Seasonal and vertical variation in the C:P ratio of suspended and settling seston of lakes

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Abstract

In the absence of field data it is often assumed that the C:P ratio of the seston in lakes corresponds to the 'ideal' ratio of 106:1, reported by Redfield *et al.* (1963) for marine phytoplankton. However, we found out that in nearly all lakes studied C:P ratios deviate systematically from this value especially during periods, when phosphorus is growth limiting. Thus, during summer the sestonic C:P ratio generally exceeds 106 in the epilimnion, but decreases with depth in the hypolimnion. Possible mechanisms which may lead to these seasonal and spatial changes in the C:P ratio are discussed.

Introduction

It is generally accepted that in most cases phosphorus is the key element in lake eutrophication. Therefore, knowledge of the links between phosphorus, carbon and oxygen cycling is of fundamental importance for understanding eutrophication and lake restoration. Information concerning the seasonal and spatial variation in the C:P ratio of particulate matter provides information on the relative net uptake or release rates of these two major nutrients.

Redfield *et al.* (1963) introduced a general stoichiometric composition of marine phytoplankton (atomic C:N:P ratio = 106:16:1). Based on such findings about average biomass composition Stumm & Morgan (1962, 1981) postulated the following general equation for primary production and mineralization of biomass:

This equation is useful to describe 'average' pro-

duction or mineralization, if large sets of data from various depths, seasons and waters are combined. However, this equation may fail to describe specific events correctly. For instance, it has recently been shown by Gächter & Mares (1985) that in the hypolimnion of Lake Lucerne production of soluble reactive phosphorus (SRP) and oxygen consumption are not coupled according to equation (1). There is experimental evidence showing that sestonic particles do not release SRP by mineralization when settling, but rather take up SRP by physical-chemical sorption or biological activity (Gächter & Mares, 1985; Currie & Kalff, 1984). This uptake of phosphorus together with a simultaneous mineralization of organic carbon, leads to a decreasing C:P ratio in settling particulate matter. Moreover, it is to be expected that during summer stratification, when algal growth becomes progressively more limited by depleting phosphorus supplies, the C:P ratio of phytoplankton is higher than during winter turnover, when phosphorus is available in excess and primary production is limited by light.

The objective of this paper is to demonstrate the variability of sestonic C:P stoichiometry in fresh-

water lakes and to discuss possible reasons for deviations from the Redfield-ratio.

Methods

Particulate organic carbon (POC) was analyzed by taking 1 l of lake water, sampled with Friedinger bottles, which was filtered through a Whatman GF/F glass fibre filter (pore size $0.7\ \mu\text{m}$), preheated at 500°C . After filtration the filters were stored at -20°C , moistened after thawing with 0.1 ml of 1 M HCl to remove inorganic C (carbonates) and dried at 40°C before being analyzed in a HERAEUS CHN Analyzer (CHN Rapid).

Particulate phosphorus (PP) was determined as the difference between total P concentration in unfiltered lake water and $0.45\ \mu\text{m}$ membrane filtered lake water. The samples were digested during 1 hour with $\text{K}_2\text{S}_2\text{O}_8$ at 120°C (Szabo, EAWAG manual, unpublished), and the phosphate (SRP) was measured with the molybdenum blue method (Vogler, 1965).

Seston was collected using cylindrical sediment traps (height 50 cm, diameter 14 cm in Lake Lucerne; height 70 cm, diameter 7 cm in Lakes Constance and Hallwil) over periods of 2–3 weeks positioned at various depths in the hypolimnion. After retrieval, the supernatant water of the traps was drained, and the remaining suspension homogeneously mixed. The Lake Lucerne samples were pre-filtered through a $300\ \mu\text{m}$ plankton net to remove larger zooplankton. All POC and PP analyses of trapped material were performed directly on Whatman GF/F glass fibre filters and Sartorius CA membrane filters, respectively, using methods described above.

