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A 50-year sediment record of algal assemblage changes in Hanabanilla Reservoir, Cuba

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Abstract Hanabanilla Reservoir, south-central Cuba, is used for electric power generation, potable water supply and tourism. We examined stratigraphic shifts in algal assemblages that accumulated in the reservoir sediments from the time of construction in 1960 through 2012, and inferred the environmental drivers of such biological changes. Historical fluctuations in algal assemblages were driven by scouring of the reservoir bottom, changing water level, and input of organic matter and nitrogen to the water body. Stage records, in conjunction with algal counts, confirm the importance of the pennate/centric diatom ratio for reconstructing past water-level changes. Although nutrient and organic matter inputs to the reservoir also influenced algal abundance and community composition, our findings suggest that regulating reservoir hydrology could be an effective strategy for preventing future cyanobacterial blooms. Shifts in the relative abundances of algal taxa, and dominance of R strategists associated with extreme fluctuations in water level, showed the strong influence of hydrology as a determinant of primary producer assemblage structure.

Keywords Reservoir · Sediment · Dam · Hydrodynamics · *Aulacoseira* · *Microcystis*

Introduction

Reservoirs provide many services to human societies, e.g. as reliable sources of water for drinking, agricultural irrigation, hydropower, industry, and recreation. But building dams to create such artificial water bodies can have negative impacts on the structure and function of aquatic ecosystems. For example, if low water levels are maintained, benthic algae taxa, some of which are less palatable, or physically difficult to consume by grazing macroinvertebrates, can dominate (Lamberti and Moore 1984). This can create potential

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problems for water users, especially if large mats and strands of filamentous algae become common. In such cases, flow releases can be implemented to promote desirable benthic algal species and densities (Martina et al. 2013).

Other common problems related to reservoirs include periodic, massive blooms of toxin-producing cyanobacteria, now a worldwide problem (Pham and Utsumi 2018). Such hazardous algal blooms (HABs) can have detrimental impacts on fisheries, aquaculture, and human and animal health (Bouaïcha and Corbel 2016). Such HABs are also aesthetically unpleasant, as they reduce water transparency, can cause foul water taste, and produce nuisance odors (Moldaenke et al. 2019).

Given the importance of reservoirs, numerous strategies have been developed to manage and monitor them. Algae have long been used in ecological assessments and phytoplankton assemblages are key bioindicators of ecosystem condition (Scheffer and Carpenter 2003). Many studies have been undertaken on short- and long-term shifts in reservoir algal assemblages (Chellappa et al. 2009; Winston et al. 2014; Monchamp et al. 2016).

Algal groups, including diatoms (Wolin and Duthie 1999), green algae (Fernandes et al. 2002), blue-greens (Cyanobacteria) (Cronberg 1986), and dinoflagellates (Quattrocchio 2009) are often preserved quantitatively in lake and reservoir sediments. Paleolimnological study of such microfossils enables inference about past water quality, human activities in drainage basins (Martina et al. 2013), and other environmental changes in and around lakes and reservoirs. Some algal groups produce thick-walled resting stages that may dwell in sediments for many years and remain viable. When suitable conditions for vegetative growth return, such resting forms produce new vegetative cells (Barsanti et al. 2008). Some algae species leave resting forms in the sediment that have been shown to grow when incubated in culture media (Li et al. 2015). It has been suggested that germination of akinetes, or recruitment of hormogonia or vegetative cells of cyanobacteria, can play an important role in bloom initiation (Brunberg and Blomqvist 2003).

Study site

Hanabanilla Reservoir is located in the Arimao River Basin, a watershed of national priority in Cuba (Fig. 1). The area is characterized by the highest elevations and slopes in central Cuba, and is dominated by geology with low permeability, which favors drainage over infiltration (Sánchez 2000). The morphometry of Hanabanilla Reservoir follows the sinusoidal shape of the rivers that underlie it (Sánchez 2000). The reservoir was constructed between 1958 and 1962 by damming the Hanabanilla and Jibacoa Rivers, and was filled with water in 1963. The reservoir provides water for the cities of Cienfuegos and Santa Clara, and other smaller towns. It is also used for electric power generation and is a tourist destination.

In 2014 and 2015, numerous floating masses of filamentous cyanobacteria appeared in the reservoir (Comas-González et al. 2017), but no quantitative study of the blooms was undertaken. Furthermore, little was known about the history of the primary producer community in the reservoir. We used a sediment core from Hanabanilla Reservoir to investigate changes in algal assemblages in the water body since its construction in 1960. We sought to: (1) characterize temporal shifts in past algal assemblages and (2) infer past environmental changes in the drainage basin and reservoir that caused the biotic changes. Knowledge of the drivers of past biological changes in the water column can be used to inform management of the reservoir, with the goal of preventing future eutrophication and harmful algal blooms.

Materials and methods

Sediment sampling, core chronology and analysis of physical/chemical variables

In 2012, a 60-cm sediment core was collected with a UWITEC® system (inner diameter: 8.6 cm) from 29 m of water near the reservoir outlet (22° 05′ 35″ N; 80° 04′ 00″ W) (Fig. 1). The coring location was selected because the site was deemed to be representative of overall reservoir water variables (nutrients, oxygen, metals, pH) (Sánchez 2000), and thus considered an appropriate location to evaluate the quality of water for human consumption (Chapman 1996). The core was kept at 4 °C to inhibit microbiological activity during transport to the lab. In the laboratory, the core was sectioned at 2-cm intervals using a

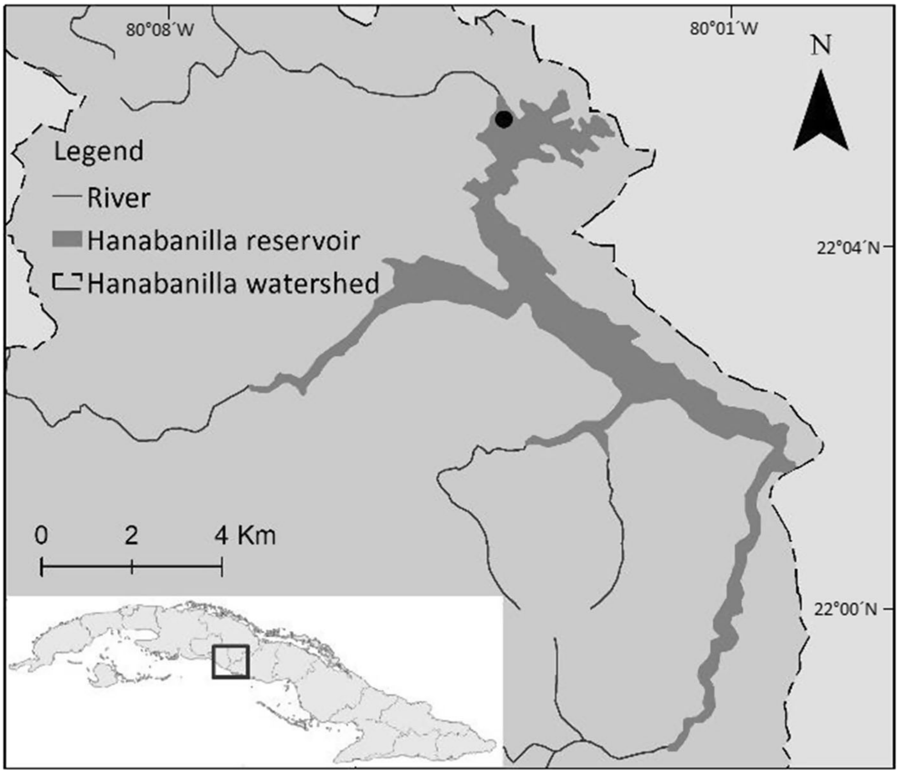


Fig. 1 Geographic location of Hanabanilla Reservoir, Cuba. Black dot indicates the outlet point of reservoir

stainless steel knife. Subsamples of sediment from each homogenized section were taken for dating, as well as for physical, chemical and biological analyses.

