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One year weekly dynamics of limnological conditions and phytoplankton in Lake Bonilla, Costa Rica

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Abstract: The detailed response of tropical lake phytoplankton to weather variations has been little studied, but it seems that composition varies in response to rain and wind variability over the course of the year. In order to gather more evidence on this variation, the weekly variability of phytoplankton composition was studied in Lake Bonilla, a low land (380 masl) 30 m deep tropical lake, from April 2010 to May 2011. Temperature variation at several depths was recorded automatically, and measurements of dissolved oxygen, water transparency, and nutrients were performed several times during the study period. The lake showed a warm monomictic pattern, with deep mixing occurring during the hemispherical winter, especially after a heavy rain period in December 2010. Phytoplankton was dominated by a few species: a colonial Cyanobacteria (*Aphanocapsa* sp., functional group F) and two colonial Chlorococcaceae (*Botryococcus braunii* and *Eutetramorus tetrasporus*, both in the functional group K). Their relative dominance shifted throughout the year, following changes in water column conditions in response to weather variations. Although changes in main functional groups indicate a shift in resource availability rather than energy, it was clear that attention should also be given to particular species adaptations beyond those used for establishing functional groups. Rev. Biol. Trop. 64 (4): 1771-1781. Epub 2016 December 01.

Key words: phytoplankton, tropical lakes, seasonality, functional groups, Costa Rica.

Lakes throughout the world respond to weather conditions (Wetzel, 2001). Although tropical regions are characterized by low variations in mean daily temperature during the year, they do demonstrate seasonality with respect to wind conditions and precipitation (Laporte, Rodríguez, & Sibaja, 1976; Coen, 1991) even though the timing and strength of the weather conditions might vary from year to year (Hidalgo, Durán-Quesada, Amador, & Alfaro, 2015). These two factors are the main drivers of lake mixing and stratification in tropical regions (Lewis, 1996; Roldán-Pérez & Ramírez-Restrepo, 2008). Mixing generally occurs at the time of the hemispherical winter period (Lewis, 1996) due to the influence of trade winds. In turn mixing events might influence the temporal dynamics of limnic inhabitants such as phytoplankton. In particular, the morphology of phytoplankton microalgae is considered one of their adaptations to environmental conditions in the pelagic habitat of lakes and oceans (Margalef, 1978; Reynolds, 1996; Padisak, Crossetti, & Naselli-Flores, 2009).

Several studies have documented the occurrence of mixing in neotropical lakes (Gunker & Casallas, 2002; Román-Botero, Gómez-Giraldo, & Toro-Botero, 2013; Umaña, 1993; Umaña, 1997; Umaña, 2006; Umaña, 2014). Although some authors have hypothesized that tropical phytoplankton should mimic the temporal variation that occurs seasonally in temperate lakes but on a shorter time schedule (Lewis, 1978; Lewis, 1986), few studies have been performed to address this suggestion. In particular, tropical lakes lack some of the most common forms that occur in temperate lakes, such as the bigger *Daphnia* species

(Fernando, 1980). Furthermore, key species in tropical lakes might not respond in a similar way, as those in lakes farther from the Equator. In a recent study on Lake Fraijanes, Umaña (2014) found that phytoplankton composition shifts seemed to follow and respond to weather conditions that affected this small lake. The sequence did not resemble the well-known seasonal pattern described, for example, by the PEG model in the 1980's (Sommer, Gliwicz, Lampert, & Duncan, 1986). In a recent review (Sommer et al., 2012), the authors expand the PEG model and include additional cases, recognizing that patterns of sequences of plankton seasonal dynamics depend on lake conditions such as eutrophic state, maximum depth and persistence of fish predation throughout the year. They also acknowledge the occurrence of year-to-year variation depending on survival of species at critical times of the year, such as winter for temperate lakes.

In this study the daily variations in temperature and weekly variations in phytoplankton composition were followed for a year in Lake Bonilla. This lake is located at middle elevation and is deep enough to stratify for several months during the year, though it mixes seasonally between November and February (Umaña, 1997). Phytoplankton species composition is expected to change according to seasonal changes in the water column condition as it is influenced by weather variations. These changes in species composition should follow a predictable pattern according to their morphological adaptations, sensu Reynolds (1984) and Padisak et al. (2009).

