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Analysis of the biological traits of diatoms in intermittent rivers

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13 CLIMATE ACTION

15 LIFE ON LAND

Abstract

Intermittent rivers predominate in Mediterranean areas; under these conditions, drying or no-flowing phases are common. Aquatic taxa have resistance and resilience strategies to withstand or recover after the drying period. In this research, we set the grounds for a rewetting experiment that analyses the reestablishment of diatoms eliminating the effect of algal recolonisation by drift. Furthermore, we also examined several diatom biological traits that may potentially be beneficial as the degree of intermittency increases; the main analysed traits were: “adnate”, “pad”, “colonial”, “ecological guilds”, “mobile”, “oxygen requirements”, “cell size”, “pioneer” and “moisture tolerance”. These coded traits were compared amongst ephemeral, intermittent and perennial rivers. Overall, the comparisons indicated that there were no statistically significant differences neither in the composition of species nor in biological traits. However, a higher variability of several of these metrics was observed for both perennial and also intermittent rivers. Notwithstanding, some constant traits were detected in intermittent rivers, indicating that lack of water flow may select pedunculated, mobile, non-colonial, no-adnate, no-pad taxa. Further physiological traits, such as mucilage secretion and other possible biofilm resistance mechanisms, should be analysed to predict the impact of climate change scenarios on diatom communities in mediterranean rivers.

Sustainable development goals

Considering future climate change scenarios for freshwater ecosystems, the study of diatom communities in intermittent rivers can be particularly significant in a long-term scale because changes in flow patterns can have effects on diatom biodiversity. This project aims to shed light into diatoms biological traits that may enable them to withstand or recover from the dry period in intermittent rivers. Most of the research done on freshwater biodiversity and intermittent rivers, has been done using aquatic macroinvertebrates, whereas diatoms have been largely neglected. The results obtained from this project could be used for predicting future diatom biodiversity patterns and their biological traits in Mediterranean river ecosystems. Our results indicate that there are no significant differences between intermittent and perennial rivers from Catalonia, nevertheless more research should be conducted to relate further biological traits that may be suitable especially under climate change conditions.

Therefore, the sustainable development goals addressed in this study are included in the issue of Planet. This impacts on Goal 13 “Take urgent action to combat climate change and its impacts”, especially regarding 13.3: “Improve education, awareness-raising and human and institutional capacity on climate change mitigation, adaptation, impact reduction and early warning”. Furthermore, it affects Goal 15 “Protect, restore and promote sustainable use of terrestrial ecosystems, sustainably manage forests, combat desertification, and halt and reverse land degradation and halt biodiversity loss”, focusing on 15.1 “By 2020, ensure the conservation, restoration and sustainable use of terrestrial and inland freshwater ecosystems and their services, in particular forests, wetlands, mountains and drylands, in line with obligations under international agreements”.

Adaptation of the TFG to the COVID-19 confinement

This project began in September 2019, starting with the setting of the rewetting experiment and the laboratory procedures in order to obtain all diatom samples. Subsequently, microscope observations, iconographies and identifications from all the samples were conducted, as well as a photographic herbarium of the taxa found. The next step was to quantify each species on each sample, nevertheless, that could not be accomplished due to the start of lockdown measures in March 2020. Consequently, this project was modified by compiling information from potential biological traits of diatom species found in the routine biomonitoring program of Catalonian rivers from the Catalan Water Agency ("Agència Catalana de l'Aigua") and comparing the different river types.

INDEX

1. INTRODUCTION

The mediterranean climate regions are located between temperate and desert climate regions in most of the continents (Dallman,1998), and usually extending between 30° and 40° latitude. The regions include areas around the Mediterranean Basin, coastal California, central Chile, the Cape area in South Africa and the south and southwestern Australia (Aschmann, 1973). These regions are characterised by summer droughts and moderate rainy winters (Bonada & Resh, 2013) and are considered biodiversity hotspots with high levels of endemisms (Myers et al., 2000; Smith & Darwall, 2006; Bonada et al., 2007). This high biodiversity level is the result of combined causes: landscape heterogeneity (Koniak & Noy-Meir, 2009), high seasonal and predictable precipitation and hydrological conditions (Bonada et al., 2007) and historical effects (e.g. the use of these areas as refuges during the Pleistocene glaciations in the northern hemisphere; Hewitt, 2004).

A large proportion of rivers in mediterranean climate regions are **intermittent** (also known as temporary), which are defined as rivers that lack of superficial flow at some period of time (Bonada & Resh, 2013). **Ephemeral** rivers are also frequent in these regions and are characterised by brief water flow periods (just after rainfalls) followed by long dry periods (Hancock, 2017). Both river types are characterised by having large variations on hydrological connectivity as they alternate between an expansion phase (lotic or wet period) to a contraction phase (lentic or dry period) (Sabater, 2008; Bernal et al., 2013). As a result, they are shifting habitat mosaics between fully aquatic and fully terrestrial habitats (Datry et al., 2016). On the contrary, **perennial** rivers are characterised for having a constant and continuous water flow, most of them constantly connected to groundwater (Meinzer, 1923). Despite their high occurrence in mediterranean climate regions, many of them are becoming intermittent due to global change (Larned et al., 2010). Flow intermittence is, however, not a unique feature of mediterranean climate regions. Intermittent rivers are present on every continent and account for more than 50% of the global river network (Tooth, 2000; Datry et al, 2014). Most of the global river network is, therefore, intermittent rather than perennial.

Intermittent (and ephemeral) rivers are considered natural disturbed ecosystems due to the extreme flow variability along the year. As a result, organisms found in these rivers have specific **resistance and resilience** strategies to withstand or recover from flow intermittence (Bogan et al, 2017). Despite following these strategies, the full recovery of the pre-drought community is unlikely to occur and generally it has a different species composition (Lawrence et al., 2010). Resistance refers to the capacity of an ecological unit (e.g. a taxon) to endure the harsh conditions in situ (Lake, 2000), summer drying in our case. It can include strategies being able to tolerate dry river beds, such as desiccation-tolerant stages (summer diapause) (Williams, 2006), or the ability to persist in a local perennial refuge like remnant pools (Boulton et al, 1992). On the contrary, resilience refers to the capacity of an ecological unit that rebounds after disturbance (Nimmo et al, 2015), and should include species with traits that allow them to colonize passively by drift (i.e. the movement with flow) or by aerial dispersion, or actively by means of their own motile structures (for example to the hyporheic zone; Del Rosario and Resh, 2000). In general, the resilience strategy is meant to be more frequent than resistance in Mediterranean rivers (Fox & Fox, 1986).

1.1 A brief introduction on Diatoms

Diatoms or Bacillariophyceae are unicellular or colonial microscopic algae characterised for having chloroplasts with four membranes, thylakoids in stacks of three, fucoxanthin as a pigment, and chrysolaminarin as a reserve product (Bhattacharya et al., 1992). The most recognisable and unique feature is a cell wall composed of silica, constituting the frustule (Pickett-Heaps et al., 1990). There is a high heterogeneity on frustule morphology, being the most diverse protists, with estimations of 100000 taxa (Mann & Drop,1996). They can be found on all kinds of moist habitats with access to light, from freshwater ecosystems to oceans, and even in soils (Falkowski, et al, 1998). Generally, they are planktonic and live in suspension or attached to a substrate, but can also be found forming filaments or colonial forms. Our study focuses on benthic taxa, which mainly includes the periphyton attached on stones or sediment surfaces in the river beds.

The frustule structure looks like an exoskeleton made of hydrated silica (SiO2) and surrounded by various organic compounds (Volcani, 1981) (Figure 1). It consists of two halves, the epitheca and the hypotheca; fitting inside one into the other, as the first covers the second one (Round et al., 1990). The frustule plays a role in gas exchange with the environment, osmotic regulation, and mucilage release to move or to adhere onto the substrate.

