Empirical relationships between nutrients, phyto- and zooplankton and relative fish biomass in lakes and reservoirs of Argentina

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Introduction

Comparative studies of lakes in the global temperate zone has shown total phosphorus is related to phytoplankton biomass and to chlorophyll (SAKAMOTO 1966, DILLON & RIGLER 1974, SCHINDLER et al. 1978, among others), to macrozooplankton biomass (HANSON & PETERS 1984, PACE 1986, YAN 1986), to microzooplankton biomass (PACE 1986), to macrobenthos biomass (HANSON & PETERS 1984, see also RASMUSSEN & KALFF 1987), to fish biomass (HANSON & LEGGETT 1982) and to bacteria (BIRD & KALFF 1984). Significant direct relationships between biological standing stocks at different trophic levels were also shown in some instances. For example macrozooplankton-chlorophyll or phytoplankton biomass (MCCAULEY & KALFF 1981, ROGNERUD & KJELLBERG 1984, see also PACE 1986), total zooplankton biomass – Carlson's chlorophyll-based index (BAYS & CRISMAN 1983). Fish yield was also shown to be strongly correlated with chlorophyll (OGLESBY 1977, JONES & HOYER 1982), and relative fish biomass as estimated from gillnetting (CPUE), is shown to be directly related to chlorophyll in a heterogeneous set of lakes and reservoirs (QUIROS 1990). However, a growing concern about the results from comparative lake studies for lakes with different kinds of trophic interactions (CARPENTER et al. 1985, CARPENTER & KITCHELL 1988) encourages studies that compare empirical relationships between nutrients and biological standing stocks for sets of lakes with different fish community composition.

The fish species of special interest in this study are facultative zooplanktivorous fish of the Atherinidae family such as *Basilichthys bonariensis* and *B. microlepidotus*, both species are widespread in Argentinian freshwaters. The former species, native to the Pampa Plain lakes, was introduced into lakes and reservoirs of the centralwestern and northwestern arid regions (Fig. 1). The latter species is native to the Patagonian Plateau and Southern Andes lakes (RINGUELET et al. 1967). The primary interest of this study was to evaluate the strength of the relationships between nutrients, chlorophyll, microzooplankton and macrozooplankton biomass, and relative fish biomass for lakes and reservoirs of Argentina, and to compare the resulting relationships for both kinds of lakes, with and without Atherinidae fish.

Lakes and reservoirs studied

The lakes and reservoirs studied are located between the 25th and 55th latitudes south throughout the central-western and northwestern arid regions of Argentina, the Pampa Plain, the Patagonian Plateau, the Patagonian Andes and Tierra del Fuego (Fig. 1). Surface lake area ranged from 0.30 to 816 km^2, and mean depth from 0.70 to 116 m (Table 1). The deepest lakes are situated in the Patagonian Andes and Tierra del Fuego. All lakes on the Pampa Plain are ponds or very shallow lakes. Mean annual air temperatures ranged from 3.0 to 20.4 °C and elevations from 2 to 3,250 m (Table 1). Patagonian and

Table 1. Mean and range for the limnological characteristics measured in 65 Argentinian lakes and reservoirs with (#ATE, n = 38) and without (#NOATE, n = 27) atherinids. A, lake area; Z$_{mean}$, mean depth; TEMP, mean annual air temperature; SDL, Secchi disk depth; K20, water conductivity at 20 °C; TP, total phosphorus; TON, total organic nitrogen; TN/TP, total nitrogen to total phosphorus ratio; CHL, total chlorophyll; MIZOO, microzooplankton biomass; MAZOO, macrozooplankton biomass; CPUEA, catch per unit effort of atherinids; CPUE, total catch per unit effort.

