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Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship?

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Abstract

Total nitrogen (TN) and total phosphorus (TP) measurements and contemporaneous measurements of chlorophyll *a* (Chl *a*) and phytoplankton nutrient deficiency have been made across a broad range of lakes and ocean sites using common methods. The ocean environment was nutrient rich in terms of TN and TP when compared with most lakes in the study, although Lake Victoria had the highest values of TN and TP. TN concentrations in lakes rose rapidly with TP concentrations, from low values to TN concentrations that are similar to those associated with the ocean sites. In contrast, the TN concentrations in the oceans were relatively homogeneous and independent of TP concentrations. The hyperbolic shape of the TN:TP relationship created a broad range of TN:TP values for both lakes and oceans. The TN:TP ratios of the surface ocean sites were usually well in excess of the Redfield ratio that is noted in the deep ocean. Phytoplankton biomass, as indicated by Chl *a,* was strongly dependent upon TP in the lakes, and there was a weaker relationship with TN. Oceanic Chl *a* values showed a positive relationship with TP, but at much higher TP values than were observed in the lakes; there was no relation with TN. P-deficient phytoplankton growth was inferred using independent indicators when TP was <0.5 μmol L^{-1} at both freshwater and marine sites. N-deficiency indicators were highly variable and did not show any clear dependence on TN concentration. The TN:TP ratio was indicative of which nutrient would become limiting for growth in both lakes and oceans. When all sites are compared, N-deficient growth was apparent at TN:TP $<$ 20 (molar), whereas P-deficient growth consistently occurred when TN:TP $>$ 50 (molar). At intermediate TN:TP ratios, either N or P can become deficient. We conclude that N or P limitation of algal growth is a product of the TN and TP concentration and the TN:TP ratio rather than a product of whether the system of study is marine or freshwater.

Limnologists and oceanographers are both concerned with the relationship of nutrients to biological production. Historically, the problems they have addressed are often very different (e.g., controlling nuisance algal blooms in freshwaters or understanding the ocean carbon [C] budget). More recently, with the increasing frequency of coastal eutrophication, many oceanographers and limnologists are working on a common problem (Smith 1998; Smith et al. 1999). However, even when the questions are similar, the physical scale of the systems they study may dictate quite different conceptual and analytical approaches. It is not surprising, therefore, that different paradigms about nutrient limitation have emerged for lakes and oceans (Smith 1984; Hecky and Kilham 1988; Howarth 1988).

Marine studies have emphasized inorganic nutrient concentrations for modeling phytoplankton growth (Kilham and Hecky 1988) and for tracing geochemical fluxes of the nutrients to productive surface waters (e.g., Smith et al. 1986). This emphasis occurs because there is a vast, relatively homogeneous reservoir of inorganic nutrients in the deep ocean, and inorganic nutrients are preferred substrates for nutrient uptake by phytoplankton. Data on organic forms of nitrogen (N) and phosphorus (P) or total N (TN) and total P (TP) for the world's oceans are still relatively sparse (Downing 1997; Vidal et al. 1999). Information on dissolved organic forms of N and P is expanding rapidly as a result of newfound appreciation for their potential roles as nutrient

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reservoirs in the upper ocean (Jackson and Williams 1985; Monaghan and Ruttenberg 1999) and for their possible trophic importance through the microbial loop (Azam et al. 1983). Our view of nutrient cycling in the ocean may still be altered as data on dissolved organic forms become more ubiquitous (Michaels et al. 1996; Vidal et al. 1999).

In lakes, during the season of most active microbial and algal growth, both inorganic N and P often become immeasurable by standard methods, thereby rendering nonfunctional those models that are dependent on inorganic nutrient concentrations. This happens because lakes are usually surrounded by productive terrestrial and urban ecosystems that yield nutrients to lakes predominantly in fixed organic forms, either in solution or as particles (Hecky et al. 1993; Meybeck 1993). As a result, limnological models of nutrient–phytoplankton relationships often emphasize TN and TP (here we mean dissolved organic and inorganic N and P plus particulate forms) rather than inorganic nutrients per se (e.g., Vollenweider 1968; Dillon and Rigler 1974).

The primary sources of new nutrients to lakes are terrestrial runoff and atmospheric input. With the exception of some of the great lakes, internal reservoirs in lakes are relatively small, and lakes are therefore very responsive to seasonal inputs. Runoff and atmospheric inputs can vary widely in the concentration and ratio of TN and TP as well as in the proportion of organic and inorganic forms of these nutrients (Duce et al. 1991; Hecky et al. 1993; Howarth et al. 1996). Oceanic deep water, with its relatively fixed ratio of largely inorganic N and P, dominates the input of nutrients to the oceanic surface mixed layer, even in coastal regimes (Nixon et al. 1996; Jickells 1998). Although biological processing produces organic compounds of N and P from the inorganic forms supplied by deep water, the stoichiometry of the particles produced in the upper layer of the oceans does not usually differ from the deep-water ratios. Net nutrient uptake and regeneration generally follows approximately Redfield proportions (Redfield et al. 1963; Hecky et al. 1993). It may therefore be expected that lakes will exhibit a much greater range of nutrient concentrations and more variable relationships between N and P than will oceans. Does this greater variability mean that lakes and oceans differ fundamentally in their nutrient–phytoplankton relationships, or is each simply a special case of a more general relationship?

To answer such a question requires a common parameterization of nutrients, nutrient deficiency indicators, and common methods across a broad spectrum of lake and ocean regimes. In the course of many studies conducted over the past 10 yr (Guildford et al. 1994; Guildford 1996; Guildford et al. 2000), we have acquired data on TN and TP, particulate C, N and P, nutrient status indicators, and chlorophyll *a* (Chl *a*) from a wide range of lake and ocean sites. The lake data include three of the largest lakes in the world, including tropical great lakes Victoria and Malawi as well as a number of other north temperate lakes spanning a range of sizes (Fee and Hecky 1992; Guildford et al. 1994). A smaller data set from the coastal Arctic Ocean and North Atlantic has been assembled with the same suite of measurements and methods. With these data, we can search for general relationships between TN and TP in freshwater and ocean environments.

