The relationship between nitrate and ammonia concentrations in the pelagic zone of lakes

Rolando Quirós

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

ABSTRACT

Both nitrate (NO_3-N) and ammonia (NH_4-N) concentrations are in general highly variable during a lake's seasonal cycle. During the growing seasonal peak, such concentrations can be very low due mainly to its' sequestration by phytoplankton. With the aim to study NO_3-N and NH_4-N mean concentration variation along the increase of the trophic state of lakes, this study simultaneously analyses the information for more than 400 lakes worldwide. Both forms of nitrogen are directly related to the trophic state of a lake when lakes are compared with total phosphorous concentration (TP) ranging across five magnitude levels. However, in lakes a pronounced non-linearity dominates the relationships among the different forms of nitrogen and phosphorous. Our results suggest that the empirical basis for both the limiting resource and inorganic nitrogen hypotheses are related. The NO_3-N: NH_4-N ratio is directly related to the TN: TP ratio for lakes in general and shallow ones in particular.

Key words: lakes, nutrients, ammonia, nitrate, lake comparisons, trophic state

RESUMEN

Las concentraciones de nitrato (NO_3-N) y de amonio (NH_4-N) generalmente son altamente variables durante el ciclo estacional de un lago. Durante el pico de la estación de crecimiento tales concentraciones pueden llegar a ser muy bajas, debido principalmente a su captación por parte del fitoplancton. Con el objeto de estudiar la variación de las concentraciones medias de NO_3-N y de NH_4-N con el aumento del estado trófico de los lagos, fue analizada información simultánea para más de 400 lagos distribuidos mundialmente. Ambas formas de nitrógeno están directamente relacionadas con el estado trófico de un lago, cuando son comparados lagos con concentraciones de fósforo total (TP) que abarcan cinco órdenes de magnitud. Sin embargo, una pronunciada no-linealidad domina las relaciones entre las diversas formas de nitrógeno y fósforo en lagos. Nuestros resultados sugieren que la base empírica de las hipótesis del nutriente limitante y del nitrógeno inorgánico están relacionadas. La relación NO_3-N:NH_4-N esta directamente vinculada con la relación TN:TP para los lagos en general y para los poco profundos en particular.

Palabras clave: lagos, nitrógeno disuelto, amonio, nitratos, estado trófico

INTRODUCTION

The change in nitrogen and phosphorus loadings to lakes led to changes in the biogeochemical cycles of these nutrients in lakes. However, the cycling of N is expected to be more affected by external loadings due to the open characteristic of the N cycle.

That increases in nutrient loadings to lakes implied the augmentation of in-lake nutrient concentrations, and the subsequent enhancement of lake biological 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). Increased levels of living and dead organic matter in eutrophic and hypertrophic lakes when compared with oligotrophic lakes permit us to predict an augmentation of reductive characteristics of the lake environment with the increase in lake trophic status (Stumm and Morgan, 1996).

Both nitrate (NO$_3$-N) and ammonia (NH$_4$-N) concentrations are highly variable during lake seasonal cycles. For deep stratified lakes nitrate is higher during mixing events and usually decreses in late summer and fall. For the trophogenic zone of shallow lakes, both concentrations would be lower during periods of water column stability and they will increase during vertical mixing events. NH$_4$-N is generated by heterotrophic bacteria as the primary nitrogenous end product of decomposition of organic matter, and is readily assimilated by plants in the trophogenic zone (see Wetzel, 2001). NH$_4$-N concentrations are usually low in oxygenated waters of oligo- to mesotrophic deep lakes because of utilization by plants in the photic zone and nitrification to N oxidized forms. At relatively low dissolved oxygen, nitrification of ammonia ceases, the absorptive capacity of the sediments is reduced, and a marked increase of the release of NH$_4$-N from the sediments then occurs. As a result, the NH$_4$-N concentration would increase for the water column of shallow lakes and of deep lakes during mixing processes. NO$_3$-N is the common form of inorganic nitrogen entering lakes from the drainage basin; in relatively aerobic waters nitrification prevails (see Wetzel, 2001). When NO$_3$-N from external sources reaches lakes it is taken by autotrophs and bacteria, transformed in organic matter that on decay and food web transmission ultimately goes to the NH$_4$-N pool. Therefore, NH$_4$-N accumulates respect to NO$_3$-N in relatively standing waters like those of lakes and reservoirs. In eutrophic and hypertrophic lakes, a large lake concentration of organic matter implies a large potential pool of ammonia. In more reductive media denitrification and nitrate reduction to ammonia would prevail (Stumm and Morgan, 1996). The removal of N from lakes is usually dominated by NO$_3$-N denitrification concomitantly with the oxidation of organic matter, but in highly productive surface waters, high pH would favor N release to the atmosphere as NH$_3$.

Therefore, and due mainly to in-lake N cycling, it has to be expected that the ratio of NO$_3$-N to NH$_4$-N (NO$_3$-N:NH$_4$-N) in lakes would be less variable in relation to natural and pollutional sources of both forms of nitrogen that in direct connection to total lake biomass and other lake characteristics like morphometry, water alkalinity and pH, and dissolved oxygen regime. For lake steady states, the supply of nutrients to lake surface waters includes both external inputs and internal inputs such as releases from sediments, transport from deep-water layers, and, in the case of nitrogen, from N$_2$ fixation. Following P and N loadings, the principal destiny of both nutrients usually is incorporation into lake biota followed by sedimentation. The principal sinks for N usually are the same as for P, the uptake by the biota followed by sedimentation. However, a lake could control TN concentration in its waters by denitrification, NH$_4$-N releases from sediments and N$_2$ fixation. All these mechanisms would contribute to determine both the TN:TP and the ratio NO$_3$-N:NH$_4$-N for lake surface waters.