| Variable	#ATE		#NOATE	
	Mean	Range	Mean	Range
A (km^2)	81.7	1.4 – 816	46.6	0.30– 580
Z$_{mean}$ (m)	24.3	1.1 – 157	55.6	0.7 – 166
TEMP (°C)	13.0	4.0 – 20.4	5.6	3 – 16.3
SDL (m)	3.3	0.15– 19	9.3	0.17– 14.5
K20 (μS)	1503	27 –9200	131	20 – 1250
TP (mg·m^{-3})	105	1 –1250	29	2 – 350
TON (μM)	118	6 – 762	43	5 – 434
TN/TP (molar ratio)	79	23 – 335	136	26 – 273
CHL (mg·m^{-3})	37.4	0.16– 405	6.9	0.21– 113
MIZOO (μg dry weight ·l^{-1})	80.0	0.44– 704.7	46.5	0.16–1165
MAZOO (μg dry weight ·l^{-1})	349.0	2.4 –2156	332.1	0.46–3432
CPUEA (kg/experimental gillnets · night)	58.5	0.2 – 435.2	–	–
CPUE (kg/experimental gillnets · night)	110.0	2.9 – 505.1	41.8	1.2 – 329.5
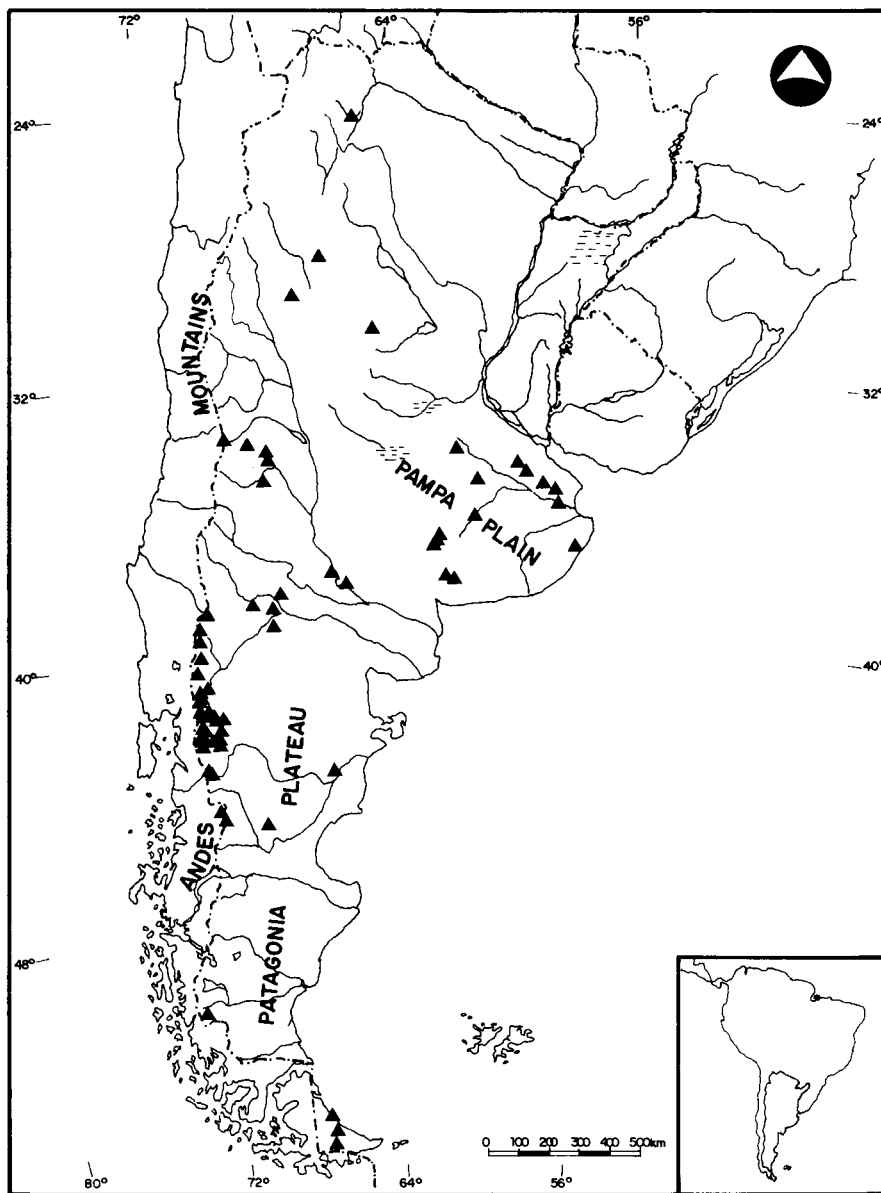
Fig. 1. Argentina showing the location of the 65 lakes and reservoirs studied.