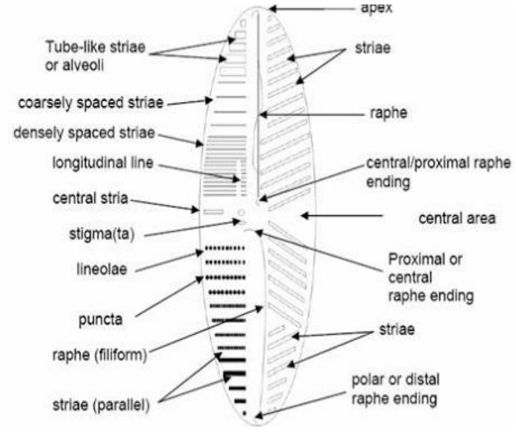

Figure 1. Diagram showing the general features of pennate diatoms (Taylor et al, 2006)

The thecae are made up of the valve, a more or less flattened plate, and the pleura on the sides and at least one cingulum, which consists of siliceous linking bands between the valve and the pleura; each band is called a copula or girdle band and is released after the vegetative cell division that produced the valve. The valves can have various ornamentations on their surface (Kroger et al., 1996). They have pores useful for nutrients intake and releasing waste (Round et al., 1990).

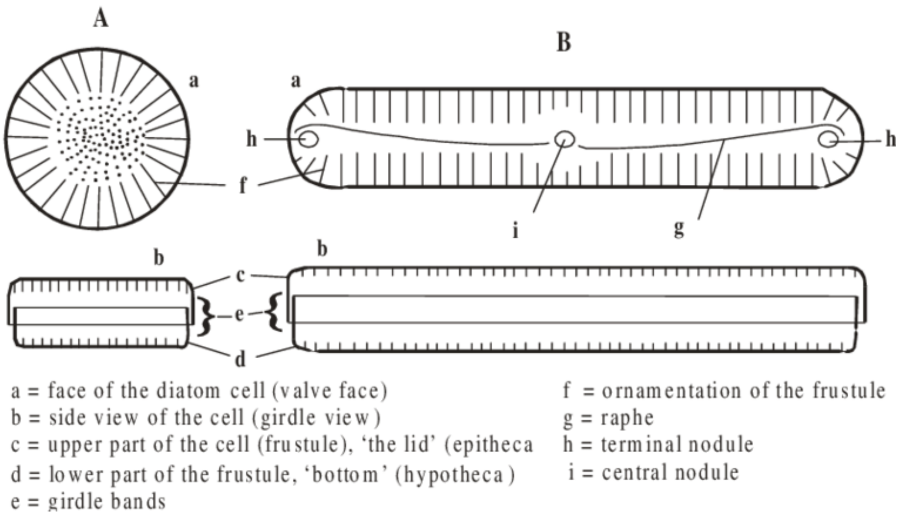

***Figure 2**. Schematic representation of typical shapes of centric (A) and pennate (B) diatoms (Sorvari, 2001)*

Considering their symmetry, they can be classified as centric (radial symmetry) or pennate diatoms (bilateral symmetry) (Schmid et al, 1981; Mann, 1986) (Figure 2). The centric ones do not have raphe and are typically planktonic, whereas pennate can have it and are generally benthic or epipelic (living at the interface of water and sediment) (Round et al., 1990). Consequently, the ability to move (in a forward and backward movement) is exclusive of the pennate diatoms that have a raphe. This movement is useful to avoid sedimentation in benthic diatoms and also facilitates sexual reproduction between genetically different individuals.

The life cycle of diatoms is diplontic, and includes a long vegetative stage during which the cells divide mitotically, and a short stage in which sexual reproduction occurs, followed by a complex developmental process leading to the formation of new vegetative cells (auxospores) (Mann, 1993). During mitosis, the two thecae become the daughter's epitheca, so each of them will have to generate the hypotheca before separation (cytokinesis). As a result, there is a gradual cell size reduction on the daughter cell that uses the mother hypotheca as the epitheca, whereas the other one is the same size as the parent cell (MacDonald, 1969; Pfitzer, 1971). Consequently, the auxosporulation process occurs, in order to re-establish the cell size and also to achieve genetic recombination. The process of sexual reproduction in centric diatoms is by means of oogamy, where gametes fuse, expand and form the auxospore that contains new thecae, which eventually form the initial free cell (Von Stosch, 1950). On the other hand, pennate diatoms carry out isogamy, forming a zygote on each parent cell, which will become the auxospore (Round et al., 1990; Chepurnov and Mann, 2004). It has also been studied apomixis, the production of auxospores without previous fecundation (Drebes, 1977). If cells do not experience a sexual phase or auxosporulation process, they will divide mitotically until they reach a critical small size threshold and die (Geitler, 1932)

Diatoms are used as **bioindicators**, that means that the presence or absence of a species or group of them can reflect the quality of that environment. They are used to assess the ecological quality of freshwater ecosystems, due to their specific ecological requirements and responses to various biogeographical and physicochemical factors. Water flow, in particular, is the factor that has a massive impact on all other physiochemical characteristics (Stevenson, 1996).

1.2 Diatoms biological traits to intermittence

Several **biological traits** can potentially provide diatoms some ability to withstand changes in water flow and intermittence, but also could be a solution to severe habitat conditions, even in perennial streams (Vander Vorste et al., 2016). Biological traits are characters or observable features that can be inherited or acquired in response to the environment. They include life history, morphological, physiological and behavioural characteristics that are related to ecological aspects (Naeem et al, 1999). This is based on the habitat template theory, which considers the habitat as a templet for natural selection to select individuals/species with traits adapted to the characteristics of the habitat (Southwood ,1977).

The analyses regarding diatoms traits can be conducted considering life-forms, cell sizes or ecological guilds (Rimet et al., 2012):

I. Regarding **life-forms**, diatoms can be solitary cells or can form colonies. The solitary ones can be not attached (if they are floating or free moving) or attached to substrates in different ways: adnate (using their valve face), mucilage pad (releasing mucilage on a pole) or mucilage stalk (the pore cells produce a stalk) (Round et al., 1990). The colonial forms can be classified in: chain colonies, ribbon colonies, zig-zag colonies, rosette colonies, star colonies, arbuscular colonies, mucous tubule colonies. Moreover, each species can show different life forms on every stage of its life-cycle.

II. The **cell size** is a property of each species but also varies in response to the nutrient availability (Finkel et al., 2009) and current velocity (Tuji, 2000).

III. **Ecological guilds** regroup the varieties of life forms (*Table 1*) considering taxa that coexist, but which may have adapted in different ways to abiotic factors (Devito et al., 2004). The following groups are described:

***Table 1**. Taxa assignment to ecological guilds, adapted from Passy (2007) and Rimet (2012)*

Ecological guilds	Taxa
Low-profile Characterised by its resistance to disturbances and not tolerating nutrient enrichment. It includes species of short size and slow moving following the r-strategy (Biggs et al.,1998). This strategy refers to the ability to reproduce and disperse rapidly and exponentially, as a result they are successful while colonising unpredictable changing environments.	*Achnanthidium, Achnanthes, Amphora, Brachysira, Cymbella, Cymbopleura, Cocconeis, Delicata, Diploneis, Discostella, Encyonema, Encyonopsis, Eucocconeis, Fragilaria, Karayevia, Kolbesia, Meridion, Nupela, Planothidium, Platessa, Rhoicosphenia, Reimeria*
High-profile Sensitive to turbulence, but it is benefited from nutrient enrichment. It includes large or colonial species.	*Aulacoseira, Achnanthidium catenatum, Diadesmis, Diatoma, Eunotia, Encyonema, Fragilaria, Frustulia Gomphonema, Gomphoneis, Gomphosphenia, Melosira, Pleurosira, Pseudostaurosira, Staurosira, Staurosirella,* *Tabularia, Ulnaria*
Motile Includes fast moving species that have the ability to select their habitat, in spite of being sensitive to high current velocities but tolerant to high nutrients (Passy, 2007).	*Adlafia, Bacillaria, Caloneis, Craticula, Delicata, Denticula, Eolimna, Epithemia, Fallacia, Fistulifera, Mastogloia* *Geissleria, Gyrosigma, Hippodonta, Luticola, Mayamaea, Navicula, Naviculadicta, Nitzschia, Nupela, Sellaphora, Simonsenia, Stauroneis, Surirella, Rhopalodia ,Tryblionella*
Planktonic Taxa with morphological adaptations for lentic habitats and able to resist sedimentation (Rimet et al, 2012).	*Cyclotella*, *Cyclostephanos*, *Nitzschia*, *Stephanodiscus*

Diatoms can withstand the dry period through several resistance and resilience strategies. Diapause can be one of the multiple **resistance** mechanisms they use to persist in a local reach during the dry period. This is possible due to the fact that diatoms are part of the periphyton, described by Sabater (2007), as a microecosystem composed of a complex mucopolysaccharide matrix with embedded autotrophic and heterotrophic microorganisms that has the natural ability to respond and recuperate from stress, such as drying. This is believed to be feasible for regrowth when water starts flowing again, but no studies have tested it so far. Furthermore, the diapause stage is not related to the auxospore formation; unlike other algae, the auxospore is neither a resting stage nor a specialised cell for dispersal (Van den Hoek et al., 1995). Another resistance mechanism could be the ability to remain active in local remnant pools (Dodds et al.,1996; Robson et al., 2008). Similarly, other refuges such as dry biofilm on stones, debris, dry sediments, organic matter and moist leaves can maintain a certain humidity for them to endure the drying periods facilitating the recovery (Webb et al. 2012).

