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Fish effects on trophic relationships in the pelagic zone of lakes

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Abstract

To examine the relationships between the biomass of pelagic communities and to study how these relationships differ between lakes with different fish assemblages, we used data on nutrients, chlorophyll, zooplankton, and fish from 96 Argentinean lakes and reservoirs. Significant differences in regressions between chlorophyll and total phosphorus, macrozooplankton and chlorophyll, and between total fish and macrozooplankton, in lakes with different fish assemblages, were found. Lakes with zooplanktivorous fishes but without piscivores, and lakes without planktivores, had the highest and the lowest phytoplankton biomass, respectively. The regression line for lakes with both types of fish were intermediate. Furthermore, lakes with planktivores, but without piscivores, had the lowest macrozooplankton. The analysis of the trend in simple regression residuals suggests that the changes in chlorophyll, macrozooplankton, and total fish with lake trophy, are related to changes in fish assemblages.

Introduction

Standing stocks of aquatic biota in lakes have often been shown to be related to nutrient content (Sakamoto, 1966; Dillon & Rigler, 1974; Schindler et al., 1978; Hanson & Leggett, 1982; Hanson & Peters, 1984; Bird & Kalff, 1984; Yan, 1986; Quirós, 1990a; among others). Moreover, significant direct relationships between those biological standing stocks at different trophic levels have been shown in some instances (Oglesby, 1977; McCauley & Kalff, 1981; Bays & Crisman, 1983; Rognerud & Kjellberg, 1984; Pace, 1986; Quirós, 1991; among others). On the other hand, nutrient content of lakes is mainly determined by nutrient loading, and by water renewal time as mediated by morphometry (Vollenweider, 1969, 1975; Dillon & Rigler, 1975).

Although Shapiro (1980) recognized that nutrients generally determine the biotic response of lakes, he stressed their dependence on the structure of the biotic community. A more internal view for relationships between biological standing stocks was proposed by Carpenter et al. (1985, 1987) in their cascading trophic interactions hypothesis. In those studies, the earlier results of Hrbacek et al. (1961) and Brooks & Dodson (1965) on the effects of fish on zooplankton and phytoplankton in individual lakes studies were further developed (Carpenter & Kitchell, 1992).

The first attempt to unify the internal and external views was developed by McQueen et al. (1986) in their bottom-up:top-down model. They stressed a symmetric abiotic and biotic two-way view, although in recent work (McQueen et al., 1989) the existence also of non symmetric effects from nutrient to fish was also recognized. The effects of fishes on the structure of freshwater ecosystems were reviewed by Northcote (1988), and the role of fish in the regulation of phosphorus availability was studied by Lamarra (1975), Nakashima & Leggett (1980), and Brabrand et al. (1990).

The principal purpose of this paper is to test the main thesis (Shapiro, 1980) that although phosphorus sets limits on the biotic responses of lakes, the actual responses are also functions of the structure of the biotic community. The data consist of simultaneous observations on nutrients, phytoplankton, zooplankton, and fish, in lakes and reservoirs of Argentina (Quirós, 1990a, 1990b; Quirós et al., 1988). A secondary purpose is to relate among lake variability in

Table 1. Limnological and fish characteristics for Argentinean lakes and reservoirs (ARLARE, $n = 96$). PLANKT +/PISCIV −, lakes with planktivores but without piscivores; PLANKT +/PISCIV +, lakes with planktivores and piscivores; PLANKT −/PISCIV ± sites without planktivores. Area (A, km^2), mean depth (ZMEAN, m), mean annual air temperature (TEMP, °C), total phosphorus (TP, mg m^{-3}), total nitrogen to total phosphorus ratio (TN:TP, molar basis), total chlorophyll (Chl, mg m^{-3}), microzooplankton biomass (MIZOO, μg dry weight l^{-1}), macrozooplankton biomass (MAZOO, μg dry weight l^{-1}), catch per unit effort of atherinids ($CPUE_{PLANKT}$, kg/night.standard gillnets), catch per unit effort of piscivores ($CPUE_{PISCIV}$, kg/night.standard gillnets), total catch per unit effort (CPUE, kg/night. standard gillnets), dissolved oxygen concentration at bottom (DOb, mg l^{-1}), mean macrozooplankton body weight (MASI, μg dry weight $ind.^{-1}$), mean depth to Secchi disk transparency ratio (ZMEAN:SDT).

