

The Effects of Fish Assemblage Composition on Lake Water Quality

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ABSTRACT

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Current trophic cascade theories predict that changes in the piscivore to planktivore biomass ratio will cascade down the food web, and will cause both chlorophyll and water clarity to deviate from nutrient - predicted values in individual lakes. An extensive survey of mid summer observations for nutrients, phytoplankton, zooplankton, and fish in Argentinean lakes and reservoirs, were used to study the effects of planktivorous and piscivorous fishes on chlorophyll concentrations and Secchi disk transparency. Regression analysis for different subsets of the data was used in this study. Regressions of chlorophyll on total phosphorus and Secchi disk on total phosphorus differed significantly among lakes with different fish assemblages. At comparable total phosphorus concentrations, lakes with planktivores but without piscivores had the highest phytoplankton biomass and the lowest water clarity. In conclusion, the results show that the fish assemblage composition has a dramatic effect on chlorophyll concentrations and water transparency when nutrient effects have been accounted for.

Key Words: TP-Chl relationships, chlorophyll, water transparency, total phosphorus, planktivore fish, lake comparisons, Argentinean lakes.

Regressions between the chlorophyll *a* concentrations (Chl) or the Secchi disk transparencies (SDT) and the total phosphorus concentrations (TP) of many lakes, are important tools to predict those water quality parameters from nutrient loading information (Vollenweider 1969, Dillon and Rigler 1975, OECD 1982). However, many different chlorophyll-on-total phosphorus regressions now exist (Dillon et al 1988), and several factors have been shown to be responsible for residual variance in these models (see Nicholls and Dillon (1978) and Quirós (1990b) for overviews). Some of these factors are usually associated with interrelated internal processes specific to individual lakes, like oxygen conditions at the sediment-water interface (Riley and Prepas 1984, Nurnberg 1988), submersed macrophyte development (Canfield et al 1984), nitrogen limitation (Smith 1979, 1982), water color (Canfield and Hodgson 1983), phosphorus availability (Peters 1981), or ecosystem biotic structure (Shapiro 1980, Pace 1984).

The effect of fish on lower trophic levels has been shown in whole-lake studies (Hrbacek et al 1961, 1978, Shapiro and Wright 1984, Carpenter et al 1987, Benndorf et al 1988, Vanni et al 1990, among others), and inter-lake comparisons (Quirós 1990b, 1991, Lyche et al 1990, Quirós submitted). Fish effects on algal biomass at different time and space scales have been

reviewed by Northcote (1988), and the role of fish in the regulation of phosphorus availability in individual lakes was studied by Kitchell et al (1979) and Nakashima and Leggett (1980). Current "biomanipulation" theories (Shapiro 1980, Carpenter et al 1985, McQueen et al 1986) predict that changes in piscivore to planktivore biomass ratio will cascade down the food web and will cause chlorophyll concentrations to deviate from nutrient-predicted values (McQueen et al 1989).

The main purpose of this paper is to describe the relations of fish community composition to algal biomass and water clarity, at comparable TP concentrations, in an inter-lake comparison. The data set is comprised of mid-summer observations of nutrients, phytoplankton, zooplankton, and fish in lakes and reservoirs of Argentina (Quirós 1988, 1990a, Quirós et al 1988, Quirós submitted).

Description of Study Area

The study lakes and reservoirs represent a wide range of trophic conditions (Table 1) and are located between 25 and 55 ° S latitude throughout the central-western and northwestern arid regions of Argentina,