MATERIALS AND METHODS

Lake Bonilla is located in the Southern downslope of Turrialba Volcano, Costa Rica, at 380 masl. It has a surface area of 30.79 hm^2, maximum depth of 27 m and mean depth of 10.2 m. Its relative depth is 4.31, which gives it a deep characteristic. It has no surface inflow but a surface out flow at its Northeast end (Mora, 1989) (9.994444° N and 83.603889° W).

On April 30^{th} 2010 a set of data loggers for temperature (Hobbo ® Water Temp Pro v2 onsetcomp.com) were suspended on a buoy moored with two anchors at the deepest point in the lake. Data loggers were placed at different depths (0; 2; 5; 10; 15; 20 and 25 m), and configured to register every hour. Data were downloaded in December 2010 and May 2011. Weather data was provided by the National Meteorological Institute (IMN for its name in Spanish) for the station located at the CATIE campus, near Turrialba (9.891394° lat. N and 83.652978° long. W).

Phytoplankton samples (100 mL) were taken every week during the same period with the assistance of a local farm worker. Samples were preserved with acidic Lugol's solution. A 50 mL aliquote per sample was settled for counting with an inverted Olympus microscope (Model IX51) according to the Utermöhl method. A total maximum count of 100 units per taxa was performed; those taxa with lower abundance were counted until 100 optical fields were observed at the highest magnification (100X submersible objective). Species were identified to the maximum possible level with available literature (Huber-Pestalozzi, 1955, Huber-Pestalozzi, 1968; John, Whitton, & Brook, 2005; Komárek, 1983; Wehr & Sheath, 2003) and web resources (www.algaebase.org). All phytoplankton species were assigned a functional group (FG) according to Reynolds (2006) classification, since it gives a better insight into the strategies followed by different phytoplankton species, rather than the recent system developed by Kruk et al. (2010) that takes into account only the morphological features.

A cluster analysis among the samples using the UPGMA clustering technique on the Bray-Curtis similarity values was performed with the five most abundant species, to evaluate phytoplankton species composition variation patterns. Correlation analysis was performed as an exploratory examination for relationships among several variables: temperature at 2 m (T2m), difference in temperature between 2 m and 10 m (Diff2-10m) as a surrogate index of water stratification status, precipitation on the date (Pptn), accumulated precipitation for the previous seven days (Pptn7d), minimum (Tmin), maximum (Tmax) and mean (Tmean) daily temperatures from the IMN weather station, and abundance of the five most dominant phytoplankton species, which were log transformed to adjust for normality. Later a Canonical Correlation Analysis was carried out with temperature at 2 m (T2m), temperature difference between 2 m and 10 m (Diff2-10m), and precipitation of the previous week (Pptn7d) as environmental variables, and the log-transformed abundance of the three most dominant species.

During several visits to the lake (July 24, 2009; April 30, 2010; June 22, 2010; August 27, 2010; September 24, 2010; December 15, 2010; February 25, 2011; and May 15, 2011) nutrients and chlorophyll *a* samples were taken at different depths, together with Secchi depth readings. A factor of 1.9 between Secchi depth and euphotic depth was assumed based on Kalff's (2002) review of the relationship for clear water lakes, such as Bonilla, in order to estimate the relationship between mixing and euphotic depths.

RESULTS

Temperature: Surface temperature was not recorded due to a failure of the data logger soon after its deployment. A few surface temperature data were obtained during field trips along the year (Fig. 1A), and it was possible to reconstruct a series of surface temperature by regression analysis between values at 0 m and 2 m from the field trips. Nevertheless,

