

Primary productivity in South American temperate lakes and reservoirs

Productividad primaria en lagos y embalses de la región templada de Sudamérica

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ABSTRACT

Latitudinal-related factors that regulate photosynthetic primary productivity (P) in temperate lakes are affected by the depth of the water body, wind exposure and nutrient loading. These factors alter the thermal regime, nutrient supply and the size of the illuminated zone where photosynthesis occurs. Community structure and grazing are also important. It has been reported that photosynthesis (P) increases linearly with phytoplankton biomass (cell volume) or chlorophyll concentration (B), although several investigators have found that specific photosynthesis (P^B) decreases with increasing phytoplankton biomass.

Bearing in mind that photosynthesis does not increase indefinitely or remains constant over a broad biomass range, the relationship between standing crop, in terms of integrated B , and integrated P^B for the entire euphotic zone, was analyzed in fourteen South American lakes and reservoirs from 33°S to King George Island in Antarctica (62°S).

Differences of two orders of magnitude or more for B and P^B relate primarily to the system's age, and are regulated by prevailing hydrological conditions. Similarities stem from hydrographical features and climatic light availability.

It was found that those systems with higher trophic status ($> \int B$) presented lower $\int P^B$ values and the same would happen within each lake during more favourable conditions. The decline in $\int P^B$ could be due to phytoplankton self-shading in nutritionally richer water and to light and nutrient limitation in poorer systems.

Most of the more "euphotic photosynthetically efficient systems", in terms of carbon fixation efficiency of the chlorophyll a content in the entire illuminated water column under a unit area, correspond to clear water lakes with euphotic depths > 40 m and low chlorophyll a concentrations (< 30 mg m⁻²), located at higher latitudes or altitudes and not to lakes considered more productive in terms of annual carbon fixation.

Key words: primary productivity, temperate lakes, temperate reservoirs.

RESUMEN

La regulación de la productividad primaria por factores latitudinales en lagos templados, está distorsionada por otros factores tales como la radiación solar, profundidad del cuerpo de agua, la exposición al viento, la altitud y la carga de nutrientes. Estos afectan el régimen térmico, el ciclo de nutrientes y el tamaño de la zona eufótica donde se realiza el proceso fotosintético. También la estructura de la comunidad debe ser considerada, fundamentalmente debido a los procesos relacionados con la herbivoría. Se ha reportado que la fotosíntesis acuática (P) se incrementa linealmente con la biomasa (volumen celular) y la concentración de clorofila (B). Sin embargo, varios investigadores han encontrado que la fotosíntesis específica (P^B) disminuye con el incremento de la biomasa fitoplanctónica.

Considerando que la fotosíntesis no puede aumentar indefinidamente o permanecer constante en todo el intervalo de biomasa, se realizó un análisis de la relación entre la cosecha estable en términos de B integrada con P^B integrada para toda la zona eufótica en 14 lagos naturales y artificiales en Sudamérica desde los 33°S hasta la Antártica (62°S).

Para estos parámetros se encontraron diferencias de más de dos órdenes de magnitud. Esto se debe a la diferente ontogenia de los sistemas, y a que son regulados en sus diferencias por las condiciones hidrológicas y en sus similitudes por las condiciones hidrográficas y disponibilidad de luz (clima).

Se detectó que aquellos sistemas de mayor nivel trófico ($> \int B$) presentan menores valores promedio de $\int P^B$ y lo mismo ocurriría en un mismo lago durante el año en los períodos más favorables.

La disminución de $\int P^B$ puede deberse al autosombreamiento del fitoplancton en lagos ricos en nutrientes y a limitación por luz y nutrientes en lagos oligotróficos.

Los lagos con "zonas eufóticas fotosintéticamente más eficientes", en términos de fijación de carbono por clorofila a contenida en toda la columna de agua iluminada y por área, corresponden a lagos más transparentes con profundidades eufóticas > 40 m y bajas concentraciones de clorofila a (< 30 mg m⁻²) localizados a mayores altitudes o latitudes y no a lagos considerados más productivos desde el punto de vista de la fijación anual de carbono.

Palabras claves: productividad primaria, lagos templados, embalses templados.

INTRODUCTION

Since the first studies of phytoplankton primary productivity in lakes located at different altitudes in Central Chile (Montecino & Cabrera 1984), oligotrophic systems were found to show a relatively higher carbon fixation efficiency of the chlorophyll *a* (Chl *a*) contained in the entire euphotic water column under a unit area than eutrophic lakes (Cabrera & Montecino, 1982a, 1987)

High phytoplankton biomass, measured as Chl *a**, has been related to elevated rates of carbon fixation, although the reverse has also been reported in the limnological literature (Talling 1973, Le Cren & Lowe-McConnell 1980, Jellison & Melack 1989). To clarify this discrepancy, we present an analysis of the information of phytoplankton primary productivity (photosynthetic carbon fixation) and biomass (Chl *a*) reported since 1980 in temperate South American water bodies.

Carbon fixation in the euphotic or trophogenic zone of lakes and other water bodies is regulated by factors such as light intensity, water temperature and the stability of the water column. Grazing by microzooplankton also plays a role and may maintain, by recycling nutrients high algal growth rates (Carney & Elser 1989).

