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STOICHIOMETRY AND PLANKTONIC COMMUNITIES STRUCTURE IN LITTORAL AND PELAGIC ZONES OF TWO LAKES WITH DIFFERENT TROPHIC TYPES IN BELARUS

(Communicated by Corresponding Member Vitaly P. Semenchenko)

Abstract. Stoichiometric C : N : P ratios were compared between primary producers in littoral and pelagic ecosystems of mesotrophic relatively shallow lake Obsterno and shallow macrophyte covered low trophic lake Nobisto from May to October over the next two years. Elemental seston ratios of lake Obsterno revealed smaller differences between littoral and pelagic zones in comparison with lake Nobisto in 2017. During the studied period, in the both lakes, the seston C : N and C : P ratios were higher than the Redfield ratio (106 : 16 : 1 C : N : P) on most dates and N : P was always more than 16. Pelagic C : P and N : P ratios in lake Obsterno were the highest in May in 2017, July and September in 2018 with significant differences between littoral and pelagic zones. N : P ratios decreased in October but there were no significant differences among habitats. In lake Nobisto in 2018, seston C : P and N : P ratios increased from May to July in littoral and pelagic zones but then decreased in September to October. Our research shows differences in stoichiometric ratios in littoral and pelagic zones of these two lakes, which indicates food quality (seston C : N : P ratios) differences for zooplankton species depending on season and location.

Keywords: Seston stoichiometry, shallow lakes, pelagic zone, littoral, phytoplankton, zooplankton

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СТЕХИОМЕТРИЯ И СТРУКТУРА ПЛАНКТОННЫХ СООБЩЕСТВ В ЛИТОРАЛИ И ПЕЛАГИАЛИ ДВУХ ОЗЕР РАЗНОГО ТРОФИЧЕСКОГО СТАТУСА В БЕЛАРУСИ

(Представлено членом-корреспондентом В. П. Семенченко)

Аннотация. Изучали стехиометрию сестона (соотношения C : N : P) двух мелководных озер разной трофности – мезотрофного озера Обстерно и дистрофного макрофитного типа озера Нобисто в течение двух последовательных лет. Сравнивали сезонные изменения в стехиометрии продуцентов в литоральной и пелагической зонах. Соотношения элементов в сестоне оз. Обстерно выявили меньшие различия между литоральной и пелагической зонами по сравнению с оз. Нобисто в 2017 г. В течение исследуемого периода в обоих озерах соотношения C : N и C : P в сестоне были выше классического соотношения Редфилда ($C_{106} : N_{16} : P_1$), а соотношение N : P всегда превышало 16. Соотношения C : P в пелагиали оз. Обстерно имели самые высокие показатели в мае 2017 г., а N : P в июле и сентябре 2018 г. со значимыми различиями между литоральной и пелагической зонами, но соотношения N : P уменьшились в октябре и не различались между местообитаниями. В оз. Нобисто в 2018 г. соотношения C : P и N : P в сестоне увеличивались с мая по июль в прибрежной и пелагической зонах, но затем снижались осенью. Как показали наши исследования, сезонные различия в стехиометрии сестона двух озер (соотношение C : N : P как показатель качества пищи) в разных местообитаниях отражают видовой состав фитопланктона, а также структуру сообществ зоопланктона, изменяющуюся в течение сезона и между местообитаниями.

Ключевые слова: стехиометрия сестона, мелководные озера, пелагиаль, литоральная зона, фитопланктон, зоопланктон

Для цитирования. Стехиометрия и структура планктонных сообществ в литорали и пелагиали двух озер разного трофического статуса в Беларуси / Ж. Ф. Бусева [и др.] // Докл. Нац. акад. наук Беларуси. – 2022. – Т. 66, № 6. – С. 595–604. https://doi.org/10.29235/1561-8323-2022-66-6-595-604

Introduction. Littoral ecosystems are important components of lakes due to their high productivity and biodiversity. Despite this, many early studies examining the causes and consequences of elemental imbalances between producers and consumers were conducted on pelagic organisms [1]. In those studies, imbalanced nutrient ratios between trophic levels resulted from the elevation of C : nutrient ratios in primary producers and more constrained elemental ratios in the bodies of zooplankton [2; 3]. Elemental imbalances between consumer and food results in slower animal growth and altered rates and ratios of nutrient release [4]. Whether these types of elemental dynamics are important for littoral ecosystems and their zoobenthos and fish consumers remains to be seen given the lack of directed studies on these communities.