Study areas—Lake Victoria and Lake Malawi are located in East Africa. General hydrological and physical limnological information about Lake Victoria and Lake Malawi as well as Lake Superior can be found in Spigel and Coulter (1996). The samples from Lake Victoria were collected throughout the years 1990 and 1992–1996, and Lake Malawi samples were collected over the years 1990–1993 and 1997. Lake Superior and Lake Nipigon were sampled over the open-water seasons during 1990 and 1991. Seven other lakes in northwestern Ontario were sampled over the open-water seasons from 1987 through 1991. For the purposes of this comparative study, we grouped the lakes from northwestern Ontario (excluding Lake Superior) into two groups based on size. The small Northwestern (NW) Ontario Lakes range in size from 29 to 706 ha, and the Large NW Ontario Lakes range from 2,220 to 484,800 ha (Fee and Hecky 1992). Coastal Arctic Ocean samples were taken during July and August 1989 and 1991 in Barrow Strait, which is located at a central part of the Northwest Passage in the Canadian Eastern Arctic (Guildford 1996). Samples from the North Atlantic Ocean were taken during a 1991 spring cruise on board the C.S.S. *Hudson* (Guildford 1996). Approximate locations were as follows: Scotian Shelf (43°20′N, 65°10′W), Continental Slope (40°20′N, 64°35′W), and Sargasso Sea (36°00′N, 63°10′W).

Field sampling and chemistry—Sample collection, chemical analyses, and nutrient status measurements are described for the Ontario Lakes in Guildford et al. (1994), for the Arctic and North Atlantic in Guildford (1996), and for Lake Malawi in Bootsma (1993) and Guildford et al. (2000). Locations of sampling stations for Lake Victoria are given in Mugidde (1993). Briefly, water samples were collected from the upper mixed layer (usually within the euphotic zone) at each location, filtered onto GF/C or GF/F filters, and dried and/or frozen until analyzed for particulate C and N, particulate P, and Chl *a* (Stainton et al. 1977). Filtrate was maintained at 4°C until it was analyzed for total dissolved P (TDP) and total dissolved N (TDN) (Stainton et al. 1977). Storage time was usually less than 2 d but ranged up to 21 d for samples collected from the North Atlantic Ocean. The analytical laboratory of the Freshwater Institute (FWI) in Winnipeg performed the chemical analyses reported here. Comparisons between similar samples collected from the North Atlantic, analyzed by both the FWI Laboratory and the Bedford Institute of Oceanography (BIO) Laboratory in Halifax, reassured us that analytical results were comparable and that we did not underestimate particulate concentrations or Chl *a* by using GF/C rather than GF/F filters (Guildford 1996). Dissolved nutrient concentrations on North Atlantic samples analyzed by BIO and FWI gave similar results.

Nutrient status measurements—Measurements of phytoplankton nutrient status consisted of three particulate composition ratios (C : N, C : P, and N : P, calculated on an atom : atom basis) and three metabolic indicators (alkaline phosphatase activity [APA], N debt, and P debt, all expressed per unit Chl *a*).

APA, an indicator of P deficiency, was measured fluorometrically (Healey and Hendzel 1979*a*) using 5-μM *o*-meth-

Table 1. Values indicative of presence or absence or degree of nutrient deficiency for nutrient status indicators used in this study. C = particulate carbon; N = particulate nitrogen; P = particulate phosphorus; chl = chlorophyll *a*; APA = alkaline phosphatase activity. Criteria are based on Healey (1975).

Indicator	Nutrient	No deficiency	Moderate deficiency	Extreme deficiency	Deficient
C:N*	N	<8.3	8.3–14.6	>14.6	
C:P*	P	<129	129–258	258	
N:P*	P	<22			>22
APA†	P	<0.003	0.003–0.005	>0.005	
N debt‡	N	<0.15			>0.15
P debt§	P	<0.075			>0.075

* Atomic ratio.
† Particulate APA, μmol P μg chl^{-1} h^{-1}.
‡ μmol N μg chl^{-1}.
§ μmol P μg chl^{-1}.

yl-fluorescein-phosphate as the substrate. Parallel determinations were made of total and soluble activities in order to distinguish between APA associated with particles and APA in solution, the soluble activity being that associated with passing through 0.2-μm filters. The difference was reported as particulate activity.

The N-debt assay was used in conjunction with particulate C:N ratios to determine N deficiency. The assay was based on the work of Healey (1977), who demonstrated that several species of algae took up more ammonium (NH_4^+) when they were N deficient than when they were N sufficient. For the N-debt assay, 100 ml of unfiltered sample was enriched with ammonium chloride to yield a final concentration of ~5 μM N. Ammonium was measured (Stainton et al. 1977) on triplicate samples at the beginning and end of a 24-h incubation period. N debt was calculated as the nutrient removed over the 24-h period per unit of Chl *a* (Healey 1977). P debt was measured in a similar way to that used to measure N debt, except that potassium dihydrogen phosphate was added (final concentration, ~5 μM). Soluble reactive P was measured on triplicate subsamples (Healey 1975).

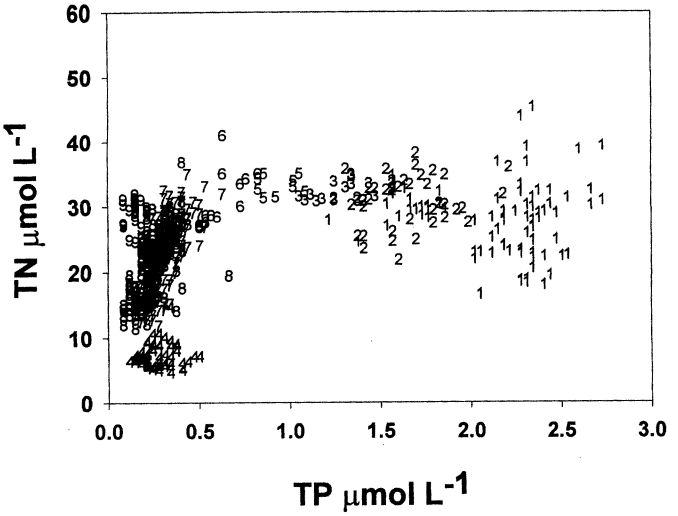

Fig. 1. Total nitrogen (TN) and total phosphorus (TP) for individual samples from within the upper mixed layer at the nine study locations. Lake Victoria = 1; Arctic Ocean = 2; Scotian Shelf = 3; Lake Malawi = 4; Continental Slope = 5; Sargasso Sea = 6; large Northwestern Ontario lakes = 7; small Northwestern Ontario lakes = 8; and Lake Superior = 9. Details about locations are in text.

