

Trophic cascade effects in a continuous series of temperate-subtropical water-bodies

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Introduction

Curvilinear relationships between total phosphorus and chlorophyll concentrations have been found for large lake data sets. PRAIRIE et al. (1989) suggested that curvilinear patterns can be explained by the different requirements of P and N for the individual algal species, and WATSON et al. (1992) hypothesized that non-linearity reflects an underlying systematic variation in the biomass of functional algal groups. Furthermore, MAZUMDER (1994) suggested that sigmoid patterns appear to be related to the transition from stratified to mixed lakes along the TP gradient. Curved lines for TP-Chl data were previously shown by STRASKRABA (1976) for more homogeneous sets of lakes, though he explained these patterns in relation to light limitation and mixing depth. However, MCCAULEY et al. (1989) called for an elucidation of the underlying biological mechanisms that produce the non-linear response with TP. Moreover, current trophic cascade theories (SHAPIRO 1980, CARPENTER et al. 1985, McQUEEN et al. 1986) predict that changes in the piscivore to planktivore biomass ratio will cascade down the food web, and will cause both chlorophyll concentrations (Chl) and Secchi disk transparencies (SDT) to deviate from nutrient-predicted values in individual lakes (McQUEEN et al. 1989). QUIRÓS (1995) found that lakes with visual

planktivorous fish, but not piscivores, showed the highest Chl and the lower water transparency than did lakes without planktivores. The regression line for lakes with both types of fish lay in between.

The main purpose of this study is to test the hypothesis that non-linear patterns in TP-Chl and TP-SDT relationships are associated with changes in fish assemblage composition for lakes with relatively simple food webs and visual planktivorous fish as dominant planktivores. A secondary purpose is to show that fish assemblage composition affects algal biomass and water clarity for both temperate and subtropical lakes.

Materials and methods

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 Argentina. 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 re-

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

Sites	temperature (n = 56)	subtropical (n = 40)
Area (km ²)	71.2 (0.3–816)	71.3 (0.09–1984)
Mean depth (m)	43.0 (1.1–166)	7.6 (0.7–31.3)
Air temperature (°C)	7.4 (3.0–14.0)	16.5 (14.5–20.4)
Latitude (°S)	42.2 (34.2–54.7)	32.8 (24.1–39.0)
Secchi disk (m)	7.6 (0.28–19.0)	1.2 (0.15–4.6)
Total phosphorus (mg·m ⁻³)	32 (1–294)	168 (13–1288)
TN:TP ratio (molar)	111 (15–335)	60 (9–147)
Chlorophyll <i>a</i> (mg·m ⁻³)	5.4 (0.16–54.1)	51.1 (1.6–405)
Planktivore biomass (kg/night per standard gillnets)	12.1 (0–335)	60.1 (0–435)
Piscivore biomass (kg/night per standard gillnets)	8.9 (0–277)	8.0 (0–76.3)
Mean macrozooplankton body weight (µg dry weight·ind ⁻¹)	3.7 (0.8–16.3)	2.4 (0.8–4.7)

servoires in the Pampa Plain and in the arid central-western and north-western 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 very low 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*) has been reported to be piscivorous as an adult. It was relatively abundant in lakes and reservoirs of the Patagonian Plateau. *Hoplias malabaricus*, a perch-like piscivore of the Erythrinidae family, was only abundant in the Pampa Plain. Piscivory is practically non-existent in central-western and northwestern reservoirs (QUIRÓS et al. 1988).

Data and data management

An extensive survey of mid-summer observations for nutrients, phytoplankton, zooplankton, and fish in Argentinean lakes and reservoirs (ARLARE data, $n = 96$) were used (QUIRÓS et al. 1988). Each site was visited once. The sampling and analytical methods used have been described previously (QUIRÓS 1990 a, 1991, 1995). Fish samples were collected using an experimental nylon gillnet. 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. Further details on the method of fish sampling are provided in QUIRÓS (1990 a). Sites with high inorganic turbidity were excluded as outliers. Other details on data screening were reported previously (QUIRÓS 1990 b, 1995).

Curvilinear trends in data were studied using robust locally weighted regression and smoothing graphic techniques (LOWESS) (CLEVELAND 1979). The "smoothness" of the smoothed points increases with the "f parameter" and $f = 0.5$ was used here, as recommended (CLEVELAND 1979). Regression analyses were made at the entire data set and at two mean annual air temperature data subsets (Table 1). These air temperature subsets were defined as: 1) temperate lakes, including lakes with air temperatures below 14.0°C ($n = 56$), and 2) subtropical lakes, including lakes with air temperatures above

14.5°C ($n = 40$). The Number Cruncher Statistical System (NCS) (HINTZE 1988) was used. 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, nutrient content, and fish assemblage composition as potential regressors. The collection frequencies of planktivores (Argentinean silver-side 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 of planktivores to that of planktivores plus piscivores ($\text{PL}/(\text{PL}+\text{PI})$) were used as surrogates of fish assemblage composition. The latter ratio was assigned a value of zero in lakes without both planktivores and piscivores. To stabilize the variance, all the variables except fish biomass ratios were log-transformed, and proportions were transformed to their arc-sine (DRAPER & 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.

