

Spatial and temporal change characterization of *Ceratium furcoides* (Dinophyta) in the equatorial reservoir Riogrande II, Colombia

Caracterização das mudanças espaciais e temporais de *Ceratium furcoides* (Dinophyta)
no reservatório equatorial Riogrande II (Entrerriós, Antioquia, Colombia)

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Abstract: Aim: To establish the dynamics of *C. furcoides* in horizontal and temporal scales; and to determine the main ecological factors related to its dynamics. **Methods:** Samples were taken in five stations between July 2002 and July 2003. Physical and chemical variables were sampled monthly. Density was evaluated by sampling carried out within the photic zone. Growth rate (r), Turnover rate (T), Generation Time (gt), Niche Width (NW), Taylor's Power Law, and the rate of population change (σ_s), were used. Canonical Correspondence Analysis (CCA) was used too. **Results:** Total density was 264163.4 cel.L⁻¹, the highest was found in Up Río Chico and the lowest in Dam. The species was more clustered in space than in time. r ranged between 0.29 and 0.3 cel.d⁻¹, gt between 1.8 and 2.4 days, T between 0.55 and 0.42 divisions per day, NW between 0.58 and 0.72, and σ_s between 0.3 d⁻¹ and 2.3 d⁻¹. The first three components of CCA explained 92.2% of the variation. Density was positively associated with chlorophyll a , NH₄⁺, RWCS and wind direction. Light attenuation, NO₃⁻, SiO₂ and O₂ were negatively associated with *C. furcoides*. **Discussion:** *C. furcoides* is a S strategist; it increases its density in the warmest periods under eutrophic conditions, low light penetration and high thermal stability; it is independent of the temperature but dependent of changes in rainfall and nutrients, – especially nitrogen – and not soluble phosphorus. Up Río Chico presented the best conditions for the increase of *C. furcoides*, since this station presented the highest levels of total nitrogen, and the highest relative stability. **Conclusion:** *C. furcoides* has a very similar ecology to that of *C. hirundinella*. It is an organism highly variable in temporal and spatial scales, with a wide niche and a clustered distribution. It belongs to the Morpho-funtional Group V and to L_o and L_M Assotiations.

Keywords: *Ceratium furcoides*, phytoplankton, dinoflagellates, temporal and spatial dynamics, tropical reservoir.

Resumo: Objetivo: determinar a dinâmica de *C. furcoides* em escalas horizontal e temporal, e determinar os principais fatores ecológicos relacionados com sua dinâmica. **Métodos:** As amostras foram coletadas em cinco estações entre julho de 2002 e julho de 2003. As variáveis físicas e químicas foram amostrados mensalmente e a densidade foi estimada a través de coletas realizadas dentro da zona fótica, a taxa de crescimento (r), taxa de rotatividade (T), Tempo de Geração (GT), Largura do nicho (NW), Power Taylor's Law, e a taxa de mudança da população (σ_s) foram utilizados. Análise de Correspondência Canônica (CCA) foi usado também. **Resultados:** A densidade total foi 264.163,4 cel.L⁻¹, a maior foi encontrada em Up Río Chico e a mais baixa na barragem. As espécie foi achada mais agrupada no espaço que no tempo. O valor de r variou entre 0,29 e 0,3 cel.d⁻¹, GT entre 1,8 e 2,4 dias, T entre 0,55 e 0,42 divisões por dia, NW entre 0,58 e 0,72, e σ_s entre 0,3 e 2,3 d⁻¹. Os três primeiros componentes da CCA explicaram 92,2% da variação. A densidade foi positivamente associado com clorofila a , NH₄⁺, RWCS e direção do vento. A atenuação da luz, NO₃⁻, SiO₂ e O₂ estiveram associados negativamente com *C. furcoides*. **Discussão:** *C. furcoides* é um estrategista tipo S, aumenta sua densidade nos períodos mais

quentes perante condições eutróficas, penetração de luz baixa e alta estabilidade térmica. A espécie é independente da temperatura, mas dependente das mudanças na precipitação e nutrientes, – especialmente nitrogênio – não fósforo solúvel. Up Río Chico apresentou as melhores condições para o aumento de *C. furcoides*, porque esta estação apresentou os mais altos níveis de nitrogênio total e a maior estabilidade relativa. **Conclusão:** *C. furcoides* tem uma ecologia muito semelhante a aquela de *C. hirundinella*; é um organismo altamente variável nas escalas temporal e espacial, com uma vasta gama de nicho e uma distribuição agregada. Pertence ao Grupo morfo-funcional V e às associações Lo e LM.

Palavras-chave: *Ceratium furcoides*, fitoplâncton, dinoflagelados, dinâmica temporal e espacial, reservatório tropical.

1. Introduction

Autoecology, a branch of Ecology introduced by Schröter in 1886, studies species dynamics. According to Margalef (1983) it explains why the specie is able to survive under certain conditions and what its relationship to the environment is. It specifies the variety of a number of ecological features generally based on density measurements which reflect the response of a population to ongoing disturbing factors.

The natural dynamics of mobile dinoflagellate populations in lakes and oceans has been subject to research in a number of occasions. It has been observed that distribution patterns of the algae are the result of three interacting components: migration, water displacement, and turbulence generated during water mixing (Heaney and Talling, 1980a). Research has mainly been focused on vertical migration which is disturbed by light and temperature gradients, nutrient availability and the age of the population. Horizontal distribution, less studied however, can be influenced by many factors such as physical, chemical, and biological, but the dominant factor is water movement caused by wind (Popovský, 1990).

Dinoflagellate growth is controlled by physical and chemical variables such as pH, temperature and organic matter concentrations, ions such as calcium, chloride, and the several forms of nitrogen and phosphorus. According to Popovský (1990), the factors which most greatly affect the presence of dinoflagellates are light intensity, light spectrum change in the water column and dissolved oxygen concentration.

As *C. hirundinella*, *Ceratium furcoides* (Levander) Langhans 1925 belongs to the Ceratiaceae family, order Peridinales. It is a relatively big dinoflagellate with a body length between 162 and 322 μm , and a variable width between 28 and 42(56) μm . It has a big horn in the epi-valve and two, rarely three, in the hypo-valve. Its life cycle comprises a vegetative

cell and benthic cysts which are the result of sexual fusion; asexual reproduction occurs by means of oblique binary fusion (Pollinger, 1988; Hickel, 1988; Popovský, 1990).

