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The forgotten lake stratification pattern: atelomixis, and its ecological importance

Francisco A. R. Barbosa and Judit Padisák

Introduction

The principal mixing patterns of lakes were described in the early decades of the 20th century (e.g. THIENEMANN 1925, YOSHIMURA 1936). Tropical high-mountain lakes were recognized as polymictic and lowland lakes as oligomictic by HUTCHINSON & LÖFFLER (1956); HUTCHINSON (1957) demonstrated the conditions associated with each of the tropical lake types, and TALLING (1969), when reviewing the thermal patterns in African lakes, suggested that a strong annual periodicity of the thermal regime was almost universal in the African tropics. However, LEWIS (1973) pointed out that such a "tropical classification scheme" was suggested with practically no information on Asian and American tropics.

Apart from these well-known (WETZEL 2001) historical lake stratification patterns, another type, atelomixis, was also identified and characterized for a tropical lake in the recent past (LEWIS 1973). According to this author, such a pattern was capable of describing the progressive layering process during the warm period of Lake Lanao, the Philippines, when diurnal temperature variations exceeded the annual variations.

During the tropical winter (20–26 °C) daytime heating leads to the development of a weak but measurable thermocline (temperature gradient: 2–5 °C). The nocturnal cooling is considerable and consequently the surface water starts to cool down, thus increasing the density. This heavier surface water then descends at about 03:00 h, breaking the thermocline. This phenomenon is repeated daily with slight variations and, consequently, the lake stratifies and destratifies on a daily basis.

These phenomena were recorded in Lake Carioca (south-east Brazil) by BARBOSA & TUNDISI (1980) and were used to explain how diurnal variations were particularly important at the onset of the stratification period.

During the last century it was increasingly recognized that tropical lakes differ from temperate lakes in some basic features. For example, anoxic hypolimnia in the stratified period do not indicate eutrophic status, N-limitation of phytoplankton growth is more frequent than in temperate lakes (TALLING 1965), and they need specific ranges for the classification of their trophic status (SALAS & MARTINO 1991).

It has been recognized also that species richness and the quantitative importance of planktonic Desmidiales (Chlorophyta) have been much higher in tropical lakes. Although this phenomenon is of great interest to algologists, there has been no discussion about how these relatively heavy and non-motile cells can be so widespread and abundant in tropical lakes, apart from drawing attention to the necessity for frequent mixing to keep them in suspension (REYNOLDS 1997a).

In this study, the manner in which the above-referred phenomena affect the composition and distribution of the phytoplankton community in two tropical lakes during the stratified summer period was assessed. The importance of atelomixis as a driving force in the selection of phytoplankton assemblages, particularly in favour of the relatively heavy and non-motile planktonic desmids, is also stressed.

Study area

The lake district of the middle Rio Doce (19° 29–48' 24" S, 42–48° 28–38' 30" W) represents one of the few natural lake systems in Brazil, formed by ca. 120 small (0.5–200 ha) and usually shallow lakes (1.5–15 m) amidst the largest remnant of the Atlantic Forest in the State of Minas Gerais, the Rio Doce State Park (36,000 ha). The area has also been subjected to extensive *Eucalyptus* spp. plantations, which, together with iron and steel plants, charcoal and cellulose production, and mining activities, exert considerable impacts. Approximately one-quarter of the lakes in this area are located within the relatively unimpacted State Park. Among these lakes, two have received considerable scientific attention: Lake Carioca and Lake Dom Helvécio.

Lake Carioca, a mesotrophic lake (SALAS & MAR-

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TINO 1991), has a surface area of 13.2 ha and a maximum depth of 11.8 m. Lake Dom Helvécio is oligotrophic with a surface area of 200 ha. With its 33-m maximum depth it is the deepest natural lake in Brazil.

Material and methods

Two diurnal cycles were investigated in the two lakes, respectively, on 11/12 February 1999 and on 17/18 February 2000 in Lake Carioca, and on 15/16 January 1999 and 15/16 February 2000 in Lake Dom Helvécio. Environmental data (temperature, conductivity, pH, dissolved oxygen, redox potential) were recorded every 3 h with a Horiba profile sensor at 0.5-m increments. Water chemistry data (main nutrients) were measured at depths corresponding to 100%, 10%, 1% surface irradiance (measured by a Li-Cor quanta sensor) and in the aphotic zone at the same time intervals. Only temperature data are discussed thoroughly herein; all others are provided as background information (Table 1).

Phytoplankton samples were taken using a van Dorn sampler at the same time intervals from water depths of 0, 1, 3, 5, 6, 7, and 9 m in Lake Carioca and 0, 1.5, 3, 4.5, 6, 7.5, 9, 12, and 20 m in Lake Dom Helvécio. Phytoplankton species were identified using contemporary phycological manuals and literature. A minimum of 400 settling units (cells, filaments or colonies) were counted in each Lugol-fixed sample, giving a counting accuracy of ± 10% for total phytoplankton. Larger species were counted on the total surface of the counting chamber in 10-mL aliquots. Phytoplankton biomass was estimated by geometrical approximations using a computerised plankton counter, following GOSSELAIN & HAMILTON (2000).