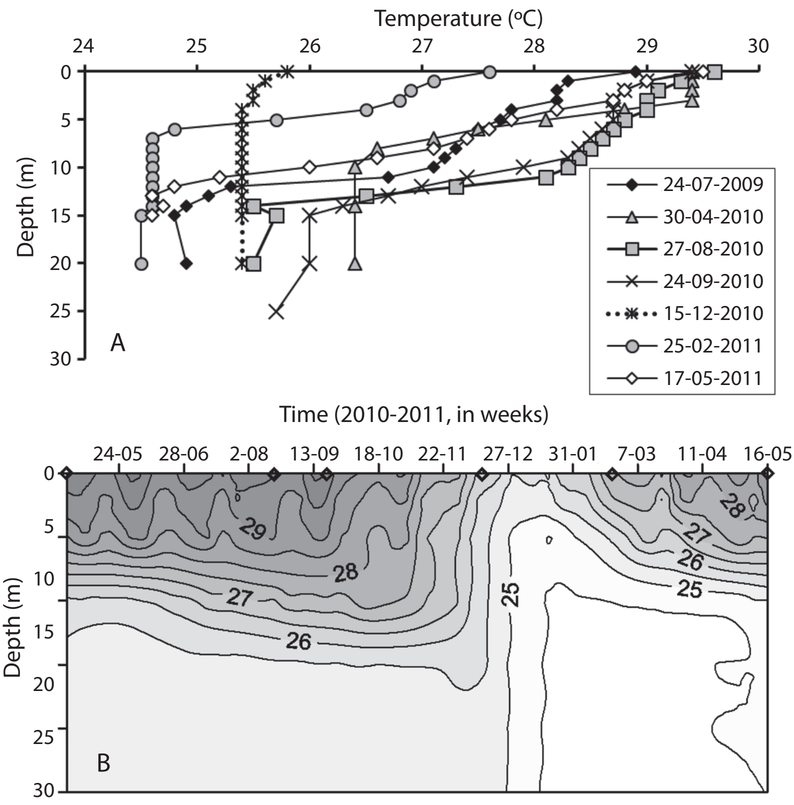

Fig. 1. A. Vertical profiles of temperature measured at the deepest point in Lake Bonilla for selected dates. **B.** Isotherms at Lake Bonilla from the data of the data loggers. Surface data was estimated with weather data from the nearest lake station, and based on the surface temperature (measured at midday on each visit to the lake).

this series is used only in figure 1B and all further analyses were performed with data from the 2 m logger. At 2 m, temperature fluctuated between 24.5 and 30.4 °C, with a mean of 27.95 ± 1.41 °C. At 5 m of depth, the temperature also fluctuated over a wide range between 24.4 and 29.5 °C, with a mean of 27.37 ± 1.46 °C. At 25 m of depth, the fluctuations were smaller, between 24.2 and 25.4 °C, with a mean of 24.97 ± 0.40 °C. Vertical profiles performed during visits to the lake showed that the lake was stratified on most occasions, with a thermocline between 8 and 15 m (Fig. 1A), although in April 2010, the thermocline was between 3 m and 8 m. In December 2010, the lake was almost homeothermal and in February 2011, the thermocline was developing again close to the surface. The data loggers showed that the lake remained stratified from April 2010 until early November 2010. At this time, the thermocline started to erode and by December 2010 the lake was homeothermal and mixing. Mixing continued until the end of February 2011, after which the stratification started to develop again (Fig. 1B).

Other observations: Daily weather data (daily temperature and mean temperature) from station No. 73010 located at CATIE campus in Turrialba, provided by the National Meteorological Institute (IMN) is summarized in figure 2A for the study period. Dissolved oxygen fluctuated between the low value of 0.65 mg/L at the surface in December 2010, up to 8.53 mg/L at 2 m depth in February 2011. Depth profiles of dissolved oxygen showed a marked oxycline between 5 and 10 m depth (Fig. 2B), with small fluctuations during most of the year at the epilimnion, except for December 15th 2010. Secchi depth varied between 1.6 and 2.5 m with no clear temporal trend. That means that mixing depth is greater than euphotic layer in this lake, and the ratio of euphotic depth to mixing depth

