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Limnology

Lake and River Ecosystems

Third Edition

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The matter was finally put to rest by the rebuttal of Vallentyne (1970), numerous subsequent investigations, and a national symposium on the subject (Likens, 1972). The effects of the controversy, however, continue to be felt both in research on the subject and in the efforts to reduce the loading of fresh waters with millions of tons of phosphorus each year, so that ultimately lakes will not become, in the words of J. R. Vallentyne, algal bowls.

E. Stoichiometry of Carbon, Nitrogen, and Phosphorus in Particulate Organic Matter

The elemental chemical composition of planktonic particulate organic matter reflects both the planktonic community structure as well as biochemical processes, such as nutrient supply ratios and turnover rates, that occurred in formulation of the composition of the biomass (reviewed in Tilman *et al.*, 1982; Kilham, 1990). For example, phosphorus or nitrogen limitation can lead to alterations in the ratios of protein, carbohydrate, and lipid content of cells, as well as the C:N ratio (cf. discussion in Chap. 12). Hence, the C:N ratio indicates not only characteristics of the nutrient availability but also an approximate evaluation of the relative proportions of cellular proteins and nonprotein structural elements (cf. Vollenweider, 1985).

A relative constancy in the molar ratio of C:N:P of 106:16:1 (or 41:7.2:1 by weight) among marine plankton, termed the Redfield ratio, is generally supported by numerous studies (Redfield *et al.*, 1963; Hecky *et al.*, 1993). The variance in this ratio is small, usually <20%. This constancy has been attributed to the relatively nutrient-sufficient growth conditions of marine plankton and the more homogeneous and stable nature of oceans (J. C. Goldman *et al.*, 1979). In contrast, marked deviations in the sestonic C:N:P proportions occur in lakes. These particulate composition ratios have been coupled to physiological indicators, such as rates of growth and productivity, to estimate the nutrient conditions to which phytoplankton of lakes have been exposed. Such relationships of nutrient stoichiometry can also give insights into species composition, growth rates, and successional patterns of phytoplankton (Kilham, 1990; Sommer, 1990).

Elemental cellular stoichiometries of natural phytoplankton communities and the seston can reflect the type and extent of nutrient limitation and availability. Ratios of elements being loaded to a lake are reflected in the elemental composition of the phytoplankton community. For example, N:P ratios in phytoplankton (seston) are strongly correlated with N:P loading rates to lakes (Table 13-17). The C:P and N:P ratios of lake

TABLE 13-17 Stoichiometric Ratios of Phytoplankton-Dominated Seston of Lakes as Approximate Indicators of Relative Nutrient Limitations^a

Ratio	Deficiency	Degree of nutrient limitation ^b		
		None	Moderate	Severe
C:N	N	<8.3	8.3-14.6	>14.6
N:P	P	<23	—	>23
C:P	P	<133	133-258	>258
Si:P	Si	<20	—	>100
C:Chl <i>a</i>	General	<4.2	4.2-8.3	>8.3
APA:Chl <i>a</i>	P	<0.003	0.003-0.005	>0.005

^a After Healey and Hendzel (1980), Kilham (1990), and Hecky *et al.* (1993).

^b Composition ratios of C:N, N:P, C:P in $\mu\text{mol } \mu\text{mol}^{-1}$; C:Chl *a* ratios as $\mu\text{mol } \mu\text{g}^{-1}$; and physiological ratio of alkaline phosphatase activity (APA):Chl *a* in $(\mu\text{mol } \mu\text{g}^{-1})\text{h}^{-1}$.

seston are generally higher than the Redfield ratio for marine waters. Phosphorus limitation of algal productivity in lakes tends to be much greater than nitrogen limitation (Healey and Hendzel, 1980; Hecky *et al.*, 1993). Streams, shallow lakes, and reservoirs with short residence times have C:P ratios <350 and N:P ratios <26, whereas lakes with longer residence times (>6 months) differentiate from their inflows typically with C:P >400 and N:P >30. Tropical lakes tend to have relatively high C:N ratios, indicative of potential nitrogen limitations, although the number of lakes sampled was relatively small (Hecky *et al.*, 1993).

Cellular elemental stoichiometry is affected by the availability of nutrients and therefore can be correlated with the extent of nutrient limitations (Table 13-17). An excellent example is observed in the spatial and temporal differences in cellular stoichiometry. Epilimnetic ratios, particularly of N:P, are often higher, indicative of high phosphorus demands in proportion to total inputs, than those of the hypolimnion, and C:P as well as N:P ratios decrease with depth (e.g., Jones, 1976; Gächter and Bloesch, 1985; Tezuka, 1985; Gálvez *et al.*, 1991). These differences with depth are usually related to high phosphorus use in relation to supply, increased nutrient pool size with depth, and respiration of organic carbon as the seston settles.

