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FISH EFFECTS ON RESERVOIR TROPHIC RELATIONSHIPS

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ABSTRACT

To study the relationships between the biomass of reservoir communities and to examine the differences between reservoirs with different fish assemblages, we used limnological and fish data for 31 Argentinean reservoirs. Despite conspicuous systemic differences with lakes, reservoirs dominated by visual zooplanktivorous fishes have had phytoplankton biomass drastically higher than reservoirs with more balanced fish assemblages where piscivorous fish biomass were more noticeable. Contrary to earlier results for a more inclusive set of lakes and reservoirs (Quirós, 1998a), our results show macrozooplankton biomass was dramatically higher for reservoirs with planktivores not controlled by piscivores, when nutrient or chlorophyll concentrations were held constant. Macrozooplankton was not strongly suppressed by planktivores, but these fish may be suspected controlling macrozooplankton size. All the biological standing stocks were higher for reservoirs with planktivores but without piscivores when nutrients were held constant, with the exception of total fish. For the latter variable, there were not significantly differences between both types of reservoirs. Our results indicate that changes in fish assemblage composition will have dramatic effects on trophic relationships in reservoirs. Heavy biased introductions and stocking of facultative planktivores may conduct to unbalanced fish assemblages with undesired effects on water quality.

Key words: reservoirs, trophic relations, fisheries.

INTRODUCTION

For lakes, it is currently theorized that pelagic trophic level biomass are controlled from below by producers (bottom-up) and from above by consumers (top-down) (McQueen et al., 1986; Brett &- Goldman, 1997). The evidence supporting this assertion comprises results of studies for individual lakes and from mesocosm and enclosure experiments (Hrbáček *et al.,* 1961; Anderson *et al.,* 1978; Shapiro &Wright, 1984; Carpenter *et al.,* 1987; Vanni *et al.,* 1990; Lazzaro *et al.,* 1992; Meijer *et al.,* 1994, among many others). Trophic cascade hypotheses were mostly developed from north temperate lake data but Lazzaro (1997) has reviewed them in order to analyze their application to tropical lakes and reservoirs. Both bottom-up and top-down likely effects have been shown from empirically derived relationships based on data from many lakes and reservoirs (Quirós, 1990, 1998a; Lyche *et al.,* 1990; Mazumder & Havens, 1998). It has been suggested that fish assemblage composition effects might cascade down the food web for both lakes and reservoirs but bottom-up and top-down effects might be unsymmetrical in character (Quirós, 1998a). Top-down trophic interactions at the macrozooplankton-phytoplankton level have been suggested as equivocal (DeMelo et *al.,* 1992), but though endogenous lake processes may modify the relationships between nutrient concentration and biological standing stocks for an individual lake, the former is essentially determined by external forces (Vollenweider, 1969, 1975). The effects of fish on the structure of freshwater ecosystems was reviewed by Northcote (1988) and their role in the regulation of nutrient availability by Schindler *et al.* (1 993). It was also suggested that, on a broad basis, fish effects would be higher for low piscivores to planktivores plus benthiyores ratio independent of lake trophy (Quirós, 1998b).

After rivers damming, resulting reservoirs have been usually stocked in order to enhance fish production. Fish introductions and stockings, though usually justified in practical (socio-economical) grounds, only occasionally were evaluated in their practical outputs and rarely supported in sound ecological science (Welcomme & Bartley, 1998). Reservoirs are generally considered structurally and functionally different from most natural lakes (Wetzel, 1990). Reservoir primary production is often limited by inorganic turbidity and water renewal time is usually chosen as the master variable for explaining reservoir function (Straškraba, 1998). Reservoirs have been considered an exception to the trophic cascade pattern because of their usual omnivorous and filter-feeding planktivorous fish populations (Stein *et al.,* 1 995). Moreover, it has been suggested that trophic interactions in reservoirs depart from the strongly linked interactions common to natural lakes and prevalent omnivorous fish may not being strongly regulated by zooplankton and phytoplankton biomass (Dettmers & Stein, 1996). Reservoirs are human created aquatic ecosystems. Most riverine biological species tend to disappear while some few of them tend to adapt to the new environment. As that, new species assemblages are usually formed. The change from a high flow to a low flow system tends to selectionate a few riverine fish species previously adapted to floodplain habitats. Although zooplanktivorous fish populations could develop, natural high population densities for visual zooplanktivorous species are usually rare. Fish communities for lakes usually have developed under evolutionary times. Fish populations are usually well adapted to the lake environment. Moreover, for lake ecosystems higher resilience than for reservoirs may be suspected. Fish species assemblages for reservoirs have usually developed under shorter, ecological times (Stein *et al.,* 1996). For the latter, it may be suspected that fish species assemblages are most prone to external disturbances and cascading trophic effects higher than lake fish communities. For reservoirs, those disturbances are usually externally induced by human action throughout fish introductions and stocking. Prevalent pattern for planktivore to piscivore ratio in reservoirs is often highly dependent on human action.

For lakes and reservoirs, a systemic view of pelagic trophic interactions (Quirós, 1998a) predicts an stepped decrease of the rate of increase of community biomass with nutrient concentrations from phytoplankton to fish. Our primary purpose in this paper is to explore the application to reservoirs of the main thesis that although nutrients set limits on the biotic responses, the actual responses are also functions of the structure of the biotic community (Shapiro, 1980). A secondary purpose is to test the hypothesis that reservoirs dominated by facultative zooplanktivorous fish have greater phytoplankton biomass when nutrient concentration is held constant.

