Analysis of plankton size spectra irregularities in two subtropical shallow lakes (Esteros del Iberá, Argentina)

Andrés Cózar, Carlos M. García, and José A. Gálvez

Abstract: Biomass irregularities in the plankton size spectra of two subtropical shallow lakes have been quantified assuming the classical observed generalities of the size spectra. During a seasonal cycle, three main functional size ranges determined the allocation of the spectra irregularities: microbial food web, nanoplankton–microplankton autotrophs, and herbivorous organisms. The structural adjustments within these trophic positions responded to the internal competition between functional guilds, mainly as the result of size-based characteristics related to the ability to eat and the susceptibility to be eaten. Despite the existence of a typical spectrum undulation resulting from self-organization (well-defined trophic positions, limnetic–benthic interaction), the biomass irregularities were an indicator of the main interactions disturbing the steady state. The mechanisms responsible for the irregularities operated jointly at ecosystem and individual levels. Thus, the irregular spectra of the eutrophic Laguna Iberá suggested a strong top-down control through cascade effects. Specific properties of peculiar organisms like filamentous cyanobacteria contributed to hold these stable irregularities. The higher spectrum regularity of the meso-oligotrophic Laguna Galarza emerged from a more balanced flow of biomass along the food chain.

Résumé : Les irrégularités de la biomasse dans les spectres de tailles du zooplancton de deux lacs subtropicaux peu profonds ont pu être quantifiées en présupposant les généralisations classiques des spectres de tailles. Au cours d'un cycle saisonnier, trois intervalles de tailles fonctionnels principaux sont responsables de l'allocation des irrégularités du spectre: le réseau trophique microbien, les autotrophes du nanoplancton–microplancton et les organismes herbivores. Les ajustements structuraux parmi ces positions trophiques sont des réactions à la compétition interne entre les guildes fonctionnelles, due principalement à des caractéristiques reliées à la taille dont la capacité de manger et la susceptibilité d'être mangé. Malgré l'existence d'une ondulation spectrale typique associée à l'auto-organisation (guildes trophiques bien définies, interactions limnétiques–benthiques), les irrégularités de la biomasse indiquent les principales interactions qui viennent perturber l'état d'équilibre. Les mécanismes responsables des irrégularités agissent conjointement aux niveaux de l'écosystème et de l'individu. Ainsi, les spectres irréguliers de Laguna Iberá, un lac eutrophe, laissent croire à l'existence d'un fort contrôle descendant qui s'exerce au moyen d'effets en cascade. Les caractéristiques spécifiques d'organismes particuliers, comme les cyanobactéries filamenteuses, contribuent au maintien de ces irrégularités stables. La plus grande régularité spectrale à Laguna Galarza, un lac méso-oligotrophe, résulte d'un flux de biomasse plus équilibré dans la chaîne trophique.

[Traduit par la Rédaction]

Introduction

The discovery of striking regularities in the size–biomass spectrum of plankton led to the consideration of this approach as a valuable tool for the analysis of aquatic ecosystems (Sheldon et al. 1972). Since then, several theoretical models have explored the flow of biomass from smallest to largest organisms with the aim of describing the functioning and organization of aquatic ecosystems. These models were based on similar assumptions, principally a continuous and unidirectional flow up of energy in steady state. Kerr (1974), Sheldon (Sheldon et al. 1977), Platt (Platt and Denman 1978; Platt 1985), and Borgmann (1982) mainly drove these first advances. The obtained conclusions were supported empirically in both marine (e.g., Rodríguez and Mullin 1986) and freshwater systems (e.g., Sprules et al. 1983; Sprules and Munawar 1986; Gaedke 1992*a*). Low-productivity pelagic ecosystems close to steady state usually show linear size spectra. This flatness reflects the dominance of those size-dependent processes operating at the primary scale of individual physiology. Ecosystems far from steady state show bumpy spectra. This undulation mainly appears as consequence of a secondary scale related to the ecological interactions (predator–prey), and attempts have been made to fit

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nonlinear functions to spectrum irregularities (Gasol et al. 1991). The theoretical model developed by Thiebaux and Dickie (1992, 1993) was precisely focused on unraveling the primary and secondary scales of the size spectra. Subsequent model validation (Sprules and Goyke 1994) and application (e.g., Sprules and Stockwell 1995) deepened the assessment of procedures for data aggregation in parabolic domes. In this sense, Kerr and Dickie (2001) recently proposed a new predator–prey theory of aquatic production on the size spectrum. Nevertheless, it could be hypothesized that other possible factors could lead to bumpy spectra, such as the trophic uncoupling between domes or the limnetic–pelagic interaction in shallow lakes. In a broad sense, we refer to the domes and troughs in biomass of the spectrum as “biomass irregularities” because they modify the regular background that emerges from the linkage between physiology and body size.

Quantitative empirical analyses of planktonic structure are usually based on the parameters generated by the straight line fitted to the size spectra (slope, *s*; intercept, *a*; coefficient of determination, R^2). The slope of the normalized biomass–size spectra (NBSS) of ecosystems close to steady state has been empirically determined to be approximately –1.0 or –1.2, depending on whether biomass is expressed as volume or carbon, respectively (e.g., Sprules et al. 1983; Rodríguez and Mullin 1986; Gaedke 1992*a*). Duarte et al. (1987) found a consistent inverse relationship between maximum organism density and body size for a wide set of aquatic ecosystems, which also would imply a –1 slope. Even in systems with discontinuities as large as the high mountain lake La Caldera (Rodríguez et al. 1990), or with high trophic uncoupling as the highly fluctuating temporary lake Fuente de Piedra (García et al. 1995), an overall slope very close to –1 is also found for the time-averaged spectrum. The biomass irregularities may be flattened if spectra are integrated over a period longer than the scale of environmental fluctuations (Gaedke 1992*a*, 1992*b*). The possibility of change of the energy dissipation rate is maximal when the slope is near –1 (Choi et al. 1999). From this slope, ecosystems have the potential to accommodate fluctuations in energy flow with only minimal structural changes. This “adaptability” of ecosystems is reflected in the small variability of *s* in nature (e.g., Kerr and Dickie 2001). However, the overall parameterization of the spectrum, and especially *s*, is often not suitable in cases when the representation is affected by a nonlinear data set.