The values suggested by Healey and Hendzel (1979*b*) were used to indicate the presence and degree of deficiency. These values (Table 1) were determined for a variety of freshwater species cultured at different growth rates in either N- or P-limited chemostats. Particulate C:P and N:P ratios exhibited by cells growing at less-than-optimum growth rate as a result of P limitation have been demonstrated to have higher particulate C:P and N:P ratios and higher APA and P debt than cells growing at or near their optimum growth rates. Similarly, N-limited cells had higher particulate C:N ratios and higher N debt. For the freshwater species studied by Healey and Hendzel (1979*b*), particulate ratios exhibited by cells growing at less than 20% of maximum growth rate were described as extremely N or P deficient. Ratios typical of cells growing at 20 to 50% of maximum growth rate were described as moderately N or P deficient (Healey 1978). APA and particulate C:N ratios have been used as indicators of P or N status in the ocean (Perry 1972; Goldman et al. 1979; Dortch et al. 1985; Smith et al. 1995; Cotner et al. 1997; Thingstad et al. 1998; Zohary and Robarts 1998).

Use of any single nutrient status indicator can be misleading. There is variability in the indicator values for particulate ratios with species and as a result of nonalgal particulate matter (Hecky et al. 1993). Not all species exhibit increased APA under P-deficient conditions (Healey and Hendzel 1979*a*). By using a combination of assays and by obtaining many measurements over time, we feel we have assembled a robust set of nutrient status data.

TN and TP in lakes and oceans—Individual TN and TP data points from all the study sites appear to follow a hyperbolic relationship (Fig. 1). Lowest and highest concentrations of TN and TP occur in lakes, and TN concentrations rise rapidly in the temperate lakes—to about 30 μmol TN L^{-1}—as TP rises to 0.5 μmol L^{-1}. Lake Superior is remarkable for its high TN (20.4–31.9 μmol L^{-1}), considering it has such low TP (0.1–0.3 μmol L^{-1}); nitrate concentrations

have been rising throughout this century, most likely as a consequence of anthropogenically enhanced atmospheric deposition of N (Bennett 1986). Lake Malawi, in contrast, has low TN (4.7–14.8 μmol L^{-1}) as well as low TP (0.1–0.5 μmol L^{-1}). These lower values are the result of the very long flushing time of Lake Malawi—700 yr (Spigel and Coulter 1996)—and of its permanently anoxic deep water, which allows relatively high rates of denitrification along the oxic–anoxic upper boundary of the monimolimnion (Kelly et al. 1987; Hecky et al. 1996). Below 0.5 μmol L^{-1} TP, there is a rapid increase in TN as TP increases, but TN plateaus at TP concentrations of >0.5 μmol L^{-1}. Lake Victoria TN concentrations fall along this plateau, although they exhibit larger variance in terms of TN than do the marine stations. This variance in Lake Victoria arises from the high rates of N fixation and denitrification in this eutrophic, tropical great lake (Hecky 1993; Hecky et al. 1996), which produce marked seasonal variation in TN concentrations (Hecky et al. 1996). The ocean stations exhibit a relatively narrow range of values of TN (21.9–41.0 μmol L^{-1}) compared to TP (0.5–2.2 μmol L^{-1}), which varies in ocean stations by a factor of four from minimum to maximum concentrations. The hyperbolic form of the TN and TP relationship creates a broad range of TN : TP ratios; means for study locations are summarized in Table 2.

The ocean sites, especially the coastal oceans, are nutrient rich compared to the lake sites in the data set. Only Lake Victoria, which would be considered very eutrophic by limnologists, is comparable to ocean stations in its TP concentrations. Oceanic TN values are uniformly higher than those associated with most freshwaters in our data set. Mean values of TN : TP for the different lakes range from 13.5 in Lake Victoria to 190 in Lake Superior. The molar TN : TP ratio for our marine stations varies from about 15 to 50, but most values are greater than the nominal Redfield ratio of 16 (Table 2). Elser and Hassett (1994) reported similar marine TN and TP values using similar methods. Their open-ocean, Gulf Stream, and Southeast Pacific TN concentrations ranged from 35 to 41 μmol L^{-1}, values that are similar to our range for ocean sites, whereas TP values ranged from 0.18 to 0.58 μmol L^{-1}. Downing (1997; fig. 1), in a comprehensive review of marine TN and TP from a large variety of studies (and using a variety of methods), found most open-ocean TN values falling in the range of 20 to 30 μmol L^{-1}, with TP values ranging from 0.2 to 4 μmol L^{-1}, a somewhat broader range than was observed in our data set (Fig. 1). Downing (1997) observed a wide range of TN : TP values for open-ocean stations in the euphotic zone (<50 m depth), with the overwhelming majority of such sites having TN : TP ratios that were greater than 20 : 1, and approximately 40% of stations had values in excess of 50 : 1 (Downing 1997; fig. 2). Based on these literature sources, we conclude that our marine samples, although limited geographically and temporally, are representative of the range of values to be found in the coastal and open ocean. In particular, the occurrence of TN : TP ratios that are well in excess of Redfield proportions occurs widely in the world's lakes and oceans as well as in our limited sampling.

Because the oceanic deep waters have TN : TP ratios near the Redfield ratio of 16 or slightly less, there must be some process or processes affecting the upper ocean, processes that enrich the water in N relative to P or that deplete the water of P relative to N (Downing 1997). In our ocean data set, the coastal Arctic Ocean and Scotian Shelf waters have the highest TP concentrations, and the Sargasso Sea has the lowest TP concentration. This trend of decreasing TP with distance from continental land mass is consistent with a coastal input of N and P from slope waters (Nixon et al. 1996), with progressive loss of P to sedimentation in deeper waters. In contrast to TP, TN is nearly constant at these marine locations (Table 2). The maintenance of a relatively low variance in TN concentrations, and of TN : TP ratios in the upper mixed layer of the ocean well in excess of 16 : 1 (Table 2), must arise from biological processes in the mixed layer. Processes that would differentially enrich the upper ocean in N relative to P would be atmospheric deposition, which is known to result in high N : P ratios (Duce et al. 1991; Prospero et al. 1996), N fixation (e.g., Karl et al. 1995; Michaels et al. 1996), and preferential regeneration of N relative to P in settling particulate matter. If preferential regeneration of N is the dominant process, then the P loss must be via fixed mineral P that is unavailable to solution, since dissolved organic P has been found to regenerate preferentially to DON (Smith et al. 1986; Clark et al. 1998). Michaels et al. (1996) infer geochemically from nutrient regeneration profiles that N fixation is a quantitatively important process in the North Atlantic. The high N : P of rain may also help to maintain TN in surface ocean waters, whereas P is lost to sedimentation. Certainly in Lake Victoria, which has a similar TN to that observed in the upper ocean and which has relatively high TP for a freshwater lake, N fixation and denitrification control TN concentrations (Hecky et al. 1996). Whether the same is true of the upper ocean is the subject of intensive debate and investigation (Capone et al. 1997; Falkowski 1997).