A large number of theories have been proposed to explain the success of pelagic cyanobacteria in lakes. These hypotheses embrace many spatial and temporal scales (see Hyenstrand et al. (1998) for a review), and the most general theories are environmentally connected and it is probable that their empirical bases would be related (Reynolds and Petersen, 2000). One of most recognized theories, the low TN:TP hypothesis (Schindler, 1977; Smith, 1982; 1983; Bulgakov and Levich, 1999), predicts that cyanobacteria will dominate lakes with a low TN:TP ratio. However, lakes with low TN:TP ratios usually also have high TP concentrations (Downing and McCauley, 1992; Quiros, 2002). With basis in their physiological requirements, it has been proposed that non-N$_2$-fixing cyanobacteria would be disfavored in nitrate rich (McQueen and Lean, 1987) oxidizing environments and favored in ammonia rich (Blomqvist et al., 1994) more reductive environments. The TN:TP hypothesis has been seriously challenged by Reynolds (1998) argumentation about selective process in the phytoplankton, and the inorganic N hypothesis had to be modified to include iron effects (Hyenstrand et al.,1999).

In this paper, the relationship between the empirical bases of the limiting resource theory (Tilman *et al*., 1982; Smith, 1983) and the inorganic nitrogen hypothesis (Blomqvist *et al*., 1994) is studied in among lake comparisons. More specifically, the relationship between the TN:TP and the NO_3-N:NH_4-N ratios is explored.

MATERIALS AND METHODS

With the purpose of exploring trophic state effects on nitrate and ammonia concentrations for the pelagic zone of lakes a variety of published and unpublished data was used, comprising measurements of total phosphorus (TP), total nitrogen (TN), total organic nitrogen (TON), dissolved inorganic N, and mean depth for 425 world lakes and ponds ranging from ultraoligotrophic to hypertrophic.

Depending on available information, the database includes data for: a) Northwest Canadian Territories (Pienitz *et al*., 1997a; 1997b), Quebec (D`Arcy and Carignan, 1997), north-temperate lakes in Wisconsin (LTER data, Bowser *et al*., 1999), and northeastern USA lakes (EMAP data, Larsen *et al*., 1991); b) world lake data for Europe (ILEC, 1994), Asia and Oceania (ILEC, 1993), and the Americas (ILEC, 1995); c) Mississippi alluvial valley lakes (Wylie and Jones, 1986); d) Southamerican reservoirs (Tundisi *et al.,* 1991) and Brazilian lakes (Mitamura *et al*., 1997); d) Andean-Patagonian lakes (Pedrozo *et al*., 1993; Diaz and Pedrozo,1996); e) fish ponds in Thailand, Kenya, and Honduras (PD/A CRSP data); f) water quality data for USA lakes and reservoirs (Nebraska (STORET, 2001) and USGS (USGS, 2001); g) others lakes and reservoirs distributed through temperate and tropical regions (Quiros files). Morphometric and nutrient data were used as published and each water body is represented once in data. Most nutrient data are mean annual values but for some lakes, available data for just one year were included.

Several data subsets were used for nutrient analyses. The total world lake and pond set (total lake data, TOTAL) comprised nutrient data for 425 lakes, reservoirs, and ponds distributed in both temperate and tropical regions, independently of their trophic conditions, morphometry, and water characteristics. A subset of the TOTAL (n = 425), is comprised by lakes and reservoirs with available morphometric data (ZLAKES, n = 191). For the latter, two lake subsets for deep (DEEP, mean depth > 10m, n = 42) and shallow (SHALLOW, mean depth < 10m, n = 149) lakes were also contemplated. To compare lake depth effects between deep and shallow lakes, a SHALLOW65 lake subset (n = 80) was defined as a part of the SHALLOW subset but only including lakes with TP concentrations ranging the same range of TP concentrations than deep lakes (< 65 mg·m^{-3}). In order to stabilize the variance for correlation and regression analysis, all the variables were log-transformed. Curvilinear trends in data were studied using robust locally weighted regression and smoothing graphic techniques (LOWESS). The Number Cruncher Statistical System (NCSS 2000) (Hintze, 1998) was used. Throughout this paper, the TP concentration will be considered as the main indicator of lake trophic state.

RESULTS

Lake data

Total lake data represents better eutrophic and hypertrophic lakes, and TP concentrations ranged over five orders of magnitude (Table 1). However, TP ranges were narrow when deep and shallow lakes were considered separately (Table 1).

As a result of lake trophic state augmentation, all lake nutrient forms increase their concentrations, as expected. Mean NO_3-N and NH_4-N concentrations in surface waters increase 7 and more than 20 times, respectively, from oligotrophic and mesotrophic to hypertrophic lakes (Table 1). Correlation analysis showed that lakes with the highest total nutrient levels tended to have higher NO_3-N and NH_4-N concen-

Table 1. General charateristics for the group of databases used for this study. Lake data sets are defined in the text. *Características generales para el conjunto de bases de datos utilizada para este estudio. Las bases de datos sobre lagos están definidas en el texto.*