The potential of the size spectrum approach lies in the use of information of the individual particles instead of integrated information of a size range of particles (e.g., filtering water samples). We propose a simple and immediate quantification of the biomass irregularities using above-mentioned generalities about size spectra. Spectrum irregularity (measured as R^2) has been considered a measurement of the perturbation regime in a given ecosystem (Sprules and Munawar 1986; Choi et al. 1999). High biomass irregularities are expected in ecosystems that are strongly perturbed (far from steady state). The location of the irregularities along size spectra could be used to examine what processes may control the planktonic structure. In this sense, Rodríguez (1994) described plankton size spectrum as a combination of physiological, physical, and ecological processes. This framework gives an interesting significance to biomass irregularities. In this study, we have tried to quantify and interpret the biomass irregularities of two poorly understood wetland lakes, Laguna Iberá and Laguna Galarza.

Methods

Study site

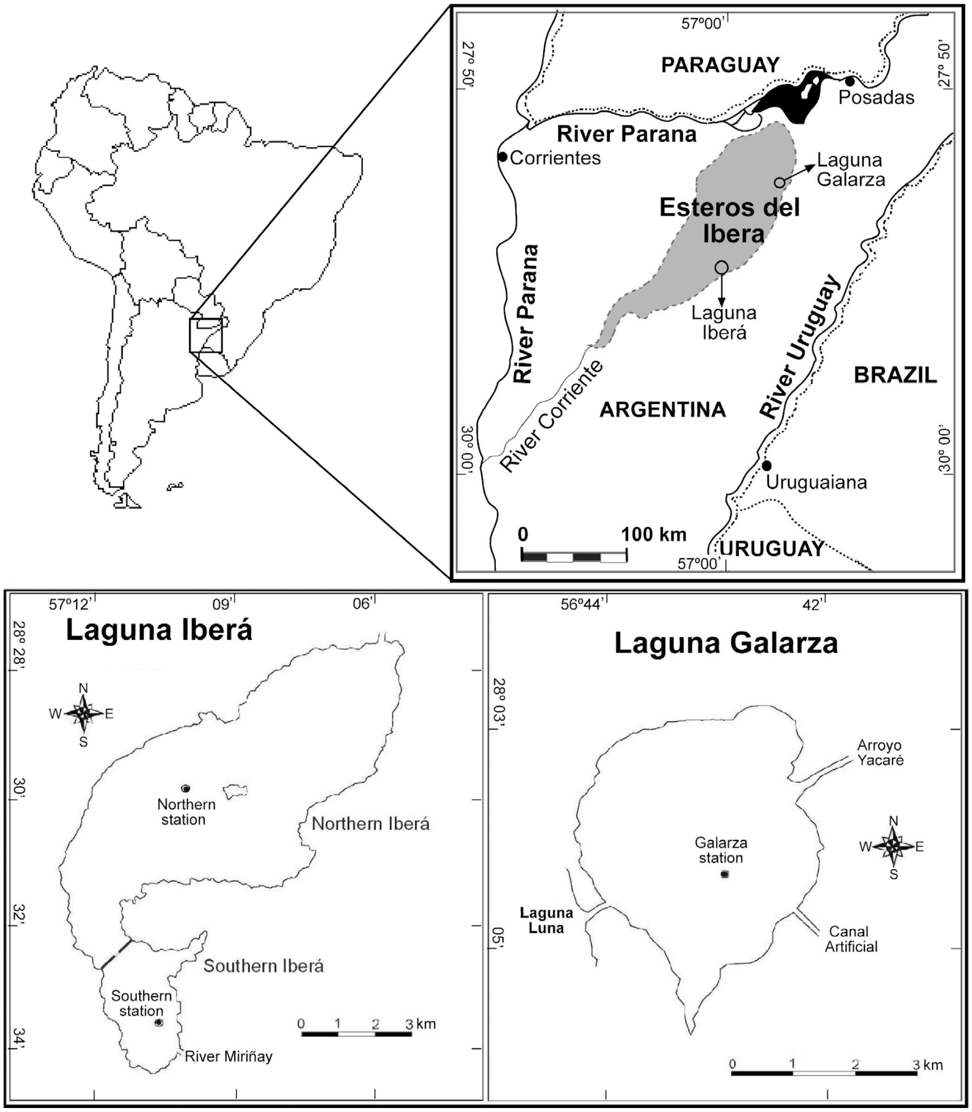
Esteros del Iberá is a vast subtropical wetland (12 000 km^2) located in the province of Corrientes (northeast Argentina). The Paraná Alto, Paraná Medio, and Uruguay rivers delimit this wetland, although it is not fed by running superficial waters (Fig. 1). The plain of Iberá constitutes the ancient bed of the Paraná, which remained connected to the river until the end of the Pleistocene. Currently the basin is mainly fed by rain and drains only through River Corriente in the south. The drainage is slow because of the flatness and the large amount of vegetation accumulated in the basin. Esteros del Iberá and the active Paraná floodplain show strong similarities (e.g., vegetation, ground, landscape). Nevertheless, following the disconnection of the Iberá macrosystem, the vegetation has progressively colonized both the littoral zone and the shores of the lakes as the result of a more predictable seasonal variability. Often, characteristic mats of floating vegetation called “embalsados” compose the shores. The Iberá macrosystem is also a reserve of a diverse community of subtropical wildlife, which is currently generating a growing tourist demand.