The cosmopolitan character of the genus *Ceratium* has been cited by many Japanese, Israeli, Canadian, British, German, Swiss, Spanish, Italian and Hungarian studies (Moore, 1981; Rengefors, 1994; Pérez-Martínez and Sánchez-Castillo, 2001; Morabito et al., 2002; Grigorszky et al., 2003) and in subtropical regions in water reservoirs in Australia and Africa (Whittington et al., 2000; Ginkel et al., 2001). All of these studies deal with the ecology and the abundance of the species *C. hirundinella*. *Ceratium* has been cited too as a pantropical species, which means that it is located in the area roughly between the two tropics (O'Sullivan and Reynolds, 2004). But for these authors, it is reasonable to replace the term 'cosmopolitan' (which means species 'occurring almost anywhere and in many kinds of lakes') by the term 'subcosmopolitan', which applies to species occurring throughout the world, but always in specialized environments. Tropical lowland lakes are rich in cosmopolitan and pantropical taxa. *Ceratium* is one of these species (O'Sullivan and Reynolds, 2004).

According to Heaney et al. (1988) and Rengefors (1994) *C. hirundinella* and *C. furcoides* can be morphologically set apart, but their ecological requisites are very similar, so they are frequently considered as *Ceratium* spp. This similarity and, in many instances, careless observations by ecologist of the taxonomical characteristics which define a species, have led to the simple observation that the presence of a similar shape to *C. hirundinella* be accepted as such, ignoring the consequences this could have.

C. hirundinella is a warm water species that grows preferably during the summer months when the water be thermally stratified and they reach higher temperatures (Hutchinson, 1967; Moore, 1981; Moyá and Ramón, 1984). Margalef et al.

(1982), Margalef et al. (1976) and De Hoyos and Negro (2004) have found that some types of *C. hirundinella* (type *robustum* and type *graciles*) are classical inhabitants of mineralized waters with high conductivity and very scarce alkaline reserve.

Because it is unknown ecological characteristics of *C. furcoides*, both in spatial and in temporal scales, and because *C. furcoides* has been found coexisting with *C. hirundinella* in England (Heaney et al., 1988), and in Lake Plusßsee in Germany by Hickel (1985), in this investigation we pretend to answer: 1) what are the factors that influence the dynamics of *C. furcoides* in the spatial and temporal scales considered; 2) if these factors are similar to those known for *C. hirundinella*; and 3) locate the species in the systems of Reynolds Associations and in the Morpho-functional groups of Kruk et al.

If in the spatial-scale, the changes in the dynamics of *C. furcoides* are influenced by the decrease in the oxygen concentration, light availability, and organic matter increase; and if in the temporal-scale changes the dynamics of *C. furcoides* are influenced principally by temperature and stratification regime, we predict: 1) that *C. furcoides* has high densities in the sampling stations located in Río Chico and Río Grande branches (spatial scale), because in these two sampling stations, for the hydrologically conditions of the reservoir, have significant signs of eutrophication which diminish the oxygen concentration and the light penetration, and increase the decomposition of organic matter and the mineralization of its waters; 2) that *C. furcoides* is present all the sampling time because the stratified and the tropical conditions of reservoir ensure optimal conditions for the species development. If so, 3) due to the taxonomic proximity between *C. hirundinella* and *C. furcoides*, the ecological characteristics of *C. furcoides* are very similar to those of *C. hirundinella* (high

temperatures, highly mineralized waters and low alkalinity, among others).

2. Material and Methods

2.1. Study area

The Riogrande II reservoir is an energy generator and a water source for the consumption of the inhabitants from the metropolitan area of Aburrá's Valley (Antioquia, Colombia) (EPPM, 1994; Roldán and Ramírez, 2008). It is located in the central region of the Department of Antioquia, in the river bed of Riogrande, located at north of Medellín city. This river bed, with a catchment area of 1294 km², makes part of the drainage of Porce River whose waters run into Nechí River, then Cauca River and finally Magdalena River (EPPM, 1994).

Its weather is cold with air temperatures between 14 °C and 18 °C (average annual fluctuation of air temperature: -2.0 °C). It is a typical equatorial reservoir located in a zone with two rainy seasons (April-June and September-November) determined mainly by the displacement of the Inter-Tropical Convergence Zone (ITCZ). The highest humidity values are recorded between October and November with averages near 83%. Dry seasons are between December and March and July and August, the first one being drier than the second (EPPM, 1994).

It is delimited by Gauss' planes coordinates (Bogotá, Colombia): X = 1'208.000-1'219.000; Y = 838.000-849.000, over 2250 m above sea level (plates number 131-III-B y 131-III-D; Geographical Institute Geográfico Agustín Codazzi (Figure 1).

Its superficial area is 12 × 10⁴ m², its volume is 220 × 10⁶ m³ with 110 × 10⁶ m³ corresponding to useful volume. Its maximum and medium depths are 42.0 and 37.9 m respectively and its maximum length is 10 km. It is exposed to high nutrients load from de municipalities of Belmira,

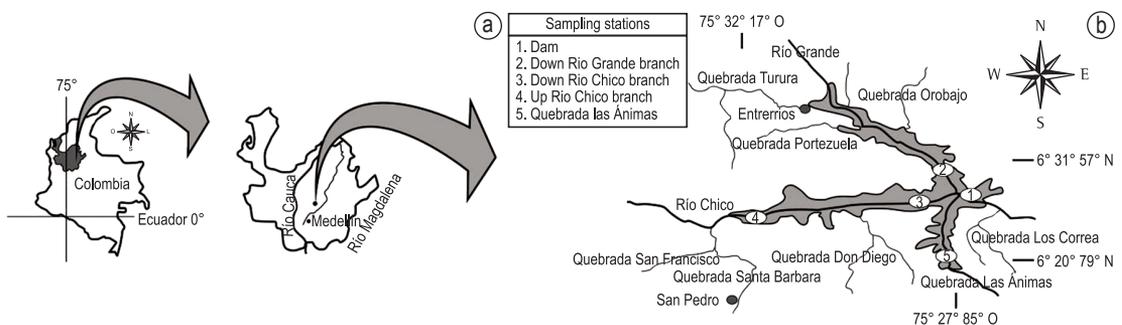


Figure 1. a) Riogrande II reservoir's map showing the location in a regional and local contexts. b) Location of the sampling stations: 1. Dam, 2. Down Río Grande branch, 3. Down Río Chico branch, 4. Up Río Chico branch and 5. Quebrada Las Ánimas branch.