	TOTAL (425)	DEEP (42)	SHALLOW (149)	SHALLOW65 (80)	TP<15 (111)	100>TP>15 (188)	TP>100 (126)
NO_3-N	255	89	224	75	69	206	492
	(0.3-5120)	(0.8-898)	(1-2685)	(1-733)	(0.8-945)	(0.3-4180)	(1.4-5120)
NH_4-N	112	28	176	39	20	64	264
	(0.3-2032)	(1.3-146)	(1-1700)	(1-347)	(1-146)	(0.3-473)	(15-2032)
TP	206	17	396	20	7.9	43	623
	(0.5-8740)	(3.4-65)	(3-3700)	(3-63)	(0.5-14.3)	(15-100)	(107-8740)
TN	1348	471	1954	744	409	970	2423
	(130-6480)	(130-1077)	(200-6480)	(220-3018)	(130-1500)	(278-5100)	(200-6480)
NO_3-N:NH_4-N	5.0	10.3	4.8	6.8	6.8	5.2	3.1
	(0.012-165)	(0.24-85)	(0.013-165)	(0.08-165)	(0.08-165)	(0.012-85)	(0.013-54)
TN:TP	32.4	34.6	20.9	40.0	87.9	26.4	8.4
	(0.11-798)	(13-79)	(0.11-129)	(10.8-128.5)	(13-798)	(3.6-111)	(0.11-26)
NO_3-N:TP	7.87	5.33	3.50	5.69	19.9	4.71	1.98
	(0.0002-582)	(0.02-37)	(0.01-71)	(0.07-71)	(0.07-582)	(0.02-84)	(0.0002-37)
NO_3-N:TN	0.17	0.11	0.14	0.12	0.20	0.15	0.23
	(0.0005-0.82)	(0.002-0.37)	(0.007-0.71)	(0.014-0.71)	(0.013-0.84)	(0.002-0.82)	(0.0005-5.1)
NH_4-N:TP	1.91	2.88	1.37	1.98	3.57	1.72	0.74
	(0.0018-78.4)	(0.02-12.6)	(0.04-12.2)	(0.08-12.2)	(0.14-78)	(0.02-12)	(0.002-9)
NH_4-N:TN	0.08	0.07	0.10	0.07	0.06	0.07	0.11
	(0.0013-0.50)	(0.001-0.28)	(0.005-0.50)	(0.005-0.30)	(0.005-0.28)	(0.001-0.30)	(0.005-0.5)
DIN:TP	9.8	7.6	4.9	7.7	23.5	6.4	2.7
	(0.002-613)	(0.043-38)	(0.053-71)	(0.15-71)	(0.15-613)	(0.031-86)	(0.002-38)
DIN:TN	0.25	0.18	0.25	0.19	0.26	0.22	0.30
	(0.003-0.9)	(0.003-0.52)	(0.019-0.83)	(0.039-0.71)	(0.023-0.86)	(0.003-1.0)	(0.006-5.3)

trations (Table 2). NH_4-N was more related with total nutrient concentrations than with NO_3-N. As expected, the TN:TP ratio was inversely related with TP but, unexpectedly, it was also inversely related with the TN concentration. Lakes with low TN:TP ratios have high NH_4-N concentrations (Table 2), though the NO_3-N concentration was not related with the TN:TP ratio. However, the higher values for the NO_3-N:NH_4-N ratio were found in lakes with intermediate TP concentrations (200 > TP > 3) and relatively high TN:TP ratios (> 7, weight basis).

Linear log-log patterns

Further analyses of nutrient ratios suggest that the relationships among different forms of dissolved N are dependent on the lake trophic state. For the total data set, both NO_3-N and NH_4-N

ratios on TP decrease with both TP (r = -0.48 and r = -0.54, P < 0.0001, respectively) and TN concentrations (r = -0.18 (P < 0.001) and r = -0.26 (P < 0.0001), respectively) (see Table 1). However, this reduction is more dramatic for the NO_3-N:TP than for the NH_4-N:TP ratio (Table 1) and, as a result, the NO_3-N: NH_4-N ratio decreases significantly with trophic state augmentation (Tables 1 and 2).

The behavior of nitrate and ammonia concentrations depends on the lake trophic state. The relationships between NH_4-N and NO_3-N had different slopes when different ranges of TP concentrations were considered (Table 3). At relatively low TP concentrations (< 15 mg m^{-3}), NO_3-N decreased (Table 3) probably by increased algal captation and denitrification whereas NH_4-N stood low (Table 1) most likely due to relatively low regeneration from sediments,

Table 2. Matrix correlation coefficients among nutrients, and some ratios for whole lake data set (TOTAL). Variables as they have been defined in the text. *Matriz de coeficientes de correlación entre los nutrientes y algunos cocientes para todo el conjunto de la base de datos (TOTAL). Las variables según han sido definidas en el texto.*

	TN	TN:TP	NO_3-N	NH_4-N	NO_3:NH_4
TP	0.75	-0.88	0.47	0.72	-0.20
TN		-0.35	0.57	0.72	-0.05 (a)
TN:TP			-0.19 (a)	-0.50	0.29
NO3				0.63	0.57
NH4					-0.27

N = 425. (a); t-test, P > 0.00001

algal uptake, and higher nitrification to more oxidized N forms. At intermediate TP (100 > TP > 10-15), both NO_3-N and NH_4-N concentrations were directly related with TP (Table 3). An increased NH_4-N regeneration from sediments and a relative acceleration of nitrification can be supposed for this range of TP concentrations. N_2- fixation usually is an important N compensation mechanism at this intermediate TP levels (Levine and Schindler, 1999). For high TP concentrations (> 100 mg m^{-3}), NO_3-N did not increase or its increse was negligible. For this range of TP, NH_4-N was directly related with TP but with a lower slope for the NH_4-N regression on TP (Table 3). Nitrification appears to be highly reduced when compared with NH_4-N regeneration from sediments. The latter fact is ultimately related to higher organic matter con-

centration and living biomass for high TP lakes. In conclusion, this is also an expected result because eutrophic and hypertrophic lakes are more reductive environments when compared with oligotrophic and mesotrophic lakes (Stumm and Morgan, 1996).