The present study is focused on the comparison of two permanent lakes located in the eastern border of the wetland (Laguna Galarza and Laguna Iberá). These lakes were selected to reflect different degrees of human influence. Laguna Iberá supports some rice farming and a human settlement of 600 habitants (Colonia Pellegrini) on its shores, whereas Laguna Galarza has remained practically unmodified by man’s activities. The high sensitivity of wetland lakes to eutrophication is unavoidably linked to the shallowness, which leads to stronger interactions with the benthos and the surrounding environment. For these reasons, Sprules and Munawar (1986) considered shallow lakes to be especially subject to biomass irregularities. It should be remarked that Laguna Iberá is divided into two basins by a narrow passage that acts as a barrier reducing the interchange of wave energy and water masses. Moreover, the inflow of River Miriñay in the southern basin produces a change in the physicochemical environment. The river is a significant source of dissolved organic substances as result of the supply of litter from the floating vegetational mats in the catchment area.

Sampling and plankton analysis

A general limnological study was carried out during a single seasonal cycle to obtain a chemical and biological characterization of the lakes. Laguna Iberá and Laguna Galarza were sampled regularly from July 1999 to June 2000 (nine sampling dates). The sampling stations were placed in the limnetic areas of the basins, with two sites in Laguna Iberá and one site in Laguna Galarza (Fig. 1). Vertical profiles of temperature, pH, and dissolved oxygen were generated at each sampling site, and water transparency was estimated with a Secchi disk (Table 1). Water samples were taken at a depth of 0.5 m. Chlorophyll *a* concentration was estimated after Talling and Driver (1963; Table 1).

Fig. 1. Location of Esteros del Iberá and the study lakes in Argentina. Two sampling sites were located in Laguna Iberá (northern and southern basins) and one in Laguna Galarza.



During the same period, the planktonic community of both lakes was sampled once a season. Three different samples were preserved to count and measure the different size fractions of the plankton. Pico- and nano-plankton samples were fixed with glutaraldehyde (final concentration 1.5%) and frozen in liquid N_2. Nano- and micro-plankton samples were placed in dark bottles and fixed with acetic Lugol's solution (final concentration 1.5%). Mesoplankton was sampled by trawling a plankton net along 400 m (diameter of the opening of attached cone, 20 cm; length, 1.5 m; mesh size, 80 µm; nearly quantitative; no filtering efficiency correction). The retained material was fixed in 4% formaldehyde and stored in plastic 250-mL bottles.

Three complementary techniques (flow cytometry, Utermöhl-inverted microscopy, and stereoscopic microscopy) were used in a way that allowed a large size-range overlap. Pico- and nano-plankton was counted using a FACSCalibur cytometer (Becton Dickinson, San Jose, Calif.). Biovolume was estimated through the calibration of the side-scatter sign with seven sized plankton cultures obtaining coefficients of determination (R^2) higher than 0.95 (Zabala 1999). SYTO-13 staining was used for the flow cytometric determination of the heterotrophic prokaryotes (del Giorgio et al. 1996). Nano- and micro-plankton were counted and measured by inverted microscopy on samples fixed with Lugol's solution. Samples were processed at magnifications of 100×, 250×, and 400×. Organisms were measured with a semiautomatic image analysis system (VIDS V; Analytical Measuring Systems, Synoptics Ltd., Cambridge, U.K.). Biovolume was calculated by using geometric formulas with the best fit to cell shape. For colonial algae, each colony was treated as an individual. These size fractions could be also identified taxonomically. Mesoplankton was processed in the same manner using a stereoscopic microscope connected with the image-analysis system. The criterion adopted with the microscopic techniques was to measure more than 400 individuals in each sample to keep the counting error within ±10%.

Building size spectra

The organisms measured covered a range of 10 orders of

Table 1. Morphometric, physico-chemical, and biological data for the lakes during nine samplings from July 1999 to June 2000.

	Mean depth (m)	Area (km^2)	Temperature (°C)	pH	DO (% saturated)	Zs (m)	Chl *a* (µg·L^{-1})	Maximum chl *a*
Laguna Iberá (north)	3.2	50.8	20.7±5.9	6.7±1.4	99±7	0.8±0.3	23±10	Spring
Laguna Iberá (south)	3.3	7.3	20.1±5.4	5.9±0.4	80±19	1.4±0.6	15±13	Summer
Laguna Galarza	1.9	16.5	21.6±4.4	5.7±0.7	93±12	1.5±0.4	4±2	Summer

Note: Values are given as mean ± standard deviation. DO, dissolved oxygen; Zs, Secchi depth; Chl *a*, chlorophyll *a*.

magnitude expressed as biovolume (0.4–800 µm equivalent spherical diameter, ESD). They ranged from bacteria to large planktonic crustaceans. This wide size range was arranged in size classes with increasing widths, following a geometric 2^n series (Sheldon et al. 1972). With this partition, the amplitude of the size class (Δw) coincides with the lower limit of it (w). The normalized biomass in each class ($\beta(w_i)$) can be calculated from biomass (B) as

$$\beta(w_i) = [B(w, w + \Delta w)]/\Delta w$$

When data are plotted on a log–log axis, the relationship is linear and it is possible to obtain the overall parameterization of the normalized biomass–size spectra (NBSS):

$$\log \beta(w) = a + s \log w$$

where a (intercept) and s (slope) are the parameters of the fitted line. We defined gap or discontinuity in the spectrum as a size class without detectable biomass. To include the gaps in the NBSS, we apply the method proposed by Tittel et al. (1998).