The limit of the trophogenic zone, where surface light declines to one percent, is usually found between 1 and 50 m depth. While the main photosynthetic organisms in this light gradient in lakes are phytoplankton and benthic macrophytes, this study focuses solely on phytoplankton microalgae and seeks to determine which parameters of primary productivity in the euphotic zone best aid in drawing comparisons between and among water bodies in similar geographical areas or in different hemispheres.

Is total annual carbon fixation the only important measurement? Or could we learn more by analysing differences in some parameters derived from the relationship between primary productivity (*P*) and light (*I*)?

The exponential gradient of light distribution in the water column determines three types of response: under low light intensity, *P* shows a linear response; at saturation light intensity, *P* is independent of *I*; and at high light intensity, *P* decreases with increasing light. Light utilization efficiency is measured in the first zone (alpha), maximum photosynthetic capacity (*P*_{max}) is measured in the second zone, and tolerance to high irradiance is measured in the third. Of these parameters, *P*_{max} and alpha have been reported to vary with phytoplankton density, lake trophic status and salinity (especially because of CO₂ availability in saline and soda lakes, Jellison & Melack 1989). Traditionally, however, phytoplankton production has been expressed as total fixed energy, carbon or chlorophyll (Le Cren & Lowe-McConnell 1980, Prairie *et al.* 1989).

Considering the horizontal, vertical, daily, seasonal and interannual variations in microalgal distribution in most lakes, my goal was to establish the relationship between Chl *a* concentrations (*B*) and photosynthetic rates (*P*) throughout the euphotic zone. The dependent variable is the integral specific productivity (*∫PB*)** in relation to integrated biomass (*∫B*) for the entire illuminated water column under a unit area. *∫PB* can be used as a measure of photosynthetic efficiency, especially when alpha is not available, and it is also more realistic because it considers the photohistories of euphotic microalgal.

This approach will answer two questions. First, is the euphotic zone of eutrophic water bodies photosynthetically more efficient per unit area than oligotrophic ones or vice versa? Second, does the high photosynthetic efficiency of a lake persist across seasons?

Primary productivity should decrease as latitude increases, mainly because of declining light availability and average water temperatures. But this relationship may be altered by trophic dynamics (Carney & Elser 1989) and further con-

* See Appendix for definition of symbols.

** This number is the integration of depth specific productivities (Carbon fixation normalized to Chlorophyll *a*) over the entire euphotic water column under a unit area.

founded by differences in mean and maximum depth of the water body, lake water retention times wind exposure, nutrient loading, and nitrogen: phosphorus ratio (Le Cren & Lowe-McConnell 1980, Prairie *et al.* 1989). In South America, these factors may be influenced by the presence of the Andean mountain range, whose geology and geography probably causes oligotrophic lakes to lie at lower latitudes than in North America.

Description of study sites

Impoundments aside, most temperate lakes in South America originated during the last glaciation, developed in Andean moraines and lie scattered more over than 4,000 km from North to South in this mountain range (Fig. 1) They are as deep, as their counterparts in the Northern Hemisphere, but they are not as large in area or volume.

Fourteen lakes located between 33°S and 62°S in Chile and Argentina (Table 1) were selected for this study. Four lie in Central Chile between 200 and 2,600 m. High mountain lakes are Laguna Negra (> 300 m maximum depth) and El Yeso Reservoir, built in 1960 (Montecino & Cabrera 1984, Universidad de Chile 1989). In the Coastal Mountain Range west of the Andes I included Rapel Reservoir, impounded in 1968 (Montecino & Cabrera 1982, Andrew *et al.* 1989), which is classified as a discontinuous warm polymictic lake (Reynolds *et al.* 1986). Eutrophic Aculeo Lake (Cabrera & Montecino 1982b) is also found in Central Chile. Farther south, four deep monomictic piedmont lakes were selected in the Araucanian Lake District of Chile: Lakes Villarrica (Campos *et al.* 1983, Universidad Austral 1987), Riñihue (Campos *et al.* 1978, 1987), Llanquihue, the largest lake in this analysis (870.5 km²; Campos *et al.* 1988, Universidad Austral 1987), and Todos los Santos (Campos *et al.* 1990). Finally, Lake Toro in the Chilean Patagonia (D. Soto, personal communication), and Lake Kitiesh, in the maritime Antarctic (62°S), the largest on King George Island in the South Shetlands (Contreras *et al.* 1990; Montecino *et al.* 1991), were studied.