Our described pattern for NO_3-N and NH_4-N variability in lakes presented some differences when deep and shallow lakes have been analyzed separately (Table 4). Shallow lakes presented higher level of nutrients when compared with deep lakes. Most of those deviations may be due to differences in lake trophic state (Table 1, compare DEEP and SHALLOW data). However, some differences between shallow and deep lakes were apparent when lakes with equivalent TP variability had been compared (Table 1, compare DEEP and SHALLOW65 data). Both NH_4-N and TN concentrations were higher for SHALLOW65 lakes, as well as the NO_3-N:NH_4-N ratio was lower for SHALLOW65 than for DEEP lakes. High data variability precludes us to conclude about significant differences for means except those for TN and TON (t-test, P < 0.01 and 0.02, respectively). When lakes were compared using multiple regression models including a "dummy" variable for lake depth, TN, TON, and TN:TP ratios were higher for shallow than for deep lakes (P < 0.05). On the other hand, NO_3-N:NH_4-N ratios were lower for SHALLOW65 lakes (P < 0.05) when TP concentration was held constant. The huge increase of NO_3-N at inter-

Table 3. Slope values for the log-log regression models between nutrient and total phosphorus (TP) for the whole data set (TOTAL) and for three data subsets as defined by its' variation range of variation. Standard error for slopes are indicated. *Valores de las pendientes para los modelos de regresión log-log entre nutrientes y el fósforo total (TP) para todo el conjunto de datos (TOTAL) y para tres subconjuntos definidos por su rango de variación. Se indican los errores estándar de las pendientes.*

|	n	NH_4-N	NO_3-N	NO_3-N:NH_4-N	TN	NH_4-N:TP	NO_3-N:TP	TN:TP
TP < 15	111	0.225 (0.151) (a)	-0.710 (0.228)	-0.947 (0.200)	0.102 (0.073) (a)	-0.775 (151)	-1.710 (0.223)	-0.904 (0.073)
100>TP>15	188	0.705 (0.131)	1.024 (0.184)	0.307 (0.186) (a)	0.479 (0.063)	-0.295 (0.131)	0.024 (0.184) (a)	-0.521 (0.064)
TP>100	126	0.486 (0.079)	-0.047 (0.118) (a)	-0.628 (0.106)	0.204 (0.057)	-0.514 (0.078)	-1.047 (0.118)	-0.787 (0.056)
TOTAL	425	0.620 (0.029)	0.490 (0.045)	-0.171 (0.041)	0.387 (0.018)	-0.380 (0.029)	-0.510 (0.045)	-0.620 (0.018)

(a), P > 0.05

mediate TP concentrations appears to be more related with deep than with shallow lakes (Table 4). More than half of lakes included in the DEEP subset (55 %) were lakes with TP < 15 mg.m^{-3}. On the other hand, the dissolved N increases for the SHALLOW65 subset at low and intermediate TP levels was related with NH$_4$-N (Table 4). That TN:TP ratios are higher for shallow than for deep lakes when TP is held constant has been shown before for a larger set of world lakes (Quirós, 2002).

Non-linear log-log patterns

As it has been shown above, NO$_3$-N and NH$_4$-N concentrations were both positively log-log correlated with TP (Table 2, Fig. 1). However, those results also suggest that the relationships between the dissolved forms of N and the lake trophic state are more complex than just log-log linear relationships. A close inspection of figure 1 shows that NO$_3$-N did not increase when TP was very high (> 100 mg m^{-3}) or even decreases when it was low (< 8-10 mg m^{-3}) (Table 3). In contrast, NO3-N showed a sharp increase when TP was between 15 and 100 mg m^{-3}. This range

of TP is in close coincidence with the TP range where lake TN increases sharply with TP (Fig. 2). For this latter TP range an acceleration of lake nitrification processes fueled by higher organic matter contents and sustained by enough dissolved oxygen, can be suspected. Moreover, a noticeable change of curvature was displayed for TP between 20 and 30 mg m^{-3} (Fig. 1). From this TP range upward NO$_3$-N diverged from NH$_4$-N up to TP near 100 mg m^{-3}. It has to be stressed here that a TP concentration of 25 mg m^{-3} has been repeatedly mentioned in literature as a lower limit for *Microcystis* plankton dominance (see Reynolds *et al.*, 2000). The NO$_3$-N:TP ratio declined for all the range of TP concentrations with exception of TP ranging between 15 and 100 mg m^{-3} (Table 3, Fig. 3a).