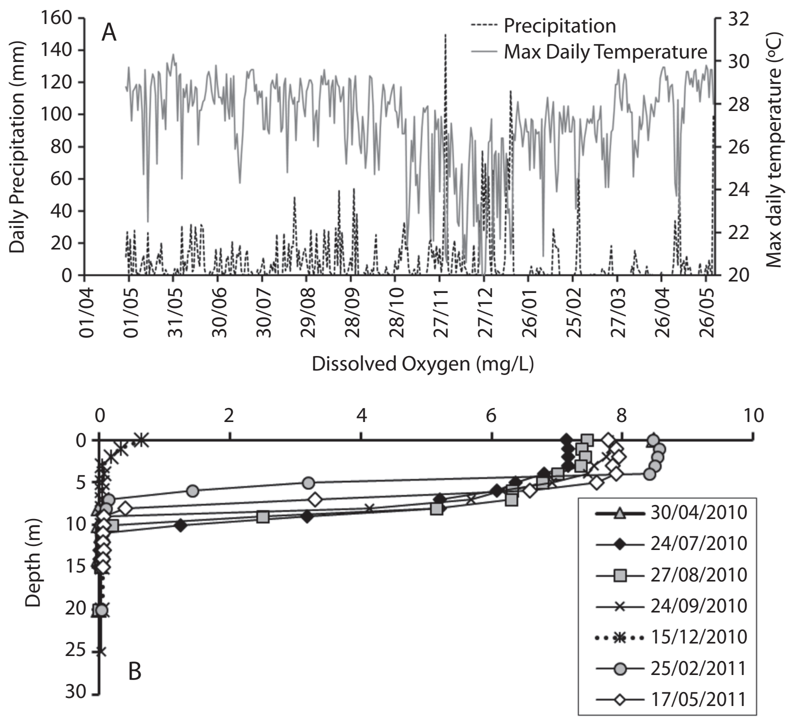

Fig. 2. A. Daily precipitation and mean temperature from station No. 73010, CATIE, Turrialba. **B.** Vertical profiles of dissolved oxygen at the deepest point in Lake Bonilla at selected dates.

varied between 0.1 when it overturned up to 0.6 especially during stratified periods.

The concentration of dissolved nitrogen inorganic forms were usually below the detection level (Table 1) in the epilimnion, and all three forms usually reached higher values below 10 m depth. The highest nitrate concentration was 25.9 µmol/L at 15 m in September 2010. Ammonium showed its highest value of 180.5 µmol/L at 15 m in September 2010. Nitrite was always below 0.5 µmol/L and reached a maximum value at the surface in August 2010. Phosphate was always detectable, with values from 0.03 up to 8.5 µmol/L, with a tendency to be higher below the thermocline. The exception occurred in December 2010, when all nutrients values were nearly homogeneous throughout the water column, since the lake was mixing at that time.

Phytoplankton: Phytoplankton species diversity was rich, with 92 different taxa. Dominant species nevertheless were only five: *Aphanocapsa* sp. (Cyanobacteria), *Botryococcus braunii* Kützing, *Eutetramorus tetrasporus* Komárek, *Oocystis lacustris* Chodat and *Chlorella* sp. (Chlorophyta) (Table 2). These five species explained most of the variation among dates (93.8 % according to SIMPER analysis), and the formation of two groups of sampling dates along the year in the cluster analysis, according to their relative contribution (Fig. 3A). *Aphanocapsa* was the dominant species of the first group, followed by *B. braunii*, it extended from April 2010 until mid December. Dominance of *E. tetrasporus* characterized the second group, which extended until middle May, when sampling was completed. Correspondence analysis with these five most common species also recognized two groups. However, both of these groups could be further divided on the grounds of the relative dominance of *Aphanocapsa* with respect to its codominant species. During the first period,

TABLE 1
Nutrient concentrations (µmol/L) in Lake Bonilla, Costa Rica (2010-2011)

	27/08/2010	24/09/2010	15/12/2010	25/02/2011	17/05/2011
Nitrate					
Upper	0.45	11.15	0.00	0.00	0.00
	0.00 - 1.36	0.00 - 21.79	0.00 - 0.00	.00 - 0.00	0.00 - 0.00
Lower	4.86	14.91	0.91	2.64	0.00
	4.35 - 5.39	0.00 - 25.94	0.00 - 2.72	0.00 - 5.42	0.00 - 0.00
Nitrite					
Upper	0.42	0.00	0.00	0.00	0.10
	0.34 - 0.53	0.00 - 0.00	0.00 - 0.00	0.00 - 0.00	0.00 - 0.17
Lower	0.10	0.00	0.00	0.33	0.10
	0.00 - 0.38	0.00 - 0.00	0.00 - 0.00	0.21 - 0.47	0.00 - 0.19
Ammonium					
Upper	4.86	0.00	6.13	0.00	0.00
	0.00 - 13.17	0.00 - 0.00	5.65 - 6.61	0.00 - 0.00	0.00 - 0.00
Lower	7.33	114.77	5.87	12.37	0.00
	4.74 - 10.19	3.10 - 180.47	5.61 - 6.30	8.11 - 18.69	0.00 - 0.00
Phosphate					
Upper	1.03	2.60	1.11	0.52	0.43
	0.61 - 1.66	2.41 - 2.86	1.09 - 1.12	0.52 - 0.52	0.41 - 0.46
Lower	1.84	5.96	1.19	1.50	1.74
	1.06 - 2.36	2.08 - 8.54	1.13 - 1.26	0.98 - 1.92	1.06 - 2.21