STUDY RESERVOIRS AND FISH ASSEMBLAGES

The study reservoirs (n = 31) are located between 25 and 43° S latitude, in the central-western (7) and northwestern (18) semi-arid regions of Argentina, the Patagonian Plateau (5), and the Patagonian Andes (1) (see Table I). The reservoirs situated in the Patagonian Andes and Plateau range from oligotrophic to mesotrophic. Most of the central-western and northwestern reservoirs range from mesotrophic to eutrophic, and more than half of the northwestern reservoirs had low dissolved oxygen concentrations in the hypolimnion at mid-summer. For northwestern silverside dominated reservoirs, several species of *Daphnia* are present during mid-summer (Bonetto *et al.,* 1976), but silverside effects on macrozooplankton size structure have been never studied.

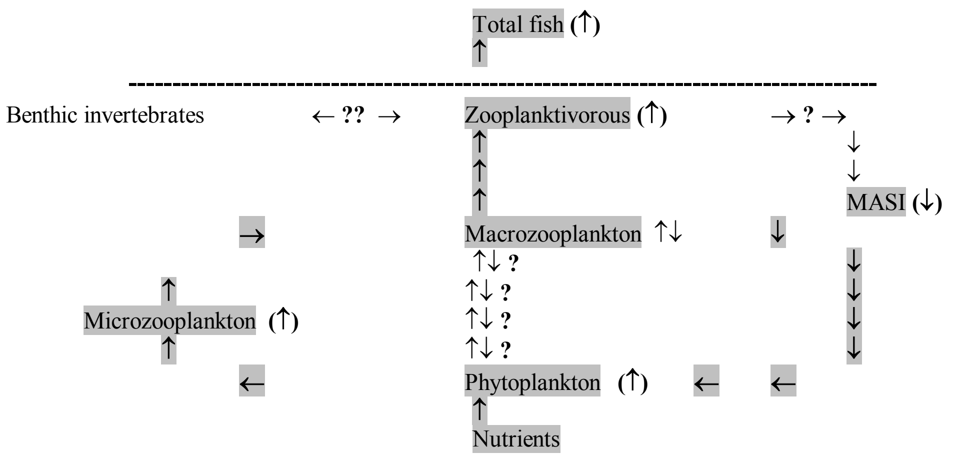
Fish management objectives in Argentina have usually been directed towards sport fisheries. Most of the fish species in the central-western and northwestern reservoirs have been introduced from outside Argentina or from other river basins in Argentina (Quirós *et al.,* 1988). A majority of the reservoirs in Patagonia have been successfully colonized by salmonids. *Odontesthes honariensis* (Argentinean silverside) is common to most reservoirs in the central-western and northwestern and regions, and *Odontesthes microlepidotus* (Patagonian silverside) is common to most Patagonian reservoirs. Both species of the Atherinidae are visual facultative zooplanktivorous fishes (Ringuelet *et al.,* 1967; Ferriz, 1987) usually highly abundant in reservoirs. Piscivory is not widespread in northwestern reservoirs. *Hoplias malabaricus,* a perch-like piscivore of the Erythrinidae, usually associated with macrophyte beds, was only present in a few of these reservoirs (Table II). Species of *Oncorhynchus and Salvelinus,* often piscivorous as adults, are relatively common in southern reservoirs, 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 (R. A, Ferriz, Buenos Aires, Argentina, pers. comm.) to be piscivorous as an adult. It was relatively abundant in Patagonian Plateau reservoirs (Quirós *et al.,* 1988).

MATERIALS AND METHODS

Limnological and fish data for 31 reservoirs were collected during an extensive survey of 110 lakes and reservoirs in Argentina (ARLARE data see http://www.geocities.com/CapeCanaveral/Lab/5028/) from 1984 to 1987 (Quirós *et al.,* 1988). Each reservoir was visited once, in mid- summer, except for one that was sampled seasonally over a period of 2 y. Data for four (4) reservoirs never used before, have been included here. Sampling stations were situated within 500 m to 2 km from the impounding dam. Chlorophyll (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. The sampling and analytical methods used have been described previously (Quirós, 1990).

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 (catch per unit effort for planktivores, CPUE, kg. night^{-1} standard gillnets). Macrozooplankton biomass (MAZOO, µg dry weight . 1^{-1}) and microzooplankton biomass (MIZOO, µg dry weight . 1^{-1}) were data used in this paper (Quirós *et al.,*1988). Cladocerans and post naupliar copepods were considered macrozooplankton, and rotifers and copepod nauplii as microzooplankton (Menu Marque & Marinone, 1986). Table I presents the main characteristics of studied reservoirs. We have distinguished two types of reservoirs. Type I reservoirs are those where zooplanktivorous atherinidae fish were introduced and heavily stocked for several years but piscivorous fish were not present at sampling. Type II includes mostly reservoirs where zooplanktivorous fish were natural components of pre-dam riverine fish assemblages and sites where both atherinids and piscivorous were introduced and stocked (Table II).

BOX 1. Type I reservoirs



Patterns displayed from correlation-regression analyses for Type I reservoir data. **(↑),** significant correlation coefficient with nutrients; ↑, significantly correlation coefficient between adjacent biological standing stocks or variables, pointing upwards: direct relationship, pointing downwards: inverse relationship.

