Factors related to variance of residuals in chlorophyll – total phosphorus regressions in lakes and reservoirs of Argentina

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Abstract

Data from an extensive mid-summer survey of Argentinian lakes and reservoirs were used to study the effects of variability in internal processes on the residual variance in chlorophyll – total phosphorus (CHL-TP) regression models. These effects were compared with those related to the external characteristics of lakes, e.g. climate, morphometry and nutrient status. Zooplanktivorous fish biomass, mean macrozooplankton size, dissolved oxygen at the sediment-water interface, and submersed macrophyte development, were shown to be significant in explaining residual variance in CHL-TP for Argentinian lakes and reservoirs. The results suggest that those variables have discontinuous or threshold effects on CHL-TP residuals among lakes. Significant differences were also shown between CHL-TP regressions for lakes with and without zooplanktivorous fish and for lakes with small or large macrozooplankton. Lakes with zooplanktivorous fish, small body size macrozooplankton, and very low hypolimnetic oxygen also have higher chlorophyll levels than predicted from CHL-TP regression models.

Introduction

Total phosphorus (TP) has been shown to be the most important variable in explaining chlorophyll (CHL) variability between lakes and reservoirs worldwide (Dillon & Rigler, 1974; Dillon *et al.*, 1988). Regional, as well as global CHL-TP regression models have been developed (Sakamoto, 1966; Dillon & Rigler, 1974; Jones & Bachmann, 1976; Schindler, 1978; Carlson, 1977; Aizaki *et al.*, 1981; OECD, 1982; Canfield, 1983; Canfield *et al.*, 1984; Pridmore *et al.*, 1985; Quirós, 1988). Several factors have been shown to be responsible for residual variance in these models: methodology (Nicholls & Dillon, 1978), time scale and data range (Nicholls & Dillon, 1978; Paloheimo & Zimmerman, 1983), dilution rate (Dillon, 1975), inorganic turbidity (Canfield & Bachmann, 1981; Jones & Novak, 1981; Hoyer & Jones, 1983), color (Canfield & Hodgson, 1983), nitrogen limitation (Sakamoto, 1966; Smith, 1979, 1982), oxygen conditions at the sediment-water interface (Riley & Prepas, 1984; Nürnberg *et al.*, 1986; Nürnberg, 1988), total dissolved solids and water chemistry (Stauffer, 1985; Campbell & Prepas, 1986), stratification (Riley & Prepas, 1985), aquatic macrophyte abundance (Canfield *et al.*, 1984), and ecosystem biotic structure (Shapiro, 1980; Pace, 1984). Some of these factors are related to internal processes specific to individual lakes while others are related to external characteristics, e.g. climate, morphometry, and edaphic conditions of the drainage basin.
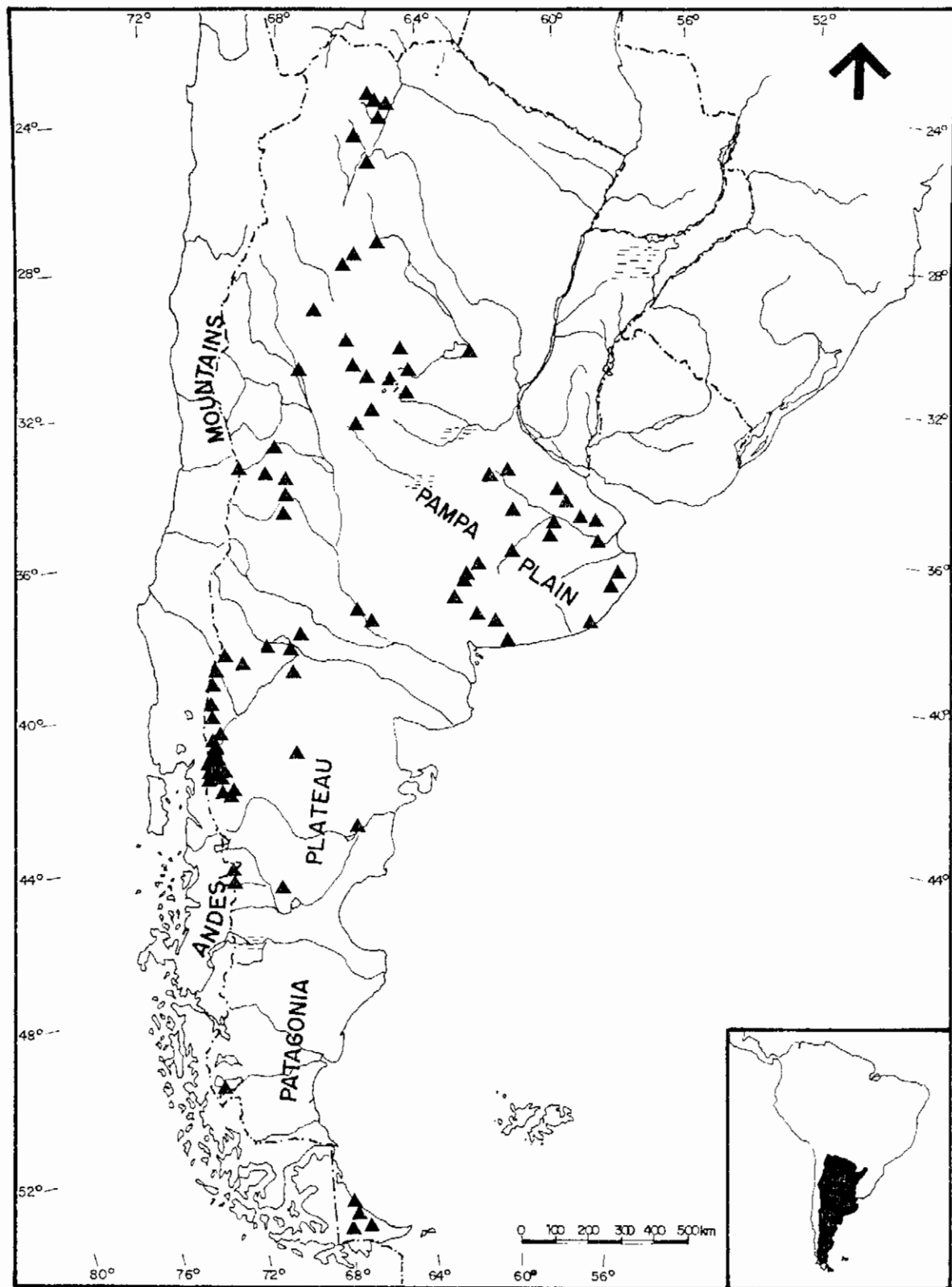
Fig. 1. Argentina showing the location of the 97 lakes and reservoirs studied.