Tierra del Fuego Andes lakes are typically ultraoligotrophic or oligotrophic. Most of the centralwestern and northwestern reservoirs and Patagonian Plateau lakes ranged from mesotrophic to eutrophic. Lake trophy of the Pampa Plain lakes ranged from eutrophic to hypertrophic. Most of the fish species of the northwestern and centralwestern reservoirs have been introduced from outside Argentina or from other river basins in Argen-

tina. A majority of the glacial lakes in Patagonia and Tierra del Fuego have been successfully colonized by salmonids (BAIGUN & QUIROS 1985, QUIROS 1987). The Pampa Plain lakes are practically the only Argentinian lakes with a relatively high fish community diversity (RINGUELET 1975) and most of the fish sampled were species native to the Pampa Plain. *Basilichthys bonariensis* (Argentinian silverside) is common to most lakes and re-

servoirs in the Pampa Plain and centralwestern and northwestern arid regions. *Basilichthys microlepidotus* (Patagonian silverside) is common to most Patagonian lakes except for those in Tierra del Fuego. Both species of the Atherinidae family have been reported as zooplanktivorous and microbenthophagous fish (RINGUELET et al. 1967). Piscivory is not widespread in Argentinian lakes and reservoirs. *Salmo trutta, Salvelinus fontinalis, Salmo salar* and *Salvelinus namaycush* were moderately abundant in some southern glacial lakes, and *Salmo gairdneri* is usually the most abundantn species there. *Hoplias malabaricus*, a piscivorous fish in the Pampa Plain lakes was only moderately abundant in about half of those lakes (QUIROS et al. 1988). Although inverse relationships between atherinids and salmonids, and also between *Basilichthys bonariensis* and *Hoplias malabaricus* have been reported (QUIROS 1987, unpubl.), those interactions have not been fully studied yet. Further relevant morphometric, chemical and fish data were presented by QUIROS (1988, 1990) and QUIROS et al. (1988).

Materials and methods

During the summers of 1984 to 1987, 110 lakes and reservoirs of Argentina were sampled (QUIROS et al. 1988). Lakes and reservoirs were visited once, except for 6 situated on the Patagonian Plateau (Fig. 1) that were studied seasonally over the course of two years. Only data for 65 lakes and resevoirs during mid-summer are considered here (Table 1).

Lake surface areas (A, km^2), mean depths (Z$_{MEAN}$, m) and mean annual air temperatures (TEMP, °C) were obtained from QUIROS et al. (1983, 1988). For each lake, vertical profiles were obtained for temperature, dissolved oxygen, conductivity, pH and total alkalinity. In lakes <25 m, a Hydrolab surveyor system was used. Secchi disk visibility (SDL, m) was recorded with a 25 cm diameter, black and white disk. Chlorophyll (CHL, mg · m^{-3}), total phosphorus (TP, mg · m^{-3}), total organic nitrogen (TON, μm), nitrate and nitrite were determined from samples collected at 0.5 m depth. Nutrients were determined according to the American Public Health Association (1975) and GOLTERMAN et al. (1978). Chlorophyll determinations were done according to STAUFFER et al. (1979). The chlorophyll results presented here are without phaeopigment corrections. The analytical methods used have all been described previously (QUIROS 1988).

Zooplankton samples were collected with 50 m long vertical tows or from 0.5 m above the bottom to the lake surface (53-μm mesh). In both cases epilimnetic waters were usually sampled. Here a 100 % net 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, unpubl. inform.). Postnauplier copepods and cladocerans were considered in MAZOO, and rotifers and copepod nauplii in MIZOO; further details are provided in MENU MARQUE & MARINONE (1986).

Relative fish biomass (CPUE, kg/night · standard gillnets) was estimated by gillnetting. Fish samples were usually collected with an experimental nylon gillnet composed of nine 50 m panels of 42, 51, 60, 70, 78, 105, 120, 140 and 170 mm stretch mesh. In the Pampa Plain lakes, nine panels of only 25 m were used. Gillnets were set in floating gangs perpendicular to the shoreline, with the smallest mesh inshore. Floating sets were made overnight, and were usually set for a period of 12 h. A measure of relative standing stocks of fish by biomass was made on the basis of mean weight in kilograms of all fish caught per overnight set for the experimental gang of gill nets. Catch was standardized as the sum of mean weights of fish per 100 m^2 of each mesh for the nine panels. Approximately equal fish vulnerability to gill nets among all lakes was assumed here. Further details on the method of fish sampling are provided in QUIROS (1990).