Results and discussion

Environmental data measured at two selected depths (representing epilimnion and hypolimnion) of both lakes during the stratification periods of 1999 and 2000 are shown in Table 1. The lakes were slightly acidic, well oxygenated within the upper layers although, as with many oligo- and mesotrophic tropical lakes, main-

Table 1. Limnological features of Lakes Carioca and Dom Helvécio at two selected depths of the water column corresponding, respectively, to a depth within the epilimnion and bottom of the thermocline, during the stratified periods of 1999 and 2000.

	Lake Carioca				Lake. Dom Helvécio			
	January 1999		February 2000		January 1999		February 2000	
Depth (m)	1.0–1.55	9.0	1.5	9.0	1.5	20.0	1.5	18–20
pH	6.4	6.1	6.1–6.8	5.6–5.9	7.4	6.3	6.8–7.7	5.7–6.4
Conductivity (µS/cm)	20	99	28	105–183	29	52	36	61–73
DO (mg/L)	5.3–7.0	0.0	7.6–8.4	0.4–0.6	7.0–7.8	0.0	8.4–8.8	0.4–0.6
Alkalinity (meq CO_2/L)	–	–	0.3	0.6–0.8	–	–	0.3–0.4	0.4–0.5
Chl. *a* (µg/L)	–	–	6.9–15.5	41.1–90.9	–	–	2.7–21.9	10.2–40.1
PO_4-P (µg/L)	4.0–376.4	4.6–39.4	0.4–14.8	0.3–2.9	2.9–6.4	5.0–127.2	0.7–4.2	0.9–2.0
P_{total} (µg/L)	8.2–111.0	32.3–148.2	13.9–20.3	33.1–52.3	7.6–452.6	17.6–27.4	6.5–16.4	7.7–15.4
NH_4^+ (µg/L)	6.3–42.1	1025.3–1640.2	8.4–62.7	716.6–1966.5	6.6–31.3	637.2–875.3	1.9–41.2	6.6–743.1
NO_2^- (µg/L)	0.8–4.3	2.4–15.8	0.5–6.2	1.3–10.7	7.4–12.3	5.3–17.0	0.1–2.3	0.6–6.3
NO_3^- (µg/L)	10.4–18.2	13.3–28.7	8.2–18.3	14.7–35.1	0.8–1.6	1.2–6.3	1.1–13.2	3.7–38.3
N_{total} (µg/L)	1.1–8.6	1.4–11.0	485.9–695.6	2320.0–4327.5	0.7–18.4	1.3–3.0	187.5–1452.0	319.9–2015.5
SiO_2 (mg/L)	3.1–4.3	3.3–4.1	2.1–2.5	1.9–3.1	4.4–5.4	3.8–4.7	2.6–3.2	2.8–3.8

taining anoxic conditions within the hypolimnion.

Temperature pattern

The water temperature between winter and summer varied from 20.3 °C to a maximum of 32.9 °C in Lake Carioca and between 22.5 °C and 31.6 °C in Lake Dom Helvécio, thus rendering seasonal temperature differences of 12.6 °C and 9.1 °C, respectively.

Figures 1 (A and B) and 2 (A and B) show diel temperature variation in Lakes Carioca and Dom Helvécio, respectively, during the stratified periods of 1999 (January) and 2000 (February). Despite their morphometric differences, the temperature patterns were very similar in both lakes, showing well defined thermoclines throughout the 24-h periods. In Lake Carioca, in January 1999, the main thermocline occurred between 5 and 7 m and a secondary (unstable) thermocline could be identified between 3 and 5 m. Instability within the upper layers was evident from 16:30 h, extending particularly during the night period, and resulting in a deepening of the main thermocline during this period. Throughout the 24 h, the water column temperature varied between 22 and 31.5 °C. In February 2000, a similar pattern was recorded, although the temperature difference between the surface and bottom waters varied between 22.3 and 33.0 °C and with greater instability within the upper layers.

Lake Dom Helvécio showed a similar pattern in both periods, with the main thermocline lying between 5 and 12 m and unstable stratification within the upper layers, particularly during the afternoon–night hours. The water column temperature varied between 23 and 31.5 °C.

Phytoplankton composition and vertical structure

The most striking feature of the phytoplankton in Lakes Carioca and Dom Helvécio was the high biodiversity: the number of species identified from the plankton was close to 200. Among the phytoplankton species, the number of planktonic desmids (belonging to genera *Desmidium, Closterium, Cosmarium, Euastrum, Gonatozygon, Micrasterias, Netrium, Staurastrum, Staurodesmus* and *Teilingia*) was very high – in qualitative samples, 39 species were found in Lake Dom Helvécio and 49 in the Carioca.

