($t = 0.17$, $p = 0.867$; Fig. 4b). The Z:S

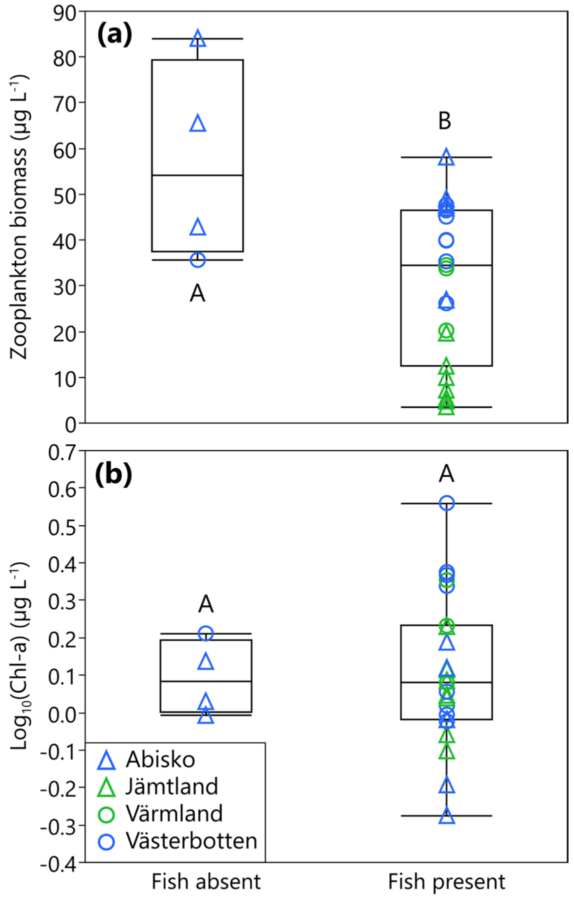

Fig. 4 **a** Zooplankton biomass and **b** chlorophyll a concentration in the lakes with and without fish. The line within the box shows median, the box ends are the 1st and 3rd quartiles, and the whiskers indicate (1st quantile − 1.5(interquartile range)) and (3rd quartile + 1.5(interquartile range)). If the data points do not reach the calculated whisker ranges, then the whiskers are determined by the upper and lower data point values (excluding outliers). Boxes with the same letter indicate no significant differences

for C, N, and P also did not differ between lakes with and without fish ($t = -1.63$–0.27, $p = 0.117$–0.786). Multiple regressions showed that the Z:S for C and N was significantly and negatively correlated with lake DIN:TP (Table 5). The Z:S for C and N was also negatively correlated with fish CPUE based on multiple regressions, although the negative correlation of Z:S for C with CPUE was nonsignificant (Table 5). There was a similar negative correlation between Z:S for P and fish CPUE, but this best model selected by the multiple regressions was not significant (Table 5).

Z:S ratio influenced by interactive effects between N deposition and lake DOC

There was consistent interaction between N deposition and DOC for all Z:S ratios, such that the Z:S differences between the low and the high N deposition regions were larger in low-DOC lakes than in high-DOC lakes (Table 4a; Fig. 3g–i). In low N deposition regions (Abisko and Västerbotten), the Z:S for C, N, and P decreased with increasing lake DOC (Table 4b; Fig. 3g–i), although the negative relationships of Z:S for C and P with DOC were insignificant (Fig. 3g, i). In high N deposition regions (Jämtland and Värmland), the Z:S for N was positively associated with DOC (Table 4b; Fig. 3h). The Z:S for C and P also tended to increase with increasing DOC in high N deposition regions, but these positive relationships were not significant (Table 4b; Fig. 3g, i). Since lake DOC is negatively correlated with the lake DIN:TP ratio in both the low and the high N deposition regions (Isles et al., 2020; Bergström et al., 2022), the Z:S trends with lake DIN:TP were generally opposite to those with lake DOC in these regions (Fig. 3a–c). In browner conditions, the Z:S for C, N, and P was more similar between regions with low and high atmospheric N deposition (Table 4b).

Table 5 Best models selected by stepwise multiple regressions of the zooplankton to seston biomass ratios (Z:S) for C, N, and P against lake dissolved inorganic N to total P molar ratio (DIN:TP), dissolved organic C (DOC) concentration, and fish biomass catch per unit effort (FishCPUE). AICc, corrected Akaike information criterion

Dependent variable	Coefficients of explanatory variables	Intercept	Model R^2
$\mathrm{Log_{10}}$(Z:S-C)	− 0.587 ($\mathrm{Log_{10}}$(DIN:TP))**, − 0.001 (FishCPUE)	0.465**	0.58**
$\mathrm{Log_{10}}$(Z:S-N)	− 0.492 ($\mathrm{Log_{10}}$(DIN:TP))**, − 0.001 (FishCPUE)*	0.911***	0.64**
$\mathrm{Log_{10}}$(Z:S-P)	− 0.0004 (FishCPUE)	0.741***	0.18

$^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Discussion

We asked four questions related on how varying N deposition and lake DOC concentrations, and presence/absence of fish, are impacting pelagic food web structure, the plankton stoichiometry, and the zooplankton-to-seston biomass ratios in northern high-latitude landscapes.