Stoichiometric dynamics could differ in littoral zones compared to pelagic ecosystems. First, the elemental composition of particulate food might be different due to differences in nutrient supply resulting from more sediment release or lateral transport from the shoreline and water level fluctuation [5; 6]. Alternatively, substantial levels of macrophyte production could result in greater nutrient competition or more C-rich particles in littoral zones. These differences in source food material and/or nutrient supply could affect the C:nutrient ratios in food material and result in more or less nutrient limitation in zoobenthic consumers.

In addition, consumer communities also differ between littoral and pelagic ecosystems, which could alter the type or severity of stoichiometric imbalances. Some taxa such as cyclopoid copepods and *Bosmina longirostris* are primarily pelagic, but also found in the littoral zone. According to the previous research on Lake Obsterno [7], the total summer population abundance of *Cladocera* is minimum in the littoral without macrophytes and considerably high in the pelagic zone and rush-covered littoral. Some of the littoral species, for instance *D. brachyurum,* dominated in pelagic zone but *C. pulchella* dominated the rush-covered littoral. These differences in species composition could affect zooplankton C : N : P ratios and the size of elemental imbalances if different zooplankton species have contrasting elemental ratios.

To assess this possibility, patterns of species composition and biomass need to be linked to individual zooplankton C : N : P content. In this study, seasonal dynamics in elemental composition (carbon (C), nitrogen (N) and phosphorus (P)) of seston was studied over two years in two shallow lakes with different trophy status. We determined whether elemental ratios differ in littoral zones from that in the adjacent pelagic zones.

Methods. Lake Obsterno is a mesotrophic relatively shallow lake with surface area of 9.89 km^2, max depth 12 m, mean depth of 5.3 m. The lake has wide macrophyte beds occupying most of the shallow water area in littoral zone. Interconnected lake Nobisto with 3.75 km^2 surface area is shallow macrophyte covered lake, has a max and mean depths of 2.8 and 1.4 m respectively. Lake Nobisto has one shoreline bounded by swamp forests and wide and dense macrophyte beds grow all around the lake.

Water samples were collected in two consecutive years 2017 and 2018 from May to October in three seasons – spring (May), summer (July) and autumn (September and/or October). All samples were taken once a day at around 10:00–12:00 o'clock. Seston samples for carbon, nitrogen and phosphorus analysis were stored in clean amber plastic bottles that were first washed and rinsed in distilled water. In the laboratory, water samples were filtered through pre-combusted (400 °C for 5 h) glass fibre GF/F filters (Microbio, pore size 0.7 μm) and dried at 60 °C for 72 h. Final volume of filtering water on GF/F for seston >100 μm was up to 0.05 liter and for seston <100 μm from 0.8–1.2 liter. Flash EA 1112 NC Soil/MAS 200, Thermo Quest, Italy, CHN analyzer was used for carbon and nitrogen determination. Particulate matter for P content was analyzed after persulfate oxidation via spectrophotometer.

At each habitat, we sampled zooplankton communities using a 100 µm mesh tow net. These samples were preserved in 4 % formalin. Preserved zooplankton communities were examined with a stereomicroscope (MBS-10) to count and measure species composition. Phytoplankton samples were kept in 1 litre jars, preserved with Lugol's solution and after sedimentation identified under a light stereomicroscope (Micros MC CAM500, Austria) measured via Fuchs–Rosenthal counting chamber method (0.0032 ml volume) at 400× magnification. Phytoplankton biomass was counted via calculation of algae biovolume equated to appropriate geometric shapes (or their combinations) and relevant sizes were measured using an ocular micrometer.

To test the significant differences among seasons and habitats, we used one-way ANOVA with Tukey post hoc test. To recognize the existence of significant relations among the abundance of zooplankton and phytoplankton dominant species in all habitats with the main hydrochemical parameters (temperature, NO_3, PO_4, NH_4) we ran Eigen analysis of the Correlation Matrix Variable with the association ($r < 0.4$ weak, $r = 0.4$ is an average and $r > 0.4$ high correlation). Data were log-transformed, if necessary, to help meet the assumptions of Normality. All statistical analyses were conducted using Minitab 17.