Chl a in relation to TN and TP—Our Chl *a* and TP concentrations split into two groups (Fig. 2), with north temperate lakes and tropical Lake Malawi forming one and the ocean sites and tropical Lake Victoria the other. Both groups exhibit a similar range of Chl *a* and a pattern of increasing Chl *a* with increasing TP. However, the north temperate and Lake Malawi freshwater group achieves those Chl *a* values at much lower TP concentrations than does the group formed by our marine stations and Lake Victoria. Others working in freshwater have also found a dependence of algal biomass, as indicated by Chl *a,* on TP (Dillon and Rigler 1974; Pridmore et al. 1985; Guildford et al. 1994). The fact that the marine stations generated less Chl *a* per unit of TP indicates that Chl *a* may be limited by other factors. Lake Victoria groups with the marine stations. In Lake Victoria, seasonal limitation of algal growth by light (Mugidde 1993) and by N for algal species that do not fix atmospheric N (Lehman and Branstrator 1993) occurs.

Chl *a* also increases with TN (Fig. 3), although the pattern is largely created by the Lake Malawi data, which have exceptionally low TN values and among the lowest Chl *a* concentrations in our study group. The range of scatter in Chl *a* increases considerably at the higher TN values that are characteristic of ocean systems. In particular, the Sargasso

Table 2. Means, standard deviations, and minimum and maximum values for variables measured at the study locations described in the text. TN = total nitrogen; TP = total phosphorus; Chl *a* = chlorophyll *a*; C:P = the ratio of particulate carbon to particulate P; N:P = the ratio of particulate N to particulate P; APA = alkaline phosphatase activity normalized to Chl *a*; and C:N = the ratio of particulate C to particulate N. P and N debt are expressed as the percent of times measured for which rates were indicative of P or N deficiency. Code numbers in parentheses are the location codes that appear in the figures. nd = not determined.

Location (code)	Statistic	TN (μM)	TP (μM)	TN:TP (molar)	Chl *a* (μg liter^{-1})	C:P (molar)	N:P (molar)	APA (μM μg^{-1}h^{-1})	P debt (%)	C:N (molar)	N debt (%)
Victoria	n	112	117	111	85	167	167	nd	27	174	26
(1)	Mean	28.8	2.5	13.6	26.5	148.5	18.3		11	8.2	19
	min	16.7	1.2	7.5	4.7	50.0	8.0			5.1	
	max	64.5	8.5	33.9	78.5	702.2	70.4			15.9	
	sd	6.5	1.4	4.0	15.9	76.4	7.6			1.7	
Arctic	n	43	43	43	48	43	43	38	11	43	43
(2)	Mean	31.1	1.6	19.2	2.3	141.0	13.0	0.010	9	11.0	51
	min	21.9	1.3	13.6	0.2	77.5	9.4	0.000		6.9	
	max	38.4	2.2	27.2	7.8	266.9	21.6	0.069		16.6	
	sd	3.8	0.2	3.3	1.7	39.1	2.9	0.014		2.6	
Shelf	n	14	14	14	14	14	14	11	nd	14	8
(3)	Mean	32.4	1.3	25.6	2.4	74.7	9.5	0.0001		8.0	13
	min	30.9	1.1	21.3	0.5	41.3	5.3	0.000		6.3	
	max	35.1	1.5	29.7	5.6	107.3	12.7	0.005		10.6	
	sd	1.5	0.1	2.3	1.6	18.5	2.4	0.002		1.4	
Malawi	n	112	130	112	171	349	349	8	25	359	32
(4)	Mean	6.9	0.3	28.4	1.4	244.3	19.4	0.002	48	12.5	63
	min	4.7	0.1	12.1	0.03	11.9	1.0	0.000		1.2	
	max	14.8	0.5	49.8	18.7	1,446.7	84.1	0.006		31.1	
	sd	1.5	0.1	9.2	2.0	154.4	8.8	0.002		3.6	
Slope	n	9	9	9	9	9	9	9	nd	9	6
(5)	Mean	33.3	1.0	35.3	0.6	66.5	8.8	0.001		7.7	33
	min	31.5	0.8	29.4	0.01	41.3	4.4	0.000		6.4	
	max	35.1	1.1	40.9	1.1	88.6	11.8	0.010		10.2	
	sd	1.4	0.1	4.0	0.3	15.5	2.5	0.005		1.1	
Sargasso	n	15	15	15	15	15	15	15	nd	15	9
(6)	Mean	30.5	0.6	50.1	0.2	97.0	8.1	0.089		11.8	33
	min	26.9	0.5	40.5	0.03	51.7	5.0	0.000		7.8	
	max	41.0	0.8	63.6	0.5	198.1	12.5	0.250		15.8	
	sd	4.3	0.1	5.8	0.2	41.9	2.3	0.079		2.2	
Large	n	165	167	165	163	169	168	160	nd	168	143
lakes	Mean	22.0	0.3	71.0	3.2	264.8	26.5	0.039		10.5	32
(7)	min	11.9	0.1	40.8	0.7	111.9	10.0	0.000		3.1	
	max	35.0	0.6	133.9	18.1	749.2	93.0	0.190		33.7	
	sd	5.6	0.1	16.6	1.9	75.4	9.9	0.033		3.2	
Small	n	225	226	224	222	230	230	172	nd	230	155
lakes	Mean	21.6	0.3	86.6	2.4	388.1	32.5	0.090		12.6	32
(8)	min	11.4	0.1	28.7	0.3	122.0	3.9	0.000		4.9	
	max	36.9	0.7	180.6	7.9	813.8	93.0	0.430		81.7	
	sd	4.6	0.1	21.0	1.5	108.9	9.7	0.071		6.0	
Superior	n	22	22	22	24	24	24	24	nd	24	24
(9)	Mean	28.3	0.2	190.1	1.0	319.6	31.1	0.082		10.3	50
	min	20.4	0.1	79.1	0.6	172.2	17.0	0.021		7.2	
	max	31.9	0.3	321.7	1.3	645.8	55.4	0.249		12.7	
	sd	2.9	0.04	62.2	0.2	101.3	8.3	0.062		1.7	