Donmatías, Entreríos, San Pedro and Santa Rosa; as a consequence, it presents clear signs of eutrophication in the different sampling stations, especially in Río Chico and particularly in Up Río Chico. Its average retention time is 72.8 days which characterizes it as a reservoir of B class or as a reservoir of intermediate retention (Straškraba, 1999) with the chance of relatively long stratification and hypolimnetical depletion of oxygen. Thus, the reservoir can be divided into two specific areas according to their quality, one characterized by the dam, which corresponds to the reservoir lentic and the other queues characterized by Chico, Grande and Ánimas branches.

Recent studies about the current regime in the reservoir have shown that Riogrande branch enters the reservoir heading towards the dam, located on the Animas sampling station, and damming the upper portion of Río Chico branch (Gómez, pers. com.), so this sampling station can be considered as the most eutrophic and the most mineralized of the reservoir.

2.2. Sample design

Five sampling stations were located in the reservoir (Figure 1):

Dam (S₁): this sampling point is located 1 kilometre away from the land structure and displays the greatest depths of the reservoir (35 to 40 m average). It is a place that features the limnetic zone of the ecosystem.

Río Grande branch (S₂): it represents waters down Riogrande, in the limits to its inflow to the reservoir. Its depths vary from 30 and 35 m. This station also represents a transitional zone of the system.

Down Río Chico (S₃) and Up Río Chico (S₄) branches: they are located on the edge of the river entrance to the reservoir and the top of it. There is a depth between 25 and 30 m. This river receives contributions from the municipalities of San Pedro and Belmira.

Las Ánimas branch (S₅): it is located 1 km from the tower of recruitment and at the entrance of the Las Ánimas stream. It's the sampling station with less depth (12 to 15 m) and that provided the least flow to the reservoir. This stream receives contributions from the municipalities of Donmatías.

2.3. Methods

This research was based on available samples at the Limnology Laboratory *Alexander von Humboldt* of the Biology Institute at the Universidad de Antioquia, collected in 36 sampling times carried

out between July 2002 and July 2003 in the five mentioned stations. Water samples were collected with a 5 L Schindler bottle. Nutrients were monthly measured in each station and others variables each ten days during biological samplings.

2.4. Physical and chemical variables

Air temperature (Thermometer), pluviosity (EEPPM), wind speed and direction (Anemometer and Weathervane), transparency (Secchi disk with 0.20 m diameter); turbidity (Turbid meter); surface radiation attenuation (Licor Datalogger), temperature and oxygen profiles (YSI Thermistor), electric conductivity (WTW conductimeter) and total suspended solids (gravimetric method) were measured. Temperature profiles and dissolved oxygen in the water column from each sampling station were taken every 0.50 m in the first 4 m of the water column. From this point on, sampling was done every meter until the bottom was reached. Relative water column stability (RWCS) was calculated in accordance with Padisák et al. (2003).

Water samples to measure total CO₂, free CO₂, HCO₃⁻, CO₃⁼ (MacKereth et al., 1978), turbidity, conductivity, alkalinity (potentiometric) and pH were extracted every five meters from the water column for the three deepest stations (Río Grande, Down Río Chico and Dam) and every 2.5 m for the stations located at the end of the reservoir (Ánimas and Up Río Chico). Total nitrogen (Kjeldhal), Ammonium (N-NH₄⁺ nesslerization), Nitrate (N-NO₃⁻) (Cadmium-Copper Reduction), soluble reactive Phosphorus (ascorbic acid) and silicates were monthly measured in each station for the photic and aphotic zones. For the multivariable analyses (CCA and cluster), only the monthly nutrients concentrations found in the photic zone (n = 12) were taken into consideration.

2.5. Biological variables

The density of *C. furcoides* was evaluated from samples gathered at three different depths of the photic zone in the water column. The samples were subsequently mixed in a bucket and one-liter sub-sample was extracted. Using the same procedure, active chlorophyll a and phaeopigment concentration (Lorenzen, 1967; Sartory and Grobbelaar, 1984) were calculated.

Phytoplankton samples were fixed with lugol-acetic acid. Sample counting was done at 10× in a Leitz Ortholux II inverted microscope in sedimentation chambers of different volumes (100, 50, 25 and 10 mL). The number of fields ranged

between 30 and 112 depending on the density of the organism. The density was reported in cells.L⁻¹ using Ross formula (Ross, 1979). The other six taxa of phytoplankton that appear in the Figure 6 are, together with *C. furcoides*, had the highest abundance, may be competitors of the species studied. The same criterion was used for the two species of zooplankton shown in that figure.

Zooplankton samples were collected using a 60 µm sieve through which filtered 35 liters of water. Fixation of organisms was performed using 30% formalin.

The growth rate (r) of the species was calculated from the density cumulative curve in each station. Generation Time (GT) was calculated based on $GT = \ln 2 \cdot r^{-1}$ Turnover rate (T), equivalent to the number of divisions in a day, was obtained taking into consideration the reciprocal of Generation Time: $T = GT^{-1}$.

In order to find the type of specie's disposition in the space and in the time the Taylor's Power Law (1975) was used. The width of standardized niche (NW) and the rate change (σ_s) between samplings in each station were calculated based on evenness of Pielou (1975) and in formulae proposed by Lewis Junior (1978), respectively.

2.6. Statistical analysis

A Two-way ANOVA using Statgraphics plus v. 4.0 was carried out to establish the statistical significance of the difference in density of *C. furcoides* between the different stations and sampling times. The data was logarithmically transformed. If significant differences were found, mean comparison (post-hoc test) was calculated using the LSD test (Least Square Difference). Sampling times were grouped using Nearest Neighbor linking strategy and squared Euclidean Distance Index.