Our prediction for the first question—*Do Z:S ratios of C, N, and P vary among lakes with contrasting atmospheric N deposition?*—was supported, with Z:S ratios of C, N, and P being higher in lakes with lower atmospheric N deposition and lower lake water DIN:TP (Abisko and Västerbotten) compared to lakes with higher atmospheric N deposition and higher lake water DIN:TP (Jämtland and Värmland). These lakes with higher Z:S ratios exhibited richer seston mineral quality, which supported higher zooplankton biomass dominated by calanoid copepods. Conversely, lakes with higher atmospheric N deposition and higher DIN:TP exhibited reduced seston mineral quality, lower zooplankton biomass, and greater proportions of cyclopoid copepods and cladocerans, which contributed to lower Z:S ratios. These findings align with previous research indicating that atmospheric N deposition enhances lake DIN:TP, promoting P-limited conditions and P-poor phytoplankton (Bergström & Jansson, 2006; Elser et al., 2009), which in turn negatively affects consumer development (Sterner & Hessen, 1994; Elser et al., 2010; Hessen, 2013; Bergström et al., 2022). Consequently, zooplankton biomass was higher in lakes with low atmospheric N deposition, where nutrient imbalances were low and seston mineral quality (lower C:P and N:P) better matched the nutrient demand of zooplankton (Bergström et al., 2022).

Our prediction for the second question—*Do zooplankton taxa differentially contribute to Z:S ratios in the lakes?*—was also supported. Lakes with low atmospheric N deposition and low DIN:TP, where phytoplankton is predominantly N-limited (Isles et al., 2020; Bergström et al., 2022), calanoid copepods contributed more significantly to higher Z:S ratios of C, N, and P than other zooplankton groups. The highest Z:S ratios were observed in Abisko, where zooplankton biomass was highest and dominated by calanoids of high body C:P and N:P. In contrast, the lowest Z:S ratios were found in Jämtland, where zooplankton biomass was lowest and dominated by cyclopoids with lower body C:P and N:P. These findings align with previous research showing that calanoids have a stronger ability to retain dietary N compared to other zooplankton taxa (Sterner, 1990; Andersen & Hessen, 1991; Bergström et al., 2022).

Further, our results suggest that the dominance of calanoid copepods in northern lakes with low atmospheric N deposition was associated with lower seston C:P and N:P, which provided better food quality for zooplankton. This result is consistent with previous studies (Sterner & Hessen, 1994; Bergström et al., 2022) that seston C:P and N:P ratios strongly influence zooplankton biomass. Additionally, we observed previously in these study lakes that seston nutritional quality, measured in terms of essential highly unsaturated fatty acid (HUFA) content, increased with increasing lake DIN:TP (Lau et al., 2021), contrasting with the decrease in seston mineral quality under more P-limited conditions (Table 2; Bergström et al., 2022). These findings highlight the complex tradeoffs zooplankton face in balancing biochemical (e.g., HUFA) and mineral nutrient (N or P) demands.

Our prediction for the third question—*Does fish predation override the effects of atmospheric N deposition on Z:S ratios in these lakes?*—was supported. Our findings indicate that while fish presence reduced zooplankton biomass, it did not exert a strong cascading effect on Z:S ratios or phytoplankton biomass. Even after considering the effects of fish predation in a subset of lakes (which mostly were in the subarctic regions), the positive impacts of lower lake DIN:TP on Z:S ratios remained evident, particularly for C and N. These results suggest that bottom-up controls (lake DIN:TP and DOC) via seston mineral quality on Z:S ratios seem to play a stronger role than the top-down control by fish.

Although zooplankton biomass was lower in lakes with fish, we observed substantial variability among lakes with similar fish predation pressures. In addition, fish presence (or absence) did not affect the relative biomass of individual zooplankton groups nor the zooplankton community composition (t-tests assuming unequal variances for Log_{10}(%Calanoids), Log_{10}(%Cyclopoids), and Log_{10}(%Cladocerans): $t = -2.05–2.17$, $p = 0.097–0.128$). This is consistent with prior findings that zooplankton community composition in oligotrophic lakes is largely determined by lake water chemistry environment, including nutrients (especially P for *Daphnia*), DOC, Ca, and pH, rather than fish predation pressure alone (Sterner et al., 1992; Hessen et al., 1995a, b; Bergström et al., 2024). Grazing by planktivorous fish is further known to impact zooplankton biomass by reducing large-bodied zooplankton (Hessen et al., 2006). Yet, we did not note any regional differences in size distribution within individual zooplankton groups. Additionally, our results suggest that fish communities in the study lakes, which are dominated by arctic char and trout (subarctic) and perch (boreal), exert relatively low to moderate predation pressure on zooplankton (Hessen et al., 2003). The lack of a strong predation effect on zooplankton biomass may be attributed to the reliance of fish on benthic prey and trophic pathways in oligotrophic lakes (Karlsson & Byström, 2005; Karlsson et al., 2009; Norman et al., 2022).