The representation of residual variations around the time-averaged spectrum allows the location of the size classes with higher susceptibility to develop biomass irregularities in the community (e.g., Rodríguez et al. 1990; Tittel et al. 1998). However, this method cannot be considered a comparable quantitative method because the deviations are referenced to a fixed level, depending on the seasonal nature of each system. The large amount of effort required to build a consistent time-averaged spectrum is a major disadvantage of this method. We have followed an immediate method to quantify irregularities based on the deviations of observed data from the observed regularities of plankton size spectra. First, we estimated a conventional reference level ($\mathrm{NBSS_p}$) that emerged from the size-dependent process operating at primary scale of individual physiology. Thus, we force the slope to be $-1(s_\mathrm{p})$ in the regression analysis of the size spectra. Because the least-squares method is by far the most common approach to regression, we use a least-squares statistic to estimate the intercept (a_p). The a_p parameter depends on the averaged biomass contained into the studied size classes:

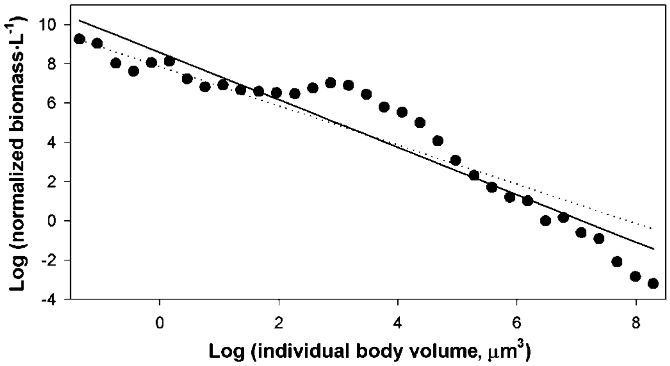
$$a_\mathrm{p} = \overline{\log \beta} - s_\mathrm{p}\, \overline{\log w} = \overline{\log \beta} + \overline{\log w}$$

The obtained straight line ($\mathrm{NBSS_p}$) allows us to calculate a theoretical normalized biomass (β_p) within each size class through the following equation:

$$\log \beta_\mathrm{p}(w) = a_\mathrm{p} - \log w$$

In this way, we can estimate a reference level for each seasonal spectrum. The fitted line resulting from the free-slope regression and $\mathrm{NBSS_p}$ can have significant differences (Fig. 2).

Fig. 2. Normalized biomass-size spectrum (NBSS) for the northern basin of Laguna Iberá during fall: fitted lines resulting from free-slope (solid line) and –1-slope regression (broken line).



In fact, the aim of conventional least-squares regression is to find the line that, on average, describes the available data with the smallest errors. When biomass irregularities occur, the regression analysis can identify the parameters estimation to obtain a better R^2. That is, the overall parameterization refers to the line that fits best the irregularities of the empirical model.

At this point, it would be possible to characterize the biomass irregularities by difference of β with respect to β_p. It is convenient to perform a logarithmic subtraction because of the wide range of biomass values along the size spectrum. An adimensional estimate is also obtained. We refer to the spectrum irregularity measured by this method as "biomass anomaly" (BA):

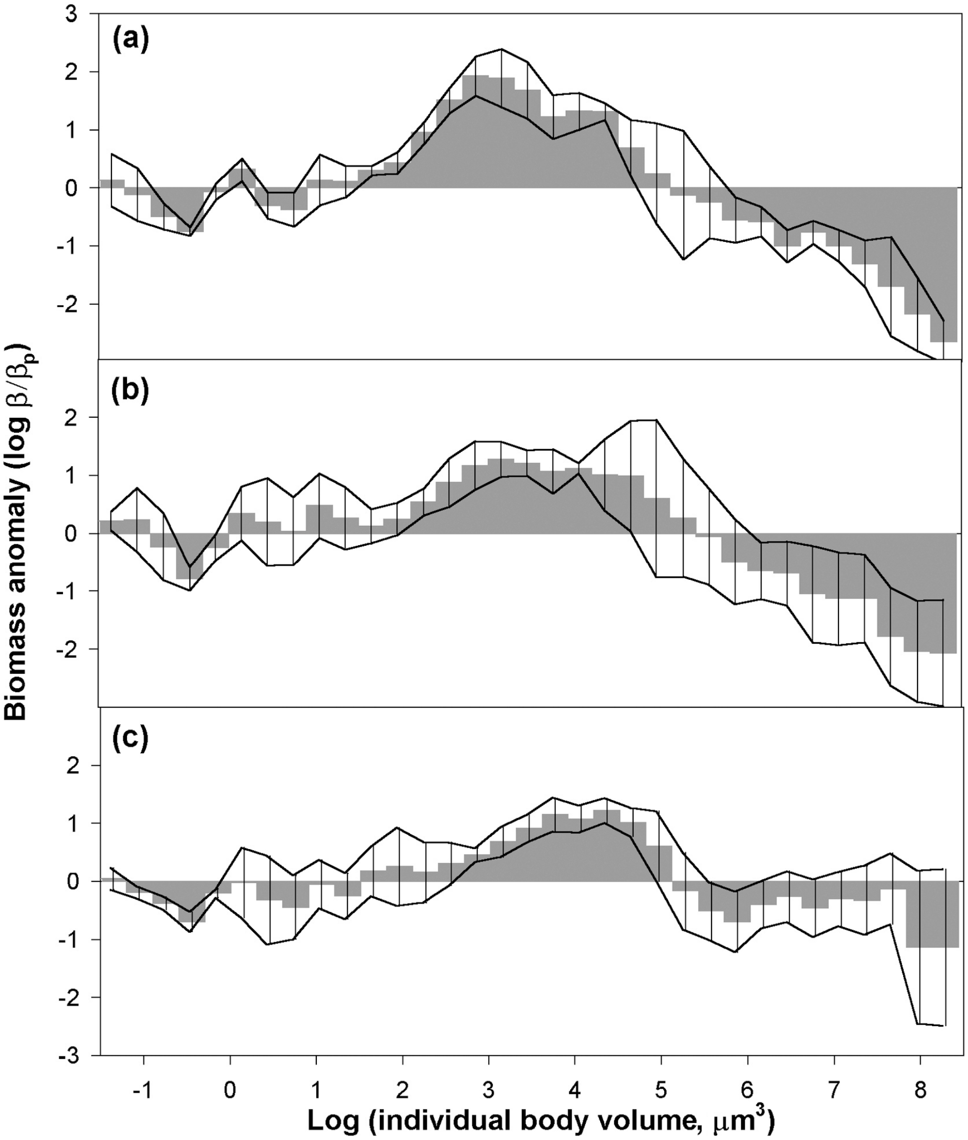
$$(1) \qquad \mathrm{BA} = \log(\beta/\beta_\mathrm{p})$$