To determine the significance the significance of the relationship between biological and environmental variables were used initially a Detrended Correspondence Analysis (DCA) (Hill and Gauch, 1980) based in density of taxa to establish if an unimodal model (Canonical Correspondence Analysis, CCA) or a lineal one (Redundancy Analysis, RDA) fit to biological data. To justify the choice rule used the length of the gradients, which states that if the gradient is less than 1.5 SD (standard deviations) should be used RDA as most of the response curves are linear taxa, and if the length of the gradient is greater than 4 SD, the response curves are monotonic and one must use a CCA. In our case, the lengths of the four axis

were greater than 4 SD, indicating that the model monotonic response is most appropriate to analyze the relationship between environmental variables and density of taxa (Leps and Šmilauer, 2003), therefore, we used a CCA using software CANOCO 4.0 (ter Braak and Šmilauer, 1998).

Data were centered and standardized. In order to purge the final diagram presented in Figures 5 and 6, samplings near the origin were eliminated. The significance of environmental variables in explaining the variance of morphological traits in the PCA was performed using Monte Carlo test with 499 permutations.

To make this the variables considered in the analysis were those that registered a $\alpha < 0.05$ and an inflation factor < 20 . Significance of environmental variables to explain the variance of morphological features in ACC was made by Monte Carlo test with 499 permutations.

3. Results

A total density of 264163.4 cells.L⁻¹ of *C. furcoides* were found. The station with the highest total density of this organism was Up Río Chico (S_3) with 103 329.5 cells.L⁻¹, followed by Río Grande (S_4) with 62 220 cells.L⁻¹, Ánimas (S_1) 44175.6 cel.L⁻¹, Down Río Chico (S_2) 40 840.1 cells.L⁻¹ and Dam (S_5) (13 598.1 cells.L⁻¹) (Figure 2a). The highest density of *C. furcoides* in the reservoir was recorded on May 12, 2003 (T_{28}) with 41 213.9 cells.L⁻¹ and the lowest was recorded on July 29, 2002 (0.96 cells.L⁻¹) (Figures 2 and 4).

ANOVA for the log (density +1) displayed highly significant differences among stations ($\alpha = 0,000$) and among sampling times ($\alpha = 0.000$). Mean comparison of density for the stations formed three groups: the first one composed by sampling station Dam (S_5), the second one included the stations Down Río Chico (S_2), Ánimas (S_1) and Río Grande (S_4); and the third one by station Up Río Chico (S_3); which fully agrees with that showed by accumulative densities for each sampling station in Figure 2, according to the mentioned current pattern in the reservoir.

In the reservoir, the highest density of *C. furcoides* was started by the end of March 2003 and decreased by the end of May, with the highest values between in April and May (Figure 3). In dendrogram on Figure 4 we can observe that samplings of April 28 (T_{27}) and May 12 (T_{28}) are well differentiated from the rest since they have the highest densities in most of the sampling stations, but especially in station Up Río Chico (S_3).

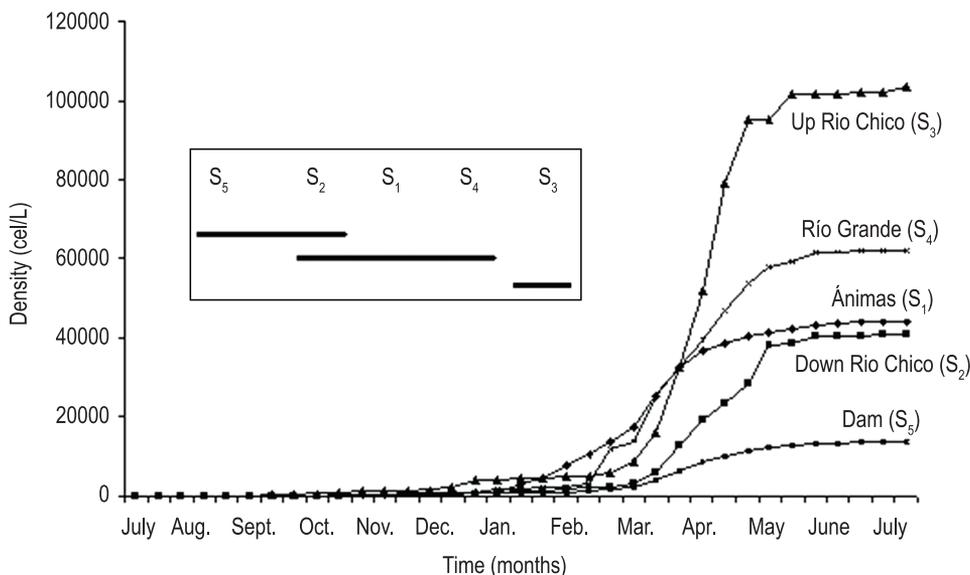


Figure 2. Riogrande II reservoir. Accumulative density in function of changes in time in each sampling station and. Inset shows the mean comparison with LSD test for the sampling stations.

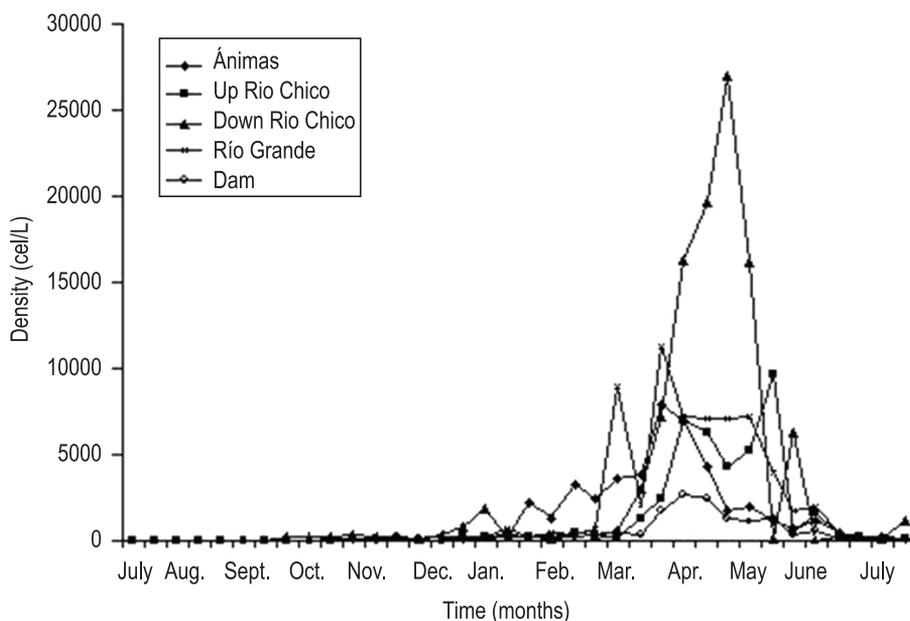


Figure 3. Riogrande II reservoir. Density of *C. furcoides* in each sampling station.