Mean values with range between minimum and maximum for two strata: Upper: above 10 m depth, and Lower: 10m depth and below.

TABLE 2
Correlation matrix among the main groups of phytoplankton and environmental parameters in Lake Bonilla

	Temp, (2m)	Dif2-10m	Pptn (7días)	Cyano	Chloro	Chryso	Crypto	Bacilla	Dinop	Euglen	Flagel
Temp, (2m)	1										
Dif2-10m	**0.60***	1									
Pptn (7dias)	**-0.32***	**-0.42***	1								
Cyano	-0.18	-0.002	0.04	1							
Chloro	**-0.63***	**-0.44***	0.03	0.05	1						
Chryso	0.12	0.15	-0.03	0.16	-0.16	1					
Crypto	0.23	-0.16	0.03	-0.04	0.02	0.01	1				
Bacilla	0.16	**-0.50***	0.18	0.03	-0.14	-0.01	**0.35***	1			
Dinop	0.05	**-0.52***	0.18	-0.03	0.08	-0.18	**0.55***	**0.52***	1		
Euglen	**0.43***	**0.52***	**-0.26***	0.17	-0.23	**0.30***	0.17	-0.15	**-0.29***	1	
Flagel	0.11	-0.02	**-0.36***	**0.29***	0.08	-0.05	-0.08	0.2	0.01	**0.27***	1

All phytoplankton data were transformed with ln (X+1). Pearson correlation index was applied for an exploratory examination of main tendencies; significant cases are marked with asterisks only as a guide.

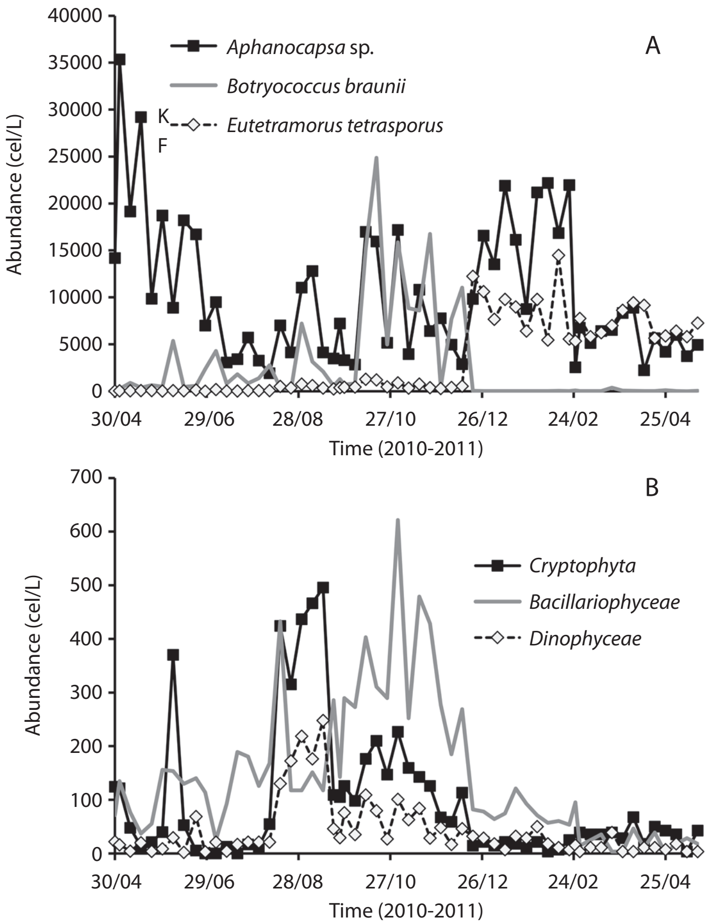

Fig. 3. A. Temporal variation of the three main phytoplankton species based on the weekly sampling at the surface of Lake Bonilla (2010-2011). **B.** Temporal variation of Cryptophyta, Bacillariophyta and Pyrrophyta at the surface of Lake Bonilla (2010-2011).