Trophic conditions, as regulated by phosphorus and nitrogen limitation, mean annual air temperature and mean depth, have been shown to explain some of the residual variance in CHL-TP regressions for Argentinian lakes and reservoirs, but fish and zooplankton effects were not discarded (Quirós, 1988, 1989a).

Data from an extensive mid-summer limnological survey of Argentinian lakes and reservoirs (Quirós *et al.*, 1988) were used to evaluate the importance of variables related to in-lake processes in explaining CHL-TP residual variance in comparative lakes studies. The biomass and structure of zooplankton and fish communities, the dissolved oxygen concentration at the sediment-water interface, and the development of submersed macrophytes were considered. Those internal variables are directly or indirectly (as refuge for herbivore zooplankton) related to biomanipulation of lakes.

Description of lakes and reservoirs

One hundred and ten lakes and reservoirs in Argentina were surveyed during the summers of 1984 to 1987. The sites are located between 25 and 55° S latitude (Fig. 1) throughout the central-western and northwestern arid regions of Argentina, the Pampa Plain, the Patagonian Plateau, the Patagonian Andes, and Tierra del Fuego. Limnological characteristics of studied sites are presented in Table 1. The deepest lakes are situated in the Patagonian Andes and Tierra del Fuego, and ranged from ultraoligotrophic to oligotrophic. All sites in the Pampa Plain are ponds or very shallow lakes and ranged from eutrophic to hypertrophic. Most of the central-western and northwestern reservoirs and Patagonian Plateau lakes ranged from mesotrophic to eutrophic, and more than half of the northwestern reservoirs had very low dissolved oxygen concentrations in the hypolimnion at time of sampling.

Crustacean zooplankton in northwestern reservoirs was studied by Bonetto *et al.* (1976). Large

Table 1. Mean and range for the limnological characteristics measured in Argentinian lakes and reservoirs ($n = 97$). #ATE and #NOATE indicate lakes and reservoirs with and without Atherinidae fish; A, lake area; ZMEAN, mean depth; SDT, Secchi disk transparency; TEMP, mean annual air temperature; K20, water conductivity at 20 °C; TP, total phosphorus; CHL, total chlorophyll; TN/TP, total nitrogen to total phosphorus ratio; CPUE, total catch per unit effort; CPUEA, catch per unit effort of Atherinidae; MAZOO, macrozooplankton biomass; MIZOO, microzooplankton biomass; MASI, mean macrozooplankton weight; DOb, bottom dissolved oxygen concentration at sampling.

Variable	#ATE ($n = 58$)		#NOATE ($n = 39$)	
	Mean	Range	Mean	Range
A (km^2)	94.4	0.09–1984	35.1	0.30–580
ZMEAN (m)	19.4	1.1 –157	40.6	0.7 –166
SDT (m)	2.7	0.15–19.0	8.0	0.17–14.5
TEMP (°C)	14.1	4.0 –20.4	7.0	3.0 –16.3
k20 (μS)	2315	27–41000	368	20–3100
TP (μg l^{-1})	120	1–1288	43	2–350
CHL (μg l^{-1})	36.7	0.16–405	6.0	0.21–113
TN/TP (molar ratio)	70	9–335	118	15–273
CPUE (kg/experimental gill nets night)	92.4	1.9 –505	42.5	0.0 –330
CPUEA (kg/experimental gill nets night)	53.2	0.1 –435	–	–
MAZOO (μg dry weight l^{-1})	289.2	2.4 –2156	286.0	0.5 –3432
MIZOO (μg dry weight l^{-1})	74.3	0.44–705	38.5	0.16–1165
MASI (μg dry weight)	2.42	0.80– 4.53	4.27	0.64–16.30
DOb (mg l^{-1})	5.88	0.01–12.20	8.71	2.80–11.10