Variable	PLANKT +/PISCIV − ($n = 42$)		PLANKT +/PISCIV + ($n = 16$)		PLANKT-/PISCIV ± ($n = 38$)	
	Mean	Range	Mean	Range	Mean	Range
A	66.6	0.1–1984	167.1	1.4–816	35.9	0.3–580
ZMEAN	12.2	1.1–59.0	38.4	1.2–157	40.6	0.7–166
TEMP	14.7	4.0–20.4	12.6	5.0–17.0	6.7	3.0–16.3
TP	104	3–1250	163	1–1288	41	2–350
TN:TP	65	16–186	85	9–335	119	15–273
Chl	40.6	0.29–405	26.3	0.16–166	5.8	0.21–113
MIZOO	66.1	0.68–705	95.8	0.44–484	38.3	0.16–1165
MAZOO	194.7	4.5–1026	537.4	2.4–2156	293.5	0.46–3432
$CPUE_{PLANKT}$	59.2	0.1–435	37.3	0.2–205	–	–
$CPUE_{PISCIV}$	–	–	14.6	0.7–52	15.5	0–277
CPUE	82.9	1.9–505	117.2	5.0–369	39.6	0–330
DOb	5.2	0.01–10.3	7.8	0.06–12.2	8.8	2.8–11.1
MASI	2.3	0.8–3.9	2.8	1.5–4.5	4.4	1.0–16.3
ZMEAN:SDT	7.5	0.7–34.4	9.2	1.4–32.5	4.4	0.4–19.0

biomass of pelagic communities to other inlake variables, beside fish community composition.

Study sites and fish assemblages

The study sites are located between 25 and 55 °S latitude, in the central-western and northwestern arid regions of Argentina, the Pampa Plain, the Patagonian Plateau, the Patagonian Andes, and Tierra del Fuego. The deepest lakes are situated in the Patagonian Andes and Tierra del Fuego, and range from ultraoligotrophic to oligotrophic. All sites in the Pampa Plain are shallow, eutrophic to hypertrophic lakes. Most of the central-western and northwestern reservoirs and Patagonian Plateau lakes range from mesotrophic to eutrophic, and more than half of the northwestern reservoirs had low dissolved oxygen concentrations in the hypolimnion at the time of sampling. The sampled lakes and reservoirs represent a wide range of trophic conditions (Table 1), and their climatic, morphometric, and edaphic characteristics are closely related (Quirós, 1990a, 1990b).

Fish management objectives in Argentina have usually been directed towards sport fisheries. Anglers' preferences have governed salmonid and silverside introductions in most lakes and reservoirs (Baigun & Quirós, 1985). 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 glacial lakes in Patagonia and Tierra del Fuego have been successfully colonized by salmonids (Baigun & Quirós, 1985). The Pampa Plain lakes are practically the only Argentinean lakes with a relatively high fish community diversity (Ringuelet, 1975) and most of the fish here are native to the lower Rio de la Plata Basin (Quirós et al., 1988). *Odontesthes bonariensis* (Argentinean silverside) is common to most lakes and reservoirs in the Pampa Plain and central-western and northwestern arid regions, and *Odontesthes microlepidotus* (Patagonian silverside) is common to most Patagonian lakes except those in Tierra del

Fuego (Table 2). Both species of the Atherinid family are visual zooplanktivorous and microbenthophagous fishes (Ringuelet et al., 1967; Ferriz, 1987). Other zooplanktivorous fish species such as the small Characidae in the Pampa lakes and northern reservoirs, the young of the year salmonids, and the native Galaxiidae and Aplochitonidae in the Patagonian lakes, were either absent or their catch was not representative of their abundance in the lakes.

Piscivory is not widespread in Argentinean lakes and reservoirs. Species of *Salmo* and *Salvelinus*, often piscivorous as adults, are relatively common in southern glacial lakes (Table 2), 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 lakes and reservoirs (Quirós et al., 1988). *Hoplias malabaricus*, a perch-like piscivore of the Erythrinidae, usually associated with macrophyte beds, was only abundant in the Pampa Plain. Piscivory is practically non-existent in central-western and northwestern reservoirs (Table 2).

Table 2. Fish species considered as piscivores or planktivores by geographic region in the analyzed data (ARLARE, $n = 96$). The number of lakes with these species present at sampling time shown in parentheses.

Piscivores	Planktivores
Patagonia and Tierra del Fuego	
Salmo trutta (14)	*Odontesthes microlepidotus* (15)
Salmo salar sebago (1)	*Odontesthes bonariensis* (1)
Salvelinus namaycush (1)	*Galaxias platei* (5) [a]
Salvelinus fontinalis (17)	
Percichthys colhuapiensis (4)	
Pampa Plain	
Hoplias malabaricus (11)	*Odontesthes bonariensis* (20)
	Odontesthes microlepidotus (1)
	small Characidae (7)[a]
Central-western and Northwestern Arid Region	
Hoplias malabaricus (1)	*Odontesthes bonariensis* (23)
	Odontesthes microlepidotus (1)
	small Characidae (8)[a]

[a] Small zooplanktivorous species not considered in main analyses.

Materials and methods

Data collection

Limnological and fish data presented in this study were collected during an extensive survey of 110 lakes and reservoirs in Argentina (ARLARE data)[1] from 1984 to 1987 (Quirós et al., 1988). Each site was visited once, in mid- summer, except for six that were sampled seasonally over a period of 2 y. 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. 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 analytical methods used have been described previously (Quirós, 1990a).

