Empirical relationships between nutrients, phyto- and zooplankton and relative fish biomass in lakes and reservoirs of Argentina

Rolando Quiros

Introduction

Comparative studies of lakes in the global temperate zone has shown that phosphorus is related to phytoplankton biomass and to chlorophyll (Sakamoto 1966, Delong & Kilger 1974, Schnitzer et al. 1978, among others). To macrozooplankton biomass (Hansson & Peters 1984, Facey 1986, Yav 1986), to microzooplankton biomass (Facey 1986), to macrobenthos biomass (Hansson & Peters 1984, see also Rasmussen & Kilger 1987), to fish biomass (Hansson & Leggett 1982) and to benthos (Berto & Kilger 1984). Significant direct relationships between biological standing stocks at different trophic levels were also shown in some instances. For example, macrozooplankton chlorophyll or phytoplankton biomass (McCauley & Kalf 1981, Rosenberg & Karlson 1984, see also Facey 1986), total zooplankton biomass = Carlson's chlorophyll-based index (Batts & Carlson 1983). Fish yield was also shown to be strongly correlated with chlorophyll (Oksanen 1977, Jones & Hoyer 1982), and relative fish biomass as estimated from ghillining (CPUU), is shown to be directly related to chlorophyll in a heterogeneous set of lakes and reservoirs (Quadas 1995). However, a growing concern about the results from comparative lake studies for lakes with different kinds of trophic interactions (Carpen ter et al. 1985, Carpenter & Hutchins 1988) encourages studies that compare empirical relationships between nutrients and biological standing stocks for sets of lakes with different fish community composition.

The fish species of special interest in this study are facultative zooplanktivorous fish of the Asterinidae family such as Balistichthys bahsiorensis and Micromiurus, these are both widespread in Argentinean freshwaters. The former species, native to the Pampa Plain lakes, was introduced into lakes and reservoirs of the centralwestern and northwestern arid regions (Fig. 1). The latter species is native to the Patagonian Plains and Southern Andes lakes (Rossetti et al. 1987). The primary interest of this study was to evaluate the strength of the relationships between nutrients, chlorophyll, microzooplankton and macrozooplankton biomass, and relative fish biomass for lakes and reservoirs of Argentina, and to compare the resulting relationships for the two kinds of lakes, with and without Asterinidae fish.

Lakes and reservoirs studied

The lakes and reservoirs studied are located between the 25th and 55th latitudes south throughout the central-western and northwestern arid regions of Argentina, the Pampa Plain, the Paraguaná Plain, the Paranaese Andes and Tierra del Fuego (Fig. 1). Surface lake area ranged from 0.10 to 81.6 km², and mean depth from 0.70 to 116 m (Table 1). The deeper lakes are situated in the Paraguaná Andes and Tierra del Fuego. All lakes on the Pampa Plain are ponds or very shallow lakes. Mean annual air temperatures ranged from 3.2 to 22.4 °C, and elevations from 0 to 2,350 m (Table 1). Paraguaná

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean Range</th>
<th>Mean Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>A (kg)</td>
<td>10.7 - 67.2</td>
<td>46.6 - 500</td>
</tr>
<tr>
<td>Zone (%)</td>
<td>24.3 - 116.7</td>
<td>50.2 - 275.0</td>
</tr>
<tr>
<td>TS (%)</td>
<td>11.2 - 32.0</td>
<td>19.4 - 116.3</td>
</tr>
<tr>
<td>DO (ppm)</td>
<td>10.1 - 27.2</td>
<td>10.1 - 27.2</td>
</tr>
<tr>
<td>pH</td>
<td>7.5 - 9.4</td>
<td>7.5 - 9.4</td>
</tr>
<tr>
<td>CHL (mg l⁻¹)</td>
<td>3.74 - 0.16</td>
<td>4.9 - 2.3</td>
</tr>
<tr>
<td>TON (ppb)</td>
<td>2.5 - 99.3</td>
<td>2.5 - 99.3</td>
</tr>
<tr>
<td>CPUU</td>
<td>0.00 - 0.00</td>
<td>0.00 - 0.00</td>
</tr>
<tr>
<td>(kg weight)</td>
<td>44.2 - 2416</td>
<td>101.2 - 2416</td>
</tr>
<tr>
<td>(kg weight)</td>
<td>0.2 - 0.4</td>
<td>0.2 - 0.4</td>
</tr>
<tr>
<td>(kg weight)</td>
<td>112.2</td>
<td>29 - 300.1</td>
</tr>
<tr>
<td>(kg weight)</td>
<td>418</td>
<td>1.2 - 329.3</td>
</tr>
</tbody>
</table>

Table 1. Mean and range for the limnological characteristics measured in 60 Argentinean lakes and reservoirs with (A AT, n = 38) and without (A NOATE, n = 27) Asterinidae. A lake area, Zone, mean depth, TEMP, mean annual air temperature, SDI, Secchi disk depth, KDL, water conductivity at 25 °C, TP, total phosphorus; TON, total organic nitrogen; TP, total nitrogen to total phosphorus ratio; CHL, total chlorophyll; MEZOO, microzooplankton biomass; MAZOO, macrozooplankton biomass; CPUU, catch per unit effort of asterinids; CPUU, total catch per unit effort.