cladocerans were not highly abundant in summer. The most commonly observed species in the three reservoirs in summer, were the copepods *Notodiaptomus incompositus* and *Acanthocyclops robustus*, and the cladocerans *Diaphanosoma brachyurum* and *Ceriodaphnia dubia* (Bonetto *et al.*, 1976). *Bosmina obtusirostris*, *Ceriodaphnia dubia* and *Diaphanosoma brachyurum* were the most commonly observed cladocerans in the Pampa Plain lakes and daphnids were observed only in some lakes (Ringuelet *et al.*, 1965). *Notodiaptomus incompositus* and *Acanthocyclops michaelseni* were common in most of the lakes. *Boeckella michaelseni* was the dominant species in Tierra del Fuego lakes (Mariazzi *et al.*, 1987). The cladoceran *Bosmina huaronensis* was common in the Patagonian plateau lakes as well as *Bosmina chilensis* in Patagonian Andes lakes (Menu Marque & Marinone, 1986). *Ceriodaphnia quadrangula* is common to deep glacial, and to shallow lakes east of the Andes; the large *Daphnia middendorffiana* and copepods of the genus *Pseudoboeckella* were present in the latter type of lakes. The copepods of the genus *Boeckella* are dominant in both the Patagonian Plateau and the Andean lakes (Menu Marque & Marinone, 1986; Margalef, 1983).

The Pampa Plain lakes are the only Argentinian lentic systems with a highly diverse fish community (Ringuelet, 1975). Most of the glacial lakes in Patagonia and Tierra del Fuego had been successfully colonized by introduced salmonids (Baigún & Quirós, 1985; Quirós, 1987). *Basilichthys bonariensis* (Argentinian silverside), native to the Pampa Plain, was also introduced into the centralwestern and northwestern reservoirs. *Basilichthys microlepidotus* (Patagonian silverside) is common to most Patagonian lakes except for the Tierra del Fuego lakes. Both species of the family Atherinidae have been reported as zooplanktivorous and microbenthophagous fishes (Ringuelet *et al.*, 1967). Piscivory is not widespread in Argentinian lakes and reservoirs. Species of the genera *Salmo* and *Salvelinus*, often piscivorous as adults, are relatively common in southern glacial lakes, but rainbow trout (*Salmo gairdneri*) was usually the most common species

there. *Hoplias malabaricus* a piscivorous fish in Pampa Plain lakes was only relatively abundant at sampling in half of those lakes (Quirós *et al.*, 1988).

Materials and methods

Lakes and reservoirs were visited once during mid-summer, except for 6 sites situated on the Patagonian Plateau which were studied once during each season over the course of two years; summer data for 97 sites are summarized here. Sampling stations were situated over the deepest part of the basin for lakes, and 500 m to 2 km from the impounding dam for reservoirs. Lake surface area (A, km^2), mean depth (ZMEAN, m) and mean annual air temperature (TEMP, $^\circ$C) were obtained from Quirós *et al.* (1983, 1988). Secchi disk transparency (SDT, m) was determined with a 25 cm diameter, black and white disk. Chlorophyll (CHL, μg l^{-1}), total phosphorus (TP, μg l^{-1}), total organic nitrogen (TON, μM), nitrate and nitrite were determined from samples collected at a depth of 0.5 m. Nutrients were determined according to American Public Health Association *et al.* (1975) and Golterman *et al.* (1978). Chlorophyll (uncorrected for phaeopigments) was measured according to Stauffer *et al.* (1979).

Zooplankton samples were collected using a 53 μm mesh net with an opening of 0.40 m. Tows were made from 0.5 m above bottom to the surface in shallow lakes and from 50 m below the surface in deeper systems; in either case, only epilimnetic waters were sampled. A 100% capture efficiency was assumed. Macrozooplankton biomass (MAZOO, μg dry weight l^{-1}) and microzooplankton biomass (MIZOO, μg dry weight l^{-1}) were calculated from size and abundance data (Menu Marque & Marinone, 1986; Quirós *et al.*, 1988). Post nauplier copepods and cladocerans were considered to be MAZOO, and rotifers and copepod nauplii as MIZOO.

Fish samples were collected using nylon gill nets. The net was composed of nine 50 m panels of 42, 51, 60, 70, 78, 105, 120, 140 and 170 mm

stretch mesh. A measure of relative fish biomass was made on the basis of mean weight in kilograms of all fish caught per overnight set for the gang of gill nets. Catch was standardized as the sum of mean weights of fishes in 100 m² of each mesh, for the nine panels (CPUE, kg/night standard gill nets) (Quirós, in press).

Two lakes with incomplete data for zooplankton and one acidic lake (Quirós, 1988) were excluded from the analysis. Sites with high inorganic turbidity were also excluded as outliers (Quirós, 1989a). Lakes and reservoirs were sampled during mid-summer but observations were not simultaneous. Notwithstanding, a synchronic view was assumed here.

Data analysis was made by simple and partial correlation, and simple and stepwise multiple regression analyses. The Number Cruncher Statistical System (NCSS) for the IBM-PC (Hintze, 1985) statistical package was used. Variables related to climate, morphometry, nutrient content, and biological standing stocks were used as potential regressors for CHL-TP residuals. Dissolved oxygen concentration at 0.50 m above the bottom (DOb, mg l^{-1}) was used as a rough estimate of oxygen conditions at the sediment-water interface, and the mean depth to Secchi depth ratio (ZMEAN/SDT) as a rough surrogate of submersed macrophyte development. The collection frequency of atherinids (%ATE = CPUEA/CPUE) was used as a rough surrogate of fish community composition. Mean macrozooplankton (MASI, μg dry weight) and mean microzooplankton body size (MISI, μg dry weight) for each lake were estimated by mean individual body weight as the ratio between biomass (μg dry weight l^{-1}) and abundance (number of individuals l^{-1}).