Fish samples were collected using a nylon gillnet composed of nine 50 m panels ranging from 42 to 170 mm stretched mesh (Quirós, 1990a). Floating sets were made overnight, and were usually set for a period of 12 h. A measure of relative standing stocks of fish by biomass was made on the basis of the mean weight of all fish caught per overnight set for the experimental gillnets (CPUE, kg/night. standard gillnets). Equal fish vulnerability to gillnets among lakes was assumed. Zooplankton samples were collected using a 53 μm mesh net with an opening of 0.40 m. Vertical 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 sampled. A 100% capture efficiency was assumed here. Macrozooplankton biomass (MAZOO, μg dry weight l^{-1}) and microzooplankton biomass (MIZOO, μg dry weight l^{-1}) were calculated from size and abundance data (Menu Marque & Marinone, 1986; Quirós et al., 1988). Cladocerans and post naupliar copepods were considered to be macrozooplankton, and rotifers and copepod nauplii as microzooplankton. Further details on the method of macrozooplankton sampling are provided in Menu Marque & Marinone (1986).

Data analyses

Sites with high inorganic turbidity were excluded as outliers (Quirós, 1989). Two lakes with incomplete data for zooplankton, one acidic lake without fish, one

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[1] A complete set of tables is available, at a nominal charge, from the National Fishery Research and Development Institute (INIDEP), Av. Victoria Ocampo 1, Escollera Norte, 7600 Mar del Plata, Argentina.

lake situated in the Pampa Plain (Indio Muerto Lake) with extremely low macrozooplankton biomass and one lake with *Mugil* sp., were also excluded (Quirós, 1990b, 1991). The resulting data base consists of 96 lakes and reservoirs. In the analyses where the variable total fish biomass was included, fishless lakes (2) or lakes where environmental stress on fish had been detected (4) (Quirós, 1990a), were also excluded. Table 1 presents the main characteristics of studied sites.

Data analysis was made by simple regression on the total data and on three data subsets (Table 1) defined as: (1) lakes with planktivorous fishes and without piscivores (PLANKT +/PISCIV −), (2) lakes with both piscivores and planktivores (PLANKT +/PISCIV +), and (3) lakes without planktivores but with or without piscivores (PLANKT −/PISCIV ±). For comparisons between regression models a general F-test (Weisberg, 1980) was used. 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 ($\%\mathrm{PLANKT} = \mathrm{CPUE}_{\mathrm{PLANKT}}/\mathrm{CPUE}$) and piscivores ($\%\mathrm{PISCIV} = \mathrm{CPUE}_{\mathrm{PISCIV}}/\mathrm{CPUE}$), and the piscivores to piscivores plus planktivores biomass ratio [%PISCIV/(%PISCIV + %PLANKT)] defined by its value except for lakes without both planktivores and piscivores for which it was defined as unity, were used as surrogates of fish community composition. Mean macrozooplankton size (MASI, μg dry weight ind.$^{-1}$) was estimated by mean body weight as the ratio between biomass (μg dry weight l^{-1}) and abundance (number of individuals l^{-1}). Dissolved oxygen concentration at 0.50 m above the bottom (DOb, mg l^{-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). In order to stabilize the variance, all the variables except DOb, and fish biomass ratios were log-transformed, and %PLANKT and %PISCIV, as proportions, were transformed to their arc-sine (Draper & Smith, 1981). 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 (partial F-value>4), but only those with low covariation with previously included regressor variables, were forced into the regression equation. Curvilinear trends in simple regression residuals were studied using robust locally weighted regression and smoothing graphic techniques (Cleveland, 1979). The Number Cruncher Statistical System (NCSS) (Hintze, 1988) was used.

Results

Simple regression models

Chlorophyll models

Lakes with planktivorous fishes but without piscivores showed the highest algal biomass, and lakes without planktivorous fishes had the lowest phytoplankton, at comparable TP concentrations. Differences among regressions between Chl and TP (Table 3) for lakes with different fish assemblages were highly significant ($F = 14.18$, $P < 0.0001$). Those differences were higher between lakes with planktivores but without piscivores (PLANKT +/PISCIV −) and lakes with both planktivorous and piscivorous fishes (PLANKT +/PISCIV +) ($F = 5.66$, $P < 0.01$), than between lakes with both planktivores and piscivores (PLANKT +/PISCIV +) and lakes without planktivores (PLANKT −/PISCIV ±) ($F = 4.36$, $P < 0.05$). Furthermore, differences between lakes with planktivores but no piscivores (PLANKT +/PISCIV −) and lakes without planktivorous fishes (PLANKT −/PISCIV ±), were highly significant ($F = 26.5$, $P << 0.0001$). As expected, both slope and intercept in TP-Chl models increase or decrease with the relative trophic relevance of zooplanktivory or piscivory, respectively (Table 3).