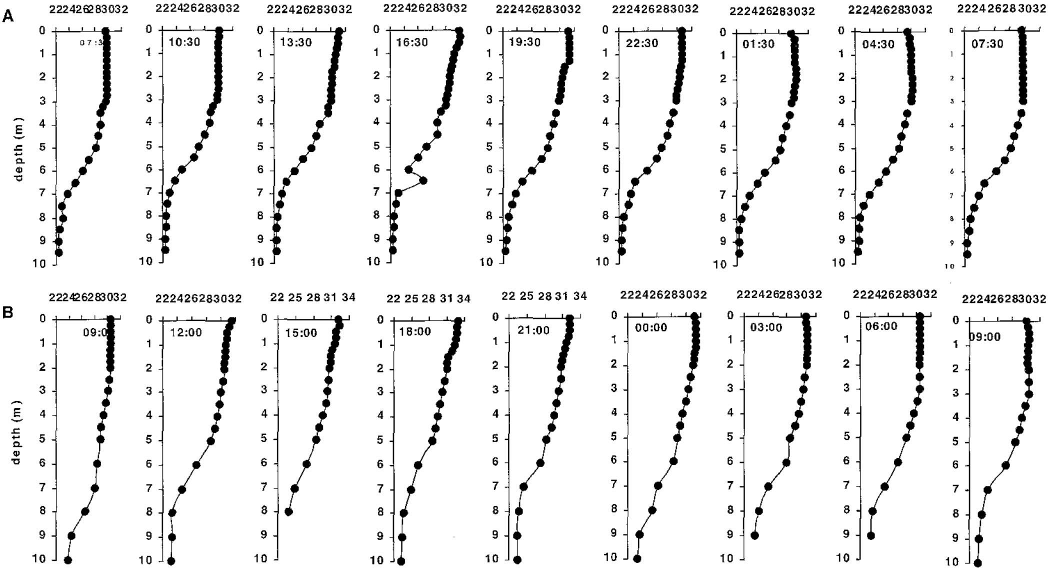

Fig. 1. Diurnal temperature variation in Lake Carioca, south-east Brazil on (A) 11/12 January 1999, and (B) 17/18 February 2000.

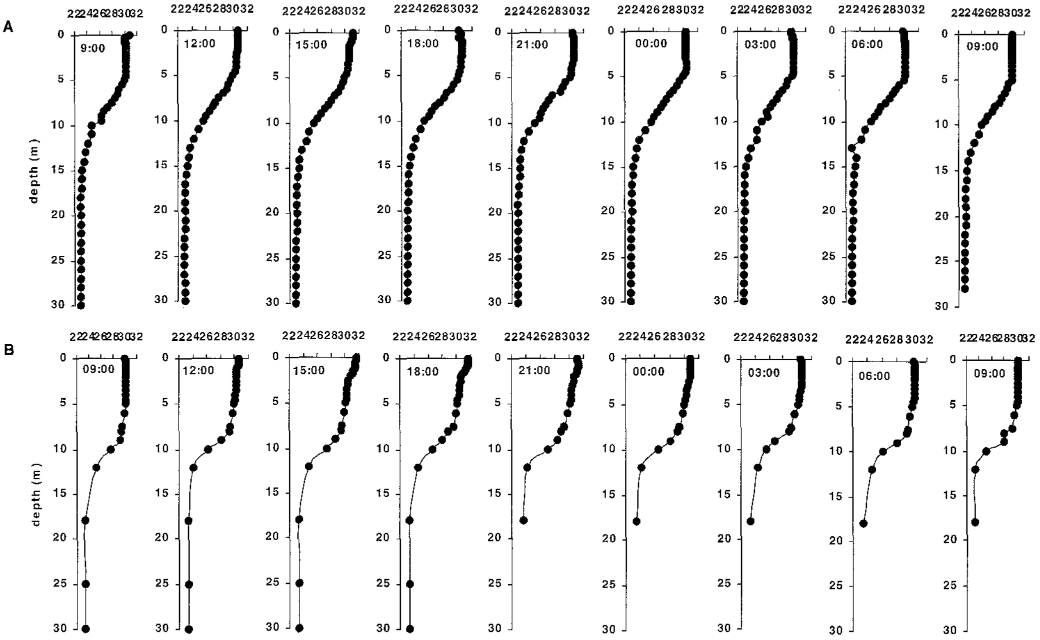

Fig. 2. Diurnal temperature variation in Lake Dom Helvécio, south-east Brazil on (A) 15/16 January 1999, and (B) 15/16 February 2000.

Occurrences of most plankton species were rare. In Lake Carioca, only *Cosmarium bioculatum* and *C. contractum* were found in large numbers, while in Lake Dom Helvécio eight species (*Closterium aciculare, Cosmarium bioculatum, C. contractum, C. tinctum, Staurastrum laeve, S. omeari, S. rotula* and *S. smithii*) of Desmidiales reached high numbers or biomass. These abundant species varied in size by a range of two orders of magnitude: the smallest one, *Staurastum smithii*, has a volume of 236 μm^3 while *Staurastrum rotula* is 29,100 μm^3 in size.

The vertical structure of phytoplankton in summer (stratified period) in many of the Rio Doce lakes is very characteristic: planktonic desmids dominate (and in some of them dinoflagellates contribute significantly) in the epilimnion and a deep-layer maximum (which is much wider than steep gradients in temperate deep lakes) is formed by cyanoprokaryota in the metalimnion.

As was noted by REYNOLDS et al. (1983), Lake Carioca supports a dense deep-layer maximum of cyanoprokaryotes, with a *Limnothrix*-like densely vacuolated species being the most abundant (Fig. 3A). Although the species number of desmids was high, they contributed less to the total biomass along the water column. In the epilimnion of Lake Dom Helvécio desmids were the most abundant (Fig. 3B), cyanoprokaryota were represented by several species, among which was *Cylindrospermopsis cuspis*. Although in this oligotrophic lake the metalimnetic maximum was not as sharp as in Lake Carioca, it was present at water depths of about 9 m and was formed almost exclusively by *C. raciborskii* (BARBOSA & PADISÁK 2001).