When sharp changes (discontinuous or threshold-like effects) on CHL-TP residuals were detected, different data subsets for the independent variable were analyzed. For comparison between regression models a general F-testing was used (Weisberg, 1980). Stepwise multiple regression analysis, using variables which were both internal and external of the aquatic ecosystem, was used to reveal patterns of residual

CHL-TP variability in data. TEMP, ZMEAN and TN/TP ratio were shown to explain residual CHL variability (Quirós, 1988), but those regressor variables covary strongly between each other and with nutrient variables (e.g. TP or TON). Here I present the 'best' multivariate models obtained using nutrient concentration and other regressor variables which have a relatively low covariation with nutrients. Therefore, significant variables (partial F-value > 4), but only those with low covariation with previously included regressor variables (Weisberg, 1980: 174), were forced into the regression equation. In order to stabilize the variance, all the variables except TEMP, DOb, and %ATE were log-transformed. %ATE, as a proportion, was transformed to arc-sine (Draper & Smith, 1981).

Results

The Argentinian lake and reservoir data base is very heterogeneous (Table 1) and climatic, morphometric, nutrient and standing crop characteristics covary strongly (Table 2) (Quirós, 1989a, 1989b). TP represented the most important variable explaining CHL variability (Quirós, 1988, 1989a) (Fig. 2a, see also Eq. 1, Table 3). The residuals of the CHL-TP regression equation were not directly related to predicted CHL, but larger positive and negative residuals were observed at intermediate and higher phosphorus concentrations respectively (see Fig. 2b). However, when residuals were analyzed against other possible independent variables certain regularities were observed (Fig. 3): a) most lakes without silversides (%ATE = 0) showed negative deviations from the regression equation while all the lakes with essentially exclusively silversides (%ATE > 0.98) had positive deviations, b) most of the lakes with MASI $\leq 1.5\,\mu$g deviated positively, while those with MASI $> 3.6\,\mu$g deviated negatively, c) lakes with DOb ≤ 2.0 mg l^{-1} deviate positively from the CHL-TP regression, and d) most of the residuals for lakes with ZMEAN/SDT < 1.3 were negative (Fig. 3). None of these variables (DOb, %ATE, MASI or

Table 2. Matrix of correlation coefficients between limnological variables for 97 Argentinian lakes and reservoirs. Chlorophyll (CHL, μg l^{-1}), mean annual air temperature (TEMP, C), mean depth (ZMEAN, m), conductivity at 20 °C (K20, μS), total phosphorus (TP, μg l^{-1}), total organic nitrogen (TON μM), total nitrogen to total phosphorus ratio (TN/TP, molar basis), frequency of atherinids in the samples (CPUEA/CPUE), mean macrozooplankton body weight (MASI, μg dry weight), mean microzooplankton body weight (MISI, μg dry weight), bottom dissolved oxygen at sampling (DOb, mg l^{-1}), macrozooplankton biomass (MAZOO, μg dry weight l^{-1}), Secchi disk transparency (SDT, m). t-test, a $p < 0.0001$, b $p < 0.001$, c $p < 0.01$.

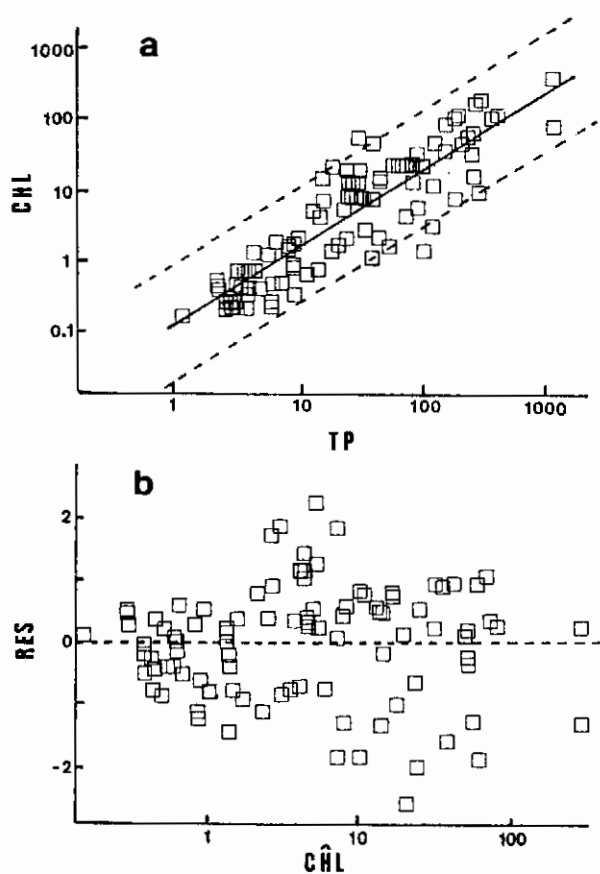| Variable	CHL	TEMP	ZMEAN	K20	TP	TON	TN/TP	%ATE	MASI	MISI	DOb	MAZOO	ZMEAN/SDT
CHL	1	0.74 a	0.78 a	0.69 a	0.88 a	0.85 a	− 0.67 a	0.56 a	− 0.26	0.06	− 0.39 b	0.65 a	0.10
TEMP		1	− 0.55 a	0.65 a	0.64 a	0.59 a	− 0.51 a	0.59 a	− 0.38 b	− 0.01	0.65 a	0.39 b	0.17
ZMEAN			1	− 0.69 a	− 0.85 a	− 0.86 a	0.58	− 0.28 c	0.01	− 0.22	0.16	− 0.74 a	0.48 a
K20				1	0.74 a	0.78 a	− 0.44 a	0.49 a	− 0.11	0.24	− 0.23	0.58 a	0.10
TP					1	0.93 a	− 0.81 a	0.38 b	− 0.04	0.21	− 0.26 c	0.73 a	− 0.11
TON						1	− 0.53 a	0.36 b	− 0.03	0.16	− 0.22	0.71 a	− 0.18
TN/TP							1	− 0.29 c	0.04	− 0.19	0.24	0.54 a	0.03
%ATE								1	− 0.34 b	− 0.04	− 0.37 b	0.26	0.29 c
MASI									1	0.40 a	0.17	0.27 c	− 0.33 c
MISI										1	0.03	0.46 a	− 0.26 c
DOb											1	− 0.11	− 0.21
MAZOO												1	− 0.22
ZMEAN/SDT													1