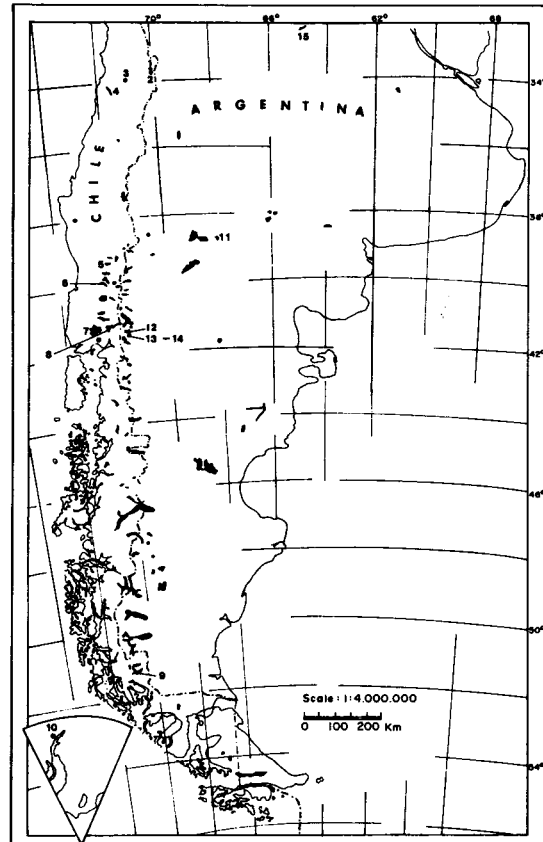


Fig. 1: Distribution of South American lakes and reservoirs (32°S - 62°S). Location of the different water bodies where information is shown with numbers. From Chile: Central zone: Embalse El Yeso (1), Laguna Negra (2), Laguna de Aculeo (3) and Embalse Rapel (4). Araucanian lake district: Villarrica (5), Riñihue (6), Llanquihue (7) and Todos los Santos (8). Patagonian lake Toro (9) and Antarctic lake Kitiesh (10). From Argentina: lakes Pellegrini (11), Mascardi (12), Guillermo (13), Hess (14) and Embalse Río Tercero (15).

Distribución de lagos y embalses sudamericanos (32°S - 62°S). La localización de los cuerpos de agua de donde proviene la información está señalada con números. En Chile: Zona central: Embalse El Yeso (1), Laguna Negra (2), Laguna de Aculeo (3) y Embalse Rapel (4). Lagos araucanos: Villarrica (5), Riñihue (6), Llanquihue (7) y Todos los Santos (8). En la Patagonia el Lago Toro (9) y en la Antártica el Lago Kitiesh (10). En Argentina: lagos Pellegrini (11), Mascardi (12), Guillermo (13), Hess (14) y Embalse Río Tercero (15).

I selected four lakes in Argentina: Lake Pellegrini, a hard-water artificial ecosystem (Conzonno *et al.* 1981) and Lakes Hess, Guillermo (INALI 1972, Margalef 1983, R. Oldani and E. Drago personal

TABLE 1

Study periods, references (numbers), geographical, and morphometric characteristics and mean values of Zeu, Pmax, and Bmax in selected lakes from Chile and Argentina

Períodos de estudio, referencias (números), características geográficas y morfométricas y valores promedio de Zeu, Pmáx y Bmáx de lagos seleccionados de Chile y Argentina. (* Embalses)

Lake/Reservoir*	References	Years	Latitude °S	Area km ²	Volume km ³	Retention years	Mean annual values		
							Zeu m	Pmax mgC/m ³ /h	Bmax mgChla/m ³
CHILE									
Laguna Negra	1	80 and 82	33	5.9	0.6	38	36.3	0.9	2.0
Aculeo	1	81-86-87	33	12.0	0.05	?	1.7	353.5	157.2
El Yeso*	1	80 and 87	33	3.5	0.25	1	21.2	3.7	1.2
Rapel*	1	80-83-84-85-87	34	134.8	0.83	0.081	4.8	72.3	19.9
Villarrica	2	84/85-86/87	39	175.8	20.9	4	26.0	8.2	2.8
Riñihue	2	85/86	39	77.5	12.5	1	29.4	5.1	1.9
Llanquihue	2	82/83-86/87	41	870.5	158.6	74	51.0	1.9	0.71
Todos los Santos	2	82/83	41	178.5	34.4	4	30.0	0.4	0.6
Toro	3	1989	51	196.4	30.2	13	8.0	1.6	0.5
ARGENTINA									
Pellegrini*	4	81/82	38	100.7	0.9	?	14(5)- 4.7 #	5.8	1.4
Mascardi	5	68/69	41	39.2	4.3	?	15(5)-23.5 #	1.8	0.7
Guillelmo	5	1969	41	5.4	0.3	?	20(5)-25.9 #	0.7	0.5
Hess	5	1969	41	?	?	?	10.0	3.9	0.8
ANTARCTIC									
Kitiesh	1	85 and 87	62	0.09	0.42 x 10 ⁻³	?	10.0	3.3	0.9

References:

1. Cabrera & Montecino 1982b, 1984, 1987; Montecino & Cabrera 1982; Reynolds *et al.* 1986; Andrew *et al.* 1989; Universidad de Chile 1989. Montecino *et al.* 1991.
 2. Campos *et al.* 1978, 1983, 1987, 1988, 1990; Universidad Austral 1987; Campos & Steffen (personal communication).
 3. D. Soto *et al.*, Campos *et al.* (personal communications).
 4. Conzonno *et al.* 1981.
 5. INALI 1972, Maglianesi *et al.* 1973, Margalef 1983.
- # Quirós 1985.

communications) and Mascardi (Maglianesi 1973, Quirós & Drago 1985), the latter three in the Andean-Patagonian region. Although several studies are available for Embalse Río Tercero (Mariazzi & Conzonno 1980, Mariazzi *et al.* 1981 and Nakaniishi *et al.* 1985), it was excluded from this analysis because of its northerly location.

METHODS

Primary productivity data are limited to radioactive measurements (^{14}C incorporation) performed *in situ* at 5 to 10 discrete depths. Incubations were terminated by filtering the phytoplankton onto membrane filters. Chl *a* was measured spectrophotometrically from acetone extracts. Details of the measurements are given in references cited in the Introduction and in Tables 1 & 2.