Deep-layer maxima of cyanoprokaryotes

The development of deep-layer maxima of cyanoprokaryotes is relatively easy to explain based on hydrological features, vertical structures of the light field and chemical gradients. As calculated from data by HENRY et al. (1987), HENRY & BARBOSA (1989) and REYNOLDS (1989, 1997a), the extent of net warming from

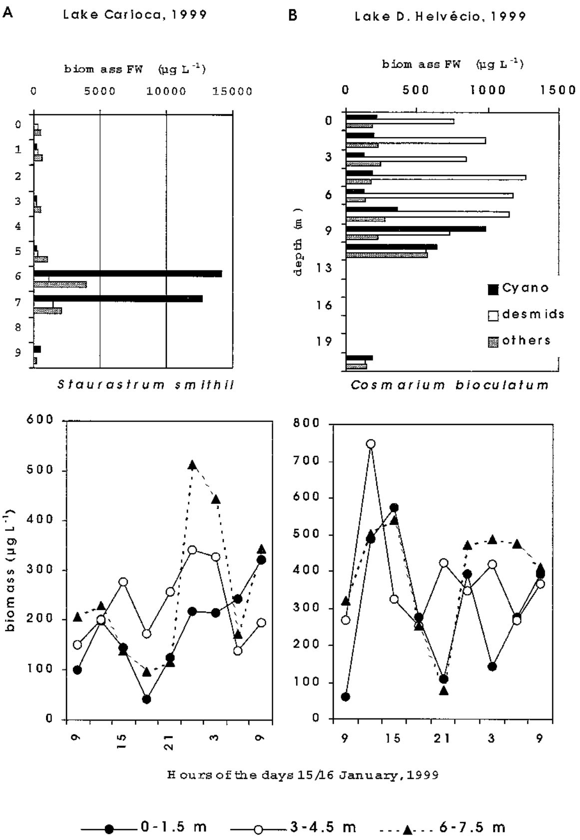

Fig. 3. (Upper two graphs) Vertical distribution of biomass (µg/L) of three main groups of phytoplankton on (A) 15/16 January 1999 in Lake Carioca and (B) 11/12 January 1999 in Lake Dom Helvécio. (Lower two graphs) Biomass changes of *Staurastrum smithii* and *Cosmarium bioculatum* on 15/16 January 1999 in three different layers of the epilimnion of Lake Dom Helvécio.

August to February, combined with the morphological features and the wind regime of these lakes, allows the development of a stable thermocline with a metalimnetic temperature gradient of about 8 °C in the summer period. Below the mixed layer, the lake is stable enough to support deep layer phytoplankton maxima. Another essential requirement is that the euphotic depth should extend through the mixing depth, which is also given in these lakes. Furthermore, algae must have some 'benefit' from living in a rather dark and, from time to time (days with cloudy sky), light-limited environment: this benefit can be traced in chemical gradients. According to the data in Table 1, P-limitation in Lake Carioca is not very likely or at least not very severe; however, there is a scarcity of inorganic N sources, and therefore phytoplankton growth in the epilimnion is probably N-limited. This does not hold for the metalimnion, with NH_4^+ concentrations between 1025.3 and 1640.2 µg/L (data for 1999). A similar situation exists for Lake Dom Helvécio (see data in Table 1) except that, based on the inorganic P concentration, a combined N + P limitation may be a possibility in the epilimnion.

In order to explain the dominance of non-motile, and therefore turbulence-dependent desmids in the epilimnion, the term '*partial atelomixis*' can be introduced.

Atelomixis and partial atelomixis

Atelomixis sensu LEWIS (1973) has been a complete atelomixis (the lake stratifies and destratifies from surface to bottom within 24 h) and can be observed only in tropical winter periods when no permanent thermocline can establish. Considering that in many tropical lakes a permanent thermocline develops during the summer period, complete atelomixis cannot occur during this time. However, the main driving force (large daily variation of air temperature) prevails and so an extension of atelomixis can establish during the stratified periods. The phenomenon (see diurnal development of temperature profiles, Figs. 1 and 2) can be described best as partial atelomixis, meaning that diurnal mixing is restricted to the epilimnion since normally a primary thermocline prevents it from proceeding downwards. Partial atelomixis is commonly observed worldwide within tropical lakes (e.g. TALLING & LEMOALLE 1998).

The results recorded in the stratified periods of both 1999 and 2000 for Lakes Carioca and Dom Helvécio represent clear examples of partial atelomixis. Daily air temperature variations recorded in February 2000 were large in both diel studies (23–34 °C during the Lake Carioca diurnal study and 23–34 °C during the Dom Helvécio study). Furthermore, during these periods both lakes remained stratified during the 24-h periods of the study and thermal instability could only be seen within the upper layers during the night periods, thus demonstrating the onset of partial atelomixis.

