

# Predictors of Relative Fish Biomass in Lakes and Reservoirs of Argentina

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Relationships between total fish biomass and chlorophyll, nutrient levels, and morphometric and climatic factors are shown for a set of 106 Argentinian lakes and reservoirs. The total data base is highly heterogeneous. Relative fish biomass (CPUE) was estimated from gill net catches. A data screening process was applied to the environmental data base to homogenize it. Nutrient, total organic matter content, and mean depth were most important in explaining relative fish biomass variability between lakes and reservoirs. In most heterogeneous sets total organic nitrogen (TON) explained most of CPUE variability. After screening for limnological anomalies (i.e. turbidity derived from inorganic sources, unsuitable conditions for fish, and TN/TP (total nitrogen / total phosphorus) < 37 (molar basis)), TP and TON were highly correlated with CPUE. Mean annual air temperature was significantly related to fish biomass, but the relationship was not significant after nutrients, morphometry, and environmental oxygen conditions had been accounted for. Several possible causes are discussed. The results support the hypothesis that fish/phytoplankton, and fish/zooplankton biomass ratios are inversely related to lake trophy.

Les relations entre la biomasse totale de poissons et la chlorophylle, la teneur en éléments nutritifs, et les facteurs morphométriques et climatiques sont présentées pour une série de 106 lacs et réservoirs argentins. La banque de données totale est très hétérogène. La biomasse de poissons relative (CPUE) a été estimée à partir des prises au filet maillant. Un tri des données a été effectué dans la banque des données environnementales afin de l'uniformiser. Les éléments nutritifs, la teneur totale en matières organiques et la profondeur moyenne ont été très importants pour expliquer la variabilité de la biomasse relative de poissons entre les lacs et les réservoirs. Dans la majorité des séries hétérogènes, la teneur en azote organique total (AOT) expliquait en majeure partie la variabilité de CPUE. Après un tri des anomalies limnologiques, c'est-à-dire : la turbidité dérivée de sources inorganiques et les conditions impropres pour le poisson, et un rapport TN/TP inférieur à 37 (base molaire), le phosphore total et l'azote organique total ont été étroitement corréliés avec CPUE. La température ambiante annuelle moyenne affichait une relation étroite à la biomasse de poissons, mais cette relation n'était pas significative une fois prises en considération la teneur en éléments nutritifs, les caractéristiques morphométriques et la teneur en oxygène de l'environnement. Plusieurs causes possibles sont envisagées. Les résultats obtenus viennent étayer l'hypothèse selon laquelle les ratios de biomasse poisson/phytoplancton et poisson/zooplancton sont inversement reliés aux caractéristiques trophiques du lac.

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**E**mpirical or predictive limnology is fundamental to fish management because it offers biologically and socially important predictions that have been confirmed in repeated trials (Peters 1986). Regression equations for predicting potential fish yields from freshwater lakes and reservoirs have become common in the fisheries literature (Schlesinger and Regier 1982); however, homogeneity of the data base has been of concern for correct use of predictive models (Henderson et al. 1973; Ryder 1982). In regions with many almost unknown water bodies, an ecosystem level, comparative approach (Regier and Henderson 1980), including limnological and fish characterization of lakes and reservoirs, seems to be more efficient than work at fish species population levels (Regier and Henderson 1980). Such an approach also allows testing the applicability of general models. Furthermore, comparative studies can provide transition between empirical management and explanatory theory (Collins and Sprules 1983; Hoenig et al. 1987).

Argentina covers a highly varied geographic area exhibiting marked diversity in climate and geology. There are more than 400 lakes and reservoirs with surface areas over 5 km<sup>2</sup> and only about 20 have been intensively studied (Quiros et al. 1983).

Most of the Argentinian lakes and reservoirs are lightly exploited for fish. Only a few very shallow lakes in the Pampa Plain and no more than three lakes in the Patagonian Plateau support a commercial fishery. The remainder of lakes and reservoirs support lightly fished or unevaluated sport fisheries. A few lakes and reservoirs have also nonintensive domestic fisheries.

My working hypothesis was that general external characteristics of an aquatic system determine many of its internal biological features (Brylinsky 1980; Kerr 1982) or that climatic, morphometric, and edaphic factors and their interrelationships determine lake productivity (Rawson 1955). I had expected that this general hypothesis could be useful for ordering Argentinian freshwaters on the basis of fish biomass. Lakes and reservoirs may be grouped by fish species composition (Tonn et al. 1983; Marshall and Ryan 1987) or by environmental factors. Here, the first aim was ordering lakes and reservoirs on the basis of fish biomass; therefore, I focused primarily on abiotic factors and chlorophyll, a measure of potential primary productivity at the lowest trophic level.

## Materials and Methods

This paper relates the mid-summer relationships between fish biomass and chlorophyll, nutrient levels, and morphometry and climatic factors for a set of 106 Argentinian lakes and reservoirs (ARLARE data set).<sup>1</sup> During the summers of 1984 to 1987, 110 lakes and reservoirs of Argentina were sampled. Four lakes without fish were excluded. Lakes and reservoirs were visited once, except for six, situated in Patagonia Plateau (Fig. 1), that were sampled seasonally over 2 yr. Reservoirs with low hydraulic residence time (<3 mo), and floodplain lakes and ponds situated in the Plata River Basin were expressly excluded (Bonetto et al. 1969; Quiros and Cuch 1983; Quiros and Cuch 1989).

### Data Collection

Lake surface area (A), latitude (LAT) and elevation (ALT) were obtained from 1 to 50 000 and 1 to 10 000 topographic maps (Quiros et al. 1983). Bathymetric surveys with a SIMRAD Skipper 411 model echosounder, a hand winch and line and lead (Welch 1948) were conducted on 47 lakes. We obtained mean depth (ZMEAN  $\pm$  10%) for each lake and reservoir. For most of the reservoirs, morphometric parameters were taken from topographic maps before impoundment (Quiros et al. 1983). For eight lakes, mean depth was estimated from the regression between mean depth and area for other lakes in the same region. Mean annual air temperature (TEMP) and frost free period (FFP) were obtained from Quiros et al. (1983); these data were considered to be of low quality especially in the Patagonian Andes Region and Tierra del Fuego (Quiros and Drago 1985), because of the sparsity of meteorological stations. 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 (Quiros 1988). For each lake, vertical profiles were obtained for temperature, dissolved oxygen, conductivity, pH, and total alkalinity. In lakes < 25 m deep, a Hydrolab Surveyor system was used. Water samples were taken from surface to bottom with a Friedinger plastic sampler (Golterman et al. 1978).

Transparency measurements (SDL) were obtained with a 25-cm black and white Secchi disk. True color (COL) was determined in the field with a Hazen platinum-cobalt scale. Conductivity (20 °C, K20), dissolved oxygen (DO, by the Winkler method) and total alkalinity (TA, by potentiometric titration), were measured in the field. Total dissolved solids (TDS) was determined as total residue on evaporation to constant weight at 105 °C, and water hardness (HARD) was determined volumetrically. Chlorophyll (CHL), total phosphorus (TP), total organic nitrogen (TDN), total organic carbon (TOC), nitrate, nitrite, major ions, and total dissolved solids (TDS) were determined from samples collected at the 0.5-m depth. Analytical methods used have been described previously (Quiros 1988).

