The nitrogen to phosphorus ratio for lakes: A cause or a consequence of aquatic biology?

Rolando Quirós (2002). Sistemas de Producción Acuática, Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, (1417) Buenos Aires, Argentina. E-mail: quiros@agro.uba.ar

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Rolando Quirós
Sistemas de Producción Acuática, Facultad de Agronomía, Universidad de Buenos Aires. Av. San Martín 4453, (1417) Buenos Aires, Argentina. E-mail: quiros@agro.uba.ar

Abstract

External gradients of matter and energy drive the behavior of dissipative structures. Therefore, it can be believed that external gradients also drive, ultimately, the behavior of self-organizing, complex, dissipative systems, like ecosystems. Nutrient gradients are ordinarily expressed between a lake and its environment and also between the lake biota and its chemical-physical environment. For the latter, some energy has to be dissipated by the biota in order to concentrate nutrients, at both high and low TN:TP ratios. Lakes exhibit a huge range of total nutrient concentrations and a great variability in relationships between total nitrogen (TN) and total phosphorus (TP). P originates primarily from soil minerals and can accumulate to a substantial degree at sediments of lakes and oceans. On the other hand, N is unique among lake nutrients, it originates from atmosphere as an inert gas, is closely tied to organic matter, exceptionally accumulates to a significant degree in lake sediments, and has a cycle either more complex than P. Most lakes distributed worldwide were P restricted before cultural eutrophication, independent of its original trophic state. Moreover, a TN:TP decrease is usually displayed during lake eutrophication processes. Therefore, the differences in biogeochemical cycles for phosphorus and nitrogen would be expected to be reflected in TN:TP ratio for lakes.

The main purpose of this study is to explore the empirical relation between the TN:TP ratio and the trophic state in lakes ranging from deep stratified to very shallow polymictic lakes. A secondary purpose is to examine the hypothesis that nonlinear patterns in TN-TP relationships for lakes are mainly associated with differences in biogeochemical cycles for N and P, and some inherent properties of living systems. A variety of published data was used comprising measurements of total nitrogen, total phosphorus, chlorophyll concentration, water transparency, lake surface area, and mean depth for more than 1500 water bodies distributed worldwide.

The relationship between lake N and P concentrations is not linear. It has a complex parabolic shape, when sets of lakes with a very wide range of trophic states are examined. Therefore, the relationship between TN:TP and TP has a decreasing hyperbolic shape. The TN:TP nutrient ratio decreases abruptly with TP from 1 to 8-10 $mg.m^{-3}$, declines more gradually between 10 and 25 $mg.m^{-3}$, and practically has a tendency to be stabilized at TN:TP values ranging between 10 and 5 (weight basis) for higher TP concentrations. Therefore, a consistent pattern emerged from the studied data set, despite a large amount of variability among individual lakes. TN:TP ratios are consistently low for eutrophic and hypertrophic lakes. Moreover, similar hyperbolic patterns are displayed for individual lakes during its seasonal cycles. For mesotrophic stratified lakes, TN:TP decreases from the mixed layer to the hypolimnia, and is a minimum at the water-sediment interface.

Since human induced nutrient loads to lakes usually have a low TN:TP ratio, would be direct to conclude that lake TN:TP mimics the TN:TP of nutrient loads to lakes. Very often N concentration increases lesser than P concentration during eutrophication.

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Nevertheless, our results show that the low lake TN:TP attained early during the eutrophication process is sustained for most of the lake trophic state change. In front of P enrichment, TN:TP ratio for lakes decreases to a limit similar to the homeostatic TN:TP ratio for living organisms. Furthermore, aquatic life is compatible with narrow upper and lower bounds of the physical-chemical parameters that qualify the ecosystem state. It appears to be that aquatic ecosystems with TN:TP ratios below 6-7 (weight basis) at surface waters were not abundant in Nature before anthropogeneic influences, the unique exceptions are naturally acidic lakes.

The mechanistic resource-based competition theory suggests that changes in the supply ratio of N and P to lakes should alter algal community composition in a predictable way. This hypothesis was seriously challenged by Reynolds (1998) argumentation about selective process in the phytoplankton. At a lower level in the hierarchy of explanations, cyanophyte dominance may be a result of nutrient unbalanced situations, expressed as low TN:TP ratios. Bloom forming cyanophytes and other algal species would thrive under light limitations (Reynolds, 1998). In front of P enrichment, lake systemic process will try to oppose to the TN:TP ratio decrease with an increase in N_2-fixation. Furthermore, our results suggest that blue-greens prevalence may be a systemic response attempting to impede TN:TP ratio descending below homeostatic levels, dangerous for a healthy aquatic biota, and besides a systemic propensity to increase the biological biomass under favorable conditions. For the lake way from oligotrophy to hypertrophy, a systemic precautionary mechanistic balance between denitrification and N_2-fixation processes can be imagined. However, the TN:TP ratio for lakes appears to be both a cause and a consequence of aquatic biology, in spite of involved mechanisms. In the wake of P enrichment of lakes, lake TN:TP ratio change to values near the homeostatic TN:TP ratio for living organisms may be anticipated.

