Algal recolonization following an extraordinary drought in permanent lowland streams

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Aʙsᴛʀᴀᴄᴛ. Droughts reduce habitat and fragment the continuity of running water systems producing lasting effects on sediment biota and affecting density and biomass of algae. When droughts occur, the survival of algae and cyanobacteria of the biofilm depends on different alternatives to overcome the stress. In Pampean streams, periods of low flow causing desiccation stress in the biofilm may be linked to El Niño/Southern Oscillation phenomenon, and to water management practices (irrigation and extraction), that can reduce stream base flows for prolonged periods, reducing wetted area and dewatering the stream bed. The aim of this study was to determine the response of epipelic algae (analyzed by greater algal groups Cyanobacteria, Euglenophyta, Dinoflagellates, Green Algae, Diatoms) to desiccation as a disturbance, in streams without frequent periods of drought. First, we studied the *in situ* vertical distribution of epipelic algae in stream sediment during the drought period as a refuge strategy, along with the vertical distribution of sediment humidity in 10 cm sediment corers divided in 6 segments at depths 0-1 cm (uppermost layer), 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm and 5-10 cm. Secondly, we analyzed the recolonization patterns of the epipelic algal assemblage after the drought by studying the succession of autotrophic organisms, in order to better understand the role of sediments as a source of algae populations. For this, 2 cm deep corers were placed with water in microcosms and monitored during 2 weeks. Our results indicate that when the streams are affected by a severe drought, algae and cyanobacteria survive; this could be related with the moisture content of the sediment. Besides, after hydratation of the sediment, the community rapidly increased its density. Cyanobacteria were the most resistant group to desiccation and the one who had the faster reaction to hydratation.

[Keywords: benthic microalgae, biofilm, disturbance, flow loss, temperate stream]

Rᴇsᴜᴍᴇɴ. Recolonización de algas tras una sequía extraordinaria en arroyos permanentes de llanura. Las sequías reducen el hábitat y fragmentan la continuidad de los sistemas lóticos, produciendo efectos duraderos en la biota de los sedimentos y afectando densidad y biomasa de algas. Al producirse sequías, la supervivencia de algas y cianobacterias del biofilm depende de diferentes alternativas para superar el estrés. En los arroyos pampeanos, los periodos de interrupción o bajo caudal que estresan el biofilm pueden relacionarse con el fenómeno de El Niño/Oscilación del Sur y con la gestión del agua (e.g., riego/extracción), que reducen los caudales base, disminuyen el área húmeda y secan el lecho del arroyo. El objetivo de este estudio fue determinar la respuesta de las algas epipélicas a la desecación, analizadas por grandes grupos algales (Cianobacterias, Dinoflagelados, Algas verdes, Diatomeas) en arroyos sin períodos frecuentes de sequía. Primero, estudiamos la distribución vertical de las algas en el sedimento del arroyo como estrategia de refugio durante el período de sequía, junto con la variación de la humedad del sedimento, en *corers* de sedimento de 10 cm divididos en seis segmentos a las profundidades 0-1 cm (superior), 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm y 5-10 cm. Segundo, analizamos los patrones de recolonización del ensamble de algas epipélicas tras la sequía, estudiando la sucesión de organismos autótrofos para comprender el papel de los sedimentos fluviales como fuente de poblaciones de algas. Para esto, *corers* de sedimento de 2 cm de profundidad fueron colocados en microcosmos con agua y estudiados durante 2 semanas. Nuestros resultados indicaron que cuando una sequía severa afecta a los arroyos, algas y cianobacterias sobreviven, pudiendo relacionarse con el contenido de humedad del sedimento. Además, tras la hidratación del sedimento, la comunidad autotrófica aumentó rápidamente su densidad. Las cianobacterias fueron el grupo más resistente a la desecación y el que más rápido reaccionó a la hidratación.

[Palabras clave: microalgas bentónicas, biofilm, disturbio, pérdida del caudal, arroyos templados]

Introduction

The alteration of flow regimes (floods and droughts) is among the major forms of natural disturbance in flowing waters (Lake 2003). With global climate change and local anthropogenic pressures, the frequency and severity of these extreme events are expected to increase (e.g., Overpeck and Cole 2006). Particularly, droughts reduce habitat and fragment the continuity of running water systems (Fazi et al. 2008). As drought progresses, water bodies may dry up or become reduced to a series of diminishing pools, and may therefore produce dramatic and lasting effects on sediment biota, both directly and by altering interactive linkages (Lake 2003). Drought affects the density and biomass of riverine algae through the direct effect of water stress on algal cell structures, also affecting algal groups and their overall diversity (Sabater et al. 2017). When droughts occur, the prevalence of algae and cyanobacteria of the biofilm depends on different alternatives to overcome the stress.

One strategy adopted by some autotrophic organisms is to migrate into the sediments. Motility seems to be a common feature of epipelic algae (Hasler et al. 2008) allowing them to migrate vertically within sediments (Round and Eaton 1966; Happey-Wood 1988). Epipelic migration in the surface sediments is a dynamic process that is generally thought to be driven by nutritional requirements and light, and often involves the positioning of algae along steep gradients of dissolved nutrients and oxygen (Round 1981; Revsbech and Jorgensen 1983). Besides this, migration into the sediments is also a common strategy to survive drying (Consalvey et al. 2004; Bogan et al. 2017). For example, a certain number of diatoms persist on the streambed after flow cessation and are widespread in moist or wet soils and sediments (Pfister et al. 2017).

Having a desiccation-resistant life stage is another viable resistance strategy to deal with dehydration. Primary producers, including chlorophytes and cyanobacteria, commonly use dormant stages to resist drying (Bogan et al. 2017), becoming active again within hours or days of flow resumption (Robson et al. 2008; Timoner et al. 2014). Besides, responses of cyanobacteria and algae to flow intermittence include specific growth forms, cellular structures, or even genetic adaptations (Sabater et al. 2017). Some cyanobacteria, especially those forms having sheaths that quickly rehydrate, are extremely quick to react to increased air moisture or resumption of stream flow (Sabater et al. 2000).