Contrasting with the behavior of NO$_3$-N, NH$_4$-N did not present huge changes of slope under TP augmentation. It increased at a low rate for TP below 8-10 mg m^{-3}, its rate of increase was maximum for TP between 15 and 100 mg m^{-3}, and increased at a declining rate for TP higher than 100 mg m^{-3} (Table 2, Fig. 1). This fact may indicate that NH$_4$-N returns from sediments increased with lake trophic state (Tables 1 and 2) but also that those returns, per unit of
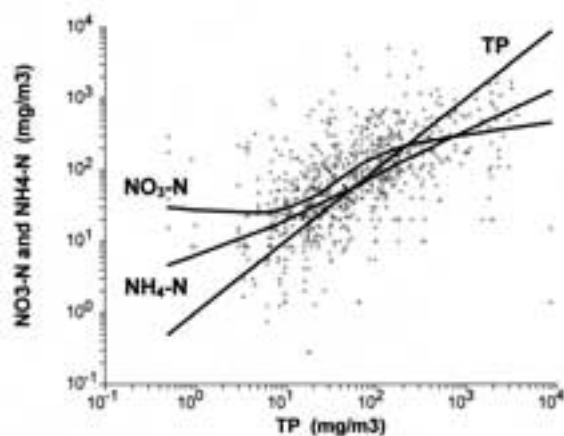
Figure 1. Relationships between nitrate (NO$_3$-N), ammonia (NH$_4$-N), and total phosphorus (TP), for all lakes and ponds (TOTAL data, n = 425). LOWESS smoothing relationships and the TP line are indicated. *Relaciones entre nitrato (NO$_3$-N) , amonio (NH$_4$-N) y fósforo total (TP), para todos los lagos y lagunas (TOTAL data, n=425). Se indican las relaciones según un suavizado LOWESS y la línea TP.*
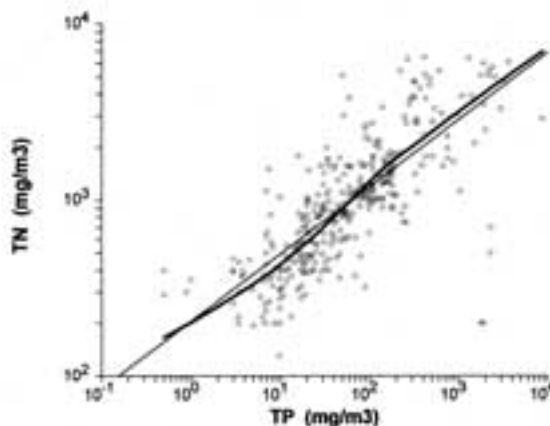
Figure 2. Relationship between total nitrogen (TN) and total phosphorus (TP). The relationship after a LOWESS smoothing is indicated. *Relación entre el nitrógeno total (TN) y el fósforo total (TP). Se indica la relación con suavizado LOWESS.*
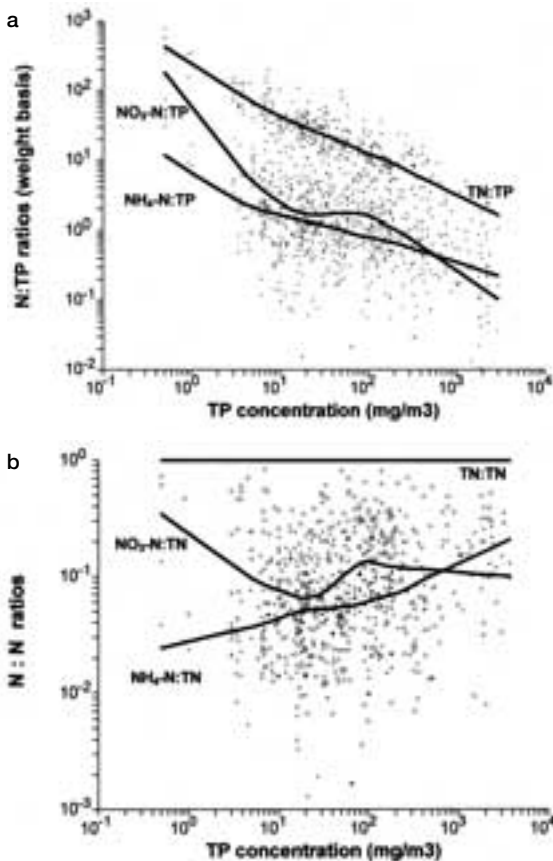
Figure 3. a) Relationships between NO_3-N:TP, NH_4-N:TP, and TN:TP ratios and total phosphorus concentration for (TP) for the whole data set; b) Relationships between NO_3-N:TN, and NH_4-N:TN, and total phosphorus concentration (TP) for the whole data set; the constant total nitrogen (TN) lines and the LOWESS smoothing relationships are indicated.
a) Relaciones entre los cocientes NO_3-N:TP, NH_4-N:TP, y TN:TP y el concentración de fósforo total (TP) para todo el conjunto de datos; b) Relaciones entre NO_3-N:TN, y NH_4-N:TN, y la concentración de fósforo total (TP) para todo el conjunto de datos; se indican las líneas de la relación constante para el nitrógeno total (TN) y para las relaciones con suavizados LOWESS.

TP, declines from oligotrophic to hypertrophic lakes (Fig. 2). One stricking result is that NH_4-N:TP ratio decline was a minimum for lakes with TP between 10 and 100 mg m^{-3} (Fig. 3a). For this latter TP range, NH_4-N returns from sediments must be higher than losses produced by nitrification to NO_3-N. Anyway, NH4-N accumulates continuously in the water column during lake eutrophication.

The proportions of NO_3-N and NH_4-N in total nitrogen both change with lake trophic state. NO_3-N and NH_4-N accounted for 30-35 % and 2 % of the N in the water, respectively, for oligotrophic lakes, and about 10% and 20%, respectively, for high TP lakes (Fig. 3b). The dissolved inorganic N had a minimum at low TP concentrations (TP = 5-6 mg m^{-3}) (Fig. 1), but for TP of about 20 mg m^{-3} the proportion of NO_3-N in TN was minimum (Fig. 3b). For total lake data, NO_3-N:TN was not log-log related to TP. However, it had its greater values for low TP lakes and decreased abruptly up to TP near 20 mg m^{-3}. From this TP concentration upwards it decreased steadily (Fig. 3b). On the other hand, NH_4-N:TN increased gently from its smaller values for low TP lakes to its higher values for high TP lakes. Other surprising result was that the LOWESS line slope for the relationship between NH_4-N:TN and TP declined considerably for TP concentrations between 20 and 50-60 mg m^{-3}. A close inspection of Figure 3b reinforce that NO_3-N was the most important form of dissolved inorganic N for oligotrophic lakes whereas NH4-N was critical for hypertrophic lakes with very high TP concentrations (> 700-800 mg m^{-3}).