key words: TN:TP ratio, world lakes, lake comparisons, ecosystem stoichiometry, lake resilience

Introduction

Nutrient gradients are ordinarily expressed between a lake and its environment and also between the lake biota and its chemical-physical environment. Lakes exhibit a huge range of total nutrient concentrations and a great variability in relationships between total nitrogen (TN) and total phosphorus (TP). P originates primarily from soil minerals and can accumulate to a substantial degree at sediments of lakes. On the other hand, N is unique among lake nutrients, it originates from atmosphere as an inert gas, is closely tied to organic matter, exceptionally accumulates to a significant degree in lake sediments, and has a cycle either more complex than P (Wetzel, 1975). The central role of P in lake ecology was shown more than 30 years ago (Schindler, 1977; Schindler et al., 1971), and most lakes distributed worldwide were P restricted before cultural eutrophication, independent of its original trophic state.

That increases in phosphorus (P) and nitrogen (N) loadings to lakes (Vollenweider, 1968; Dillon and Rigler, 1975), and the subsequent augmentation of in-lake nutrient concentrations, implied the enhancement of lake community standing stocks is now widely recognized (Sakamoto, 1966; Dillon and Rigler, 1974; Schindler et al., 1978; Hanson and Leggett, 1982; Hanson and Peters, 1984; Bird and Kalff, 1984; Yan, 1986; Quiros, 1990; Brown et al., 2000; among many others). These results are in close agreement with the modern thermodynamic (Kondepudi and Prigogine, 1998) view of ecosystems as dissipative systems (Kay and Schneider, 1994; Straskraba et al., 1999; Kay, 2000). As expected, lake entropy production per unit of lake volume increases with nutrient enrichment and enhanced biomass (Aoiki, 2000). Moreover, ecosystems are the place where biological organisms thrive under favorable gradients of energy and matter. Aquatic organisms have to concentrate nutrients. For P and N, there are concentration differences of several order of magnitude between the homeostatic internal media and the lake concentrations. Therefore, some energy has to be dissipated by the biota in order to concentrate nutrients.

The TN:TP ratio for lakes has been studied previously. Obtained results were suggested as related to N:P differences for nutrient sources, and to the trophic state of lakes (Downing and McCauley; 1992). However, results were usually interpreted (Smith, 1982, 1983; McCauley et al., 1989; Guilford and Hecky, 2000) under the light of the mechanistic resource-based competition theory (Tilman, 1977). Moreover, it has been suggested that the occurrence of blooms of cyanobacteria is causally related to low TN:TP ratios (Smith, 1986; Bulgakov and Levich, 1999; Guilford and Hecky, 2000, among many others). Nevertheless, recently, Reynolds´ objections to a deterministic role for N:P ratios (Reynolds, 1999) cast many doubts on the theoretical understanding of causal links between the TN:TP ratio and the blue-green dominance in some water bodies.

The TN:TP concentration ratio has been a problematic and messy variable for lake limnology. First, it is a ratio variable and, therefore, is not a good state variable to study lake processes. It usually varies inversely with lake trophic state and biological standing stocks (Smith, 1982; Downing and McCauley; 1992; Quiros, 1990b). However, the TN:TP ratio may be a good variable to study state change in lakes. As it was stated before, the TN:TP ratio and the trophic status are closely and inversely related for lakes. Furthermore, the differences in biogeochemical cycles for phosphorus and nitrogen would be expected to be reflected in TN:TP ratio for lakes.

The N:P composition of the aquatic biota is fairly restricted (Elser et al., 1996) in comparison to the wide range of N:P found in lakes and oceans. Moreover, the TN:TP ratio for the upper mixed layer is usually higher than for the hypolimnion. However, for both lakes and oceans the N:P stoichiometry of the organisms produced in the upper layer does not usually differ from the deep-water TN:TP ratios.

The main purpose of this study is to explore the empirical relation between the TN:TP concentration ratio and the trophic state in lakes ranging from deep stratified to very shallow polymictic lakes and ponds. A secondary purpose is to examine the hypothesis that nonlinear patterns in TN-TP relationships for lakes are mainly associated with differences in biogeochemical cycles for N and P, and some inherent properties of living systems. A variety of published and not yet published data was used, comprising measurements of total nitrogen, total phosphorus, chlorophyll concentration, water transparency, lake surface area, and mean depth for more than 1500 water bodies distributed worldwide.