© 1991 E. Schmitzler und H. Verlagshaus. BDZ 1991 Stuttgart 1

O164-0770/91/0224-1198 $ 2.25
Tierra del Fuego Andes lakes are typically ultralotrophic or oligotrophic. Most of the centralwestern and northwestern reservoirs and Patagonian Plateau lakes ranged from mesotrophic to eutrophic. Lake trophy of the Pampa Plain lakes ranged from eutrophic to hypertrophic. Most of the fish species of the northwestern and centralwestern reservoirs have been introduced from outside Argentina or from other river basins in Argentina. A majority of the glacial lakes in Patagonia and Tierra del Fuego have been successfully colonized by salmoids (Bedin & Quiros 1983, Quiros 1987). The Pampa Plain lakes are practically the only Argentinean lakes with a relatively high fish community diversity (Ringuet 1975) and most of the fish sampled were species native to the Pampa Plain. Basildichthyus thomsonii (Argentinian silverside) is common to most lakes and re-
servors in the Pampa Plain and centralwestern and northwestern arid regions. Boleophthalmus microlepidus (Paratrogaster silverspinus) is common to most Patagonian lakes except for those in Tierra del Fuego. Both species of the Asterinidae family have been reported as zoo- planktonivores and microbenthic feeding fish (Boschetti et al. 1987). Pelagic fish is widespread in Argentinean lakes and reservoirs. Salmo trutta, Salvelinus fontinalis, Salmo salar and Salvelinus nanaycota were moderately abundant in some southern glacial lakes, and Salmo gairdneri is usually the most abundant species there. Holocentrus wallago, a piscivorous fish in the Pampa Plain lakes was only moderately abundant in fish of those lakes (Quinones et al. 1988). Although inverse relationships between aleurinids and salmlondids, and also between Boleophthalmus microlepidus and Holocentrus wallago have been reported (Quinones 1987), unreported, those inter- actions have not been fully studied yet. Further relevant morphometric, chemical and fish data were presented by Quinones (1988, 1990) and Quinones et al. (1988).

Materials and methods

During the summers of 1984 to 1987, 110 lakes and re- sevoirs of Argentina were sampled (Quinones et al. 1988). Lakes and reservoirs were visited once, except for 6 stu- tioned on the Paraguanado (Fig. 1) that were studied seasonally over the course of two years. Only data for 65 lakes and reservoirs during mid-summer are considered here (Table 1).

Lake surface area (A, km²), mean depth (Zmax, m) and mean annual air temperatures (TEMP, °C) were ob- tained from Quinones et al. (1983, 1986). For each lake, vertical profiles were obtained for temperature, dis- solved oxygen, conductivity, pH and total alkalinity. In lakes <25 m, a Hydrolab survey system was used. Secchi disk visibility (SDL, m) was recorded with a 25 cm diameter, black and white disk. Chlorophyll (CHL, mg·m⁻³), total phosphorus (TP, mg·m⁻³), total nitrogen (TN, mg·m⁻³); nitrates and nitrites were determined from samples collected at 0.5 m depth. Nutrients were determined according to the American Public Health Association (1977) and Getteman et al. (1978). Chlorophyll determinations were done according to Scourfield et al. (1979). The chlorophyll results pre- sented here are without phaeophytin corrections. The analytical methods used have all been described pre- viously (Quinones 1988).

Zooplankton samples were collected with 50 m long vertical tows or from 0.5 m above the bottom to the lake surface (53-am mon). In both cases epilimnetic waters were usually sampled. Have a 100 μm net efficiency was assumed. Macrozooplankton biomass (MAZOO, ag dry weight -1') and microzooplankton biomass (MIZOO, ag dry weight -1') were calculated from size and abundance data (Méndez & Marques, unpublished data). Pontoporeia copepods and cladocerans were considered in MAZOO and rotifers and copepods nauplii in MIZOO. More details are provided in Méndez & Marques (1986).