Raw data for all the lakes and reservoirs studied are available from the Instituto Nacional de Investigacion y Desarrollo Pesquero (QUIROS et al. 1988).

Lakes were classified according to the presence of fish or degree of human intervention. Accordingly, I exclude here 4 lakes without fish and 7 lakes and reservoirs known to be subject to high stress levels due to human influences on fish (QUIROS 1990). Lake Indio Muerto situated in the Pampa Plain with extremely low macrozooplankton biomass and the only lake with *Mugil* sp. at sampling, was also excluded. To homogenize the data base, further screening was made for turbid lakes where the turbidity was derived from inorganic sources, lakes with low dissolved oxygen at the water-sediment interface (below 2.0 mg · l^{-1}), with Secchi readings above the mean depth (Z$_{MEAN}$/SDL <1) or with TN/TP (molar basis) below 22; all those variables were shown to be related to phytoplankton or fish after nutrient effects had been accounted for (QUIROS 1988, 1989 b, 1990).

Data study was made by simple correlation and regression analyses. The total data set (n = 65) and subsets for sites with (#ATE, n = 38) and without (#NOATE, n = 27) atherinid fish were considered. General F-testing was used for regression models comparisons (WEISBERG 1980). All the variables except mean annual air temperature (TEMP) were log$_e$-transformed in order to stabilize the variance and linearize the data.

Results

For the total data set (n = 65), phytoplankton, micro and macrozooplankton, and total fish standing stocks were highly correlated with each other and also with climatic, morphometric and nutrient related variables (Table 2). Similar results were obtained from the correlation analyses of the #ATE and #NOATE data subsets. As expected, biological standing stocks were directly related to nutrients (Fig. 2), total organic matter in the water column and mean annual air temperature, and in-

Table 2. Matrix of correlation coefficients between environmental and standing stock variables for 65 Argentinian lakes and reservoirs. Area (A, km^2), mean depth (Z$_{mean}$ m), mean annual air temperaure (TEMP, °C), Secchi disk lecture (SDL, m), conductivity at 20 °C (K20, μS), total phosphorus (TP, mg · m^{-3}), total organic nitrogen (TON, μm), total chlorophyll (CHL, mg · m^{-3}), microzooplankton biomass (MIZOO, μg dry weight · l^{-1}), macrozooplankton biomass (MAZOO, μg dry weight · l^{-1}), catch per unit effort of atherinids (CPUEA, kg/night · standard gillnets), total catch per unit effort (CPUE, kg/night · standard gillnets).

Variable	A	Z$_{mean}$	TEMP	SDL	K20	TP	TON	CHL	MIZOO	MAZOO	CPUEA	CPUE
A	1	0.43 b	−0.11	0.23	−0.10	−0.31	−0.29	−0.26	−0.31	−0.42	−0.12	−0.23
Z$_{mean}$		1	−0.64 a	0.89 a	−0.75 a	−0.91 a	−0.90 a	−0.90 a	−0.87 a	−0.81 a	−0.61 a	−0.77 a
TEMP			1	−0.78 a	0.78 a	0.70 a	0.62 a	0.76 a	0.73 a	0.54 a	0.65 a	0.50 a
SDL				1	−0.78 a	−0.93 a	−0.88 a	−0.96 a	−0.86 a	−0.73 a	−0.65 a	−0.76 a
K20					1	0.76 a	0.75 a	0.77 a	0.77 a	0.65 a	0.66 a	0.58 a
TP						1	0.94 a	0.94 a	0.87 a	0.79 a	0.63 a	0.79 a
TON							1	0.91 a	0.89 a	0.78 a	0.62 a	0.77 a
CHL								1	0.88 a	0.75 a	0.69 a	0.75 a
MIZOO									1	0.83 a	0.61 a	0.72 a
MAZOO										1	0.45 b	0.67 a
CPUEA											1	0.68 a
CPUE												1

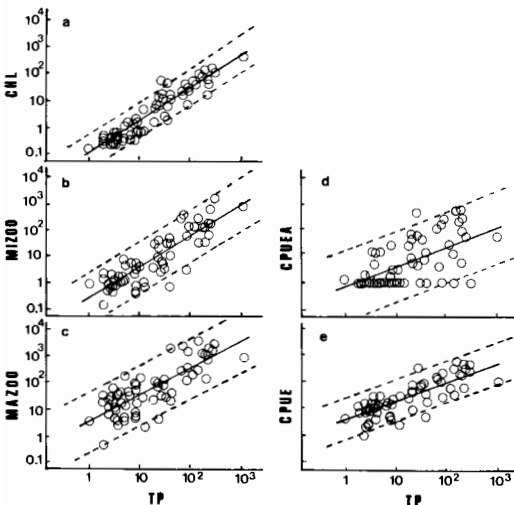t-test, a p < 0.0001, b p < 0.001, c p < 0.01.