three subgroups were discernible: a first one, when *Aphanocapsa* had a high dominance over *Botryococcus*; a second one, when both were codominants; and a third, when *Botryococcus* increased in abundance and dominated over *Aphanocapsa*. The second group could also be divided in two, when *E. tetrasporus* replaced *B. braunii*. At first *Aphanocapsa* dominated over *E. tetramorus,* and later both codominated. Although *Aphanocapsa* was present throughout the study period, it did not contribute much to the separation of the two main groups. The analysis of other algal groups, such as Cryptophyta, Bacillariophyta and Pyrrophyta showed an increase from August to early November 2010. However, their abundance was much lower when compared to the dominant species (Fig. 3B).

The correlation analysis showed that temperatures from consecutive depths were positively correlated among them; and due to the lack of surface data as noted before, all further multivariate analysis were performed with the temperature at 2 m, and the difference in temperature between 2 m and 10 m depth as a surrogate of water column stratification status (Table 2). Precipitation of the previous week (Pptn7d) showed a stronger negative correlation with temperature difference between 2 m and 10 m depth (Diff2-10m) than precipitation of the same day. Among the five dominant species, *Aphanocapsa* showed no correlation with environmental variables, or with the other species included in the analysis. *B. braunii* showed positive relationships with temperature, whereas *E. tetrasporus*, *O. lacustris* and *Chlorella* showed a negative relationship with temperature. All these latter species were negatively related with Diff2-10 m. Only *Chlorella* showed a weak positive trend with the precipitation of the previous week. The canonical correlation analysis (CCA) confirmed the tendencies just described (Fig. 4). *B. braunii* was negatively correlated with *E. tetrasporus*, while, *Aphanocapsa* was not related to either of them. *E. tetrasporus* was negatively related to temperature, and *B. braunii* showed the opposing trend. *Aphanocapsa* was weakly and negatively related to the precipitation of the previous week and the difference of temperature between 2 and 10 m depth. *Chlorella* was positively related to Pptn7d and negatively to Diff2-10 m. Finally *O. lacustris* did not show any trend in the CCA analysis. Among the other groups analyzed, Bacillariophyta and Pyrrophyta were negatively correlated with Diff2-10m, and Cryptophyta showed only a weak correlation with temperature at 2 m (Table 2).

A total of 19 functional groups were identified, however, only five of the groups accounted for most of the abundance and are further described in what follows. The most abundant FG was Group K, mainly due to the dominance of the colonial Cyanobacteria *Aphanocapsa* sp. The second most abundant was Group F, to which belonged the colonial Chlorococcal algae such as *B. braunii* and *E. tetrasporus*. Other relevant FG's were Groups X1 to which *Chlorella* sp. belongs, as well as J and Y, but with much lower abundances. The temporal variation of FG's abundances is depicted in figure 5, as expected, the two main groups followed closely the variation shown by dominant species, but the other three groups follow

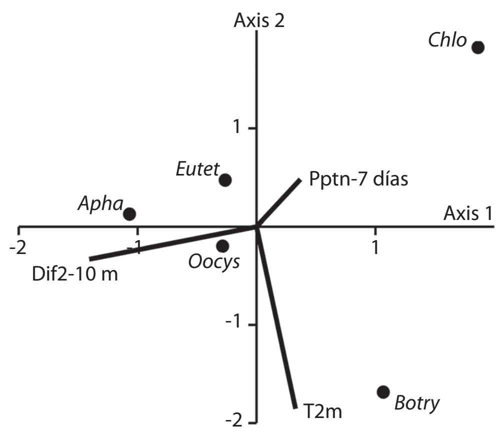

Fig. 4. Plot of the Canonical Correlation Analysis of phytoplankton and environmental variables. Chlo: *Chlorella* sp.; Eutet: *Eutetramorus tetrasporus*; Apha: *Aphanocapsa* sp.; Oocys: *Oocystis lacustris*; Botry: *Botryococcus braunii*; Pptn-7days: Precipitation in the previous 7 days, T2m: Temperature at 2m depth, Dif2-10m: difference in temperature between 2 and 10m depth.