The behaviors of NH_4-N and TN concentrations under TP augmentation were similar (Fig. 3a, and compare Figures 1 and 2). The change of slopes for the TN:TP ratio was close to the changes displayed for the NH_4-N:TP ratio when different ranges of TP concentrations were considered (Table 3).

Relationship between TP-TN and NO_3-N:NH_4-N ratios

Lakes with high TP concentrations and low TN:TP ratios also tend to have low NO_3-N:NH_4-N ratios (Table 2). For total lake data, both TN:TP and NO_3-N:NH_4-N ratios were inversely related to TP (r = -0.88 (P < 10^{-6}) and r = -0.20 (P < 10^{-4})). Both ratios were significantly correlated between them (r = 0.29, P < 10^{-6}).

For the low range of TP (< 10-15 mg m^{-3}), the slope for the TP-TN relationship was the smallest when compared with upper ranges of TP (Fig. 2,

Table 4. Slope values for log-log regression models between nutrients and total phosphorus (TP) for the whole data set (ZLAKES) and three data subsets as defined in the text. *Pendientes de los modelos de regresión log-log entre los nutrientes y el fósforo total (TP) para el total de los datos (ZLAKES) y tres subconjuntos de datos que se definen en el texto.*

|	n	NH_4-N	NO_3-N	NO_3-N:NH_4-N	TN	NH_4-N:TP	NO_3-N:TP	TN:TP
DEEP	42	0.178 (0.293) (a)	0.867 (0.328)	0.652 (0.327) (a)	0.632 (0.102)	-0.822 (293)	-0.133 (0.328) (a)	-0.402 (0.103)
SHALLOW65	80	0.823 (0.135)	0.312 (0.199) (a)	-0.495 (0.193)	0.488 (0.068)	-0.177 (0.135) (a)	-0.688 (0.199)	-0.532 (0.073)
SHALLOW	149	0.691 (0.039)	0.498 (0.058)	-0.256 (0.057)	0.354 (0.034)	-0.309 (0.039)	-0.502 (0.058)	-0.657 (0.034)
TOTALZ	191	0.692 (0.039)	0.496 (0.053)	-0.263 (0.054)	0.403 (0.027)	-0.308 (0.039)	-0.504 (0.053)	-0.607 (0.028)

(a), P > 0.05
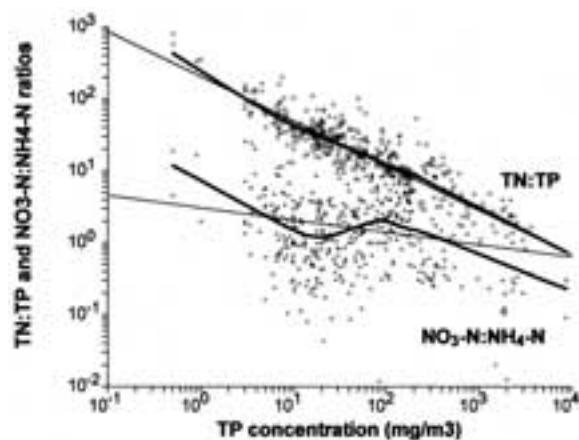
Figure 4. Relationships between TN:TP and NO_3-N:NH_4-N ratios and total phosphorus concentration (TP) for the whole data set. LOWESS smoothing relationships are also presented. *Relaciones entre los cocientes TN:TP y NO_3-N:NH_4-N y la concentración de fósforo total (TP) para todo el conjunto de datos. Se presenta, además la relaciones según un suavizado LOWESS.*

Table 3) and both ratios, TN:TP and NO_3-N:NH_4-N, decrease abruptly with TP augmentation (Fig. 4). At intermediate TP, a huge impulse to nitrification may be suspected. The NO_3-N:NH_4-N ratio changes its decreasing tendency and stabilizes or even increases whereas the TN:TP ratio maintains its decreasing tendency but with a lower slope (Fig. 4). At high TP concentrations (> 100 mg m^{-3}), there appears to be no lake mechanism completely able to resiliate successfully TN:TP lowering; both ratios continue their decreasing tendency with TP. Moreover, high primary productivity for these lakes usually conduces to pH increasing that may also favors N (as NH_3-N) evolution to the atmosphere.

When deep and shallow lakes were considered separately, shallow lakes followed a similar pattern to that for total lakes; NO_3-N:NH_4-N and TP were inversely correlated for SHALLOW and SHALLOW65 data sets (r = -0.35, P < 0.0001, and r = -0.28, P = 0.01, respectively). On the contrary, NO_3-N:NH_4-N and TP were directly correlated for the DEEP data set (r = 0.30, P = 0.05). These differences between deep and shallow lakes at similar TP concentrations may be related to different lake mechanisms involved in N processing for deep and shallow environments (Levine and Schindler, 1992 and 1999).