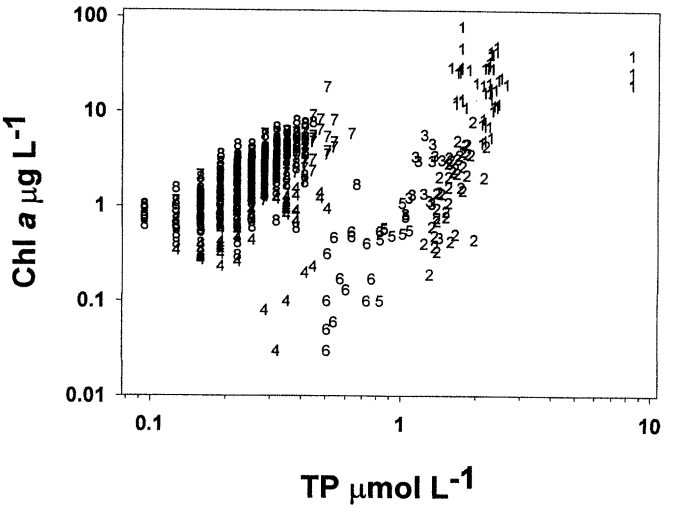

Fig. 2. Chlorophyll *a* and total phosphorus for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1).

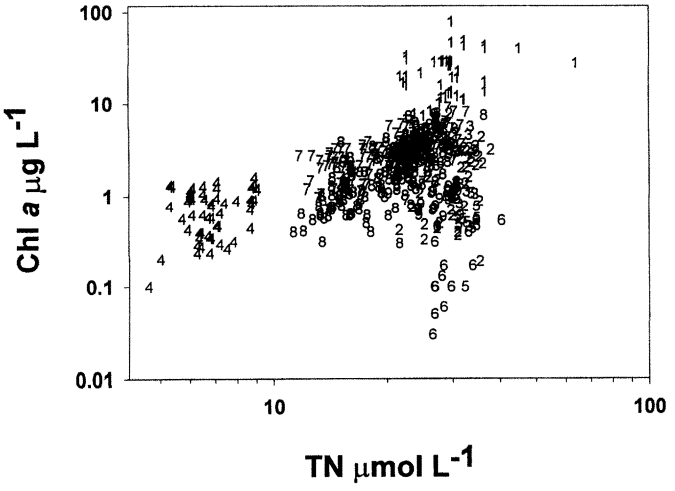

Fig. 3. Chlorophyll *a* and total nitrogen for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1).

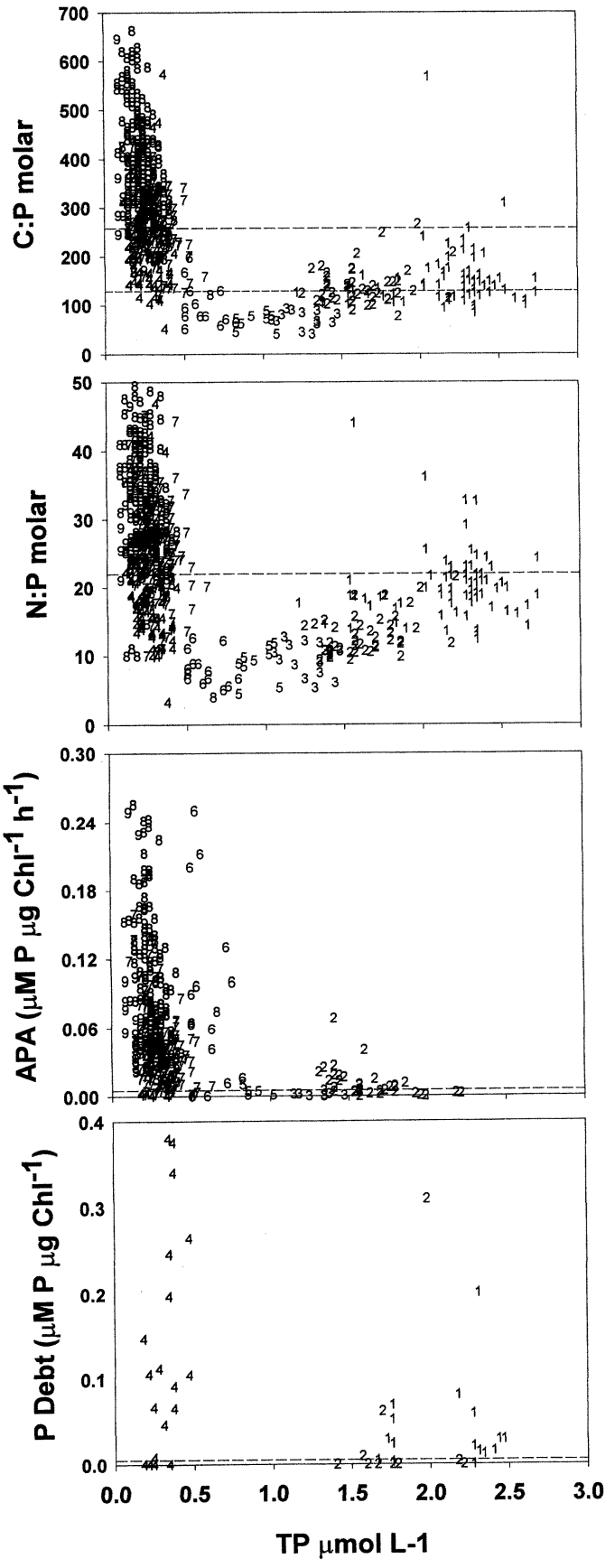

Fig. 4. Indicators of phosphorus deficiency plotted against the total phosphorus (TP) concentration for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1). The C:P ratio is particulate carbon:particulate phosphorus; N:P ratio is particulate N:particulate P; APA is alkaline phosphatase activity normalized to chlorophyll *a*, (Chl *a*); P debt is uptake of PO_4 in the dark normalized to Chl *a*. Values below the lower dashed lines are considered to be not P deficient; values above the dashed line are considered to be P deficient. If there are two dashed lines, values that fall in between are considered moderately P deficient, and values that fall above are considered severely P deficient.

Sea has much lower Chl *a* than would be expected from the general trend, whereas Lake Victoria Chl *a* concentrations are nearly two orders of magnitude higher than those of the Sargasso Sea for the same TN concentration. In fact, nearly all the data contributing to the upward trend in Chl *a* with increasing TN concentration are from lakes, whereas the ocean data set, with its restricted range of TN, shows a very high variance in Chl *a* concentration. A wider range of TN in our marine stations might demonstrate a significant trend, but the scatter observed over a limited range of TN would still be much greater than that observed in the relationship between TP and Chl *a* for the lakes in Fig. 2. For the ocean sites in our data set, Chl *a* is more highly correlated with TP (r^2 = 0.601) than with TN (r^2 = 0.079).