A sediment core chronology was developed by ^{210}Pb dating, using the Constant Rate of Supply (CRS) Model (Appleby 2008; Appleby and Oldfield 1978; Baskaran et al. 2015), and was corroborated with ^{137}Cs (Díaz-Asencio et al. 2017). Total nitrogen (TN) content in sediment was determined by the Kjeldahl method. Total phosphorus (TP) content in sediment was determined colorimetrically, using the vanadium-molybdenum method and Cuban Standard NC 34:1999, with color read on a spectrophotometer. Organic matter (OM) content was determined by weight loss on ignition (LOI) at 550 °C for 4 h, from which organic carbon was estimated using the van Bemmelen factor [$OC_{(\%)} = OM_{(\%)}/1.724$], which we consider to be a reasonable means to approximate OC content (Heaton et al. 2016).

Granulometry of sediment samples was analyzed using mechanical agitation sifters of 63 and 2 µm, and samples were separated into three size fractions, reported as % mass: particle size (ps) $\geq$ 63 µm, 63 µm > ps $\geq$ 2 µm, and ps < 2 µm. Historical data on hydrologic variables associated with the reservoir, such as maximum volume (V_{max}) and minimum volume (V_{min}), were obtained from the Institute of Hydraulic Resources (INRH) of Villa Clara Province. Sediment Mass Accumulation Rate (MAR; g m^{-2} year^{-1}) was determined from output of the CRS dating model. Details of methods for analysis of physical–chemical variables in the sediment (TN, OC, TP and granulometry) and reservoir hydrology (V_{max}, V_{min} and residence time) were described in Labaut et al. (2018). Details regarding core dating, development of the chronology and MAR calculations appear in Díaz-Asencio et al. (2017).

Algae samples

Sediment samples for biological analysis were weighed on a Sartorius analytical balance (error = 0.0001 g), and reported as wet weight (ww). Samples were preserved with 1 mL of neutral formaldehyde (3%) prior to analysis. Next, samples were washed/sieved with filtered water through 63-

and 20-µm sieves, until the resulting water was clear. This was done to reduce interference from sediment particles during microscope analysis. Subsamples of 1 mL were then diluted with filtered water, keeping track of volumes so that algal concentrations could be reported in terms of amount in the initial wet sample mass.

The sieve size class between 63 and 20 µm was used for qualitative and quantitative analysis. A Laborlux Leica-Leitz microscope (640× and 1600×) was used to identify algae. Species identifications were made using the appropriate taxonomic literature (Bourrelly 1972; Krammer and Lange-Bertalot 1986). The AlgaeBase World-wide electronic publication (Guiry and Guiry 2018) was also consulted. Species were classified according to Ruggiero et al. (2015), which represents a consensus opinion regarding boundaries between taxa and ranks of major taxa, including kingdoms. The term 'algae' is not strictly taxonomic and includes a number of phyla, including both prokaryote and eukaryote species (Guiry and Guiry 2018). We focused on the value of individual algal species or groups as indicators of environmental conditions, thereby avoiding debates about systematics.

A Motic inverted microscope (400×) and sedimentation chamber were used for algae quantification. Algal counting was carried out using a method based on the Utermöhl technique (Utermöhl 1958). In some previous phytoplankton studies, colonies (e.g. colonial cyanobacteria) were counted as single units. This counting method, however, resulted in a high coefficient of variation among analyses. Thus, we used individual cell counts (Vuorio et al. 2007).

Data analysis

Spearman and Pearson correlation analysis were applied to MAR and algal abundance, and to MAR and loss on ignition (LOI), respectively. The Mann–Whitney test was applied to independent samples to compare species abundance and taxa richness (TR) means in sediments deposited during the intervals 1960–1976 and 1977–2012 (InfoStat v. 2014). The concept of functional groups, i.e. Competitive, Stress-tolerant and Ruderal strategists (C–S–R) (Reynolds 2006), was applied to the phytoplankton assemblages.

A Jaccard similarity (presence/absence species) matrix was calculated and hierarchical cluster analysis was performed using the complete linking method to produce a dendrogram. A SIMPROF test (999 permutations) was carried out on the clusters (PRIMER 6.1.6). The SIMPROF routine is based on the concept of a "similarity profile," which represents the matrix of pairwise similarity values between any set of objects, and is a test used to decide which clusters can be identified as distinguishable groups, statistically speaking (Clarke and Gorley 2015).

Ordination analyses were used to explore relationships between microalgae (classes or species) and physical–chemical variables. The exploratory variables were: hydrodynamics (V_{min}, V_{max}), TP, TN, OC, particle size ($ps \geq 63$ µm; 63 µm $> ps \geq 2$ µm, $ps < 2$ µm), and abundance of species/classes by year. Redundancy Analysis (RDA) and Canonical Correspondence Analysis (CCA) were chosen because preliminary analyses showed that classes and species variations were better described by linear response modeling (RDA) and unimodal models (CCA), respectively (ter Brak and Smilauer 1998). Both analyses were performed using CANOCO 4.5 software. In the CCA, only species with ≥ 1% relative abundance in at least one sample were used, thereby eliminating stochastic/rare taxa. Abiotic and biotic data were log $(x + 1)$ transformed for ordination analysis. Variables with high correlations (inflation factor > 20) were eliminated to avoid collinearity, and to remove the weakest ones (Ter Braak and Smilauer 2002). The significance of axes and the species/classes-environment relation was calculated with a Monte Carlo test (999 permutations).

Results

Algae abundance and assemblage composition

A total of 58 species were identified across five major taxonomic categories: Cyanophyceae (6), Chlorophyta (17), Euglenophyceae (6), Bacillariophyceae (27), Zygnemaphyceae (2) (Table 1). A *Rhodomonas* sp. individual was registered in 2004, but was excluded from the analysis, as were other rare species (relative abundance < 1%). The most abundant algae throughout the sediment profile were Cyanophyceae (32%) and Chlorophyceae (27%); Euglenophyceae (0.14%) were the least abundant (Fig. 2). Whereas diatoms (Bacillariophyceae) were the most diverse

Table 1 List of the recorded algae taxa in Hanabanilla Reservoir sediment [classification according to Ruggiero et al. (2015)]