Results

Seasonal and vertical variation of C:P ratios in the suspended seston of lakes

In several Swiss lakes, the atomic C:P ratio in suspended epilimnetic seston differed systematically from Redfield's 'ideal' C:P ratio (Fig. 1). Primarily during summer stratification, but also during winter turnover, the C:P ratios in surface layers (0–5 m) clearly exceeded 106 except in Lake Zürich

(site Thalwil), where values scattered closely to the Redfield-ratio. These observations are in agreement with those made in Lake Ontario by Stadelmann & Munawar (1974), and they are supported by high C:P ratios determined in natural phytoplankton samples obtained from Lakes George (207:1; Viner, 1970), Kinneret (235 to 645:1; Serruya *et al.*, 1976) and Lugano (209:1; Premazzi & Marengo, 1982).

As indicated in Fig. 1, the C:P ratio of suspended particulate matter just above lake bottoms is usually lower than in the surface waters (in 67 to 100% of all observations, in every lake). Fig. 2 shows this depth dependent decrease of the C:P ratio in more detail for the period of highest epilimnetic C:P ratios. Despite considerable variation it is evident that the C:P ratio decline is greatest in the sub-surface layers. In the eutrophic lakes (Greifensee, Lake Zürich and Baldegg) the ratio decreased to 106 at about 10 m, whereas in the oligotrophic to mesotrophic lakes (Walensee and Lake Lucerne) this required at least 60 m. In extremely oligotrophic Lake Tahoe the atomic C:P ratios reached 385 at the surface and still exceeded 106 at 400 m (Holm-Hansen, 1972).

Seasonal and vertical variation of C:P ratios in the entrapped seston of lakes

As shown for suspended material the composition of seston collected by sediment traps at the lower border of the epilimnion also differs systematically from the Redfield-ratio. Although all data sets showed considerable annual variation (examples in Fig. 3), the trends are evident when mean values for stratification and turnover periods are compared (Table 1). In all lakes, Lake Constance excepted, the C:P ratios of entrapped epilimnetic material exceeded 106 during summer. During turnover these ratios were all lower than during stratification, with values well below 106 for Lakes Constance, Zug and Lucerne (1983, 1984).

In several lakes the C:P ratio of trapped seston decreased with depth (Table 2), but this change appears less pronounced than found for suspended seston collected on filters (Fig. 2). No significant vertical differences occurred in Lake Hallwil and Lake Constance. However, these small changes or even the lack thereof are comprehensible, because the uppermost trap is usually situated *below* the

Fig. 1. Seasonal variations of sestonic C:P ratios in the epilimnion (average value for the layer 0 to 5 m: $\bigcirc$ — $\bigcirc$) and above the lake bottom (X). Shaded areas = period of summer stratification.

Fig. 2. Average C:P profiles during the period of maximum epilimnetic C:P ratios.

epilimnion, and greatest vertical differences in suspended seston were observed *within* the epilimnion. Accordingly, the greatest dynamics in both particle formation and dissolution which lead to changes in chemical particle composition take place in the epilimnion, whereas these processes are delayed or diminished in the hypolimnetic layers.

Discussion

The various data compilations presented demonstrate that in nearly all lakes studied the stoichio-

Fig. 3. C:P ratios of seston collected by sediment traps at the lower border of the epilimnion in several Swiss lakes. Shaded area = period of summer stratification. Original data and data from Bloesch (1974) and Bloesch & Sturm (1984).

Table 1. C:P ratios in seston collected by sediment traps at the lower border of the epilimnion of lakes. TP = average total phosphorus ($\text{mg} \cdot \text{m}^{-3}$) during spring turnover.

Lake	TP	Trophic state	Trap depth m	Stratification		Turnover		Reference
				C:P	n	C:P	n	
Lucerne, Horw Bay	20	mesotrophic	15	171	11	134	14	Bloesch, 1974
Lucerne, Horw Bay	20	mesotrophic	20	117	12	76	9	1983–84, this work
Rotsee	370	polytrophic	5	204	7	190	10	Bloesch, 1974
Hallwil	215	eutrophic	13	124	36	104	43	1984, this work
Zug	210	eutrophic	20	149	17	64	20	Bloesch & Sturm, 1985
Zürich	80	meso-eutrophic	9	193	1	—	—	Giovanoli <i>et al.</i> , 1980
Lugano	185	eutrophic	15	194	10	142	7	Premazzi & Marengo, 1982
Erie	35	mesotrophic	7–20	339	6	—	—	Bloesch, 1982
Constance	90	meso-eutrophic	40–53	98	6	82	4	1982, this work
Lawrence	n.s.	oligo-mesotrophic	6	668	13	325	6	White & Wetzel, 1975
Piburg	15	oligo-mesotrophic	10	364	18	166	17	Dörrstein, 1977
Blelham Tarn	n.s.	eutrophic	7	119	16	—	—	Jones, 1976

n.s. = not specified.