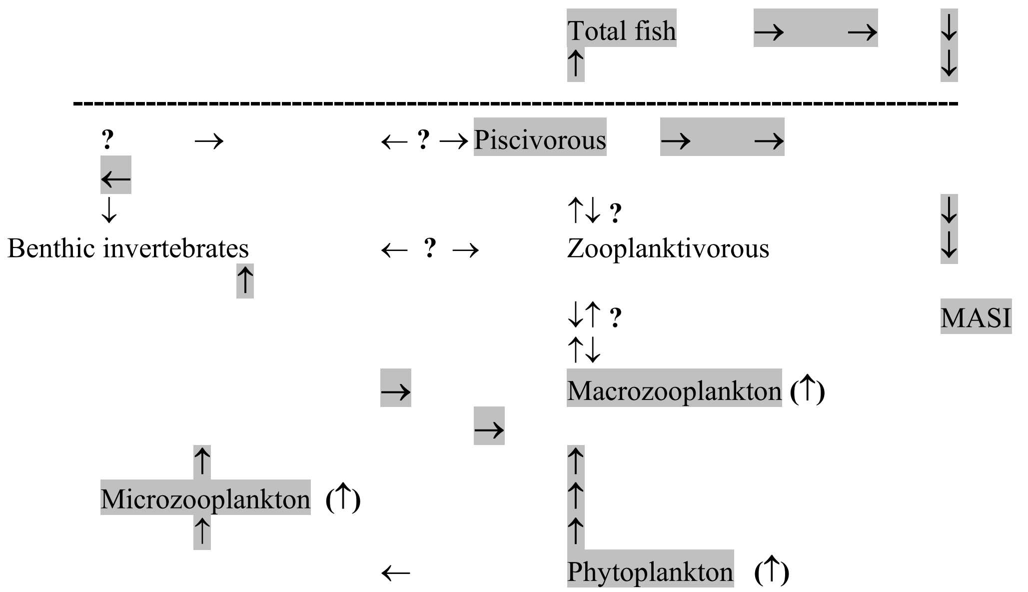
Data analysis was made by simple regression on the total data and on two data subsets (Table I) defined as: 1) reservoirs with planktivorous fishes and without piscivores (Type I), and 2) reservoirs with both piscivores and planktivores (Type II). Stepwise multiple regression analysis was applied to the total data using variables related to climate, morphometry, nutrient content, fish community composition, and biological standing stocks as potential regressors.

The collection frequencies of planktivores (ZOF:TOF = CPUEPLANKT / CPUE) was used as surrogate of fish assemblage composition. Mean macrozooplankton size (MASI, µg dry weight . individual^{-1}) was estimated by mean body weight as the ratio between biomass (µg dry weight . 1^{-1}) and abundance (number of individuals . 1^{-1}).

Table 1. Limnological and fish characteristics for Argentinean reservoirs. Type I: reservoirs with planktivores but without piscivores. Type II: reservoirs with planktivores and piscivores. Catch per unit effort of atherinids (ZOF, kg/night.standard gillnets), catch per unit effort of piscivores (PIF, kg/night.standard gillnets), total catch per unit effort (TOF, kg/night.standard gillnets), mean macrozooplankton body weight (MASI, ug dry weight.ind^{-1}), mean depth to Secchi disk depth ratio (Zmean:SDL).

	Total (n = 31)		Type I (n = 23)		Type II (n = 8)	
Surface area (km^{1})	80.0	816 - 1.5	20.4	100.7 - 1.5	251.4	816 - 13.5
Mean depth (Zmean, m)	21.6	79.4 - 3.0	15.3	36.2 - 3.0	39.5	79.4 - 5.3
Secchi disk depth (SDL, m)	2.5	10.5 - 0.28	2.0	5.8 - 0.28	3.8	10.5 - 0.40
Total phosphorus (TP, mg m^{-1})	61	477 - 3	63	477 - 5	58	322 - 3
Total organic nitrogen (TON, uM)	49	352 - 6	57	352 - 13	29	61 – 6
Total nitrogen (TN, mg m^{-3})	1843	11200 - 223	2045	11200 - 653	1262	2752 - 223
TN:TP	64	273 - 6	59	128 - 6	80	273 - 7
Chlorophyll concentration (Chl, mg m^{-1})	17.1	218 - 0.66	21.8	218 - 0.93	3.6	10.4 - 0.66
Microzooplankton biomass (ug dry weight.l^{-1})	16.7	79.2 - 0.44	21.3	79.2 - 0.83	3.8	17.0 - 0.44
Macrozooplankton biomass (ug dry weight.l^{-1})	53.2	177 - 7.4	66.4	177 - 11.1	15.4	40.4 - 7.4
Total fish (TOF)	36.6	283 - 1.9	39.5	283 - 1.9	28.3	90.7 - 2.7
Zooplanktivorous fish (ZOF)	23.0	283 - 0.0	29.6	283 - 0.1	4.1	13.5 - 0.0
Piscivorous fish (PIF)	4.2	70.7 - 0.1	0.0		16.1	70.7 - 0.1
ZOF : TOF	0.43	1.0 - 0.0	0.53	1.0 - 0.02	0.14	0.43 - 0.0
Macrozooplankton size (MASI)	2.4	3.7 - 0.92	2.3	3.2 - 0.92	2.6	3.7 - 1.5
DO at bottom (mg.l^{-1})	4.4	9.7 - 0.01	3.6	9.7 - 0.01	6.6	9.4 - 0.06
Relative inorganic turbidity (ITurb)	3.1	28.8 - 0.24	2.8	28.8 - 0.24	3.9	15.2 - 0.79
Zmean : SDL	11.2	49.3 - 0.69	9.9	34.4 - 0.69	17.6	49.3 - 6.2
Water renewal time (yr^{-1})	1.04	3.0 - 0.11	0.86	3.0 - 0.11	1.45	3.0 - 0.64

BOX 2. Type II reservoirs



Dissolved oxygen concentration at 0.50 m above the bottom ($D0_b$, mg. 1^{-1}) was used as a rough estimate of oxygen concentrations at the water-sediment interface, and the mean depth to Secchi depth ratio (Zmean : SDT) as a rough surrogate of submersed macrophyte development and subsurface light availability (Reynolds & Walsby, 1975). Because reservoirs are usually light limited by clay turbidity, to take account of inorganic turbidity effects an index of relative inorganic turbidity (ITurb) was defined as the ratio between TP-estimated Chl concentration from a regression model for a highly homogeneous set of lakes with very low inorganic turbidity (Quirós, 1991) and the actual Chl concentration as measured, for each reservoir.