Fig. 2. Relationships between a) chlorophyll (CHL, mg · m^{-3}); b) micro-zooplankton biomass (MIZOO, μg dry weight · l^{-1}); c) macrozoo-plankton biomass (MAZOO, μg dry weight · l^{-1}); d) Atherinidae fish relative biomass (CPUEA + 1, kg/night · standard gillnets); and e) total fish biomass (CPUE, kg/night · standard gillnets), with total phosphorus (TP, mg · m^{-3}) for 65 lakes and reservoirs.

versely related to mean depth and Secchi depth (Table 2).

After Secchi depth, TP was the second strongest estimator of CHL for total data (r^2 = 0.88), as

well as for #ATE and #NOATE data subsets (r^2 = 0.87 and r^2 = 0.84 respectively). The total coincident regression model (Eq. 1, Table 3) was not adequate when compared to regressions for #ATE and #NOATE data subsets (F = 5.56, P < 0.01).

TON was as good as CHL, TP or Z$_{MEAN}$ to explain MIZOO variability for the total data set (Table 2) and #ATE data subset, but CHL was the strongest variable related to MIZOO for #NOATE (r^2 = 0.77, P < 0.001). There were no significant differences between MIZOO regressions for lakes with and without atherinids, for example F = 0.15 (P > 0.25) for MIZOO-TP regressions. Macrozooplankton biomass (MAZOO) was more closely related to microzooplankton biomass (MIZOO) than to any other variable considered (Table 2) for all data sets. TP was as good as mean depth to explain MAZOO variability for total data and #ATE subset, but its correlation to MAZOO for #NOATE subset was lower. The total composite MAZOO regression model on TP (Eq. 7, Table 3) or TON could not be rejected (F = 1.66, P > 0.90, and F = 1.17, P > 0.75, respectively). Nevertheless, for both MAZOO-CHL and MAZOO-MIZOO regressions, a single composite model was not adequate (F = 4.31, P < 0.05, and F = 3.82, P < 0.05, respectively).

Total fish standing stock (CPUE) was more related to TP than to any other considered regressor variable for all of the data combined (r^2 = 0.63, P < 0.0001) and #NOATE data subset (r^2 = 0.60, P < 0.0001), but was slightly more closely relat-

Table 3. Simple regression models relating total chlorophyll (CHL, mg·m⁻³) microzooplankton biomass (MIZOO, μg dry weight·l⁻¹), macrozooplankton biomass (MAZOO, μg dry weight·l⁻¹), catch per unit effort of Atherinidae (CPUEA, kg/night·standard gill nets), total catch per unit effort (CPUE, kg/night·standard gill nets), total phosphorus (TP, mg·m⁻³), and total organic nitrogen (TON, μm). #ATE, lake data subset with atherinids; #NOATE, lake data subset without atherinids. Standard error of slope (SE), root mean square error of regression (RMSE) and the coefficient of determination (r^2) are presented.