Results and Discussion. During this study, in Lake Obsterno in 2017 and 2018, water temperature varied from 18.4–18.7 °C in May with maximum of 19.1–21.9 °C in July to 10.60–14.1 °C in October. In lake Nobisto in 2017–2018, water temperature varied from 16.7–19.6 °C in May with maximum of 18.7–22.4 °C in summer within pelagic zone location to October 9.6–12.3 °C. The Secchi disc transparency in Obsterno differed from spring to autumn shifted from 4.1–5.0 m in May to 3.5–4.0 m in July and 5.1–2.5 m in October. The transparency in Nobisto shifted seasonally from 1.8–2.3 m in May and 2.2–3.0 m in July and 2.9–2.3 m in October. Year 2018 was warmer but transparency was lower in Nobisto lake from July to October. Contrary, in lake Obsterno transparency was higher from May to July in the same warmer year 2018. The other hydrochemical parameters are presented in Table 1.

T a b l e 1. **Hydrochemical parameters of lakes Obsterno and Nobisto (2017–2018)**

Lake	Month	Habitats	*T*, °C	Secchi depth, m	PO_4, mg/l	NO_3, mg/l	NH_4, mg/l	O_2, mg/l	TDS, mS/cm
2017									
Obsterno	May	Pelagic	18.4	4.1	1.56	1.1	0.37	13.2	120
		Littoral	19.1		1.1–2.0	0.5–1.3	0.23–0.28	13.2–14.0	120
	July	Pelagic	19.1	3.5	0.27	0	0.19	7.4	120
		Littoral	18.3–18.5		0.53–1.4	0	0.14–1.15	8.0–8.6	120
	Oct	Pelagic	10.8	5.1	1.84	0	0.5	10.5	115
		Littoral	10.6–10.7		1.39–3.86	0–1.0	0.4–1.12	8.7–9.4	115
Nobisto	May	Pelagic	16.9	2.3	1.04	0	0.07	10.7	130
		Littoral	16.7–16.9		1.3–2.04	0	0.05–0.41	4.3–4.5	130
	July	Pelagic	18.7	3.0	0.6	0.2	0.41	6.9	120
		Littoral	18.6		0.57–2.6	0	0.31–0.41	5.7–6.8	130
	Oct	Pelagic	9.6	2.9	2.0	0	0.77	10.0	110
		Littoral	9.6–9.8		1.04–1.84	0–0.2	0.93–1.56	7.7–8.6	100–110
2018									
Obsterno	May	Pelagic	19.0	5.0	0.14	0	0.2	13.7	120
		Littoral	18.5–19.0		0.15–1.56	0–0.5	0.39–2.57	nd	120–130
	July	Pelagic	21.8	4.0	0.55	0.8	0.45	14.6	140
		Littoral	21.9		0.35–0.87	0.1–1.2	0.28–0.37	12.3–15.5	130
	Sept	Pelagic	21.1	5.0	2.43	0	0.18	nd	130
		Littoral	20.9–21.4		1.02–1.45	0–0.5	0.17–0.38	nd	130
	Oct	Pelagic	14.9	2.5	1.1	2.2	0.43	nd	140
		Littoral	14.1–15.2		0.48–0.58	0–0.6	0.11–0.47	nd	140
Nobisto	May	Pelagic	20.4	1.8	0.2	0.3	0.36	nd	130
		Littoral	19.6–20.8		0.16–0.41	0.1–0.4	0.19–0.29	nd	130
	July	Pelagic	22.2	2.2	1.58	1.4	0.25	14.6	130
		Littoral	22.1–22.4		0.12–1.15	0.1–0.2	0.23–0.6	15.4–15.5	130
	Sept	Pelagic	20.5	2.0	0.3	0	0.27	nd	130
		Littoral	20.3–20.4		1.01–1.05	0–0.8	0.13–0.3	nd	130
	Oct	Pelagic	13.0	2.3	0.16	1.4	0.43	nd	145
		Littoral	12.3–12.8		0.19–0.65	0.7–1.4	0.3–0.37	nd	135–140

N o t e s. Data for two/three littoral locations of each lake represent min-max values. Oct – October; Sept – September; nd – no data.