In order to stabilize the variance, all the variables except D0b, MASI, and fish biomass ratios were log-transformed.

The "best" multivariate models, obtained using nutrients or biological standing stocks, and other regressor variables that have a low covariation with the former variables ($R^2 < 0.40$) are presented here. Therefore, significant variables (T-value > 2), but only those with low covariation with previously included regressor variables, were forced into the regression equation.

Curvilinear trends in data were studied using robust locally weighted regression and smoothing graphic techniques (LOWESS). The Number Cruncher Statistical System (NCSS 2000) (Hintze, 1998) was used.

RESULTS

Trophic relationships for Type I and Type II reservoirs

Because reservoirs located in arid and semi-arid regions are usually nitrogen limited and more turbid by clays than lakes and reservoirs situated on hard-rock basins (Horne & Goldman, 1994), we analyzed TP-Chl and TON-Chl relationships for total data and the two data subsets. The TP-Chl relationship for both types of reservoirs are significantly different from that for natural lakes (Quir6s, 1998a). Regression slopes are noticeable lower; it may be due to higher inorganic turbidity for study reservoirs than for natural lakes (Quirós, 1991). Anyway, reservoirs with planktivores but without piscivores showed the highest algal biomass (Figure 1a). The regression equations for the relationship between nutrient concentrations and Chl were as follows.

All reservoir data

$$\log_e \mathrm{Chl} = -\ 0.800\ (0.545) + 0.793\ (0.156) \log_e \mathrm{TP} \qquad (1)$$

$(R^2 = 0.47, p < 0.0001, n = 31)$

$$\log_e \mathrm{Chl} = -\ 3.665\ (0.656) + 1.537\ (0.180) \log_e \mathrm{TON} \qquad (2)$$

$(R^2 = 0.72, p < 0.0001, n = 31)$

Type I reservoirs

$$\log_e \mathrm{Chl} = -\ 0.850\ (0.758) + 0.871\ (0.212) \log_e \mathrm{TP} \qquad (3)$$

$(R^2 = 0.45, p = 0.0005, n = 23)$

$$\log_e \mathrm{Chl} = -\ 3.840\ (0.829) + 1.611\ (0.220) \log_e \mathrm{TON} \qquad (4)$$

$(R^2 = 0.72, p < 0.0001, n = 23)$

Type II reservoirs

$$\log_e \mathrm{Chl} = -\ 0.661\ (0.451) + 0.528\ (0.139) \log_e \mathrm{TP} \qquad (5)$$

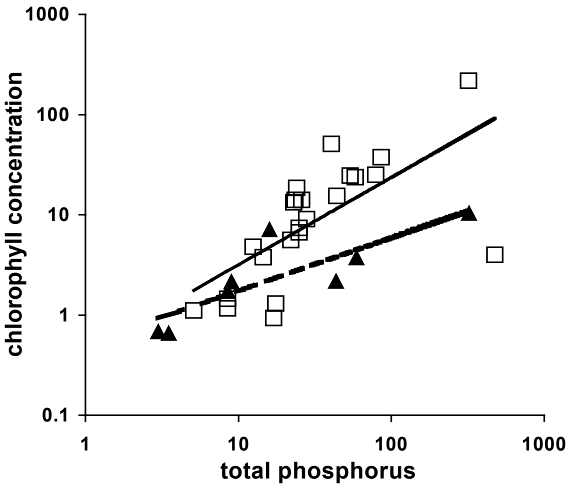
$(R^2 = 0.71, p = 0.009, n = 8)$

$$\log_e \mathrm{Chl} = -\ 2.283\ (1.076) + 1.004\ (0.335) \log_e \mathrm{TON} \qquad (6)$$

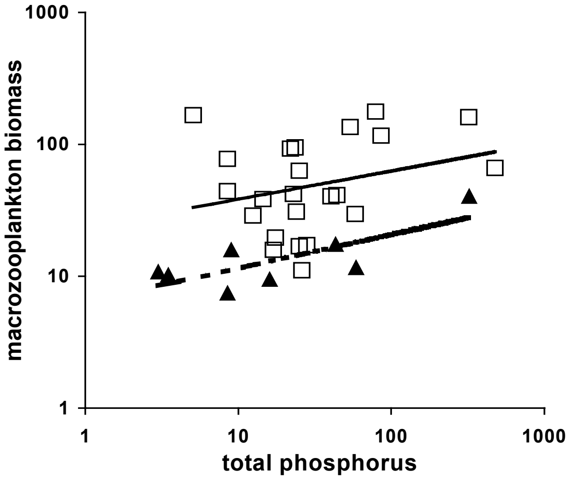
$(R^2 = 0.60, p = 0.024, n = 8)$

The greater slopes for TON-Chl and TN-Chl than for TP-Chl regressions may be indicating that nitrogen limitation was increasing with reservoir trophic state for both kinds of reservoirs. Moreover, lower slopes in TP-Chl equations for reservoirs than for a comprehensive set of Argentincan water bodies (Qt@!r6s, 199 1) indicate higher inorganic turbidity effects for reservoirs than for laces.

The phytoplankton and microzooplankton biomass were strongly related to nutrient concentrations for both types of reservoirs whereas macrozooplankton biomass was related to nutrients just for reservoirs with piscivorous (Type 11). Macrozooplankton biomass was also higher for planktivore dominated reservoirs (Figure lb). This was a significant but unexpected result. The general pattern for lakes and reservoirs with balanced fish assemblages (Quir6s, 1998a) predicts an steady decrease of slope and explained variance for regressions of biological standing stocks on nutrients from phytoplankton to piscivorous fishes. However, both types of reservoirs considered here have highly unbalanced fish assemblages and depart from the most general proposed pattern depending on fish assemblage composition (see Figures 2a and 2b).