the Pampa Plain, the Patagonian Plateau, the Patagonian Andes, and Tierra del Fuego. More than half of the northwestern reservoirs had very low dissolved oxygen concentrations in the hypolimnion at the time of sampling. Most of the fish species there have been introduced from outside Argentina or from other river basins in Argentina (Quirós et al 1988). The deepest lakes are situated in the Patagonian Andes and Tierra del Fuego. A majority of these lakes has been successfully colonized by introduced salmonids (Baigun and Quirós 1985). All sites in the Pampa Plain are shallow eutrophic to hypertrophic lakes, and they are practically the only Argentinean lakes with a relatively high fish community diversity (Ringuelet 1975). Two species of the Atherinidae family, *Odontesthes bonariensis* (Argentinean silverside) and *Odontesthes microlepidotus* (Patagonian silverside), have been reported to be visual zooplanktivorous and microbenthophagous (Ringuelet et al 1967, Ferriz 1987). The former species is common to most lakes and reservoirs in the Pampa Plain and in the arid central-western and northwestern regions. The latter is common to most Patagonian lakes except Tierra del Fuego lakes. Other zooplanktivorous fish species such as the small Characidae in the Pampa lakes and northern reservoirs, and the native Galaxiidae and Aplochitonidae in the Patagonian lakes, were either absent in the samples or their catch was not repre-

sentative of their abundance in the study lakes. On the other hand, piscivory is not widespread in Argentinean waters. Species of the genera *Salmo* and *Salvelinus*, often piscivorous as adults, are relatively common in southern glacial lakes, but rainbow trout (*Oncorhynchus mykiss*) are usually the most common salmonid species found there. Moreover, the large mouth Patagonian perch (*Percichthys colhuapiensis*), a fish native to Patagonia, has been reported to be piscivorous as an adult (R. A. Ferriz, pers. comm., MACNBR, Ictiologia, Av. Angel Gallardo 470, 1405 CF, Buenos Aires, Argentina). It was relatively abundant in lakes and reservoirs of the Patagonian Plateau (Quirós et al 1988). *Hoplias malabaricus*, a perch-like piscivore of the Erythrinidae family associated with macrophyte beds, was only abundant in the Pampa Plain. Piscivory is practically non-existent in central-western and northwestern reservoirs (Quirós et al 1988).

Methods and Data Management

Limnological and fish data used in this study were collected during an extensive mid-summer survey of 110 lakes and reservoirs in Argentina (ARLARE data)

Table 1.—Mean and range for some limnological and fish characteristics measured in Argentinean lakes and reservoirs.

Sites	with planktivores but without piscivores (n = 42)		with both piscivores and planktivores (n = 16)		without planktivores (n = 38)	
Area (km ²)	66.6	(0.09 - 1984)	167.1	(1.4 - 816)	35.9	(0.3 - 580)
Mean depth (m)	12.2	(1.1 - 59.0)	38.4	(1.2 - 157)	41.6	(0.7 - 166)
Secchi disk (m)	2.3	(0.18 - 16.5)	3.9	(0.15 - 19.0)	8.2	(0.17 - 14.5)
Total phosphorus (mg m ⁻¹)	104	(3 - 1250)	163	(1 - 1288)	41	(2 - 350)
TN:TP ratio (molar)	65	(16 - 186)	85	(9 - 235)	119	(5 - 273)
Chlorophyll <i>a</i> (mg m ⁻³)	40.6	(0.29-405)	26.3	(0.16 - 166)	5.8	(0.21-113)
Planktivore biomass (kg night ⁻¹ per standard gillnet)	59.2	(0.1-435)	37.3	(0.20 - 205)	-	
Piscivore biomass (kg night ⁻¹ per standard gillnet)	-		14.6	(0.69 - 51.6)	15.5	(0 - 277)
Mean macrozooplankton body weight (µg dry weight ind ⁻¹)	2.3	(0.8 - 3.9)	2.8	(1.5 - 4.5)	4.4	(1.0 - 16.3)
Dissolved oxygen at sediment-water interface (mg L ⁻¹)	5.2	(0.01 - 10.3)	7.8	(0.06 - 12.2)	8.8	(2.8 - 11.1)

from 1984 to 1987 (Quirós 1988, 1990a, 1990b, Quirós et al 1988). Each site was visited once. Sampling stations were situated over the deepest part of the basin for lakes, and within 500 m to 2 km from the impounding dam for reservoirs. Secchi disk transparency (SDT, m) was determined with a 25 cm black-and-white disk. Chlorophyll *a* (Chl, mg m^{-3}), total phosphorus (TP, mg m^{-3}), total organic nitrogen, nitrate, and nitrite were determined from samples collected at a depth of 0.5 m. Nutrients were determined according to APHA (1975) and Golterman et al (1978). Chlorophyll *a* (uncorrected for phaeopigments) was measured according to Stauffer et al (1979). The analytical methods used have been described previously (Quirós 1988, 1990a).