Superkingdom Prokaryota	Group*
Class Cyanophyceae [= Phycobacteria]	
Aphanocapsa delicatissima W. et G.S.West 1912	D
Coelomoron sp.	A
Cylindrospermopsis sp.	F
Geitlerinema sp.	E
Microcystis panniformis Kom. et al. 2002	D
Phormidium sp.	D
Superkingdom Eukaryota	Group*
Kingdom Protozoa	
Class Euglenophyceae	
Euglena sp	D
Lepocinclis texta (Duj.) Lemm. emend. Conrad 1934	C
Phacus sp.	C
Trachelomonas curta Da Cunha 1913	E
Trachelomonas sp.	D
Trachelomonas volvocina Ehrenb. 1833	C
Kingdom Chromista	
Class Conjugatophyceae [= Zygnematophyceae]	
Staurastrum gracile Ralfs 1848	E
Staurastrum grallatorium Nordstedt 1870	E
Class Bacillariophyceae [= Diatomeae]	
Amphipleura pellucida (Kütz.) Kütz. 1844	A
Amphora libyca Ehrenb. 1846	A
Aulacoseira granulata (Ehrenb.) Simonsen 1979	E
Bacillaria paxillifera (O.F.Müller) T.Marsson	G
Craticula cuspidata (Kütz.) Mann in Round et al. 1990	F
Cyclotella meneghiniana Kütz. 1844	D
Cymbella affinis Kützing	A
Navicymbula pusilla (Grunow) Krammer	A
Eunotia sp.	C
Eunotia pectinalis (O.F. Müller) Rabenh. 1864	A
Fragilaria rumpens (Kütz.) Carlson 1913	D
Gomphonema lanceolatum Ehrenberg	A
Gyrosigma acuminatum (Kütz.) Rabenh. 1853	B
Hantzschia sp.	C
Navicula sanctaecrucis Oestrup 1913	F
Navicula sp.	B
Neidium sp.	A
Nitszchia linearis (Agardh) W. Smith 1853	A
Nitzschia sp.	B
Tryblionella scalaris (Ehrenberg) Siver et Hamilton	A
Pinnularia maior (Kütz.) Rabenh. 1833	A
Rhopalodia gibba (Ehrenb.) O. F. Müller 1895	E
Iconella linearis (W.Smith) Ruck et Nakov in Ruck et al.	A
Iconella tenera (W.Gregory) Ruck et Nakov in Ruck et al.	F
Synedra spp.	G
Ulnaria acus (Kütz.) Aboal 2003	E
Trybionella victoriae Grunow 1862	B
Kingdom Plantae	
Phylum Chlorophyta	
Class Chlorophyceae	
Coelastrum indicum Turner 1892	C
Coenococcus spp.	E
Coenocystis asymmetrica Komárek 1983	G
Coenocystis spp.	F
Desmodesmus serratus (Corda) An et al. 1999	E
Desmodesmus sp.	E
Hariotina reticulata Dangeard 1889	E
Monactinus simplex (Meyen) Corda 1838	E
Sphaerellopsis sp.	C
Tetraëdron regulare Kützing 1845	E
Tetrastrum sp.	E
Willea apiculata (Lemmermann) John, Wynne et Tsarenko	E
Class Trebouxiophyceae	
Hindakia fallax (Komárek) Bock, Proschold et Krienitz	C
Dictyosphaerium spp.	D
Micractinium pusillum Fresenius 1858	E
Oocystis lacustris Chod. 1897	D
Oocystis sp.	C

Groups were defined by the authors, rather than having been distinguished statistically by CCA

class (Table 1), overall Chlorophyceae was the only group represented in all years in the reservoir (Fig. 2). In sediments dated to 1963, no algae were found.

Diatoms were abundant during the first years after reservoir construction, about 1960 (87.4%) and 1962 (81.5%), but diminished between about 1963 and 1988 (0–19%), only to increase again from ca. 1990 to 2008, especially about 1996 (78%) (Fig. 2). Centric diatoms *Aulacoseira granulata* and *Cyclotella meneghiniana* appeared for the first time ca. 1964 and 1965, respectively, with relatively low abundances compared to later years of the record, ~ 1990 to 2010

(Fig. 3). From about 1965 to 1976, the assemblage was dominated by Chlorophyceae/Cyanophyceae, and from about 1977 to 2010 Chlorophyceae/Cyanophyceae/Bacillariophyceae dominated. Between 1965 and 1976, Euglenophyceae first appeared and had the highest abundance.

Conjugatophyceae was represented by only two desmid species, *Staurastrum grallatorium* and *S. gracile*, which were least abundant from about 1960 to 1976 (0–0.4%), increased in 1977 (9.8%), and were most abundant in model years 2006, 2008 and 2010 (35.6, 44.2 and 13.7%, respectively) (Figs. 2, 3). The most abundant species were: *Staurastrum gracile*, *Aulacoseira granulata*, *Microcystis panniformis*, *Monactinus simplex*, *Aphanocapsa delicatissima* and *Hariotina reticulata* (abundance > 10^5 cells/g ww in some intervals).

The core was divided into five clusters according to presence/absence of species ($p < 0.01$): 1965 and 1972, period 1 (1960–1966), period 2 (1968–1976), period 3 (1977–2010) and 2012 (Fig. 4). Years 1965, 1972 and 2012 were not analyzed as periods, because the two earliest represent anomalous years in the time intervals (periods) 1960–1966 and 1968–1976, respectively, according to the clustering, and 2012 represents the topmost sample in the core.

Fig. 3 Changes in Hanabanilla Reservoir, Cuba, between 1960 ▶ and 2012. [Maximum water volume: Vmax, total phosphorus: TP, organic carbon: OC, relative abundances of C–S–R (Competitive, Stress tolerant and Ruderal strategists) functional groups, and abundances of selected algal groups in the sediment core]

Years 1960–1976 (periods 1 and 2) had generally lower abundances (6.4×10^3–1.8×10^5 cells/g ww), compared to period 3 (1.3×10^4–2.3×10^6 cells/g ww) ($p < 0.01$), with some samples coinciding with times of lowest taxonomic richness (TR) (Fig. 5). TR varied with sediment depth, with both high and low values at the top and bottom of the profile: TR = 3–9 (1965–1977). The years from 1979 to 2010 were characterized by relatively stable, high values, with the highest in 1982 (TR = 18), and lowest in 2012 (TR = 2). Average TR for all depths was 10.

Application of the C–S–R (Competitive, Stress-tolerant and Ruderal) functional group approach (Reynolds 2006) indicated dominance of S strategists in model years 1964, 1974, 1979, 1986 and 1988,