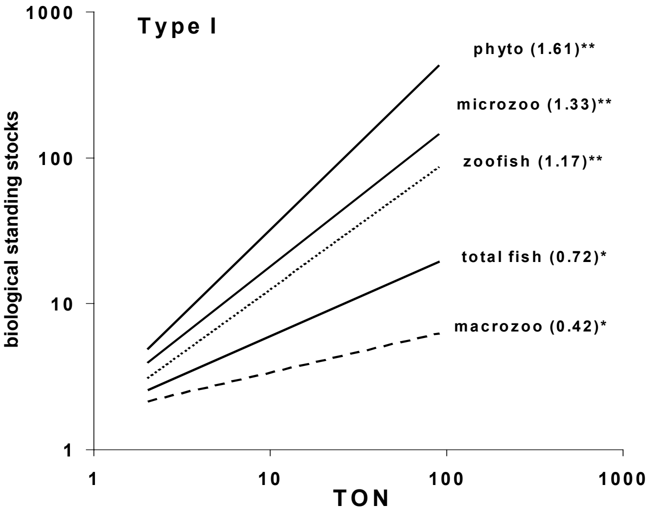
(a)



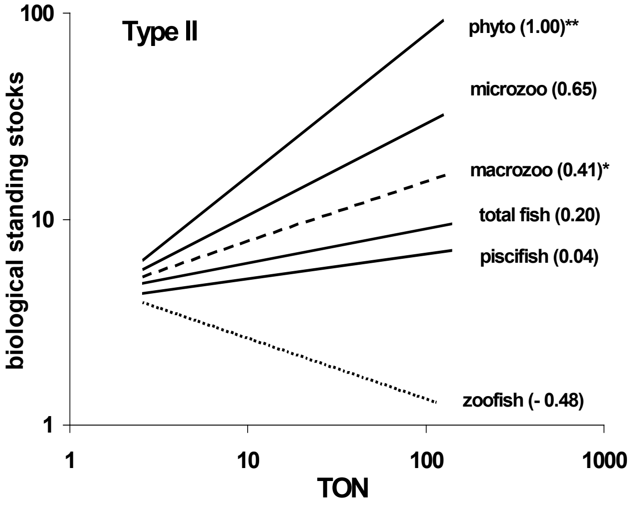
(b)

Figure 1 Relationships between: a) total phosphorus and chlorophyll concentrations, and b) total phosphorus and macrozooplankton biomass, for planktivore reservoirs with (▲) and without (□) piscivorous fish.

For reservoirs with planktivores but without piscivores (Type I), the planktivore biomass constitutes 53% of the total fish biomass and it was directly related to nutrient contents ($r = 0.50$ and $r = 0.56$, for TP and TN, respectively, $p < 0.05$). For this subset, the macrozooplankton size was inversely related to nutrient content ($r = - 0.45$ and $r = -0.51$, for TP and TN, respectively, $p < 0.05$), but rnacrozooplankton biomass was directly related to planktivores ($r = 0.83$, $p < 0.0001$). In some sense, the latter was also an unexpected result. However, these results are in agreement with Pace (1984) results that macrozooplankton size, but not biomass, explain differences for TP-Chl relationships.



(a)

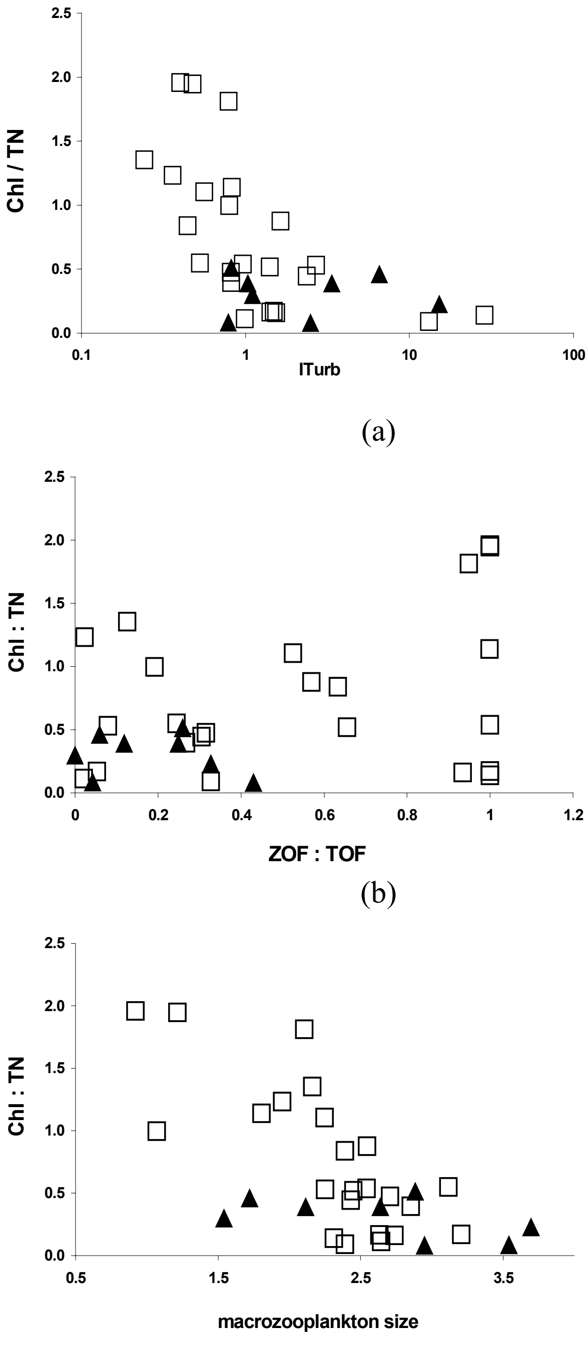


(b)

Figure 2 Slope values for simple regression models between total organic nitrogen and biological standing stocks for planktivore reservoirs: a) without (Type I), and b) with (Type II) piscivorous fish, respectively. (**), $P < 0.01$; (*), $P < 0.05$. The axes are not at scale.