The recovery rates of the algal assemblages after droughts are dependent on their recolonization ability. Algal taxa differ in the timing and mode of colonization processes such as drift, local reproduction (Peterson 1996) and growth from dry biofilm (Robson et al. 2008), and assemblage composition will reflect those differences (Chester and Robson 2014). According to Peterson and Boulton (1999), succession of benthic algae in intermittent desert streams originates from 'clean' substrata, whereas succession in perennial streams originates from resistant (basal) cells on the substratum. This implies that patterns of algal growth and community structure in perennial streams reflect earlier growth patterns, but that patterns observed in intermittent streams do not (Robson 2000).

In general, full recovery of algal biofilms occurs within 12 weeks of flow resumption, but the duration of the flow conditions preceding the dry period can alter the recovery timing and assemblage trajectories (Robson et al. 2008; Chester and Robson 2014; Timoner et al. 2014). For example, previous field studies show that when drying occurs rapidly, there is a devastating effect on algal recovery from dry biofilm (Benenati et al. 1998; Mosisch 2001). In contrast, when drying occurred naturally and slowly, regrowth from dry biofilm is apparent (Robson 2000; Robson and Matthews 2004). Hence, algal communities in watercourses subjected to frequent low-flow periods (e.g., because of seasonal changes in the flow regime) are expected to be better able to survive desiccation stress, while algae in streams which rarely experience conditions of low flow would be most affected if subjected to desiccation (Mosisch 2001).

Lowland streams across the Pampa Region (Argentina) are characterized by high basal nutrient concentrations, particularly N and P (Giorgi 1998), as they run through depositional areas that are dominated by volcanic sediments rich in phosphates and silicates (Martínez and Osterrieth 1999; Giorgi et al. 2005). Their slope ranges between 1.15 m/km in the highest areas (10% of the total area) and 0.25 m/km in the lowest areas, and water enters mostly by precipitation and underground flow (Gómez and Licursi 2001). They are characterized by the lack of riparian autochthonous forest vegetation; a very high growth of primary

producers such as algae and macrophytes (Acuña et al. 2011), and their streambed is usually made up of fine sediments (silt and clay) and covered by epipelic biofilms.

The Pampean plain contains the highest demographic and industrial concentrations in the country, the greatest agriculture and livestock production (Rodrigues Capítulo et al. 2010). Such a heavy exploitation of the land is accompanied with different water management practices, including irrigation and water extraction, that along with seasonal droughts can lower stream base flows for extended periods, that extraordinarily can dry the streambed (Extence et al. 1999; Stromberg et al. 2005; Gómez et al. 2022). By comparison, the ecological effects of floods in the Pampean Region are better understood (Zaplara et al. 2018; Solari et al. 2018) than the drought disturbance, even though periods of low discharge are recognised as disturbance capable of controlling stream communities (Bogan et al. 2017).

Given the local anthropogenic pressures, including irrigation and water extraction, it is important to understand the responses of aquatic communities to flow alteration events. The primary aim of this study was to determine the response of epipelic algal communities to desiccation as an extraordinary disturbance in permanent streams, which are not subjected to drought periodically. Our first objective was to determine if during a drought epipelic algae would use the stream sediment as a refuge strategy; for this purpose, we studied the *in situ* vertical distribution of algae in stream sediments during the drought period along with the vertical distribution of sediment humidity. We hypothesized that algal cells can survive embedded in the sediment during extraordinary droughts; therefore, we expected to find algal cells up to several centimeters deep within the sediment, even when the surface of the streambed would be completely desiccated. Our second objective was to analyze the recolonization pattern of the benthic assemblage after the drought; we hypothesized that once the streambed rehydrated, the algal cells embedded in the sediment would regrow the biofilm.

Materials and Methods

Study area

Three permanent streams that run through agricultural areas near the city of La Plata

(Carnaval stream: -34°55′2.24″, -58°6′30.53″; Del Gato stream: -34°58′26.6″, -58°3′13.1″; and a tributary of the Pescado stream: -35°2′57.8976′′, -57°59′20.9472′′) had first order reaches affected by an unusual drought during the year 2018. The main hydrological characteristics of the sites are shown in Table 1 (modified from Altieri 2022). None of these streams had been subject to drought for at least 4 years; during the summer drought, first order reaches dried up completely exposing the clay and silt bedstream to direct sunlight. At these reaches, sites were sampled after they had been dry for at least seven days. These streams run through the 5000 ha agricultural area near the city of La Plata, of which 3000 ha are covered by greenhouses (Mac Loughlin et al. 2017). The main land-use activities are horticulture, floriculture and extensive agriculture, primarily cultivating soybeans, corn and wheat. Although the streams are classified as permanent, since irrigation water from the fields provides water flow all year long, their connection to groundwater is not constant throughout their entire length. Due to the natural lithology of the area and the input from agriculture, the streams can be classified as eutrophic when phosphorus is considered, or as mesotrophic when nitrogen is considered.

The study was conducted in early March (Figure 1). In the previous months (January and February), a period of low rainfall occurred, coincident with a La Niña phase of the ENSO phenomenon (Gómez et al. 2022).

Sample collection

To measure the vertical distribution of algae during the drought, six sediment replicates were collected at each site. Each replicate consisted of a 10 cm deep sediment core collected with a plastic corer (1.9 cm internal diameter). Additionally, each core was divided in six segments at depths 0-1 cm (uppermost layer), 1-2 cm, 2-3 cm, 3-4 cm, 4-5 cm and 5 - 10 cm. Each segment from each replicate was placed in a separate 25 mL plastic jar, with 6 mL of distilled autoclaved water and fixed with 2% formaldehyde.