Active or passive movement from refuges or perennial pools to new flowing habitats are considered **resilience** mechanisms. These are linked to species with a raphe that enables them to actively migrate or to species more prone to be passively dispersed by drift, colonising downstream areas appears such in perennial rivers (Peterson 1996). Other resilience mechanisms would be related to passive dispersal through wind (Ehrenberg, 1849), waterbirds (Figuerola et al., 2002) or on moist surfaces of several animals (Stoyneva, 2016). Despite all these potential resistance and resilience mechanisms, Robson (2008) suggested that diatoms mainly used dry biofilm on stones (resistance) and drift (resilience) to recolonise after the dry period in intermittent rivers.

It has also been studied that only a week of dry period has a long-term effect on diatoms metacommunity, and that it did not returned to the initial state after a 28-day rewetting (Barthès et al, 2015). In addition, there are recognised differences on taxonomic composition of diatoms meta-communities considering flow intermittence. Tornés et al. (2013) found that a perennial flowing stream shows the highest proportion of nestedness in diatom communities of the Iberian Peninsula, while on the contrary, idiosyncratic taxa and lower species richness seems to be typical on intermittent rivers. Nestedness occurs when the taxa of a community with lower numbers of species tends to be subsets of the taxa at richer sites (Wright et al, 1992); following different patterns consisting of connecting local communities by dispersal of multiple interacting species (Leibold et al., 2004). Idiosyncratic taxa do not follow this pattern, they are characterised for being present in unexpected poor species sites or absent in species-rich sites (Atmar & Patterson, 1993). Diatoms have efficient passive dispersal strategies (mainly drift) which are meant to lower nested patterns; hence, unexpected presences and absences would be common (Soininen, 2008; Ruhí et al., 2013).

2. HYPOTHESES

Following the biological traits of aquatic invertebrates analysed on “The biota of intermittent rivers and ephemeral streams” by Stubbington et al (2017), we built up a table regarding the possible diatom traits to endure the dry period in intermittent rivers, considering both resistance and resilience traits. Contrary, perennial rivers may be characterised by the absence or less presence of these studied traits. This table constitutes a summary of the hypotheses of this study. Besides the listed traits, some others could be also considered, such as pH, salinity, nitrogen uptake metabolism, trophic state, or the chlorophyll-a levels (Van Dam, 1994; Falasco et al., 2016). However, more autoecological information is needed about all these traits and therefore, we focused on more simple traits mostly related to morphology (*Table 2*).

Table 2. *Potential diatom biological traits that may promote resistance and/or resilience strategies to intermittence.*

Resistance traits	**Rationale**
Large cell size	Large diatoms tend to be epipelic, at the interface of sediments and water (Round et al.,1990), therefore having more potential abilities to survive in dry sediments.
Adnate	The adhesion to the substrate by their valve face or girdle view, promotes a moist microhabitat in which they may withstand the drying period.
Pad	The production of mucilage on a pole that sticks to substrate may be useful to stay hydrated.
Colonial	Promotes the adhesion to the substrate by creating a moist microhabitat useful to withstand the drying period.
Planktonic guild	Taxa included in this guild are adapted to lentic environments, having morphological adaptations that enable them resisting to sedimentation. (Passy, 2007)
Low Oxygen requirements	May be able to endure the anoxic conditions in remnant pools with accumulated organic matter.
Mobile (raphe)	They can move on the stone surface, remaining in contact with the water, as the upper part of the river dries faster.
Motile guild	May be able to select their habitat and locally migrate to parts with moisture under the stone.

Resilience traits	Rationale
Small cell size	Taxa with a fast-growing rate, may be competitive in recolonising.
Non-Colonial	Free moving individual cells may be able to disperse easily.
Pioneer	Able to endure harsh drying conditions, these species are the first to colonise the disrupted environment. (Passy, 2007)
Low profile guild	Enhances resistance to disturbances, by reproducing and dispersing exponentially, following the r strategy. (Passy, 2007)
Moisture tolerance	May be able to survive on wet and moist or temporarily dry places. (Van Daam, 1994)

3. OBJECTIVES

The main aim of this research is to assess the responses of flow intermittence on diatoms by setting up and experiment and by compiling and analysing diatom community data in perennial and intermittent rivers. The specific objectives are as follows:

> OBJECTIVE 1: To assess the temporal dispersal ability of diatom species (resistance strategies) in intermittent rivers by setting a rewetting experiment that avoids the recolonization by resilience strategies.
>
> OBJECTIVE 2: To create a list of biological resistance/resilience traits of diatom species collected in several perennial and intermittent mediterranean rivers in Catalonia.
>
> OBJECTIVE 3: To compare trait composition of diatom species in perennial and intermittent mediterranean rivers in Catalonia.

4. MATERIAL AND METHODS

4.1 Methods for Objective 1

The study area

Three rivers from Sant Llorenç del Munt i l'Obac Natural Park, located in Vallés Occidental county in central Catalonia, were selected: Sanana, Talamanca and Santa Creu[1]. They are very close to each other but differ in the degree of flow intermittence, with Sanana being the most permanent, Talamanca having intermediate values of flow intermittence, and Santa Creu being the most ephemeral.

The area has a typical mediterranean climate, with an average annual rainfall of 682 mm, mainly falling in autumn, followed by spring and summer being the driest. We obtained the following temperature data from sensors (HOBOs) placed several sites along the three rivers (Figure 4); the mean temperature in all three rivers oscillates from 5-9 ºC in winter, while reaching 20-26 ºC in summer. The year 2019 was extremely dry in winter and the precipitation rate obtained by sensors oscillated around 0mm.

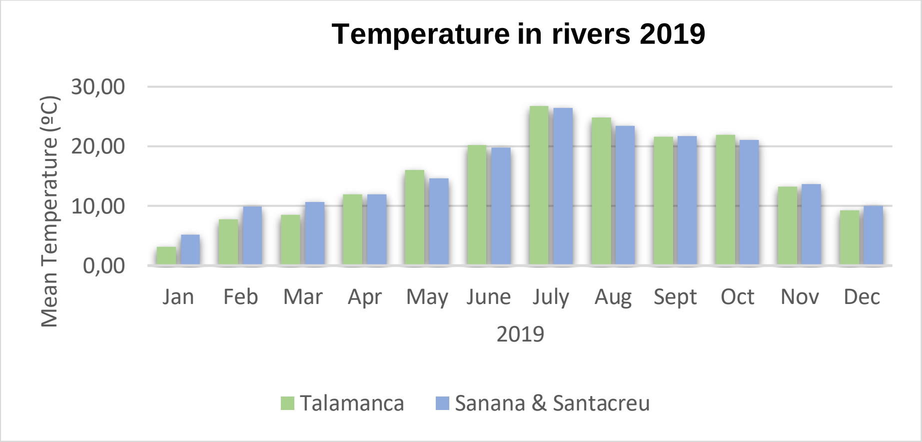

***Figure 3**. Mean temperature variations on the three rivers during 2019. Data collected from HOBOs located in several sites along the three rivers.*

Sampling

Field work was carried out during May 2019, as part of the MECODISPER project sampling campaign. The diatom sampling started with the collection of 3 stones of each river. Then, the upper surfaces of the stones were scrubbed with a toothbrush and samples were fixed in 4% formaldehyde. A total of 9 (3 from each chosen river) samples of diatoms were collected.