Relative fish biomass (CFUP, kg·m⁻² - standard gill-

net) was estimated by gillnetting. Fish samples were usually collected with an experimental nylon gillnet composed of 50 cm panels of 42, 61, 70, 75, 125, 150 and 175 mm stretch mesh. In the Pampa Plain lakes, nine panels of only 25 m were used. Gillnets were set in floating gates perpendicular to the shoreline, with the smallest mesh inshore. Floating nets were made over- night, and were usually set for a period of 12 h. A mea- sure of relative standing stocks of fish by biomass was made on the basis of mean weight in kilograms if all fish caught per overnight set for the experimental gang of gill nets. Catch was standardized as the sum of mean weights of fish per 100 m² of each mesh for the nine panels. Approximately equal fish vulnerability is gill nets among all lakes was assumed here. Further details on the method of fish sampling are provided in Quinones (1986).

Raw data for all the lakes and reservoirs studied are available from the Instituto Nacional de Investigación y Desarrollo Pesquero (Quinones et al. 1988).

Lakes were classified according to the presence of fish or degree of human intervention. Accordingly, I exclude here 4 lakes without fish and 7 lakes and reservoirs known to be subject to high stress levels due to human influence on fish (Quinones 1990). Lake Lago Missouri si- tuated in the Pampa Plain with extremely low macro- zooplankton biomass and the only lake with Megalops at sampling, was also excluded. To homogenize the data base, further screening was made for turbid lakes where the turbidity was derived from inorganic sources, lakes with low dissolved oxygen at the water-sediment inter- face (below 2.0 mg·l⁻¹), with Secchi readings above the mean depth (Zmax<SDL<1) or with TN/TP (molar basis) below 22; all those variables were shown to be re- lated to phytoplankton or fish food nutrient effects had been accounted for (Quinones 1988, 1989, 1990).

Data study was made by simple correlation and regression analyses. The total data set (n = 65) and subsets for simple (n = 40) and without (n = 27) artificial fish were used. Further analysis was performed for regression models comparisons (Wennergren 1982). All the variables except mean annual air tempera- ture (TEMP) were log transformed in order to stabilize the variance and linearize the data.

Results

For the total data set (n = 65), phytoplankton, micro and macrozooplankton, and total fish stand- ing stocks were highly correlated with each other and also with climatic, morphometric and nutrient related variables (Table 2). Similar results were ob- tained from the correlation analyses of the n = 40 and n = 27 subsets data. As expected, biological standing stocks were directly related to TEMP and water column and mean annual air temperature, and in-
Table 2. Matrix of correlation coefficients between environmental and trophic variables for 68 Argentinean lakes and reservoirs. Axes (A, km²), mean depth (Zmean, m), mean annual air temperature (TEMP, °C), Secchi disk depth (SDL, m), conductivity at 20 °C (KD), total phosphorus (TP, mg m⁻³), total nitrogen (TON, µg), chlorophyll (CHL, mg m⁻³), microzooplankton biomass (MIZOO, µg dry weight⁻¹), and macrozooplankton biomass (MAIZOO, µg dry weight⁻¹), catch per unit effort of athereoids (CPEUE, kg/night - standard gillnets), total catch per unit effort (CPU, kg/night - standard gillnets).