The ratio of fluxes of nutrients into the dissolved nutrient resource pool (i.e., the supply rates of essential nutrients) can markedly influence the community structure of the phytoplankton (Tilman, 1982). As correctly pointed out by Sterner *et al.* (1992), external sources of nutrient loading can be and have been evaluated with some degree of accuracy, but rates and controls of internal regeneration of nutrients by physical (e.g., resuspension and mixing) and biological (e.g., nitrogen fixa-

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tion, denitrification, food web regeneration by all heterotrophs, including viruses) processes are much less quantified to levels that allow effective use of predictive models. For example, denitrification was the most important mechanism for reducing N:P ratios in the water column, whereas both nitrogen fixation and sediment resuspension raised N:P ratios (Levine and Schindler, 1992). Sediments tend to be a major nitrogen source, particularly in littoral areas.

The N:P and Si:P supply ratios are fundamental axes along which phytoplanktonic community structures vary (Hecky and Kilham, 1988; Kilham, 1990). Diatoms and some chrysophyte algae have absolute silica requirements. Although total algal biomass is not limited by silica availability, the algal community composition, interspecific competition, and succession can be altered markedly (cf. Chaps. 15 and 19). Species of diatoms with low Si:P requirements, for example, often develop maximally during seasonal periods of lowest Si:P ratios (Kilham, 1984). In another example, many cyanobacteria are capable of nitrogen fixation, which allows these species to maintain high growth rates in habitats low in available combined inorganic nitrogen. The relative competitive capacities and proportions of cyanobacteria in epilimnetic phytoplankton communities are thus indicated by the N:P ratio; cyanobacteria tend to be rare at N:P >29 (Smith, 1983).

Zooplankton and higher animals usually constitute small portions of the total dissolved and seston pools of nitrogen and phosphorus. For example, in an alpine lake in California, zooplankton always constituted <5% and <10% of the pelagic storage compartments for nitrogen and phosphorus, respectively (Elser and George, 1993). However, during brief periods of high zooplankton biomass, the zooplanktonic contributions to total sestonic elemental stoichiometry can be significant. Although the N:P and C:P ratios do not vary greatly intraspecifically among zooplankton, considerable differences occur interspecifically (Watanabe, 1990; Gulati *et al.*, 1991; Sterner *et al.*, 1992; Elser and George, 1993; Urabe, 1995). Zooplanktonic N:P ratios may be altered by the N:P ratio of seston as certain individual species populations of zooplankton, which grow and reproduce most efficiently at a given N:P supply ratio, come to dominate the zooplankton community. Because the biochemical requirements of crustacean zooplankton for a N:P ratio in their tissues is below the ratio of most sestonic assemblages, there is a tendency for crustacean zooplankton to retain P preferentially to N. As a result of this process, nutrient regeneration via feces of zooplankton can be skewed toward nitrogen and thereby enhance phosphorus limitations to phytoplankton during short periods of intense cladoceran grazing (e.g., "clear water phase").

In examining the chemical composition of particulate organic matter, large zooplankton can be effectively separated from smaller particles. However, detrital particles nearly always dominate (>50–80%) over algal and bacterial biomass in the remaining seston (Saunders, 1972a; Uehlinger and Bloesch, 1987; Gálvez *et al.* 1989). If the planktonic microbiota are reproducing rapidly, much of the detritus present can have chemical composition relatively similar to that of the living plankton. Appreciable loadings of particulate organic matter from the structural tissues of terrestrial and littoral plants, however, can result in seston relatively rich in carbon and lesser amounts of nitrogen and lead to high C:N, C:P, and N:P ratios. Although much of the particulate organic matter from external sources tends to be deposited in near-shore regions in natural lakes, importation from the drainage basin is much greater in reservoir ecosystems (Chaps. 15 and 21). In addition, because of the high ratio of drainage basin area to reservoir area, large quantities of inorganic particles (e.g., clay) can be imported to the pelagic zone. These particles of the seston can contain high and variable quantities of nutrients that are undifferentiated from particulate organic matter of biota and can lead to skewed results, requiring care in interpretation. However, in most lakes with water residence times of several months or longer, sestonic composition ratios reflect the general status of the availability of nitrogen and phosphorus for planktonic growth in these waters.

Furthermore, the predictive value of nutrients present in the seston as a reflection of nutrient availability has been extended by the obvious relationship of energy available as light for photosynthesis to nutrient available and incorporated into the seston (Sterner *et al.*, 1997). When phosphorus availability is low, C:P ratios of particulate organic matter will tend to be low and photosynthetic productivity low. Differences in nutrient use efficiency may occur at different light availability, and these ratios will be translated to higher trophic levels feeding upon them. Low light:phosphorus ratios of seston likely indicate simultaneous carbon and organic matter (energy) limitation in other dependent trophic levels, whereas high light:phosphorus ratios suggest phosphorus limitation among several dependent trophic levels.

VIII. PHOSPHORUS AND NITROGEN LOADING AND ALGAL PRODUCTIVITY

When phosphorus is added as a pulse to unproductive lakes or ponds, either experimentally, for purposes of intentional fertilization or in effluents resulting from

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