Chlorophyll was determined according to Stauffer et al. (1979) without pheopigment corrections. All nutrient and chlorophyll determinations were done in duplicate. For 71 lakes and reservoirs in northern Patagonia, and central-western and north-

western arid region, nitrate and nitrite were determined with an ORION D793-07 electrode and the diazotation method (APHA et al. 1975), respectively. On average, the nitrate plus nitrite-N fraction was 0.24 of Kjeldahl-N (SE = 0.16, range: 0.03–1.16). For 35 lakes in the Pampa Region, southern Patagonia and Tierra del Fuego, I assumed nitrate plus nitrite was 20% of the total Kjeldahl nitrogen concentration. Nitrate and nitrite were used only to estimate TN:TP ratios.

Fish were collected by nylon gillnets. The experimental net was 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 25 m were used. Gillnets were set in gangs of floating nets, perpendicular to the shoreline, with the smallest mesh inshore. The sets were remote from stream mouths, protected bays or islands. Lakes larger than 20 km<sup>2</sup> or with irregular shorelines were fished for 2 d at two locations. Floating sets were made overnight, usually for 12 h. I used only data from the overnight catches. Relative biomass of fish was approximated using mean weight (kg) of fish caught per overnight set for the experimental gang of gillnets (Northcote and Larkin 1956). Catch was standardized as the sum of mean weights of fish in 100 m<sup>2</sup> of each mesh, for the nine panels (CPUE).

Zooplankton samples were collected by 50-m vertical tows or from 0.5 m above the bottom to the surface. In both cases epilimnetic waters were sampled. 100% net efficiency was assumed; Menu Marque and Marinone (1986) detailed enumeration and biomass determination methods. Total zooplankton biomass (TOZOO,  $\mu$ g dry weight·L<sup>-1</sup>) was used herein.

### Data Analysis

The data (ARLARE) is highly heterogeneous and the climatic, morphometric, and edaphic variables are closely related (Quiros 1987). All lakes and reservoirs are contained within 24 and 55 °S latitudes (Fig. 1).

Exploratory analyses of the data base were made by simple and partial correlation and simple and stepwise multiple regression analyses (Weisberg 1980; Davis 1986). Number Cruncher Statistical System (NCSS) for IBM PC (Hintze 1985) statistical package was used. For comparison between regression models, ANCOVA analysis and general *F*-testing was used (Weisberg 1980). Environmental variables were log-transformed except LAT, TEMP, and DO<sub>b</sub> levels. Water type was characterized as differences in anionic (A/A, carbonate plus bicarbonate to chloride plus sulfate) and cationic (C/C, calcium plus magnesium to sodium plus potassium) ratios (equivalent basis). Environmental ordination of lakes and reservoirs was performed by principal components analysis (PCA) (Davis 1986). A correlation matrix analysis was used because variables were in different units. Here I present the results of an environmental PCA ordination of lakes and reservoirs with 19 variables. All the variables except LAT, TEMP, and DO<sub>b</sub> were log-transformed to linearize the relations and to reduce the disproportionate effect of the untransformed data from a few lakes and reservoirs (Peters 1986). The results of the PCA did not change appreciably if CHL was or was not included in the analysis.

Different pathways of data screening were tried to improve predictive ability. Here we present the pathway that leads to explaining the highest proportion in CPUE variance using the fewest variables. Lakes and reservoirs with limnological anomalies or unsuitable conditions for fish were removed in a stepwise procedure. Lakes and reservoirs known to be subject to

<sup>1</sup>Complete set of tables is available, at a nominal charge, from the repository of unpublished data CISTI, National Research Council of Canada, Ottawa, Ont. K1A 0S2, or from the Instituto Nacional de Investigacion y Desarrollo Pesquero, C.C. 175, 7600 Playa Grande, Mar del Plata, Argentina.

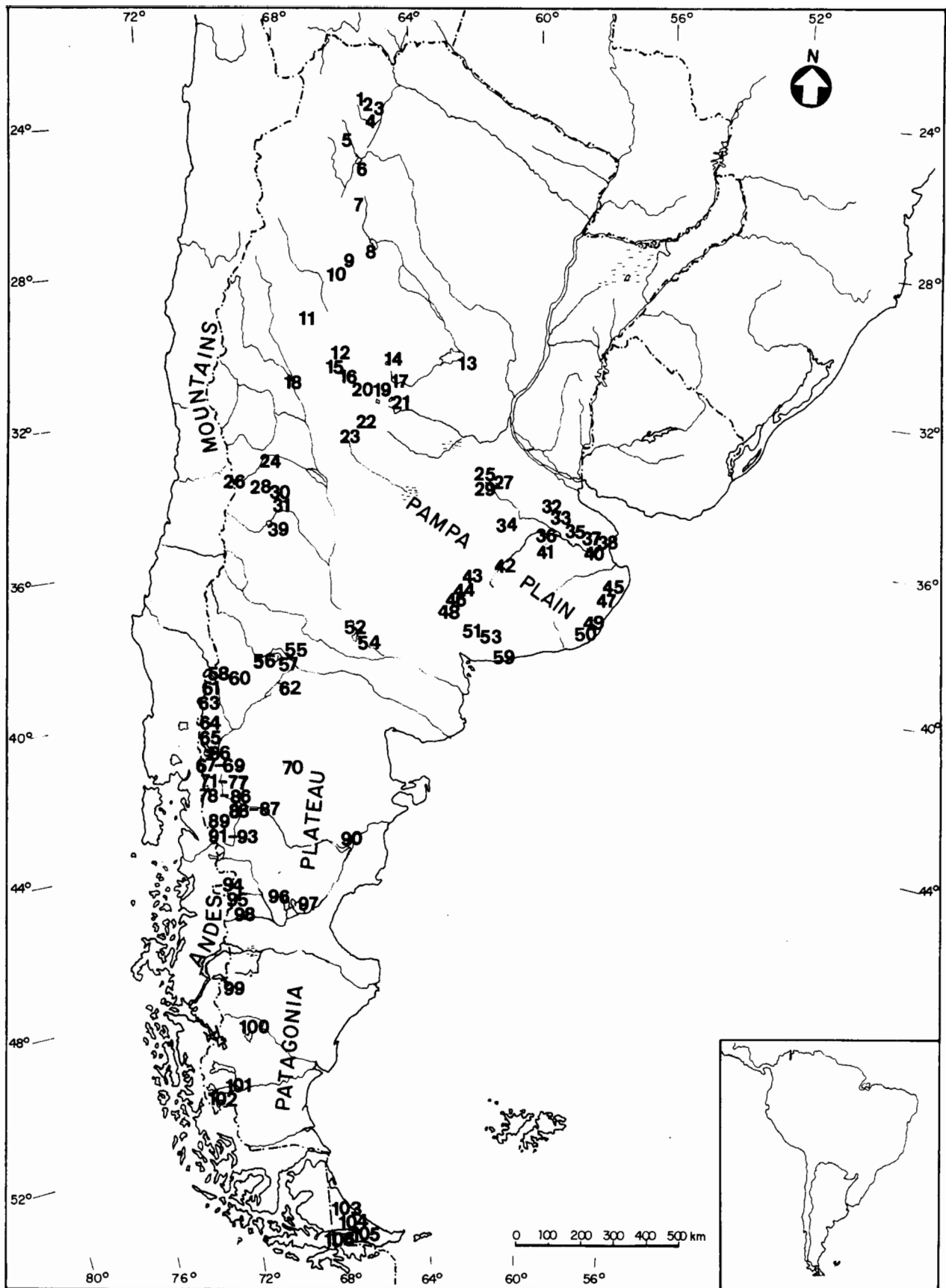


FIG. 1. Argentina showing the location of the 106 lakes and reservoirs studies.