Integrated specific photosynthesis values (fPB) for the data base were obtained as follows: carbon fixation (P) at any depth in the vertical gradient was normalized to Chl *a* concentrations at the same depth. Each resulting PB value was averaged with the next nearest PB value and multiplied by the depth interval between them. This was done throughout the euphotic zone. The final sum of all layers corresponds to the specific primary productivity for the water column per m^2 . The same procedure was followed to calculate fP and fB in each experiment.

The maximum depth of the euphotic zone (Z_{eu}) was established in most cases on the basis of the known mean extinction coefficient (\bar{k}) of the photosynthetically active radiation (P.A.R.), measured with an underwater quantum sensor. Z_{eu} was estimated to be that depth where surface irradiance (I_0) declines to one percent:

$$Z_{eu} = \ln 100/\bar{k}$$

Where \bar{k} was unknown, Z_{eu} depth was estimated as three times the Secchi depth.

Data frequency varied widely. For some lakes, data correspond either to monthly measurements made at a single station or taken at more than one station in different

seasons. Other measurements were performed at the same station but at different times of day or on different days of the same month. In some cases, measurements were available from different years, but because of substantial daily, seasonal and interannual variability, individual results are plotted in the graphs and they do not represent averages. For comparative purposes in the tables, annual carbon fixation was obtained by multiplying the fP mean value in $\text{mgC m}^{-2} \text{h}^{-1}$ by the estimated daylight hours in one year at different latitudes. For lakes in Central Chile: 3,285 h; for southern Chilean and Argentine lakes: 2,146 h; for Lake Toro in Patagonia: 1,839 h and for Lake Kitiash in Antarctica: 1,533 h.

RESULTS

Biomass (fB) and primary productivity (fP)

Study periods and selected characteristics of lakes are summarized in Table 1. P_{max} annual mean values ranged from $0.4 \text{ mgC m}^{-3} \text{h}^{-1}$ in Lake Todos los Santos to $353.5 \text{ mgC m}^{-3} \text{h}^{-1}$ in Lake Aculeo. B_{max} ranged from $0.4\text{--}0.6 \text{ mg Chl } a \text{ m}^{-3}$ in oligotrophic lakes up to $157.2 \text{ mg Chl } a \text{ m}^{-3}$ in Aculeo. fB annual mean values varied tenfold among lakes. Maximum values of fB were found in Rapel Reservoir and Lake Aculeo (70.9 to $100.3 \text{ mg Chl } a \text{ m}^{-2}$) and minimum values in Lakes Toro, Hess and Kitiash, 2.9 ; 5.5 and $6.6 \text{ mg Chl } a \text{ m}^{-2}$ respectively. (Fig. 2a). With the exception of the high mountain lakes Laguna Negra and El Yeso in Central Chile, fP followed the same trend as $fChl a$, with mean values higher than $149.9 \text{ mgC m}^{-2} \text{h}^{-1}$ for those lakes located at lower latitudes, and less than $31.7 \text{ mgC m}^{-2} \text{h}^{-1}$ for lakes south of 41°S .

The depth of the euphotic zone varied greatly, between 1.7 and 51.0 m . Retention time also varied significantly, from 0.08 years in Rapel Reservoir to 74.0 years in Lake Llanquihue (Table 1).

PB_{max}, fPB, P and Annual Carbon fixation

As shown in Fig. 2b, no latitudinal trend was found for PB_{max} , unlike fB (Fig.

TABLE 2

Lowest, highest and mean values for fPB , fP , and estimated annual carbon fixation in South American temperate lakes and reservoirs. fP and annual P of other systems are also included at the bottom

Valores mínimos y máximos de fPB , fP , y estimaciones de fijación anual de carbono en lagos y embalses templados de Sudamérica.
Se incluyen también datos de fP y P anual para otros sistemas

Lake/Reservoir*	fPB mgC(mgChl <i>a</i>) - 1 m ⁻² h ⁻¹			fP mgC m ⁻² h ⁻¹			Annual carbon fixation gC m ⁻² y ⁻¹
	min	max	mean	min	max	mean	
CHILE							
Laguna Negra	7.2	29.4	19.2	1.7	22.7	12.4	40.7
Aculeo	0.3	15.4	4.3	25.3	1,233.0	237.0	778.5
El Yeso*	4.3	148.0	51.5	8.6	49.6	27.0	88.7
Rapel*	2.0	26.5	10.1	1.0	428.1	149.9	492.4
Villarrica	3.1	129.5	41.4	3.1	228.7	84.6	181.6
Riñihue	16.0	344.5	125.6	53.4	127.5	80.9	173.6
Llanquihue	4.0	350.6	66.1	3.5	94.1	31.7	68.0
Todos los Santos	6.0	60.2	22.0	4.7	11.3	6.4	13.7
Toro (1)	11.9	19.8	15.9	4.3	8.1	6.2	11.4
ARGENTINA							
Pellegrini*	19.1	59.4	35.3	19.9	69.6	36.3	77.9
Mascardi (2)	—	—	15.8	10.6	29.6	20.1	43.1
Guillermo (2)	—	—	54.7	—	—	16.4	35.2
Hess (2)	—	—	56.4	—	—	29.3	63.0
ANTARCTIC							
Kitiesh (1)	20.1	33.2	26.7	5.3	39.08	22.05	34.5
OTHER SYSTEMS							
Inland aquatic ecosystems	Likens (1975)			—	—	—	2.0 – 950.0
47 lakes	Hammer (1980)			—	—	—	8.3 > 1,000
14 lakes	Vincent <i>et al.</i> (1986)			10.0	414.0	103.0	—
Mono Lake	Jellison & Melack (1988)			—	—	—	540.0
Marine Environments	Kelly (1989)			—	—	—	350.0

NOTE: (1) Two measurements only.