Fig. 2. a. Relation between chlorophyll (CHL, μg l^{-1}) and total phosphorus (TP, μg l^{-1}) for 97 lakes and reservoirs. Broken lines show 95% confidence limits. b. Relation between CHL-TP residuals (RES) and predicted chlorophyll (CHL, μg l^{-1}) for 97 sites.

ZMEAN/SDT) were highly correlated with TP. TEMP was highly and positively correlated with CHL-TP residuals, but it covaried with DOb, %ATE and MASI (Table 2). Other variables positively related to residuals were MIZOO, CPUEA, TON and TN/TP, however all covaried strongly with TP.

The discontinuous effects of MASI, %ATE and DOb on variability in the CHL residuals were studied using subsets of data such as defined by the CHL-TP residual analysis (Fig. 3). Three subsets were considered for each variable: a) MASI $\leqslant 2\ \mu$g, > 2 and $\leqslant 3.6\ \mu$g, and $> 3.6\ \mu$g; b) DOb $\leqslant 2$ mg l^{-1}, > 2 and $\leqslant 7$ mg l^{-1}, and > 7 mg l^{-1}, and c) %ATE equal 0, > 0 and $\leqslant 0.20$, and > 0.20. In all the cases, CHL-TP regressions were highly significant ($P < 0.001$). The CHL-TP equations for the MASI, DOb or %ATE subsets provided a better fit than did the total coincident model ($n = 97$, Eq. 1 in Table 3) ($P < 0.01$, $F = 3.75$, 4.91 and 10.61 for MASI, DOb and %ATE subsets respectively). However, testing for differences between models for MASI < 2 and $3.6 \geqslant$ MASI > 2, $7 \geqslant$ DOb > 2 and DOb > 7, or %ATE > 0.20 and $0.20 \geqslant$ %ATE > 0, against their respective coincident model ($n = 75$, 83 and 58 for MASI, DOb and %ATE data respectively) did not yield positive results ($F = 0.86$, 0.39 and 0.39 for MASI, DOb and %ATE subsets respectively). Therefore, only two
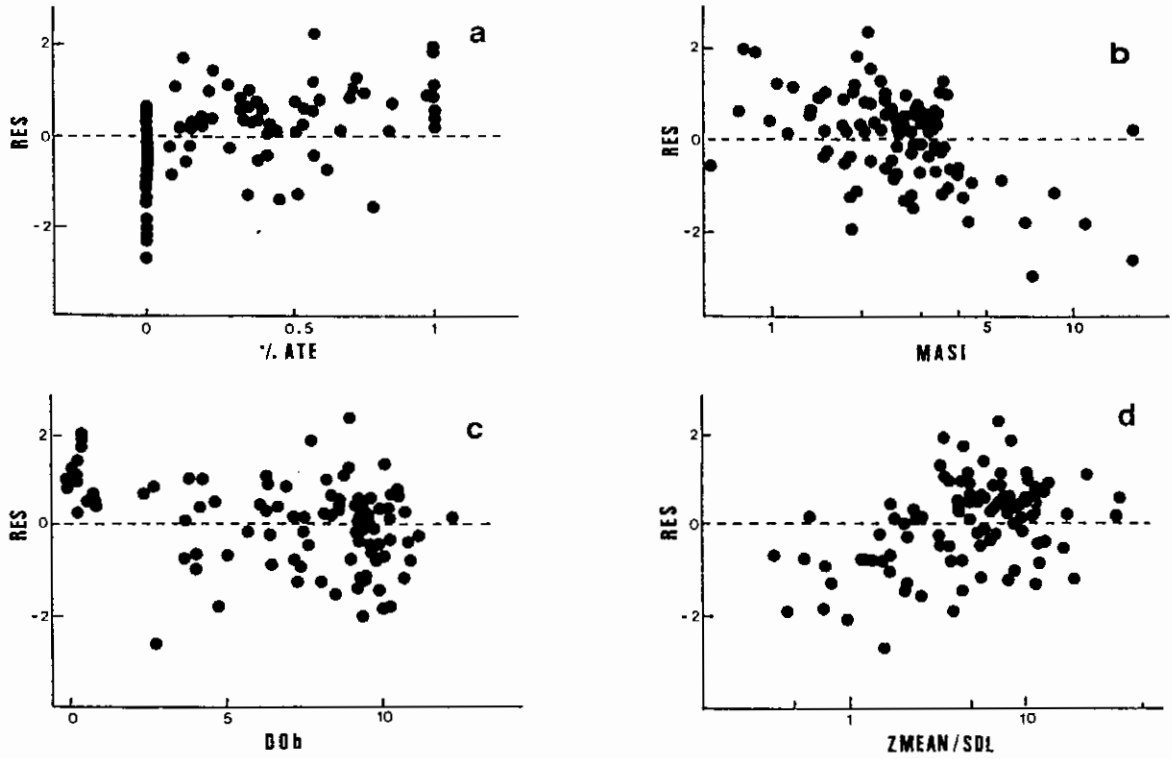
Fig. 3. a. Relation between CHL-TP residuals and frequency of atherinids at sampling (%ATE) arc-sin transformed. b. idem for mean macrozooplankton body weight (MASI, μg dry weight) loge-transformed. c. idem for bottom dissolved oxygen (DOb, mg l⁻¹). d. idem for mean depth to Secchi disk transparency ratio (ZMEAN/SDT) loge-transformed.