Ecological relevance of partial atelomixis

Little has been known about the ecological relevance of either complete or partial atelomixis. REYNOLDS (1997a) pointed out that the distribution of desmids in the lake at the beginning of March (start of isothermal conditions) cannot be explained without assuming a recent or a frequent intervention of intermittent mixing (atelomixis), and TALLING & LEMOALLE (1998) intuitively suggested that atelomixis, through shaping the thickness of the epilimnion and affecting nutrient return, might have some ecological relevance.

Partial atelomixis represents a robust water movement within the epilimnion; it occurs regularly, moreover, its scale is shorter than the lifetime of most phytoplankton species. This means that this hydrodynamic process must be a key factor in keeping in epilimnetic suspension all those phytoplankton species whose daily sinking amplitude, on average, is smaller than the thickness of the epilimnion.

A particular feature of many tropical waters is that, among the phytoplankton, desmids are the major non-motile group, which is not the normal situation among temperate waters where desmids are often an insignificant group during the stratified period. In Lakes Carioca and Dom Helvécio, as well as in many other lakes in the middle Rio Doce area, this group is abundant and frequently dominates within the epilimnion.

From an ecological point of view, the most interesting aspect is how a non-motile group can be dominant during the stratified period. This is particularly applicable for the desmids, since they are the heaviest algae after diatoms. For example, a specific density of 1.067 g/cm^3 was found for *Cosmarium* sp., which is only slightly lower than that of the lightest diatoms (>1.08 g/cm^3) and much higher than that of the lightest green algae, for example *Pandorina morum* (1.019 g/cm^3) (PADISÁK in press).

Moreover, according to the Stokes equation (WETZEL 2001), further aspects to consider are the viscosity of the water, and the cell form resistance factor. Despite the lack of specific data on the latter for the involved species, it is reasonable to suppose that the form resistance factor of desmids, with their 'complicated' shape, is higher than that of the much simpler diatoms, thus decreasing terminal sinking velocities. Furthermore, epilimnetic water temperature can reach ca. 34 °C during summer and this will decrease the viscosity of the water by ca. 40–50% as compared with temperate waters when diatoms are dominant and this results in faster sinking. The latter factor leads to increased terminal sinking velocities.

It would be reasonable to demonstrate the role of atelomixis in keeping desmids in suspension, using temperature and Desmidiales quantitative data from studies in Lake Dom Helvétio in 1999 or 2000. Despite many trials and, in particular, because of confusing results in the uppermost (1–3 m) layers, it was not possible to carry out such an analysis for desmids as a group. This can be attributed to several reasons: wind-induced daytime mixing and waves may interfere with the mixing pattern deriving from partial atelomixis; horizontal water currents may impose further 'stochasticity' upon the process; for many species statistically reliable counting is difficult; net growth of algal species, as well as loss by grazing, interferes with sinking patterns; human disturbance (turbulence induced by motor-boats when sampling) can also be source of confusion, etc.

For the above reasons, *Staurastrum smithii* and *Cosmarium bioculatum* were selected to demonstrate the possible effect of partial atelomixis on the diurnal pattern of desmids (counting error for individual records in Fig. 4 is about 20% for these species).

The abundance of both species increased between 09:00 h and 12:00 h, which might be the combined effect of delayed upwelling drifting from deeper strata and division. However, between 12:00 h and approximately 18:00–21:00 h, a net decrease could be observed for each species, especially *Cosmarium bioculatum*. Daytime sinking can be traced in the *Staurastrum smithii* data: in the period between approximately 11:00 and 16:00 h, cell numbers were the lowest in the upper (1- to 1.5-m) layer, higher in the 3- to 4.5-m layer and highest in the 6- to 7.5-m layer. Complete nocturnal overturn (see Fig. 2) occurred in the early morning hours and was completed some time between 06:00 and 09:00 h. As data for *C. bioculatum* show, the population was evenly distributed in the water column at 09:00 h (end of observation period).

An unfortunate coincidence when demonstrating the effect of partial atelomixis was the fact that the sampling interval was a period when daytime primary production resulted in a considerable increase in cell numbers. Epilimnetic net growth rates on the day of the investigation were 0.79/day (*Staurastrum smithii*) and 0.53/day (*Cosmarium bioculatum*), which correspond to doubling times of 0.88 and 1.32 days, respectively. These records are among the fastest that can be observed in populations of phytoplankton species growing in natural conditions.

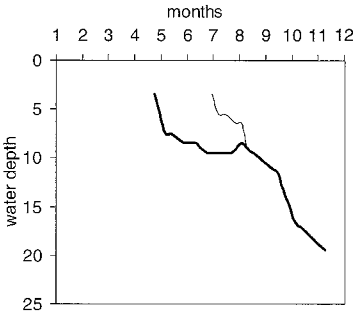

Fig. 4. Development of the main (thick line) and secondary (thin line) thermocline in Lake Stechlin (Germany) in 1994.

The main characteristics of the vertical structures (deep-layer maximum of cyanoprokaryota and non-motile desmids in the epilimnion) of phytoplankton in the investigated tropical South American systems are, therefore, paradoxical: one of the assemblages (deep layer assemblage) requires thermal stability and the other requires frequent (daily) mixing. These contrasting demands can be explained by the above-defined term, partial atelomixis.