A histogram plot of biomass anomaly–size spectrum (BASS) can then be obtained following this simple method. The sign of BA indicates the shape of the spectrum irregularity, dome (+) or trough (–). In the next section, we use this BASS as tool to analyze the plankton size structure.

Results and discussion

The studied lakes showed clearly different limnological characteristics (Table 1). Laguna Iberá showed concentrations of chlorophyll *a* higher than in Laguna Galarza. The concentrations registered in the northern basin of Laguna Iberá were particularly high. Both lakes showed a seasonal bloom, although the chlorophyll maxima of Laguna Galarza and southern Iberá had a lag time compared with the northern basin of Iberá. These limnological differences were also reflected in different BASS (Fig. 3). It is interesting to note that the three studied basins held planktonic organisms in all size classes of the averaged spectra, despite their shallow-

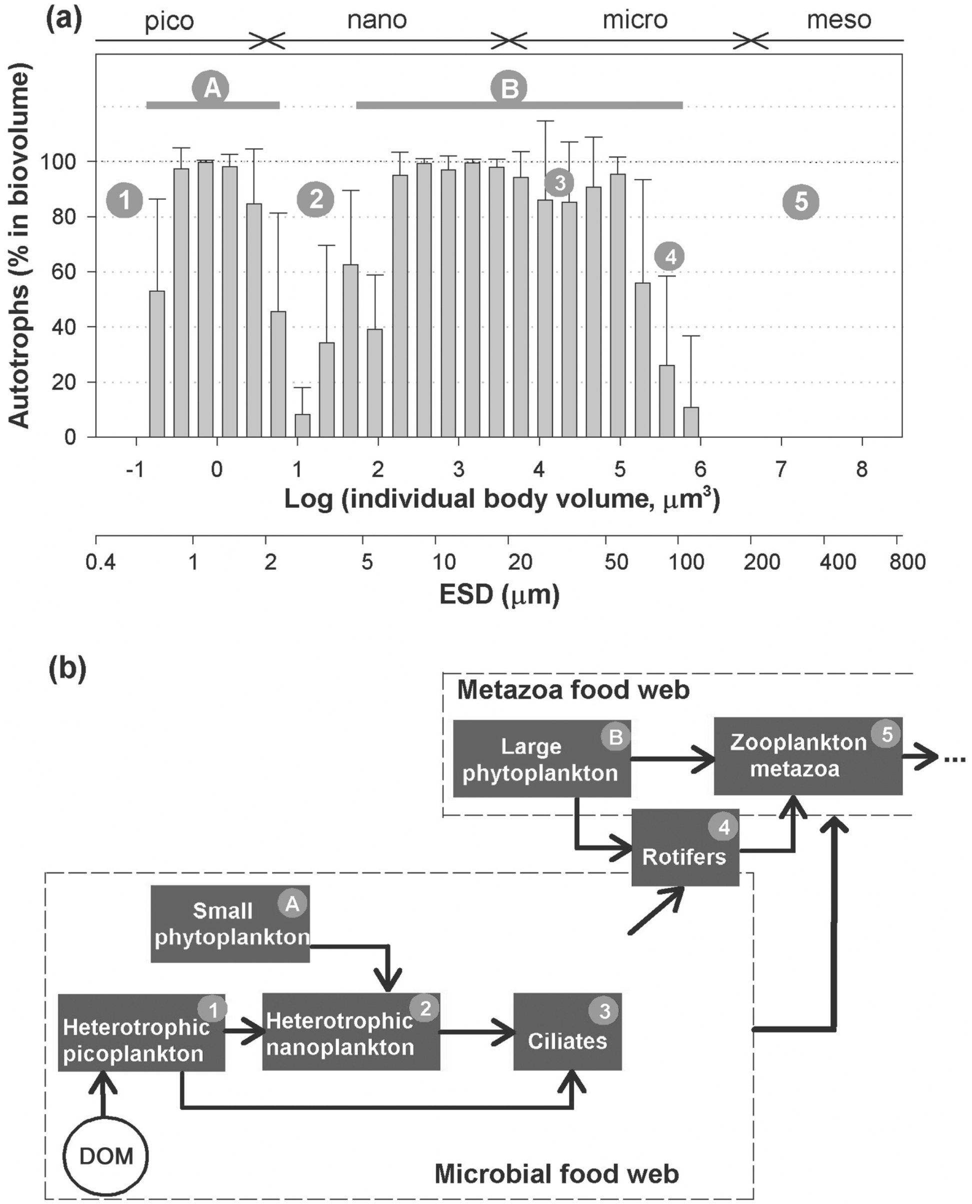
Fig. 3. Seasonal averaged biomass anomaly–size spectra (BASS) for (*a*) northern and (*b*) southern basins of Laguna Iberá and (*c*) Laguna Galarza. The averages included a whole BASS per season. Standard deviations during the seasonal cycle are shown in each size class.



ness. Gaps or size classes without detectable biomass appeared only in the largest size classes (crustaceans) of some seasonal spectra, mainly during the low-productivity phase of Laguna Iberá. A continuous size spectrum has been interpreted as a continuum of functional guilds, an expected feature of highly developed food webs (Gaedke 1992*b*). The higher diversity of species of the equatorial and subtropical regions could contribute to a relatively lower frequency of gaps and irregularities at low latitudes (Sprules 1988). Furthermore, a linear spectrum with slope close to –1 has been interpreted as indicative of a more developed community (Gasol et al. 1991). The total biomass anomaly of the eutrophic northern Iberá was the highest; Laguna Galarza shows the most linear spectrum, and southern Iberá shows an intermediate pattern.