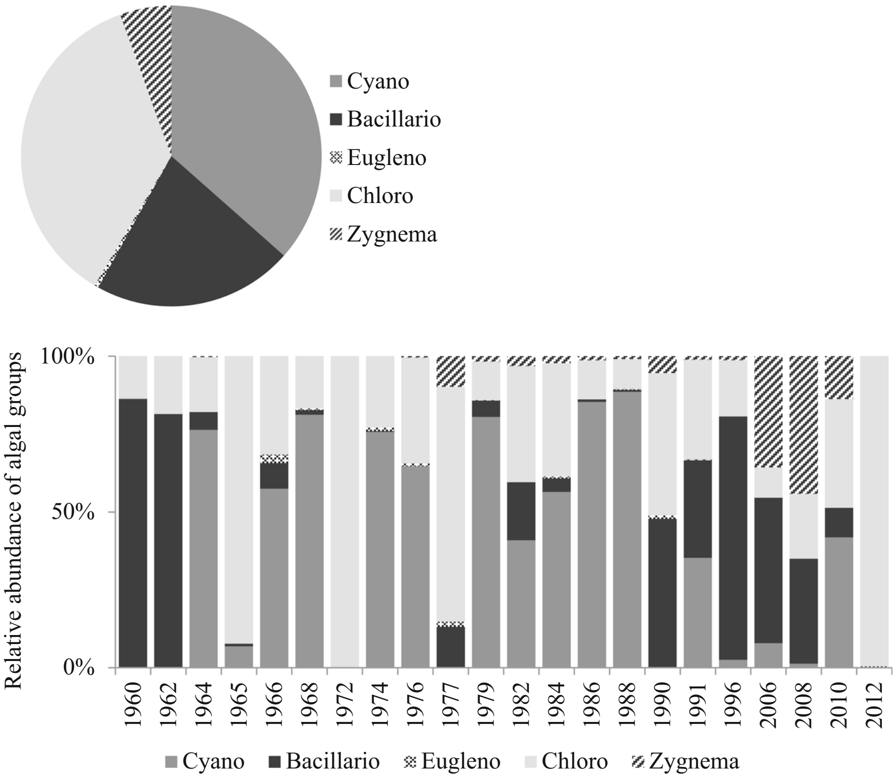
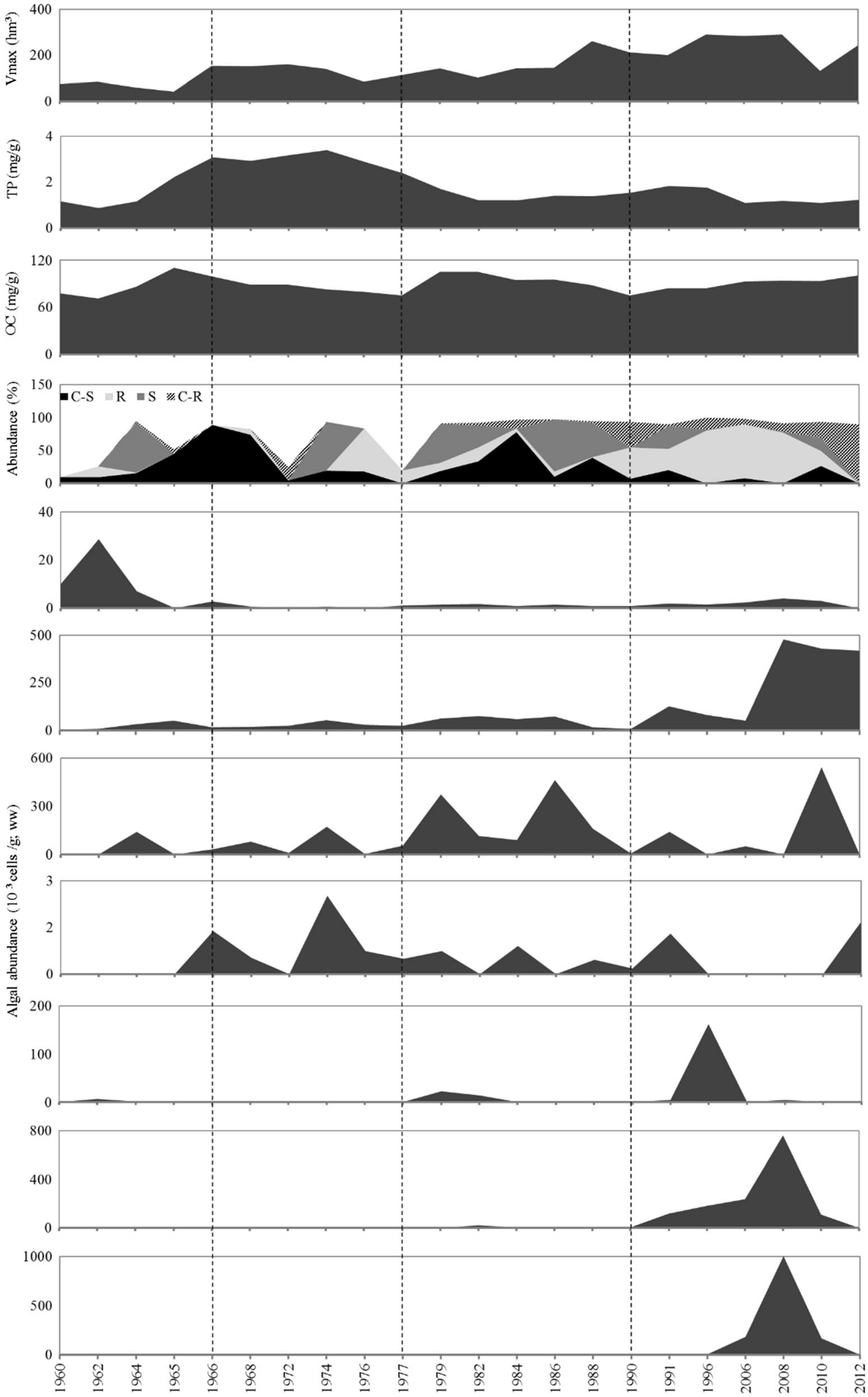


Fig. 2 Relative abundances of algal groups in the sediment profile from Hanabanilla Reservoir, Cuba, versus year of sediment deposition. Cyano: Cyanophyceae, Bacillario: Bacillariophyceae, Chloro: Chlorophyta, Eugleno: Euglenophyceae, Conjugato: Conjugatophyceae


Vmax (hm³)
400
200
0
TP (mg/g)
4
2
0
OC (mg/g)
120
60
0
Abundance (%)
150
100
50
0
■ C-S
R
■ S
▨ C-R
40
20
0
500
250
0
600
300
0
3
2
1
0
200
100
0
800
400
0
1000
500
0
Algal abundance (10³ cells /g; ww)
1960
1962
1964
1965
1966
1968
1972
1974
1976
1977
1979
1982
1984
1986
1988
1990
1991
1996
2006
2008
2010
2012

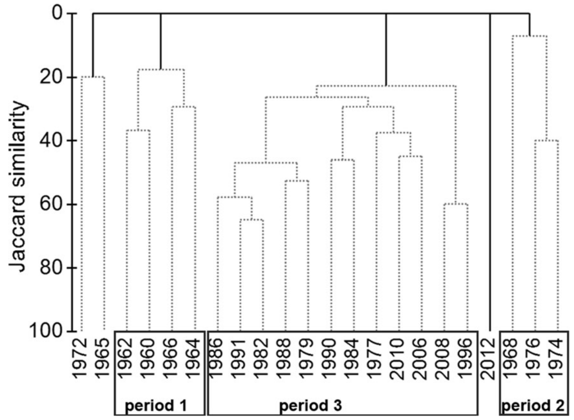


Fig. 4 Hierarchical clustering by Jaccard similarity of presence/absence of abundant species (relative abundance ≥ 1% in any sample) by date. Dotted lines indicate groups of samples not separated ($p < 0.01$) by the SIMPROF test

when they contributed between 52% and 80% to the algal assemblages (Fig. 3). From 1974 to 1984, C–S strategists represented 18–78%. From 1990 to 2012, R and C–R strategists were the main groups, contributing between 24.3 and 90% to the assemblages, except in 2010, when there were similar abundances of the S, C–S, R and C–R groups. Succession of the functional groups through time occurred as follows: R → S → C–S → C–R → S→R → S → S/C–S → S → R/C–R. C strategists were represented by the genera *Euglena, Lepocinclis, Trachelomonas,* and *Coenocystis*; C–S strategists by *Aphanocapsa, Dyctiosphaerium* and *Oocystis*; S strategists by *Microcystis* and *Cylindrospermopsis*; C–R strategists by *Monactinus*, *Coelastrum* and *Hariotina*; and R strategists by *Aulacoseira, Fragilaria, Synedra, Phormidium, and Staurastrum* (Reynolds 2006).