TABLE 1. Mean and range for the limnological and fish characteristics measured in Argentinian lakes and reservoirs (data set #2,  $n=99$ ). Area (A,  $\text{km}^{-2}$ ), mean depth (ZMEAN, m), mean annual air temperature (TEMP,  $^{\circ}\text{C}$ ), elevation (ALT, m), total dissolved solids (TDS,  $\text{g} \cdot \text{m}^{-3}$ ), total phosphorus (TP,  $\text{mg} \cdot \text{m}^{-3}$ ), total organic nitrogen (TON,  $\mu\text{M}$ ), total chlorophyll (CHL,  $\text{mg} \cdot \text{m}^{-3}$ ), carbonate plus bicarbonate to chloride plus sulfate (A/A, equivalent basis), calcium plus magnesium to sodium plus potassium (C/C, equivalent basis), bottom dissolved oxygen concentration at sampling (DOb,  $\text{mg} \cdot \text{L}^{-1}$ ), catch per unit effort of Atherinidae (CPUEA, kg/night per standard gillnets), total catch per unit effort (CPUE, kg/night per standard gillnets), and number of fish species at sampling (NUM).

Variable	lakes ( $n=70$ )		reservoirs ( $n=29$ )	
	Mean	Range	Mean	Range
A	80.0	0.09–1466.0	81.6	1.5–816.0
ZMEAN	32.4	0.7–166.0	21.9	3.0–79.0
TEMP	9.7	3.0–16.5	15.9	5.0–20.4
ALT	464	2.0–3250.0	764	169.0–1339.0
TDS	1043	19.0–13800.0	640	33.0–6780.0
TP	131	1.0–1288.0	63	3.0–477.0
TON	104	5.0–762.0	50	6.0–352.0
CHL	26.1	0.16–405.0	17.7	0.66–218.0
A/A	5.56	0.03–26.6	2.47	0.04–9.83
C/C	2.47	0.03–16.0	2.62	0.18–8.05
DOb	8.2	0.5–12.2	4.2	0.01–9.7
CPUEA	34.8	0–435.2	23.5	0–283.0
CPUE	88.2	1.2–505.1	37.3	1.9–283.0
NUM	3.3	1.0–9.0	3.6	1.0–10.0

TABLE 2. Data screening conditions for total lakes and ponds (LA) and reservoir (RE) data sets analyzed. DOb (bottom dissolved oxygen at sampling;  $\text{mg} \cdot \text{L}^{-1}$ ), CHL:TP (chlorophyll to total phosphorus ratio), TN:TP (total nitrogen to total phosphorus ratio, molar basis), NUM (number of fish species at sampling).

Data set	$n$	Data screening conditions
#1	106	—
#2	99	—
#2RE	29	Reservoirs
#2LA	70	Lakes
#3	74	CHL:TP>0.05, DOb>2.0 $\text{mg} \cdot \text{L}^{-1}$
#3LA	47	Lakes, CHL:TP>0.05, DOb>2.0 $\text{mg} \cdot \text{L}^{-1}$ , TN:TP>37
#4LA	37	Lakes, CHL:TP>0.05, DOb>2.0 $\text{mg} \cdot \text{L}^{-1}$ , TN:TP>37, NUM>1

extensive human influence were excluded (set #2, Table 1). The data screening process and the lakes and reservoirs used in this analysis are in Table 2.

In many lakes and reservoirs in Patagonian Andes, Tierra del Fuego, and the central-western and northwestern regions, fish components have not coevolved with each other and with their environment, due to fish introductions and fish transfers. As a result, I used water temperature and dissolved oxygen levels at sampling, number of fish species (NUM) in the catch and frequency of Atherinidae (%ATE) as surrogate variables.

Flushing rate modifies thermal stratification of reservoirs in general (Wunderlich and Elder 1967; Wunderlich 1971) and Argentinian reservoirs in particular (Viana and Quiros 1989). Furthermore, flushing rate is related to nutrient loading. Therefore, differences in fish biomass may be attributable in part to flushing rate (Jenkins 1982). The relationship between fish biomass and mean hydraulic residence time ( $T_w$ ) was examined here for a subset of 43 lakes and reservoirs, for which flushing rates were known.

## Results

### Lake Characteristics by Region

#### Central western and northwestern arid region

Throughout the arid region 29 lakes and reservoirs were examined, 25 of which were reservoirs. Mar Chiquita Lake and El Cadillal Reservoir were removed from our set #2 analysis. The former is a saline lake with very high total dissolved solids (28 157  $\text{mg} \cdot \text{L}^{-1}$ ). The latter has been developed for live-stock, has high relief, significant land erosion and therefore, high reservoir inorganic turbidity. The high-mountain lake (El Diamante) was used within the Patagonian data set.

TEMP ranged from 11 to 16  $^{\circ}\text{C}$  for the central western to 20.4  $^{\circ}\text{C}$  for the northwestern lakes and reservoirs. There were 12 reservoirs and two lakes (most ( $n=13$ ) in the northwest) with DOb below 3.0  $\text{mg} \cdot \text{L}^{-1}$ . CPUE ranged from 1.9 to 283.0 kg/night.

Most of the fish species of the reservoirs have been introduced (Baigun and Quiros 1985; Quiros 1987) from outside Argentina or from other river basins in Argentina. Salmonid introductions were attempted but without much success (Baigun and Quiros 1985; Quiros 1987). Argentinian silverside (*Basilichthys bonariensis*, Atherinidae), introduced from the Pampa Plain region, was the most common (frequency of occurrence: 0.49). Rainbow trout (*Oncorhynchus mykiss*), reintroduced principally from southern Patagonia, had a low mean frequency of occurrence (0.2) and was captured only in the western reservoirs and in one northern lake at an elevation of 1446 m. One species of Percichthyidae had been introduced from Patagonia and was captured in the western reservoirs and in one northern lake (mean frequency of occurrence: 0.13). Remaining species were carp (*Cyprinus carpio*), or species native to their respective catchment basins (Quiros et al. 1988). More than 80% of the fish biomass arose from exotic species in the central-western and northwestern arid region.

## Patagonia and Tierra del Fuego

Fifty lakes and reservoirs were sampled throughout Patagonia and Tierra del Fuego; most ( $n = 45$ ) were lakes. Ne-Luan, Cronometro, Blanco, and Escondido lakes were included only in the set #1 analyses. The former is a small lake used for experimental introductions of rainbow trout and Patagonian silverside (*Basilichthys microlepidotus*, Atherinidae) and was heavily fished, experimentally (Quiros and Baigun 1986). Cronometro Lake was suspected to have pesticide generated environmental stress (Quiros and Baigun 1986) while Blanco Lake is shallow, turbid, fluctuates considerably in surface area and depth, and was practically without fish. Escondido is a dammed lake used for saw-mill activities and was practically without fish. El Diamante lake, a high-mountain lake in central Andes Mountains, was also included in the regional analysis because of its altitude and its salmonid fish population.