Both kinds of models, parallel regressions or concurrent regressions, were as good as the most general three regressions model for which all the parameters are different ($F = 2.08$, $P = 0.15$, and $F = 0.80$, $P = 0.46$, respectively), but differences were lower for concurrent regressions. From those results, whether fish effects increase or whether they are equally distributed with lake trophy cannot be securely discriminated. That those effects are not higher in temperate oligotrophic conditions can be assured for ARLARE data, even if higher differences may be suspected for eutrophic-hypertrophic conditions (Quirós, 1995).

Zooplankton biomass models

Differences among regressions between macrozooplankton and chlorophyll for lakes with different fish assemblages were highly significant ($F = 7.98$,

Table 3. Simple regression models for total chlorophyll (Chl, mg m^{-3}), macrozooplankton biomass (MAZOO, μg dry weight l^{-1}), catch per unit effort of planktivores ($CPUE_{PLANKT}$, kg/night.standard gillnets), catch per unit effort of piscivores ($CPUE_{PISCIV}$, kg/night. standard gillnets), total catch per unit effort (CPUE, kg/night.standard gillnets). TP (total phosphorus, mg m^{-3}). The coefficient of determination (R^2), the root mean square error (RMSE), and the standard error for slope (SEs), are presented. PLANKT + and PLANKT −, sites with and without planktivores, respectively. PISCIV + and PISCIV −, sites with and without piscivores, respectively.

Data set	*n*	Equation	SEs	RMSE	R^2
total	96	$\log_e \text{Chl} = -1.949 + 1.08 \log_e \text{TP}$	0.060	0.956	0.78
PLANKT +/PISCIV −	42	$\log_e \text{Chl} = -1.347 + 1.08 \log_e \text{TP}$	0.093	0.776	0.77
PLANKT +/PISCIV +	16	$\log_e \text{Chl} = -1.738 + 0.98 \log_e \text{TP}$	0.088	0.711	0.90
PLANKT −/PISCIV ±	38	$\log_e \text{Chl} = -1.897 + 0.83 \log_e \text{TP}$	0.084	0.773	0.73
total	96	$\log_e \text{MAZOO} = 3.160 + 0.63 \log_e \text{Chl}$	0.070	1.369	0.47
PLANKT +/PISCIV −	42	$\log_e \text{MAZOO} = 2.985 + 0.52 \log_e \text{Chl}$	0.108	1.109	0.37
PLANKT +/PISCIV +	16	$\log_e \text{MAZOO} = 2.561 + 1.00 \log_e \text{Chl}$	0.161	1.343	0.74
PLANKT −/PISCIV ±	38	$\log_e \text{MAZOO} = 3.606 + 1.09 \log_e \text{Chl}$	0.138	1.242	0.63
PLANKT +/PISCIV + plus PLANKT −/PISCIV ±	54	$\log_e \text{MAZOO} = 3.346 + 0.93 \log_e \text{Chl}$	0.101	1.338	0.62
total	96	$\log_e \text{CPUE}_{\text{PLANKT}} = -0.181 + 0.46 \log_e \text{MAZOO}$	0.070	1.369	0.47
#PISCIV −	49	$\log_e \text{CPUE}_{\text{PLANKT}} = -0.266 + 0.62 \log_e \text{MAZOO}$	0.108	1.109	0.37
#PISCIV +	41	$\log_e \text{CPUE}_{\text{PLANKT}} = -0.294 + 0.31 \log_e \text{MAZOO}$	0.161	1.343	0.74
total	90	$\log_e \text{CPUE} = 2.776 + 0.42 \log_e \text{Chl}$	0.058	1.122	0.37
PLANKT +/PISCIV −	40	$\log_e \text{CPUE} = 2.323 + 0.46 \log_e \text{Chl}$	0.130	1.318	0.25
PLANKT +/PISCIV + plus PLANKT −/PISCIV ±	50	$\log_e \text{CPUE} = 2.977 + 0.58 \log_e \text{Chl}$	0.062	0.808	0.65
total	90	$\log_e \text{CPUE} = 1.418 + 0.49 \log_e \text{MAZOO}$	0.059	1.064	0.44
PLANKT +	56	$\log_e \text{CPUE} = 1.059 + 0.60 \log_e \text{MAZOO}$	0.079	1.037	0.52
PLANKT −	34	$\log_e \text{CPUE} = 1.838 + 0.32 \log_e \text{MAZOO}$	0.087	1.026	0.30

$P<0.001$) (Table 3). Despite these differences, a model composed of two concurrent regressions, one for lakes with planktivores but without piscivores (PLANKT +/PISCIV −) and another for lakes without planktivores or with both planktivores and piscivores (PLANKT −/PISCIV ± plus PLANKT +/PISCIV +) (Table 3), fitted the data better than a model with three concurrent regressions ($F = 2.38$, $P = 0.14$). Similar results were obtained from the analysis of the relationship between macrozooplankton and microzooplankton ($F = 10.92$, $P<0.0001$, for a two regressions model). However, there were no significant differences between macrozooplankton on TP regressions for fish data subsets, though the regression for lakes without planktivores (PLANKT −/PISCIV ±) predicted higher macrozooplankton biomass. In summary, the macrozooplankton was significantly lower for sites with planktivores not controlled by piscivores (PLANKT +/PISCIV −), when chlorophyll or microzooplankton was held constant. Moreover, the effects of the fishes were greater for eutrophic-hypertrophic conditions than for oligotrophic conditions (Table 3).