Materials and methods

With the purpose of exploring trophic state effects on TN:TP concentration ratio, a database was constructed, depending on available information. A variety of published data was used comprising measurements of total nitrogen, total phosphorus, chlorophyll concentration, water transparency, lake surface area and mean depth, and latitude for more than 1500 water bodies from both temperate and tropical regions (Table I). The database includes published nutrient and chlorophyll data for: a) subartic Alaskan lakes (Edmundson and Carlson, 1998; Edmundson data), and northtemperate lakes in Ontario (Hutchinson et al., 1991), Montreal (Prairie data), and northeastern USA (Larsen et al., 1991; EMAP data); Missouri reservoirs (Jones and Knowlton, 1993); Mississippi alluvial valley lakes (Wylie and Jones, 1986); Florida lakes (Bachmann et al., 1996; Terrell et al., 2000); b) Costa Rica (Jones et al. 1993), and Brazilian reservoirs (Tundisi et al., 1991); Argentinean lakes and reservoirs (Quiros, 1988); New Zealand shallow lakes (Jeppesen et al., 2000); c) lakes in Poland (Gizinski et al. 1997; Kufel and Kufel 1997), The Netherlands (Meijer and Hospers, 1977), Germany (Nixdorf and Deneke, 1997; Rucker et al., 1997), England (Moss et al., 1997), northern and western Europe (data in Thyssen, 1999), reservoirs in Spain , Italy (Sardinia), and Portugal (data in Thyssen, 1999); d) fish ponds in Thailand, Kenya, and Honduras (PD/A CRSP data); e) others lakes, reservoirs and ponds distributed through temperate and tropical regions, including urban and experimental lakes (Quiros files). Chlorophyll and nutrient data were used as published. Nutrient data for the estimation of N and P concentrations in aquatic organisms were taken from Davis and Boyd (1978), Elser and Hasset (1994), Schindler and Eby (1997), Hasset et al. (1997), Burkhardt et al., 1999), Hillebrand and Sommer (1999), Fernandez-Alaez et al. (1999), Sterner and George (2000), and Tanner et al. (2000).

Several data subsets were used for chlorophyll and nutrient analyses. The total world lake and pond set (total lake data, TLD) comprised nutrient and chlorophyll data for more than 1600 lakes, reservoirs, and ponds distributed in both temperate and tropical regions, independently of their trophic conditions, morphometry, and water characteristics. A subset of the TLD (n = 1535), comprised only by lakes and reservoirs without distrophic characteristics or oxygen devoid, and not with lakes under experimentation, was considered as a “healthy” lake data subset (“healthy” lake data, HLD). For the latter, two lake subsets for deep (HLDD, mean depth > 10m) and shallow (HLDS, mean depth < 10m) lakes were also contemplated. Anycase, an arbitrary TP maximum lake limit (1400 mg.m^{-3}) for inclusion in the “healthy” lake set, was fixed. This is the maximum TP concentration found for some hypertrophic but relatively healthy, Pampean very shallow lakes. Only results for total nitrogen (TN, mg.m^{-3}) and total phosphorus (TP, mg.m^{-3}) concentrations, total chlorophyll *a* concentration (Chl, mg.m^{-3}), and TN:TP ratio (weight basis), will be presented here.

In order to stabilize the variance for regression analysis, all the variables except nutrient ratios were log-transformed. Curvilinear trends in data were studied using robust locally weighted regression and smoothing graphic techniques (LOWESS and Median). The Number Cruncher Statistical System (NCSS 2000) (Hintze 1998) was used.

Results

As expected, for all the analyzed data sets, TN, TP, and Chl concentrations were related highly and significantly among them, in log-log analyses (Table 1). However, a close analysis on log-log data shows sigmoid-like patterns in data (Fig. 1). These patterns are analogous for the TP-TN and the TP-Chl relationships. In other words, each relationship resembles each other. Moreover, the TN concentration approximates to the TP concentration with the increasing in TP (Fig. 1).

Therefore, we have two remarkable results here. First, the TN-TP curved relationship has an appearance similar as has the TP-Chl regression (Fig. 1). However, similar appearance not implies similar shape. For both TLD and HLD lake sets, TN-TP and TP- Chl regressions show noticeable change of slopes at TP equal to 3-4, 25-30, and 100-200 mg.m^{-3}. For TP concentrations between 1 and 3-4 mg.m^{-3}, or greater than 100-200 mg.m^{-3}, TP-Chl regression slope resembles the slope for the TP-TN regression. On the other hand, for TP between 25-30 and 100-200 mg.m^{-3}, TP-Chl slope resembles TP increases.

Table 1. Simple regression models for total nitrogen (TN, mg.m^{-3}), and total chlorophyll *a* (Chl, mg.m^{-3}) on TP (total phosphorus, mg.m^{-3}). The coefficient of determination (R^2), the root mean square error (RMSE), and the standard error for slope (SEs), are presented. TLD, total world lakes and ponds set (total lake data); HLD, "healthy" lakes data subset; HLDD, deep lakes; HLDS, shallow lakes; all sets of lakes as defined in the text.

data set	n	Equation	SEs	RMSE	R^2
TLD	1655	$\log_e TN = 4.758 + 0.505 \log_e TP$	0.038	0.665	0.58
TLD	1356	$\log_e Chl = -0.826 + 0.870 \log_e TP$	0.017	0.947	0.65
HLD	1535	$\log_e TN = 4.601 + 0.568 \log_e TP$	0.012	0.626	0.58
HLD	1276	$\log_e Chl = -0.937 + 0.918 \log_e TP$	0.021	0.929	0.61
HLDD	229	$\log_e TN = 4.655 + 0.471 \log_e TP$	0.048	0.846	0.30
HLDD	146	$\log_e Chl = -2.086 + 1.066 \log_e TP$	0.070	0.972	0.62
HLDS	323	$\log_e TN = 4.494 + 0.669 \log_e TP$	0.027	0.704	0.66
HLDS	249	$\log_e Chl = -0.611 + 0.846 \log_e TP$	0.038	0.889	0.66