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[1] Maps of the studied rivers and MECODISPER campaign sampling points are on the *Appendix 1.*

Experimental design

Nine calcareous stones of different sizes were placed on each river on 28th may 2019 to allow the colonisation by diatoms. On 9-12 July 2019, stones and encrusted substrate were extracted and left to dry out during the whole summer at the terrace of the Section of Ecology at the University of Barcelona, in order to simulate the drying period in natural conditions. Experimentally, all stones experienced drought for the same period of time, regardless of belonging to rivers with a different degree of intermittency. Encrusted algae from bedrock was also collected to ensure that colonisation of stones was completed. On 26th September 2019, just after the summer period, the experimental rehydration of the substrates started. Firstly, the substrates were placed in plastic tuppers and treated water without chlorine was added to simulate the rewetting. A hole was made on each tupper lid to insert aerators, which would provide oxygen into the water. The lid helped to isolate each sample from the outside, to minimise the risk of contamination by propagules from the air. A total of 27 tuppers with one stone each and 27 more with a sample of encrusted substrate (9+9 samples per river) were set up and randomly placed at the terrace's shelves, bearing in mind that there might be some variations in weather conditions and light according to their location.

The growing in the community was monitored over time on both substrates. Three stones and 3 pieces of encrusted substrate from each river were randomly extracted at three different times. Nevertheless, the experimental design was different for each type of substrate, due to the fact that different stones were taken on each extraction, whereas for encrusted substrate the extractions were always collected from the same samples; thus, we also aimed to study the succession of the exact same community over time.

For stones, the three extractions were conducted every 20-25 days, whereas for encrusted substrates, the first extractions were done after 30 days, and the last one after 25 days. This difference in the extractions was due to the fact that the encrusted substrate seemed to have more cyanobacteria after the rewetting.

Laboratory protocol

Each sample, stone or encrusted substrate, was scraped using a toothbrush. For the encrusted substrate sample, the green part was detached from the original substrate using a blade, and then the obtained periphyton were poured in flasks. Then, it was fixed using 4 % formaldehyde and the sediments were allowed to settle for 24 hours. Part of each sample was poured on a digestion tube and 110 volume hydrogen peroxide was added, in order to eliminate the organic matter. The tubes were let to digest on a sand bath in a hot plate, at 100ºC. After 24h, the hydrogen peroxide was removed while keeping the sediments, filling with distilled water and adding drops of hydrochloric acid to acidify and remove calcium carbonate. After 24h, the supernatant was removed and cleaned with distilled water again. A day later, the sediment material was taken and resuspended on flasks, verifying with an optical microscope that the density of frustules was the ideal for observation. Using a pipette, the sample was mixed and a drop was put on a cover glass. Then it was let to dry for a day and after that permanent samples were mounted using Naphrax resin.

The identification was based on the frustule shape, size and structure, mostly considering the valve surface ornamentation. The observations were conducted using a Zeiss microscope and its camera. After having identified the taxa present, all the species on each sample should have been quantified. The ideal would have been that 400 valves were counted for each sample using an optic microscope. After that, in order to infer whether the diatoms found and identified were actually able to regrow from dry substrates, a viability study should have been conducted, in which the proportion of alive cells (full frustules and chloroplasts) between dead cells (empty frustules, no chloroplasts) had been determined. This procedure can still be done at any time, due to the fact that all samples and extractions were first preserved in formaldehyde, preserving both alive and dead cells.

$$\%viability = \frac{alive\ diatoms}{dead\ diatoms} x100$$

4.2 Methods for Objective 2

This objective focused on analysing data from the Catalan Water Agency ("Agència Catalana de l'Aigua"), consisting on diatom inventories from different types of rivers: 6 perennial (Bruguent, Portella, Merlès, Major, Òsor and Guilla) 6 intermittent (Glorieta, Santa Creu,Guanta, Avencó, Daró and Orlina) and 1 ephemeral (Riudaura). Samples from 1 ephemeral river were included for comparison with perennial and intermittent ones as an extreme case of flow intermittence. No more data from other ephemeral rivers was available. Perennial and intermittent rivers include 3 calcareous and 3 siliceous sites each, as diatoms are very sensitive to geology and physico-chemical characteristics of the substrate (Cantonati et al., 2009). These rivers were sampled in 2016-2018. For each taxon identified on each river, biological traits were obtained from Rimet & Bouchez (2012) and Van Daam (1994) (*Appendix 2*).

4.3 Methods for Objective 3

In order to compare trait composition of diatom species in perennial and intermittent (and also ephemeral) rivers, data from the Catalan Water Agency was divided and built in two different excel matrixes. The first matrix (A) refers to taxa identified as columns and different rivers as rows; it contains the abundance of each taxon for each river. The second matrix (B) includes biological traits as columns and species as rows. Therefore, a third matrix (C)[2] was obtained. This matrix included the proportion of each biological trait in each river. Statistical analyses were done first on the taxonomic matrix (A) by means of richness, Shannon diversity, Multidimensional Scaling (MDS) and ANOSIM analysis. Richness refers to the total number of unique species found at a site, whereas Shannon-Weiner diversity index represents species weighted by abundance. While MDS allows to have a better view of diatoms communities organization in a multidimensional space, ANOSIM tests for differences in community composition among groups (perennial, intermittent and ephemeral rivers in our case). Kruskal-Wallis tests were applied to test for significant differences between taxonomic metrics (richness and Shannon diversity) and the proportion of each biological trait among the three river types. All these statistical analyses were carried out in R (R Development Core Team, 2019) and using the packages *vegan* (*v2.5-6*; Oksanen & Blanchet, 2019), for richness and diversity, and *ade4* (*v1.7-15*; Dray & Dufour, 2018) to obtain the C matrix. In addition, a Principal Components Analysis (PCA) was conducted using the Excel software XLSTAT in our matrix B, regrouping taxa for each type of river.

5. RESULTS

5.1 Results for Objective 1

The taxa identified in all three studied rivers were the following:[3]

- *Achnantes* cf *trinoidis*
- *Achnantidium minutissimum*
- *Brachisyra liliana*
- *Brachisyra vitrea*
- *Cyclostephanos dubius*
- *Cyclotella meneguiniana*
- *Cymbella* cf *compacta*
- *Cymbella* cf *laevis*
- *Cymbella* cf *lancettula*
- *Cymbella cymbiformes*
- *Cymbella excisa*
- *Cymbopleura amphicephala*

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[2] This C Matrix is on the *Appendix 3*.

[3] For further identification and taxonomic details, consult the photographic herbarium attached on the *Appendix 5*.

- *Denticula tenuis*
- *Diploneis elliptica*
- *Encyonema silesiacum*
- *Encyonopsis cesatii*
- *Encyonopsis minuta*
- *Eucocconeis flexella*
- *Eunotia bidens*
- *Eunotia denticulata*
- *Fragilaria* cf *radians*
- *Fragilaria dilatata*
- *Fragilaria ulna*
- *Gomphonema gracile*
- *Gomphonema lateripunctatum*
- *Gomphonema micropus*
- *Gomphonema parvulis*
- *Gomphonema vibrio*
- *Gyrosigma* cf *attenuatum*
- *Hantschia abundans*
- *Mastogloia lacustris*
- *Mastogloia smithii*
- *Navicula criptotenella*
- *Navicula vandamii*
- *Nitzschia denticula*
- *Pinnularia* cf *sinistra*
- *Pinnularia* cf *subcapita*
- *Pinnularia nobilis*
- *Rhopalodia parallela*
- *Stephanodiscus minutulus*

5.2 Results for Objective 2

The coded biological traits for each species are found on a table in the *Appendix 2*.