A pattern similar to that for TP-Chl regressions (Table 3) was obtained for regressions of microzooplankton on TP. Microzooplankton was greater for sites with planktivorous fishes, and a concurrent two-way regression model for sites with and without planktivores, fitted the data better that a three-way regression model ($F = 0.98$, $P = 0.35$). Otherwise, there were no significant differences for regressions of microzooplankton on chlorophyll.

Fish biomass models

Planktivorous fish biomass increased with lake trophy (Quirós, 1990a, 1991), but regression differences were only significant for regressions with macrozooplankton ($P<0.0005$) (Table 3), microzooplankton ($P<0.005$), and TP ($P<0.05$), for sites with and without piscivorous fish.

Piscivorous fishes were not significantly related to nutrient or planktonic variables, but had a weak significant negative relation with planktivorous fishes ($R = -0.25$, $P = 0.02$) for total data. However, for sites where both planktivores and piscivores had been present (PLANKT +/PISCIV +), both variables were positively related (loge $\mathrm{CPUE}_{\mathrm{PISCIV}} = 1.460 + 0.33$ (0.15) $\log_e \mathrm{CPUE}_{\mathrm{PLANKT}}$, $R^2 = 0.25$, $P = 0.05$). Moreover, for those sites macrozooplankton explained just 50% of the variability in both planktivore ($R^2 = 0.53$, $P<0.001$) and piscivore ($R^2 = 0.52$, $P<0.002$).

As shown before (Quirós, 1990, 1991), total fish biomass (CPUE) was significantly related to nutrient and planktonic variables, but there were no significant differences between regressions of total fish on TP or on microzooplankton, for the fish data subsets considered here. However, differences were significant for regressions of total fish with chlorophyll and with macrozooplankton. For the relationship between total fish and chlorophyll, a two- way parallel regression model for lakes with not controlled planktivores (PLANKT +/PISCIV −), and for lakes with controlled planktivores or without these fishes (PLANKT +/PISCIV + plus PLANKT −/PISCIV data subsets) fitted the data better ($F = 0.04$, $P>0.80$) (Table 3). For a given chlorophyll concentration, lakes with planktivores but without piscivores presented a lower total fish biomass than the other lakes. For the relationship between total fish and macrozooplankton, a two-way concurrent regression model for sites with and without planktivorous fish fitted the data better ($F = 1.50$, $P>0.20$). As shown in Quirós (1991), sites with planktivorous fishes presented a higher total fish when compared with lakes without those fish after macrozooplankton effects have been accounted for; this is so, at least for early eutrophic conditions. In summary, total fish biomass is more related to chlorophyll in lakes without planktivores or lakes where both planktivores and piscivores are absent, and more related to macrozooplankton in lakes with planktivorous fish.

Regression slope comparisons

For total data, both the slopes of the regressions for biological standing stocks on total phosphorus and the explained variances diminished steadily from phytoplankton to planktivorous fishes (Figure 1). A similar relationship occurred in an earlier mostly homogeneous data set (Quirós, 1991). However, this pattern was not apparent for each fish data subset. Although the explained variance usually diminished towards the top of the food web, there were gaps between regression slopes (Figure 1). For lakes without visual planktivores, the gap in slope values was, as expected, between regressions of macrozooplankton and total fish biomass on TP. The patterns obtained for regressions between standing stocks, ordered as in an idealized (and incomplete) pelagic food web, are qualitatively similar to those described above (Figure 2).

To check that the observed differences among lakes are more closely related to fish composition differences than to other factors not considered here, the simple regressions were also analyzed considering subsets of lakes on a typological regional basis (Quirós, 1989). Although differences for regional, climatic, morphometric, and nutrient data subsets were significant (Quirós, 1990b, 1996), in every instance, the models for the fish data subsets explained most of the variability in biological standing stocks. Moreover, there were no significant differences in regressions when stratified and mixed lake subsets were analyzed.