Despite the ataxonomic nature of the size spectrum, it seems convenient to outline a trophic background to analyze the spectrum irregularities. Aiming to simplify the intricate structural interactions of the food web, we have established the rough limits of functional groups along the size gradient by calculating the approximate autotrophs to heterotrophs ratio (Fig. 4). The clearest heterotrophic-dominant classes are located at the lower and upper end. These size classes include heterotrophic bacteria and large zooplankton (crustaceans), respectively. The totality of limnetic autotrophs is confined within these limits. The transition between autotrophs and metazoan zooplankton shows a narrow size overlap, supporting the scheme of size-related pelagic food chains of discrete levels (Kerr and Dickie 2001). However, some other heterotrophic organisms (ciliates and rotifers) fall into the size range of large phytoplankton, showing a less clear size – trophic position relationship. There is also a clear dominance of heterotrophs in the nanoplanktonic classes mainly because of heterotrophic flagellates. The general pattern in the data shows strong similarity with other similar trophic analysis of plankton (e.g., Sprules and Goyke 1994; del Giorgio and Gasol 1995). Different functional groups rarely occur simultaneously in the same location. The steadi-

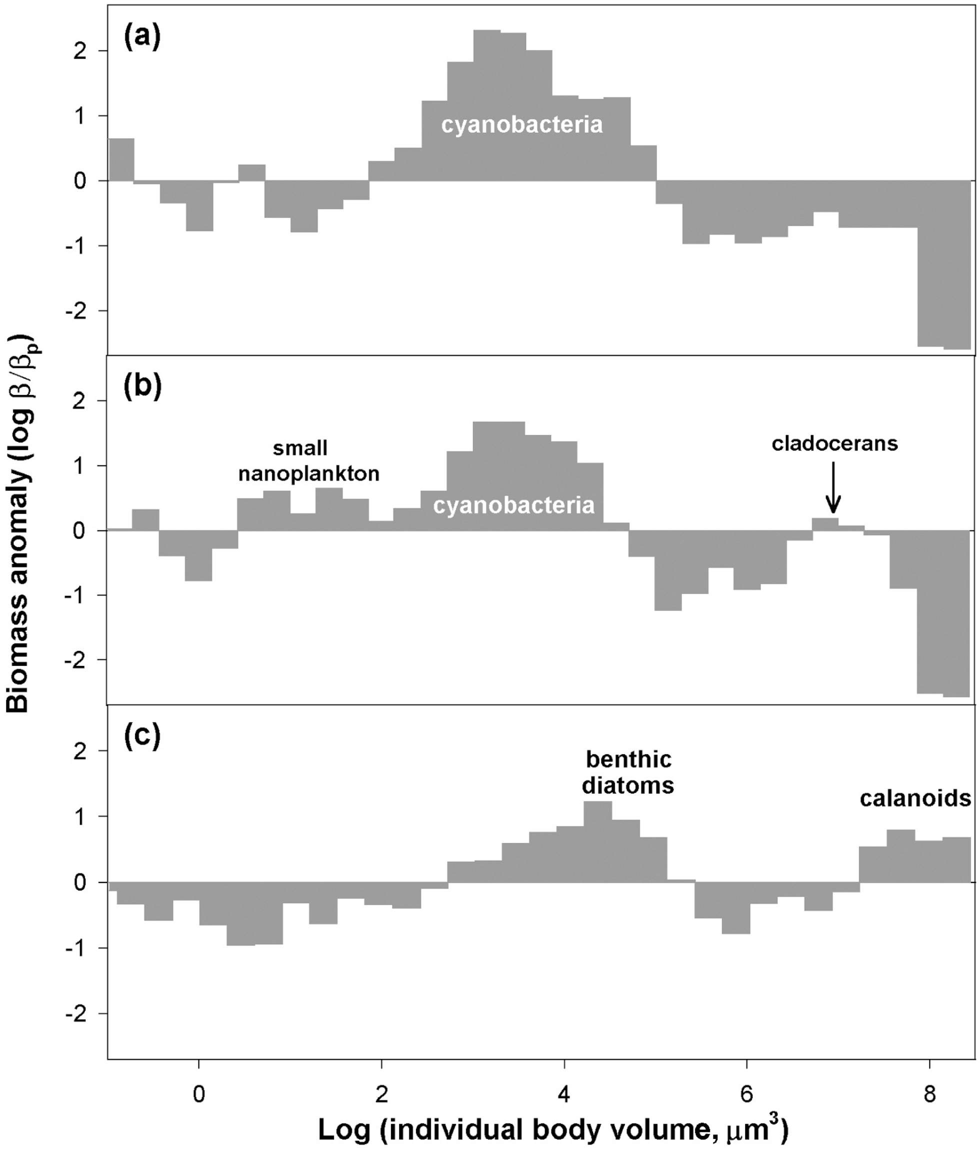
Fig. 4. Trophic size spectrum. (*a*) Percentage of autotrophs with respect to the total biomass of each size class. The averages were obtained from all size spectra performed during the study in Laguna Iberá and Laguna Galarza. Standard deviations are shown in each size class. (*b*) The lower conceptual diagram represents the correspondence between food web components and windows of the trophic spectrum, and a simplified interpretation of energy flow intrinsic to the plankton size spectra. Capital letters A and B indicate the size ranges in which the small and the large phytoplankton are located. Numbers 1, 2, 3, 4, and 5 indicate the components responsible for the heterotrophic windows.



ness of the trophic positions would be the cause of the existence of a typical pattern of spectrum undulation describing these main functional size ranges. This pattern has been described in detail from the measurement of the parabolic curvature of each trophic position (Kerr and Dickie 2001). The use of polimodal functions fitted to the overall spectrum has received less attention (e.g., Gasol et al. 1991), probably because of the higher complexity of this task. In this sense, the new view offered by BASS shows a simultaneous comparison of every dome along the spectrum. Note that this tool enhances the vertical shifts between parabolas.