Most of the obtained values are coherent to each taxon, although there is a lack of data in reference to “Oxygen requirements” and “Moisture tolerance” traits.

5.3 Results for Objective 3

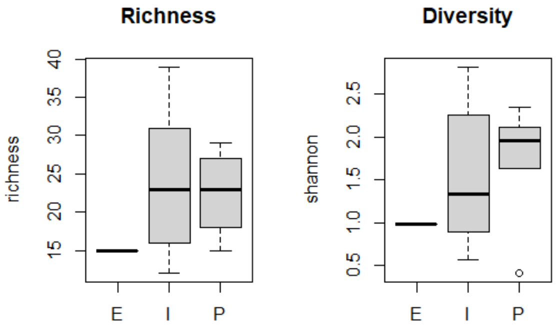


***Figure 3**. Boxplot of the distribution of species richness and diversity in the three river types. For each type, the horizontal line represents the median value of the distribution, and the whiskers reach the highest and lowest value within 95% of the distribution. (E)= Ephemeral, (I)=Intermittent and (P)=Perennial.*

```
Kruskal-Wallis rank sum test
richness by temp1
Kruskal-Wallis chi-squared = 1.4628, df = 2,
p-value = 0.4812

Shannon by temp1
Kruskal-Wallis chi-squared = 0.91209, df = 2,

p-value = 0.6338
```

Species richness was visually higher in intermittent rivers, followed by perennial ones but no significant differences were found (*Figure 3*). Moreover, perennial rivers appeared to have a higher diversity than ephemeral rivers but overall, no significant differences were found. In both graphics, it is noticeable that intermittent rivers have a higher variability in both taxonomic metrics.

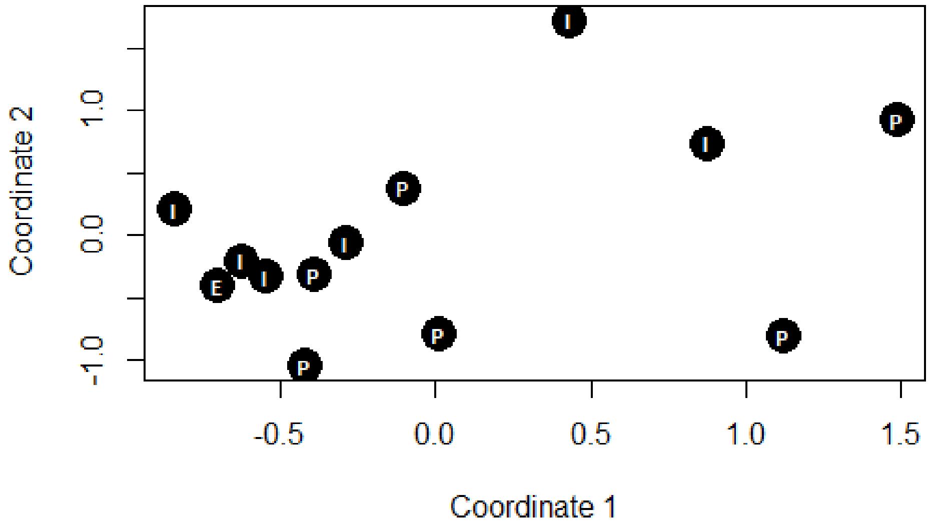


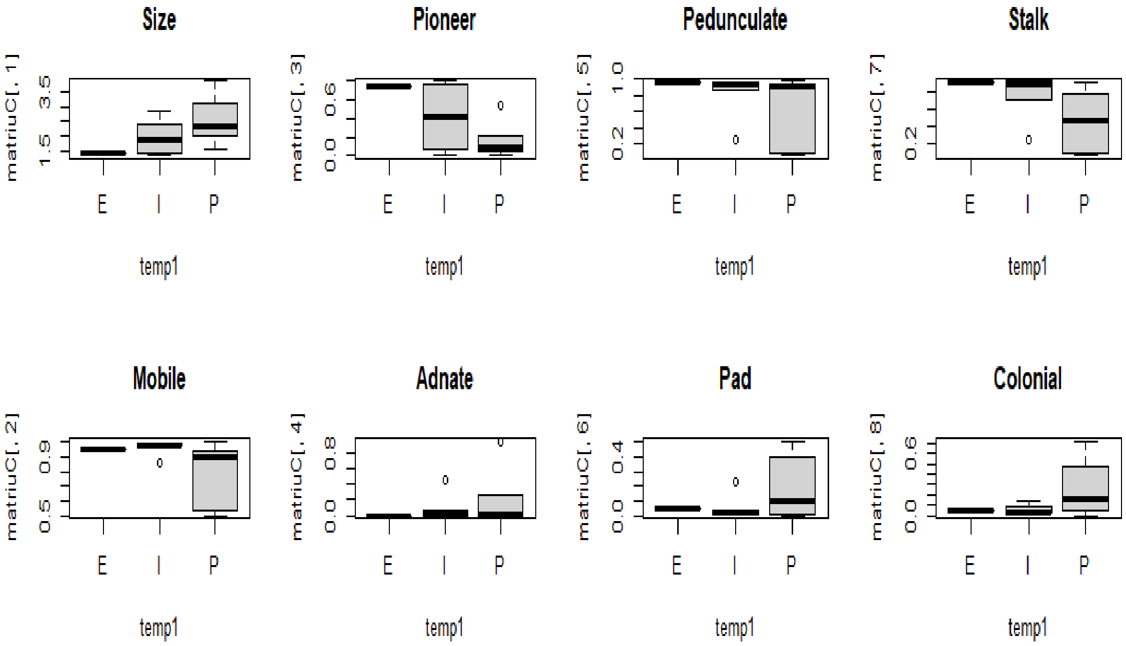
***Figure 4**. Dimension reduction via multidimensional scaling (MDS) showing the three types of rivers. I (Intermittent), E (Ephemeral) and P (Perennial)*

There seemed to be a high similarity between communities from the three river types (*Figure 4*) and no significant differences were observed with the ANOSIM analysis (*Table 4*).

***Table 4**. ANOSIM for communities and traits between the three types of rivers.*

For communities:	For traits:
ANOSIM statistic R: -0.1201 Significance: 0.835	ANOSIM statistic R: -0.04028 Significance: 0.58

This indicates that there are no differences neither in communities nor in traits between intermittent, ephemeral and perennial rivers. Moreover, the negative *R* values in both analyses suggest more similarity between rivers than within rivers.



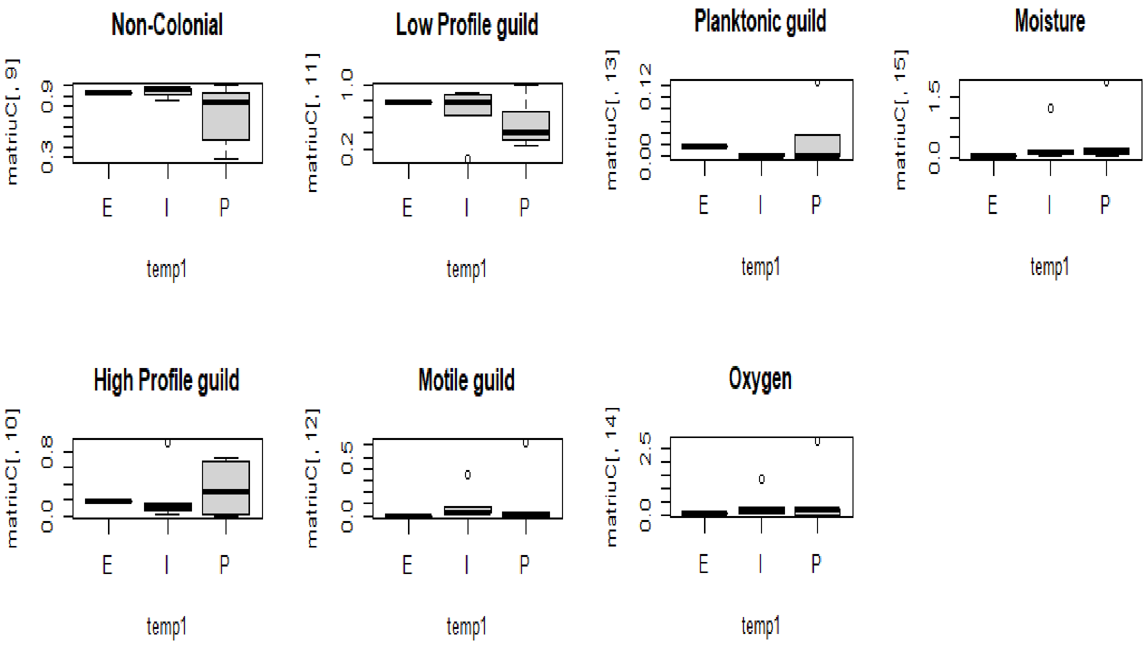


***Figure 5**. Boxplots of the distribution of each trait in the three river types. For each type, the horizontal line represents the median value of the distribution, and the whiskers reach the highest and lowest value within 95% of the distribution. (E)= Ephemeral, (I)=Intermittent and (P)=Perennial.*