Fish samples were collected using an experimental nylon gillnet composed of nine 50 m panels ranging from 42 to 170 mm stretched mesh. Floating sets were made overnight, usually for 12 h. A measure of relative standing stocks of fish by biomass was made on the basis of the mean weight of all fish caught per overnight set for the experimental gillnets. Equal fish vulnerability to gillnets among all lakes was assumed. Further details on the method of fish sampling are provided in Quirós (1990a).

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, epilimnetic waters were usually sampled. A 100% capture efficiency was assumed. Macrozooplankton biomass was calculated from size and abundance data (Menu Marque and Marinone 1986, Quirós et al 1988). Cladocerans and post naupliar copepods and considered to be macrozooplankton. Further details on the method of zooplankton sampling are provided in Menu Marque and Marinone (1986).

Sites with high inorganic turbidity were excluded as outliers (Quirós 1990b). Two lakes with incomplete data for zooplankton, one acidic lake without fish, and one lake situated in the Pampa Plain (Indio Muerto Lake) with extremely low macrozooplankton biomass and the only lake with *Mugil* sp. at sampling, were also excluded (Quirós 1990b, 1991). The resulting data base consisted of 96 lakes and reservoirs.

Regression analyses were made of the entire data set and of three fish data subsets (Table 1). These fish subsets were defined as: 1) lakes with planktivorous fishes and without piscivores ($n = 42$); 2) lakes with both piscivores and planktivores ($n = 16$); and 3) lakes without planktivores, but with or without piscivores ($n = 38$). To study trophic state effects, three TP data subsets were also analyzed. A general F-test (Weisberg 1980) was used to compare regression models. Stepwise multiple regression analysis was applied to the total data and the data subsets using aspects of climate, lake

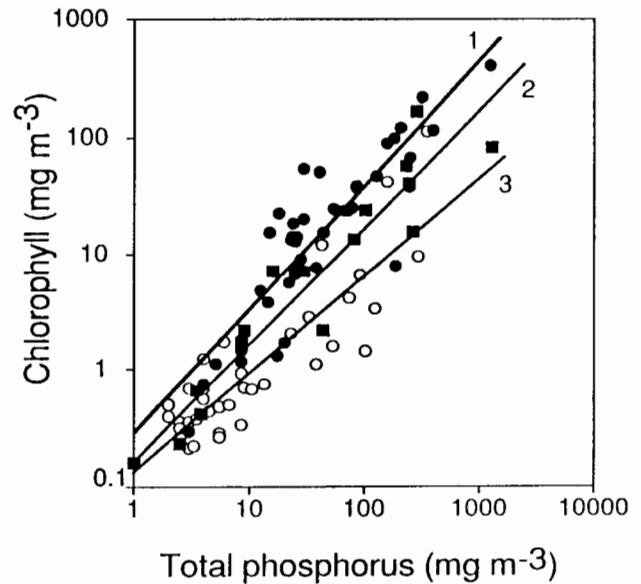


Fig. 1.—The relationship between total phosphorus and chlorophyll concentrations for study lakes and reservoirs. The regression lines for: 1. sites with planktivores but without piscivores (●), 2. sites with both planktivores and piscivores (■), and 3. sites without planktivores and with or without piscivores (○), are presented.

morphometry, nutrient content, fish assemblage composition, and biological standing stocks as potential regressors. The collection frequencies of planktivores (Argentinean silverside and Patagonian silverside) and of piscivores (*Hoplias malabaricus*, *Salmo trutta*, *Salmo salar sebago*, *Salvelinus fontinalis*, *Salvelinus namaycush*, and *Percichthys colhuapiensis*), and the ratio of the biomass