To analyze the dry-weight of the sediment at each depth, another three 10 cm-deep core replicates per site were collected, and divided in the same six segments as previously described. Each segment was transported to the laboratory, pre-weighed and placed to dry at 60 °C for 48 h until constant weight

Table 1. Mean width, depth and water velocity of the sampled sites under normal hydrological conditions (modified from Altieri [2022]).

Tabla 1. Valores medios de ancho, profundidad y velocidad media en los sitios de muestreo bajo condiciones hidrológicas normales (modificada de Altieri [2022]).

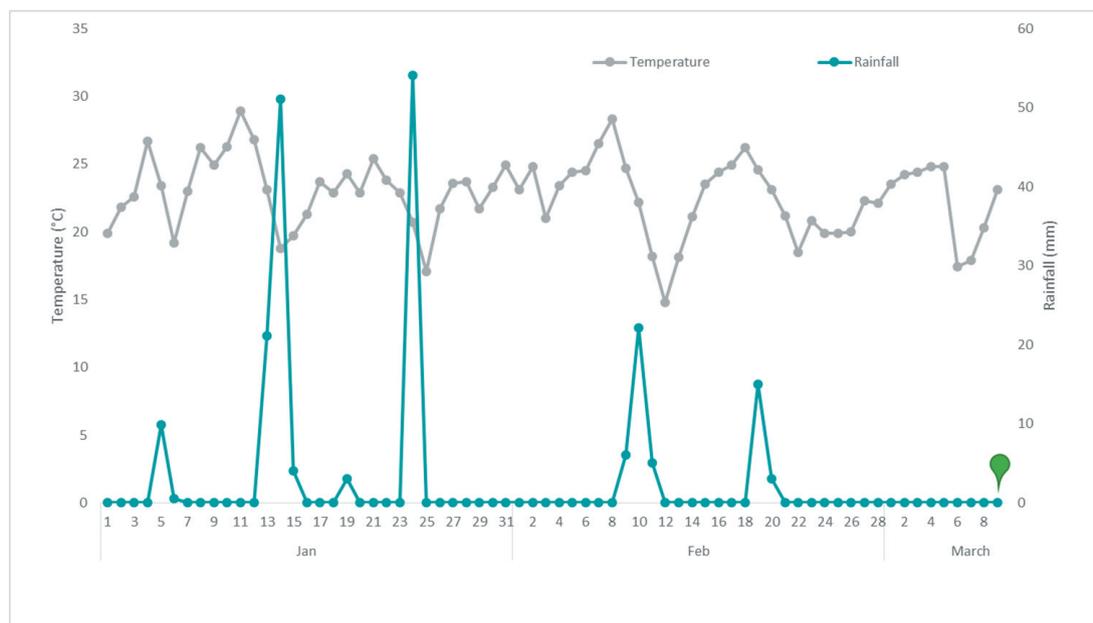| Stream	Carnaval	Del Gato	Pescado
Site (coordinates)	-34°55′2.24″ -58°6′30.53″	-34°58′26.6″ -58°3′13.1″	-35°2′57.89″ -57°59′20.94″
Width (m)	2.26	1.21	1.32
Depth (m)	0.13	0.08	0.10
Velocity (m/s)	0.09	0.03	0.06

Figure 1. Mean temperature and precipitation during the months previous to sampling. Sampling day is indicated in green. Source: 875930 (SADL).

Figura 1. Temperatura media y precipitaciones durante los meses anteriores al muestreo. El día de muestreo se indica en verde. Fuente: 875930 (SADL).

(APHA/AWWA 2012). The differences in the wet weight and the dry weight was considered the loss of humidity (expressed as % of the wet weight). Samples were then muffled at 450 °C for 3 h to remove all organic material (ash-free dry mass) to use as reference biomass for the biological data.

With the purpose of analyzing the recolonization patterns of the benthic assemblage after the drought, 21 replicates per site were collected with a 2 cm deep corer and placed in a microcosm (50 mL round plastic jars), following Nejadsattari (1992), who found the major fraction of benthic algal assemblage in the top 2 cm of sediment. Each sample was taken in coolers to the laboratory and placed in closed plastic boxes that acted as a humid enclosed environment, and 10 mL of filtered stream water was added (36 μm pore mesh first, and through GF/C Sartorious filters), enough to cover the sediment sample. These microcosm were left outside under natural conditions, so that it would be exposed to a natural photoperiod, light intensity and temperature.

For the following two weeks, 3 microcosms collected from each stream were sampled at fixed times (T0: day of collection; T1: 24 h; T2: 48 h; T3: 72 h; T4: 96 h; T5: 1 week; T6: 2 weeks) and fixed with 2% formaldehyde. The volume of filtered stream water in each microcosm was replaced daily to maintain the 10 mL level.

All fixed samples from both the vertical distribution samples and the recolonization samples were analyzed under an Olympus BX-51 microscope in 1 mL Sedgewick-Rafter chambers. Only algae with intact chloroplasts were considered in the counting, to discard empty diatom frustules that might be part of the sediment, according to Gottlieb et al. (2005). Algae were counted by greater algal groups (Cyanobacteria, Euglenophyta, Dinoflagellates, Green Algae, Diatoms) and their density referred to the ash-free dry mass of the sediment.