Within 2017–2018, seston stoichiometry showed significant differences between littoral and pelagic zone in Obsterno lake from May to October. During whole study period in lake Obsterno, C : N ratio varied from 7.97 to 13.57 in pelagic zone and ranged from 9.10 to 9.41 in littoral, N : P 18.39 to 47.8 in pelagic zone but from 23.3 to 56.53 in littoral and finally C : P varied from 193.9 to 397.3 in pelagic zone and 221 to 514 in littoral (Table 2, Obsterno lake). Synchronously, seston C : P and N : P ratios in lake Nobisto increased in July in both years, in comparison with May in littoral and pelagic zone. Seston C : P and N : P ratios also showed similar decreasing tendencies but not statistically significant in October. In contrast, although mean seston C : N ratios was significantly higher in May, this difference of C : N ratios were not significant within littoral and pelagic zone in October (Table 2, Nobisto lake). Both N : P and C : P ratios did not show significant differences among habitats but were highest at pelagic habitat in July and generally lower at littoral for C : P.

T a b l e 2. **Seston elemental ratios (seston fraction <100 μm) of lakes Obsterno and Nobisto in 2017–2018**

Lake	Month	Habiats	C : N	N : P	C : P
2017					
Obsterno	May	Pelagic	11.01 ± 1.64[abc]	38.13 ± 13.83[ab]	408.4 ± 89.7[b]
		Littoral zone	11.61 ± 2.04[abc]	48.57 ± 15.36[ab]	570.33 ± 238.0[ab]
	July	Pelagic	10.38 ± 2.41[abc]	46.5 ± 28.6[ab]	437.0 ± 225.0[b]
		Littoral zone	9.60 ± 1.1[bc]	26.17 ± 3.47[b]	247.56 ± 43.23[b]
	October	Pelagic	15.62 ± 4.86[a]	235 ± 300[a]	4408 ± 5828[a]
		Littoral zone	10.18 ± 2.91[abc]	31.6 ± 10.62[ab]	317.03 ± 80.86[ab]
Nobisto	May	Pelagic	13.34 ± 2.18[a]	23.96 ± 9.43[b]	309.3 ± 73.5[b]
		Littoral zone	10.0 ± 2.45[ab]	51.47 ± 19.64[b]	514.5 ± 250.6[b]
	July	Pelagic	7.23 ± 0.49[b]	149.2 ± 152.5[b]	1045 ± 1015[b]
		Littoral zone	7.79 ± 0.18[ab]	152.0 ± 6.1[a]	1355.4 ± 65.25[a]
	October	Pelagic	10.74 ± 0.92[ab]	31.1 ± 13.84[b]	340.0 ± 177.0[b]
		Littoral zone	11.42 ± 2.27[ab]	45.29 ± 29.09[b]	883.5 ± 860.5[b]
2018					
Obsterno	May	Pelagic	10.68 ± 0.478[ab]	18.39 ± 8.38[a]	193.9 ± 79.3[a]
		Littoral zone	9.10 ± 2.58[b]	30.08 ± 18.32[a]	275.6 ± 177.4[a]
	July	Pelagic	7.979 ± 0.949[b]	47.8 ± 23.1[a]	387.0 ± 206.0[a]
		Littoral zone	10.77 ± 2.14[ab]	29.97 ± 11.99[a]	302.7 ± 103.63[a]
	September	Pelagic	8.747 ± 0.053[ab]	45.44 ± 6.60[a]	397.3 ± 55.3[a]
		Littoral zone	9.16 ± 0.285[ab]	56.53 ± 35.7[a]	514.3 ± 318.3[a]
	October	Pelagic	13.52 ± 0.202[a]	31.23 ± 2.84[a]	255.61 ± 16.64[a]
		Littoral zone	9.41 ± 0.85[ab]	23.3 ± 3.36[a]	221.27 ± 46.66[a]
Nobisto	May	Pelagic	10.25 ± 1.087[a]	35.79 ± 10.15[ab]	373.5 ± 146.4[ab]
		Littoral zone	9.79 ± 1.8[a]	34.87 ± 12.58[ab]	319.65 ± 76.0[ab]
	July	Pelagic	9.279 ± 0.76[a]	41.96 ± 13.06[ab]	383.2 ± 86.6[ab]
		Littoral zone	10.20 ± 1.31[a]	45.07 ± 20.48[ab]	486.2 ± 297.75[ab]
	September	Pelagic	8.97 ± 0.43[a]	45.4 ± 18.0[ab]	411.0 ± 181.0[ab]
		Littoral zone	9.62 ± 1.29[a]	27.44 ± 5.25[ab]	255.15 ± 23.66[ab]
	October	Pelagic	9.26 ± 0.55[a]	23.99 ± 12.66[ab]	218.8 ± 111.3[b]
		Littoral zone	10.16 ± 2.155[a]	22.69 ± 11.56[ab]	217.25 ± 70.6[b]