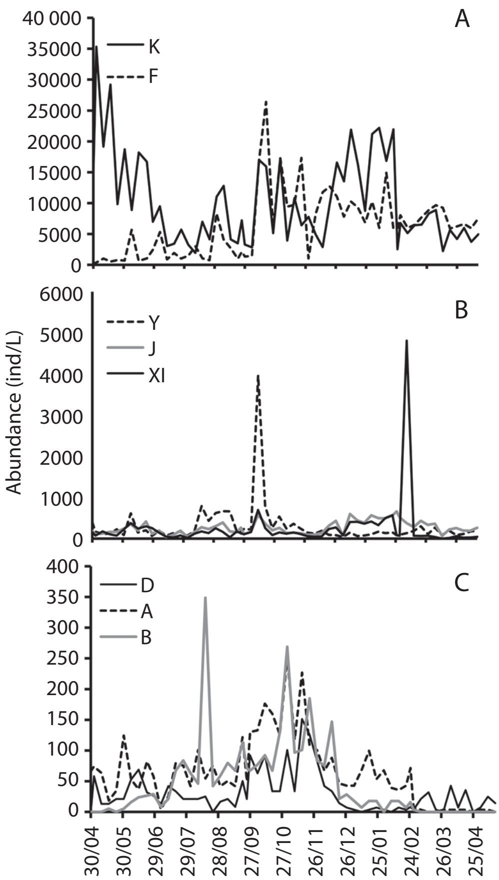

Fig. 5. Temporal variation of Functional Groups of phytoplankton in Lake Bonilla, Costa Rica, 2010-2011: **A.** Functional groups K and F. **B.** Functional groups Y, J and XI. **C.** Functional groups D, A and B.

a different pattern, some of them showing small increases just before or during the mixing event.

DISCUSSION

Lake Bonilla is located on the Southeastern side of the Turrialba volcano, in the Caribbean watershed of Costa Rica. The weather on this side of the country is characterized by a short dry period in February and March, and in some locations, there is no real dry season, rather a brief, less rainy period, coinciding with the lower temperatures occurring from November to February of the next year (Herrera, 1985). During this study, data from the meteorological national institute (IMN) showed that there were rainy days almost all year round, with a lower frequency between January and April 2011. Lower temperatures occurred between November 2010 and January 2010. This subtle seasonality was enough to produce a shift in the water column conditions of the lake, which was stratified until November, when surface temperatures started to decrease and the thermocline moved a little deeper in the water column. Complete mixing finally occurred in mid December, after several days of heavy rains during a cold spell. The mixing period was brief and stratification started to develop again in March. This behavior confirms the results of previous studies in the lake based on monthly or quarterly samplings (Mora, 1989; Umaña, 1997). It also agrees well with results from other tropical lakes, as summarized by Lewis (1996) and Roldán-Pérez and Ramírez-Restrepo (2008), who point out the occurrence of deep mixing in deep tropical lakes during the hemispherical winter. The deep mixing event in December also produced a pronounced reduction in dissolved oxygen in the upper water column, even at the surface. In addition, the sulfidic smell that was detected in previous samplings was not perceived at the time of the deep mixing event, nor during subsequent sampling events. Nutrient levels were distributed more evenly in the water column as well at this time. All of this information is indicative that a complete mixing of the lake was occurring. The ratio of mixing depth relative to water transparency in this tropical lake is an indication that photosynthesis was often light limited according to values suggested by Cloern (1987) and later confirmed by other researchers.