Although the total irregularity increased with the trophic status, we registered similar shapes of BASS according to the allocation of the trophic levels. The clearest change of sign of BASS coincides with the compositional change from autotrophs to metazoan zooplankton. The lower limit of the positive biomass anomalies (BAs, eq. 1) coincides with the heterotrophic nanoplankton classes of the size spectrum in both lakes. Pico- and small nano-plankton (<100 µm^3) did not exceed a |BA| = 1 during all sampling dates. This result indicates a small deviation between the physiological primary slope and the structure of the microbial food web. Presumably, the smaller organisms are metabolically more active, reacting rapidly to the biomass irregularities in these size classes. Gaedke (1992*b*) hypothesized that a regular size distribution emerges from local interactions, essentially from

Fig. 5. Comparison of the spring biomass anomaly–size spectrum (BASS) in (*a*) northern and (*b*) southern basins of Laguna Iberá and (*c*) Laguna Galarza. Benthic diatoms were the dominant algal group during this season in Laguna Galarza, although chlorophyceans and cyanobacteria also reached significant biomass.



the interspecific competition and the successful invasion into "empty" size classes. Following this argument, positive BAs would indicate size ranges in which competition presumably is acting as an important agent in shaping the structure of the assemblage. Negative BAs, in turn, would indicate niches with a lower utilization, in which some other restrictions would shape the structure. Micro- and large nano-plankton reached the highest positive BA in the lakes. The biomass accumulation in the phytoplankton size range seems to be frequently observed in freshwater lakes (e.g., Sprules et al. 1983; Tittel et al. 1998) and is probably related to the strong nutrient control of this spectrum segment (Rodríguez et al. 1990). Nutrient availability determines the potential of this positive BA; however, zooplankton grazing is what determines how much and how this potential is developed (Cottingham 1999). This consideration shows the complexity of the interaction between top-down and bottom-up controls in the ecosystem. Positive BAs corresponding to zooplankton are only observed during spring (Fig. 5). Nevertheless, these biomass accumulations were always substantially lower than those registered in the phytoplanktonic range. Northern Iberá showed the clearest unimodal distribution along the seasonal cycle. We could hypothesize for this basin relatively higher algal competition for the resources (light and nutrients) without a relevant control by grazing.

The possible mechanisms responsible for the apparition of biomass irregularities will be classified according to the theoretical assumptions of the size spectrum modelling (e.g., Sheldon et al. 1977; Platt and Denman 1978; Borgmann 1982). Firstly, the idealized regular spectrum is based on general allometric relationships. It seems evident that organisms with peculiarities that cause a deviation of the size-related processes can alter the energy flow along the size spectrum (Gaedke 1992*b*). The specific feeding pattern of daphnids (efficient filter feeders in a broad size range) has been identified as a source of biomass irregularities (Tittel et al. 1998). The presence of large ciliates (*Fabrea salina*) with high trophic flexibility and adapted to high salinity stress was also proposed as a cause of irregularities in a temporary, saline inland lake (García et al. 1995). Thus, the properties of the constituent species of the main positive BAs should be taken into account. The high BA within the time-averaged spectrum of the northern basin of Laguna Iberá is remarkable. *Lyngbya* spp. appears as the dominant species, representing 63% of the algal biomass (58% *L. limnetica*, 5% *L. contorta*). The increase in lake productivity decreases species diversity (Dodson et al. 2000); likewise, the success of one species implies an increment of biomass into few size classes. The specific characteristics of *Lyngbya* spp. contribute to support the spectrum undulation. The high shade tolerance and inedibility of the filamentous cyanobacteria (e.g., Scheffer 1998) leads to a double positive feedback with eutrophic conditions and low zooplanktonic biomass, respectively. On the other hand, the sedimentation does not contribute excessively to the dissipation of the excess of energy influx in the ecosystem. *Lyngbya limnetica* seems to have the capacity of buoyancy regulation (Reynolds et al. 1983). The southern basin of Laguna Iberá, however, showed a more regular spectrum. This basin even reached positive BAs in the zooplanktonic size range coinciding with the maximal bacterial abundance during spring (Fig. 5*b*). The zooplanktonic positive BAs were composed by medium-sized cladocerans (mainly *Bosmina* spp.). The elements of the microbial web reached the highest concentrations in the southern Iberá, probably because of the higher concentration of dissolved organic substances. Prey size range corresponding to cladocerans covers the pico- and small nano-plankton. We hypothesize that in these conditions, the accumulation of small fast-growing edible cells in certain suitable size classes is easily transferable to larger organisms. The development of a complex microbial food web, including high concentrations of ciliates, rotifers, and cladocerans, contributes to a more regular spectrum. In this case, the community structure adapted rapidly to the energy inflow, balancing the bacterial growth. Excess of primary production can also move ecosystems away from the steady state. Primary production is often much higher than consumption because of a delay in the herbivorous reaction. A winter bloom in the Mediterranean was used to show bottlenecks in the propagation of a fluctuation up the planktonic size spectrum (Jiménez et al. 1989). Sedimentation rapidly acted as a relaxing mechanism of this destabilizing energy inflow. The temporal scale of the biomass uncoupling is usually relatively short because of the rapid adaptability of the ecosystems (Choi et al. 1999).