Thus, atelomixis (both complete and partial) can play a key role in keeping these relatively heavy and non-motile algae suspended in the epilimnion of tropical lakes, allowing them to account for as much as 51% of total biomass, as recorded in more lakes than included in this study. Atelomixis has a profound impact on the formation of tropical phytoplankton communities.

Atelomixis in textbooks

From the point of view of hydrodynamics, atelomixis differs from the 'classical' stratification types that originate from convectional currents repeated daily, while all others originate from seasonality and wind-driven mixing. It was described by Lewis (1973), and, in theory, a quarter of a century represents sufficient time to introduce the term to basic education in limnology. This has not been done yet; instead, there is considerable confusion regarding descriptions and explanations of diurnal convectional currents and their role in lakes, whether the term 'atelomixis' is specified or not.

Atelomixis is not mentioned in POURRIOT & MEYBECK's (1995) "Limnologie Générale", and in none of the revised editions of WETZEL's (1975, 1983, 2001) "Limnology". In SCHWOERBEL's (1999) "Einführung in die Limnologie" atelomixis, as a term, is not introduced; however, the lake type "warm monomictic" is described for tropical lakes with frequent complete circulation if nocturnal cooling is strong ("warm monomiktisch: Tropenseen mit häufigen Vollcirkulationen bei stärkerer nähtlicher Abkülhung" page 55), which essentially corresponds to the description of atelomixis. The lakes discussed in the present paper can also be characterised as warm monomictic by the classical system. However, from the point of view of selection of phytoplankton assemblages, the atelomixis (both complete and partial) is probably equally important as, or even more important than, annual stratification patterns.

In LAMPERT & SOMMER's "Limnoökologie" (1993) and its English edition ("Limnoecology" 1997), atelomixis, as a terminus technicus, also has not been introduced, although it is roughly described as "This change between stratification and circulation that takes place on an annual cycle in the temperate latitudes can occur daily in shallow, tropical lakes. Very small temperature differences can sustain stable thermal stratification in warm, tropical lakes, since the relative density differences per degree temperature change are greatest at high temperatures. These lakes stratify during the day as the surface waters are heated, and each night, as the surface waters cool, the wind destratifies them" (p. 32–33 of the English edition and p. 43 of the German edition). A slight misunderstanding here can be traced to two points: one is that the phenomenon is not exclusive to tropical shallow lakes, and the other is that it is not the wind that leads to (complete or partial, epilimnetic) overturn during the night, but the heat loss and the consequent density increase in the surface layers. In addition to that, it is not the wind that destratifies the lake during the nights, as found by REYNOLDS (1997a), who explained that Lake Carioca ought to be isothermal throughout the year based on model assumptions by its depth, heat income, etc., and its stable stratification can develop only because it is surrounded by a dense forest that efficiently protects it from wind action.

The above misunderstanding is completely corrected in SOMMER's (1994) "Planktonologie" when describing polymictic lakes as "Anderseits tritt dieses Typ in tropischen Klimaten auf, wenn die Tagesamlitude starker ist als die Jahresamplitude. Dann bildet sich am Tag eine thermische Schichtung aus, während es in der Nacht zur konvektiven Durchmischung kommt" (p. 61). Nevertheless, atelomixis, as a term, is not mentioned in this book.

BOULTON & BROCK's (1999) recently published "Australian Freshwater Ecology: Processes and Management" does not contain the term 'atelomixis'; however, polymictic lakes are defined as "Polymictic (poly, many). Explanation: Mix often, sometimes continuously. Stratify in response to diel temperature changes. Examples: Common in arid Australia in shallow basins that cool at night and heat during the day" (page 30). The cause of atelomixis can be clearly traced here; however, it is restricted to shallow lakes. Moreover, wind-driven polymixis, the common case in temperate shallow lakes, is not even mentioned. It is hard to believe that only atelomixis would lead to polymixis in Australia. Wind-driven mixing must not be neglected at such a definitive way.

The effects of seasonal versus daily stratification can be clearly separated in temperate lakes during the period of the most stable stratification. It has been known for decades that in such periods if there is a long-lasting calm period with no (or minimal) wind a 'secondary thermocline' develops within the epilimnion (WETZEL 1975: 75, 1983: 81, 2001: 79); see also the example on Fig. 4 (Lake Stechlin, 53° N, Germany). In such a situation, the primary (main) thermocline designates the depth until wind-driven mixing can make the given layer (epilimnion) isothermal, while the secondary thermocline indicates the mixing capacity of convectional currents due to daily heating and nocturnal cooling (partial atelomixis). These examples extend the importance of partial atelomixis to higher latitudes, and its ecological significance for phytoplankton development is evident: in such periods turbulence-dependent re-occurrence of planktonic diatoms cannot be expected (since hypolimnion with inocula are physically well separated from the upper layer mixed by convectional currents); rather, the assembly of phytoplankton is driven towards species with excellent floating abilities (large flagellates, buoyant cyanoprokaryota).

In his detailed textbook "Limnología" MARGALEF (1983) similarly did not mention atelomixis although he explained the limited thermal instability of the surface layers as being due to the prevalence of small vertical temperature differences that would allow the lake to circulate only near to the surface, sometimes every night, as for example Lakes Ukerewe and Valencia. Accordingly, such stability is more a consequence of dissolved organic material in deep waters than temperature differences: "En los grandes lagos tropicales las diferencias verticales de temperatura son muy pequeñas y el lago circula verticalmente en un espesor limitado, cerca de la superfície, a veces cada noch (por ejemplo, el Ulerewe y el Valencia hasta los 20 m). La estabilidad, más que a diferecias de temperatura, puede deberse a la presencia de material disuelto u organico en profundidad" (p. 100).