Evidence for algal growth limitation by TP and TN—Higher TP concentrations generally relieve P deficiency (Fig. 4). Small and large lakes in northwestern Ontario, Lake Superior, and Lake Malawi had TP concentrations that were, on average, <0.5 μmol L^{-1} (Table 2). These locations were often strongly P deficient, as indicated by the particulate ratios of C:P, N:P, and/or the physiological assays, APA and P debt (Fig. 4). Although Lake Malawi had particulate C:P and N:P ratios and P-debt uptake indicative of P deficiency, the APA assay, which we performed on three separate visits to Lake Malawi, had measurable rates (mean = 0.002 μmol P μg Chl a^{-1} h^{-1}, standard deviation [SD] = 0.002, n = 8) that were not indicative of P deficiency. In contrast, the Sargasso Sea, with an average TP concentration of 0.62 μmol L^{-1} during our spring visit, had APA rates that were indicative of severe P deficiency but had particulate ratios that were indicative of no P deficiency. At locations with TP concentrations of >0.62 μmol L^{-1}, P deficiency did not occur consistently, although rates of APA in the Arctic and C:P ratios in Lake Victoria (Fig. 4) were at times indicative of moderate P deficiency.

There is no apparent minimum threshold of TN below which severe N deficiency consistently occured (Fig. 5). There is a general decline in C:N ratios as TN increases, but high N-debt values can occur at any TN (Fig. 5). We observed moderate to severe N deficiency at the lowest TN location, Lake Malawi (mean C:N, 12.5, and N debt indicative of N deficiency on 63% of dates measured [N-debt frequency]; Table 2). We also observed similarly moderate to severe N deficiency in the Arctic Ocean (mean C:N, 11, N-debt frequency 52%), even though the mean TN concentration was much higher (31 μmol L^{-1}) than that observed in Lake Malawi (6.9 μmol L^{-1}). Although Lake Malawi and the Arctic Ocean are the only two locations in which high C:N ratios were accompanied by high N-debt frequency (over 50%; Table 2), we observed particulate C:N ratios that were indicative of moderate N deficiency in Lake Superior as well as in the large and small lakes in northwestern Ontario. Only Lake Victoria, Scotian Shelf, and Continental Slope water had average C:N ratios and N-debt frequencies that were indicative of no N deficiency. The high C:N ratios in the highly P-deficient lakes (Lake Superior, small and large lakes in northwestern Ontario) were not surprising. Severely P-deficient algae with high C:P ratios (in culture and in experimental lakes) also had high C:N ratios, although

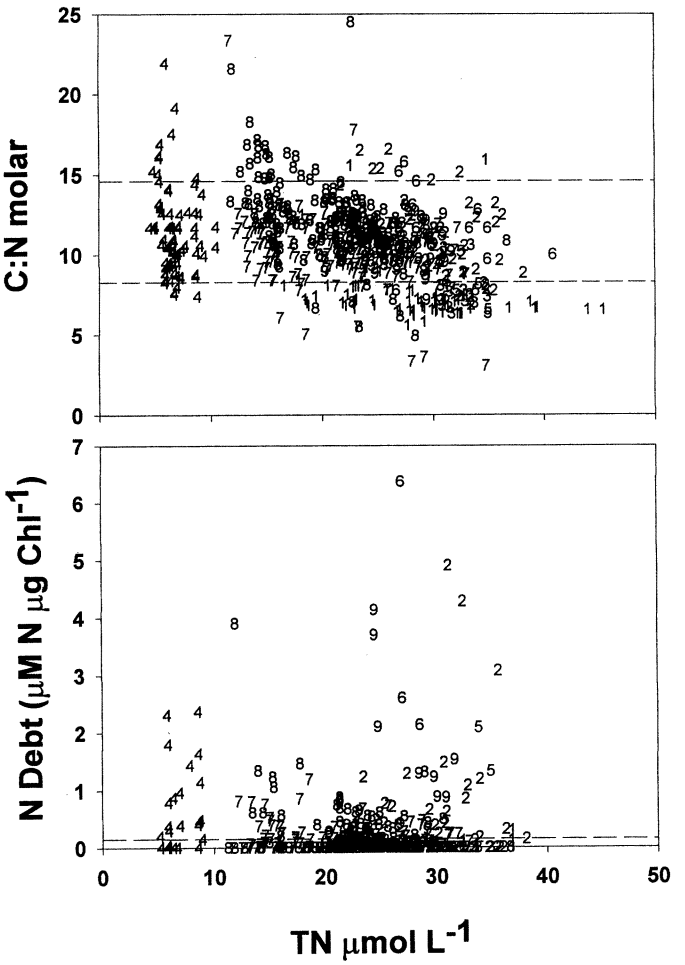

Fig. 5. Indicators of nitrogen deficiency plotted against total nitrogen (TN) for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1). The C:N ratio is particulate carbon:particulate nitrogen; N debt is uptake of NH_4 in the dark normalized to chlorophyll *a*. Values below the lower dashed lines are considered to be not N deficient; values above the dashed line are considered to be N deficient. If there are two dashed lines, values that fall in between are considered moderately N deficient, and values that fall above are considered severely N deficient.

they had infrequent N debt (Healey and Hendzel 1979*b*, 1980). Lack of predictability of N deficiency by the TN concentration could also mean that N deficiency was not usually severe or consistently present because of the physical conditions at our locations. In regularly deeply mixed waters like the Scotian Shelf and Continental Slope locations, severe nutrient deficiency may occur rarely, because new nutrients are made available by mixing with the high-nutrient deep waters. Also, cell growth may be controlled by light, as mean water column light intensity in deeply mixed water columns may be below the threshold value for light limitation (e.g., Hecky and Guildford 1984).