Notwithstanding discrete and striking changes of slope for log-log regressions, the slopes for both TP-TN and TP-Chl relations appear to change continuously (Fig. 1). The linear plotting of both relationships shows that neither TN nor Chl vary linearly with the TP concentration (Figures 2 and 3). On the contrary, both functions have a complex sigmoid parabolic-like shape with decreasing slopes but ascending steps. As expected, these "steps" are situated approximately at the same TP concentrations where the log-log regressions change their slopes. Moreover, both functions attain very low slope increases from relatively low TP concentrations (100-200 mg.m^{-3}) upwards (Fig. 1). In other words, both TN concentration and algal biomass appear to reach a plateau, under heavy TP loading. However, there are significant differences between patterns for deep and shallow lakes (Fig. 4). For TP higher than 7-8 mg.m^{-3}, TN concentrations were dramatically higher for shallow than for deep lakes, when TP concentrations were held constant.

Second, the TN concentrations approached the TP concentrations as long as lake trophic status increases. This result illustrates why TN:TP concentration ratios are inversely related to lake trophic states. Moreover, the functionality of the TN:TP lowering with the TP concentration increases is far to be linear. At first glance, the relationship between TN:TP and TP has a decreasing hyperbolic shape (Fig. 5). For the "healthy" lake susbset (HLD), TN:TP decreases abruptly from more than 100 to approximately 25-30 when TP increases from very low values for ultraoligotrophic lakes (< 1 mg.m^{-3}) to 8-10 mg.m^{-3} (Fig. 6). The nutrient ratio declines more gradually to approximately 30 for TP between 10 and 25 mg.m^{-3}, reaching values of 10 and 6-5 at TP approximately 200 mg.m^{-3} and 400 mg.m^{-3}, respectively. From the later TP concentration and above, TN:TP ratio is stabilized between 5 and 6 (weight basis). As expected from TP-TN and TP-Chl regression analyses for deep and shallow lakes separately, the TN:TP ratios for shallow lakes are higher than for deep lakes, when TP concentrations were held constant (Fig. 7). However, there was not a clear tendency to stabilize the TN:TP ratio at high TP concentrations for deep lakes (see Fig. 8).

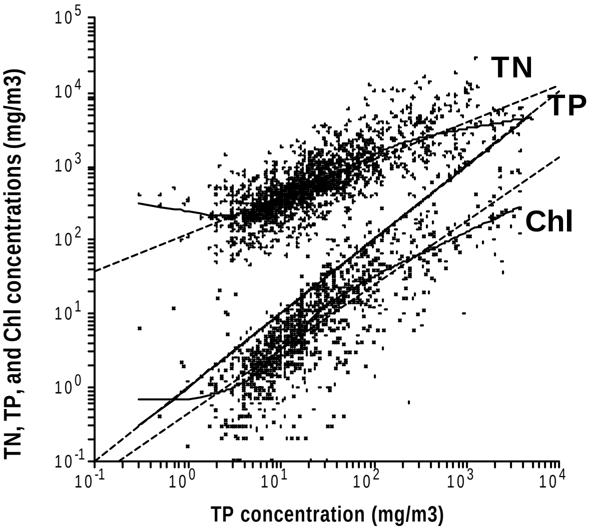

Figure 1. Relationships between total nitrogen (TN), total phosphorus (TP), and chlorophyll (Chl) concentrations for all lakes and ponds (TLD data, n=1655). LOWESS smooth relationships are presented.

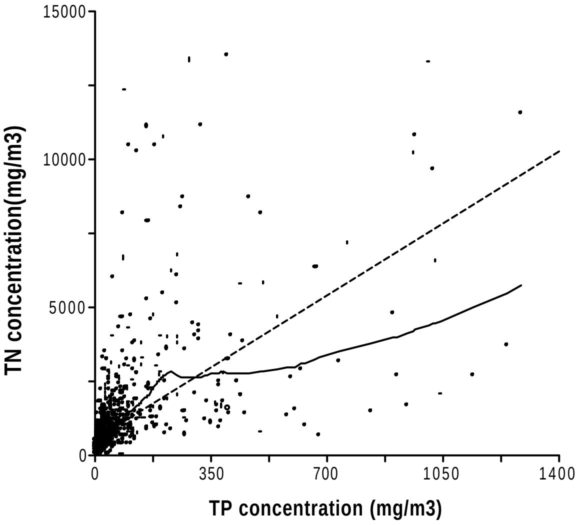

Figure 2. Relationship between total nitrogen (TN) and total phosphorus (TP) concentrations for "healthy" lake data (HLD data, n = 1535). LOWESS smooth relationship is presented.