Statistical analyses

To explore the vertical distribution of the principal groups of algae and the sediment humidity a two-way analysis of variance (ANOVA) was performed with Depth and Site as factors. The Depth factor had 4 levels (0-1cm, >1-2 cm, >2-3 cm, >3-4 cm) in the algae analysis, and 6 levels in the sediment humidity analysis (0-1cm, >1-2cm,>2-3cm, >3-4cm, >4-5cm, >5-10cm). The Site factor had three levels (Carnaval, Del Gato, Pescado) in both analyses. To analyze the recolonization patterns of the different greater algal groups another two-way ANOVA was performed with Time having 7 levels (T0, T1, T1, T3, T4, T5 and T6) and Site having 3 levels (Carnaval, Del Gato, Pescado) as factors. If the interaction between the factors was significant, one-way ANOVA was conducted to analyze differences in the effects of sediments on each date. Normality was previously checked by the Shapiro-Wilks test (Shapiro and Wilk 1965) and homogeneity of variance by Cochrane's test (Cochran 1951). If the normality test was not significant, variables were transformed to log(x+1) (for cell density) or arcsine square root (for percentage data). Partial η2 (Cohen 2013) was computed as a measure of the effect size.

The relationship between the density of the greater algal groups, depth and percentage of humidity were analyzed using Spearman correlation coefficient (significance level=0.05). Growth curves for each algal group in the recolonization pattern experiment were also fitted by non-linear regression to lineal, exponential and logistic (sigmoid) models. The best fit (higher R^2) is reported, which was the logistic model with three parameters for all algal groups:

$$Y = K / (1 + e^{\wedge[-(X-X_{50})/b]})$$

where K is the ln of the carrying capacity, b the growth rate, Y the dependent variable, x the independent variable (time), and X_{50} the time to reach 50% of the carrying capacity. All analyses were conducted in R (3.5.2) in Rstudio (1.2.5033), using the rstatix package to test normality and to conduct the ANOVA analyses. The agricolae package was used for the a posteriori tests and ggplot2 for plotting.

Results

Sediment humidity

Sediment humidity in all streams was below 35% of the sample wet weight. The overall humidity in the sediment was higher in the Carnaval stream when compared to the other two streams. In the topmost 1 cm and 2 cm of the sediment the humidity was higher than in the final 6-10 cm of the corer (Table 1, Figure 2).

Vertical distribution of benthic algae

The density of the different algal groups found in the segments of the sediment corers varied between streams. In the Carnaval stream, cells with intact chloroplasts were found at depths of 1 cm, 2 cm, 3 cm and 4 cm (total density=3.86x10^7±3.22x10^7 cell/cm^3; 2.07x10^6±1.20x10^6 cell/cm^3; 3.76x10^5±4.27x10^5 cell/cm^3; 9.82x10^5±1.15x10^6 cell/cm^3, respectively). In the Pescado stream, cells were found at depths of 1 cm, 2 cm, and 3 cm (total density=1.34x10^7±4.95x10^6 cell/cm^3; 3.99x10^6±1.52x10^6 cell/cm^3; 4.42x10^6±2.02x10^6 cell/cm^3, respectively). In Del Gato stream, cells were found at depths of 1 cm and 2 cm of depth (total density=1.21x10^7±4.53x10^6 cell/cm^3; 4.51x10^5±2.63x10^5 cell/cm^3, respectively) (Figure 3). Algal densities were significantly higher at 1 cm and 2 cm in Del Gato stream, at 1 cm, 2 cm and 3 cm in the Pescado stream, and at the first cm in the Carnaval stream (Table 1).

The analysis of the algal groups in the sediment corer showed that cyanobacteria were the dominant taxa group in all streams (Figure 3). In the Carnaval and Del Gato streams the cyanobacteria density was significantly higher at the two first centimeters of depth, meanwhile in the Pescado stream the density of cyanobacteria was higher at 1 cm, 2 cm and 3 cm when comparing to the deepest segment of the sediment (eta^2=0.37)

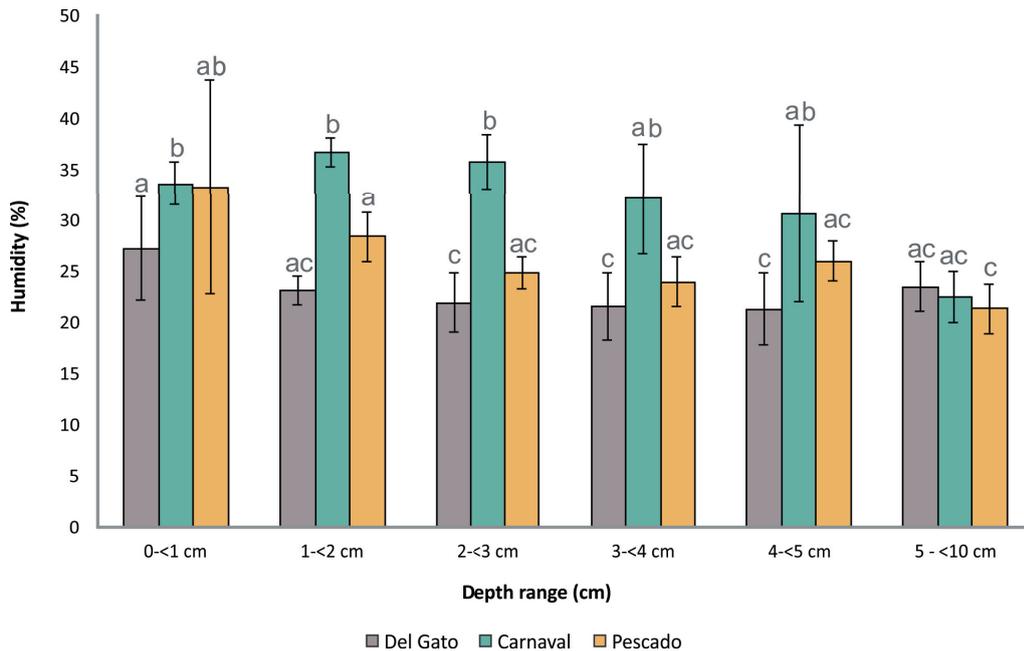**Figure 2.** Percentage (%) of humidity in the sediment (bars) from each stream at each depth. Statistical differences among treatments are shown (P<0.05).