Lakes with low TN:TP ratios tend to present low NO_3-N:NH_4-N ratios. A close inspection of figure 5 shows that lakes with TN:TP ratios higher than 50 (weight basis) also tend to have the higher values for the NO_3-N:NH_4-N ratio. This
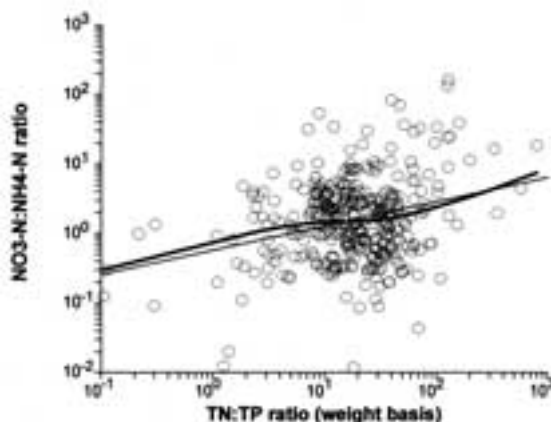
Figure 5. Relationships between NO_3-N:NH_4-N and TN:TP ratios the whole data set. LOWESS smoothing relationship is also presented. *Relaciones entre los cocientes NO_3-N:NH_4-N y TN:TP con TN:TP para el total de datos. Se presenta, además, la relación según un suavizado LOWESS.*

ratio have a tendency to be stabilized for TN:TP ratios between 50 and 10 and decreases for TN:TP ratios lesser than 8-7. A change of curvature for the fitting line is noticeable when TN:TP equals 25 (Fig. 5). However, when the relationships between NO_3-N:NH_4-N and TN:TP have been analyzed for deep and shallow lakes separately there were not noticeable differences in between. NO_3-N:NH_4-N and TN:TP were directly related for both deep and shallow lakes though it was not significant for deep lakes (r = 0.27, P = 0.14, and r = 0.44, P < 0.01, for DEEP and SHALLOW65 data sets, respectively).

DISCUSSION AND CONCLUSIONS

Our results strongly support that the concentration of NH_4-N and the proportion of NH_4-N in total nitrogen in lake surface waters rise steadily with lake trophic state for lakes and shallow lakes. The analysis of our data for deep lakes did not show that NH_4-N increase for deep lakes with TP concentrations lower than 65 mg m^{-3}. However, our results also support that NH_4-N will also increase for deep eutrophic and hypertrophic lakes with very high TP concentrations. The behavior of NO_3-N under lake eutrophication is relatively more complex than NH_4-N behavior. The concentrations of NO_3-N in lake surface waters increase clearly with lake trophic state only for lakes with TP concentrations between 10 and 100 mg m^{-3}, as well as for deep and shallow lakes, but it did not show a clear intensification for shallow lakes with TP concentrations lower than 65 mg m^{-3}. As well as for total nitrogen, when the total trophic continuum is considered, both forms of inorganic N decline per unit of TP, but that declination is reduced for TP concentrations between 10-15 and 100 mg m^{-3}.

The NO_3-N:NH_4-N ratio decreases with TP for lakes and shallow lakes, but it increased for deep lakes with TP concentrations lower than 65 mg m^{-3} in our total lake data set. NH_4-N was greater than NO_3-N for TP concentrations from 600-700 mg m^{-3} upwards (Fig. 1). When only shallow lakes were considered, it was higher than

NO_3-N for TP concentrations from 70-90 mg m^{-3} upwards. These results are consistent with the view that shallow lakes compensate high TP loadings better than deep lakes, mainly through NH_4-N processing. Moreover, total nitrogen, as well as total organic nitrogen, is higher for shallow than for deep lakes at equivalent concentrations of total phosphorus (Quiros, 2002; this paper). However, both NO_3-N:TP and NH_4-N:TP ratios decrease with lake trophic state for lakes and shallow lakes, but neither NO_3-N:TP nor NH_4-N:TP decreased for deep and shallow lakes, respectively, when lakes have had TP concentrations lower than 65 mg m^{-3}. This latter result suggests that NO_3-N is a major form in N dynamics for surface waters of deep lakes whereas NH_4-N is prominent for shallow lakes, at low and intermediate TP concentrations (< 70-100 mg m^{-3}).

Some similarities are apparent between the behaviors of inorganic N dissolved forms displayed for low and very high TP lakes. The NO_3-N:TP and NH_4-N:TP ratios both decrease with TP for oligotrophic and hypertrophic lakes. The proportion of NO_3-N in total nitrogen decreases with TP for low and very high TP concentrations, whereas the proportion of NH_4-N increases for both oligotrophic and hypertrophic lakes. An increase of the reductive characteristics of the environment with the lake trophic state (Stumm and Morgan, 1996) may explain both NH_4-N intensification and NO_3-N reduction. It is to be expected that both deep and shallow lakes will present a similar pattern for NO_3-N reduction and NH_4-N rise for high TP concentrations. However, a change for in-lake operating mechanisms is apparent for TP concentrations between 8-15 and 100 mg m^{-3}. This range of TP is coincidental with non-linear nitrogen and phytoplankton biomass increases showed for several data sets distributed worldwide. The lower part of this range of TP is where occur most of the changes in species composition for lake communities (e.g.: Colby et al., 1972; Leach et al., 1977; Quiros, 1998; Reynolds et al., 2000).