(2) From Margalef (1983)

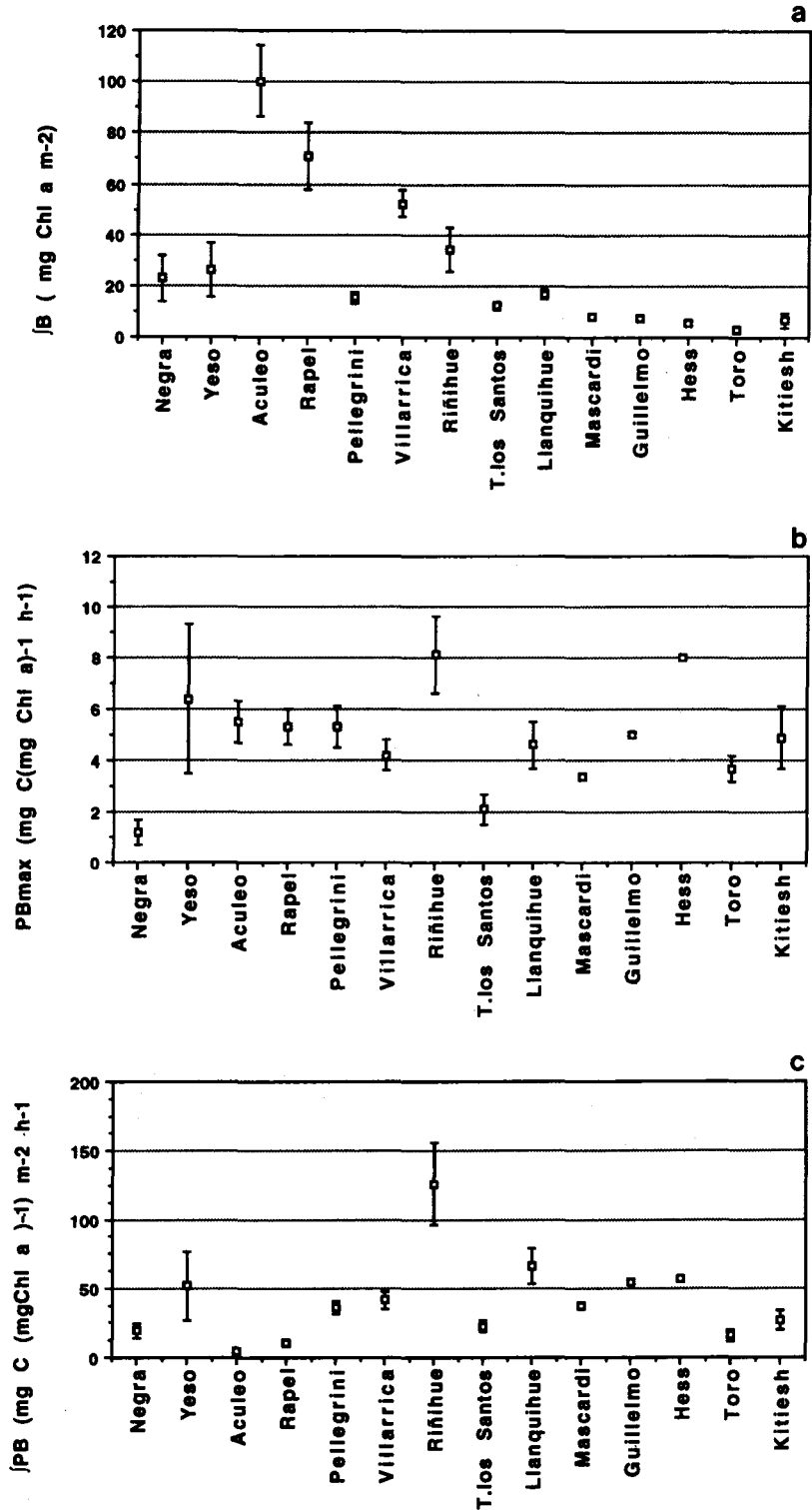


Fig. 2: Biomass as mean fB (a), mean PB_{max} (b) and mean fPB (c) of the different lakes in a relative latitudinal sequence starting from the north at the left. Standard error is also shown.

Biomasa como promedio de fB (a), promedio de PB_{max} (b) y promedio de fPB (c) de los diferentes lagos en una secuencia latitudinal partiendo a la izquierda desde el norte. También se señala el error estándar.

2a). Large differences in PB_{max} were observed, especially among the oligotrophic lakes (i.e. 6.38 ± 2.9 and 8.1 ± 1.5 for El Yeso and Riñihue respectively).

Mean integrated specific primary productivity (fPB) had an overall range from 4.3 to 125.6 $\text{mgC} (\text{mg Chl } a)^{-1} \text{m}^{-2} \text{h}^{-1}$ (Fig. 2c). With the exception of Laguna Negra, the largest difference between minimum and maximum values and the highest mean fPB values ($> 100 \text{ mgC} (\text{mg Chl } a)^{-1} \text{m}^{-2} \text{h}^{-1}$) were found in lakes of greater euphotic depth. The more eutrophic lakes, located mainly in valleys, attained maximum values less than 26.5 $\text{mgC} (\text{mg Chl } a)^{-1} \text{m}^{-2} \text{h}^{-1}$ (Table 2).