<table>
<thead>
<tr>
<th>Variable</th>
<th>A</th>
<th>Zmean</th>
<th>TEMP</th>
<th>SDL</th>
<th>KD</th>
<th>TP</th>
<th>TON</th>
<th>CHL</th>
<th>MIZOO</th>
<th>MAIZOO</th>
<th>CPUA</th>
<th>CPUE</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>1</td>
<td>0.43</td>
<td>-0.11</td>
<td>0.23</td>
<td>-0.10</td>
<td>-0.31</td>
<td>-0.29</td>
<td>-0.26</td>
<td>-0.35</td>
<td>-0.42</td>
<td>-0.12</td>
<td>-0.23</td>
</tr>
<tr>
<td>Zmean</td>
<td>1</td>
<td>-0.64</td>
<td>0.49</td>
<td>-0.75</td>
<td>0.91</td>
<td>-0.90</td>
<td>0.93</td>
<td>-0.90</td>
<td>-0.87</td>
<td>0.81</td>
<td>-0.65</td>
<td>-0.77</td>
</tr>
<tr>
<td>TEMP</td>
<td>1</td>
<td>-0.79</td>
<td>0.72</td>
<td>0.72</td>
<td>0.63</td>
<td>0.79</td>
<td>0.73</td>
<td>0.84</td>
<td>0.68</td>
<td>0.52</td>
<td>0.60</td>
<td>0.53</td>
</tr>
<tr>
<td>SDL</td>
<td>1</td>
<td>-0.38</td>
<td>0.93</td>
<td>-0.88</td>
<td>0.96</td>
<td>-0.79</td>
<td>0.73</td>
<td>-0.65</td>
<td>0.77</td>
<td>0.56</td>
<td>0.58</td>
<td>0.56</td>
</tr>
<tr>
<td>KD</td>
<td>1</td>
<td>0.76</td>
<td>0.75</td>
<td>0.77</td>
<td>0.77</td>
<td>0.65</td>
<td>0.66</td>
<td>0.58</td>
<td>0.56</td>
<td>0.58</td>
<td>0.58</td>
<td>0.58</td>
</tr>
<tr>
<td>TP</td>
<td>1</td>
<td>0.94</td>
<td>0.94</td>
<td>0.87</td>
<td>0.79</td>
<td>0.74</td>
<td>0.63</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.61</td>
<td>0.79</td>
</tr>
<tr>
<td>TON</td>
<td>1</td>
<td>0.91</td>
<td>0.89</td>
<td>0.78</td>
<td>0.82</td>
<td>0.77</td>
<td>0.74</td>
<td>0.63</td>
<td>0.63</td>
<td>0.63</td>
<td>0.63</td>
<td>0.63</td>
</tr>
<tr>
<td>CHL</td>
<td>1</td>
<td>0.98</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
<td>0.79</td>
</tr>
<tr>
<td>MIZOO</td>
<td>1</td>
<td>0.83</td>
<td>2.63</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
<td>0.72</td>
</tr>
<tr>
<td>MAIZOO</td>
<td>1</td>
<td>0.43</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
<td>0.67</td>
</tr>
<tr>
<td>CPUA</td>
<td>1</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
</tr>
<tr>
<td>CPUE</td>
<td>1</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
<td>0.68</td>
</tr>
</tbody>
</table>

*P* < 0.0001, *b* < 0.0001, *c* < 0.01.

Fig. 2. Relationships between a) chlorophyll (CHL, mg m⁻³) and b) micro- and macrozooplankton biomass (MIZOO, µg dry weight⁻¹) of algae (MAIZOO, µg dry weight⁻¹), c) macrozooplankton biomass (MAIZOO, µg dry weight⁻¹), and d) 68 lakes and reservoirs. CHL, TON, and CPUA were more closely related to mean depth and Secchi depth (Table 2).

After Secchi depth, TP was the strongest estimator of CHL for total data (*r²* = 0.88), as well as for NOATE data subsets (*r²* = 0.87 and *r²* = 0.84 respectively). The total coincident regression model (Eq. 1, Table 3) was not adequate when compared to regressions for NOATE and NOATE data subsets (*F* = 5.56, *P* < 0.01). TON was as good as CHL, TP, or Zmean to explain MIZOO variability for the total data set (Table 2) and NOATE subset, but CHL was the strongest variable related to MIZOO for NOATE (*r²* = 0.77, *P* < 0.01). There were no significant differences between macro and microzooplankton biomass (MAIZOO) and any other variable considered (Table 2) for all data sets. TP was an important mean depth to explain MIZOO variability for total data and NOATE subset, but its correlation to MIZOO for NOATE subset was lower. The total composite MIZOO regression model on TP (Eq. 1, Table 3) or TON could not be rejected (*F* = 1.66, *P* > 0.05, and *F* = 1.17, *P* > 0.75, respectively). Nevertheless, for both MIZOO-CHL and MIZOO-MIZOO regressions, a single composite model was not adequate (*F* = 4.31, *P* < 0.05, and *F* = 3.82, *P* < 0.05, respectively). Total fish standing stock (CPUE) was more related to TP than to any other considered regressor for variable of all the data combined (*r²* = 0.63, *P* < 0.0001) and NOATE data subset (*r²* = 0.26, *P* < 0.0001), but was slightly more closely relat-
Table 3. Simple regression models relating total chlorophyll (CHL, mg m⁻²) microzooplankton biomass (MIZOO, µg dry weight⁻¹), microzooplankton biomass (MAZOO, µg dry weight⁻¹), catch per unit effort of Asterinidae (CPEU, kg night⁻¹ standard g net), total catch per unit effort (CPEU, kg night⁻¹ standard g net), total phosphorus (TP, mg L⁻¹) and total organic nitrogen (TON, µmol). #ATE, lake data subset with asterisks, #NOATE, lake data subset without asterisks. Standard error of slope (SE), root mean square error of regression (RMSE) and the coefficient of determination (r²) are presented.