metric composition of suspended and entrapped seston does differ systematically from the 'ideal' composition of algal biomass proposed by Redfield *et al.* (1963). Especially during summer stratifica-

tion, the C:P ratios in the epilimnion mostly exceeded 106 considerably (Fig. 1, Table 1), and decreased with depth primarily in the epi- and metalimnion. Accordingly, chemical changes of seston

Table 2. Vertical differences in the C:P ratios of seston collected by sediment traps at various lake depths. The lowest trap is positioned between 1.5 and 12 m above lake bottom.

Lake	Trap depth m	Stratification		Turnover		Reference
		C:P	n	C:P	n	
Lucerne, Horw Bay	7.5	170	11	125	14	Bloesch, 1974
	15	171	11	134	14	
	25	175	11	131	14	
	45	151	11	139	14	
	60	127	11	118	14	
Lucerne, Horw Bay	20	117	12	76	9	1983–84, this work
	60	86	12	65	9	
Rotsee	2.5	226	7	191	10	Bloesch, 1974
	5	204	7	190	10	
	14	184	7	200	10	
Hallwil, mid stn. 4	13	128	12	107	14	1984, this work
	30	131	12	86	14	
	43	131	12	86	14	
Hallwil, stn. 2	13	123	12	114	15	
	30	134	12	101	15	
Hallwil, stn. 6	13	120	12	90	14	
	30	112	12	78	14	
Zug, North Basin	20	152	9	61	10	Bloesch & Sturm, 1984
	52	126	9	56	10	
Zug, South Basin	20	146	8	66	10	
	185	139	8	54	10	
Zürich	9	193	1	—	—	Giovanolli <i>et al.</i> , 1980
	82	132	1	230	1	
	123	112	1	115	1	
	133	119	1	122	1	
Lugano	15	194	10	142	7	Premazzi & Marengo, 1982
	45	165	9	147	7	
Erie	7–20	339	6	—	—	Bloesch, 1982
	32	138	1	—	—	
	37	124	6	—	—	
Constance	40 ¹	96	2	78	2	1982, this work
	53 ²	97	5	85	2	
	92	94	5	82	4	
	152 ³	98	6	83	2	
	247 ⁴	102	6	84	3	
Lawrence	2	784	13	267	6	White & Wetzel, 1975
	6	668	13	325	6	
	10	420	13	240	6	
Piburg	5	628	18	224	17	Dörrstein, 1977
	10	364	18	166	17	
	15	268	18	162	17	
	23	238	18	123	16	
Blelham Tarn	7	119	16	—	—	Jones, 1976
	13	89	16	—	—	

¹ 20 m ² 60 m ³ 120 m ⁴ 210 m in the period of 18.6. – 8.7.82.

associated with particle formation or dissolution occur mainly in the epi- and metalimnion and to a less extent in the hypolimnion.

Equation(1) postulates that algal growth requires 1 mol P (as HPO_4^{2-}) per 106 mol C (as CO_2). However, our data show that the biomass C:P ratio increases during summer, when most likely phosphorus is growth-limiting. Thus, the nutrient supply seems to regulate the stoichiometric composition of biomass. This was experimentally shown by Goldman *et al.* (1979) for marine phytoplankton, by Uehlinger (1981) for *Aphanizomenon flos-aquae* and confirmed by us for *Chlamydomonas reinhardtii* (Fig. 4): During sufficient or excess P supply, the *Chlamydomonas* C:P ratio was less than 106, while growth rate was at the maximum of about 0.11 h^{-1} . If the SRP supply was decreased, the C:P ratio increased to values larger than 106, and simultaneously growth rate decreased in proportion to the increasing C:P ratio. From this we conclude in agreement with Goldman *et al.* (1979) that C:P ratios close to the Redfield-value occur only when phytoplankton growth is not limited by phosphorus, a situation not typical for temperate freshwater lakes during summer. In phosphorus limited environments this nutrient is much more efficiently used by algae for biosynthesis of organic matter than it is assumed by equation(1), allowing the phytoplankton to synthesize much more than 106 mol of carbon per mol of phosphorus.