Figura 2. Porcentaje (%) de humedad en el sedimento (barras) de cada arroyo en cada profundidad. Se muestran las diferencias significativas entre tratamientos (P<0.05).

(Table 1). Green algae were more abundant at the first centimeter in the Pescado and Del Gato stream, whereas in the Carnaval stream their density was significantly higher at the two first centimeters of depth (eta^2=0.34) (Table 1). Diatoms were more abundant in the first 1 cm and 2 cm in Del Gato stream, and in 1 cm, 2 cm and 3 cm in the Pescado stream (eta^2=0.33) (Table 1). The total density of algae was significantly higher in the first centimeter of depth with a low effect size (eta^2=0.38) (Table 1). The Euglenophytes and the Dinoflagellates were not considered for analyses because of their low proportion in the samples. All the algae groups were negatively correlated with depth (P>0.05), but none of them correlated with the percentage of humidity.

Recolonization patterns of the benthic algal assemblage

The dominant taxonomic group at the three sediment sites was the cyanobacteria, reaching a maximum of 99% of the overall composition in all the streams analyzed (Figure 4). Diatoms were the second most dominant group, reaching a maximum of 59% at the Carnaval sediment, 68% in the Del Gato sediment, and 18% in the Pescado stream (Figure 4). The green algae represented less than 13% of total algal density at all sediment sites (Figure 4).

The total algal density in the Carnaval sediment remained similar at T0 to T2 and started to increase from T3 to T6, where it reached its maximum value. In the Pescado stream, the density remained similar until T1, had its maximum at T4 and then remained similar until T6. In Del Gato stream, the algal density gradually increased and reached its maximum at T6 (Table 2). The increase in total algal density during the experiment at the sediment streams fitted a logistic function with similar rates and X_{50} values (P<0.01) (Table 3).

In the rehydration experiment, the cyanobacteria presented the same response as the total algal densities in all the sediments (Table 2, Figure 4), confirming that they are the main algal group in the community. Cyanobacteria' growth rates in the three sediments fitted significantly to a logistic curve (P<0.01), with the X_{50} for cyanobacterial growth being lower at the Carnaval sediment (0.79 days), when compared with the Del Gato (1.63 days) and the Pescado (2.14 days) (Table 3).

The green algae in the Carnaval sediment were similar from T0 to T2, increasing gradually from T3 reaching its maximum at two weeks (T6). In the Del Gato stream, the

Table 2. Results of two-way ANOVA (Factors: Site [C=Carnaval, P=Pescado, G=Del Gato], Depth [1, 2, 3, 4 cm] and Site*Depth) for the density of the different algal groups (cyanobacteria, green algae and diatoms) and the percentage of humidity. *Post hoc* test results are also shown for the Site and Depth factors (Tukey test) and partial eta^2 is shown as a measure of the effect size.

Tabla 2. Resultados del ANOVA de dos vías (Factores: Sitio [C=Carnaval, P=Pescado, G=Del Gato], Profundidad [1, 2, 3, 4 cm] y Sitio*Profundidad) para la densidad de los diferentes grupos de algas (cianobacterias, clorofitas y diatomeas) y el porcentaje de humedad. Se muestran los resultados de las pruebas *post hoc* para los factores Sitio y Profundidad (prueba de Tukey) y el eta^2 parcial como medida del tamaño del efecto.

| | | Factors | | | *Post hoc* tests | |
		Site	Depth	Site*Depth	Site	Depth
Cyanobacteria	F	6.71	31.09	3.48	C	1=2>3=4
	p	0.00	0.00	0.01	P	1=2=3>4
	η2	0.27	0.72	0.37	G	1=2>3=4
Green algae	F	2.71	60.28	3.07	C	1=2>3=4
	p	0.08	0.00	0.02	P	1>2=3=4
	η2	0.13	0.83	0.34	G	1>2=3=4
Diatoms	F	10.37	18.83	2.94	C	1=2=3=4
	p	0.00	0.00	0.02	P	1=2=3>4
	η2	0.37	0.61	0.33	G	1=2>3=4
Total density	F	37.39	98.97	16.13	C	1=2>2=3=4
	p	0.00	0.00	0.00	P	1=2=3>4
	η2	0.68	0.89	0.73	G	1=2>3=4
Humidity %	F	19.92	4.96	1.62		
	p	0.00	0.00	0.14	G<P<C	1cm=2cm≥3cm=4cm=5cm≥6cm
	η2	0.34	0.21	0.14		

Table 3. Results of the two-way ANOVA (Factors: Site [C=Carnaval, P=Pescado, G=Del Gato]; Time [T0=day of collection; T1=24 h; T2=48 h; T3=72 h; T4=96 h; T5=one week; T6=two weeks]; Site*Time) for the density of the different algal groups and the total algal density for the recolonization pattern experiment. *Post hoc* test results are also shown for the Time and Site factors (Tukey test) and partial eta^2 is shown as a measure of the effect size.