N o t e s. Elements in μg/l, seston fraction <100 μm. Grouping information using Tukey test for C : N : P ratios, different labels (a, b, c) show significant differences ($p < 0.05$) of ratios among habitats (a, b) and seasons (c)

Seston phosphorus content of the lake Obsterno in 2017 was recorded from 2–10 μg/l by spring to autumn. But in Nobisto from 0.02–13 μg/l. In 2018, phosphorus (P) content of seston in lake Obsterno increased from 6–28 μg/l and 4–14 μg/l in lake Nobisto. Within 2017–2018, we observed higher phosphorus in warm season in littoral than in pelagic zone as well as in Nobisto lake but higher in pelagic zone during May and October.

In both Obsterno and Nobisto, seston C : N and C : P ratios were higher than the Redfield ratio (106 : 16 : 1 C : N : P) on most dates and N : P was frequently more than 16, suggesting a general excess of N relative to P, which is consistent with high dissolved N : P values in late summer. Seston C : P and N : P ratios exceeded Redfield proportions on most dates, showing the existence of P-limited phytoplankton growth. Increases in seston C : P and N : P ratios during the sampling season indicated that phytoplankton P limitation in pelagic zone habitats became more intense in Obsterno. Both N : P and C : P ratios were higher at pelagic habitat in July and October and generally lower than in littoral. Throughout the study period in 2017 in Obsterno lake, nutrient ratios in seston showed marked temporal changes, it peaked once in late May, maintained a relatively lower level in July specially in littoral, and increased again in October (Table 2, Obsterno lake). However, no studies have quantified differences between pelagic and littoral food stoichiometry but a logical way to achieve this goal is to characterize the species composition of zooplankton and their body stoichiometry of dominant zooplankton taxa in both habitats. Given the compared results of those factors with seston stoichiometry of shallow lakes could be an outstanding step for future stoichiometric investigations. Together, these differences in the elemental composition of suspended food would alter the frequency and severity of growth limitation of these secondary consumers. In addition, this could affect their rates of nutrient release and the resupply ratios of nutrients back into the littoral environment.

Regarding to phytoplankton, lake Obsterno in May and July 2017 and 2018, *Chrysophyta* and then *Bacillariophyta* were the most abundant algae groups in pelagic zone, bare littoral, rush beds and yellow water-lily zone respectively but with almost 4 fold more abundance in May 2018 in comparison with May 2017. In autumn 2017, *Bacillariophyta* but in 2018 *Cryptophyta* was also the most widespread group in all habitats. During these two years, *Cyanophyta* were absent in May in pelagic zone and bare littoral and had minimum values in rush beds and yellow water lily zone.

According to the phytoplankton community composition of lake Nobisto in May 2017 *Chrysophyta* and then *Bacillariophyta* in pelagic zone, bare littoral and bulrush were registered as the most abundant ones. In summer, phytoplankton community composition did not substantially change but its total abundance decreased to almost two folders in all habitats; just in bulrush we registered more *Bacillariophyta* than *Chrysophyta.* During autumn in pelagic zone *Chrysophyta* but in bare littoral and bulrush, *Bacillariophyta* were the dominant groups. In lake Nobisto, we identified minimum values of *Cyanophyta* in all habitats in autumn. In Nobisto lake in 2018, only total abundance of phytoplankton community composition increased in comparison with 2017. In May, *Chrysophyta* and then *Bacillariophyta* in pelagic zone, bare littoral and bulrush, in July, *Chlorophyta* and *Bacillariophyta* in all habitats and finally in October, *Euglenophyta* in all habitats specially in pelagic zone then *Bacillariophyta* were the most abundant groups. Correlation analysis expressed mostly weak correlation between phytoplankton groups and C : N : P as well as water chemistry (Tables 3, 4). *Chrysophyta* in May and July and *Bacillariophyta* and *Euglenophyta* in October were identified as the most abundant groups in lake Nobisto within 2017 and 2018.