Phytoplankton composition also showed a shift in composition, and five periods were discernible. These groups correspond to different conditions of the water column. The first group coincides with a time of stable stratification and a thermocline located at a depth of 5 to 10 m. The second group began when the thermocline started to sink slowly by about one meter. The third group corresponded with the time of thermocline disruption and deep mixing, until complete overturn of the lake. The fourth group was in place when the lake started to warm again and developed a thermocline. The fifth group occurred when the lake was again stratified. Nevertheless, there are differences between the first and fifth groups, and this might be a result of the variation among years. Dominant groups at each stage of the cycle also conform to the expected response of phytoplankton functional adaptations. During the periods of stratification, the cyanobacteria *Aphanocapsa* (of the K functional group), was the dominant or codominant species, together with *B. braunii* (F functional group), both of which have adaptations to enhance buoyancy. During the deep mixing period *E. tetrasporus* (F functional group), a colonial green algae, became dominant. When stratification began to reestablish *Aphanocapsa* started to increase again and became codominant together with *E. tetrasporus*.

The shift from *B. braunii* to *E. tetrasporus* explained most of the observed variation in phytoplankton composition, although both were assigned to the same functional group. This difference can be the result of the stronger susceptibility of *B. braunii* to deep mixing like the one observed during the sampling period. Ramírez & Corbacho (2005) found that this species was negatively affected by light attenuation, such as occured during deep mixing periods. Both green colonial algae are non-motile but differ in the shape of their colonies and amount of mucilaginous cover, and perhaps also in their metabolism (specifically in their lipid accumulation). Happey-Wood (1988) suggested that non-motile Chlorococcaceae green algae need turbulence to sustain a sufficient growth rate to overcome sinking, as long as the mixing depth is less than the double of the euphotic zone, and gave, as an example, the colonial species *Sphaerocystis schroeteri*. Thus, there is a clear distinction between the different requirements of *B. braunii* and *E. tetrasporus*, which explained their temporal succession in Bonilla Lake. In this case, the use of Reynold´s functional groups did not perform well, since both species belong to the same category. A similar conclusion was reached recently by Salmaso, Naselli-Flores & Padisak (2014) where they warn about the misuse of functional groups without taking into consideration the species identity, since classification criteria distinguishing functional groups might not include all ecological variation that exist among different species sharing similar morphologies. Yet, the functional classification gives a broad view of the successional events in this tropical lake, where the two main FGs show a shift between S (Stress tolerants) and C (Competition) strategies, as proposed by Reynolds (1996, 2006) following Grime's (1977) criteria. This is an indication that in this tropical lake a shift in resource availability is more influential than a shift in energy levels in terms of light. This general finding agrees with a previous work in this lake, where a shift from N to P limitation of phytoplankton has been noted (Petersen & Umaña, 2002; Umaña, 1997). It also follows a pattern of variation in functional groups, similar to that of Lake Fraijanes (Umaña 2014), where the shift in functional groups was also related to changes in resource abundance rather than energy availability.

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RESUMEN

La respuesta detallada del fitoplancton de lagos tropicales a las variaciones climáticas ha sido poco estudiada, sin embargo al parecer la composición de especies varía en respuesta a la variabilidad de la precipitación y de los vientos a lo largo del año. Con el fin de recabar más evidencia de esta variación, se estudió semanalmente la composición del fitoplancton en el lago Bonilla, un lago tropical de zonas bajas (380 msnm), de 30 m de profundidad, entre abril 2010 y mayo 2011. Se registró la temperatura del agua a varias profundidades, y se realizaron mediciones de oxígeno disuelto en la columna de agua, trasparencia del agua y concentración de nutrientes varias veces a lo largo del año de estudio. El lago es monomíctico cálido, con una mezcla profunda durante el invierno hemisférico, especialmente luego de un periodo de fuertes precipitaciones en diciembre 2010. El fitoplancton estuvo dominado por pocas especies: una Cyanobacteria colonial (*Aphanocapsa* sp., grupo funcional F), y dos Chlorococcaceae coloniales (*Botryococcus braunii* y *Eutetramorus tetrasporus*, ambas del grupo funcional K). Sus abundancias relativas cambiaron a lo largo del año, siguiendo los cambios en las condiciones de la columna de agua que es influenciada por variaciones en el tiempo atmosférico. Aunque los cambios en los grupos funcionales indican que hubo un cambio en la disponibilidad de recursos en vez de energía radiante, fue evidente que se debe prestar también atención a las adaptaciones particulares de las especies más allá de las que se usan normalmente para establecer los grupos funcionales.

Palabras clave: fitoplancton, lagos tropicales, estacionalidad, grupos funcionales, Costa Rica.

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