Tabla 3. Resultados del ANOVA de dos vías (Factores: Sitio [C=Carnaval, P=Pescado, G=Del Gato]; Tiempo [T0=día de recolección; T1=24 h; T2=48 h; T3=72 h; T4=96 h; T5=una semana; T6=dos semanas]; Sitio*Tiempo) para la densidad de los diferentes grupos de algas y la densidad total de algas para el experimento de recolonización. Se muestran los resultados de las pruebas *post hoc* para los factores Tiempo y Sitio (prueba de Tukey) y el eta^2 parcial como medida del tamaño del efecto.

| | | ANOVA 2-way | | | Post-hoc |
		Site	Time	Site*Time	Site*Time
Cyanobacteria	F	3.21	30.64	2.27	C → T0=T1=T2<T3=T4<T5<T6
	p	0.05	0.00	0.02	G → T1<T0<T2=T3=T4=T5<T6
	η2	0.02	0.71	0.11	P → T0=T1<T2<T3<T4=T5=T6
Green algae	F	12.97	2.05	2.39	C → T0=T1=T2<T3=T4=T5<T6
	p	0.00	0.08	0.02	G → T1=T2<T0=T3=T5=T6
	η2	0.24	0.11	0.26	P → T1<T0=T2=T3=T4=T6
Diatoms	F	36.81	1.88	5.61	C → T0=T1=T2<T3=T4=T5<T6
	p	0.00	0.11	0.00	G → T0=T1=T2<T3=T4=T5=T6
	η2	0.38	0.06	0.35	P → T6<T0=T1=T2=T3=T4=T5
Euglenophytes	F	8.35	7.48	3.27	C → T2 < T3 = T4 = T5 < T6
	p	0.00	0.00	0.00	G →-T1=T2<T3=T4=T5=T6
	η2	0.12	0.31	0.27	P → T2<T1<T0<T3=T4=T5=T6
Total density	F	18.69	66.64	3.92	C → T0=T1=T2<T3=T4<T5<T6
	p	0.00	0.00	0.00	G →T1<T0<T2=T3=T4=T5<T6
	η2	0.21	0.74	0.04	P → T0=T1<T2<T3<T4=T5=T6
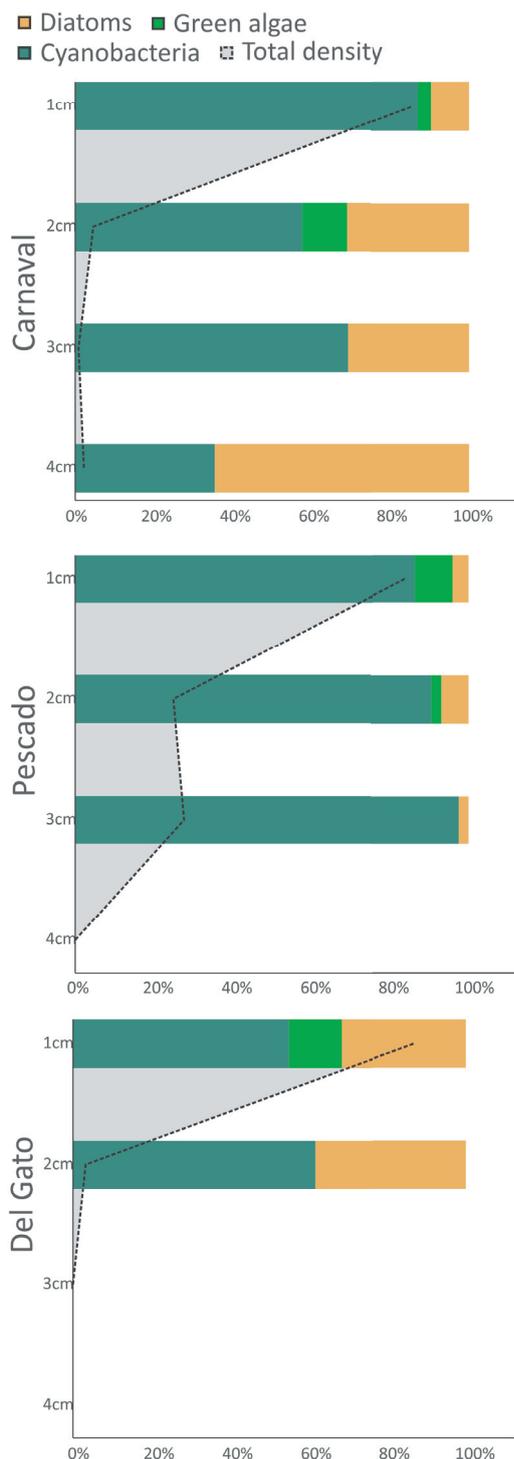
Figure 3. Percentage of the main taxonomic algal groups found at different depths in the sediment corers of the three streams (left axis, bars) and the total algal density (right axis, shaded area).

Figura 3. Porcentaje de los principales grupos taxonómicos de algas encontrados a diferentes profundidades en los *corers* de sedimentos de los tres arroyos (eje izquierdo, barras) y la densidad total de algas (eje derecho, área sombreada).

green algae density was lower at T1 and T2, increased at T3 and remained stable until T6. In the sediment of the Pescado stream, the density of green algae remained similar from T2 onwards. The increase in the density of green algae during the experiment in all three streams followed a logistic function with the highest X_{50} value at the Del Gato sediment (P<0.01) (Table 3). There are two particular cases where the density was zero (Del Gato T4; Pescado T5), although it was likely related to a methodological issue when analyzing those samples.

Regarding diatoms, in the sediment of Carnaval stream, the density gradually increased reaching its maximum at T6. In the Del Gato sediment, diatom density reached its highest value at T3, remaining similar to T6. In the Pescado stream, diatom density remained similar over the first week (T0-T5), and decreased after two weeks (T6) (Table 2, Figure 4). The increase in diatom density during the experiment fitted a logistic function with similar rates and X_{50} values at Carnaval and Del Gato, and with the lowest value at the Pescado stream sediment (P<0.01) (Table 3).

The density of euglenophytes at the Carnaval sediment increased from T2 to T6. In Del Gato sediment, the euglenophyte density was similar during the first 48 h, increased at T3 remaining invariant until the end of the experiment. At the Pescado sediment the density varied during the first sampling times, reaching its maximum at T4 and remaining without variation until the end of the experiment. (Table 2, Figure 4). Euglenophyte growth at the three stream sediments fitted significantly to a logistic curve with similar rates and X_{50} values (P<0.01) (Table 3). The dinoflagellates were not considered for analyses because of their low proportion in the samples.