T a b l e 3. **Results of Eigen analysis of the Correlation Matrix Variable between elements and their ratios in seston with biomass of dominant zooplankton species, biomass of dominant phytoplankton groups and hydrochemical parameters in Obsterno and Nobisto lakes (2017)**

Index	Lake Obsterno						Lake Nobisto					
	C	N	P	C : N	N : P	C : P	C	N	P	C : N	N : P	C : P
Bosmina	0.151	0.394		0.309						0.401	0.248	
Daphnia				0.341	0.120	0.318				0.378	**0.704**	
Ceriodaphnia					**0.640**						0.299	
Diaphnosoma		**0.595**	0.062				**0.708**				0.298	
Eudiaptomus			**0.512**	0.309	0.328	0.372				0.332		
Thermocyclops		0.322		0.318		0.340				**0.416**	0.345	
T, °C	0.140	0.143	0.245	**0.433**							0.271	
O_2		0.183	**0.434**			0.301			**0.782**			
NO_3	**0.705**	0.219				0.351		**0.702**		0.229	0.261	
NH_4	**0.442**		**0.558**		0.203				**0.558**	**0.423**		

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Index	Lake Obsterno						Lake Nobisto					
	C	N	P	C : N	N : P	C : P	C	N	P	C : N	N : P	C : P
PO_4					**0.661**		0.265	0.388			**0.704**	
Cyanophyta	**0.789**	**0.698**	0.339	0.343	0.041							0.236
Chlorophyta	0.044		0.334	0.389	**0.675**					**0.486**		
Chrysophyta			**0.482**	**0.436**						0.375		
Cryptophyta				**0.424**							**0.482**	
Bacillariophyta				**0.410**						**0.475**		
Dinophyta										0.303	0.392	0.209

N o t e s. Correlations are weak at PC < 0.4, average at PC = 0.4, strong PC > 0.4 ($p > 0.05$); only positive correlations are presented. Significant correlations with significance level $p < 0.05$ are highlighted bold.

T a b l e 4. **Results of Eigen analysis of the Correlation Matrix Variable between elements and their ratios in seston with biomass of dominant zooplankton species, biomass of dominant phytoplankton groups and hydrochemical parameters in Obsterno and Nobisto lakes (2018)**

Index	Lake Obsterno						Lake Nobisto					
	C	N	P	C : N	N : P	C : P	C	N	P	C : N	N : P	C : P
Bosmina			0.374						**0.423**	**0.603**		
Daphnia								**0.423**	0.278		**0.664**	
Ceriodaphnia			**0.727**	**0.413**			0.106	**0.443**	0.121			0.101
Diaphnosoma	0.263	**0.674**			**0.864**		**0.723**	**0.440**	0.234			
Eudiaptomus				**0.502**			0.301	0.331	0.112			0.174
Thermocyclops								**0.442**	0.205			0.120
T, °C					0.365	0.292		0.399	0.431			
NO_3					**0.533**			**0.576**				
NH_4		**0.656**	0.285	0.326								
PO_4				0.375	**0.680**				0.221			
Cyanophyta	0.105	**0.604**		**0.634**			**0.721**					
Chlorophyta	0.297		0.199	0.278	**0.784**					0.265	**0.655**	**0.542**
Chrysophyta							0.142	0.233	0.039			
Cryptophyta	0.347	0.316	0.179				0.391	0.371				
Bacillariophyta	0.335	0.342	**0.683**	0.289								

N o t e s. The same as for table 3.

The zooplankton community composition was strikingly similar for both these lakes. The three dominating groups were *Bosmina* spp. (mostly *B. longispina* and *B. longirostris*), *Daphnia* (mostly *D. cucullata*) and *Thermocyclops* (*Th. oithonoides*). Small cyclopoides were rare in both lakes but with maximum densities in midsummer, while both small *Bosmina* and *Daphnia* had peak densities in early summer. Copepods were most abundant in late summer and fall. The number of all species was lowest in autumn when P content peaked, but it is hard to separate the seasonality effect from the food quality. Neither of the dominant zooplankton species significantly correlated either with food quality in terms of seston C, except *Diaphanosoma* in Nobisto lake within two years (Tables 3, 4).