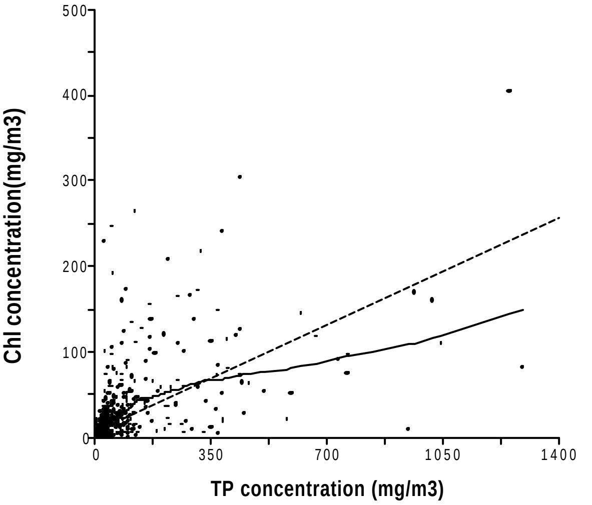

Figure 3. Relationship between chlorophyll (Chl) and total phosphorus (TP) concentrations for "healthy" lake data (HLD data, n = 1276). LOWESS smooth relationship is presented.

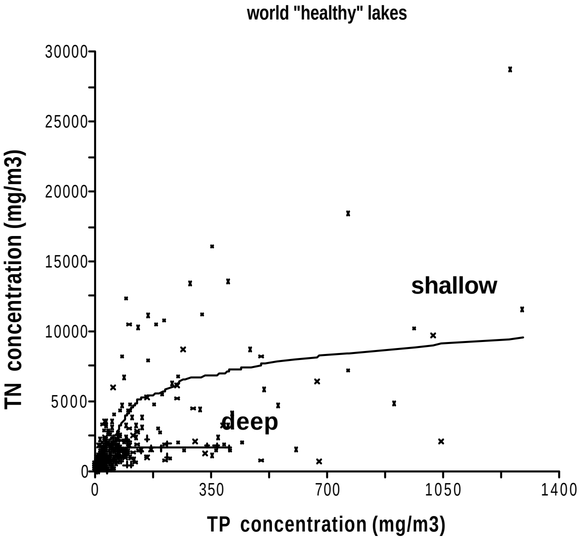

Figure 4. Relationship between total nitrogen (TN) and total phosphorus (TP) concentrations for shallow (HLDS data, n = 323) and deep lake data (HLDD data, n = 229). LOWESS smooth relationships are presented.

When dystrophic and oxygen devoid lakes, lakes under experimentation, naturally acidic lakes, and heavy N-loaded fish ponds were included in the analyses (TLD lake analyses), the mean value for TN:TP reach 1 at TP = 5000 mg.m^{-3} (Fig. 9). Moreover, there was not a defined pattern for the relationship between the TP:TN ratio and the TN concentration.

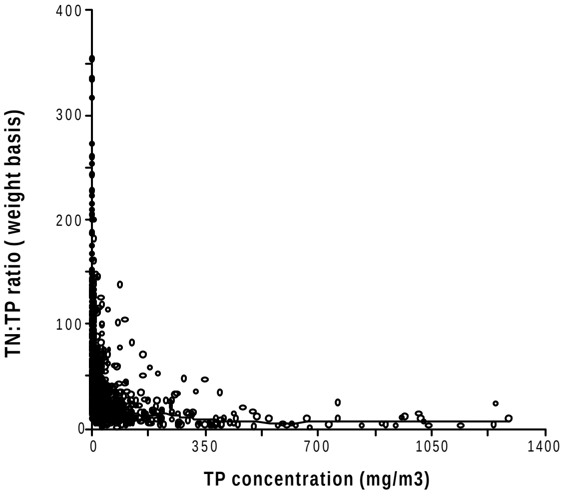

Figure 5. Relationship between TN:TP ratios and total phosphorus (TP) concentrations for “healthy” lake data (HLD data, n = 1535) (just for lakes with TN:TP < 400). LOWESS smooth relationship is presented.

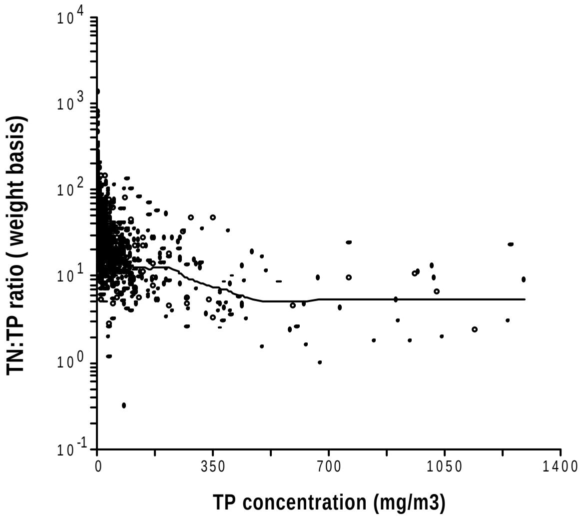

Figure 6. Relationship between TN:TP ratios and total phosphorus (TP) concentrations for “healthy” lake data (HLD data, n = 1535). LOWESS smooth relationship is presented.