Our fourth question—*Does DOC counteract the effects of atmospheric N deposition on Z:S ratios in these lakes?*—and the corresponding prediction was supported since we found that increasing DOC moderated the negative effects of higher atmospheric N deposition on Z:S ratios by enriching seston mineral quality and promoting more similar zooplankton community composition. Higher DOC concentrations reduced differences in Z:S ratios associated with contrasting levels of atmospheric N deposition and lake DIN:TP. In boreal regions (Västerbotten and Värmland), where DOC was higher, zooplankton biomass and community composition were more similar among lakes, leading to reduced differences in Z:S ratios compared to in subarctic lakes. Consequently, Z:S ratios were only 1.3 times higher for C, similar for N, and 0.6 times lower for P in Västerbotten than in Värmland, whereas they were 10 times higher for C, 7 times higher for N, and 3 times higher for P in Abisko than in Jämtland.

DOC's role in moderating Z:S differences is likely due to its effect on reducing the ratio of light to nutrient availability (e.g., reduced DIN:TP ratios and light availability following increases in lake water DOC and associated TP concentrations; see Isles et al., 2020), improving seston mineral quality (Urabe et al., 2002; Bergström et al., 2022), and promoting more similar zooplankton community composition. However, multiple regression analyses did not identify DOC as a significant predictor of Z:S ratios, likely because high-DOC boreal lakes were excluded due to missing fish CPUE data.

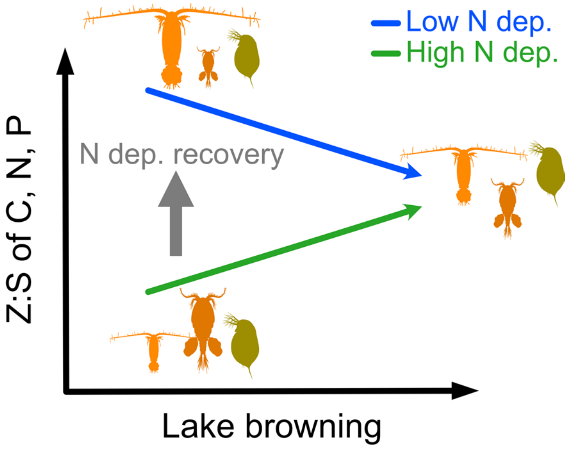

Fig. 5 Conceptual model illustrating trajectories in the zooplankton to seston biomass ratios (Z:S) of C, N, and P in northern oligotrophic lakes following atmospheric N deposition recovery and lake browning. Our findings provide evidence that lake browning lowers the enhanced response in Z:S ratios caused by atmospheric N deposition recovery via its impacts on seston mineral quality and the relative biomass of calanoids in zooplankton. Blue and green lines indicate the Z:S ratio trajectories with browning in regions with low and high atmospheric N deposition, respectively. Gray arrow illustrates the positive impact of atmospheric N deposition recovery on lake Z:S ratios. A larger symbol size of the zooplankton group (i.e., calanoids, cyclopoids, or cladocerans) reflects a higher relative biomass in dry weight in the zooplankton community

Conclusion

Our findings provide evidence that atmospheric N deposition and lake browning jointly influence the Z:S ratios of C, N, and P by altering seston stoichiometry and zooplankton community composition (Fig. 5). Lakes with higher atmospheric N deposition and higher DIN:TP exhibit lower Z:S ratios due to reduced seston mineral quality and shifts in zooplankton community composition. However, increasing DOC moderates these differences by improving seston mineral quality and homogenizing zooplankton community composition. Fish predation has a limited effect on Z:S ratios, as the positive impact of lower lake DIN:TP on Z:S ratios remains strongly evident even in lakes with fish. Overall, our results suggest that recovery from atmospheric N deposition and concurrent lake browning will likely result in lower Z:S ratios and nutrient accumulation in planktonic food chains, with potential repercussions for ecosystem productivity in northern lakes.

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Author contributions Ann-Kristin Bergström conceived the study together with Danny Lau and Irena Creed. Field work was conducted by Peter Isles, Erik Geibrink, Anders Jonsson, and Ann-Kristin Bergström. Data assessment and analyses, as well as figure and table illustrations, were performed by Ann-Kristin Bergström and Danny Lau. Ann-Kristin Bergström and Danny Lau wrote the paper with contributions from all co-authors.

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Data availability The data that support the findings of this study are openly available in Zenodo at https://doi.org/10.5281/zenodo.15776055.

Declarations

Conflict of interest The authors have no competing or conflict of interest to declare.

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