The comparison of each trait amongst river types resulted in a tendency of some traits (“size”, “pad”, “adnate”, “colonial” and “high-profile guild”) to increase progressively as the degree of intermittence decreases (*Figure 5*). However, it also seemed to be a high variability for perennial rivers, including taxa with wide ranging values for “colonial”, “pad”, “mobile”, “stalk” and “high-profile”.

On the other hand, while intermittent rivers also showed variability in some traits such “pioneer”, it seemed that several are constant, including presence of “non-colonial”, “low-profile guild”, “mobile”, “pedunculate”, “stalk” and absence of “pad” and “adnate” traits. In addition, regarding the ephemeral river, the traits that appeared to predominate are: “pioneer”, “stalk” and “planktonic guild”. Nevertheless, Kruskal-Wallis tests[4] were conducted for each river type per trait and all the obtained P-values showed non-significant differences.

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[4] The Kruskal-Wallis analyses and P-values are attached in the Appendix.

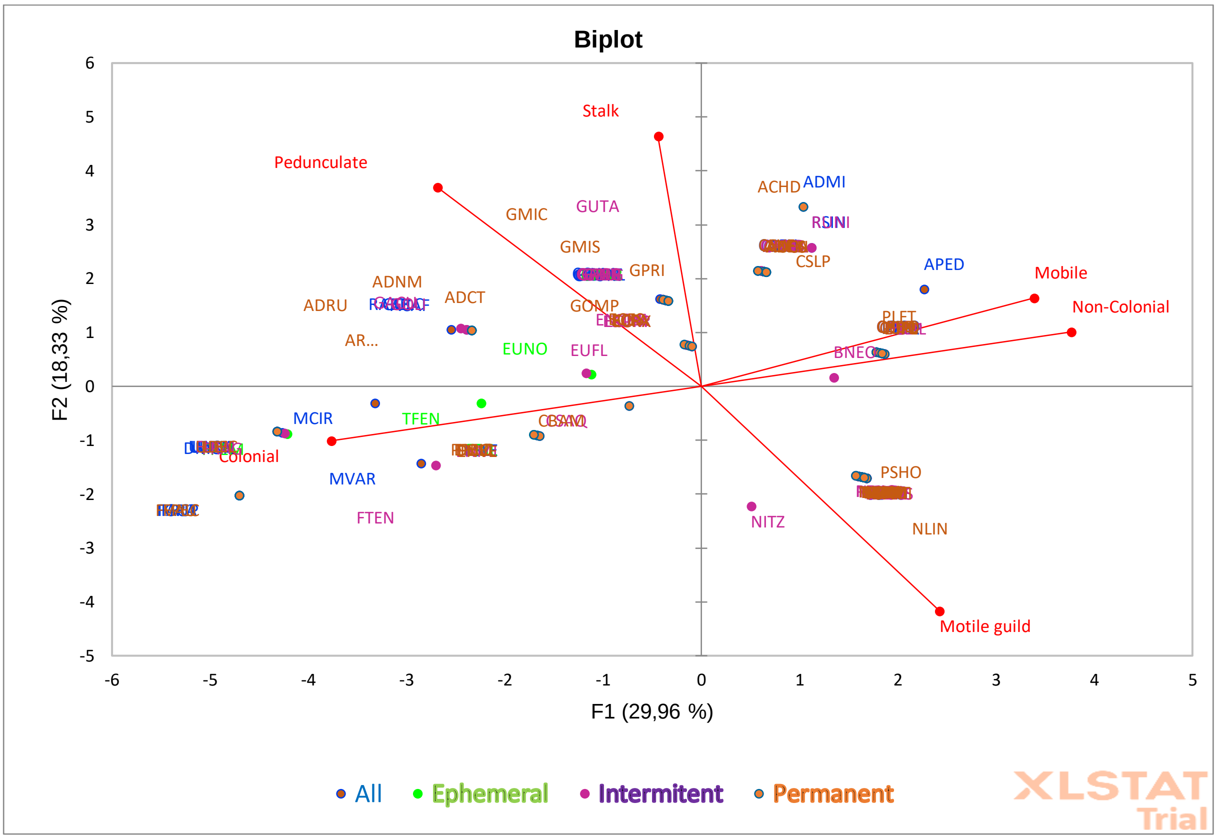

Figure 6*. Principal Components Analysis (PCA) for species with biological traits as variables and considering hydrological groups: “Perennial”, “Intermittent”, “Ephemeral” and “All”. Main Species codes*[5] *: Achnanthes pyrenaica (APYR), Amphora pediculus (APED), Brachysira neoexilis(BNEO) , Cocconeis placentula(CPPL), Cymbopleura subaequalis (CSAQ), Diploneis separanda(DSEP), Eucocconeis flexella (EUFL), Eunotia sp (EUNO), Eunotia bilunaris (EBIL), Encyonema minutum (ENMI), Encyonopsis microcephala (ENCM), Fragilaria perminuta (FPEM), Gomphonema utae (GUTA), Gomphonema parvulum (GPAR),), Nitzschia sp. (NITZ), Pinnularia schoenfelderi (PSHO), Reimeria uniseriata (RUMI), Tabellaria fenestrata (TFEN).*

Our PCA (*Figure 6*), showed that the first component accounted for 29,96% of the information, and the second component for 18,33%; together they contained 48,82%. The influential variables are the following biological traits: Mobile, Non-colonial, Motile guild, Colonial, Pedunculate and Stalk. The first component separated species with mobile, non-colonial traits and motile guild on the right and colonial and pedunculate traits on the left (Table 5). For the second component, the variables that weigh are: stalk, pedunculate, low profile guild and also motile guild with a negative value. Thus, high values of this component indicate species that have traits such as stalk, peduncle and belong to the low-profile guild, whereas low values of this component refer to species without these traits that facilitate attachment to the substrate and belong to the Motile-guild.

One of the centromeres from species belonging to ephemeral rivers is located negatively on both axes, these taxa are colonial and belong to the high-profile guild or

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[5] All species Codes can be found on *Appendix 2.*

planktonic guild. The other cluster is located below the first component and above the second component.

Regarding species belonging to intermittent rivers, it appears to be a high variability, with multiple centromeres: two below both axis, these include colonial species belonging to the high-profile guild. Another centromere is positive for the first component and negative for the second component, characterised for being non-colonial and belonging to the motile guild. There are two more clusters located positive on both axes, includes taxa with traits to attach to the substrate and belonging to the low-profile guild and non-colonial. In addition, Moreover, there are also 3 clusters located on a negative first component and a positive second component, composed of colonial species belonging to low profile guild and having structures such as a stalk or peduncle.

In reference to species belonging to perennial rivers, there seems to be a high variability on the traits found and consequently their distribution is wide along all axes.

Table 5. Factor loadings for each component.