Algal relations with environmental variables

Sediment mass accumulation rate (MAR) was correlated with loss on ignition (LOI) (r = 0.51, $p < 0.05$), but not to algal abundance. The exploratory ordination analysis indicated collinearity between V_{max} and V_{min}, TP and ps < 2 µm, and between OC and TN. Therefore, V_{min}, ps < 2 µm and TN were eliminated. Also, the variable 63 µm $>$ ps ≥ 2 µm was eliminated because of the very small contribution of the vector projections to axes of all exploratory ordination analysis. The Monte Carlo test was significant for the first axis and all canonical axes of RDA (classes/environment) and CCA (species/environment) (Table 2), indicating that these environmental variables were important in explaining the algal classes and species composition in the reservoir.

In the RDA, the first two axes explained 93% of the cumulative variance of class-environment relations. It

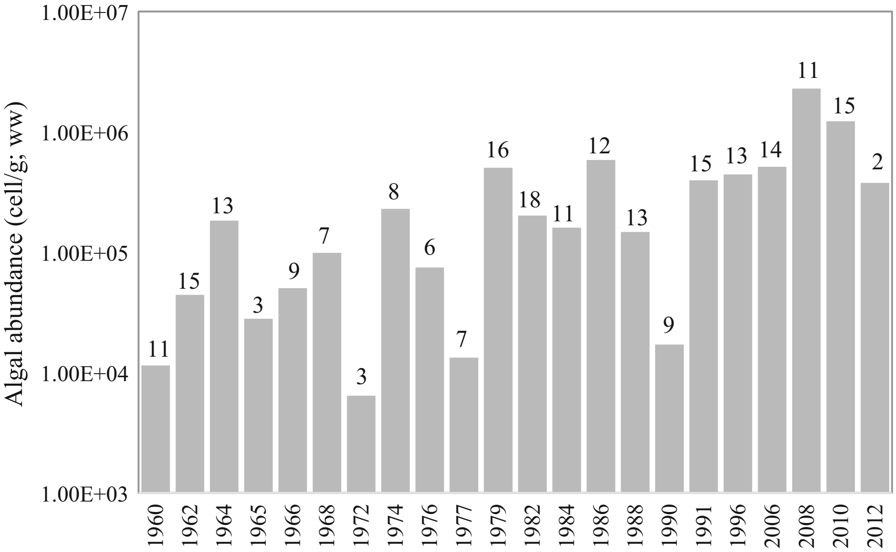


Fig. 5 Total algal abundance (vertical gray bars) and taxa richness (numbers above bars) versus date in sediment record from Hanabanilla Reservoir

Table 2 Summary of redundancy analysis (RDA) and canonical correspondence analysis (CCA)

Monte Carlo permutation test

RDA 1: F-ratio = 9.656**; All canonical axes RDA: F = 4.169**

CCA 1: F-ratio = 1.981*; All canonical axes ACC: F = 1.435*

*$p < 0.05$, **$p < 0.01$

Variable	First axis			
	RDA 1	RDA 2	CCA1	CCA2
≥ 63 µm	− 0.6	0.02	0.56	0.38
TP	−0.32	− 0.56	− 0.31	0.81
OC	0.39	− 0.49	− 0.61	− 0.03
V_{max}	0.39	− 0.05	− 0.51	− 0.51
Eigen values	0.35	0.1	0.48	0.33
Species-environment correlation	0.8	0.7	0.9	0.91
Percentage of cumulative variance				
Species data	34.9	44.7	10.4	17.6
Species-environment relation	72.6	93	41.4	69.8

describes a "shift" from shallow waters (quadrant I) with the largest particle sizes (≥ 63 µm) in the bottom, during the first years of the reservoir, to years with high quantities of TP and presence of Euglenophyceae (quadrant III) (both quadrants with lowest algal abundance), and finally to deep waters (with sediments rich in organic matter) in the last years, and four representative algal classes

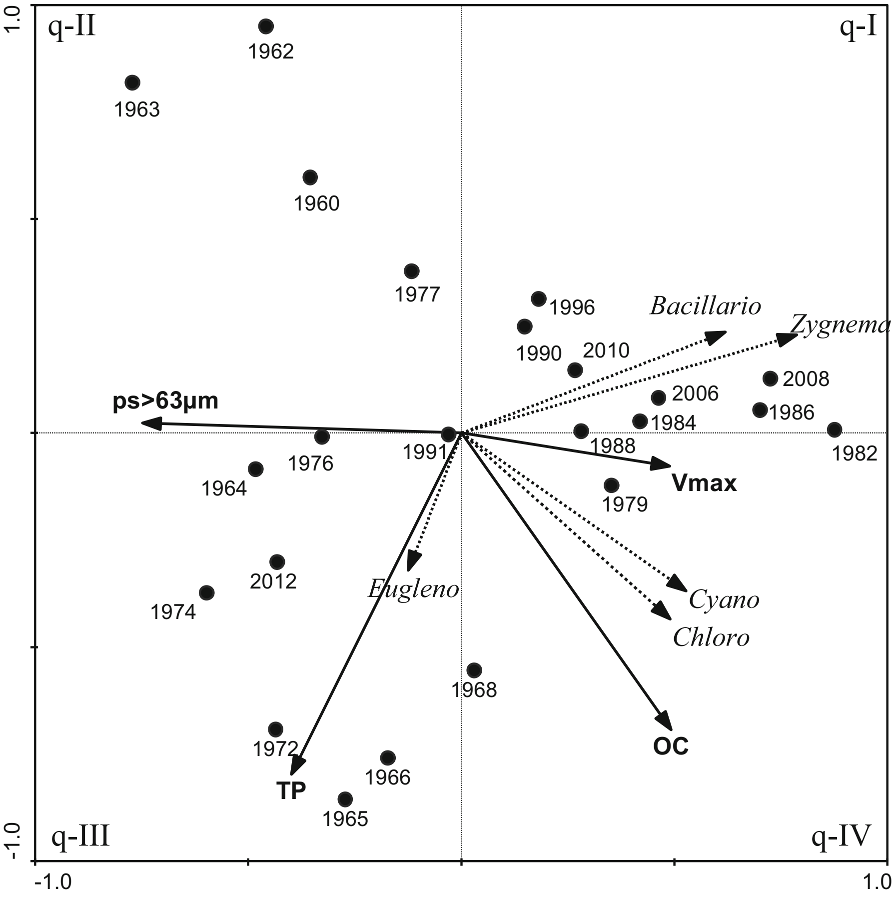


Fig. 6 Redundancy analysis (RDA). Black circles represent the date, black arrows the environmental variables and dotted arrows the microalgae groups. Arrows point in the direction of maximum change. Cyano: Cyanophyceae, Bacillario: Bacillariophyceae, Chloro: Chlorophyta, Eugleno: Euglenophyceae, Conjuga: Conjugatophyceae. q-I–IV = quadrants I–IV