Table 3. Chlorophyll (CHL, μg l⁻¹) on total phosphorus (TP, μg l⁻¹) regression models for different data sets. MASI, mean macrozooplankton body weight (μg dry weight); DOb, bottom dissolved oxygen (mg l⁻¹); %ATE, frequency of atherinids at sampling. Intercept (a), slope (b), standard error of slope (SE), coefficient of determination (r^2), and root mean square error of regression (RMSE) are presented. All regressions with $P < 0.001$ (*F*-test).

Eq.	*n*	Limits	TP range	Regression coefficients			r^2	RMSE
				a	b	SE		
1	97	Total data	1–1288	− 1.943	1.08	0.06	0.78	0.953
2	75	MASI ⩽ 3.6	1–1288	− 1.879	1.12	0.06	0.82	0.839
3	22	MASI > 3.6	2–398	− 2.646	1.10	0.14	0.75	1.093
4	14	DOb ⩽ 2	15–398	− 0.338	0.89	0.13	0.80	0.505
5	83	DOb > 2	1–1288	− 2.045	1.06	0.06	0.80	0.920
6	58	%ATE > 0	1–1288	− 1.432	1.04	0.07	0.80	0.854
7	39	%ATE = 0	2–350	− 1.916	0.84	0.08	0.74	0.728
8	57	TP ⩽ 30	1–30	− 2.593	1.44	0.11	0.75	0.767
9	40	TP > 30	31–1288	− 2.030	1.06	0.20	0.44	1.104

data subsets for each variable are presented here (Table 3). The results show that a unique CHL-TP regression model is not adequate; significant differences were observed between Eq. 2 and 3 (see Table 3) for MASI $\leq$ 3.6 and MASI > 3.6 μg respectively ($F = 6.83, P < 0.01$), as well as between Eq. 4 and 5 for DOb $\leq$ 2 mg L^{-1} and DOb > 2 mg L^{-1} ($F = 9.51, P < 0.001$), and between Eq. 6 and 7 for %ATE > 0 and %ATE = 0 ($F = 21.06, P < 0.0001$). On the other hand, there were no significant differences between slopes for the MASI ($F = 0.23$, $P = 0.34$) and DOb ($F = 0.30$, $P = 0.39$) data subsets, but the difference was significant between slopes for %ATE subsets ($F = 3.55$, $P < 0.05$). Similar results were obtained when analysis of covariance was performed, over a similar range of the independent variable TP.

Simultaneous condition for internal variables

To study the effect of extreme values for MASI, DOb and %ATE on CHL-TP regressions, three data subsets were considered (see Table 4). When the total coincident model (Eq. 1, Table 3) was compared against the CHL-TP regressions presented in Table 4 (Eqs 10 to 12), highly significant differences were observed ($F = 12.15, P < 0.001$). The CHL-TP relationships were also different ($F = 11.60$, $P < 0.0005$) between lakes with DOb > 2, MASI > 3.6 and %ATE = 0 (Eq. 12), and the remainder lakes except those with DOb $\leq$ 2, MASI $\leq$ 3.6 and %ATE > 0 (Eq. 11). The sites included in Eq. 10 (Table 4) are also included in Eq. 4 (Table 3, DOb $\leq$ 2 condition). Because of that, the latter is more representative for lakes with the conditions stated in Table 4 for Eq. 10 than for lakes with just anoxic, sediment-water interfaces.

MASI was significantly different between lakes with (#ATE, $n = 58$) and without (#NOATE, $n = 39$) atherinids ($F = 15.07, P < 0.0001$). There were no significant differences for MASI between Pampa Plain and centralwestern and northwestern sites ($F = 1.67, P > 0.80$) where silversides were usually abundant. On the other hand, MASI was significantly higher (3.1 μg) in the southern glacial lakes, where silversides were absent or very low at sampling, when compared with Pampa Plain (2.6 μg) and centralwestern and northwestern sites (2.2 μg) ($F = 6.94$, $P < 0.01$). There were no lakes with both atherinid fish and mean macrozooplankton weight above 4.6 μg (Fig. 4). Moreover, most of the lakes with MASI > 4.6 μg ($n = 8$) also had no fish or very low fish at sampling, a high turbidity or a high development of submersed macrophytes; most of these systems are situated in the Patagonian Plateau with TEMP below 10 °C.

Table 4. Chlorophyll (CHL, μg l^{-1}) on total phosphorus (TP, μg l^{-1}) regression models for different data sets. DOb, bottom dissolved oxygen (mg l^{-1}); MASI, mean macrozooplankton body weight (μg dry weight); %ATE, frequency of atherinids. Intercept (a), slope (b), standard error of slope (SE), coefficient of determination (r^2), and root mean square error of regression (RMSE) are presented. All regressions with $P < 0.001$ (F-test).