The results obtained from among lake comparisons presented here, are similar to those obtained with other regional but more intensive lake data sets not yet included in our studied lake data base (e.g. LTER north temperate lakes (Bowser et al., 1999), and Florida lakes (LAKEWATCH, 1998), as well as for individual lakes during its annual seasonal cycle (Quiros, unpublished results).

Moreover, our obtained pattern for TN:TP lowering with TP concentration increases may be of wide application also to oceans and estuarine environments, given that the published TN:TP data for estuaries and oceans (Downing, 1997; Guilford and Hecky, 2000) fits our obtained pattern.

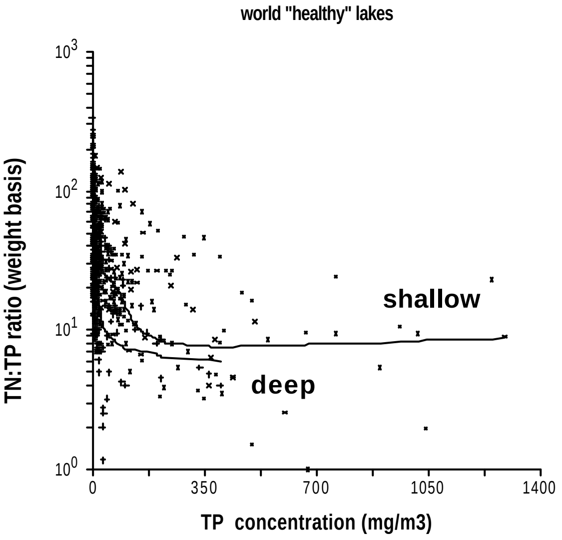

Figure 7. Relationship between TN:TP ratios and total phosphorus (TP) concentrations for shallow (HLDS data, n = 323) and deep lake data (HLDD data, n = 229). Median smooth relationships are presented.

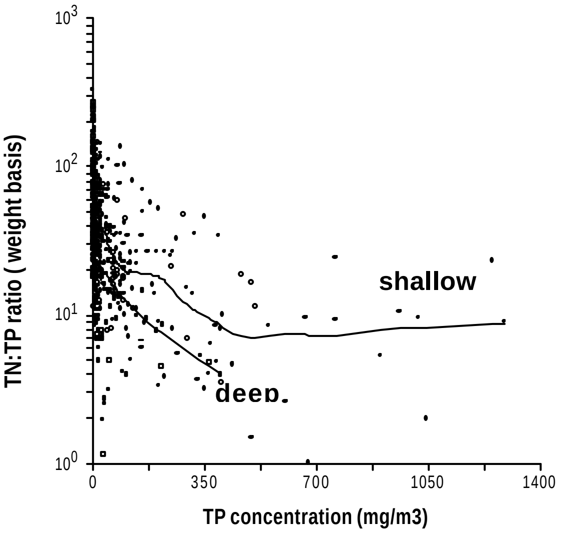

Figure 8. Relationship between TN:TP ratios and total phosphorus (TP) concentrations for shallow (HLDS data, n = 323) and deep lake data (HLDD data, n = 229). LOWESS smooth relationships are presented.

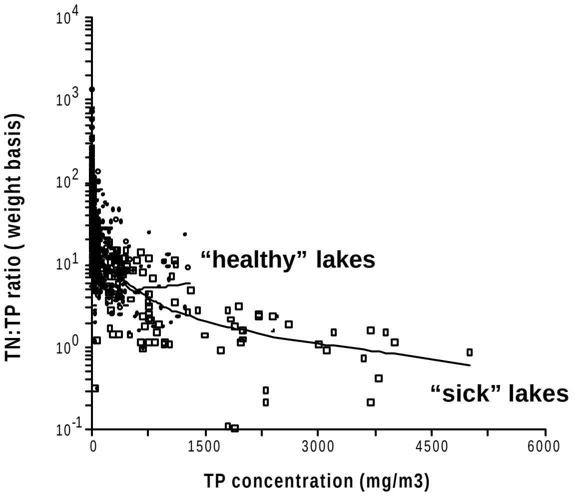

Figure 9. Relationship between TN:TP ratios and total phosphorus (TP) concentrations for "healthy" (HLD data, n = 1535) and "sick" lake data (TLD minus HLD data, n = 120). LOWESS smooth relationships are presented.

Discussion and conclusions

During lake nutrient enrichment, water nitrogen and phosphorus concentrations do not vary linearly between them. Their relative concentrations can be influenced by a complex set of interrelated biogeochemical mechanisms (Schindler, 1977; Downing and McCauley; 1992).

Despite a large amount of variability among individual lakes, a consistent pattern emerged from the studied data sets. As was stated before, TN:TP ratios were consistently low for eutrophic and hypertrophic lakes. It has been suggested that the decline in TN:TP with increased TP may be due at least in part to the differences in the TN:TP ratio of the nutrient sources of lakes (Downing and McCauley; 1992). However, low TN:TP for nutrient loadings appears not to be enough to explain the pattern of TN:TP ratio decrease for surface waters neither to elucidate the cyanophyte dominance for eutrophic and hypertrophic lakes (Reynolds et al., 2000).