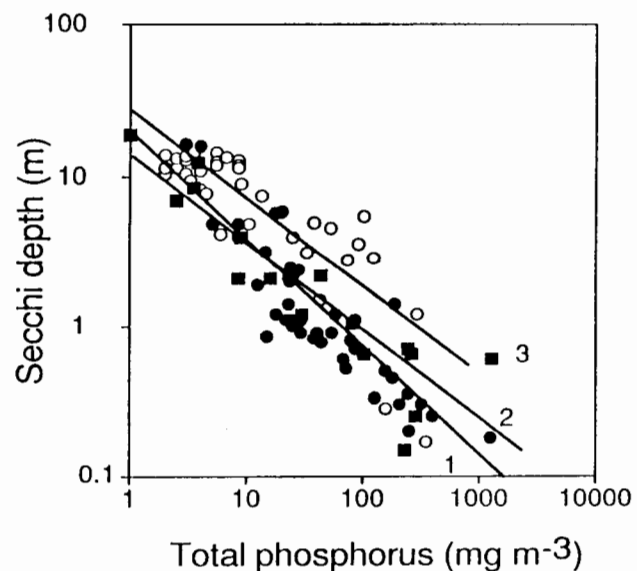


Fig. 2.—The relationship between total phosphorus concentration and Secchi disk transparency for study lakes and reservoirs. The regression lines for: 1. sites with planktivores but without piscivores (●), 2. sites with both planktivores and piscivores (■), and 3. sites without planktivores and with or without piscivores (○), are presented.

of piscivores to that of planktivores plus piscivores were used as surrogates of fish assemblage composition. The latter ratio was assigned a value of unity in lakes without both planktivores and piscivores. Mean macrozooplankton size (MASI) was estimated by mean body weight (μg dry weight per individual) as the ratio between biomass (μg dry weight L^{-1}) and abundance (number of individuals L^{-1}). The dissolved oxygen concentration at 0.50 m above the bottom was used as a rough index of oxygen concentration at the water-sediment interface, and the lake mean depth to Secchi depth ratio (ZMEAN/SDT) was used as a surrogate for submersed macrophyte development (Quirós 1990b) and subsurface light availability (Reynolds and Walsby 1975). To stabilize the variance, all the variables except dissolved oxygen concentration and fish biomass ratios were log-transformed, and proportions were transformed to their arc-sine (Draper and Smith 1981). In multiple regression models, only significant variables (partial F-value > 4) with low covariation with previously included regressor variables ($R^2 < 0.40$), were forced into the regression equation. The Number Cruncher Statistical System (NCSS) (Hintze 1988) was used.

Results

Fish Data Subsets

The total phosphorus - chlorophyll (Fig. 1, Table 2) relationship differed significantly among regressions for lakes with different fish assemblages ($F = 14.2$, $P < 0.0001$). A three TP-Chl lines regression model fits to the data much better (Fig. 1). Lakes with planktivores but without piscivores showed the highest phytoplankton biomass, at comparable TP concentrations. As shown before (Quirós submitted), the TP-Chl regressions differed more between sites with planktivores but without piscivores, and sites with both ($F = 5.66$, $P < 0.01$), than between the latter sites and those without planktivorous fishes ($F = 4.66$, $P < 0.05$).

On the other hand, the total phosphorus - Secchi disk (Fig. 2) relationship also differed significantly among regressions for lakes with different fish assemblages ($F = 10.2$, $P < 0.0001$). Lakes with planktivores but without piscivores showed the lowest

Table 2.—Simple regression models for chlorophyll *a* concentration (mg m^{-3}) and Secchi disk transparency (m) on total phosphorus concentration (mg m^{-3}). All the variables were log_e transformed.

Data Set	n	Parameters		SE slope	R ²
		a	b		
chlorophyll					
Total	96	-1.949	1.08	0.06	0.78
PLANKT+/PISC-	42	-1.347	1.08	0.09	0.77
PLANKT+/PISC+	16	-1.738	0.98	0.09	0.90
PLANKT-/PISC±	38	-1.897	0.83	0.08	0.73
Secchi disk					
Total	96	3.178	-0.72	0.04	0.77
PLANKT+/PISC±	58	2.760	-0.68	0.05	0.79
PLANKT-/PISC±	38	3.220	-0.58	0.06	0.71

Note: all the regressions significant with $P < 0.001$ (F-test)

PLANKT+ = sites with planktivores, PLANKT- = sites without those fish

PISC+ = sites with piscivores, PISC- = sites without those fish

PISC± = sites with or without piscivores

Table 3.—The coefficient of determination (R^2) for simple regression models of chlorophyll *a* and Secchi disk depth on total phosphorus (TP) for fish and TP data subsets.