TEMP ranged from 3 to 5°C in the high-mountain lake and the glacial lakes in the southern Andes and from 12 to 14.5°C in the northern Patagonian Plateau lakes and reservoirs (Quiros and Drago 1985). Salmonid species have been introduced from the beginning of the century onward in this set of lakes. Salmonids are presently known to have established breeding populations in some Patagonian lakes. Most glacial lakes in Patagonia and Tierra del Fuego have been successfully colonized by salmonids (Baigun and Quiros 1985; Quiros 1987). CPUE ranged from 0.2 to 400.0 kg/night. Fifty-eight percent of the fish biomass captured in our sampling was introduced salmonids. East of the Andes, there are many small lakes in which salmonid populations are maintained almost entirely by periodic stocking. Nevertheless, the fish community in the Patagonian Plateau lakes and reservoirs was dominated by indigenous percichthyds and atherinids. The climatic, edaphic, and morphological attributes of lakes, especially TEMP, explained the relative abundance of salmonids in Patagonia (Quiros and Baigun 1986; Quiros 1987).

## Pampa Plain

Twenty-six lakes were sampled for fish in the Pampa Plain. Melincue Lake was only included in our set #1 analysis. It is a very turbid lake, subject to earth embankment construction activities during sampling, has the lowest A/A ratio and the highest TP content of the ARLARE set.

Lakes are shallow (0.7 to 5.2 m), and TEMP ranges from 13.8 to 16.5°C. CPUE ranged from 17.4 to 505.1 kg/night. Most of the fish captured in the sampling were species native to the Pampa Plain. Forty-five percent of biomass was the Argentinian silverside and the common carp was captured only in five lakes. The fish community composition was related to the amount of open water and vegetated areas and wetlands, and to the organic matter (R. Quiros, unpubl. data).

## Ordination of Lakes and Reservoirs

Climatic, morphometric, and edaphic characteristics were highly interrelated in the ARLARE data base (Table 3). Nineteen variables of different hierarchical levels were used in principal components ordination analyses (Table 4). Edaphic variables are commonly related to or determined by climate and morphometry, but must be tested in each case (Quiros 1987). I am also conscious of the log-linear structure that I have imposed to data in the ordination analyses (Gauch 1982; Zimmerman et al. 1983; Bolter and Meyer 1986).

The first component (PC1) explained 54.6% of total variance and loaded highly and positively on ZMEAN and SDL, and negatively on nutrient and organic matter variables, TEMP and CHL (Table 4). This first component represents a contrast between shallow lakes and reservoirs with high nutrient concentrations, high total and dissolved organic matter, high phytoplanktonic biomass, and high mean annual air temperatures, and deep lakes and reservoirs with higher water transparency, higher elevations and latitudes, belonging to the calcium plus magnesium and carbonate plus bicarbonate chemical water type, and with high TN:TP ratios. The second component explained 13.8% of the total variance and loaded heavily and negatively on DO<sub>B</sub> and LAT, and positively on CHL:TP ratio. The second component contrasts lakes and reservoirs at high elevations, high mean annual air temperature and belonging to the calcium plus magnesium water type, with large lakes at high latitudes and high oxygen levels at the water-sediment interface.

A continuum of lakes and reservoirs was defined on the ordination space of the two first components (Fig. 2). However, three spatial groups were distinguishable depending on region. A first group (A) includes the lakes and reservoirs of Patagonia and Tierra del Fuego, and a second group (B) includes most of the reservoirs of the central-western and northwestern arid region. The central-western reservoirs without an oxygen deficit in the hypolimnion are positioned near the Patagonian lakes and overlapped with the small, shallow Patagonian lakes situated immediately west of the Andes Mountains. A third group (C) includes the very shallow lakes located on the Pampa Plain. The shallowest northwestern reservoirs in group B overlapped the Pampa Plain lakes in group C.

The third and fourth components explained 9.0 and 6.3% of total variance, respectively and represent particular characteristics of the Argentinian lakes and reservoirs, such as regional distribution of large lakes and reservoirs with high dissolved solids and  $\text{Cl}^-$  or  $\text{SO}_4^{2-}$  water type, and sites with both high TN:TP and CHL:TP ratios.

The lakes and reservoirs with the highest CPUE are included in a zone of the principal components space that have low and intermediate values of PC1 and PC2, respectively (Fig. 3). In that zone are lakes and reservoirs with the lowest mean depths, the highest nutrient concentrations, the highest mean annual air temperatures, and intermediate values of CHL:TP ratios. All the sites with CPUE > 150 kg/night and many of those with CPUE > 60 kg/night are included there. However, those lakes and reservoirs with favorable climatic, morphometric, and edaphic conditions for high fish biomass, but with low bottom dissolved oxygen, and those with very low CHL:TP ratios are excluded (Fig. 3).

## Factors Related to Fish Biomass

Correlation analyses results show that lakes and reservoirs with the highest nutrient levels, the lowest mean depths, and the highest mean annual air temperatures, tended to have, as expected, higher fish biomass (Table 3). For unscreened data (set #1,  $n = 106$ ; Fig. 4) ZMEAN explained 31% of CPUE variance, and TON, TP, CHL, and TEMP explained 29, 19, 23, and 9% of it, respectively. For set #2 ( $n = 99$ ), CPUE variance explained by the same variables was higher than for set #1, and TON was the most important single variable (Table 3). In this data set, a series of sites with high nonalgal suspended solids and others with an extensive aquatic macrophyte development were still included. Many of the northwest region

TABLE 3. Matrix correlation coefficients between environmental and fish variables for ARLARE data set #2 ( $n=99$ ), Area (A,  $\text{km}^2$ ), mean depth (ZMEAN, m), mean annual air temperature (TEMP,  $^{\circ}\text{C}$ ), total dissolved solids (TDS,  $\text{g} \cdot \text{m}^{-3}$ ), total phosphorus (TP,  $\text{mg} \cdot \text{m}^{-3}$ ), total organic nitrogen (TON,  $\mu\text{M}$ ), total nitrogen to total phosphorus ratio (TN/TP), total chlorophyll (CHL,  $\text{mg} \cdot \text{m}^{-3}$ ), carbonate plus bicarbonate to chloride plus sulfate (A/A), calcium plus magnesium to sodium plus potassium (C/C), bottom dissolved oxygen concentration at sampling (DOb,  $\text{mg} \cdot \text{L}^{-1}$ ), number of fish species at sampling (NUM), catch per unit effort of Atherinidae (CPUEA,  $\text{kg}/\text{night}$  per standard gillnets), total catch per unit effort (CPUE  $\text{kg}/\text{night}$  per standard gillnets), and frequency of atherinids at sampling (%ATE).