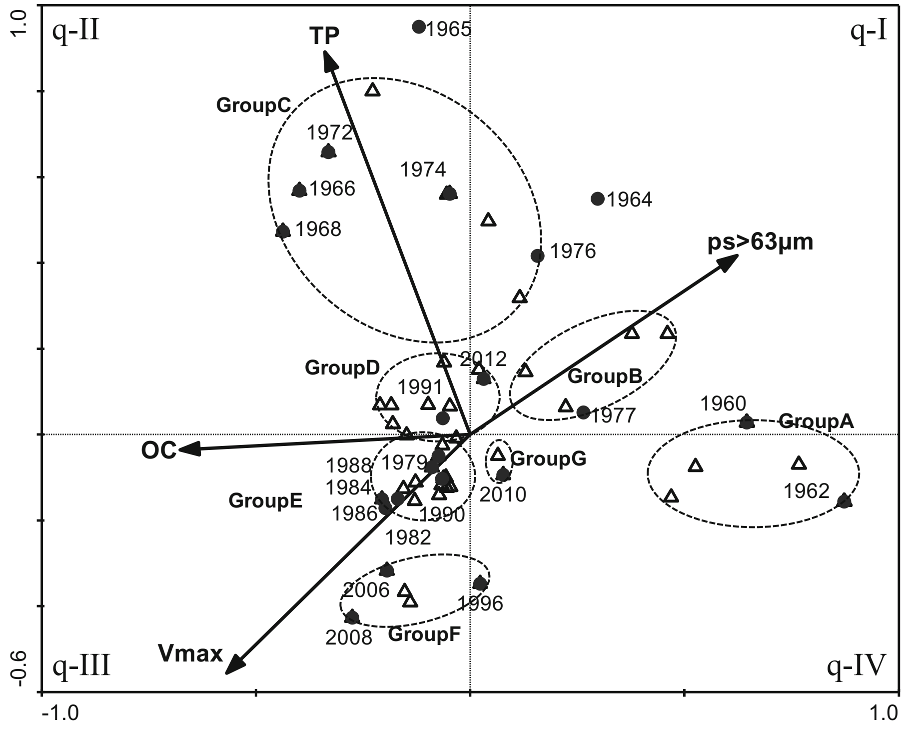


Fig. 7 Canonical correspondence analysis (CCA) for algae species (white triangles), environmental variables (black arrows), dates (black dots) and taxa groups (dotted circles and ellipses, which were defined by the authors, rather than having been distinguished statistically by CCA (Table 3); q-I–IV = quadrants I–IV

Table 3 Grouped taxa of Fig. 7 (*Groups were defined by the authors, rather than having been distinguished statistically by CCA)

Group*	Taxa
A	*Amphipleura pellucida, Amphora libyca, Coelomoron* sp., *Cymbopleura affinis, Eunotia pectinalis, Gomphonema lanceolatum, Iconella linearis, Navicymbula pusilla, Neidium* sp., *Nitszchia linearis, Pinnularia maior, Trybionella scalaris*
B	*Gyrosigma acuminatum, Navicula* sp., *Nitzschia* sp., *Trybionella victoreae*
C	*Coelastrum indicum, Eunotia* sp., *Hantzschia* sp., *Hindakia fallax, Lepocinclis texta, Oocystis* sp., *Phacus* sp., *Trachelomonas volvocina, Sphaerellopsis* sp.
D	*Aphanocapsa delicatissima, Cyclotella meneghiniana, Dyctiosphaerium* sp., *Euglena* sp.; *Fragilaria rumpens, Microcystis panniformis, Oocystis lacustris, Phormidium* sp., *Trachelomonas* sp.
E	*Aulacoseira granulata, Coenoccocus* sp., *Desmodesmus serratus, Desmodesmus* sp., *Geitlerinema* sp., *Hariotina reticulata, Micractinium pussillum, Monactinus simplex, Rhopalodia gibba, Staurastrum gracile, Staurastrum grallatorium, Tetraëdron regulare; Tetrastum* sp., *Trachelomonas curta, Ulnaria acus, Willea apiculata*
F	*Cilindrospermopsis* sp., *Craticula cuspidata, Coenocystis* sp., *Iconella tenera, Navicula sanctaecrucis*
G	*Bacillaria paxillifera, Coenocystis asymmetrica, Synedra* spp.

(Cyanophyceae, Bacillariophyceae, Chlorophyceae and Conjugatophyceae) (quadrants IV and I) (Fig. 6). Vector length indicates the goodness of fit of each taxon's abundance to the displayed ordination, and acute angles between two vectors indicate a high positive correlation (Ter Braak and Smilauer 2002).

Thus, Euglenophyceae was related to TP and OC, Cyanophyceae and Chlorophyceae to TP, OC and V_{max}, and Bacillariophyceae and Conjugatophyceae to OC and V_{max}.

In the CCA, the first two axes explained 69.8% of the cumulative variance of the species-environment relation. It also described a "shift" (as RDA) from shallow waters (quadrant I and IV), with the biggest particle size and pennate (benthic) diatom numbers in the first years of the reservoir, to years when planktonic species predominated, linked to TP (quadrant II), V_{max}, and OC (quadrant III) (Fig. 7; Tables 1, 3). Some years (1964–1976) of the first two decades were included in quadrant II, in which species such as *Microcystis panniformis, Aphanocapsa delicatissima* and *Phormidium* sp. were relatively abundant. Most years of the last 3 decades (ca. 1979–2008) were grouped in quadrant III, in which species with the highest abundance values (e.g. *Staurastrum gracile, Aphanocapsa delicatissima, Microcystis panniformis, Aulacoseira granulata, Monactinus simplex,* and *Hariotina reticulata*) were related to OC and V_{max}.

Discussion

Algae in Hanabanilla Reservoir sediment

Algal abundance was not correlated with sediment mass accumulation rate (MAR). This suggests a small contribution of algal biomass to net sedimentation in Hanabanilla Reservoir. Although net sedimentation rate increases with increasing epilimnetic algal biomass, multiple factors affect sedimentation (Larocque et al. 1996). The positive correlation between LOI and MAR could be related to deposition of allochthonous organic matter of terrestrial origin, derived from vascular plants, as inferred from high C/N ratios (> 20) in all layers of the profile (Labaut et al. 2018). Also, Díaz-Asencio et al. (2017) related the higher values of MAR in the core to intense rain events in the region, which cause rapid soil erosion in the catchment and consequent high particulate loading and sedimentation.

The sedimentation rate of plankton can be affected by many factors in lakes and reservoirs, such as the presence of grazers, buoyancy of cells, and water currents, all of which may also influence the proportions of phytoplankton cells found in the sediments (Monchamp et al. 2016). For example, taxa richness (TR) in the sediments ($TR_{maximum}$ = 18), was lower than the mean TR (46) of recent phytoplankton samples (2015) from surface waters (depth = 0.5 m) of this reservoir (Comas and Labaut 2016). This probably reflects the fact that some taxa are not transferred from the water column to the sediment, or are not preserved in the sediment. For instance, Dynophyceae, a common group in lakes, was not found in the reservoir sediment, but several dinoflagellate species were found as components of the phytoplankton (Comas and Labaut 2016). Dinoflagellate cysts in the sediments suggests recent introduction of this group into the ecosystem.