However, most of the existing literature indicates that both N_2-fixing cyanophytes and bloom forming algae usually dominate lakes with relatively low TN:TP ratios. We believe this fact could be explained under an ecosystemic view of lakes. This view is supported in the hypothesis that ecosystems are dissipative systems (sensu Kay and Schneider, 1994) where dissipative structures (e.g. individual organisms, waves, and tornadoes) "play the game" of dissipate energy (Prigogine, 1967). Dissipative structures lie in between external gradients in order to organize space and trying to destroy external gradients producing as much entropy as they can.

The decrease of the TN:TP ratios for lakes when TP loading increases is very sharp, reaching N:P values near the homeostatic range very abruptly. Moreover, these relatively low values are sustained for several orders of magnitude in TP change, during the eutrophication process. It suggests that under external nutrient loading, an ecosystemic lake mechanism is working to oppose TN:TP lowering in order to sustain it near the range of the biological homeostatic values (Elser et al., 1996). However, living organisms have to concentrate nutrients. For P and N, there are concentration differences of several order of magnitude between the homeostatic internal media and the lake concentrations (Fig. 10). Some energy has to be dissipated by the aquatic biota in order to concentrate nutrients, at both high and low TN:TP ratios (Fig. 11). Anycase, lake eutrophication decreases the gradients between the external and the internal homeostatic media (Fig. 10). Therefore, system history and lack of genetic variability (throughout evolution) may be a limitation for lake life at very heavy P-loading (TP>1500–2000 $mg.m^{-3}$).

However, this result also implies an expected conclusion, just the energy gradient drives living dissipative structures development in aquatic ecosystems. The interplay of energy and matter availability, in the organimistic near environment, determines how much it is achieved the individual goal of growth and reproduction.

For ultraoligotrophic and oligotrophic

lakes, a portion of the available energy for aquatic production can not be used because of nutrient limitations. On the contrary, energy limitations can be suspected when the lake state changes from eutrophy to hypertrophy. Lake ecosystems "resiliate" external nutrient loadings with usually low TN:TP ratios in order to sustain a "healthy" water environment with TN:TP nutrient ratios no so far of homeostatic internal media for aquatic organisms.

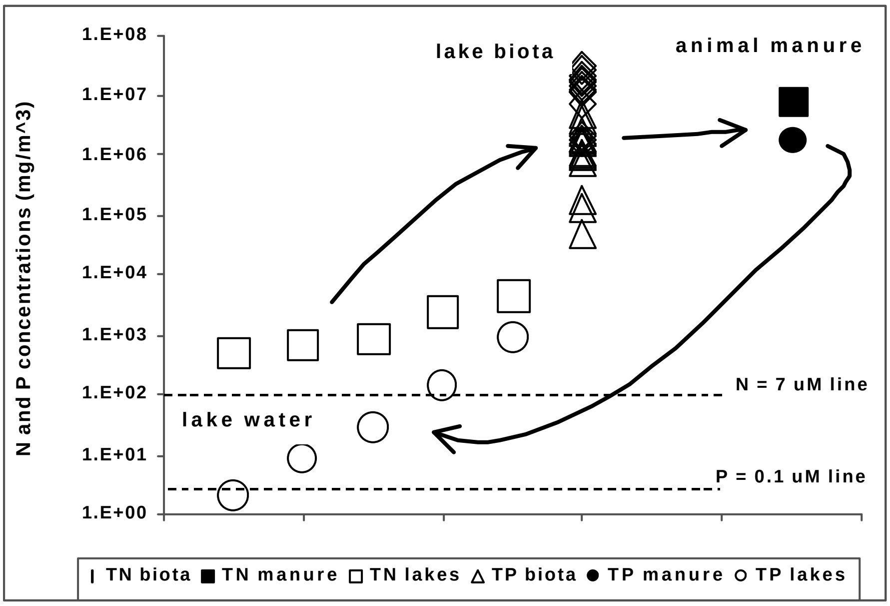

Figure 10. Nitrogen and phosphorus concentrations for lakes (ultraoligotrophic to hypertrophic), lake biota (several sources, details in text), and animal manure. The lines for algal physiological requirements of dissolved nutrients (Reynolds, 1999) are presented.

From this view, it can be concluded that N_2-fixing cyanophytes and bloom forming algae are both natural ecosystemic mechanisms directed to ameliorate ecosystem changes and to maximize dissipative structures (number of organisms and, therefore, biomass) under appropriate external gradients. Under increasing nutrient loading, the eutrophication process proceeds from lower to higher trophic states. Lakes reorder their internal states to the new environmental conditions. The biological standing stocks (e.g. phyto and zooplankton, and fish communities) usually increase (Quiros, 1990a, 1991). Therefore, more living biomass is displayed for the higher lake trophic states. As was shown by Aoki (2000), an increase in lake entropy production per unit lake volume have to be expected during eutrophication. This last statement implies more living biomass, throughout more individuals, an empirical observation for lake nutrient enrichment.