Variable	A	ZMEAN	TEMP	TDS	TP	TON	TN/TP	CHL	A/A	C/C	DOb	NUM	CPUEA	CPUE	%ATE
A	1														
ZMEAN	0.41 <sup>a</sup>	1													
TEMP	-0.16	-0.57 <sup>a</sup>	1												
TDS	-0.01	-0.69 <sup>a</sup>	0.64 <sup>a</sup>	1											
TP	-0.18	-0.82 <sup>a</sup>	0.64 <sup>a</sup>	0.77 <sup>a</sup>	1										
TON	-0.26 <sup>c</sup>	-0.86 <sup>a</sup>	0.59 <sup>a</sup>	0.76 <sup>a</sup>	0.89 <sup>a</sup>	1									
TN/TP	0.02	0.49 <sup>a</sup>	-0.50 <sup>a</sup>	-0.51 <sup>a</sup>	-0.81 <sup>a</sup>	-0.46 <sup>a</sup>	1								
CHL	-0.27 <sup>c</sup>	-0.80 <sup>a</sup>	0.72 <sup>a</sup>	0.67 <sup>a</sup>	0.82 <sup>a</sup>	0.86 <sup>a</sup>	-0.51 <sup>a</sup>	1							
A/A	-0.23	0.34 <sup>b</sup>	-0.46 <sup>a</sup>	-0.78 <sup>a</sup>	-0.36 <sup>b</sup>	-0.36 <sup>b</sup>	0.20	-0.33 <sup>b</sup>	1						
C/C	-0.03	0.66 <sup>a</sup>	-0.45 <sup>a</sup>	-0.81 <sup>a</sup>	-0.79 <sup>a</sup>	-0.78 <sup>a</sup>	0.54 <sup>a</sup>	-0.59 <sup>a</sup>	0.48 <sup>a</sup>	1					
DOb	0.28 <sup>c</sup>	0.19	-0.63 <sup>b</sup>	-0.21	-0.23	-0.24	0.13	-0.41 <sup>a</sup>	0.12	0.00	1				
NUM	0.19	-0.34 <sup>b</sup>	0.43 <sup>a</sup>	0.28 <sup>c</sup>	0.37 <sup>b</sup>	0.39 <sup>b</sup>	-0.21	0.39 <sup>a</sup>	-0.19	-0.29 <sup>c</sup>	-0.13	1			
CPUEA	-0.17	-0.49 <sup>a</sup>	0.52 <sup>a</sup>	0.56 <sup>a</sup>	0.52 <sup>a</sup>	0.55 <sup>a</sup>	-0.29 <sup>c</sup>	0.66 <sup>a</sup>	-0.35 <sup>b</sup>	-0.49 <sup>a</sup>	-0.14	0.18	1		
CPUE	-0.15	-0.68 <sup>a</sup>	0.32 <sup>b</sup>	0.51 <sup>a</sup>	0.64 <sup>a</sup>	0.69 <sup>a</sup>	-0.36 <sup>a</sup>	0.61 <sup>a</sup>	-0.25	-0.60 <sup>a</sup>	0.07	0.37 <sup>b</sup>	0.62 <sup>a</sup>	1	
%ATE	-0.22	-0.29 <sup>c</sup>	0.50 <sup>a</sup>	0.44 <sup>a</sup>	0.33 <sup>b</sup>	0.33 <sup>b</sup>	-0.22	0.51 <sup>a</sup>	-0.34 <sup>b</sup>	-0.28 <sup>c</sup>	-0.28 <sup>c</sup>	-0.09	0.57 <sup>a</sup>	0.28 <sup>c</sup>	1

<sup>a</sup>t-test  $p < 0.0001$ .

<sup>b</sup>t-test  $p < 0.001$ .

<sup>c</sup>t-test  $p < 0.01$ .

TABLE 4. Eigenvalues, percent variance explained and factor loadings for principal components analysis with 19 variables defined in the text, for set #2 ( $n=99$ ).

Factor	I	II
Eigenvalue	10.38	2.63
Percent variance explained	54.6	13.8
A	0.19	-0.44
ZMEAN	0.87	0.01
SDL	0.89	-0.04
COL	-0.79	-0.15
TEMP	-0.79	0.42
ALT	0.59	0.50
TA	-0.92	-0.17
K20	-0.88	-0.12
HARD	-0.75	0.07
TP	-0.95	-0.13
TON	-0.92	-0.04
TOC	-0.93	-0.06
CHL	-0.88	0.28
LAT	0.41	-0.76
A/A	0.53	0.08
C/C	0.81	0.40
CHL:TP	-0.12	0.68
TN:TP	0.64	0.20
DOb	0.33	-0.76

reservoirs had an anoxic hypolimnion or low dissolved oxygen levels ( $< 2.0 \text{ mg} \cdot \text{L}^{-1}$ ), a summer characteristic of most of the northwest arid region deep reservoirs. These reservoirs are monomictic in the spring only (Bonetto et al. 1976; Viana and Quiros 1989). When screening sites where  $\text{CHL}/\text{TP} < 0.05$  or  $\text{DOb} < 2.0 \text{ mg} \cdot \text{L}^{-1}$  (set #3,  $n=74$ ), the CPUE variation explained by both TON and TP increased (Table 5). Half of the reservoirs were screened in this step, but TEMP was still negatively related to DOb ( $r = -0.54$ ,  $P < 0.001$ ).

System surface area ranged over six orders of magnitude in the ARLARE data base. Although A and ZMEAN were correlated (Table 3), there was no highly significant relationship

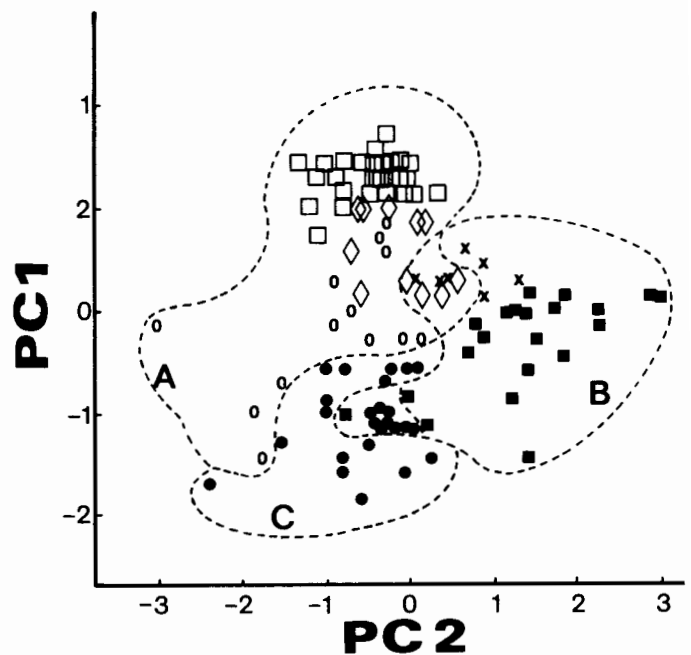


FIG. 2. Position of Argentinian lakes and reservoirs in the two first principal components space. (A). Patagonia and Tierra del Fuego. (□) Andean lakes; (◇) small lakes located east of the foothills of the southern Andes; (○) Patagonia Plateau lakes and reservoirs. (B) Arid region. (■) northwestern lakes and reservoirs; (X) central-western reservoirs. (C) Pampa Plain lakes (●).

between CPUE and A in any analyzed case. Similar results were obtained for the relationship between fish biomass and mean hydraulic residence time ( $r = -0.05$ ,  $n=43$ ). The same as TEMP, both surface ( $T_s$ ) and bottom ( $T_b$ ) water temperature at sampling were significantly related to CPUE.