Data set	n	Equation		SE	r^2	RMSE
1 Total	65	$\log_e$CHL	= −2.260 +1.20 $\log_e$TP	0.06	0.88	0.753
2 #ATE	38	$\log_e$CHL	= −1.863 +1.15 $\log_e$TP	0.07	0.87	0.746
3 #NOATE	27	$\log_e$CHL	= −2.283 +1.06 $\log_e$TP	0.09	0.84	0.637
4 Total	65	$\log_e$MIZOO	= −1.543 +1.15 $\log_e$TP	0.08	0.76	1.107
5 Total	65	$\log_e$MIZOO	= −4.069 +1.60 $\log_e$TON	0.11	0.78	1.042
6 Total	65	$\log_e$MIZOO	= 0.692 +0.91 $\log_e$CHL	0.06	0.77	1.079
7 Total	65	$\log_e$MAZOO	= 1.148 +0.97 $\log_e$TP	0.09	0.63	1.259
8 Total	65	$\log_e$MAZOO	= 3.093 +0.72 $\log_e$CHL	0.08	0.56	1.376
9 Total	65	$\log_e$MAZOO	= 2.586 +0.77 $\log_e$MIZOO	0.06	0.69	1.158
10 #ATE	38	$\log_e$MAZOO	= 2.450 +0.74 $\log_e$MIZOO	0.08	0.72	1.032
11 #NOATE	27	$\log_e$MAZOO	= 2.706 +1.03 $\log_e$MIZOO	0.14	0.69	1.211
12 Total	65	$\log_e$(CPUEA+1)	= −0.378 +0.71 $\log_e$TP	0.11	0.39	1.502
13 Total	65	$\log_e$(CPUEA+1)	= 0.941 +0.62 $\log_e$CHL	0.08	0.48	1.391
14 #ATE	38	$\log_e$(CPUEA+1)	= 0.645 +0.64 $\log_e$TP	0.13	0.39	1.321
15 #ATE	38	$\log_e$(CPUEA+1)	= 1.743 +0.53 $\log_e$CHL	0.11	0.41	1.303
16 #ATE	38	$\log_e$(CPUEA+1)	= 0.712 +0.47 $\log_e$MAZOO	0.12	0.33	1.392
17 Total	65	$\log_e$CPUE	= 1.489 +0.68 $\log_e$TP	0.07	0.63	0.884
18 Total	65	$\log_e$CPUE	= 1.582 +0.47 $\log_e$MAZOO	0.06	0.45	1.070
19 #ATE	38	$\log_e$CPUE	= 1.485 +0.54 $\log_e$MAZOO	0.09	0.52	1.017
20 #NOATE	27	$\log_e$CPUE	= 1.795 +0.31 $\log_e$MAZOO	0.09	0.30	1.031*

F-test, all $P < 0.001$, except * $P < 0.005$.

ed to Z_{MEAN} for #ATE subset (r^2 = 0.62, $P < 0.0001$). There were no significant differences between the CPUE simple regression models on TP, TON, CHL or MIZOO, for #ATE and #NOATE subsets, but a single composite model was not adequate for CPUE-MAZOO (F = 3.97, $P < 0.05$) (Table 3). For both total and #ATE data, CHL was the strongest single estimator of atherinids relative biomass (r^2 = 0.48, $P < 0.0001$, and r^2 = 0.41, $P < 0.0001$, respectively).

The slope of the relationships between biological standing stocks and total phosphorus generally diminished from phytoplankton to zooplanktivorous fish (Fig. 2) and an inverse trend was shown by the standard error in the slope (Fig. 3 a). An exception was MAZOO-TP relationship for #NOATE data subset; both the slope and its standard error were higher than for both CHL-TP and MIZOO-TP regressions (Fig. 3 a). The same pattern for slope variation was observed between standing stocks regressions (Fig. 3 b). For #NOATE data subset, MAZOO was again an exception. The slope of the MAZOO-CHL regression was almost the same and greater than the slope for CHL-TP and MIZOO-CHL regressions

respectively, but the standard error for the former was considerably higher (Fig. 3 b).