Similarly, ESTEVES (1988) in his "Fundamentos de Limnologia", without mentioning atelomixis provides a clear explanation of this stratification pattern (p. 138) as "Durante o período de estratificação térmica pode ocorrer a formação de várias termoclinas. Este fenômeno pode ocorrer em qualquer latitude. Sua origem está ligada a três fenômenos principais: 1°) o não estabelecimento muito acentuado da termoclina original; 2°) à força dos ventos que não são suficientemente fortes para movimentar toda a massa d'água que comprende o epilímnio; e 3°) perdas acentuadas de calor a partir da superfície para atmosfera durante a noite". In this chapter, the author not only discussed the known causes for atelomixis (weak main thermocline, wind action, and heat loss through the surface) but also cited the work of LEWIS (1973) in Lake Lanao in order to explain the onset of daily thermoclines, also using the example of Lake Carioca (south-east Brazil) described by BARBOSA & TUNDISI (1980).

It is likely that TALLING & LEMOALLE's (1998) "Ecological Dynamics of Tropical Inland Waters" has been the only widely used review in which 'atelomixis' can be found in the index. The process is dealt with in the section (p. 202–203) dealing with patterns of environmental change within time, and repeats the original description of atelomixis, indicating its worldwide (tropics) importance in many kinds of lakes. However, in the section "Phytoplankton: Diel variability" (p. 261–262) no reference is provided to atelomixis as a mixing pattern that may keep non-buoyant and non-motile species (such as diatoms, desmids and many Chlorococcales) in suspension, and thus being a major factor in tropics for species selection and assembly of phytoplankton.

CASADO-SANCHO (2001) in her "Glosarío de limnologia" describes atelomixis as "mezclado vertical incompleto de masas de aguas estratificadas homogeneizando capas de propiedades químicas diferentes sin perturbar el hipolimnion. Típico de lagos tropicales" which corresponds to the description of partial atelomixis used herein.

Atelomixis cannot be found in REYNOLD's (1997b) "Vegetation Processes in the Pelagic: a Model for Ecosystem Theory" as it is not a textbook, and consequently has no index. However, atelomictic lakes are described as essentially polymictic systems (p. 45); moreover, the ecological importance of atelomixis for phytoplankton is mentioned and graphically demonstrated in the section "Development of Pelagic Plant Populations" (p. 137 and 139).

Conclusions

As indicated above, there appears to be considerable confusion surrounding atelomixis and its ecological significance, and even its recognition worldwide is doubtful. This is certainly due to the fact that this term is absent from the widely used textbooks or monographs. A possible explanation for this lack of acceptance possibly lies in the fact that atelomixis is essentially a tropical phenomenon and so far has been demonstrated in only a few lakes. On the other hand, given that it is a macroclimate-driven phenomenon, it must have an overall importance within the tropical regions, acting similarly in stratified lakes of different sizes.

As demonstrated in this study, desmids can be seen as the 'diatoms' of the temperate lakes, a group that can remain in suspension only if the mixing depth and frequency are considerable. Nonetheless, when compared to the huge body of ecological knowledge about diatoms, knowledge has been very limited about other adaptive features (nutrient uptake kinetics, light/shade preferences, avoidance of grazing, etc.) of desmids. At an evolutionary scale, the hypothesis that atelomixis has been a driving force for evolutionary speciation of planktonic Desmidiales is proposed.

Phytoplankton, as the major primary producers, have a basic role in aquatic ecosystems. The composition and structure are very likely influenced by atelomixis, which as a mixing event, acts within the lifetime of individual species. Therefore, through the phytoplankton, atelomixis may affect entire food chains and thus interfere with most ecological processes within aquatic ecosystems. In conclusion, its recognition as an important phenomenon deserving to be recognised and accepted as a separate mixing pattern is strongly argued.

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References

BARBOSA, F. A. R. & TUNDISI, J. G., 1980: Primary production of phytoplankton and environmental characteristics of a shallow quaternary lake at eastern Brasil. – *Arch. Hydrobiol.* **90**: 139–161.

BARBOSA, F. A. R. & PADISÁK, J., 2001: Algumas considerações sobre desenho amostral para estudos de longa duração. [Some considerations on sampling design for long-term studies] – In: BICUDO, C. E. M. & BICUDO, D. C. (eds): *Amostragem em limnologia.* – Maringá: Editora da Universidade Estadual de Maringá. p. 00–00. (in press)

BOULTON, A. J. & BROCK, M. A., 1999: *Australian Freshwater Ecology: Processes and Management.* – Gleneagles Publishing, Glen Osmond.

CASADO-SANCHO, C., 2001: Glosarío de Limnologia. Universidad Autónoma de Madrid, http://www.adi.uam.es/~ccasado/8limnologia.html

ESTEVES, F. A., 1988: *Fundamentos de Limnologia.* Editora Interciência Ltda, Rio de Janeiro.