Results

Both chlorophyll concentration and Secchi disk transparency vary non-linearly with TP (Figs. 1 A and B). The LOWESS analyses also show that zooplanktivorous fish biomass (PL), piscivorous fish biomass (PI), and the ratio $\text{PL}/(\text{PL}+\text{PI})$ vary non-linearly with total phosphorus (Fig. 1 C). Moreover, the change in slope for TP-Chl and TP-SDT curves is concurrent to the change in slope for fish biomass curves (compare Figs. 1 A and 1 B with 1 C). Five main sections for each curve can be distinguished and are visually apparent (see Figs. 1 A, B, and C). An estimation of slopes was obtained for the curve sections where the increase in the independent variables was almost linear with TP (Figs. 1 A and 1 B). The increments in chlorophyll concentration per unit change in total phosphorus concentration and the decreases in Secchi disk transparency per unit change in TP are intensified where the increases of planktivore and the decreases of piscivore biomass per unit TP are higher (Fig. 1). Correlation analyses show that slopes for chlorophyll are positively related to slopes for the $\text{PL}/(\text{PL}+\text{PI})$ biomass

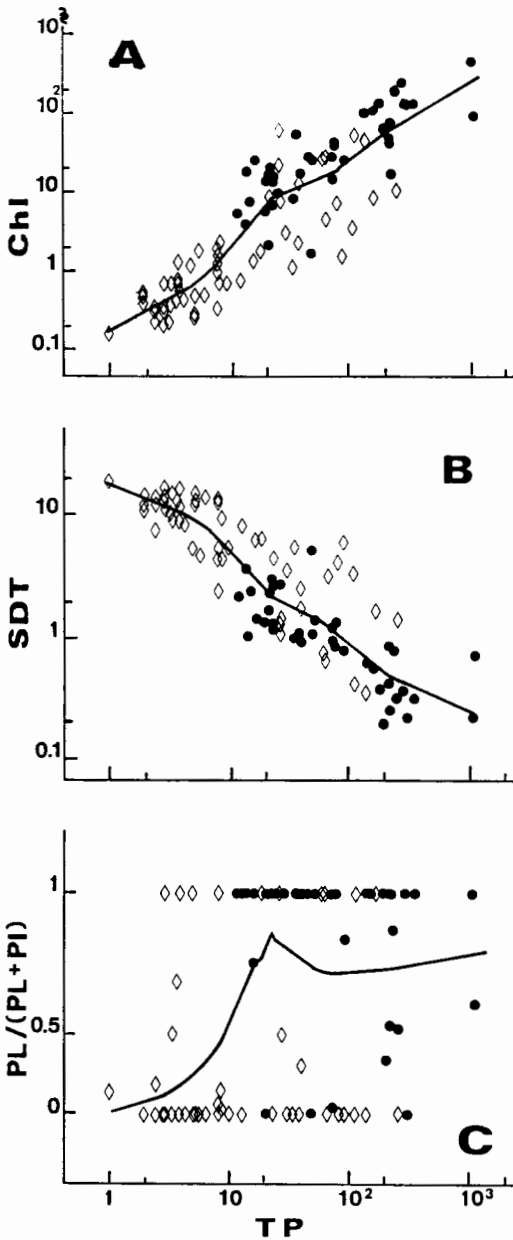


Fig. 1. Locally-weighted sequential smoothing fitted curves for the relationships between: A) TP and Chl, B) TP and SDT, and C) TP and PL/(PL+PI). (\diamond), temperate lakes. (\bullet), subtropical lakes. Chl, chlorophyll concentration ($\text{mg} \cdot \text{m}^{-3}$). TP, total phosphorus concentration ($\text{mg} \cdot \text{m}^{-3}$). SDT, Secchi disk transparency (m). PL/(PL+PI), biomass of planktivores to that of planktivores plus piscivores.

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

Data Set	n	Regression coefficients		SE slope	R ²
		a	b		
chlorophyll					
Total	96	-1.949	1.08	0.06	0.78
Temperate	56	-1.856	0.90	0.08	0.69
Subtropical	40	-0.333	0.82	0.10	0.65
Secchi disk					
Total	96	3.178	-0.72	0.04	0.77
Temperate	56	3.131	-0.62	0.06	0.68
Subtropical	40	2.199	-0.56	0.07	0.65

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

ratio ($r = 0.98$, $P < 0.01$). On the other hand, for the Secchi disk curve its slope was inversely related to the slope for the PL/(PL+PI) biomass ratio ($r = -0.81$, $P < 0.05$).