For the reservoirs with piscivorous fish (Type II), piscivorous constitute 47% of the total fish biomass, but their biomass were not significantly related to the nutrient contents. For these reservoirs, total fish was directly related to piscivorous ($P = 0.01$).

For both types of reservoirs, the biomass variability of phytoplankton and microzooplankton were mostly explained by nutrient concentrations, in spite of fish assemblage effects on macrozooplankton biomass. Moreover, the biomass of microzooplankton increased relative to that of macrozooplankton as reservoir trophy increased (see Figures 3a and 3b).



(a)

(b)

(c)

Figure 3 Relationships between: a) relative inorganic turbidity (ITurb), b) planktivores to total fish biomass ratio (ZOF : TOF), and c) macrozooplankton size (ug dry weight.individual^{-1}), and the Chl : TN ratio for planktivore reservoirs with (▲) and without (□) piscivorous fish.

For type 1 reservoirs (Box 1), total fish biomass was highly related to planktivorous fish ($r = 0.82$, $p < 0.0001$) and all biological standing stocks, with exception of macrozooplankton, were highly related to nutrient concentrations. The link between phytoplankton and macrozooplankton appears to be lightly connected. Bottom-up effects from nutrients to microzooplankton were apparent, but macrozooplankton was more heavily connected to the bottom throughout microzooplankton than to phytoplankton biomass. Moreover, for this type of reservoirs, macrozooplankton biomass was highly related ($r = 0.83$, $p < 0.0001$) to zooplanktivorous fish biomass, and a significant ($r = -0.67$, $p < 0.001$) inverse relationship between rnacrozooplankton size and phytoplankton biomass was displayed for mid-summer.

For Type II reservoirs, total fish biomass was related to piscivorous biomass ($r = 0.80$, $p = 0.01$), and bottom-up effects are evident from nutrient to macrozooplankton biomass (Box 2). Zooplanktivorous fish was not related to any macrozooplankton blomass or size, and piscivorous biomass was positively related to macrozooplankton biomass ($r = 0.68$, $p < 0.05$) and inversely related to size ($r = - 0.62$, $p < 0.06$). However, a more significant inverse relationship between macrozooplankton size and fish biomass was shown for total fish ($r = - 0.73$, $p < 0.04$). All the biological standing stocks, with the exception of total fish blomass, were higher for Type I silverside dominated reservoirs than for Type II reservoirs. The grade of connection between fish and nutrients was lower (not significant relationships) than for planktivore dominated reservoirs. How much is it related with a higher connection of fish with benthic fauna is something that we can not resolve here.

Table II Fish species considered as piscivores or planktivores by geographic region in the analyzed data. The number of reservoirs with these species present at sampling time shown in parentheses.

Piscivores	Planktivores
Patagonia	
Salmo trutta (2)	*Odontesthes microlepidotus* (5)
Salvelinus fontinalis (1)	*Odontesthes bonariensis* (1)
Percichthys colhuapiensis (4)	
Central-western and Northwestern Arid Region	
Hoplias malabaricus (3)	*Odontesthes bonariensis* (25)
Salminus maxillosus (1)	*Odontesthes microlepidotus* (1)
	small Characidae * (10)

- Small zooplanktivorous species not considered in main analyses.

Multiple regression models for reservoirs

For all Chl reservoir data, several equivalent multiple regression models were developed (Table III). These models are compatible with some concurring mechanisms to explain phytoplankton biomass variability.

As expected,,Chl is directly related to nutrient concentrations [Equations (1) to (6), but is lower for muddy or very shallow macrophyte dominated reservoirs (Table III, model 1). These latter reservoir characteristics ordinarily represent potential refuge for grazers. Therefore, it was also to be expected that phytoplankton blomass had been lower for reservoirs with higher grazer sizes (Table III, models 3 to 6). Zooplanktivorous fish biomass was also an important variable to explain Chl residual variability (Table III, models 2 and 6), Some of those relationships are displayed in Figures 3a to 3c. When inorganic turbid reservoirs were excluded from analyses (n = 27), we obtained similar results but explained variance was still higher and TP was the most relevant nutrient variable.

Table III Multiple regression models for total reservoir data. Phytoplankton biomass (as chlorophyll concentration) to total nitrogen ratio (Chl/TN, n=31), T-value for each variable, RMSE, root mean square error.