TN:TP ratio as a determinant of the limiting nutrient—Although the absolute value of TN may not be a strong predictor of N limitation, the TN:TP ratio may be useful in

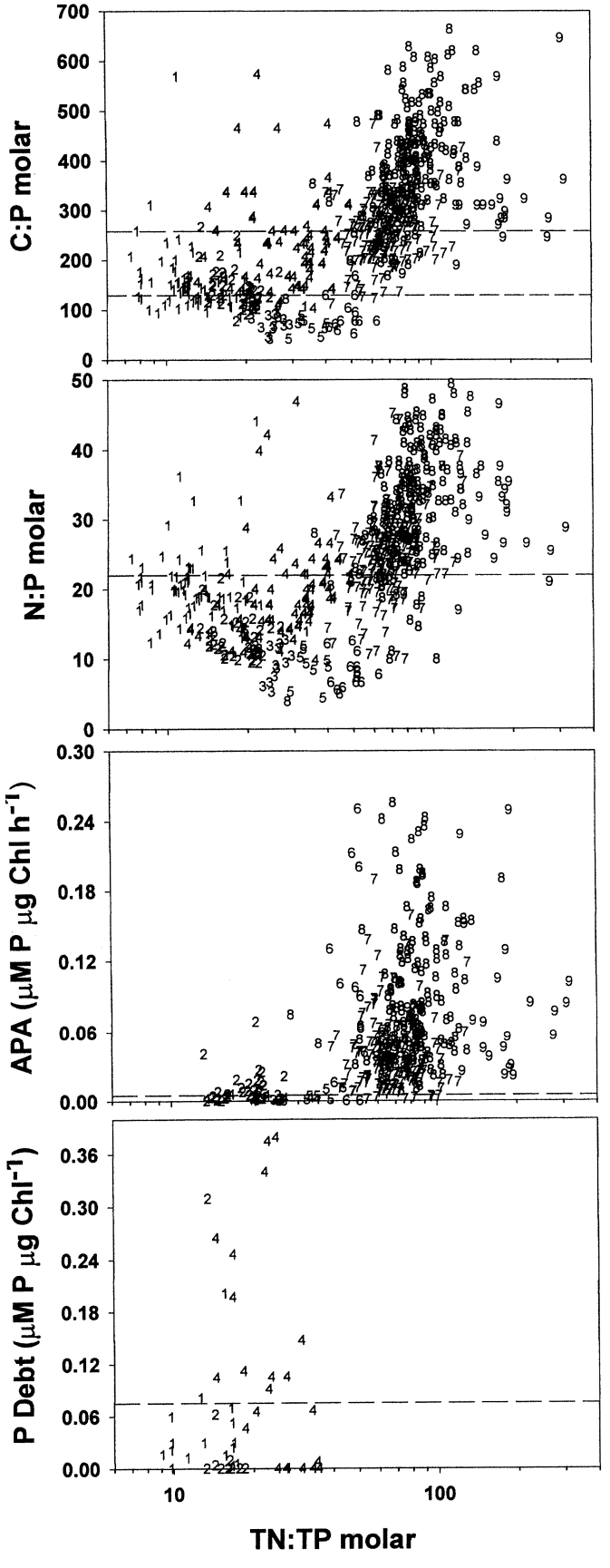

Fig. 6. Indicators of phosphorus deficiency plotted against the TN:TP ratio for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1). The C:P ratio is particulate carbon:particulate phosphorus; the N:P ratio is particulate N:particulate P; APA is alkaline phosphatase activity normalized to chlorophyll *a*, (Chl *a*); P debt is uptake of PO_4 in the dark normalized to Chl *a*. Values below the lower dashed lines are considered to be not P deficient; values above the dashed line are considered to be P deficient. If there are two dashed lines, values that fall in between are considered moderately P deficient, and values that fall above are considered severely P deficient.

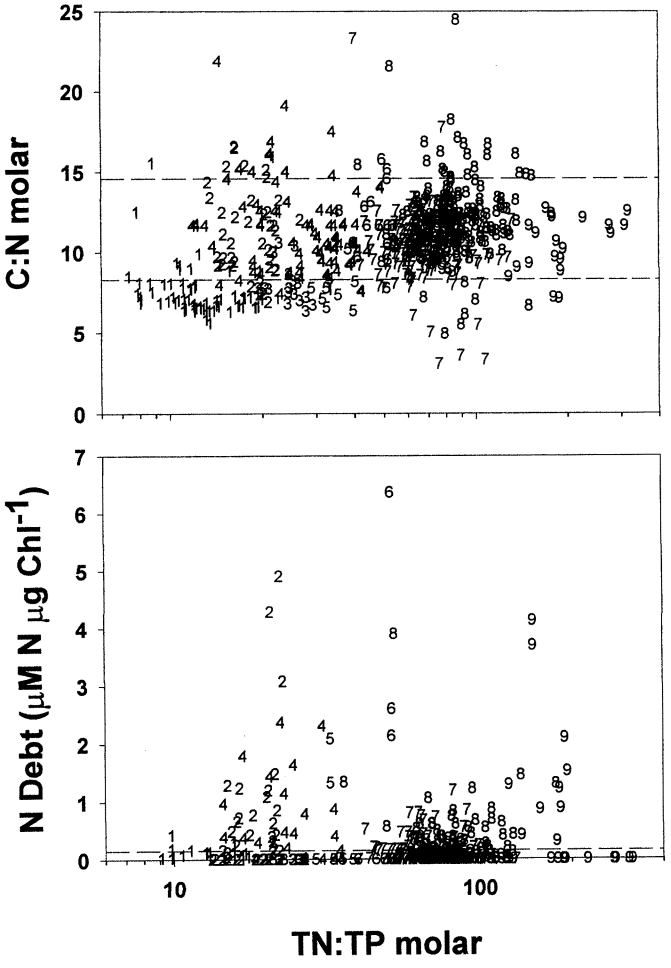

Fig. 7. Indicators of nitrogen deficiency plotted against the TN:TP ratio for individual samples from within the upper mixed layer at the nine study locations (*see* Fig. 1). The C:N ratio is particulate carbon:particulate nitrogen; N debt is uptake of NH_4 in the dark normalized to chlorophyll *a*. Values below the lower dashed lines are considered to be not N deficient; values above the dashed line are considered to be N deficient. If there are two dashed lines, values that fall in between are considered moderately N deficient, and values that fall above are considered severely N deficient.