Taxonomic composition of the phytoplankton community varies among lakes and reservoirs (Reynolds 2006). Nevertheless, the primary producer groups found in the sediment of Hanabanilla Reservoir were the common major groups found in tropical reservoirs (Dodds 2002). Phytoplankton numbers and species composition were also similar to what is presently found in the water column of the reservoir (Comas and Labaut 2016).

Highest abundances of Cyanobacteria in sediment (10^5 cells/g ww) in model years 1964, 1974, 1979, 1982, 1988, 1991 and 2010, were comparable to recent phytoplankton densities in the water column (10^4 cells/mL) (Comas and Labaut 2016), and to the highest diatom abundances (10^5 cells/g ww) between 1991 and 2010 in the same sediment profile, suggesting sedimented algae were well preserved and representative of the phytoplankton. Abundance data in sediments should be interpreted with caution, but if richness is high and the relation between cyanobacterial assemblage composition in sediments and water is strong, past diversity can be inferred (Monchamp et al. 2016).

Models of algal sinking patterns indicate that larger cells sink faster than smaller cells (Blottiere 2015). Some cyanobacteria develop large aggregates (colonies) of coccoid cells or filaments, which sink faster than small ones (Mur et al. 1999). This may explain why only colonial species of cyanobacteria were registered in the reservoir sediment. Among other groups, colonial species such as *Aulacoseira granulata*, *Hariotina reticulata*, and *Monactinus simplex* also dominated.

A decrease in algal abundance with greater sediment depth (age) might be related to algae decomposition through time (Fallon and Brock 1979), but both algal abundance and richness fluctuated throughout the Hanabanilla Reservoir sediment profile, with abundance declining in the last few years (Fig. 5). Highest algal abundance values (in 10^6 cells/g ww) were higher than abundances in surface sediment samples from an urban reservoir (10^3 cells/g; ww) (Li et al. 2015) and similar to diatom abundance, on the order of 10^6 cells/mL, in a sediment profile from a reservoir of similar age (Winston et al. 2014), suggesting algae are well preserved in the Hanabanilla Reservoir sediment.

Past environmental conditions inferred from algae in the sediment

RDA on algal classes showed that lower values of algal abundance in the first few years of reservoir operation were related to lower nutrient availability (Labaut et al. 2018). Nitrogen and phosphorus are critical nutrients that often limit phytoplankton growth (Reynolds 2006). The highest and lowest values of TN and maximum water level (V_{max}), respectively, were registered in 1965, and with respect to these variables, 1965 was an anomalous year in the time period 1960–1966, according to clustering by similarity of presence/absence of taxa. Lowest values of TN, along with low V_{max} in 1963, may have stressed algal assemblages, accounting for an absence of remains in the sediment.

In subsequent years, high concentrations of TP, associated with $ps < 2$ µm, were registered, but phytoplankton abundance was not as high as during period 3 (1977–2010). Phosphorus retention in sediment (Labaut et al. 2018) could have limited algal growth in the water column, causing the differences in sediment algal abundance between periods. Higher fine-particle concentrations were strongly correlated with a rise in water level (Wolin and Duthie 1999) during those years.

The last three decades (period 3) were characterized by increased anthropogenic disturbances in the drainage basin, mainly agricultural activities (Sánchez 2000) that coincided with increases in OC and TN (Labaut et al. 2018). The relation between Cyanophyceae and Chlorophyceae and both OC and TN, suggests that these algal groups can be used as indicators of trophic state conditions (Comas 2008). Cyanophyceae are favored under conditions of nutrient (especially P) enrichment (GEOHAB 2006), and some blue-green taxa fix atmospheric nitrogen.

Pennate diatom species dominated in the first years of reservoir operation, i.e. 1960, 1962, 1964 (Fig. 7; Tables 1, 3). Processes such as bottom scouring can reset the successional status back to an early-stage community dominated by diatoms, via physical removal of taxa on the substrate (Davie et al. 2012). Excavation and removal of substrate during reservoir construction may have had an effect similar to scouring, resulting in predominance of pennate diatoms in the first years. Such taxa are common in the benthos (Dodds 2002) and are related with $ps \geq 63$ µm, a particle-size class associated with the riverbed over which the reservoir lies (Labaut et al. 2018). Furthermore, lower water levels in the first few years imply abundant shallow-water habitat, ideal sites for benthic and epiphytic diatoms (Wolin and Duthie 1999), thereby favoring bottom-dwelling over planktonic species.

Comparison of taxa richness among years enables evaluation of environmental influences on algal diversity. Mean taxa richness ($TR_{1960–1964} = 13$) in the first years of the record (Fig. 5), when water levels were low and shallow-water habitats predominated, was similar to means from shallow lakes in Australia (Davidson et al. 2013), at times when benthic diatoms also dominated.

High abundance of centric diatoms in recent years can be related to the increase of water level. An increase in silica concentration in the water at the end of the 1990s (Sánchez 2000), in particular in 1996, reveals the relation between water quality and sediment algal composition. In freshwater lakes, stratigraphic changes in the sediment of the benthic (pennate) to planktonic (centric) diatom ratio are used as an indicator of past water level fluctuations (Wolin and Duthie 1999).

Freshwater diatom assemblages respond indirectly to changes in the aquatic environment that result from fluctuations in water level, but similar environmental conditions can also result from other factors (Wolin and Duthie 1999). This may explain why year 1966 was included in period 1, based on species composition, whereas the CCA put this year closer to other years in the profile. V_{max} in 1966 was 152.3 hm^3, whereas the mean of the first few years was 69.4 hm^3, years in which succession was difficult to detect. Coexistence of euplanktonic *Microcystis* with benthic diatoms, as occurred in 1964 (Fig. 3), has also been seen in other freshwater ecosystems (Abonyi 2015).

Sustained low water levels can lead to domination by late-succession benthic algae, sometimes in the form of large, filamentous mats (Lamberti and Moore 1984). In Hanabanilla Reservoir, however, the increase of V_{max} led to a change in assemblage structure, from early-succession, benthic (pennate) diatoms, to domination by planktonic species. Planktonic time interval was divided into three periods, as inferred from species assemblage composition (Fig. 4). CCA also revealed differences between these years (Fig. 7). In deep-water cores from large lakes, water-level changes may be reflected by changes in dominant planktonic forms, which respond to physical or chemical variables (Wolin and Duthie 1999).

Predominance in 1964 of *Microcystis panniformis,* an S strategist (stress-tolerant), could be related to the fact that at low latitudes, nutrient-enriched shallow systems may experience monospecific, steady-state *Microcystis* blooms. The ability of *Microcystis* to regulate its buoyancy helps it avoid excessive light near the water surface during the day, and enables it to re-establish its position in the water column after nocturnal water-column mixing (Reynolds 2006). According to Connell (1978), a community under intermediate-frequency disturbance may re-establish its pioneer species (C strategists) many times, and competing populations may coexist. Under high-frequency disturbance conditions, few pioneer species become established after each disturbance event and low diversity is maintained (Lopes et al. 2009). *Microcystis*, however, is relatively slow to establish in newly nutrient-enriched lakes, even though the habitat seems amenable for growth (Sas 1989), and no *Microcystis* blooms have been recorded in recent phytoplankton studies in Hanabanilla Reservoir.