Up Rio Chico, the station where *C. furcoides* was more abundant, showed the highest values of density (26967 cells.L⁻¹) and chlorophyll a concentration (523.1 µg.L⁻¹) in the entire reservoir on May 12 (Figures 2 and 6). During this sampling, the temperature in the photic zone of this station was 23.4 °C, ammonia nitrogen 1.15 mg.L⁻¹, nitrate 0.61 mg.L⁻¹ and the relative stability of water column (RWCS) was 1495.6.

Taking into account the results presented by Taylor's law, *C. furcoides* was found slightly more clustered in space ($b = 2.2$) than in time ($b = 1.9$).

The variation between niche width values were generally high and stables (mean value = 0.66, CV = 8.8%, Figure 5a). The growth rate did not have a significant change; it varied between 0.29 cells.d⁻¹ in Up Rio Chico and 0.3 cells.d⁻¹ in Riogrande (Figure 5b). Generation Time was low

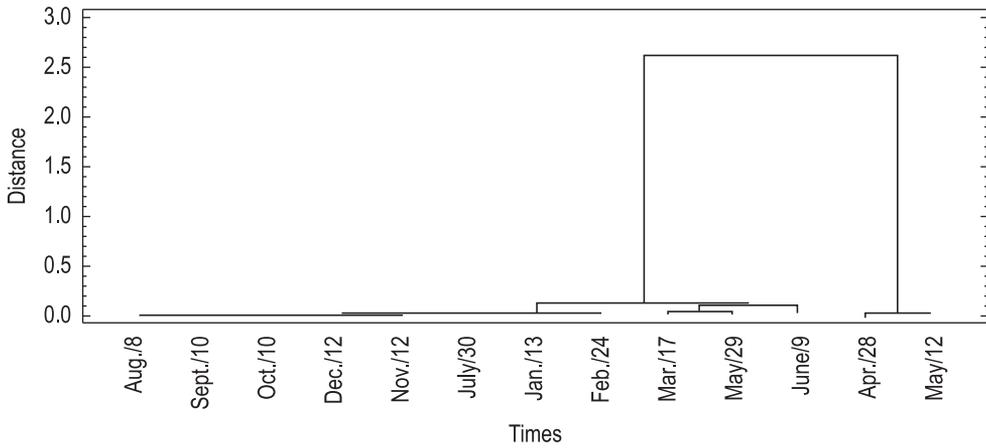


Figure 4. Riogrande II reservoir. Classification Analysis for the sampling times.

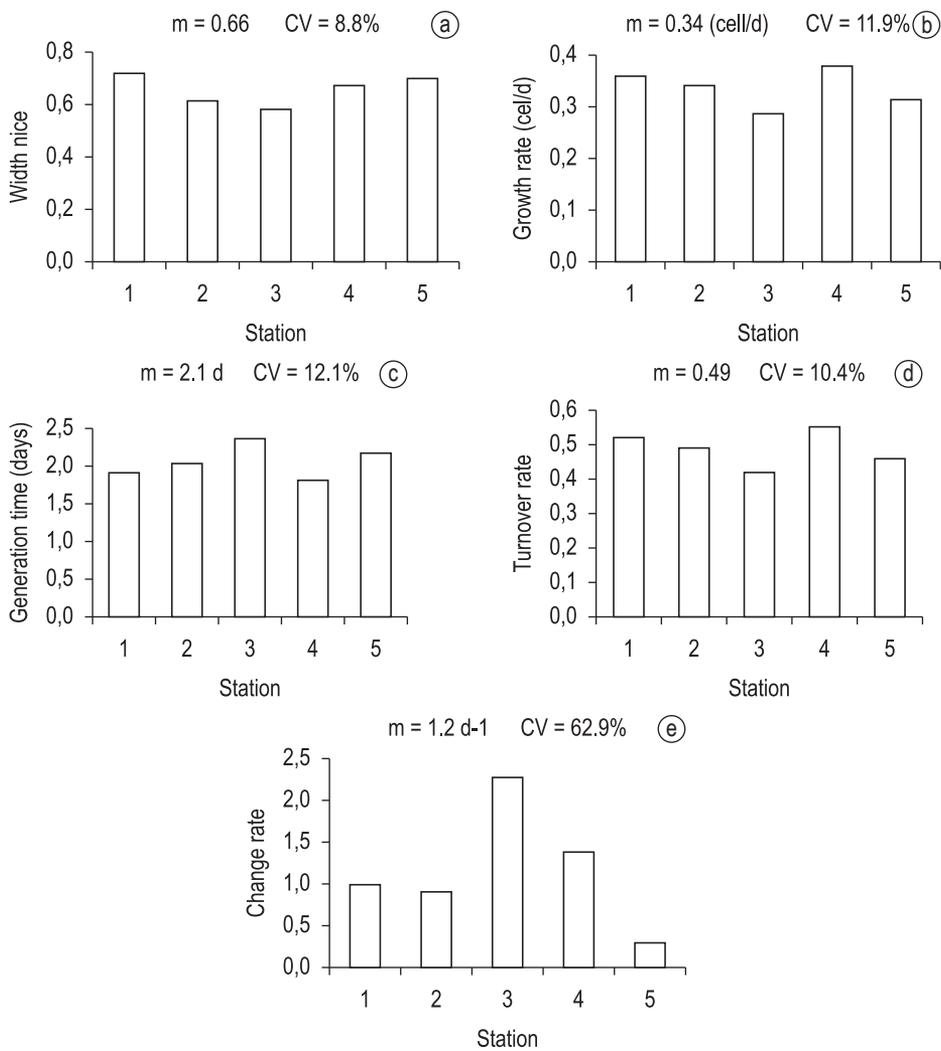


Figure 5. Riogrande II reservoir. Mean and relative dispersion values of niche width, growth rate, generation time, turnover rate and rate of population change of *C. furcoides* (m = mean value, CV = coefficient of variation).