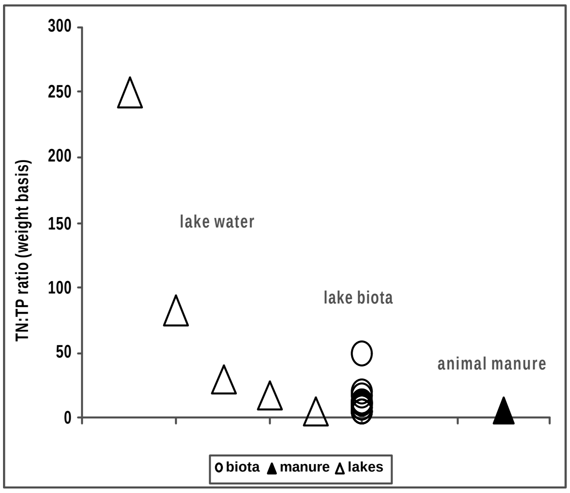

Figure 11. The TN:TP ratios for lakes (ultraoligotrophic to hypertrophic), lake biota (several sources, details in text), and animal manure.

Under eutrophication process, the lake ecosystem reorganizes itself in order to sustain ecosystem integrity. To explain this fact at lower hierarchic level, it is not necessary to postulate markedly different mechanisms of loss of N and P from the pelagic zone among lakes of differing trophic status. Species structure may be the key. It is enough to suppose similar mechanism operating at different rates. The change in species structure for aquatic communities under nutrient loading, may be the way to achieve ecosystemic capacity of resilience. It is not our intention here to discuss why some groups of species tend to increase in biomass rather more strongly than others under given conditions. However, our results suggest that the proposed systemic response to TN:TP ratio lowering may be supported by species pre-adaptations to nutrient and light conditions (Reynolds, 1998). Therefore, under this view, community structure change is a ecosystemic resilience response to a change in the lake nutrient environment, and N_2-fixing cyanophytes would start to act before bloom forming algae or other algae adapted at low light conditions.

The former argumentation could be extended to other lake species assemblages. They usually change irreversibly under eutrophication (Colby et al., 1972; Leach, et al., 1977). Anyway, for most of the lakes distributed worldwide, an expected change of functional species groups may be predicted under nutrient loading increase. This last statement is not the same that suppose that increased nutrient content is directly implicated in a mechanistic species selection by nutrient contents (Reynolds, 1999, 2000). Our results shown that, during lake enrichment, N increases more slowly than P up to the point where lake ecosystems lost diversity and alternative periodical cycles of predominant autotrophy and heterotrophy, may be expected.

The role of N_2-fixing cyanophytes contributing to resiliate lake TN:TP lowering has been suggested before (see Moss et al., 1997), but partially justified on mechanistic nutrient limitation theories. It is not highly probable that a lake shifts from an external determination at low nutrient loads to an internal determination at high loads. Lake resilience mechanisms to environmental change would be at operation for any lake state. They probably operate at different rates for different lake nutrient status. The huge changes in community's structure under lake enrichment could be part of the operation of ecosystemic mechanisms under the necessary increase in total lake biomass.

Under this view, two parallel process will operate under lake enrichment, one conducted to resiliate external changes in order to assure living conditions, and the other directed to maximize biomass (entropy production) under favorable nutrient conditions. This is the type of changes that would be expected under the postulates of the far from equilibrium thermodynamics (Kay and Schneider, 1994; Kondepudi and Prigogine, 1998).

However, the lake capacity of resilience to nutrient loading would have a limit; for TN:TP ratios below 5-4 (weight basis), an unhealthy lake state can be anticipated. When the grade of hypertrophy attains levels where the TN:TP ratio decreases below the homeostatic biological levels, it would be the moment when the lake state is incompatible with a "healthy" aquatic life. On the other hand, there is not a defined pattern for the relationship between TP:TN and TN. This result reflects the different characteristics of N and P biogeochemical cycles in aquatic ecosystems.

Shallow lakes appear to defend themselves better from TN:TP ratio lowering under high TP-loading and high in-lake TP concentrations. The first fact is probably related to shallow lake higher capacity to retain P at sediments during early eutrophication (Sas, 1989). The second may be related with a higher capacity to produce algal biomass than deep lakes for a similar TP concentration (see Table I).

For the lake way from oligotrophy to hypertrophy, a systemic precautionary mechanistic balance between denitrification and N_2-fixation processes can be imagined. However, the TN:TP ratio for lakes appears to be both a cause and a consequence of aquatic biology, in spite of involved mechanisms. Biogeochemical fluxes of nutrients to lakes and oceans has been profoundly modified by man. Many lakes distributed worldwide are under heavy nutrient loading and suffer eutrophication processes. In the wake of P enrichment of lakes, lake TN:TP ratio change to values near the homeostatic TN:TP ratio for living organisms may be anticipated.

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