	TP data subsets			Fish data subsets		
	TP<9	9≤TP≤50	TP>50	PLANKT+ PISC-	PLANKT+ PISC+	PLANKT- PISC±
Chlorophyll	0.39	0.23	0.37	0.77	0.90	0.73
Secchi disk	0.23	0.27	0.32	0.78	0.83	0.71

PLANKT+ = sites with planktivores, PLANKT- = sites without those fishes

PISC+ = sites with piscivores, PISC- = sites without those fishes

PISC± = sites with or without piscivores

transparency, at comparable TP concentrations. However, this regression did not differ from that from lakes with both planktivores and piscivores ($F = 1.67$, $P = 0.21$). Therefore, a two-line regression model, one for lakes with planktivores and the other for lakes without those fishes, fits the transparency data better (Table 2).

As expected, there were no significant differences among regressions when the chlorophyll concentration-Secchi disk transparency relationship was analyzed.

Total Phosphorus Data Subsets

Multiple regression techniques were used to study the relative effects of total phosphorus and other internal variables on chlorophyll concentration and Secchi disk transparency (Quirós 1990b, 1991, Quirós

submitted, this study). For the overall data set and for subsets of different fish assemblages, total phosphorus was the best single predictor of chlorophyll concentration and Secchi disk transparency (Tables 3 and 4). However, the variability explained by TP decreased appreciably when subsets of the data representing smaller ranges of TP data subsets were analyzed. This was unexpected, but a more surprising result was that other variables were more effective than total phosphorus in explaining chlorophyll and Secchi disk variation (Table 4). This is especially for TP ranging between 9 and 50 mg m⁻³, where sharp changes in planktivore and piscivore biomass are displayed (Table 5). In summary, the effectiveness of total phosphorus in explaining the changes in algal biomass and in water clarity decreases drastically when sudden changes in piscivore to planktivore ratio occur (Table 5).

Table 4.—The most important variables explaining chlorophyll (Chl) and Secchi disk (SDT) variability.

Data Set	Chl	SDT
Total	TP	TP
Fish subsets	TP	TP
TP < 9	TN:TP, DO _b	TP
9 < TP < 50	PI/(PI+PL) %PL, MASI	PI/(PI+PL) %PL, %PI, MASI
TP > 50	ZMEAN/SDT	ZMEAN/SDT

TN:TP = total nitrogen to total phosphorus ratio

PI/(PI+PL) = piscivore to piscivore plus planktivore ratio

%PL = frequency of planktivorous fish

%PI = frequency of piscivorous fish

MASI = mean macrozooplankton body weight

ZMEAN/SDT = mean depth to Secchi depth ratio

Discussion and Conclusions

Fish assemblage composition greatly affects algal biomass and water clarity in cross-lake comparisons (Quirós 1990b, 1991, Quirós submitted, this study), in enclosures and in whole-lake biomanipulations (Anderson et al 1978, Shapiro and Wright 1984, Carpenter et al 1987, Vanni et al 1990, McQueen et al 1990a for an overview), as expected from the current trophic cascade theories (Shapiro 1980, Carpenter et al 1985, McQueen et al 1986). However, other variables are also important (Quirós 1990b, Quirós submitted).

The results suggest that the fish affect algal biomass through food web interactions. The highest differences in chlorophyll were found between lakes where planktivores were not controlled by piscivores and lakes where planktivores were controlled or absent. On the other hand, the effects of fish on water clarity may be related both to trophic cascades and to bottom

disturbance where atherinid fish feed on the benthos. There were no significant differences in water clarity between lakes where planktivores were uncontrolled and those where planktivores were controlled.