(1.8 days in Río Grande branch and 2.4 days in Up Rio Chico branch) corresponding to 0.55 and 0.42 divisions per day respectively (Figure 5c). Growth rate ($CV = 11.9\%$, Figure 5b), Generation

Time ($CV = 12.1\%$, Figure 5c) and Turnover rate ($CV = 10.4\%$, Figure 5d) were stables too. The Rate of population change were highly variable (Figure 5e).

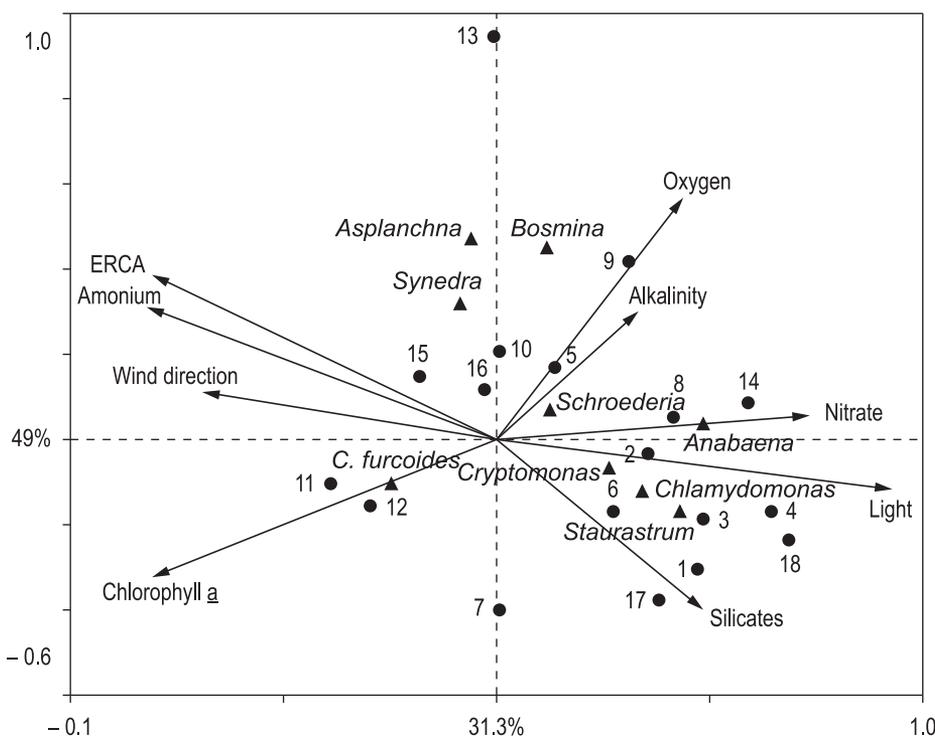


Figure 6. Vectorial diagram of species, environmental variables and sampling times in each sampling station on first and second canonical axes in CCA. Sampling times in each one of the stations are designed as: **Ánimas** (1. August 8-2002. 2. September 10-2002. 3. December 12-2002. 4. January 23-2003. 5. May 29-2003. 6. July 30-2003). **Down Rio Chico** (7. April 28-2003). **Up Rio Chico** (8. October 10-2002. 9. November 12-2002. 10. February 24-2003. 11. April 28-2003. 12. May 12-2003. 13. May 29-2003). **Río Grande** (14. November 12-2002. 15. May 12-2003. 16. May 29-2003). Dam (17. August 8-2002. 18. September 10-2002).

The results provided by the ACC showed that the three first axes explained 92.2% of matrix inertia; the first axis explained 49.3% of the total variation ($\lambda_1 = 0.70$), and the second one 31.3% ($\lambda_2 = 0.44$). The species association with the first axis was 39.6%, and with the second one 25.2%.

The most related variables with *Ceratium*'s density were chlorophyll a ($R = 0.90$), RWCS ($R = 0.69$), ammonium ($R = 0.68$) and wind direction ($R = 0.47$). The variables that affected negatively the organism were light ($R = -0.84$), alkalinity ($R = -0.72$), nitrate and oxygen ($R = -0.49$), and silicates ($R = -0.34$) (Figure 6).

The sampling stations and sampling times nearest to *C. furcoides* in Figure 6 correspond to those with the higher density values (Up Rio Chico: April 28 and May 12); those farthest to the specie are those with the lowest densities: Up Rio Chico (S3) in November 12 (T11) 2002 and Mayo 29 (T30) 2003, Ánimas in January 23 (T18), Dam in September 10 (T5), and Río Grande in November 12 (T11) 2002.

Phytoplankton taxa negatively related with *C. furcoides* were *Schroederia setigera*, *Cryptomonas* sp.,

Staurastrum spp., *Chlamydomonas* sp. and *Anabaena* sp.; in zooplankton were *Bosmina* sp. and *Asplanchna girodi* (Figure 6).

In April, May and at the beginning of July 2003 high ammonium and soluble reactive phosphorus values were present in Up Rio Chico (S3) and especially in April 28 (T₁₁) and May 12 (T₁₂). In this station the highest values of chlorophyll a were present coinciding with the highest densities of *C. furcoides*; simultaneously the major relative stability in the water column (ERCA) and the lowest light, nitrate and oxygen values were found.

4. Discussion

All organisms tend to cluster for different reasons. In Phytoplankton, the existence of clusters highlights this condition and shows that even microscopic organisms “choose” places offering the best conditions to live. For this reason, *C. furcoides* was found slightly more clustered in space than in time (Figure 2), and Up Rio Chico station between the times April 28 and May 12 offered the best conditions to increase its density, favored by the relatively high concentrations of ammonium, as well

as by the thermal stability of the water column, the low light penetration, and lower concentration of nitrate and alkalinity, that favored the highest rate of population change to the species (Figure 5e).