Our results support that there are not relatively simple log-log models to explain relationships between lake nutrient concentrations. Both

NO_3-N and NH_4-N concentrations presented complex non-linear log-log patterns when have related with TP. The multiple changes of slope for log-log regressions may reflect the complex interplay of internal mechanisms and the influences of external forces. The relationships in lakes are still more complex because all the analyzed forms of N and the biomass for lake communities are really a potentially decreasing function of lake TP (Quiros, 2000). Curvilinear relationships among total phosphorus, total nitrogen, and phytoplankton biomass have been shown for many lake data sets (Straskraba, 1976; Prairie *et al*., 1989), but we still have a rudimentary understanding of the factors that determine TP-TN and TP-Chl sigmoid patterns. McCauley *et al*. (1989) called for an elucidation of the underlying biological mechanisms that produce the nonlinear response with TP. Furthermore, Watson *et al*. (1992) suggested that non-linearity reflects an underlying systematic variation in the biomass of functional algal groups. Mazumder (1994) showed that sigmoid patterns appear to be related to the transition from stratified to mixed lakes along the TP gradient, and Quiros (1998) have related those patterns to the transition from lakes with balanced fish populations to planktivore dominated lakes. Our earlier results (Quiros, 2002) suggest that previous explanations for nonlinear patterns might be included in a systemic view for N variability under P loading and its differences between deep and shallow lakes. It has been proposed that underlying mechanisms for observed nonlinear patterns are hidden behind differences in the N biogeochemical cycling for lakes with different trophic states and that an impulse to lake nitrification process may be suspected for intermediate lake trophic states (Quiros, 2002).

The physical-chemical characteristics of lake water are influenced by external and in-lake processes. The complexity of these processes often limits us to discriminate between internal and external causes for some in-lake process. As is usual in studying open systems with complex behaviors, a mix of both internal and external influences on in-lake processes can be identified.

It has been proposed two sources of change for the TN:TP ratio change in lakes. The first, mostly external (Downing and McCauley, 1992) hypothesis, proposes that the lake TN:TP ratio decreases under nutrient enrichment is due related primarily with the N:P ratio for the nutrient loads. A second mostly internal theory (Schindler, 1977) considers that lakes compensate high P loadings throughout the most open N cycling. However, our results suggest that internal and external influences may be not equally distributed throughout the trophic continuum. The quantities of NO_3-N and NH_4-N from external sources are highly diverse and variable because of marked differences in the inputs from surface and groundwater sources, particularly as affected by human activities (see Wetzel, 2001). NH_4-N is oxidized rapidly to nitrate in aerobic waters of rivers and streams. However, in lakes, NO_3-N is rapidly reduced into organic compounds within organisms and liberated as ammonia during the metabolism of these organisms. External influences would be most important at low and very high TP concentrations but in-lake N processing is highly active in determining nutrient relationships for lakes at TP concentrations between 10-15 and 100 mg m^{-3}. The more holistic external-internal view (Quiros, 2002) suggests that in-lake processes always work against external changes but they are particularly successful in opposing external influences only at intermediate lake trophic states. Experimental results support part of our contentions; the external sources may dominate the N inputs to lake waters for high TN:TP lakes whereas waters of low TN:TP lakes could receive more than half of their N from internal lake sources such as NH_4-N from sediments or N2 fixation (Levine and Schindler, 1992).

The TN:TP and NO_3-N:NH_4-N ratios are dependent on lake trophic state but also on lake morphometry. The NO_3-N:NH_4-N ratio is consistently very low for eutrophic and hypertrophic lakes. However, it appears to be relatively low also for ultraoligotrophic lakes (Fig. 4). Maximum values for NO3:NH4 were displayed at TP concentrations between 3 and 30 mg m^{-3}. Anyway, our results suggest that the em-

pirical basis for both the limiting resources (Tilman *et al*., 1982; Smith, 1982; Smith and Bennett,1999) and the inorganic nitrogen hypotheses (Blomqvist *et al*., 1994) are related. The NO_3-N:NH_4-N ratio is directly related to the TN:TP ratio for lakes and shallow lakes. A similar relationship was shown for deep lakes but it is something that needs to be investigated further. As was repeatedly suggested in literature (see Hyenstrand et al. (1998) for a review), NO_3-N and NH_4-N would not be equivalent forms of dissolved inorganic N for different species composing the phytoplankton community. A high organic matter content in a high trophic state lake implies a more reductive environment where ammonia accumulates respect to nitrate (Fig. 3b). Therefore, it is to be expected, that different proportions of NO_3-N and NH_4-N in total nitrogen or some other factors (e.g. some elements other than N or P) related with the continuum that goes from high oxidizing to more reductive environments throughout the trophic continuum, may be reflected in phytoplankton structure.

Our results suggest that leading mechanisms responsible of N cycling in lakes would be different for different lake trophic states and between deep and shallow lakes. 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 phosphorus (P) restricted before cultural eutrophication, independent of its original trophic state. However, the role of N has been discussed for many years in literature. The effect of internal compensating processes is to increase rather than lower, the TN:TP ratio (Fig. 2). Internal mechanisms that can compensate low TN:TP nutrient loadings include: N_2 fixation, sedimentation of N and P at a ratio different from the external supply ratio, differential P and N releases from sediments, and denitrification. At the lake system level, these mechanisms would operate differently for deep than for shallow lakes. It is not our intention here to hypothesize about hidden mechanisms behind described patterns. We believe that an adequate mix of well-known

N processing mechanisms may explain quite adequately our described behavior for inorganic dissolved forms. The high variability in our data precludes us to conclude that some of those differences are significantly.

Our obtained relationships will be only valid for stagnant surface waters. Therefore, for the NO_3-N:NH_4-N ratio, a variable dependence on the water renewal time may be suspected. Flowing waters usually have higher dissolved oxygen contents that modify N processing and conduct to higher NO_3-N:NH_4-N ratios for running waters when lakes and rivers were compared at constant TP concentration (Quirós, unpublished results).

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