Mean fP values varied between 6.2 and 237.0 $\text{mgC} \text{m}^{-2} \text{h}^{-1}$, with minimum values of 1.0 to 53.4 $\text{mgC} \text{m}^{-1} \text{h}^{-1}$ and maximum values between 8.1 and 1,233.0 $\text{mgC} \text{m}^{-2} \text{h}^{-1}$ (Table 2).

Estimates of carbon fixation on a yearly basis (Table 2) attained maximum values in Lake Aculeo and Rapel Reservoir and were lowest for the high mountain and piedmont lakes ($< 200 \text{ gC} \text{m}^{-2} \text{y}^{-1}$). For Antarctic Lake Kitiesh, only summer values were available and calculations may be seriously overestimated. Nevertheless, results lie between the low values reported for the permanently ice covered Vanda Lake and Fryxell Lake in the Dry Valley region and the high values reported for Heywood Lake, Signy Island (Montecino *et al.* 1991). Since calculations for lakes Mascardi, Guillermo, and Hess were performed on the basis of a single measurement, their corresponding annual carbon fixation was included only for comparative purposes.

Relationship between fB and fPB

In Fig. 3a the relationship between fB and fPB is shown for Central Chile lakes and reservoirs. Values for El Yeso Reservoir and Laguna Negra concentrate in the upper left corner of the graph, while values for eutrophic Lake Aculeo cluster in the lower right half. Rapel lies in between. Fig 3b show lakes of more southern latitudes. Data for Lake Pellegrini in Argentina are similar to those of El Yeso,

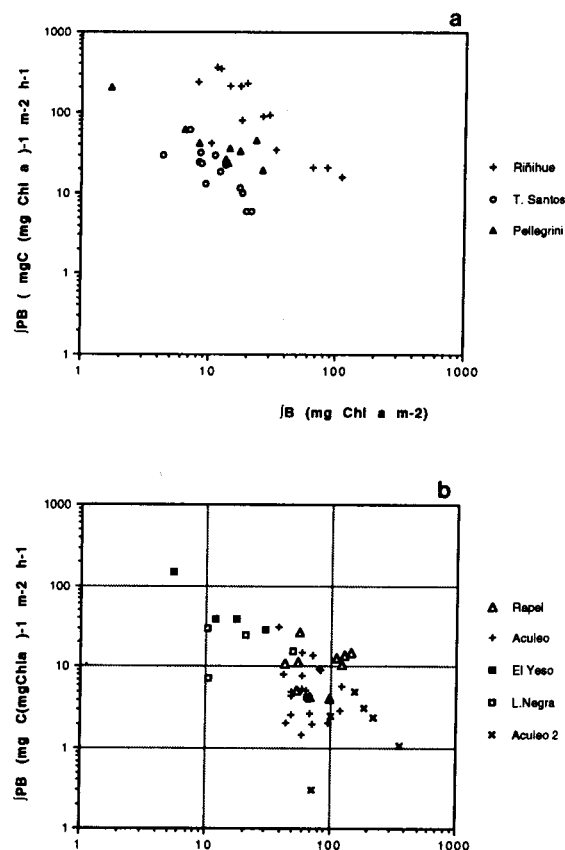


Fig. 3: Relationship between fB and fPB in a log/log scale for a) Central Chile water bodies: El Yeso, Aculeo, Laguna Negra and Rapel Reservoir; b) Southern lakes: Pellegrini, Riñihue and Todos los Santos.

Relación entre fB y fPB en escala log/log de cuerpos de agua de a) la zona central de Chile: El Yeso, Aculeo, Laguna Negra y Embalse Rapel; b) la zona sur: lagos Pellegrini, Riñihue y Todos los Santos.

Laguna Negra and Lake Todos los Santos. Lake Riñihue attains the highest fPB values in relation to fB .

In Fig. 4 values of fB and fPB for all lakes were plotted. Relatively high values of fPB tend to be associated with low values of fB and low values of fPB associated with high values of fB . Although this relationship is significant ($r^2=0.25$ $n = 152$ $p < 0.001$) its interpretation is difficult because of mathematical considerations (see Discussion). Nevertheless, as every point represents a different date within each lake, the slopes reveal the behavior of the two variables with time or across seasons.