GOSSELAIN, V. & HAMILTON, P. B., 2000: Algamica: Guide Manual. Version 4.0 for PC Computers. – *Hydrobiologia* **438**: 139–142.

HENRY, R. & BARBOSA, F. A. R., 1989: Thermal structure, heat content and stability of two lakes in the National Park of Rio Doce Valley (Minas Gerais, Brazil). – *Hydrobiologia* **171**: 189–199.

HENRY, R., TUNDISI, J. G., CALIJURI, M. DO D. & IBAÑEZ, M. DO S. R. DE, 1987: A comparative study of thermal structure, heat content and stability during summer in three lakes of the Rio Doce Valley Park (Minas Gerais, Brazil). – In: SAIJO, Y. & TUNDISI, J. G. (eds.): *Limnological Studies in the Rio Doce Lakes and Pantanal Wetland, Brazil* (2nd Report): 15–20 – Water Research Institute, Nagoya.

HUTCHINSON, G. E., 1957: *A Treatise on Limnology, Vol. 1*, part 1. – Wiley.

HUTCHINSON, G. E. & LÖFFLER, H., 1956: The thermal classification of lakes. – *Proc. Natl. Acad. Sci. U.S.A.* **42**: 84–86.

LAMPERT, W. & SOMMER, U., 1993: *Limnoökologie.* – Thieme, New York.

LAMPERT, W. & SOMMER, U., 1997: *Limnoecology: the Ecology of Lakes and Streams.* – Oxford University Press, New York, Oxford.

LEWIS JR., W. M., 1973: The thermal regime of Lake Lanao (Philippines) and its theoretical implications for tropical lakes. – *Limnol. Oceanogr.* **18**: 200–217.

MARGALEF, R., 1983: *Limnología.* – Ediciones Omega, S. A. Barcelona.

PADISÁK, J., in press: Chapter 10. The Phytoplankton. – In: O'SULLIVAN, P & REYNOLDS, C. S. (eds): *The Lakes Handbook.* – Blackwell Science Ltd. Oxford.

POURRIOT, R. & MEYBECK, M. (eds), (1995): *Limnologie Générale.* – In: *Collection d'Ecologie* 25 – Masson, Paris.

REYNOLDS, C. S., 1989: Physical determinants of phytoplankton succession. – In: SOMMER, U. (ed.): *Plankton Ecology*: 9–56. – Brock/Springer, Madison.

REYNOLDS, C. S., 1997a: On the vertical distribution of phytoplankton in the middle Rio Doce Valley Lakes. – In: TUNDISI, J. G. & SAIJO, Y. (eds): *Limnological Studies on the Rio Doce Valley Lakes, Brazil*: 227–241. – Brazilian Academy of Science, São Carlos.

REYNOLDS, C. S., 1997b: *Vegetation Processes in the Pelagic: a Model for Ecosystem Theories.* – Ecology Institute, Oldenburg/Luhe.

REYNOLDS, C. S., TUNDISI, J. G. & HINO, K., 1983: Observations on a metalimnetic Lyngbya population in a stably stratified tropical lake (Lagoa Carioca, Eastern Brazil). – *Arch. Hydrobiol.* **97**: 7–17.

SALAS, H. J. & MARTINO, P., 1991: A simplified phosphorus trophic state model for warm-water tropical lakes. – *Water Res.* **25** (3): 341–350.

SCHWOERBEL, J., 1999: *Einführung in die Limnologie.* – Gustav Fischer, Stuttgart.

SOMMER, U., 1994: *Planktonologie.* – Springer, Berlin.

TALLING, J. F., 1965: Comparative problems of phytoplankton production and photosynthetic activity in a tropical and a temperate lake. – *Mem. Ist. Ital. Idrobiol. Suppl.* **18**:

399–424.

TALLING, J. F., 1969: The incidence of vertical mixing, and some biological and chemical consequences in tropical African lakes. – *Int. Ver. Theor. Angew. Limnol. Verh.* 17: 998–1012.

TALLING, J. F. & LEMOALLE, J., 1998: *Ecological Dynamics of Tropical Inland Waters.* – Cambridge University Press, Cambridge, UK, 441 p.

THIENEMANN, A., 1925: *Die Binnengewässer Mitteleuropas.* – Das Binnengewässer 1. Verlag Schweizerbart, Stuttgart.

WETZEL, R. G., 1975, 1983: *Limnology.* – W. B. Saunders Company, Philadelphia, London, Toronto.

WETZEL, R. G., 2001: *Limnology: Lake and River Ecosystems.* 3rd ed. – Academic Press, San Diego.

YOSHIMURA, S., 1936: A contribution to the knowledge of deep water temperatures of Japanese lakes. Part I. summer temperatures. – *Jpn. J. Astron. Geophys.* 13: 61–120.

Authors' addresses:

F. A. R. BARBOSA, Department of General Biology, Federal University of Minas Gerais. P. O. Box 486, 30161-070 Belo Horizonte, Minas Gerais, Brazil.
E-mail: barbosa@mono.icb.ufmg.br

J. PADISÁK, Institute of Biology, Veszprém University, Veszprém, H-8200 Veszprém, P. O. Box 158, Hungary.
E-mail: padisak@tres.blki.hu