We found significant differences in seston stoichiometry between littoral and pelagic zone in both lakes. In Obsterno lake in spring of 2017, both N : P and C : P ratios were highest at pelagic habitat whilst this variability was related to higher zooplankton biomass (especially *Bosmina*, *Ceriodaphnia*, *Daphnia*) and less to *Diaphanosoma*. In 2018 in lake Obsterno, the highest N : P and C : P ratios were recorded in July and September and decreased in October without significant differences among habitats which were related to higher zooplankton biomass (especially *Cer. pulchella* and *Diaphanosoma*) and less to *Daphnia*, *Bosmina*, *Thermocyclops* and *Eudiaptomus* (Tables 3, 4, lake Obsterno).

In lake Nobisto in 2017, seston C : P and N : P ratios, increased in July in comparison with May in littoral and pelagic zone. C : P and N : P ratios were more positively correlated to large *Bosmina* and *Daphnia* and less to *Ceriodaphnia*, *Diaphnosoma*, *Thermocyclops* and *Eudiaptomus*. In lake Nobisto in 2018, seston C : P and N : P ratios increased from May to July in littoral and pelagic zones then decreased in September to October. These ratios were statistically different between littoral and pelagic zoneswhile N : P was more correlated to *Daphnia* and C : P to copepods (tables 3 and 4, lake Nobisto). Variability of seston C : P ratios may be partly related to this fact that zooplankton taxa differ considerably in their body construction, which affects their elemental composition, as its shown *Daphnia*, *Ceriodaphnia*, *Bosmina* with lower C : P ratios and copepods with higher C : P [2].

Seston elemental ratios of lake Obsterno revealed smaller changes between littoral and pelagic zone in comparison with lake Nobisto from May to October. As it was reported by Elser et al. (2000) [8] C : N ratio of seston limits in freshwater systems are ranged in 6–14 (by mass). In our studied lakes these ratios didn't differ a lot between lakes and locations showing insignificant decrease in summer in both lakes. Lakes' seston have high N and C relative to P ratios because of phosphorus-limited growth and usually don't exceed 14–54 for N : P and 123–1842 for C : P. Elser & Hassett (1994) [9] showed that majority of lakes have seston C : P values higher than 200 : 1 (by mass) possibly reflecting the contribution of allocthonous detritus that is high in C relative to P (rather than phytoplankton composition). In our studied lakes, we registered low abundance *Daphnia* species in summer and autumn in both lakes whereas *Eudiaptomus* spp. and *Bosmina* spp. in lake Obsterno greatly contributed in pelagic communities within autumn and spring. In lake Nobisto *Ceriodaphnia pulchella* and plant-dwelling detritovorous Cladocera were abundant within all seasons. Also *Cyanophyta* were the least abundant group respectively from late spring to autumn in Obsterno and Nobisto within two years but they had their highest abundance during periods increasing of temperature and lower nitrate. These temperature effects are supported by chemostat experiments reported by Tilman et al. (1986) [10] who showed that at N : P ratios ranging from 0.1 to 500. In Lake Superior, *Cyanophyta* were outcompeted by diatoms and green algae when the temperature was held at 10 and 17 °C, but that at 24 °C, *Cyanophyta* dominated up to an N : P ratio of 30 : 1. In our lakes, *Cyanophyta* was the least widespread algal group but increases in abundance in summer when N : P ratio was more or less near to 30 : 1. Jasser (1995) [11] showed that release of organic compounds by macrophytes apparently contributed to a decline of cyanobacteria by changing the phytoplankton dominance structure by increases green algae. This is in agreement with our data from lake Nobisto with high N : P and C : P specially in summer when the C : P values exceeded 1000 (Table 2) unless biomass of *Cyanophyta* was twice lower in littoral than in pelagic zone (2.44 and 5.01 $mg \cdot l^{-1}$ respectively). High N : P and C : P values in littoral locations show strong P-limitation and that might reflect the influence of allochthonous organic matter. According to Frost et al. (2006) [12], detritovorous invertebrates have higher body C : P ratios than their grazing and predatory counterparts consequently. Due to this, detritivores are predicted to have relatively lower P requirements for growth metabolism compared with grazers and predators, which is in agreement with our data where detritovorous zooplankton were dominant in late September and early October within both lakes (Table 2). When the food C : P ratios exceed 200, it may reduce the growth rates of some zooplankton taxa such as *Daphnia* spp. but would not strongly affect the development of some taxa which are not typically P limited. Such taxa would include *Bosmina* spp. and calanoid copepods and other herbivorous-detritovorous species [13]. Eigen analysis of our data showed positive correlation with copepods such as *Eudiaptomus* spp. (0.502) and seston C : P ratios by more biomass in studied lakes having nutrient poor food.