The C:P ratio of seston could also be influenced by allochthonous particulate matter superimposing upon the biological processes of production and respiration in equation(1). Sturm *et al.* (1982) showed that at our sampling site in Lake Constance sedimentation was periodically dominated by inorganic allochthonous material from the alpine Rhine River (Müller & Quakernaat, 1969). Thus, the low

Fig. 4. Growth rate of *Chlamydomonas reinhardtii* as a function of the C:P ratio. Points represent average steady state conditions of several turbidostat and chemostat experiments conducted at 25°C and optimum light intensity.

C:P ratios in this lake appear attributable to dilution of autochthonous organic matter by allochthonous P-containing inorganic material. This explains why the seston C:P ratio never reached 106, although it is unlikely that algal growth would not be phosphorus-limited in Lake Constance (Mohammed & Müller, 1981).

Several events may contribute to the observed vertical decrease of the C:P ratio during summer stratification: (1) Rhee & Gotham (1981) showed that a temperature decrease from 20°C to 10°C resulted in a decrease in the C:P ratio of *Scenedesmus* cultures from 160 to 50. However, these results cannot be transferred quantitatively to *in situ* conditions, since the suspended and collected seston consist mainly of detritus and not of healthy growing algae. Accordingly, the effect of temperature is likely of minor importance for the observed decrease of the C:P ratio with increasing depth. (2) As demonstrated in Lake Erie (Bloesch, 1982) resuspension of bottom sediments with low C:P ratio decreases the C:P ratio of near bottom trap material. However, turbulent Lake Erie cannot be directly compared with our lakes featuring a comparably small wind fetch. Although resuspension of sediment particles with high water content occurs already at near bottom currents of a few $\text{mm} \cdot \text{s}^{-1}$ (Terwindt, 1977; Rosa *et al.*, 1983), our finding that the major decrease in the C:P ratio occurred in the uppermost layers rather than close to the lake bottom (Fig. 2, Table 2) indicates that resuspension is not responsible to a great extent for the vertical decrease in the C:P ratios of smaller lakes. (3) The results obtained can only be understood, if during decomposition of settling particles more carbon is mineralized than phosphorus is dissolved. There is strong evidence that settling material takes up SRP while decomposing, either through purely physical-chemical processes, such as sorption onto particle surfaces or precipitation, or through active SRP uptake by sinking algae or heterotrophic organisms colonizing on detritus (Currie & Kalff, 1984; Gächter & Mares, 1985; Stöckli, 1985). This together with the intensive mineralization of organic carbon within the epilimnion (Uehlinger *et al.*, 1984) helps explain the significant decrease of the C:P ratio in the lower part of this layer.

In conclusion, our data show that the C:P ratio of particulate matter in most freshwater lakes stu-

died systematically deviate from the 'ideal' Redfield-ratio: The observed ratio is generally higher in the epilimnion during summer stratification, but decreasing with increasing sampling depth. Mechanisms leading to these deviations are most probably reduction of the phosphorus supply to algae during summer plus uptake of phosphorus by seston which respire organic carbon while settling through the trophogenic layer.

Dynamic lake models, used to predict the course of lake restoration, should be based on realistic parameters so as to improve their capabilities. Use of the inappropriate Redfield-stoichiometry to link carbon with phosphorus will result in the underestimation of primary production in phosphorus limited lakes. The commonly assumed C:P ratio of about 106 appears to be the result of averaging large data sets from various lakes, depths and seasons but unsuitable for modelling the behavior of a specific lake.

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