<table>
<thead>
<tr>
<th>Data set</th>
<th>Equation</th>
<th>SE</th>
<th>r²</th>
<th>RMSE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Total</td>
<td>log(theses) = 2.26 + 1.2 log(TP)</td>
<td>0.06</td>
<td>0.88</td>
<td>0.753</td>
</tr>
<tr>
<td>2 #ATE</td>
<td>log(CHL) = 1.86 - 1.3 log(TH)</td>
<td>0.07</td>
<td>0.87</td>
<td>0.746</td>
</tr>
<tr>
<td>3 #NOATE</td>
<td>log(CHL) = 2.28 - 1.06 log(TH)</td>
<td>0.09</td>
<td>0.84</td>
<td>0.637</td>
</tr>
<tr>
<td>4 Total</td>
<td>log(MIZOO) = 1.54 + 1.15 log(TH)</td>
<td>0.08</td>
<td>0.76</td>
<td>1.107</td>
</tr>
<tr>
<td>5 Total</td>
<td>log(MIZOO) = 4.06 + 1.06 log(TON)</td>
<td>0.11</td>
<td>0.78</td>
<td>1.044</td>
</tr>
<tr>
<td>6 Total</td>
<td>log(MIZOO) = 0.692 + 0.91 log(CHL)</td>
<td>0.06</td>
<td>0.77</td>
<td>1.079</td>
</tr>
<tr>
<td>7 Total</td>
<td>log(MAZOO) = 1.148 + 0.97 log(TH)</td>
<td>0.09</td>
<td>0.65</td>
<td>1.259</td>
</tr>
<tr>
<td>8 Total</td>
<td>log(MAZOO) = 3.093 - 0.72 log(TH)</td>
<td>0.08</td>
<td>0.56</td>
<td>0.576</td>
</tr>
<tr>
<td>9 Total</td>
<td>log(MAZOO) = 2.386 - 0.57 log(MIZOO)</td>
<td>0.06</td>
<td>0.69</td>
<td>1.158</td>
</tr>
<tr>
<td>10 #ATE</td>
<td>log(MAZOO) = 2.450 + 0.74 log(MIZOO)</td>
<td>0.08</td>
<td>0.72</td>
<td>1.358</td>
</tr>
<tr>
<td>11 #NOATE</td>
<td>log(MAZOO) = 2.706 - 1.03 log(MIZOO)</td>
<td>0.14</td>
<td>0.69</td>
<td>1.354</td>
</tr>
<tr>
<td>12 Total</td>
<td>log(CPEU1) = 0.378 + 0.71 log(TH)</td>
<td>0.11</td>
<td>0.39</td>
<td>1.352</td>
</tr>
<tr>
<td>13 Total</td>
<td>log(CPEU1) = 0.941 + 0.62 log(TH)</td>
<td>0.08</td>
<td>0.48</td>
<td>1.395</td>
</tr>
<tr>
<td>14 #ATE</td>
<td>log(CPEU1) = 0.645 + 0.64 log(TH)</td>
<td>0.13</td>
<td>0.39</td>
<td>1.352</td>
</tr>
<tr>
<td>15 #ATE</td>
<td>log(CPEU1) = 1.743 - 0.53 log(TH)</td>
<td>0.11</td>
<td>0.41</td>
<td>1.352</td>
</tr>
<tr>
<td>16 #ATE</td>
<td>log(CPEU1) = 0.712 - 0.47 log(MAZOO)</td>
<td>0.12</td>
<td>0.33</td>
<td>1.396</td>
</tr>
<tr>
<td>17 Total</td>
<td>log(CPEU2) = 1.489 + 0.66 log(TH)</td>
<td>0.07</td>
<td>0.63</td>
<td>0.884</td>
</tr>
<tr>
<td>18 Total</td>
<td>log(CPEU2) = 1.582 + 0.47 log(MAZOO)</td>
<td>0.06</td>
<td>0.45</td>
<td>1.070</td>
</tr>
<tr>
<td>19 #ATE</td>
<td>log(CPEU2) = 1.485 - 0.54 log(MAZOO)</td>
<td>0.09</td>
<td>0.52</td>
<td>1.217</td>
</tr>
<tr>
<td>20 #NOATE</td>
<td>log(CPEU2) = 1.795 + 0.31 log(MAZOO)</td>
<td>0.09</td>
<td>0.30</td>
<td>1.031*</td>
</tr>
</tbody>
</table>

*test, P<0.001, except * P<0.05.