	F1	F2	F3	F4	F5
Size class	-0,072	0,022	-0,164	0,759	-0,339
Mobile	0,758	0,287	-0,326	0,004	0,109
Pioneer	0,106	0,264	0,219	-0,219	0,667
Adnate	0,334	0,219	0,526	0,584	0,129
Pedunculate	-0,602	0,647	-0,018	-0,338	-0,276
Pad	-0,657	-0,150	0,456	-0,120	-0,350
Stalk	-0,099	0,814	-0,395	-0,261	-0,005
Colonial	-0,844	-0,177	-0,050	0,223	0,360
Non-Colonial	0,844	0,177	0,050	-0,223	-0,360
High-Profile guild	-0,622	0,211	-0,605	0,229	0,037
Low-Profile guild	0,272	0,610	0,628	0,153	-0,003
Motile guild	0,543	-0,730	-0,239	-0,226	-0,014
Planktonic guild	-0,457	-0,257	0,471	-0,376	-0,050

6. DISCUSSION

According to predictions on climate change and human alterations, low-flow and drying periods are expected to increase in Mediterranean regions, with intermittent and ephemeral rivers being even more frequent (Datry et al., 2014). We found that diatoms did not show statistically significant differences on taxonomic or trait patterns amongst different river types, most probably due to the fact that diatoms have short life cycles and are able to quickly respond to environmental changes.

While resilience is studied as the leading cause for algal recolonization by means of drift, there is a lack of knowledge especially regarding diatom physiological traits that may enable them with resistant strategies. Our original experiment aimed to be the stepping stone to further analyses of biofilm resistance to drying periods, shedding light into the pattern of recolonisation considering both the degree of intermittence and habitat heterogeneity, experimentally eliminating the effect from drift. Nevertheless, our final study results are mostly based on morphological traits and ecological guilds, which cannot consider all the possible stresses that may have an impact on the diatom communities and distribution patterns. The ecological guilds defined by Passy (2007) are an interesting mechanism to regroup other biological traits; in our study, the low-profile guild appears to increase following the degree of intermittency, contrary to the high-profile guild. However, this approach does not seem convenient when analysing several biological traits and hence, analysing traits independently is essential. Furthermore, Van Dam (1994) and Falasco (2016) defined several physiological traits: pH, salinity, Nitrogen uptake metabolism, trophic state, or the Chlorophyll-a levels, but there is a lack of data for the majority of species sampled by Catalan Water Agency and for this reason, our results comparing oxygen and moisture traits between different types of rivers do not seem significant. Further research should also incorporate traits considering mucilage production as potential and essential strategy to withstand drying conditions. Other valuable biological traits that should be addressed may be aerial dispersal by animals or wind and the occurrence of taxa in drift

While comparing traits between river types, one of the major traits that appears to respond to flow intermittence is diatom size, which increased as the degree of intermittence decreases, suggesting resistance. However, Round et al. (1990) stated that large diatoms tend to be epipelic, growing and adhering at the interference of sediments and water, while Leira et al. (2009) suggested that small cell sizes thrive on flowing rivers with low nutrients levels. Our different approach is based on the fact that a small cell size implies a fast-growing and recolonisation rate, usually being pioneer taxa, predominant in changing habitats like intermittent rivers. On the contrary, a large cell size seems better adapted to stable conditions like perennial streams. For this river type, most of the analysed traits seemed to have a wide variability, hinting that other variables may be more influential in shaping diatoms communities in perennial rivers.

Our results also found variability in intermittent rivers, regarding richness, diversity and the pioneer trait, as well as in the dispersion on the MDS, and multiple centromeres on the “Principal Components Analysis”. This is likely to be due to the different timings since the drying periods started for each river. Unlike macroinvertebrates or other aquatic taxa, diatoms complete their life cycle rapidly, recolonising and re-establishing the community in short periods of time; therefore, the information about the perturbation is lost in a short time and for this reason, the analysed rivers should be on the same desiccation stage for a more objective insight into changes in diatom communities.

However, some other traits appeared to be constant in most intermittent rivers, such as mobile, pedunculate, non-colonial, no-adnate, no-pad; indicating potential resistance and resilience strategies. The traits mobile and non-colonial could possibly be correlated, free individual cells may be able to move locally on a stone, reaching remaining water. In reference to the peduncle structure, it is thought to be merely structural as a main response to reach light (Round et al., 1990), but may also be considered as a resistance strategy in intermittent rivers, whereas the assumed structures to stay attached (adnate and pad) are mostly absent, suggesting that these traits are not probably resistance mechanisms. Despite the fact that these traits show no statistically significant differences, the tendency to predominate in the majority of intermittent rivers seems to evoke that the temporary lack of water flow can potentially act as an environmental filtering, shaping the community composition, selecting taxa with these apparent constant traits.

Regarding ephemeral streams, the tendency in traits correlates to intermittent rivers, but includes pioneer taxa. Nevertheless, the analysed data only corresponds to a single river; hence, a complete study should have included the same number of samples for each river type classification.

7. CONCLUSION

In this research, we were not able to test for resistance traits of diatoms from the initial rewetting experiment; however, our obtained laboratory samples can still be analysed. Our main study tried to assess potential biological traits that may influence resistance and also resilience strategies in intermittent rivers. This was carried out by coding traits and assigning them to real data of diatom communities belonging to several rivers differing in the degree of flow intermittence.

To sum up, we found no statistically significant differences on traits or community composition between river types. Although both perennial and intermittent rivers showed a wide variability, some constant tendencies were observed especially regarding intermittent rivers. Our approach identifies traits such as mobile, pedunculate, non-colonial, no-adnate and no-pad to be favourably selected in this river type. In reference to our hypotheses, it seems that resistance traits predominate, but resilience strategies are also implied. In addition, we suggest that conducting more species inventories on each river type would be likely to have statistically significant results. Further research should also aim to study rivers that are on a similar stage in the drying period, in order to reduce the variability.

Acknowledgements

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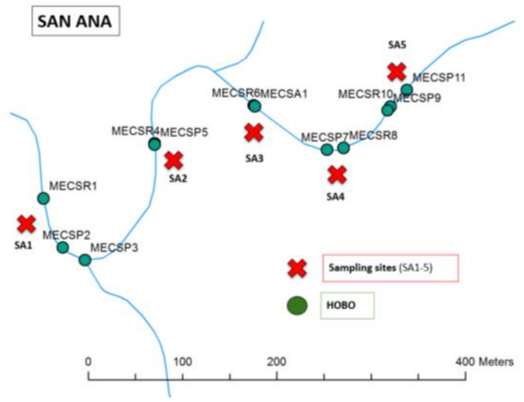
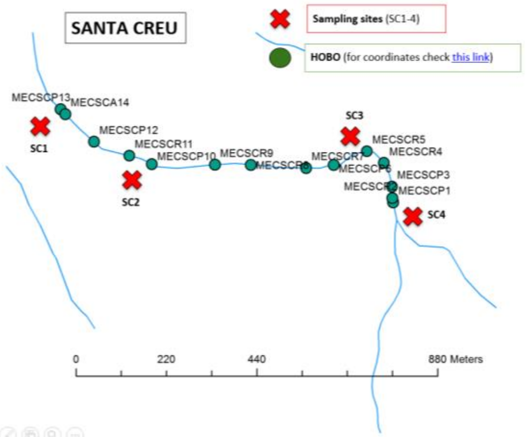
9. APPENDIX

A.1 Maps of the three studied rivers

***Figure 7**. Topographic map of the three rivers location. a)Talamanca, b) Santa Creu and C) San Ana https://www.google.es/maps*