Residuals and multiple regressions

Curvilinear trends in residuals to TP-Chl linear regression shown previously described patterns (Quirós, 1990b). Residuals were positive for lakes with low dissolved oxygen concentration at the water-sediment interface or sites with planktivorous fish, and negative for lakes with low ZMEAN/SDT ratio or sites with piscivorous fish. Residuals also changed from positive to negative with the increase in mean macrozooplankton body weight. On the other hand, those residuals showed a bell-shaped curve when regressed on TN:TP ratio between 7 and 120 (molar ratio), and a maximum is displayed for TN:TP near 60. The results described above are in concordance with the multiple regression models for chlorophyll concentration developed before (Quirós, 1990b, 1995).

The explained variability in macrozooplankton was lower than for chlorophyll, both in the single and multiple regression models. For the total data, macro-

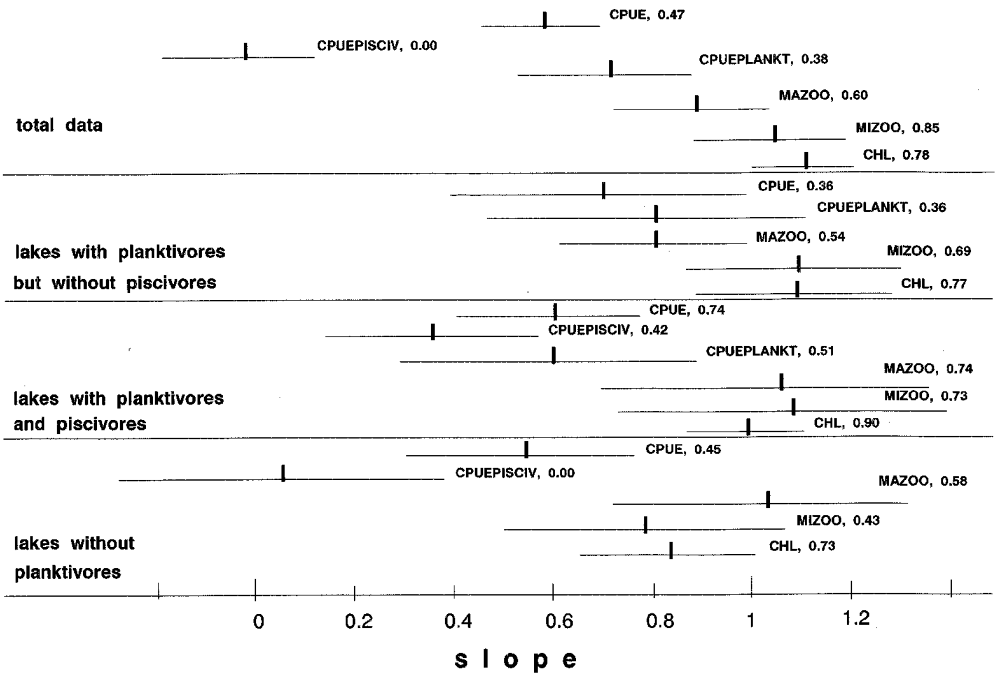

Figure 1. Slope values are for simple regression models between biological standing stocks and total phosphorus for total data and three fish data subsets as defined in the text. The number next to the biological stock variable name is the coefficient of determination (R^2) for the regression. Points and lines represent slope values and two times the standard error for slope respectively. Total data ($n = 96$); sites with planktivores but without piscivores ($n = 42$); sites with both planktivores and piscivores ($n = 16$); sites without planktivores ($n = 38$).

zooplankton was more related to TP ($R^2 = 0.60$) than to chlorophyll ($R^2 = 0.47$), but mean depth was the most important single variable to explain its variability ($R = -0.79$, $P < 0.0001$). Residual analysis showed macrozooplankton body weight, frequency of piscivores, and mean depth to Secchi disk transparency ratio to be potential independent variables after TP or chlorophyll effects had been accounted for. Nutrient variables (e.g. TP or TN) or chlorophyll were, by far, the most relevant in explaining macrozooplankton variability for total data in multiple regressions (Table 4).

Frequencies of planktivores and piscivores were important inversely related variables to explain the variability of piscivore and planktivore biomass for multiple regression models (not presented here), respectively. Those models both show the dissolved oxygen concentration at the bottom to be positively related to fish biomass. Moreover, chlorophyll and macrozooplankton were most relevant than TP in explaining planktivore and piscivore variability, respectively.

Discussion and conclusions

Differences in fish assemblage composition among lakes were reflected in distinct relationships between nutrient levels and biological standing stocks, and between those relationships at different trophic levels. However, fish effects were not clearly separated from other internal differences among lakes, like dissolved oxygen concentration at the bottom, the relative importance of aquatic macrophytes, or macrozooplankton body size. Partially independent effects of macrozooplankton size and planktivorous fish on chlorophyll, and a significant ($P < 0.001$) inverse relationship between macrozooplankton size and the ZMEAN:SDT ratio, have been shown before for the ARLARE data (Quirós, 1990b). Furthermore, a direct relationship ($R = 0.39$, $P < 0.001$) between frequency of piscivores and dissolved oxygen at the sediment interface is shown here.