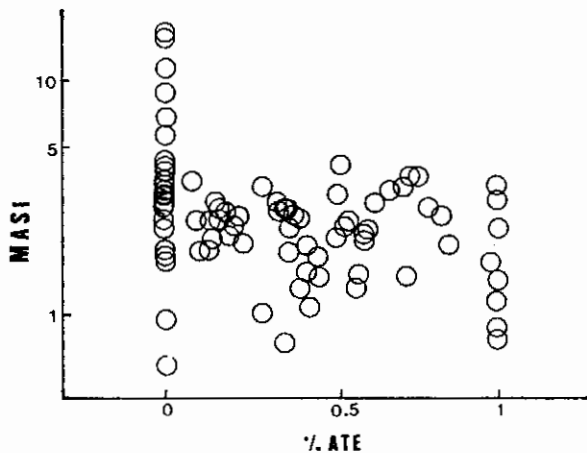| Eq.	n	Limits	TP range	Regression coefficients			r^2	RMSE
				a	b	SE slope		
10	13	DOb $\leq$ 2, MASI $\leq$ 3.6, %ATE > 0.	15–320	-0.569	0.96	0.17	0.74	0.517
11	69		1–1288	-1.963	1.10	0.06	0.85	0.809
12	15	DOb > 2, MASI > 3.6, %ATE = 0.	2–294	-2.236	0.84	0.14	0.72	0.855

Fig. 4. Relation between mean macrozooplankton body weight (MASI, μg dry weight) and frequency of atherinids (%ATE) for total data ($n = 97$).

Therefore, Eq. 12 is also representative of those conditions.

Multiple regression models

In multiple regression analysis of the total data set ($n = 97$), successive incorporation of %ATE and MASI improved the explained variation in CHL, from 77% to 83 and 86% respectively. Further inclusion of DOb into the equation did not yield a further improvement in predictive ability, but diminished the residuals (Eq. 13, Table 5). A similar result was obtained for ZMEAN/SDT, but its covariation with water transparency prevents its incorporation into multiple regression equation. Frequency of atherinids was not a significant variable to explain CHL-TP residual variation in lakes with %ATE > 0 (as shown in Eq. 14, Table 5). This result could support the discontinuous effect of zooplanktivorous fish on variability in CHL residuals. Furthermore, dissolved oxygen at the sediment-water interface was not significant in lakes with %ATE = 0. This result is not surprising because there are no lakes in the total data base both without atherinids and with DOb $\leqslant 2.0\,\mu$g L^{-1}.

The effect of 'trophic state' on CHL-TP regressions and variability in their residuals was studied using subsets on the TP data base. Results for the TP $\leqslant 30\,\mu$g l^{-1} and TP > 30 μg l^{-1} subsets are presented in Table 3 (Eqs 8 and 9). Frequency of atherinids and mean macrozooplankton size were significant in explaining variability

Table 5. Chlorophyll (CHL, μg l^{-1}) multiple regression models for total data ($n = 97$), for data subsets with (#ATE, $n = 58$) and without (#NOATE, $n = 39$) atherinids, and with total phosphorus below (TP $\leqslant 30$, $n = 57$) or above (TP > 30, $n = 40$) 30 μg l^{-1}. Not included variables: *, significant but high covariation; **, significant and low covariation; ns, no significant. Intercept, regression coefficients (standard error) for independent variables, determination coefficient (R^2), and root mean square error (RMSE), are presented. %ATE, frequency of atherinids at sampling (CPUEA/CPUE); MASI, mean macrozooplankton body weight (μg dry weight); DOb, dissolved oxygen at the sediment-water interface (mg l^{-1}); TN/TP, total nitrogen to total phosphorus ratio; ZMEAN/SDT, mean depth to Secchi transparency ratio.

	Total data	#ATE	#NOATE	TP $\leqq$ 30	TP > 30
Equation	13	14	15	16	17
n	97	58	39	57	40
Intercept	− 0.923 (0.311)	− 0.410 (0.344)	− 1.529 (0.303)	− 1.833 (0.390)	− 1.742 (0.794)
TP	0.959 (0.052)	1.048 (0.062)	0.869 (0.080)	1.279 (0.109)	0.955 (0.152)
%ATE	0.670 (0.178)	ns	–	0.612 (0.234)	0.859 (0.261)
MASI	− 0.561 (0.151)	− 0.718 (0.239)	− 0.375 (0.192)	− 0.638 (0.281)	− 0.511 (0.196)
DOb	− 0.057 (0.024)	− 0.077 (0.026)	ns	ns	ns
TN/TP	*	*	ns	ns	*
ZMEAN/SDT	**	**	ns	ns	*
R^2	0.864	0.845	0.768	0.809	0.685
RMSE	0.754	0.722	0.739	0.682	0.848
F-test	145.68	100.37	59.48	74.85	26.03
P <	0.001	0.001	0.001	0.001	0.001

in CHL-TP residuals for both oligo-mesotrophic and eutrophic-hypertrophic lakes (Eqs 16 and 17, Table 5), but those effects appear to be more marked in eutrophic-hypertrophic systems (compare Eq. 8 with 16 and Eq. 9 with 17). DOb did not yield significant improvement when introduced to either Eq. 16 or 17. This result also supports the discontinuous effect of DOb on variation in CHL-TP residuals.