ed to ZIOOAN for #ATE subset (P = 0.62, P<0.001). There were no significant differences between the CPEU simple regression models on TP, TON, CHL or MIZOO, for #ATE and #NOATE subsets, but a simple composite model was not adequate for CPEU-MAZOO (F = 3.97, P<0.001) (Table 3). For both total and #ATE data, CHL was the strongest single estimator of asterinidae relative biomass (r² = 0.49, P<0.001), and r² = 0.49, P<0.001, respectively). The slope of the relationships between "bio logical standing stocks and total phosphorous" generally diminished from phytoplankton to zooplanktonivorous fish (Fig. 2) and an inverse trend was shown by the standard error in the slope (Fig. 3). An exception was MAZOO-TP relationship for #NCATE data subset; both the slope and its standard errors were higher than for both CHL-TP and MIZOO-TP regressions (Fig. 3). A similar pattern for slope variation was observed between standing stocks regressions (Fig. 3b). For #NOATE data subset, MIZOO was again an exception. The slope of the MIZOO-CHL regressions was almost the same and greater than the slope for CHL-TP and MIZOO-CHL regressions respectively, but the standard error for the former was considerably higher (Fig. 3b).

Discussion

Total phosphorus has been shown to be the most important variable to explain chlorophyll variability (SARAMOTO 1966, DILLON & ROYLER 1974, among others) in both the northern and southern hemispheres (FERRIS & TULL 1985). As previously indicated (QUIROZ 1988, 1989 b), total phosphorus was one of the strongest estimators of total chlorophyll for Argentine lakes and reservoirs. There were no significant differences between regressions for lakes and for reservoirs, or between man-made and natural lakes (QUIROZ 1988, 1989 a). However, when facultative zooplanktonivorous fish of the Asterinidae family are present, chlorophyll predicted from general CHL-TP models will be usually lower, and accordingly, two different models for lakes with and without zooplanktonivorous fish should be used (compare Eq. 1 with Eq. 2 and 3 in Table 3). When the total CPE-TP model (Eq. 1, Table 3) was applied to 14 lakes with bottom dissolved oxygen below 2.0 mg
Fig. 3. Slope values for simple regression models a) between biological standing stocks and total phosphorus, and b) between different standing stocks. Points and lines represent slope value and two times standard error for slope respectively. Number in parentheses is the coefficient of determination (r²) for the regression. **TOTAL** total data (n = 63); **ATE** and **NOATE** mean lake data subsets with (n = 38) and without (n = 27) atherines in the samples.

1-2 (not included here), most of estimations (13) were below measured chlorophyll concentrations. Similar results were obtained for 9 lakes with ZMAX/SEIL < 1.0 (also not included here) for 8 lakes, predicted chlorophyll was above actual chlorophyll concentrations at sampling. When Equation 1 (Table 3) was used to estimate chlorophyll concentrations for 23 non-turbid lakes with mean macrozooplankton body weight 3.6 mg dry weight, 20 of those lakes showed a negative departure from CHL-TP regression. Furthermore, the hypothesis of independent effects of zooplanktonivorous fish and macrozooplankton size on phytoplankton standing stocks in comparative lake studies, after nutrient effects had been accounted for, was supported by results obtained for Argentinean lakes and reservoirs (Quirós 1989 a, b).