The content of chlorophyll a in phytoplankton depends on factors such as the taxonomic group, light conditions and nutritional state of the phytoplankton. According to Olrik (1994), the content of this photosynthetic pigment is generally higher in green algae and relatively low in the cyanobacteria and the dinoflagellates. For *C. hirundinella*, Reynolds (1984) records a value of chlorophyll a of 1.26% dry weight and 5.4 µg of chlorophyll a per mm³ of bio-volume, while Harris et al. (1979) cites a cellular content of chlorophyll of 250×10^{-9} mg.cel⁻¹ for *Ceratium*.

Species with the ability to adjust their vertical position in the water column (via buoyancy or swimming) can actively select that part which is optimal for their own photosynthesis. For example *Ceratium hirundinella* tends to cluster in water layers receiving 125-440 mEm⁻².s⁻¹ PAR (Harris et al., 1979; Padisak, 1985). In Riogrande II coincided that when the *C. furcoides* density was high, the chlorophyll a concentration in Up Rio Chico was also high. The increase of *Ceratium* density could have determined the increase in the concentration of this pigment. Deep-layer Chlorophyll Maxima (DCM) occurs at depths rather greater than the thermocline, frequently at the nitricline. In the La Concepcion Reservoir, southern Spain, *Ceratium hirundinella* was found to be abundant in the DCM that occurs in the metalimnion, where it receives 1-3% of surface incident light (Galvez et al., 1988).

Although dinoflagellates seem to prefer abundant light and are frequently found in the upper strata of the water column, its requirements seem to be completely flexible (Pollinger, 1988). For Moore (1981) changes in light conditions seem to be important, but the quantity of light in the water column was not the main factor controlling the growth of *Ceratium* in six Canadian lakes. *C. furcoides* was highly dense in the station where the light faded faster, but due to the fact that we integrated the photic zone, we can't tell at what depth the highest density was found. It would possibly be found just as for *C. hirundinella* at a depth in which the range of radiation is optimal thanks to its ability to compensate for low levels of radiation by swimming to the surface layers, and at the same time its ability to swim away from the surface when it is bright (Frempong, 1984). The

high number of *Ceratium* could have influenced in the low light entrance presented in Up Rio Chico, since in the CCA analysis, this variable showed an inverse behavior to the *C. furcoides* density.

The niche width found in this research is probably similar to that of many other dinoflagellates. There are many reasons for this behavior. One of these is that *C. furcoides* can grow in the dark displaying heterotrophic nutrition, and phagotrophia (Bruno and McLaughlin, 1977) because its mobility allows it to exploit resources in the vertical and horizontal dimensions even under stable stratification conditions. For this reason, we consider that this organism is similar to *C. hirundinella* in the use of space and time.

Because of its relatively big body and in some cases the presence of horns, many dinoflagellates cannot be used as food by zooplankton, which prevents lost by grazing (Margalef, 1983; Pollinger, 1988). Despite this, it has been found *Peridinium* in the stomach content of *Bursariella truncate*, and several species of *Asplanchna* have been known for eating *Ceratium* (Pollinger, 1988), and such it happens in Riogrande II, where some pieces of *C. furcoides* were found in *Asplanchna*'s stomach contents (Estrada, pers. comm.). However, it is not possible to determine if the grazing by this specie was determinant in the *C. furcoides* control yet. Everything indicates that according to the relatively high retention time of the reservoir, its incomplete atelomic type of mixing (Mazo, 2008) and the *C. furcoides* relatively big size, of the four mortality causes (hydraulic washout, sedimentation, grazing and physiological death), physiological death could be considered the main factor causing the population control of this specie.

Regarding the presence of the cladoceran *Bosmina*, we believe that its effect on the density of *C. furcoides* is not considerable, because spiny appearance of this species prevents its filtration by *Bosmina*. Besides this, we could not find in the literature any report that refer to *Bosmina* as predator of *Ceratium* or other dinoflagellate. We believe that, as with other blooms forming species, *Bosmina* (like other cladocerans and copepods) could coexist with *Ceratium* increases. Needless to say, that *Bosmina longirostris* has long been a representative taxon and also one of the most abundant zooplankton species in time and space in the reservoir. It is also an indicator species for eutrophic sites.

Many dinoflagellates are eutrophic forms and its blooms occur during summer months, how

a lot of studies about *C. hirundinella* in Europe have shown (Hutchinson, 1961; Harris et al., 1979; Heaney and Talling, 1980b; Moore, 1981; Frempong, 1984; Hickel, 1985; Padišák, 1985; Pollingher, 1988; Sandgren, 1988; Ginkel et al., 2001; Gliora et al., 2003). A similar behaviour seems to have *C. furcoides*.

In Riogrande II reservoir, the air temperature (CV = 10%) and the stability pattern (atelomictic pattern, Mazo 2008) did not have a significant variation throughout the year, as it is usual in the Equatorial zone, where seasonality is a function of rainfall and wind patterns and not of the variations in light and temperature. We consider that this is the reason why *C. furcoides* was present throughout the sampling year. However, the highest abundance of *C. furcoides* coincided with the beginning of the rainy season. As in Plußsee lake where *C. furcoides* bloom diminished abruptly after a strong rain period (Hickel, 1985), in Riogrande II the reduction of density also coincided with the highest level of rainfall on May 29, 2003 (34.8 mm).

C. furcoides in Riogrande II reservoir coincided with the characterization given to this genus, as an organism of warm waters, with an optimum temperature range between 15 and 25 °C (Heaney et al., 1988; Pollingher, 1988; Ginkel et al., 2001), though Moore (1981); although Pérez-Martínez and Sánchez-Castillo (2002) have found it at 4 °C.

The horizontal distribution of *C. furcoides* in the reservoir displayed significant differences among the stations showing a clustered pattern. Kawabata and Kagawa (1988) in Berh dam found that *C. hirundinella* was less abundant in the dam reservoir and was mostly present towards the “tails” of the reservoir. In our research, *C. furcoides* was also less abundant in the Dam station of the reservoir (S₅) and the highest density was present in one of the “tails” of the reservoir corresponding to the station Up Rio Chico (S₃) which is according to wind direction, positively related to the density in Figure 6, and to the described local current pattern within the reservoir (*see study area*) linked also to chemical structure of the reservoir (Harris et al., 1979).