Both the TP-Chl and the TP-SDT (Table 2, Fig. 1 A and B) relationships differed significantly among regressions for lakes with distinct mean annual air temperatures ($F = 17.6$ and $F = 12.4$, $P < 0.0001$, respectively). Therefore, a two TP-Chl lines regression model and a two TP-SDT lines regression model fit the data better (Table 2). Chlorophyll concentration is higher and water clarity is lower for subtropical lakes than for temperate lakes. However, underlying fish effects are still apparent for both temperate and subtropical lake subsets. Therefore, multiple regression techniques were used to examine the relative effects of total phosphorus and fish variables on chlorophyll concentration and Secchi disk transparency (QUIRÓS 1995). For temperate lakes, PL/(PL+PI) increased Chl and SDT explained variances by 5% and 4%, respectively. On the other hand, the fish biomass ratio increased Chl explained variance by 10% for subtropical lakes (Table 3). However, for the latter, fish biomass ratio increased SDT variance by 6% after TP, water color and inorganic turbidity effects have been accounted for. Subsequently, multiple regression models including TP and PL/(PL+PI) as regressor variables were compared (Table 3). Differences between temperate and subtropical systems decreased sharply for both Chl and SDT ($F =$

Table 3. Multiple regression models for chlorophyll *a* ($\text{mg} \cdot \text{m}^{-3}$) on total phosphorus (TP, $\text{mg} \cdot \text{m}^{-3}$) and biomass of planktivores to that of planktivores plus piscivores (PL/(PL+PI)).

Data Set	n	Regression coefficients			R ²
		a	TP	PL/(PL+PI)	
Total	96	-2.136	0.94 (0.05)	0.80 (0.12)	0.85
Temperate	56	-1.944	0.85 (0.08)	0.53 (0.17)	0.74
Subtropical	40	-1.647	0.89 (0.09)	0.77 (0.21)	0.75

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

4.05, $P = 0.008$, and $F = 3.06$, $P = 0.025$, respectively). Moreover, non-linear patterns almost disappear when Chl was related to predicted Chl on both TP and PL/(PL+PI) biomass ratio. In conclusion, for both temperate and subtropical regions, lakes with visual planktivores but without piscivores showed the highest phytoplankton biomass and the lowest water clarity, at comparable TP concentrations.

Non-linear patterns in TP-Chl relationships related to contrasting thermal stratification regime were also tested here. However, there were not significant differences between stratified and mixed lakes for both total data ($F = 0.55$, $P \geq 0.10$), and temperate ($F = 2.72$, $P > 0.05$) and subtropical ($F = 1.59$, $P > 0.05$) lake subsets.

Discussion and conclusions

Curvilinear trends in total phosphorus – chlorophyll relationships have been related to various ecosystem processes by different authors: limiting physical factors (STRASKRABA 1976), lake mixing regime (MAZUMDER 1994), changes in algal nutrient requirements (PRAIRIE et al. 1989), changes in the balance between average growth and loss rates of algae related to internal mechanisms, like herbivory, that might change with lake enrichment (MCCAULEY et al. 1989), a systematic contribution of inedible algae to total phytoplankton biomass along the TP gradient (WATSON et al. 1992), and underlying changes in fish assemblage cascading through the food web (this study). The fish effects might also be related to the relative increase of P availability in TP with increasing levels of predation and foraging activity in planktivore-dominated lakes (QUIRÓS 1990 b, SCHINDLER et al. 1993). All these processes may be relevant to explain curvilinear relationships

in comparative lake studies. Nevertheless, the effects of these internal variables are not evenly distributed along the trophic continuum (QUIRÓS 1990 b). Mazunder's hypothesis relating TP-Chl non-linearity to thermal stratification was not confirmed with the data used here. However, the percent of blue-green algae in net phytoplankton along the TP gradient roughly corresponds with the hypothesis of WATSON et al. (1992).

The regression models for the temperate and subtropical subsets predict better than the single regression model based on all the data. However, those results are more closely related to changes in the relative abundance of visual planktivorous fish with site temperature than to a difference in the climate itself.

Although the results require testing against independent data for general applicability, they support early obtained results (QUIRÓS 1990 b, 1995) and suggest that the fish affect algal biomass and water clarity through food web interactions for both temperate and subtropical systems where visual planktivores are present. Fish assemblage composition greatly affects algal biomass and water clarity in cross-lake comparisons (LYCHE et al. 1990, Fig. 1 a, MCQUEEN et al. 1990, QUIRÓS 1990 b, 1991, 1995, this study), in enclosures and in whole-lake biomanipulations (ANDERSON et al. 1978, SHAPIRO & WRIGHT 1984, CARPENTER et al. 1987, VANNI et al. 1990, LAZZARO et al. 1992), as expected from the current trophic cascade theories (SHAPIRO 1980, CARPENTER et al. 1985, MCQUEEN et al. 1986). However, further research will be necessary to test the hypothesis that changes in fish community structure underlie non-linear responses with TP for both cool and warm lakes.

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