Several regression models and curvilinear trends in data have been related to various ecosystem processes by different authors (Straskaba, 1976; Prairie et al., 1989; McCauley et al., 1989; Watson et al., 1992;

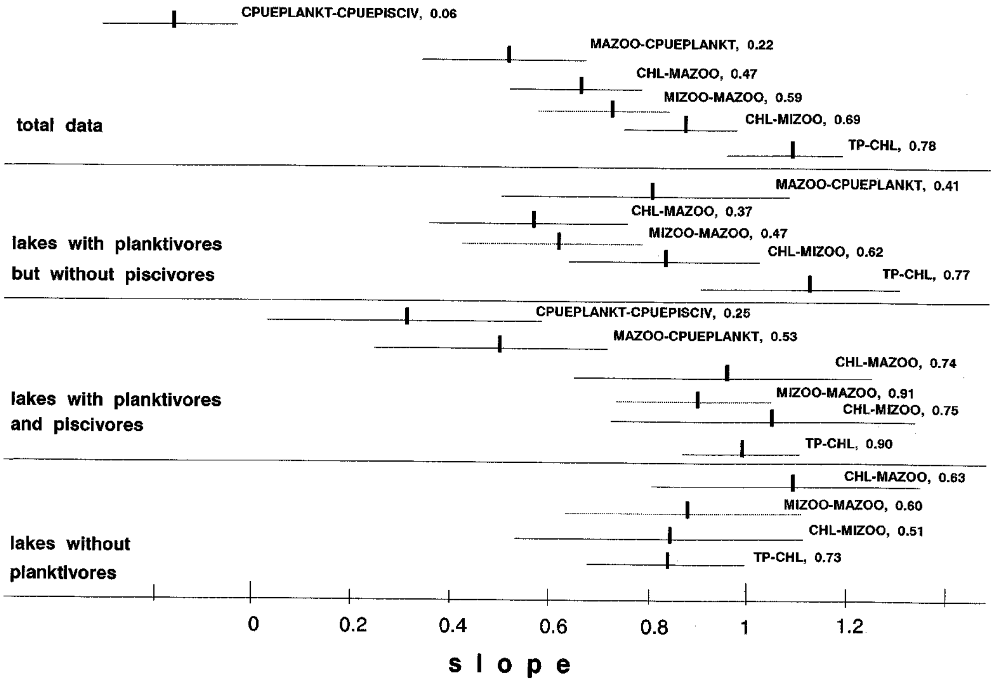

Figure 2. Slope values for simple regression models between different standing stocks for total data and three fish data subsets as defined in the text. Points and lines represent slope values and two times the standard error for slope respectively. The number next to each line is the coefficient of determination (R^2) for the regression. The standing stock variables as defined in the text. total data ($n = 96$); sites with planktivores but without piscivores ($n = 42$); sites with both planktivores and piscivores ($n = 16$); sites without planktivores ($n = 38$).

Mazumder, 1994). In this paper we propose changes in fish assemblage cascading through the food web. Regional differences have been considered in stepwise multiple regression analyses. Climatic, morphometric, and nutrient variables have been included as potential regressors. Nevertheless, fish assemblage composition variables remain the ‘best’ regressors to explain residual variability in biological standing stocks (Quirós, 1990b, 1995, this paper).

Lakes with three level pelagic communities (planktivores not controlled by piscivores) had chlorophyll concentrations drastically higher than lakes with four level communities (planktivores controlled by piscivores). Moreover, lakes without planktivorous fishes showed the lowest chlorophyll concentrations after nutrient effects have been accounted for. These results coincided with the predictions of the biomanipulation concept (Shapiro et al., 1975), the cascading trophic interactions hypotheses (Carpenter et al., 1985), and the bottom-up:top-down model (McQueen et al., 1986) for individual lakes. However, fish effects were not weaker towards the bottom of the food web. Moreover, the differences in visual planktivore biomass regressions were only displayed between lakes with and without piscivores, and not between lakes with planktivores controlled or not by piscivores, respectively. The latter result may be related to the control effects of piscivores on the small planktivores species and planktivorous young of other species that were not considered here. However, though the gillnets used selected strongly against small fish, some of those fish were captured nevertheless. Furthermore, the results were qualitatively similar when small planktivorous species were considered in the analyses.