Theoretical models of the aquatic size structure have been developed in closed systems. Nevertheless, a littoral or benthic input of biomass can also alter the spectrum regularity of a limnetic food web (e.g., Rodríguez et al. 1990). This situation can be exemplified in Laguna Galarza. The autotrophic BAs in Galarza (BA_{max} = +1.5 at 40 μm ESD) appeared centered on a different size range and showed lower values than in Laguna Iberá (BA_{max} = +2.3 at 10 μm ESD). The algal structure of Laguna Galarza was generated under conditions of higher grazing pressure than that of Laguna Iberá (Fig. 5). An increase of average individual volume of the phytoplankton is a rough indicator of a higher resistance to grazing (e.g., Gaedke 1992*a*; Cottingham 1999). Diatoms, colonial cyanobacteria, and large chlorophyceans compound the algal biomass accumulation in the microplanktonic classes of Laguna Galarza. Large benthic diatoms such as *Surirella* spp. and *Navicula* spp. contributed significantly to enlarge the microplanktonic subdome. They represented about 20% of the algal biomass measured in the water column throughout the year and were the dominant group during the spring calanoid copepods proliferation (BA_{max} = +0.8 at 500 μm ESD). The size structure of phytobenthos seems to differ from the phytoplankton size structure because of the different size ratios between prey and predator (Warwick and Joint 1987). Thus, the different constraints on body size of prey in both ecosystems (benthos and pelagic) would facilitate the occurrence of microbenthic diatoms in the water column. This fact supports the hypothesis of diatom resuspension as a viable adaptive strategy in shallow lakes (Carrick et al. 1993). Carrick et al. (1993) also provided evidence supporting this hypothesis in terms of nutrients and light availability. The higher transparency and shallowness of Galarza facilitated the growth and the frequent wind resuspension of the phytobenthic assemblage. The consequent spectrum undulation should be considered as a typical shape in shallow lakes. The self-organization of the deep aquatic environments generates a higher spectrum flatness that in shallow environments, with a better connection to benthos (e.g., Choi et al. 1999). Sedimentation is not an efficient mechanism with which to dissipate destabilizing factors, as occurs in deep environments.

The theoretical models of the aquatic size structure rest on the assumption of a unidirectional energy flow upward. This assumption would be equivalent to a bottom-up control in which the growth of the whole food chain would be directly proportional to the growth of the lower trophic levels. When the predation controls the biomass of the lower trophic level (downward forcing), the ecosystem is headed to a spectrum undulation. The obtained time-averaged BASS in Laguna Iberá could be also explained from this viewpoint. We suggest a strong top-down control of the food web of Laguna Iberá. Grazing should be a relevant process promoting a more regular biomass distribution in this lake. However, the transference of the accumulated algae towards larger organisms is quite inefficient, appearing as a bottleneck in the energy flow. An overgrazing on the zooplankton size range by fishes seems to promote high algal accumulations. Comparing the food web of Iberá with the regular biomass distribution of Galarza, we found five times more biomass of autotrophs in Iberá compared with a 15-fold increase in biomass of crustaceans in Galarza. Quantitative fishing has confirmed that the fish stock is, in turn, about six times higher in Laguna Iberá (W. Jacobo, ACUICOR, Corrientes, Argentina, personal communication). Nevertheless, a detailed trophic analysis of the fish community needs to be undertaken.

The analysis of the different size distribution patterns observed for the zooplanktonic size ranges supports the aforementioned hypothesis of trophic control in the studied lakes. Selective predation by planktivorous fishes removes the larger zooplankters. Therefore, small rotifers make up the only zooplanktonic group that showed relevant growth. In the southern Iberá, medium-sized cladocerans represent a significant percentage of the herbivorous biomass (26% throughout the year), although the rotifers are also the dominant group (55%). The zooplankton of Laguna Galarza is mainly represented by larger copepods (62%). Brooks and Dodson (1965) described similar structural and compositional differences in the zooplankton as a consequence of the different zooplanktivorous pressure.

The limnetic community of Laguna Iberá could be defined as a “wasp-waist” food chain in which the zooplanktonic trophic position, in the middle, has crucial importance in defining the trophic control. The biomanipulation could be a useful tool for management and restoration of Laguna Iberá. However, the presence of abundant filamentous cyanobacteria making up a large positive BA questions the effectiveness of this alternative. Cottingham (1999) showed that the increase of the average zooplankton size decreased the spectrum irregularity in a lake dominated by chrysophytes, dinoflagellates, and cryptophytes. However, a similar increase in size led to even higher spectrum irregularities in two other lakes dominated by filamentous cyanobacteria. Combined strategies that include a specific reduction of the proportion of filamentous cyanobacteria would be most likely to be effective.

Attempts to deal with size spectra, including this study, usually use taxonomic information. This information, gathered previously by microscopic inspection, often helps to find the answers to the study goals. However, this brings into question the subsequent usefulness of size spectrum analysis. Nevertheless, the size spectrum offers a well-known approach to the analysis of ecosystem structure. This groundwork provides a systematic and suitable framework for the integration of whole-community information (microbial food web, phytoplankton, zooplankton, etc.). The validity of the concept of “trophic positions” demonstrates the compatibility of the structural and functional information in aquatic ecosystems. The spectrum approach allows the generation of size compartments composed by organisms having roughly similar physiological rates and ecological functionality. The synthesis of wide and diverse information within the spectrum should facilitate the understanding of the ecosystem organization. Integral descriptions of the food chains may simplify the difficult question of how perturbations act on the ecosystems through the identification of the more relevant species and processes. On the other hand, the development of automatic particle counters like the flow cytometer, which offers individualized information of body size and trophic characteristics, allows us to predict a hopeful future for the use of size spectrum as a first exploratory approach.

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