As in other lakes comparisons, microzooplankton ( Pace 1986) and macrozooplankton biomass (McCaulley & Kalf 1981, Hamson & Peters 1984) increased with lake trophy. Site comparisons with Pace's data (1986) are not possible because of the shortcomings of micro and macro-
zooplankton data presented here. However, total phosphorus was highly significant in explaining microzooplankton biomass variation in Argentinian lakes, but the regression slope was higher than for Quebec lakes (Pace 1986). As in Hanson & Pettis's (1984) results, the slope for macrozooplankton biomass - total phosphorus relation- ship did not differ significantly from unity for the total data set and for both types of lakes, with and without aliphatic nitrogen. Nevertheless, although slope for the macrozooplankton biomass - chlorophyll relationship was well below 1.0 for the total data set and for lakes with zooplanktivorous fish, it was not significantly different from unity for lakes without aliphatic nitrogen. On the other hand, macrozooplankton - micro- zooplankton relationships were significantly dif- ferent for both types of lakes, with and without aliphatic nitrogen respectively. Regression slopes were below 1.0 for the former and not significantly different from unity for the latter (see Equations 12 and 11, Table 3). To test whether the presence of zooplanktivorous fish or lake trophy, is more re- lated to changes in macrozooplankton/micro- zooplankton biomass ratio, two lake subsets with TP < 30 mg·m⁻³ (n = 42) and TP > 30 mg·m⁻³ (n = 23) were considered. Regression slopes for MAZOO-MIZO regressions were not signifi- cantly different but the equation intercept for MAZ 0ATE (a = 3.815) was higher than for MAZ 0ATE (a = 2.480) lakes. The stronger differences between macrozooplankton - microzooplankton regression for lakes with and without aliphatic nitrogen (P = 3.82, P < 0.05) than between regressions for oligotrophic - mesotrophic and eutrophic - hypertrophic lakes (P = 2.45, P = 0.10), suggest that zooplankton relative biomass changes are more related to fish community composition than to lake trophy. In summary, despite statistical dif- ferences between regression models, lakes with zooplanktivorous fish showed lower macrozooo- plankton biomass when lake trophy state was re- duced to a common denominator. Relative fish standing stocks (biomass), as es- timated by Gillikin, was shown to be correlated with measurements of lake trophy in Argentinian lakes and reservoirs (Quintas 1990), as has been found for fish biomass (Hanson & Leggett 1982) and fish yield (Ryder 1963, Ouellet 1977, Herrick 1982, Jones & Hoyle 1982) in other studies. The slope of the regression for relative fish biomass on total phosphorus, 0.68, 0.46 and 0.69 for total data, and MAZ 0ATE and MAZ 0ATE subsets respectively) were not signifi- cantly different from the slope of Hanson & Leggett (1982) equation of fish standing crop on total phosphorus. Macrozooplankton biomass ex- pressed 52% and 36% of total fish variation for lakes with and without zooplanktivorous fish re- spectively. The results suggest that when macro- zooplankton biomass is held constant, lakes with zooplanktivorous fish will have a higher fish biomass than lakes without those fish. However, residual variation is high, how much it is related to other unconsidered variables, sampling bias, gear selectivity or simple error is something I have not resolved here. Both "bottom-up" and "top-down" effects (McQueen et al. 1986, Northcote 1988) are in- volved, but the latter was not analyzed here. Macrozooplankton size effects on the CHL·TP re- siding variation was shown for Argentinian lakes and reservoirs (Quintas 1989 b). However, only in the eutrophic - hypertrophic lake subset (TP > 30 mg·m⁻³), zooplanktivorous fish were significant, and inversely related, to reduce MAZOO-TP residual variation (Quintas unpubl.). As was shown before for other data sets (McQueen et al. 1986), slopes were stronger near the bottom of the food web, and variability around the regression lines increased with every step up the food chain until zooplanktivorous fish were reached; in lakes where those fish were scarce or absent from the fish community, maximum variability among the lakes was transferred to ma- crozooplankton (Fig. 3 a and b). The obvious quantitative limitations of fish and zooplankton sampling and the sparseness of data for each lake, precludes the formulation of broad generalizations, even though a wide range of lim- nological characteristics were sampled. Notwith- standing, the results provided valuable observa- tions of how biological standing stocks vary among lakes, and especially how those standing stocks vary among lakes with or without zooo- planktivorous fish. Similar patterns were obtained for most heterogeneously set lakes and reservoirs studied, but the explained variances and regression slopes were lower (Quintas 1988, 1990). The re- sults also support the notion that large differences in nutrient status among lakes will be manifested in measurable differences in biological standing stocks (Broenkien et al. 1973, Yen 1986). On the basis of Volkwein's (1969, 1973) models of nutrient loading, a hypothesis may also be ex- pressed that the most general external character- istic of the ecosystem dependent on the degree of the internal variability in standing stocks of com-
mammals because of the inherent system cons-
ervation e.g. Rawson 1932, 1955, Ryder 1965, 
Vollenweider 1969, 1975, Dillon & Rigler 1975, 
Schindler et al. 1978, Britteny 1982, Kerr 1982, 
Quinn 1990, and many others. Internal fea-
tures modulate those standing stocks (Stanford 
1960) between relatively narrow limits in sym-
chronic lakes comparisons.

Acknowledgements
Research was supported by the Instituto Nacional de De-
veloping and the Fundo Nacional de Investigacao Cientifica e Tecnica (FONUCAV) to the au-
tor. I thank S. Moniz, M. Marques and M. C. Marques for the use of their abundance and biomass zooplankton 
data. Special thanks are due to R. A. Ryder for his advice to the research program.