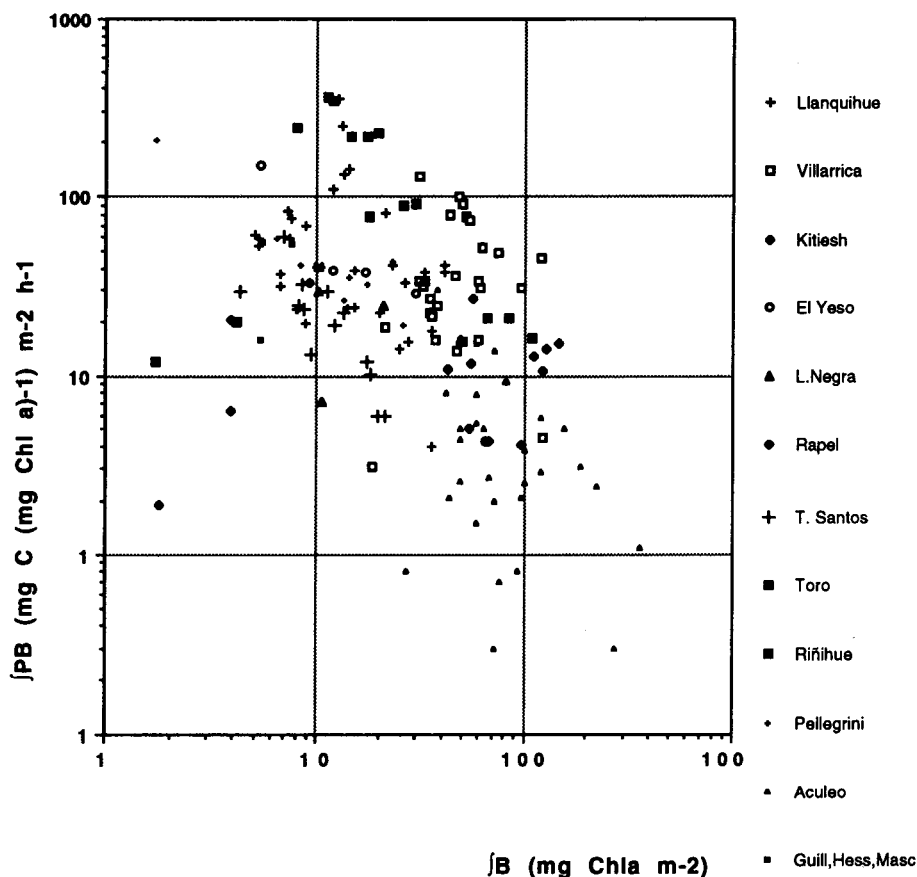


Fig. 4: Relationship between single values of fB and fPB of fourteen lakes shown with numbers in Fig. 1 in a log/log scale.

Relación entre cada uno de los valores de fB y fPB de los 14 lagos identificados en la Fig. 1 en una escala log/log.

These results suggests, that carbon fixation efficiency of Chl *a* contained in the entire euphotic water column under a unit area decreases at higher integrated biomass under the same area.

DISCUSSION

Brylinsky (1980) analysing ^{14}C results found that the primary productivity of 43 lakes of North America, Africa and Europe correlated well with latitude.

In temperate South American lakes, light as a function of latitude does not seem to be the most consistent environmental variable affecting photosynthesis, as it has been reported (Vincent *et al.* 1986). This is probably because the lakes analysed vary considerably in trophic

state, size, and altitude, and because some are natural and others are man-made. Also lakes with similar mixing regimes (Campos *et al.* 1983, 1987, 1988, 1990) respond quite differently both in terms of biomass specific productivity and total annual carbon fixation in temperate South America.

In an analysis of 47 lakes Hammer (1980) concluded that PB_{max} varies broadly over a range of latitudes and altitudes and that the capacity (assimilation) of a lake to produce and sustain algae is unrelated to latitude.

The importance of light in controlling photosynthesis throughout the year was demonstrated in a fjord by Erga (1989). He also reported that optimal photosynthetic conditions often were found in conjunction with low standing stocks of phy-

toplankton and that high PB_{max} values occurred at almost undetectable nitrate and orthophosphate concentrations. He proposed that, at least during summer, this high photosynthetic assimilation could be attributed to the recycling of nutrients by micro and macrozooplankton. The microbial loop dominates in oligotrophic oceans and in strongly stratified waters during the temperate summer (Cushing 1989). Water column stability and nutrient availability are proposed by Reynolds (1980) to be the two major environmental variables interacting to determine phytoplankton periodicity.

In relation to nutrients, retention time in lakes is another important factor, especially in oligotrophic natural systems.

Carney & Elser (1989) suggested that when biomass was low, photosynthetic efficiency increased because zooplankton enhanced nutrient recycling. On the other hand, light may be a more important limiting factor in eutrophic than in oligotrophic systems, where microzooplankton play a larger role.

Comparing the productivity data in Table 2, Vincent *et al.* (1986) from the study of 14 temperate lakes gives a range of 10.0 to 414.0 mgC m⁻² h⁻¹, with a mean of 103.0 mgC m⁻² h⁻¹ that is somewhat higher than the mean of 65 mgC m⁻² h⁻¹ in this analysis (mean values range 6.4 to 237.0 mgC m⁻² h⁻¹). Likens (1975) gives values for temperate aquatic ecosystems ranging from 5 to 3,600 mgC m⁻² day⁻¹. For annual carbon fixation Jellison & Melack (1988) reported 540 gC m⁻² y⁻¹ for hypersaline Mono Lake in California (38°N). In this study a maximum of 758 gC m⁻² y⁻¹ is calculated for Lake Aculeo (33°S). Likens (1975) reported a maximum of 950.0 gC m⁻² y⁻¹. Kelly (1989) gives annual carbon fixation values for marine environments using data from Whittaker & Likens of 350 gC m⁻² y⁻¹.

Since mean assimilation numbers (PB_{max}) showed no trend in relation to latitude (Fig. 2b), I selected for primary productivity comparisons the parameter fPB , which permits finer discrimination and normalises both for Chl *a* at each depth and for the different sizes of the euphotic

zones of the lakes. The relationship between the size of the euphotic zone and fB was highly significant, although the correlation was rather low ($r=0.43$).

The relationship of this photosynthetic efficiency parameter (fPB) with the declining trend of fB observed in Fig. 2a, then was investigated bearing in mind what Westlake *et al.* (1980) had reported a curvilinear relationship between daily integral photoassimilation and biomass in terms of volume, starting to level out at quite low cell volumes.