Discussion

Total phosphorus has been shown to be the most important variable to explain chlorophyll variability (SAKAMOTO 1966, DILLON & RIGLER 1974, among others) in both the northern and southern hemispheres (FERRIS & TYLER 1985). As previously indicated (QUIROS 1988, 1989 b), total phosphorus was one of the strongest estimators of total chlorophyll for Argentinian lakes and reservoirs. There were no significant differences between regressions for lakes and for reservoirs, or between mixed and stratified lakes (QUIROS 1988, 1989 a). However, when facultative zooplanktivorous fish of the Atherinidae family are present, chlorophyll predicted from general CHL-TP models will be usually lower, and accordingly, two different models for lakes with and without zooplanktivorous fish should be used (compare Eq. 1 with Eq. 2 and 3 in Table 3). When the total CHL-TP model (Eq. 1, Table 3) was applied to 14 lakes with bottom dissolved oxygen below 2.0 mg
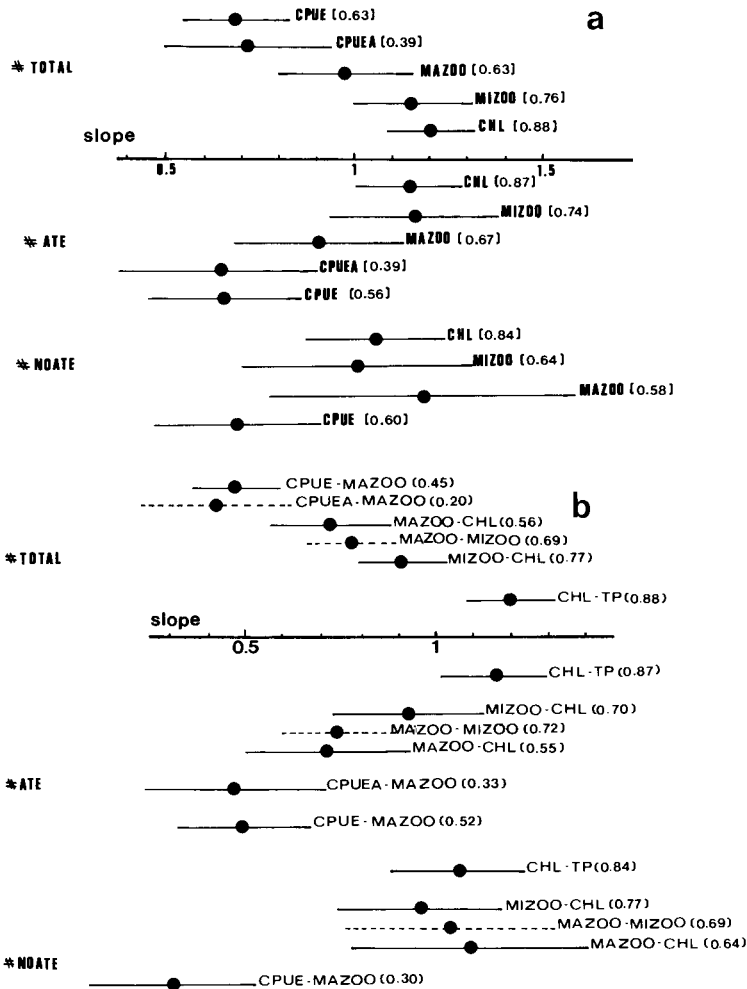
Fig. 3. Slope values for simple regression models a) between biological standing stocks and total phosphorus, and b) between different standing stocks. Points and lines represent slope value and two times standard error for slope respectively. Number in parentheses is the coefficient of determination (r^2) for the regression. #TOTAL, total data (n = 65); #ATE and #NOATE mean lake data subsets with (n = 38) and without (n = 27) atherinids in the samples.

· l^{-1} (not included here), most of estimations (13) were below measured chlorophyll concentrations. Similar results were obtained for 9 lakes with $Z_{MEAN}/SDL < 1.0$ (also not included here); for 8 lakes, predicted chlorophyll was above actual chlorophyll concentrations at sampling. When Equation 1 (Table 3) was used to estimate chlorophyll concentrations for 23 non-turbid lakes with mean macrozooplankton body weight above 3.6 μg dry weight, 20 of those lakes showed a negative departure from CHL-TP regression. Furthermore, the hypothesis of independent effects of

zooplanktivorous fish and macrozooplankton size on phytoplankton standing stocks in comparative lake studies, after nutrient effects had been accounted for, was supported by results obtained for Argentinian lakes and reservoirs (QUIROS 1989 a, b).

As in other lakes comparisons, microzooplankton (PACE 1986) and macrozooplankton biomass (MCCAULEY & KALFF 1981, HANSON & PETERS 1984) increased with lake trophy. Strict comparisons with PACE's data (1986) are not possible because of the shortcomings of micro and macro-

zooplankton data presented here. However, total phosphorus was highly significant in explaining microzooplankton biomass variation in Argentinian lakes, but the regression slope was higher than for Quebec lakes (PACE 1986). As in HANSON & PETER's (1984) results, the slope for macrozooplankton biomass – total phosphorus relationship did not differ significantly from unity for the total data set and for both types of lakes, with and without atherinids. Nevertheless, although slope for the macrozooplankton biomass – chlorophyll relationship was well below 1.0 for the total data set and for lakes with zooplanktivorous fish, it was not significantly different from unity for lakes without atherinids.