In our both lakes, there was a pattern with decreased P-content and increased C : P ratio in seston coinciding with the increase in water temperature. Sestonic C : P ratios increased over the growing season, suggesting that seasonal dynamics among autotrophs with high P-uptake in colder months. These seasonal changes in elemental ratios were also associated with disparity in macrophytes covering of both lakes that reflects contributions an allochthonous detritus potentially from the macrophytes and surrounding forested territories what may influence on P depletion in seston in summer. Shallow macrophytes covered lake Nobisto revealed more variable seston elemental ratios than mesotrophic lake Obsterno. Generally, seston C : N ratios varied the least across all habitats of lakes, but in lake Obsterno in 2017, C : P and N : P ratios varied widely and showed a significant seasonal pattern with lower ratios of N : P and C : P in littoral than pelagic zone during colder seasons and higher ratios in the warm seasons. Contrary, in lake Nobisto in 2017, C : P and N : P ratios were higher ratios in most littoral locations compared to adjacent pelagic zone seasonally. In 2018, Obsterno exhibited higher C : P and N : P ratios in littoral seston than that in pelagic zones seasonally unlike what was seen in lake Nobisto that year.

Correlation analysis revealed weak relationships between the biomass of zooplankton species and sestonic C : P, suggesting that the variability in the zooplankton community was not primary due to food P content. The weak correlation between sestonic C : P and temperature also could be a seasonal effect but one altered by zooplankton (Tables 3, 4). Temperature follows the seasonality of light, and controls the growth cycle of the autotrophs. Lower temperature could induce changes in stoichiometry so dramatic shifts in seston C : P in autumn could be explained as a seasonal effect of reduced temperature, less light, and increased nutrient supply [14]. The fact that P concentration in seston was rather constant in the lakes over the seasons, but the C : P ratios markedly increased in summer (Table 2), suggests that an increase in seston C with the temperature rise reflects phytoplankton growth almost entirely due to C assimilation. So this could explain most of the increase in C : P ratios of seston from spring to late summer [15]. On the other hand, an increased share of detritus in seston in autumn would tend to increase the sestonic C : P ratio specially in littoral than in pelagic zone in our studied lakes. Beside this, *Cyanophyta* and their predominance during autumn would increase C and N of the seston content (Tables 3, 4) specially in mesotrophic lake Obsterno.

Eigen analysis of the Correlation Matrix Variable suggest that temperature played a minor role for seston C : P and N : P. Changes in composition within the zooplankton community, between dominance of daphniids and copepods, could induce shifts in elemental ratios at the community level [2; 16]. The previous studies show that when P-rich cladocerans like *Daphnia* or *Diaphanosoma* are present, N : P ratio of seston is higher specially in late spring or early summer but the total dominance of the relatively P-poor small *Bosmina* and copepods is high in mid-summer and early autumn when C : P ratio of seston is higher [16; 17] as in our lakes. Finally, dietary changes in C : P may also affect consumer stoichiometry, the very high sestonic C : P would surely pose an additional constraint on P-demanding species such as *Daphnia* and *Diaphanosoma*.

Conclusions. Our field studies found that the relationship between seston elemental ratio and phytoplankton biomass differs between habitats. In addition, zooplankton (*Daphnia*, *Ceriodaphnia* and *Diaphnosoma*) biomass were further explained both by variables but appeared more related to food quality and variables that are primarily a measure of organic matter. The phytoplankton composition played a role as well with the relative biomass of *Cyanophyta* showing a stronger positive relationship with elements in Obsterno lake. We also found that the relative abundance of *Dinophyta* and *Chlorophyta* in both lakes had a positive relationship with C : N : P ratio within two years. Both plankton species composition and hydrochemical parameters were the best predictors of different seston stoichiometry in different habitats. We hypothesize that in these systems, light regime is also important in determining the seston composition, which is a good predictor for zooplankton growth. These proposed relationships between light regime, content of the seston, phytoplankton and zooplankton structure need experimental confirmation in future.

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