In Figs. 3 & 4, the increase in fPB with decreasing fB is probably the result of a lower Chl *a* concentration in each cell which prevents them from harvesting more light than can be used for growth in nutrient-limited situations, therefore their fB carbon fixation efficiency increases.

Jellison & Melack (1988) found that another parameter, PB_{max} , was higher when algal biomass was low and Talling (1973) reported that high population densities depressed photosynthetic rates. On the other hand, when fB is high, self-shading may reduce photosynthetic performance. Rather similar observations were reported by Cabrera & Montecino (1990) in Antarctic marine environments. Although Antarctic waters are often nutrient rich, Sommer (1988) suggested nutrient limitation during the austral summer.

According to Prairie *et al.* (1989) temperate lakes are phosphorus limited, but they note that phosphorus is a poor predictor of phytoplankton biomass in nitrogen-limited lakes. Other conclusions are that algae use nutrients with reduced efficiency in eutrophic lakes, and that high Chl *a* concentrations occur in lakes with low total nitrogen: total phosphorus ratios. Elser & McKay (1989) found herbivores to be important in regulating resource availabilities. By varying zooplankton biomass, they established experimentally that specific productivity increased significantly with increasing zooplankton biomass, indicating and improvement in algal physiological status and the occurrence of compensatory growth in response to grazing pressure and nutrient regeneration.

In this study lakes are segregated spatially (Figs. 3 & 4). More eutrophic systems tend to be located on the lower right side of the graphs (i.e. $f\text{Chl } a$ increase in a overall comparatively shallower euphotic zone). This may also be true in the case of temporarily more favourable conditions within each lake. Since fPB somehow includes fB , the negative correlation shown in the figures 3, 4 would hold even for randomly selected values for P and B . In fact, since PB is an integrated form of P_i/B_i for all layers, relatively small (large) B_i values will produce high (low) integrated PB , regardless the value of P . In any case the tendency for relatively high (low) values of fPB associated with low (high) values of fB seems to stand according to the analysis of individual PB for the different lakes (Fig. 2c). This suggests that the more eutrophic lakes at lower latitudes and altitudes, have lower fPB , and that the highest fPB are found at intermediate latitudes.

Since PB_{max} was unrelated to latitude we conclude that in eutrophic and oligotrophic systems fB can be equally efficient, probably due to optimization of photon capture in the latter because of their comparatively larger light-limited zone. It also seems that the trend of fPB , is quite distinct for each lake across seasons. The higher photosynthetic efficiency is observed in Lake Riñihue (Figs. 2c and 3b). Lake Riñihue showed the highest PB_{max} and highest fBP values, and with the exception of Rapel Reservoir, has the shortest (1 year) retention time (Campos & Steffen, personal communication).

Further studies are needed to establish the validity of an increase of euphotic $\text{Chl } a$ carbon fixation efficiency per area (fPB) with decreasing biomass (fB), measured as an independent variable.

Peters (1986) suggested that before more measurements are made, existing data must be compiled and scrutinized. With some exceptions, existing information does not allow statistical interannual comparisons, especially in Central Chile, which regularly presents rainfall anomalies (Rutllant & Fuenzalida 1990). Long-term surveys should be made, and day-to-day

variations pursued. At temperate latitudes, where insolation shows a sinusoidal seasonal variation, investigation should focus on periods when light is decreasing or increasing in order to avoid limiting or inhibiting conditions.

Future studies in South America should consider temperate lakes at different latitudes and altitudes, and take into account variations in trophic including saline habitats, areas in which primary productivity measurements are virtually lacking. Most importantly, primary productivity measurements should be coordinated with zooplankton and grazing experiments because, as Jellison & Melack (1989) have pointed out, PB_{max} is highest and coincident with the onset of grazing and out of phase with algal abundance. Achieving this coordinated approach will also require further refinement of chemical measurements. The broader data set resulting from such a coordinated effort would probably add uncertainties, but studies incorporating complex interactions and biochemical data, such as carbon flux measurements at the ecosystem level, would also improve hemispheric comparisons and aid in developing a capability to predict on a global scale.

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APPENDIX

Symbols

<i>B</i>	Biomass (Chlorophyll <i>a</i> concentration)	mg Chl <i>a</i> m ⁻³
Chl <i>a</i>	Chlorophyll <i>a</i> concentration	mg Chl <i>a</i> m ⁻³
<i>B</i> _{max}	Maximum biomass (Chlorophyll <i>a</i> concentration) in the water column	mg Chl <i>a</i> m ⁻³
$\int B$	Integrated Chlorophyll <i>a</i> over the euphotic zone	mg Chl <i>a</i> m ⁻²
<i>P</i>	Photosynthetic primary productivity (Carbon fixation)	mg C m ⁻³ h ⁻¹
$\int P$	Integrated photosynthetic primary productivity	mg C m ⁻² h ⁻¹
<i>pB</i>	Specific photosynthesis	mg C (mg Chl <i>a</i>) ⁻¹ h ⁻¹
$\int pB$	Integrated specific photosynthesis over the euphotic zone	mg C (mg Chl <i>a</i>) ⁻¹ m ⁻² h ⁻¹
<i>P</i> _{max}	Maximum photosynthetic primary productivity (C fixation) in the water column	mg C m ⁻³ h ⁻¹
O-Zeu	Euphotic zone: 1% light level	m