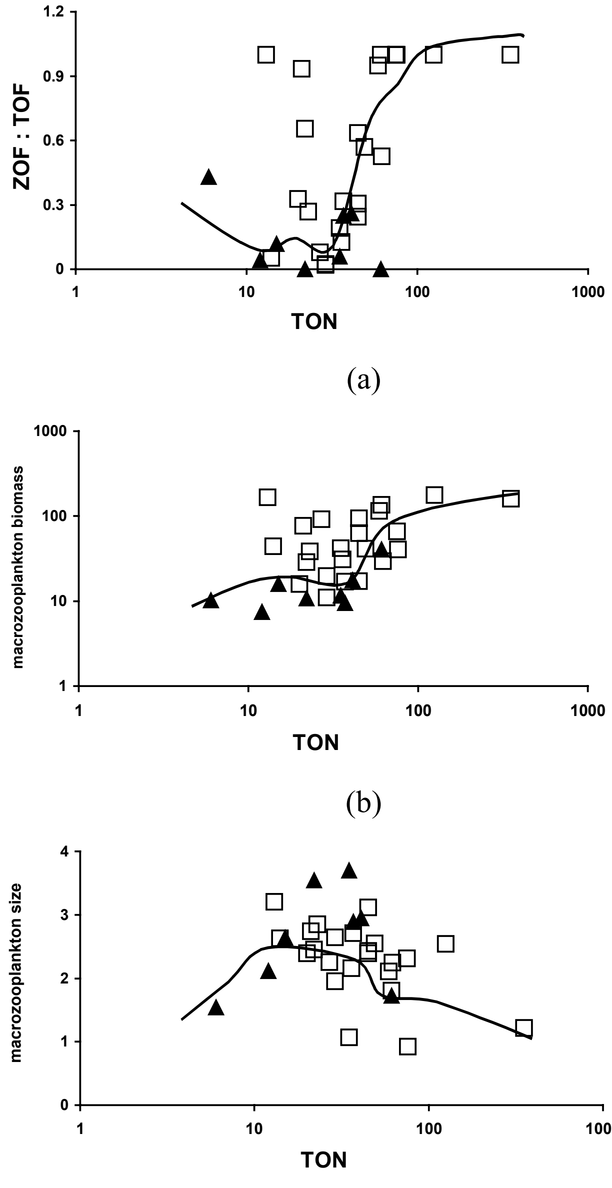
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
ITurb	- 5.0	- 5.2		-4.7	- 4.4	- 4.9
Z_m/SDL	2.8	2.8		2.5	2.8	2.6
MASI			- 5.0	- 4.4	- 4.4	- 4.0
DO_b			- 3.0			
ZOF/TOF		2.5				2.1
PIF					- 2.5	
R^2	0.48	0.58	0.58	0.69	0.75	0.75
P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
RMSE	0.0041	0.0038	0.0037	0.0032	0.0029	0.0030

Some insights from LOWESS analyses

Interplay between bottom-up and top-down effects would change with reservoir fish assemblage composition (Quirós, 1998a). For low nutrient contents, fish assemblage composition was balanced between piscivorous and zooplanktivorous (Figure 4a). The planktivores to total fish biomass ratio (ZOF/T0F) is comparatively lower in reservoirs with low nutrient concentrations. When it decreases, both macrozooplankton biomass and size increase (Figure 4b and 4c).

For an intermediate range of nutrient concentrations where fish assemblage composition (ZOF/TOF) remains constant, the changes for both macrozooplankton biomass and size were not noticeable. For eutrophic conditions, when zooplanktivorous were clearly dominant, macrozooplankton size decrease but macrozooplankton biomass increased dramatically.

In conclusion, for the total data we have analyzed, both bottom-up and top-down effects were displayed for the same group of reservoirs depending on fish assemblage composition. For low planktivore content reservoirs, both biomass and size for macrozooplankton had decreased or remained unchanging, but when the collection frequency of planktivores had increased dramatically a huge increase for macrozooplankton biomass and a decrease for size were noticeable (Figure 4c).



(a)

(b)

(c)

Figure 4 LOWESS relationships between: a) planktivores to total fish biomass ratio (ZOF : TOF), b) macrozooplankton biomass (ug dry weight.l^{-1}), and c) macrozooplankton size (ug dry weight.individual^{-1}), and total organic nitrogen concentration (TON, uM) for planktivore reservoirs with (▲) and without (□) piscivorous fish.

DISCUSSION AND CONCLUSIONS

In spite of conspicuous systemic differences with lakes, reservoirs dominated by visual zooplanktivorous fishes have had phytoplankton biomass drastically higher than reservoirs with more balanced fish assemblages where piscivorous fish biomass were more noticeable. This fact is coincident with predictions from trophic cascade hypotheses (Shapiro, 1980; Carpenteret *al.,* 1985), but as was stated before (Quir6s, 1998a), many other in lake characteristics contribute to conform that pattern. For both kind of reservoirs, bottom-up effects from nutrient to algae were strong, but top-down increasing effects on phytoplankton were apparent for planktivorous dominated reservoirs. Contrary to earlier results for a more inclusive set of lakes and reservoirs (Quirós, 1998a), our results show macrozooplankton biomass was dramatically higher for reservoirs with planktivores not controlled by piscivores, when nutrient or chlorophyll was held constant. Therefore, in reservoirs, macrozooplankton was not strongly suppressed by planktivores, but these fish may control macrozooplankton size. Moreover, a phytoplankton control by large grazers (Brooks & Dodson, 1965) may be suspected for planktivore dominated reservoirs. In some sense, our results are coincident with the view that for reservoirs where facultative planktivores are dominant, these fish play a central role in reservoir ecosystem function (Stein *et al.,* 1996) but controlling just zooplankton size, and with Pace (1984, 1986) hypothesis that zooplankton size structure, but not biomass, influences nutrient-phytoplankton relationships.

For lakes and reservoirs with balanced fish assemblages, it is expected that efficiency of nutrient transference from the bottom up in the trophic web would diminish from algae to piscivorous fishes; slopes are predicted to decrease from the bottom to the top of the food web (Quirós, 1998a). Those patterns were not entirely displayed here for reservoirs with fish assemblages largely dominated by facultative planktivorous fish. Some reasons could he speculated to explain the obtained results. Human'actions influence both the bottom (nutrient loading) and the top of the web (fish stocking and introductions). For reservoirs, fish assemblage composition is usually dependent on human actions throughout fish introductions and stocking. Facultative planktivorous fish dependence on benthic resources may also explain some of our results for both types of reservoirs. In Argentina, most of planktivore dominated reservoirs have been heavily stocked with sliversides as long as other reservoirs have been usually stocked with piscivorous fish and rainbow trout. Some previous results suggest that as facultative visual planktivores (Brooks, 1969), silversides also feed on benthic invertebrates (Luchini *et al.,* 1984), but we can not define here how much were they related to benthic fauna.