As was shown before (Quirós, 1990b), ‘top-down’ effects increase from oligotrophic-mesotrophic to eutrophic-hypertrophic conditions, but those changes are more related to fish assemblage composition change than to regional, climatic, morphometric or edaphic lake differences, and were greater with the increase of the planktivore biomass (Quirós, 1990b, 1995, this paper). Similar fish effects on TP-Chl regressions were displayed for a set of Norwegian lakes with different intensity of fish predation (Lyche et al., 1990: Fig. 1a), and planktivore effects on chlorophyll deviations from current TP-Chl regressions have been shown

Table 4. Multiple regression equations relating macrozooplankton biomass (MAZOO, μg dry weight l^{-1}) to total phosphorus (TP, mg m^{-3}), mean macrozooplankton body weight (MASI, μg dry weight ind.$^{-1}$), frequency of piscivores (%PISCIV), mean depth to Secchi disk transparency ratio (ZMEAN:SDT), chlorophyll concentration (Chl, mg m^{-3}). The coefficient of determination (R^2), and the root mean square error of regression (RMSE) are presented.

	Regression coefficient	Standard error	*F*-value ($b_i = 0$)
	Model 1		
Intercept	1.322	0.396	11.16
TP	0.947	0.078	148.60
%PISCIV	0.712	0.279	6.50
ZMEAN:SDT	−0.300	0.125	5.76
$R^2 = 0.655$	RMSE = 1.112		
F (overall) = 58.17	$P<0.001$		
	Model 2		
Intercept	2.163	0.392	30.58
Chl	0.808	0.062	169.00
MASI	1.152	0.227	25.70
ZMEAN:SDT	−0.415	0.124	11.16
%PISCIV	0.693	0.274	6.40
$R^2 = 0.696$	RMSE = 1.050		
F (overall) = 52.07	$P<0.001$		

by McQueen et al. (1990) for a small lake set. Although it was not possible to compare adequately planktivore effects for different trophic conditions because there are relatively few lakes with both low TP concentration and high frequency of visual planktivores (20% for TP below 9 mg m^{-3}), I conclude that, for ARLARE data, both the effects of macrozooplankton on phytoplankton, and of planktivores on macrozooplankton, are greater when TP is higher, but that pattern would be reversed for sets of lakes with high planktivore biomass in oligotrophic-mesotrophic conditions. That suggests a change of the framework for the discussion of fish effects on phytoplankton and zooplankton (McQueen et al., 1986; Benndorf, 1987, 1988). On a broad basis, fish effects would be higher for low piscivores to planktivores plus benthivores ratio independent of lake trophy, all else being equal. Other effects, like trophically induced changes in algal species (McQueen et al., 1986) cannot be ignored.

A decrease in epilimnetic phosphorus has been found in lakes subjected to whole-lake fish manipulations (Benndorf, 1989 for a review), and exceptions appear to be restricted to very shallow ponds and small lakes, densely colonized by macrophytes or subjected to high flushing rates (Benndorf, 1989). For large enclosure experiments, Mazumder et al. (1989) concluded that planktivorous fishes can reduce the loss of P from the epilimnion. However, the highly significant differences among the various fish subsets shown for ARLARE data suggest that the decrease in TP, following an impressive decrease in planktivores is not as important as the decrease in Chl, all else being equal. The opposite view would show a single line as a better representative for the TP-Chl total data.

The existence of three types of lakes depending on the number of components and the existence of gaps in the pelagic trophic web has been suggested (Persson et al., 1988). In ARLARE lakes with two and four level pelagic assemblages, total fish biomass was closely related to chlorophyll concentration. However, it was better related to macrozooplankton for lakes with three and four trophic level (with visual planktivores) assemblages. Those results are in agreement with a bifurcated pathway view for the food web (pelagic and benthic), from phytoplankton to fish. In contrast to that for the relationships between total fish biomass and phyto or macrozooplankton, there were no significant differences for relationships between total fish biomass and TP among fish data subsets, for the data analyzed here as well as for a more homogeneous data set (Quirós, 1991). Those results reinforce the integrative character of fish assemblages, including benthivorous, in aquatic systems (Ryder et al., 1974; Ryder, 1978).

Some of the most important limitations of the ARLARE data, such as limited sampling and shortcomings in fish and zooplankton sampling, were emphasized before (Quirós, 1990a, 1990b, 1995), but some of its advantages, e.g. the wide geographic representation, the broad range of limnological characteristics that have been sampled, which include nutrient, phytoplankton, zooplankton, and fish data, and almost synchronic data, are stressed here.

The results also show that contrary to the apparent global value of the relationships among nutrients, phytoplankton, zooplankton, and total fish standing stocks (expected from thermodynamics and trophic web interaction theories), there is no prevalent pattern for piscivore to planktivore ratio change with lake trophy valid for any set of lakes (Quirós, 1995, 1996). The present results also reinforce a previously stated (Quirós, 1990a) systemic view that effects of variables related to endogenous lake processes, and not directly determined or linked to external characteristics, are not maintained throughout the trophic continuum. When sharp threshold-like changes in internal variables are produced in a narrow range of nutrient variation, the effect of input variables to take account of community biomass change, should be notably lower, resembling short-term changes in some lakes (Quirós, 1996). The effect of endogenous lake variables and the functionality of their variability with lake trophy for lakes with different fish assemblage is worthy of further attention.

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