Stepwise regression analysis was used to identify the environmental and fish variables that take account of CPUE variability and to quantify their relative magnitude. Most of the

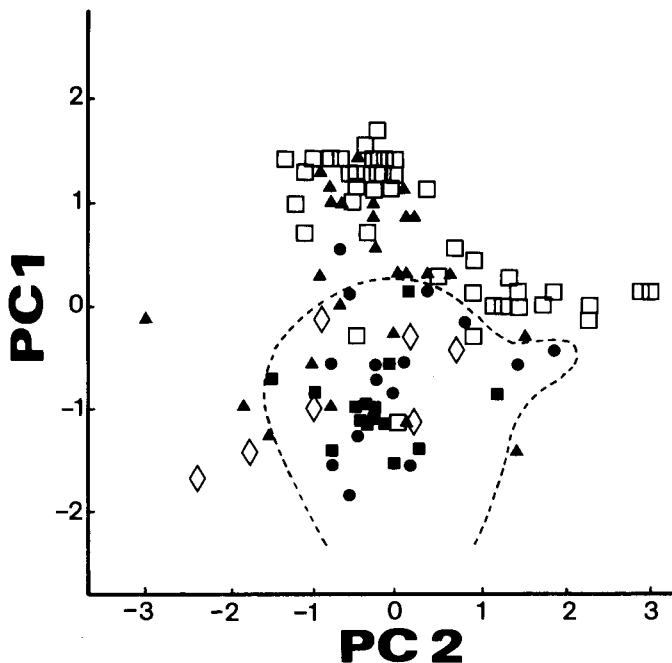


FIG. 3. Position of lakes and reservoirs in the two first principal components space and catch per unit effort (CPUE, kg/night per standard gillnets). (■) CPUE >150; (●) 150 > CPUE >60; (▲) 60 > CPUE >20; (□) 20 > CPUE; (◇) lakes and reservoirs removed from main analyses.

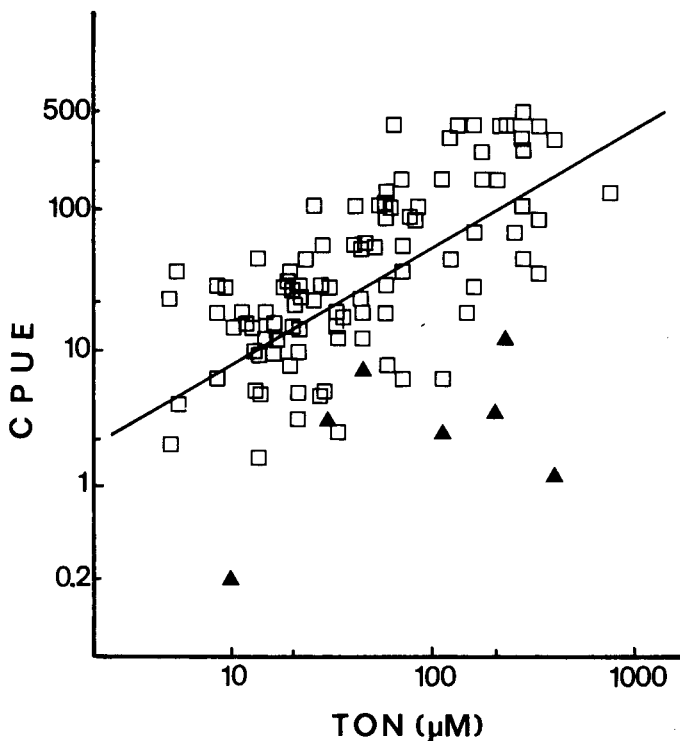


FIG. 4. Relation between fish biomass (CPUE, kg/night per standard gillnets) and mid-summer total organic nitrogen (TON,  $\mu\text{M}$ ) for 106 lakes and reservoirs. (▲) lakes and reservoirs removed from main analyses.

lakes and reservoirs with  $\text{DOb} < 2.0 \text{ mg}\cdot\text{L}^{-1}$  or  $\text{CHL}/\text{TP} < 0.05$  deviate negatively from the CPUE-TP (Fig 5) and CPUE-TON regressions. As was stated before, TON was the most important variable to explain CPUE variability in data set #2 ( $n=99$ ).

When DOB was introduced in the regression equation, CPUE variance explained improved by 5% (Table 5 and 6). The mean value of the residuals to the regression of CPUE against TON were positive for the geographic data sets Patagonia (#PAT+1) and Pampa Plain (#PAM), and negative for the central and northwestern (#NOR-1) set where most of the sites with low oxygen levels in their hypolimnia were. However, the introduction of DOB in the regression equation diminished the residual mean values but did not modify that situation. CHL and ZMEAN were highly correlated to TON (Table 3), therefore, to avoid collinearity problems, they were forced not to enter to the regression equation.

Fish community composition and number of fish species at sampling take account of some CPUE residual variability after nutrients and dissolved oxygen. Both %ATE or NUM were positively related to the residuals of CPUE on TON and DOB and accounted for an additional 4% in CPUE explained variance (Table 6). Their covariation with both nutrient and oxygen variables was low (Table 3), and the inclusion in CPUE regression models has the advantage of improving fit.

Low chlorophyll to total phosphorus ratio resulted in lower fish biomass than predicted for most heterogeneous data sets. When CHL/TP was forced into the equation after TP, it improved the CPUE explained variability by 7%. But unlike CHL, it was not highly related to TP or DOB ( $r^2 = 0.01$  and  $r^2 = 0.14$ , respectively). Besides, DOB and CHL/TP effects on CPUE-TP or CPUE-TON equations appear not to have a continuous character. Most of residuals were negative when  $\text{DOb} < 2.0 \text{ mg}\cdot\text{L}^{-1}$  or  $\text{CHL}/\text{TP} < 0.05$ , but were random distributed for  $\text{DOb} > 2.0 - 1 \text{ mg}\cdot\text{L}^{-1}$  or  $\text{CHL}/\text{TP} > 0.05$ . These facts justified the data screening that have conducted from set #2 ( $n=99$ ) to set #3 ( $n=74$ ). CPUE variability was more explained in single variable models for the latter, more homogeneous data set (Table 5) than in multiple regression models for the former (Table 6). TN/TP ratio was the most important variable to explain the residual variance in CPUE after TON, when most of the variability due to inorganic turbidity, macrophyte abundance, and hypolimnetic oxygen deficits had been removed (#3,  $n=74$ ), and ZMEAN had been forced not to enter to the equation. But it only marginally improved CPUE explained variance in 2% (Table 6). Similar results were obtained when TN/TP was introduced after TP, but they were highly related (Table 3).

When lakes and reservoirs were considered separately, the level of CPUE variance explained was improved for lakes (Table 5, #2LA,  $n=70$ ). For reservoirs the CPUE variability explained was lower when all the variables were considered (Table 5, #2RE,  $n=29$ ). When screening was applied to lake data subset, the level of CPUE variance explained increased, and TP was the most important single variable to explain CPUE variation after screening for  $\text{CHL}/\text{TP} < 0.05$ ,  $\text{DOb} < 2.0 \text{ mg}\cdot\text{m}^{-3}$  and  $\text{TN}/\text{TP} < 37$  (#3LA,  $n=47$ , Table 5). Reservoir differences with lakes appear to be more related to the facts that half of them have hypolimnia devoid of oxygen, introduced fishes, or suffer human influences that I cannot quantify here, than to its own characteristics as reservoirs.