References
APHA (American Public Health Association), American Water Works Association, and Water Pollution Control Federation, 1975: Standard method for the examination of water and wast-
Bagnol, C. R. M. & Quinn, R., 1985: Introduction de pe& quot;„;me stounst in the Republic Argentina. In-
formesTécnicos del Departamento de Aguas Con-
tinuas No. 2. – Instituto Nacional de In-
vagGncias y Desarrollo Pesquero, Mar del Plas, Argentina, 90 pp.
Beer, K. F. & Kerr, S., 1986: Empirical relationships be-
tween bacterial abundance and chlorophyll con-
centation in fresh and marine waters. – Can. 
J. Fish. Aquat. Sc. 43: 1013–1023
Brockman, R., M., Davis, G. E. & Warren, C. E., 1973: 
Analysis of trophic processes on the basis of den-
sity-dependent functions. – Int. Rev. (Ed.): Marine food chains, 484–498. – Oliver and Boyd, 
Edinburgh, 523 pp.
Britteny, M., 1982: Estimating the productivity of lakes and reservoirs. – In: Cane, E. D. 1st Ed. Low-
Campbell, S. R. & Kotzela, J. F., 1988: Consumer control of lake productivity. Large-scale experi-
Campbell, S. R., Kotzela, J. F. & Hogston, J. R., 1985: Cascading trophic interact and lake pro-
Dallen, P. J. & Ryder, F. E., 1974: The phosphorus-
chlorophyll relationship in lakes. – Limnol. Ocea-
Ferreira, J. M. & Tyler, P. A., 1985: Chlorophyll-totall phosphorus relationships in Lake Barragga, 
New South Wales, and some other Southern Ho-
mpshire lakes. – Aust. J. Mar. Fresh. Res. 36: 
157–168.
Gutierrez, Y. L., Cama, R. S. & Owusu, M. A., 1978: Methods for physical and chemical analysis of 
Hannos, J. M. & Loganget, W. C., 1982: Empirical pro-
duction of fish biomass and yield. – Can. J. Fish. 
Hannos, J. M. & Peters, R. H., 1984: Empirical predic-
tion of cranefish zooplankton biomass and pro-
found macroinvertebrates biomass in lakes. – Can. 
Jones, J. R. & How, M. V., 1982: Sportfish harvest be-
due to warmer chlorophyll a concentration in midwestern lakes and reservoirs. – Trans. Am. 
Fish. Soc. 111: 176–179.
160–170.
McCauley, E. & Kerr, S. J., 1981: Empirical relation-
McQuaid, D. J., Port, J. R. & Malle, L. E., 1986: 
Trophic relationships in freshwater pelagic eco-
Moniz, S. & Marques, M. C., 1986: The zool-
oplankton of two lakes of the Chuwar (Argentina) and 
some probable relations with the ichthyofauna and 
algae complex of the lake. – Atti VII Convegno 
Intervento sullo Stato della Zona Marittima, Libri, 133–136.
Northcote, T. G., 1986: Fish inshore structure and func-
tion of freshwater ecosystems. A "top-down" view. – 
Ogawa, T., 1977: Relationships of fish yield to lake phytoplankton standing crop, production, and 
Price, M. L., 1996: An empirical analysis of zooplankton community structure across lake trophic gra-
Verhandlungen – Proceedings – Travaux
of the International Association for Theoretical and Applied Limnology, Congress in Munich 1989

If you are a member of this association you receive these "Proceedings" against your yearly membership fee of Swiss Francs 50.–

Please notice also the

Archiv für Hydrobiologie
an official organ of the International Association for Theoretical and Applied Limnology (SIL), and its Supplements.
Edited by: Prof. Dr. H. KAUSCH, Hamburg, Germany West and Prof. Dr. W. LAMPERT, Plön/Holstein, Germany West.

Editorial Board: Prof. Dr. CAROLYN W. BURNS, Dunedin, New Zealand; Prof. Dr. Z. MAJER GŁUBICKI, Warszawa, Poland; Prof. Dr. J. OVERBECK, Plön, Germany; Prof. Dr. ERIC PATTÉ, Villeurbanne, France; Prof. Dr. COLIN S. REYNOLDS, Ambleside, Great Britain; Prof. Dr. ROBERT G. WETZEL, Tuscaloosa, Alabama, USA.

As a member of SIL you are entitled to receive this important journal at a special membership price.

True to its tradition this periodical serves freshwater research in the widest sense, including treatment of problems of brackish and seawater as far as they bear a relationship to limnology. It is the editors' aim to devote increased attention to ecology in association with experimental, above all physiological works corresponding to the more recent developments in limnology. Finally, it is intended that the "Archiv" should continue to form a bridge between theoretical and applied water research.

For details please write to the Publishers E. Schweizerbart'sche Verlagsbuchhandlung (Nägele u. Ostermiller), Johannesstraße 3 A, D-7000 Stuttgart 1.

If you are interested in

Archiv für Hydrobiology, Supplements
and in the special issue:

Ergebnisse der Limnologie/Advances in Limnology
these are available also against a special membership price; for details please ask the Publishers (for address see above).

If you are interested in being a member of the International Association for Theoretical and Applied Limnology, please write to the General Secretary-Treasurer:

Prof. Dr. R. G. WERTZ, Department of Biology,
The University of Alabama, Tuscaloosa, Alabama 35487-0344/USA