Low taxonomic richness was maintained between 1965 and 1968 because new conditions led to predominance of C–S strategists. During high-water periods, the watershed supplies the reservoir with abundant nutrients and suspended sediment, which may appear as a “nutrient pulse,” transported advectively into the reservoir. The intermediate disturbance hypothesis would seem to be applicable to these types of successional events. During periods of high nutrient availability in Hanabanilla Reservoir, when physical and/or chemical disturbances occur, e.g. V_{max} and probably transparency variations, C–S species tend to predominate the algae biomass. Sometimes only two species of *Dyctiosphaerium* and one of *Aphanocapsa* make up $> 80\%$ of phytoplankton biomass under these conditions (Naselli-Flores 2000). C–S species display intermediate ecological characteristics, between those of C (competitive-invasive) and S (stress-tolerant) species. They are characterized by stress tolerance, but also an ability to exploit and conserve nutrients (Reynolds 2006).

Higher nutrient concentrations and organic matter may play a role in reducing diatom and chlorophyte numbers, and the rise to dominance of Cyanobacteria and Euglenophyta, in shallow, hypereutrophic lakes, particularly during the warm season (Çelik and Ongun 2006). In Hanabanilla Reservoir the second phase of primary producers was characterized by Chlorophyceae and Cyanophyceae (i.e. C–S species), with the highest Euglenophyceae abundances in the entire profile. Environments with high levels of organic matter favor euglenoids (Borics et al. 2003) and species such as *Phacus* sp., *Trachelomonas volvocina* and *Lepocinclis texta* were abundant in this period. Association of euglenoids (*Phacus, Lepocinclis*) with other unicellular forms reflects the presence of shallow-lake phytoplankton assemblages characterized by C-type, invasive, fast-growth-rate strategies (Reynolds 2006).

In 1972, C–R strategists displayed their highest abundance (20%). They included species with different tolerances for turbidity, which are associated with nutrient-enriched shallow ecosystems (Reynolds 2006). *Coelastrum,* a dominant species that year, is typical of shallow, nutrient-enriched lakes with low light conditions (Reynolds 2006). Hence, we infer that this period was characterized by a well-mixed water column, high concentrations of OC and TN, but relatively low V_{max}.

Predominance in 1974 of the S strategist *Microcystis panniformis*, representing 74% of the algal assemblages, probably indicates a stable water column. The photosynthetic efficiencies of some bloom-forming genera (e.g. *Microcystis*) are lower in turbid, mixed water columns, and they tolerate high daytime light intensities (Reynolds 2006). Some studies suggest that better-illuminated water columns favor the growth of green algae, which have growth rates much higher than *Microcystis* spp. (Lürling et al. 2013). Relatively stable thermal stratification in tropical lakes, a consequence of the large density difference per degree temperature change at higher temperatures, may lead to *Microcystis* dominance (Reynolds 2006).

In 1976, *Phormidium* sp. replaced *Microcystis* in abundance. This phenomenon has been seen in other reservoirs, where *Microcystis* was replaced by filamentous blue-greens *Phormidium* and *Oscillatoria*, and is attributed to an increase in the N/P ratio (Takamura et al. 1992), perhaps because some *Phormidium* species require more nitrogen for growth than does *Microcystis* (Fujimoto et al. 1997). From 1974 to 1976, the N/P ratio displayed only a slight increase, from 1.33 to 1.55 (Labaut et al. 2018), but V_{max} decreased from 139.2 to 84 hm^3, indicating the ability of *Phormidium,* an R strategist (disturbance-tolerant ruderal), to take advantage of transient habitats and convert resources into biomass (Reynolds 2006).

Since 1977 the reservoir developed a new period of phytoplankton dynamics, revealed by RDA, CCA and cluster analysis, mainly related to changes in V_{max} (hydrodynamics) and an increase in OC and TN. The return to S strategist dominance in 1979 demonstrates a shift to conditions that prevailed earlier, with less disturbance. The relatively constant conditions in the water column persisted for several years, marked by alternation of predominant C–S and S strategists, until the rise of R and C–R strategists ca. 1990. During the interval 1977–2010, values of TR were higher than those between 1960 and 1976 (Fig. 5). If higher diversity can be equated with a healthier ecosystem, these years were characterized by better water quality than in previous periods.

The R strategists were mainly represented by diatoms (*Aulacoseira granulata, Synedra* spp. and *Fragilaria* sp.) and desmids (*Staurastrum gracile* and *S. grallatorium*), and C–R strategists were mainly represented by Chlorophyceae (*Hariotina reticulata* and *Monactinus simplex*). The transition from S/C–S (S: *Microcystis, Ceratium, Anabaena* and C–S: colonial Volvocales) to R was the fourth stage in the phytoplankton succession, and was characterized by assemblages of diatoms (*Fragilaria, Aulacoseira granulata*) and desmids (*Closterium* and several species of *Staurastrum*) (Reynolds 2006).

This diatom/desmid assemblage, common phytoplankton in reservoirs (Hart 2006), is related inversely to water column stability, and vertical mixing is usually an important factor for ruderal taxa (Hart 2006; Reynolds 2006). For instance, *Aulacoseira* and *Staurastrum*, two R strategists (Reynolds 2006), dominated in the Volta Grande Reservoir in Brazil, where a power generation plant draws water from the base of the reservoir, which consequently has a near-isothermal water column that fails to stratify (Reynolds 1987).

Lund (1966) argued that turbulent mixing in reservoirs favors *Aulacoseira* and Reynolds (2006) suggested that reservoirs could be managed by promoting intermittent mixing and by keeping retention times short, thereby preventing any phytoplankton group from becoming too numerous/dominant. In Hanabanilla Reservoir, water residence times were long, i.e. more than a year (380–832 days) during the period 1990–2012. Use of water for power production, however, caused extreme fluctuations in stored water during those years, with consequent high variability in residence time, V_{max}, and V_{min} (Labaut et al. 2018), leading to dominance of R strategists *Aulacoseira*, *Fragilaria*, *Synedra* and *Staurastrum* (Fig. 3).

The functional approach has advantages over use of simple species composition when using algal remains in lake and reservoir sediments to infer past conditions. Forecasting the responses of functional groups (e.g. 'ruderals') is a more practical approach than trying to predict details of community composition (Hart 2006). Similar relative abundances of C–S, S, R, and C–R groups in Hanabanilla Reservoir in 2010, indicate the reservoir is vulnerable, under certain conditions, to an increase in "stress-tolerant" species, especially *Microcystis*, a species that has been present at generally low concentrations throughout the history of the reservoir, but could become a major component of cyanobacterial blooms.

Conclusions

Historical changes in the algal community of Hanabanilla Reservoir, Cuba, were driven by multiple mechanisms, including scraping of the reservoir bottom, changing water level, and anthropogenic input of nutrients and organic matter to the water body. Correlation between diatom assemblage composition and records of hydrodynamic changes in the reservoir confirm the utility of this primary producer group for inferring past water-level changes in reservoirs. Although human activities influence nutrient delivery to the reservoir, the primary importance of hydrodynamics in controlling algal abundance and community composition suggests that reservoir hydrology could be managed to prevent future cyanobacteria blooms.

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