Discussion

The vertical distribution of epipelic algae in the stream sediment during an extraordinary drought period along with the recolonization patterns of the benthic assemblage after the rehydration of dry sediment were studied in order to determine the response to desiccation of epipelic algal communities in streams that are not subjected to frequent periods of drought. The main results showed that algae and cyanobacteria are able to recolonize the sediment after the drought, and cyanobacteria were the principal group found, both in the
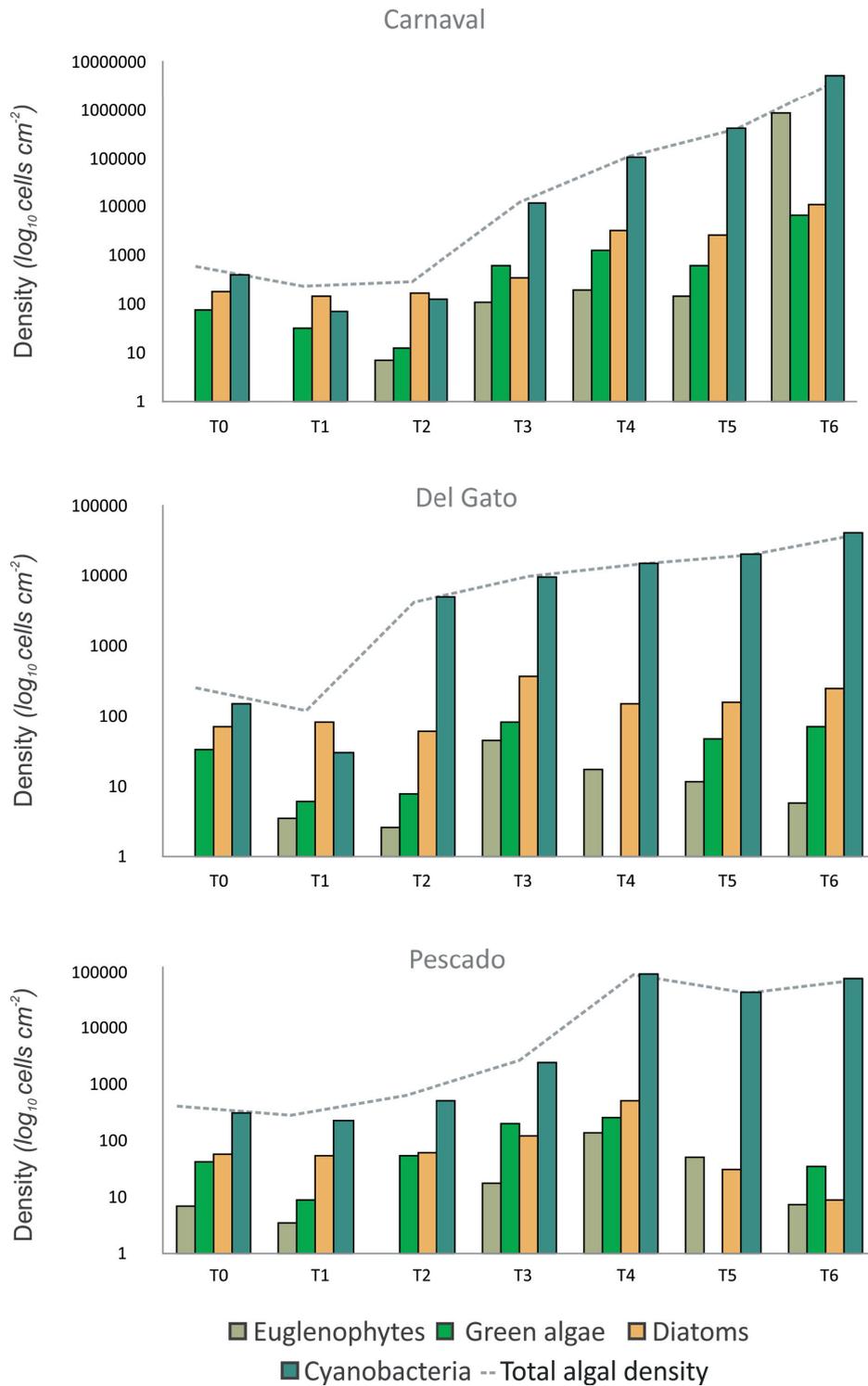
Figure 4. Density of the higher taxonomic algal groups in the rehydrated sediment from the three sites during all sampling dates (left axis, bars) and the total density (right axis, dotted line).

Figura 4. Densidad de los grandes grupos taxonómicos de algas en el sedimento rehidratado de los tres sitios durante todas las fechas de muestreo (eje izquierdo, barras) y la densidad total (eje derecho, línea de puntos).

Table 4. Parameters for the logistic model of each algal group at each site. K=ln of the carrying capacity; r=growth rate; X_{50}=time (days) at which the variable reaches 50% of the carrying capacity.

Tabla 4. Parámetros para el modelo logístico de cada grupo de algas en cada sitio. K=ln de la capacidad de carga; r=tasa de crecimiento; X_{50}=tiempo (días) en que la variable alcanza el 50% de la capacidad de carga.

Stream	Variable	Parameters (logistic model)			
		K	r	X_{50}	P
Carnaval	Total algal density	0.841	0.196	0.654	0
	Cyanobacteria	0.803	0.241	0.789	0
	Green algae	0.876	0.286	0.733	0.006
	Diatoms	0.907	0.213	0.595	0
	Euglenophytes	0.708	0.817	1.804	0
Del Gato	Total algal density	0.871	0.252	0.631	0.00001
	Cyanobacteria	0.839	0.688	1.631	0
	Green algae	1.162	0.323	0.757	0
	Diatoms	0.972	0.258	0.568	0.00001
	Euglenophytes	0.965	0.861	1.093	0.0001
Pescado	Total algal density	0.868	0.227	0.521	0.00001
	Cyanobacteria	0.723	0.678	2.142	0.0001
	Green algae	1.206	0.228	0.516	0.0001
	Diatoms	1.185	0.155	0.367	0
	Euglenophytes	0.989	0.622	0.851	0

vertical humidity gradient in the sediment and during its rehydration.