Stepwise regression models for lakes were qualitatively similar to those for total sets, but CPUE variance explained was comparatively higher (Table 6). For most homogeneous lake set (#3LA,  $n=47$ ), ZMEAN, %ATE or NUM only marginally improved CPUE explained variance (Table 5 and 6). However, NUM also appear to be a discontinuous character variable; sum of residuals to CPUE-TP regression for NUM=1 lakes was

TABLE 5. Simple regression models relating catch per unit effort (CPUE, kg/night per standard gillnets) to total organic nitrogen (TON,  $\mu\text{M}$ ), total phosphorus (TP,  $\text{mg} \cdot \text{m}^{-3}$ , total chlorophyll (CHL,  $\text{mag} \cdot \text{m}^{-3}$ ), mean depth (ZMEAN, m) and mean annual air temperature (TEMP,  $^{\circ}\text{C}$ ), for different levels of data screening. All the variables except TEMP were log transformed. Intercept (a), slope (b), and the coefficient of determination ( $r^2$ ) are presented. LA = lakes, RE = reservoirs. *F*-test,  $P < 0.001$ .

	Independent variable				
	TP	TON	CHL	ZMEAN	TEMP
	set #2 ( $n = 99$ )				
a	1.695	0.226	2.769	4.886	2.245
b	0.513	0.831	0.427	-0.625	0.084
$r^2$	0.404	0.475	0.372	0.464	0.100 <sup>a</sup>
	set #2LA ( $n = 70$ )				
a	1.839	0.250	2.942	4.987	1.838
b	0.530	0.856	0.501	-0.616	0.182
$r^2$	0.502	0.581	0.586	0.543	0.375
	set #2RE ( $n = 29$ )				
a	1.588	1.099	2.588	4.316	1.513
b	0.397	0.503	0.165	-0.524	0.086
$r^2$	0.168 <sup>b</sup>	0.110 <sup>c</sup>	0.039 <sup>c</sup>	0.147 <sup>b</sup>	0.066 <sup>c</sup>
	set #3 ( $n = 74$ )				
a	1.540	0.124	2.863	5.182	2.112
b	0.657	0.917	0.514	-0.675	0.135
$r^2$	0.598	0.607	0.539	0.573	0.224
	set 3LA ( $n = 47$ )				
a	1.499	-0.093	3.010	5.251	1.695
b	0.761	0.983	0.558	-0.659	0.216
$r^2$	0.727	0.688	0.700	0.636	0.481

<sup>a</sup>*F*-test,  $P < 0.01$ .

<sup>b</sup>*F*-test,  $P < 0.05$ .

<sup>c</sup>*F*-test, non-significant.

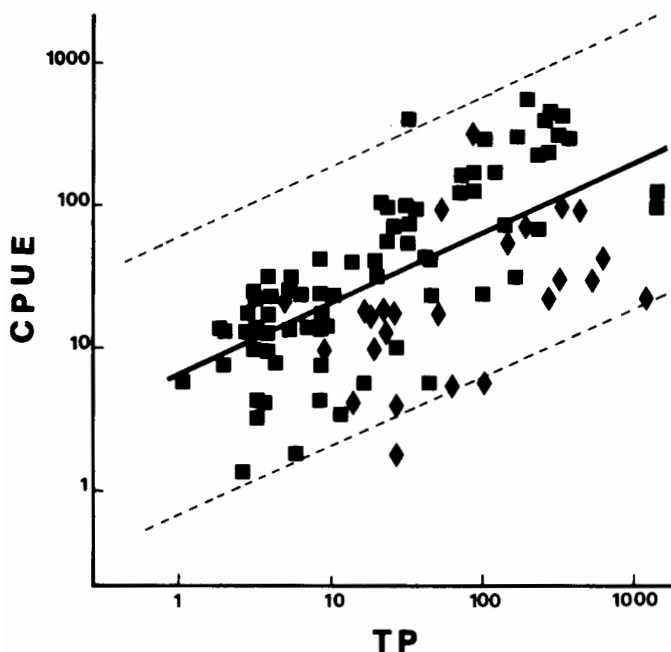


FIG. 5. Relation between fish biomass (CPUE, kg/night per standard gillnets) and mid-summer total phosphorus (TP,  $\text{mg} \cdot \text{m}^{-3}$ ) for data set #2 ( $n = 99$ ). ( $\blacklozenge$ ) lakes and reservoirs with  $\text{DO}_b < 2 \text{ mg} \cdot \text{L}^{-1}$  (bottom dissolved oxygen) or  $\text{CHL}:\text{TP} < 0.05$  (chlorophyll to total phosphorus ratio). Broken lines show 95% confidence limits.

highly negative when compared with  $\text{NUM} > 1$  lakes. When lakes with  $\text{NUM} = 1$  were removed, TP explained 76% of CPUE variability (#4LA,  $n = 37$ ), and the inclusion of ZMEAN and  $\text{DO}_b$  accounted for an additional 5%. In this last data set TEMP was still negatively related to  $\text{DO}_b$  ( $r = -0.45$ ,

$P < 0.001$ ), and mean frequency of salmonids at sampling was 0.44.

Simple regression models for CPUE were developed mainly to compare with existing models in the literature (Table 5). For CPUE against ZMEAN, there was no evidence against a coincident ( $n = 99$ ) regression model ( $F(2,95) = 3.10 > F = 1.74$ ;  $P = 0.05$ ), and the difference in means of residuals of regression models for lakes and for reservoirs was not significant ( $F = 3.51 < F(1,96) = 3.94$ ;  $P = 0.05$ ). For CPUE against TP a unique regression model is not adequate ( $F(2,95) = 3.10 < F = 4.58$ ;  $P = 0.05$ ), but there was no significant difference between slopes for lake and for reservoir models ( $F = 0.37 < F(1,95) = 3.90$ ;  $P = 0.05$ ). TA was the most important single variable to explain CPUE variability in reservoirs, before  $\text{DO}_b < 2.0 \text{ mg} \cdot \text{L}^{-1}$  screening ( $\log_e \text{CPUE} = 2.509 + 0.955 (\text{SE} = 0.279) \log_e \text{TA}$ ;  $r = 0.30$ ,  $n = 29$ ,  $\text{RMSE} = 1.025$ ,  $P = 0.002$ ). For total sets and for lakes, CPUE variance explained and regression equation slope increased with the screening process (Table 5). The slopes were in general higher for the lake subset than for the reservoir subset equations.

There were no significant differences between regression models of fish biomass on environmental variables for sites with and without atherinids. Atherinids at sampling (% ATE) was highly correlated with TEMP, CHL, and TDS (Table 3), and correlation coefficients practically did not change with data screening. For set #3 ( $n = 74$ ) two subsets, with (#ATE) and without (#NOATE) atherinids, were considered. CPUE was most related to TEMP, TP, and CHL in the #ATE subset, and to ZMEAN and TON in #NOATE, but in each case there was no evidence against a coincident simple regression model. *F*-ratio was 0.03, 0.47, 1.39 and 1.50 for TON, TP, ZMEAN, and CHL models, respectively against  $F(2,68) = 3.12$



TABLE 6. Multiple regression equations relating CPUE (kg/night per standard gillnets) to total organic nitrogen (TON,  $\mu\text{M}$ ), total phosphorus (TP,  $\text{mg} \cdot \text{m}^{-3}$ ), mean depth (ZMEAN, m), bottom dissolved oxygen (DOb,  $\text{mg} \cdot \text{L}^{-1}$ ), chlorophyll to total phosphorus ratio (CHL:TP), total nitrogen to total phosphorus ratio (TN:TP, molar basis), and frequency of atherinids (%ATE). The coefficient of determination ( $R^2$ ), and the root mean square error of regression (RMSE) are presented.