The regression models for the fish subsets predict better than the single regression model based on all the data. For chlorophyll, the three lines for different fish classes explain from a two-fold difference in oligotrophic lakes of similar TP concentration to more than an eight-fold difference in hypertrophic lakes. On the other hand, the regressions explain differences of 1.5 to 3 times for Secchi disk range. Those results are more closely related to increases in the relative abundance of planktivorous fish with lake trophic state than to an increase of the trophic state itself.

Both total nitrogen concentration and the TN:TP ratio had slight effects on chlorophyll and Secchi disk variability after TP effects had been accounted for (less than 1%). However, TN:TP ratio was a significant variable when included in multiple regression models after TP, fish, and zooplankton variables (Quirós 1990b). An unexpected result was that TN:TP explained some residual variability in chlorophyll and Secchi disk only for lakes where planktivores were not controlled and where the mean TN:TP was the lowest (Table 1). TN:TP was not effective for the other two types of lakes.

The three regression lines for different fish assemblages and the multiple regressions are all consistent in their descriptions of lake data. The three

regressions pattern for separated fish assemblages is confirmed by results from multiple regression analyses: the models for both chlorophyll concentration and Secchi disk transparency include TP, the ratio of piscivore biomass to piscivore plus planktivore biomass, and the mean macrozooplankton body weight as independent variables (Table 5). These models fit the data better than the several regression lines (Table 2). The effects of these internal variables might not be evenly distributed along the trophic continuum (Quirós submitted, this study), and also might reflect complex interactions among system components in individual lakes (Carpenter and Kitchell 1988).

Similar fish effects are displayed for a set of Norwegian lakes with different intensities of fish predation (Lyche et al 1990, Fig. 1a). Planktivore effects on water clarity and on chlorophyll deviations from current TP - Chl regressions have been shown by McQueen et al (1990a) for a small lake set.

The control of nutrient loading combined with the manipulation of fish communities has been recommended to improve water quality in eutrophic lakes (Benndorf 1987, 1988, 1989, McQueen et al 1990a, Shapiro 1993 among others). However, the management of lake water quality by biomanipulation techniques is still controversial (McQueen et al 1986, Benndorf 1987, DeMelo et al 1992, Carpenter and Kitchell 1992, Shapiro 1993, MS). My results reinforce the worldwide importance of total phosphorus in

Table 5.—The percent change in the root mean square error (%RMSE) that would result if the indicated variable were removed from the multiple regression equation.

Independent variables	Lake sets							
	Total (n = 96)		9 ≤ TP ≤ 50 (n = 32)		PLANKT+/PISC- (n = 42)		PLANKT+/PISC+ (n = 16)	
	Chl	SDT	Chl	SDT	Chl	SDT	Chl	SDT
TP	118.4	100.0	17.8	20.7	111.5	120.6	202.9	131.8
MASI	5.6	4.4	7.5	7.3	5.8	7.5	ns	ns
PI/(PI+PL)	11.6	5.4	13.0	7.2	-	-	ns	ns
TN:TP	*	*	ns	ns	*	*	ns	ns
COLOR	**	*	ns	ns	ns	ns	ns	ns
R ²	0.867	0.837	0.629	0.594	0.800	0.817	0.898	0.826

Note 1: all the regressions significant with $P < 0.001$ (F-test)

Note 2: Not included variables: *, significant ($P < 0.05$) but high covariation

** , significant ($P < 0.05$) but positively related

ns, not significant ($P > 0.05$) for the presented models

TP = total phosphorus, MASI = mean macrozooplankton body weight, COLOR = water color

PI/ (PI+PL) = piscivore to piscivore plus planktivore biomass

PLANKT+ = sites with planktivores, PISC+ = sites with piscivores, PISC- = sites without piscivores

determining algal biomass in lakes and show dramatic effects of fish on algal biomass and water clarity. However, the change in piscivorous to planktivorous fish biomass appears to be more an effect than a cause of the eutrophication processes (Quirós submitted) and this conclusion raises important questions concerning how changes in fish assemblage composition are related to trophic state changes for lakes.

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