The depth up to which algae are still found with intact chloroplasts and cytoplasmic content varied between streams, probably due to the variation in sediment humidity, but never exceeded 5 cm of depth. The stream where cells were found at lower depths was the Carnaval, which presented the higher percentage of moisture in the sediment. The exposed substratum becomes the ultimate refuge for algae until flow returns and refuge prevalence depends on its ability to retain moisture but also on the severity of the drought. Some substrata have greater ability to retain moisture than others and may be where algae better resist desiccation (Sabater et al. 2017). The sediments of the studied streams in this experiment could be efficient at retaining moisture, as they are mostly composed of slime-clay with low proportions of gravel and sand, providing suitable conditions for algae survival (Licursi and Gómez 2001).

In general, remnant pools offer the best refuge, but when they dry, inocula may persist in temporarily wet microenvironments or even in dry biofilms on cobbles or subsurface sediments (Sabater et al. 2017). The survival during the recolonization process may depend on the origin of the inocula available for the recolonization (Robson et al. 2008). Epipelic biofilm in the studied region is dominated by cyanobacteria and diatoms, with a lesser proportion of green algae and euglenophytes (Sierra and Gómez 2007; Sierra et al. 2013). In the results for this research, cyanobacteria were also the dominant group in all streams, followed by diatoms.

Cyanobacteria present the greatest resistance to desiccation (Davis 1972; Robson 2000) due to the presence of specific pigments to protect vegetative cells from desiccation and the formation of sheath which react quickly to humidity or water return (Robson 2000; Sabater et al. 2016; Sabater et al. 2017), while pioneer species are generally a few diatom species (Sabater et al. 2017). Although the sampled streams do not have regular wet/dry cycles, the main taxonomic groups found in our results also support the ability of cyanobacteria to withstand drought. This

group of autotrophs also becomes dominant in the biofilm of Pampean streams in summer (Vilches et al. 2003), while their natural nutrient-rich condition with increasing levels due to intensive agricultural practices (Licursi et al. 2016), further magnifies their biomass in the benthic assemblage (Perez et al. 2007; Griffith et al. 2009).

Diatoms were the second most important group in both experiments. They represent a sensitive group to desiccation (Timoner et al. 2020), yet they are not able to withstand complete desiccation such as other groups of algae (Sabater 2016). Despite this, some of them present strategies that allow them to survive in dry conditions, such as the generation of mucilage or the ability of migration from superficial to deeper sediments (McKew et al. 2011). The former could explain the fact that in two of the streams analyzed in this study, the density of diatoms was higher in the deepest segments of the corers.

During the rehydration experiments, the response of diatoms was more variable depending on the stream analyzed, but, in general, increased their density after 72 h and remained invariant until the end of the experimental period. Previous studies in streams of the region suggest that diatoms lead colonization processes of biofilms under normal flow conditions (Cochero et al. 2018; Nicolosi Gelis et al. 2020; Nicolosi Gelis 2021), but it seems that after a drought the response of the assemblage is different. Extreme physical disturbance (e.g., floods or drying up) significantly rearranges the composition of benthic algal and cyanobacterial assemblages, typically shifting them towards the dominance of one group (Lukács et al. 2021). Since extreme flow events act as main drivers of aquatic organisms, only those with specific adaptive capabilities persist under these conditions (Larson and Passy 2012), and our results support the idea that, rather than diatoms, cyanobacteria are faster to overcome the drought period.

Green algae, on the other hand, presented the lowest abundance in the analyzed sediment, with lower densities and growth rate during the rehydration experiment than both diatoms and cyanobacteria. Despite being reported as resistant to desiccation (Robson 2000; Ledger et al. 2008; Sabater et al. 2017), this is to be expected in epipelic biofilms, as they have the lowest representation among the major algal groups (Sierra et al. 2013).

Hence, we hypothesize that the rapid growth of cyanobacteria in the microcosmos could directly affect the development of the other algal groups. In this way, Robson et al. (2008) reported that some diatoms and green algae possess resilience traits that promote the rapid exploitation of patches opened by drought, although this was contingent upon disturbance timing and initial species composition.

Lastly, although euglenophytes were present in the recolonization process, they presented the lowest densities, in agreement with other studies in the region. These studies reported this group does not have a dominant role in sediment communities (Solari and Claps 1996; Cochero et al. 2015).

Non-flow periods disturb permanent stream biofilms (Timmoner et al. 2019), and temporary stream biofilms are said to have greater adaptive capacity since have evolved to provide themselves with protection and damage repair mechanisms (Karsten and Holzinger 2014), attributes that are not common in the phototrophic communities of perennial streams (Timoner et al. 2020). Despite this, the phototrophic community analyzed in this study has been shown to respond rapidly to rehydration.

Our results indicate that when the streams were superficially dried, benthic algae and cyanobacteria, among the most important primary producers in Pampean streams (Vilches and Giorgi 2010; Vilches et al. 2013), can recolonize the sediment. Their survival might be related with the moisture content of the sediments, and after rehydration the autotrophic community reacts quickly increasing their density. Yet, these compositional changes may have a major impacts altering the entire trophic network and the main ecosystem functions.

Knowledge on how the substrate can offer conditions for the survival of some producers, and how the recolonization processes occur after a drought event, are fundamental to understanding how algae will adjust to changes in flow regime, including those arising from unexpected events (e.g., La Niña influence) and those related to anthropogenic pressures, including irrigation and water extraction. Further challenges remain, including the studies of longer periods of drought, the community composition prior to the event, and the contribution of water pools to the ecological succession process.

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