Reynolds (1984, 1997, 2006) considers to *Ceratium* as an organism belonging to the phytoplanktonic canopy, able to operate and dominate among the plankton for long periods after the nutrients in the surface waters have been depleted. Their mobility allows to this genus to live successfully in highly stratified lakes, segregated

resources and their effectiveness to “harvest” makes no difference whether the initial resources are high or low. For this reason, the relatively high correlation (R = 0.69) with the stability test chosen for this research (RWCS) (Figure 6). Olrik (1994), states that the species of *Ceratium* often bloom in lakes with strong thermal stability. As with *P. willei* and *P. cinctum*, *Ceratium* can develop high densities and biomasses from mesotrophic to eutrophic lakes which are rich in organic matter as organic nitrogen. This is one reason, why they can compete for dominance with the blooming Cyanobacteria; they can even precede their blooming, more often follow them and hardly ever co-dominate with them (Reynolds, 1997, 2006).

Dinoflagellates generally display low growth rates and long generation times when compared to other algae; as an example, Reynolds (1997, 2006) cites *Synechococcus* – a well known C strategist – whose growth rate in laboratory conditions is 7.97 cells.d⁻¹ for a generation time of 2.09 hours (=0.087 days); this organism divides at 41 °C, 11.5 times a day. Under the field conditions of this research, *C. furcoides* showed low growth and turnover rates and a high generation time. This organism, under the above conditions, divides 0.49 times per day; this means, it divides 23.6 times less than *Synechococcus*.

The growth rate found for *C. furcoides* in this research (0.34 cells.d⁻¹) is very high when compared to that of *Peridinium* (0.06 cells.d⁻¹, under laboratory conditions), but similar to that of *C. hirundinella* under the same conditions (0.21-0.27 cells.d⁻¹) by Reynolds (1984) and 0.14-0.24 cells.d⁻¹ by (Padišák, 1985); under field conditions Pollingher (1988) found a value oscillating between 0.12-0.27 cells.d⁻¹. This value (0.34 cells.d⁻¹) is also low when compared to that registered by Moore (1981) in Canada (6.1 cells.d⁻¹). However, in the temperate zones, Heaney and Talling (1980a) (0.016-0.092 cells.d⁻¹) and Whittington et al. (2000) (0.1 cells.d⁻¹) have registered too lower speed growth for *Ceratium*.

Because nutrient depletion prevents explosive growth of edible algae, phytoplankton composition shifts towards taxa which can utilize high hypolimnetic phosphorus concentrations, as *Ceratium* spp. (O’Sullivan and Reynolds, 2004).

The generation time found for *C. furcoides* in this study is very lower when compared with that was registered for other dinoflagellates as *Peridinium* with generation times of 11 days (Pollingher, 1988). Padišák (1985) cites several generation times for

C. hirundinella during summer under stable thermal conditions which vary between 2.9 and 24.8 days. This suggests that the growth of dinoflagellates and *C. furcoides* in particular, is influenced by nutrients availability and light, which explains the differences among the sampling places where it was found; this explains too its position in the Figure 6: opposite to the light and to oxidized nutrients as nitrates and silicon.

C. furcoides – as *C. hirundinella* – is a big unicellular organism (volume $> 10^4 \mu\text{m}^3$), S-strategist, stress tolerant, K-selected, with a slow growth rate even under good conditions; with a low SV^{-1} ratio ($< 0.3 \mu\text{m}^{-1}$) and relatively low metabolic rate. These apparent disadvantages are compensated with resistance to herbivory and high capacity to store phosphorus (since it showed a low inhibition constant for this nutrient, but a high affinity for it); for this reason, it tolerates nutrient stress, exploits organic particles (mixotrophy) and has a low breathing rate. It has the potential ability to increase its population through the recruiting of stocks of cysts available in the sediment. Its lack of inhibition under the presence of strong light is due to its lower capacity to obtain light per unit of volume (low projected area per unit of mass) when compared to the small forms (see the position of the organism related with light in Figure 6). In despite of its growth rates and reduced breathing rates, it prefers high temperatures; so, its main disadvantage is its reduced tolerance to the low temperatures.

For these reasons, we think that *C. furcoides* belongs to Assotiations L_0 and L_M in Reynolds et al. (2002) and Reynolds (2006) classification systems; and – that like *C. hirundinella* – *C. furcoides* belongs to the Morpho-functional Group V of Kruk et al. (2009), which includes most single-celled dinoflagellates, small to large with a variety of types ranging from r-selected species to K-selected as *C. hirundinella*, with moderate value of SV^{-1} and possession of flagella, reducing their sinking rates and facilitating access to nutrients, which together with the production of cysts and the ability of phagotrophy and mixotrophy in some species may increase tolerance to low concentrations of them. Its relatively high value of MLD and the presence of flagella can supplement a substantial resistance to grazing. Similarly, *C. furcoides*, can be located in Morpho-functional Group 1b of the system proposed by Salmaso and Padisák (2007).

5. Conclusion

Relating to the question that motivated this research about the population dynamics of *C. furcoides* we can conclude that it has a similar

ecology to that of *C. hirundinella*, since it is an S-strategist which increases its density in the warm periods of the year under eutrophic and mineralized conditions, low light penetration and high thermal stability. It is a warm water organism which belongs to Morpho-functional Group V and to L_0 and L_M Assotiations. This is also an organism which in Riogrande II reservoir shows a wide niche and clustered distribution in space as well as in time. As a consequence, the hypothesised was accepted.

The variables negatively influencing the ecology of *C. furcoides* density were alkalinity, light, nitrates, and to a lower extent water temperature and oxygen; as a consequence, in Ánimas, Down Rio Chico and Dam, where these variables were the highest, the organism density was lower throughout the sampling year.

In the sampling year in Riogrande II reservoir, Up Rio Chico station presented the best conditions for the highest density of *C. furcoides*, since it presented the highest levels of total nitrogen, and the highest relative stability in the water column.

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