For our study reservoirs, all the biological standing stocks were higher for reservoirs with planktivores but without piscivores when nutrients were held constant, with the exception of total fish. For the latter variable, there were not significantly differences between both types of reservoirs. The figure of zooplanktivorous fish cascading by predation and pumping nutrient up throughout the food web may illustrate our obtained patterns.

So much could be speculated about reasons to explain uncoupling between macrozooplankton biomass and phytoplankton for planktivore dominated reservoirs. One of the tenets of the trophic cascade hypothesis was not displayed for Argentinean reservoirs. Macrozooplankton biomass was higher for planktivore dominated reservoirs. A coincident and equal bottom-up and top-down effect on macrozooplankton biomass may be not a good explanation, because macrozooplankton biomass was highly connected to zooplanktivorous fish but lightly related to nutrients or algae in our data. An alternative though partial explanation may be related with that actual macrozooplankton standings would be of small size not connected to phytoplankton throughout grazing. However, phytoplankton biomass was inversely related to macrozooplankton size. Therefore, what could explain the facts that macrozooplankton biomass is lightly coupled to phytoplankton for planktivore dominated reservoirs and that macrozooplankton biomass is dramatically higher for these reservoirs, are open questions for Argentinean reservoir ecology.

We can not conclude that top-predators can control zooplanktivorous fish biomass for reservoirs, but we have shown planktivore biomass exerts an important control on macrozooplankton size that cascades down the food web. It has been suggested that most planktivorous are facultative planktivorous also feeding on benthic invertebrates (Brooks, 1969; Jeppessen, 1998), It is highly probably that heavy facultative planktivore biomass put these fish out of control from top-predators (Stein *et al.,* 1996). For natural lakes, the development of high facultative planktivore biomass is promoted by human action throughout nutrient load increase (Brooks, 1969). For reservoirs, very often fish introduction and stockings contributes still more to the rise of planktivore biomass. We are not able to quantify here how much fish assemblage composition changes may modify trophic relationships through non-cascading (Brabrand *et al.,* 1990) or more diffuse, and not yet clearly understandable processes.

We have to be very cautious in order to generalize our results to other kind of reservoirs, but some of our results are in coincidence with those expected from current aquatic ecology science applied to reservoirs. The main tenets of the biomanipulation concept are of application for reservoirs situated in and and semi-arid region with fish assemblages dominated by facultative visual planktivorous. For example, reservoirs with three level pelagic communities (planktivores not controlled by piscivores) have had chlorophyll concentrations drastically higher than reservoirs with four level communities (planktivores partially (?) controlled by piscivores), notwithstanding the effects of other endogenous reservoir variables could not be diminished.

Both bottom-up and top-down effects would be operational for lakes and reservoirs (Quirós, 1998b). However, bottom-up effects might be modulated by the actual fish assemblage composition. These changes in trophic dependence are particularly influential for human-made aquatic ecosystems like reservoirs. This study indicates that changes in fish assemblage composition will have dramatic effects on trophic relationships in reservoirs.

MANAGEMENT IMPLICATIONS

Earlier results for more comprehensive lake and reservoir data had been shown (Quirós, 1998a) roughly in coincidence with the predictions of the biomanipulation concept (Shapiro *et al.,* 19 75), the cascading trophic interactions hypotheses (Carpenter *et al.,* 1985), and the bottom-up:top-down model (McQueen *et al*., 1986) for individual lakes. Some more deviations from those concepts have been shown here for more narrow data, notwithstanding the basic recommendations of the biomanipulation concept remains for application to reservoirs. Many alternative nutrient pathways are not included in current trophic cascade hypotheses (Carpenter *et al.,* 1985; Burns, 1998; among many others) and consumer and resource controls for pelagic food webs are often ideal abstractions (Peters, 1991) sustained mainly from results usually obtained from simple system experiences. As was stated before (Quirós, 1990), we may believe that simple internal views including one or two control factors for freshwater pelagic food webs practically does not apply for any actual complex aquatic ecosystem. In order to get reliable scientific knowledge we have to search for similarity as well as for difference. Patterns obtained from system comparisons may help to display some similarities. The patterns we have obtained for the Argentincan reservoirs are based on the premise of similar behavior among reservoirs. As was stressed before, each reservoir and its environment are unique (Reckhow *et al*., 1980; Burns, 1998). One weakness of obtained patterns lies in the fact that they are not reservoir-specific, so that models and data are not directly transferable to other individual reservoir within each reservoir subset. Therefore, a more mechanistic approach knowing more about endogenous lake interactions must be necessary in order to apply successfully trophic web manipulations to reservoir management (Stein *et al.,* 1996).

Heavy biased introductions and stocking of planktivores may conduct to unbalanced fish assemblages with undesired effects on water quality. For most reservoirs distributed worldwide, both bottom-up and top-down effects are externally driven. The former throughout nutrient load, and the latter by usual introduction and stocking of fish. Stocked fish are very often facultative zooplanktivorous for undeveloped country reservoirs. Our results suggest that total fish abundance may not be higher for these reservoirs, but the potential impairing effects on fish production of stocking fish near the bottom of the food web could not be diminished. Some related facts from siverside introduction cases support our results. The Argentinean silverside has been introduced in lakes of reservoirs of central Chile and the Titicaca Lake. Self-sustained populations were developed and a heavy increase of phytoplankton biomass was noticed there. Some other countries have been considering silversides to be stocked in their lakes and reservoirs. However, the capacity of these fish to magnify eutrophication processes should be weighed.

As reservoir management measures, the obtained results support to apply a careful control of fish introductions and stockings. The overstocking of planktivorous fish will conduct to deteriorate water quality throughout increased algal biomass and diminished water transparency. The concurrent stocking of piscivorous will produce most balanced trophic interactions at the bottom of the food webs.

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