Covariation among regressor variables was not a problem in multiple regression equations, as shown by the fact that partial regression coefficients for TP in Eqs 13 to 17 (Table 5) have almost the same value as in simple regressions (Eq. 1, Eqs 6 and 7, and Eqs 8 and 9 for total data, %ATE and TP data subsets respectively). Macro (MAZOO) and microzooplankton (MIZOO) biomass, as well as total fish (CPUE) and atherinid biomass (CPUEA) were highly and positively related to TP (Quirós, 1989b). MAZOO and MIZOO were also positively related to CHL residuals after TP, DOb, %ATE and MASI had been controlled ($r = 0.22$, $P < 0.05$, and $r = 0.29$, $P < 0.01$ respectively). Similar results were obtained for MIZOO and MAZOO in all analyzed subsets (Table 5). For MAZOO, sites with atherinids were an exception: there was no significant relationship between variability in CHL residuals and macrozooplankton biomass.

Discussion and conclusions

Negative effects of large herbivorous zooplankton on phytoplankton have been shown in whole-lake studies and a number of experimental enclosure studies (Hrbacek et al., 1961; Shapiro & Wright, 1984; Northcote, 1988, for a review), as well as individual lake studies (Edmonson & Litt, 1982; see Shapiro & Wright, 1984, for a review). Results from multiple lake comparisons showed the influences of large zooplankton on CHL-TP relationships, but its effect is weak (Pace, 1984). The present results show clearly, that lakes with mean macrozooplankton individual weights above 4.0 μg, deviate negatively from CHL-TP regres-

sions, and also that any negative effect of total macrozooplankton biomass should be rejected for Argentinian lakes and reservoirs.

Fish effects on phytoplankton at different time and space scales have been recently reviewed by Northcote (1988) and the role of fishes in the regulation of phosphorus availability in individual lakes was studied and reviewed earlier by Nakashima & Leggett (1980). Results from Argentinian lakes indicate positive relationship between variability in CHL residuals and frequency of atherinids at sampling. Macrozooplankton and atherinid biomass was also positively related to CHL-TP residuals, but they covaried strongly with TP. Two hypotheses have been proposed to explain the mechanism of phytoplankton enhancement by zooplanktivorous fish: a) fish predation reduces zooplankton grazing pressure on phytoplankton and b) zooplanktivorous fish increase nutrient cycling and thereby enhance phytoplankton (Northcote, 1988). However, predation and grazing, as well as nutrient cycling, are processes, and are expressed in individual lakes. On the other hand, when time is fixed, a CHL-TP regression is just a comparison among lakes; it represents a projection of a multiple variable state space, where there is no causality at all (Quirós, 1989a). As was stated by D'Elia et al. (1986), in situ recycling cannot increase the standing stocks of organic matter that are ultimately controlled by nutrient concentration. Therefore, a hypothesis for macrozooplankton and fish effects on CHL-TP regression residuals, might be also related to the relative increase of P bioavailability in TP with increasing levels of predation and foraging activity or perhaps with a general increase of metabolic activity and cycling.

Phosphorus is released from the sediments when the sediment surface has become anoxic. Furthermore, direct relationships between lake productivity and P release rates, and high availability of P release from internal sources to phytoplankton have been shown (Nürnberg et al., 1986; Nürnberg, 1988). My results showed that all the lakes with low dissolved oxygen levels at the sediment-water interface deviate positively

from the CHL-TP regression. How much it was related to an increase of P release rates or to a relative increase of P bioavailability is worthy of further attention.

The inclusion of mean macrozooplankton size and frequency of zooplanktivorous fish in CHL regression models shows the importance of those variables in improving the explained variability in CHL. These variables also have the advantage of having a relatively low covariation with nutrient levels and biological standing crops. Those findings, in addition to the observation of greater intercepts for the CHL-TP regression lines for lakes with mean macrozooplankton size below 3.6 μg, or lakes with zooplanktivorous fishes, support the findings of complementary and also partially independent effects of mean macrozooplankton size and zooplanktivorous fish variables on phytoplankton standing stock, in comparative lake studies.

Effects of lake productivity on macrozooplankton size were not significant, but size was negatively related to abundance of atherinids and ZMEAN/SDT (Table 2). For the total data set ($n = 108$), including the turbid lakes, MASI was also positively related to inorganic turbidity (Quirós data files). Although mean macrozooplankton size was below 4.6 μg for lakes with atherinids, it was not related to total relative fish biomass (CPUE); lakes with MASI > 4.6 μg had from no fish to high fish biomass. The relationships between fish predation on large herbivores and invertebrate predators, macrozooplankton size, and macrozooplankton refuges in turbid lakes, or lakes with high standing crop of submersed macrophytes, are worthy of further attention for the Argentinian lakes.

A wide range of limnological characteristics was sampled, but the obvious limitations of fish and zooplankton sampling, lack of data on zooplankton community internal structure, and the sparseness of data for each lake prevent wide generalizations. In summary, the effects of macrozooplankton size, dissolved oxygen levels at the sediment-water interface and zooplanktivorous fish abundance on CHL-TP residual variability were shown to be statistically significant in a comparative lake study. As expected, lakes with mean macrozooplankton body weight below 3.6 μg dry weight, an anoxic sediment-water interface or zooplanktivorous fish, tended to have the highest phytoplankton standing stock after nutrient effects had been taken into account. The results also suggest that the abundance of submersed macrophyte is negatively related to CHL-TP residuals. Scale effects, from heterogeneous to the most homogeneous sets of lakes should be further investigated.

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