determining the potentially limiting nutrient. If we examine the indicators of nutrient status along the TN : TP gradient for the nine locations used in this study, the patterns that emerge can be explained by the TN : TP ratio and by various physical conditions, as follows. (1) A TN : TP ratio of >50: Three of the locations fall within this range: Lake Superior and the large and small lakes in northwestern Ontario. Phytoplankton were extremely P deficient according to the nutrient status indicators of particulate C : P, particulate N : P, and APA (P debt was not routinely measured in these lakes) (Fig. 6). These lakes stratify strongly during the summer months and are driven to extreme P deficiency with very low TP concentrations. The particulate C : N ratio at these locations indicated moderate N deficiency (Fig. 7), but as discussed above, extremely P-deficient algae with high C : P ratios will also have high particulate C : N ratios. Although on several occasions N-debt measurements were indicative of N deficiency at these three locations (Fig. 7), the overall frequency of N debts indicative of N deficiency was low for the northwestern Ontario lakes, although this was not the case for Lake Superior (Table 2). For these high TN : TP freshwaters, TP is a good predictor of algal biomass, as indicated by Chl *a* (Fig. 2). (2) TN : TP ratio of <20: Two of the locations (Lake Victoria and the Arctic) fall within this range, suggesting that N was the limiting nutrient. The Arctic Ocean was consistently N deficient according to the high particulate C : N ratio (average 11) and N-debt frequency (51%; Table 2). We were able to sample the Arctic Ocean under both stratified and unstratified conditions, which changed over weekly and even daily time periods (Guildford 1996). Although TN concentrations were high at all times in the Arctic Ocean, the inorganic pool became depleted quickly under stratified, high-light conditions in summer (Guildford 1996). Rates of nutrient regeneration in these Arctic waters may also be slow because of the cold temperatures. Under these conditions, strong N deficiency developed quickly but was relieved when stratification broke down.

The TN : TP ratio would suggest that Lake Victoria would become N limited under stratified conditions. However, Lake Victoria may not exhibit high particulate C : N ratios (Fig. 7) or high N-debt frequency (Table 2) for two reasons. First, during the windy season, the open offshore areas of this large lake are mixed to the bottom (maximum depth, 60 m), and the phytoplankton are light limited (Mugidde 1993). Second, at the onset of stratification, large blooms of N-fixing cyanobacteria quickly develop and persist, fueled by the high P levels (Hecky 1993). The presence of these blooms is itself a strong positive indication of N deficiency for the many algal species that do not fix N. (3) TN : TP ratios of 20–50: Locations in this range are Lake Malawi, the Sargasso Sea, the Scotian Shelf, and the Continental Slope water. This range appears to be transitional from N to P deficiency. We observed indications of both N and P deficiency in Lake Malawi and the Sargasso Sea. Lake Malawi, with an average TN : TP ratio of 28, was N deficient according to the particulate C : N ratio (average 12.5) and N-debt frequency (63%; Table 2). Lake Malawi also exhibited indications of moderate P deficiency according to the particulate C : P ratio (Fig. 6) and P-debt frequency (48%; Fig. 6 and Table 2). Lake Malawi was not considered P deficient according to the particulate N : P ratio (average 19) or by the APA assay, however. We interpret this to mean that Lake Malawi is not as strongly or consistently P deficient as are lakes with similarly low TP concentrations but higher TN (Lake Superior, large and small lakes in northwestern Ontario). The Sargasso Sea was moderately N deficient according to the particulate C : N ratio (average 11.75) and severely P deficient according to the APA assays (Fig. 6). Other indicators of N deficiency (N-debt frequency, 37%) and P deficiency (particulate C : P average, 97; particulate N : P, average 8) did not indicate consistent N or P deficiency, respectively. Cotner et al. (1997) measured rates of alkaline phosphatase and particulate C : P and N : P ratios indicative of P deficiency in the Sargasso Sea. As would be expected at these transitional values along the TN : TP gradient, under stratified conditions, both N and P deficiency can and do occur in Lake Malawi and the Sargasso Sea. Scotian Shelf and Continental Slope waters were not N or P deficient during our spring visit to these locations. This may have been the result of deep mixing below the euphotic zone or excessive loss rates attributable to grazing.

Many factors modify the demand and supply of N and P to phytoplankton in the upper waters of lakes and oceans. The amount of light available (mixed depth, water clarity), supply of nutrients from external sources, nutrient regeneration rates by micrograzers, mineralization rates by bacteria, and loss rates due to grazing and sedimentation are just some of these factors. However, the TN : TP ratio can serve as a predictor for which of the two most commonly limiting macronutrients will become limiting for growth under well-illuminated, stratified conditions. The TN : TP ratio reflects the total pool of these nutrients available for cycling (not just the inorganic pool), and it reflects the in situ ratio at which they may be made available to the algae. Phytoplankton, whether they are freshwater or marine, appear to have a common response to the TN : TP ratio. As more total nutrient data become available, along with more measurements of nutrient status, the generality of our proposed relationship may be tested in locations in which we have few data points and in areas with different concentrations and ratios of TN and TP.

Conclusions—If TN and TP concentrations are indicative of available N and P to support algal growth, it might be expected that the oceans are not as frequently or strongly nutrient limited as are many freshwater systems. Freshwater systems exhibit a broad range of TN and TP concentrations, but most often they have concentrations that are well below those observed in the ocean. In our data set, P control of algal biomass (as indicated by Chl *a* concentration) and algal growth rate (as indicated by nutrient status indicators) were evident in most of the freshwater systems, especially when TP was less than 0.5 μmol L^{-1}. The relatively nutrient-rich marine sites less frequently displayed strong or consistent nutrient limitation that would indicate growth-rate limitation. Although we did observe a significant correlation between Chl *a* and TP in the marine sites, the TP concentrations were high relative to the freshwater TP concentrations, and the

Chl *a* concentrations per unit of TP were low. There was no evidence that Chl *a* was controlled by TN.

Marine and freshwater systems have overlapping TN : TP ratios, and these ratios appear to predict equally well in both environments which of these two nutrients can become limiting for growth when nutrient concentrations are low. N limitation of growth, as determined by nutrient status indicators, can occur at low TN : TP ratios (<20) in both freshwater and oceans. Similarly P limitation can occur in both environments when the TN : TP ratio is high (>50). Downing (1997), in his review of TN : TP ratios in the marine environment, found that the great majority of values reported for the upper euphotic zone of the ocean had TN : TP greater than 20, and many ratios exceeded 50. He concluded that strong limitation by N would not be expected to occur in much of the open ocean. Our data on nutrient status indicators and their relations to TN : TP ratios support this conclusion. N or P limitation of growth is a product of the TN and TP concentration and of the TN : TP ratio and not of whether the system of study is marine or freshwater. Total nutrient concentrations and nutrient status data from marine and freshwater sites presented here indicate that freshwater systems are more consistently and strongly nutrient deficient than are marine systems. This aspect, rather than whether N or P is the critical nutrient, may be the greatest difference between lakes and oceans.

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