Equation	$R^2$	RMSE	$F^a$
set #2 ( $n = 99$ )			
log <sub>e</sub> CPUE = $-0.764 + 0.903 \log_e \text{TON} + 0.102 \text{DOb}$	0.534	0.966	54.97
log <sub>e</sub> CPUE = $1.079 + 0.595 \log_e \text{TP} + 0.142 \text{DOb}$	0.524	0.982	34.87
log <sub>e</sub> CPUE = $-0.968 + 0.769 \log_e \text{TON} + 0.119 \text{DOb}$ + $0.651 \% \text{ATE} + 0.120 \text{NUM}$	0.568	0.941	30.86
log <sub>e</sub> CPUE = $3.191 - 0.550 \log_e \text{ZMEAN} + 0.109 \text{DOb}$ + $0.806 \% \text{ATE} + 0.152 \text{NUM}$	0.562	0.947	30.11
set #2LA ( $n = 70$ )			
log <sub>e</sub> CPUE = $-1.013 + 0.943 \log_e \text{TON} + 0.112 \text{DOb}$	0.619	0.897	54.31
log <sub>e</sub> CPUE = $-0.617 + 0.918 \log_e \text{TON} + 0.128 \text{DOb}$ + $0.213 \log_e \text{CHL/TP}$	0.646	0.870	40.20
log <sub>e</sub> CPUE = $-0.865 + 0.766 \log_e \text{TON} + 0.110 \text{DOb}$ + $0.780 \% \text{ATE} + 0.117 \text{NUM}$	0.656	0.865	30.91
set #3 ( $n = 74$ )			
log <sub>e</sub> CPUE = $1.921 + 0.819 \log_e \text{TON}$ - $0.331 \log_e \text{TON/TP}$	0.627	0.904	59.79
set #3LA ( $n = 47$ )			
log <sub>e</sub> CPUE = $1.340 + 0.639 \log_e \text{TP} + 0.644 \% \text{ATE}$ + $0.112 \text{NUM}$	0.756	0.740	44.37

<sup>a</sup>F-test,  $P \leq 0.01$ .

TABLE 7. Correlation coefficients ( $r$ ) of chlorophyll to total phosphorus (CH/TP), total zooplankton biomass to chlorophyll (TOZOO/CHL), fish biomass to chlorophyll (CPUE/CHL), and fish biomass to total zooplankton biomass (CPUE/TOZOO) ratios, with several variables defined in the text, for ARLARE data set #2 ( $n = 99$ ).

	TOZOO/ CHL	CPUE/ TOZOO	CPUE/CHL	CHL/TP
ZMEAN	0.07	0.38 <sup>b</sup>	0.40 <sup>a</sup>	-0.15
TEMP	-0.39 <sup>b</sup>	-0.33 <sup>b</sup>	-0.63 <sup>a</sup>	0.29 <sup>c</sup>
TP	-0.17	-0.37 <sup>b</sup>	-0.47 <sup>a</sup>	-0.08
TON	-0.16	-0.37 <sup>b</sup>	-0.47 <sup>a</sup>	0.15
CHL	-0.46 <sup>a</sup>	-0.36 <sup>b</sup>	-0.72 <sup>a</sup>	0.50 <sup>a</sup>
TN:TP	0.13	0.24	0.33 <sup>b</sup>	0.33 <sup>b</sup>
DOb	0.33 <sup>b</sup>	0.33 <sup>b</sup>	0.58 <sup>a</sup>	-0.38 <sup>b</sup>
%ATE	-0.34 <sup>b</sup>	-0.12	-0.39 <sup>b</sup>	0.38 <sup>b</sup>

<sup>a</sup>t-test,  $P < 0.001$ .

<sup>b</sup>t-test,  $P < 0.001$ .

<sup>c</sup>t-test,  $P < 0.01$ .

( $P = 0.05$ ). Similar results were obtained for set #2 ( $n = 99$ ) analysis.

#### Factors Related to CPUE:CHL and CPUE:TOZOO Ratios

Both fish/phytoplankton and fish/zooplankton biomass ratios were negatively related to nutrient concentrations and temperature, and positively related to mean depth (Table 7). CPUE and CHL spanned three and four orders of magnitude, respectively, for the ARLARE data set #2 (Table 1), and CPUE:CHL ratio ranged from 0.11 to 116. It was higher for Patagonia (from 1.5 to 115.7), than for Pampa Plain and arid regions (from 0.31 to 22.9, and from 0.11 to 33.4, respectively). CHL has been the most relevant variable related to CPUE:CHL variation in the studied lakes and reservoirs (Table 5, Fig. 6a). The negative relationship was maintained for most homogeneous data sets

(Table 5). The analysis of the limits of CPUE:CHL distribution for untransformed data clearly shows negative dependence on CHL. The 25 lakes and reservoirs that have CPUE:CHL > 30, have CHL < 2.5  $\text{mg} \cdot \text{m}^{-3}$ , and the 10 lakes with CPUE:CHL < 6 also have CHL > 60  $\text{mg} \cdot \text{m}^{-3}$ .

For relative fish biomass to total zooplankton biomass ratio (CPUE:TOZOO) the pattern of variable dependence was qualitatively similar to that obtained for CPUE:CHL ratio but relationships were weaker (Table 7). TOZOO explained 48% of CPUE variation for data set #2 (log<sub>e</sub> CPUE =  $1.381 + 0.494$  (SE = 0.059) log<sub>e</sub> TOZOO;  $n = 99$ ,  $F = 69.89$ ,  $P < < 0.001$ ) and 46% for #3LA (log<sub>e</sub> CPUE =  $1.685 + 0.458$  (SE = 0.074) log<sub>e</sub> TOZOO;  $n = 47$ ,  $F = 38.62$ ,  $P < 0.001$ ). Obviously, CPUE:TOZOO diminished when TOZOO increased (Fig. 6b).

#### Discussion

Catch per unit effort, as estimated by gillnetting, is not an unbiased estimate of fish biomass. It is possible that relative fish biomass bias increases with the true biomass; this will result in the slope of the log-log equations for CPUE being below the true slope by an amount for any correlate. However, for the most homogeneous sets, simple regression equations for relative fish biomass have slopes similar to equations for yield and fish biomass developed from northern hemisphere lake comparisons. In the CPUE against TON regressions, the slopes were in general not significantly different from one. Similar results were shown by Hrbacek (1969) for fish yield and Kjeldahl nitrogen relationships in ponds. The TP exponent in the CPUE on TP models for most homogeneous sets (Table 5) ranged from 0.66 to 0.72 for total data and from 0.70 to 0.76 for lakes; it is 0.71 for the Hanson and Legett (1982) equation of fish standing crop on total phosphorus, and 0.70 for Lee and Jones (1981) equation of fish yield on phosphorus load, developed with Oglesby's (1977) fish data. However, CHL exponent in CPUE