On the other hand, macrozooplankton – microzooplankton relationships were significantly different for both types of lakes, with and without atherinids respectively. Regression slopes were below 1.0 for the former and not significantly different from unity for the latter (see Equations 10 and 11, Table 3). To test whether the presence of zooplanktivorous fish or lake trophy, is more related to changes in macrozooplankton/microzooplankton biomass ratio, two lake subsets with TP < 30 mg $\cdot$ m^{-3} (n = 42) and TP > 30 mg $\cdot$ m^{-3} (n = 23) were considered. Regression slopes for MAZOO-MIZOO regressions were not significantly different but the equation intercept for #NOATE (a = 3.815) was higher than for #ATE (a = 2.480) lakes. The stronger differences between macrozooplankton-microzooplankton regressions for lakes with and without atherinids (F = 3.82, P < 0.05) than between regressions for oligotrophic – mesotrophic and eutrophic – hypertrophic lakes (F = 2.65, P < 0.10), suggest that zooplankton relative biomass changes are more related to fish community composition than to lake trophy. In summary, despite statistical differences between regression models, lakes with zooplanktivorous fish showed lower macrozooplankton biomass when lake trophic state was reduced to a common denominator.

Relative fish standing stocks (biomass), as estimated by gillnetting, was shown to be correlated with measurements of lake trophy in Argentinian lakes and reservoirs (QUIROS 1990), as has been found for fish biomass (HANSON & LEGGETT 1982) and fish yield (RYDER 1965, OGLESBY 1977, HANSON & LEGGETT 1982, JONES & HOYER 1982) in other studies. The slope of the regression for relative fish biomass on total phosphorus (0.68, 0.66 and 0.69 for total data, and #ATE and #NOATE subsets respectively) were not signif-

icantly different from the slope of HANSON & LEGGETT (1982) equation of fish standing crop on total phosphorus. Macrozooplankton biomass explained 52 % and 30 % of total fish variation for lakes with and without zooplanktivorous fish respectively. The results suggest that when macrozooplankton biomass is held constant, lakes with zooplanktivorous fish will have a higher fish biomass than lakes without those fish. However, residual variation is high, how much it is related to other unconsidered variables, sampling bias, gear selectively or simple error is something I have not resolved here.

Both "bottom-up" and "top-down" effects (McQUEEN et al. 1986, NORTHCOTE 1988) are involved, but the latter was not analysized, here. Macrozooplankton size effects on the CHL-TP residual variability was shown for Argentinian lakes and reservoirs (QUIROS 1989 b). However, only in the eutrophic – hypertrophic lake subset (TP > 30 mg $\cdot$ m^{-3}), zooplanktivorous fish were significant, and inversely related, to reduce MAZOO-TP residual variation (QUIROS unpubl.). As was shown before for other data sets (McQUEEN et al. 1986), slopes were stronger near the bottom of the food web, and variability around the regression lines increased with every step up the food chain until zooplanktivorous fish were reached; in lakes where those fish were scarce or absent from the fish community, maximum variability among the lakes was transfered to macrozooplankton (Fig. 3 a and b).

The obvious quantitative limitations of fish and zooplankton sampling and the sparseness of data for each lake, precludes the formulation of broad generalizations, eventhough a wide range of limnological characteristics were sampled. Notwithstanding, the results provided valuable observations of how biological standing stocks vary among lakes, and especially how those standing stocks vary among lakes with or without zooplanktivorous fish. Similar patterns were obtained for most heterogeneous sets of lakes and reservoirs studied, but the explained variances and regression slopes were lower (QUIROS 1988, 1990). The results also support the notion that large differences in nutrient status among lakes will be manifested in measurable differences in biological standing stocks (BROCKSEN et al. 1973, YAN 1986). On the basis of VOLLENWEIDER's (1969, 1975) models of nutrient loading, a hypothesis may also be expressed that the most general external characteristics of an aquatic ecosystem determine most of the internal variability in standing stocks of com-

munities because of the inherent system conservatisms (e.g. RAWSON 1952, 1955, RYDER 1965, VOLLENWEIDER 1969, 1975, DILLON & RIGLER 1975, SCHINDLER et al. 1978, BRYLINSKY 1980, KERR 1982, QUIROS 1990, and many others), and internal features modulate those standing stocks (SHAPIRO 1980) between relatively narrow limits in synchronic lakes comparisons.

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