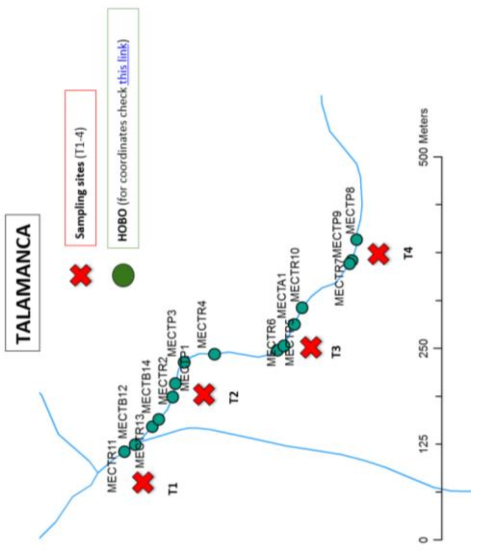


***Figure 8**. Maps of the three studied rivers. FEHM-lab*

A.2 Table of Results for Objective 2

***Table 6**. Analysis of biological traits for each species (Data from ACA)*

	CODE	Hydrology	Size class	Mobile	Pioneer	Adnate	Pedunculate	Pad	Stalk	Colonial	Non-Colonia	High-Profile	Low-Profile	Motile guild	Planktonic g	Oxygen	Moisture
Achnanthes	APYR	Intermitent	2	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ACAF	All	1	1	0	0	1	0	1	1	0	1	0	0	0		
Achnanthidi	ADCA	Permanent	1	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ADCT	Permanent	1	1	0	0	1	0	1	1	0	1	0	0	0		
Achnanthidi	ADRU	Permanent	1	1	0	0	1	0	1	1	0	1	0	0	0		
Achnanthidi	ADEU	Permanent	1	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ADEX	Permanent	2	1	0	0	1	0	1	0	1	0	1	0	0		
ACHNANTHI	ACHD	Permanent	1	1	1	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ADGL	Intermitent	1	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ACLI	Permanent	1	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ADMI	All	1	1	1	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ADNM	Permanent	1	1	0	0	1	0	1	1	0	1	0	0	0		
Achnanthidi	ADPY	All	2	1	0	0	1	0	1	0	1	0	1	0	0		
Achnanthidi	ARPY	Permanent	1	1	0	0	1	0	1	1	0	1	0	0	0		
Achnanthidi	ADCS	Permanent	1	1	0	0	1	0	1	0	1	0	1	0	0		
Adlafia minu	ADMS	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Amphora pe	APED	All	1	1	1	1	0	0	0	0	1	0	1	0	0	2	3
Brachysira ne	BNEO	Intermitent	2	1	0	0	0	0	0	0	1	0	1	0	0		
COCCONEIS	COCO	All	5	1	0	1	0	0	0	0	1	0	1	0	0	3	2
Cocconeis eu	CEUG	All	5	1	0	1	0	0	0	0	1	0	1	0	0		
Cocconeis eu	CEUO	Permanent	5	1	0	1	0	0	0	0	1	0	1	0	0		
Cocconeis pe	CPED	Permanent	5	1	0	1	0	0	0	0	1	0	1	0	0	2	1
Cocconeis pl	CPPL	Intermitent	4	1	0	1	0	0	0	0	1	0	1	0	0	3	2
Cocconeis pl	CPLE	Intermitent	5	1	0	1	0	0	0	0	1	0	1	0	0	3	2
Cocconeis pl	CPLI	All	5	1	0	1	0	0	0	0	1	0	1	0	0	3	2
Cocconeis ps	COPL	Permanent	4	1	0	1	0	0	0	0	1	0	1	0	0	3	2
Craticula acc	CRAC	Permanent	3	1	0	0	0	0	0	0	1	0	0	1	0		
CYMBELLA C	CYMB	Intermitent	3	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella aff	CAFF	Intermitent	3	1	0	0	1	0	1	0	1	0	1	0	0	1	2
Cymbella cyr	CCYM	All	5	1	0	0	1	0	1	0	1	1	0	0	0	1	2
Cymbella ex	CAEX	All	4	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella ex	CEXF	Permanent	4	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella lae	CLAE	Intermitent	2	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella pa	CPAR	All	2	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella pe	CPPV	Intermitent	2	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella sul	CSLP	Permanent	4	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbella sul	CSUT	All	3	1	0	0	1	0	1	0	1	0	1	0	0		
Cymbopleur	CBAM	Permanent	4	1	0	0	0	0	0	1	0	0	1	0	0		
Cymbopleur	CSAQ	Intermitent	4	1	0	0	0	0	0	1	0	0	1	0	0		
Delicata deli	DDEL	Permanent	3	1	0	0	0	0	0	1	0	1	0	0	0		
Denticula te	DTEN	Permanent	3	1	0	0	0	0	0	0	1	0	0	1	0	1	1
Diatoma mo	DMON	All	3	0	0	0	1	1	0	1	0	1	0	0	0		
DIPLONEIS C	DIPL	Permanent	2	1	0	1	0	0	0	0	1	0	1	0	0		
Diploneis ob	DOBL	Intermitent	2	1	0	1	0	0	0	0	1	0	1	0	0	1	4
Diploneis se	DSEP	Intermitent	2	1	0	1	0	0	0	0	1	0	1	0	0		
Encyonema	ENMI	Intermitent	2	1	0	0	0	0	0	1	0	1	0	0	0		
Encyonema	ESLE	All	3	1	0	0	0	0	0	1	0	1	0	0	0		
Encyonema	ENVE	Permanent	2	1	0	0	0	0	0	1	0	1	0	0	0		
Encyonopsis	ECES	Permanent	4	1	0	0	1	1	0	0	1	0	1	0	0		
Encyonopsis	ECFA	Permanent	2	1	0	0	1	1	0	0	1	0	1	0	0		
Encyonopsis	ECKR	Intermitent	1	1	0	0	1	1	0	0	1	0	1	0	0		
Encyonopsis	ENCM	Intermitent	3	1	0	0	1	1	0	0	1	0	1	0	0		
Encyonopsis	ECPM	Intermitent	1	1	0	0	1	1	0	0	1	0	1	0	0		
Encyonopsis	ESUM	Intermitent	1	1	0	0	1	1	0	0	1	0	1	0	0		
Eolimna cras	ECRX	Permanent	1	1	0	0	1	1	0	0	1	0	1	0	0		
Eolimna min	EOMI	All	1	1	0	0	0	0	0	0	1	0	0	1	0		
Eolimna sub	ESBT	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Eolimna sub	ESBM	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Eucocconeis	EUFL	Intermitent	5	1	0	0	1	1	0	0	1	1	0	0	0		
EUNOTIA C.(	EUNO	Ephemeral	3	1	0	0	1	1	0	0	1	1	0	0	0		
Eunotia bilur	EBIL	Ephemeral	4	1	0	0	0	0	0	1	0	1	0	0	0	2	3
Eunotia micr	EMIC	Permanent	4	1	0	0	0	0	0	1	0	1	0	0	0	1	4
Fallacia subh	FSBH	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Fistulifera sa	FSAP	Permanent	1	1	0	0	0	0	0	0	1	0	0	1	0		
FRAGILARIA	FRAG	Intermitent	2	0	0	0	1	1	0	1	0	1	0	0	0		
Fragilaria au	FAUT	All	1	0	0	0	1	1	0	1	0	0	0	0	1	1	
Fragilaria gra	FGRA	All	1	0	0	0	1	1	0	1	0	0	0	0	1	1	
Fragilaria pe	FPEC	Permanent	1	0	0	0	1	1	0	1	0	0	0	0	1	1	
Fragilaria pe	FPEM	Ephemeral	1	0	0	0	1	1	0	1	0	1	0	0	0		
Fragilaria rec	FRCP	All	1	0	0	0	1	1	0	1	0	0	0	0	1	1	
Fragilaria ter	FTEN	Intermitent	2	0	0	0	1	1	0	0	1	0	0	0	1	1	2
Fragilaria ulr	FULN	Intermitent	5	0	0	0	1	1	0	1	0	1	0	0	0	3	2
Fragilaria va	FVAU	Permanent	1	0	0	0	1	1	0	1	0	0	0	0	1	1	
GOMPHONE	GOMP	Permanent	3	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GACU	Intermitent	5	1	0	0	1	0	1	1	0	1	0	0	0	2	2

Gomphonem	GANG	All	3	1	0	0	1	0	1	0	1	1	0	0	0	1	
Gomphonem	GANT	Intermitent	4	1	0	0	1	0	1	0	1	1	0	0	0	1	
Gomphonem	GCBC	All	3	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GELG	Intermitent	3	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GEXL	All	3	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GGRA	All	4	1	0	0	1	0	1	0	1	1	0	0	0	1	3
Gomphonem	GLAT	All	4	1	0	0	1	0	1	0	1	1	0	0	0	1	3
Gomphonem	GMIC	Permanent	4	1	0	0	1	0	1	0	1	1	0	0	0	2	3
Gomphonem	GMIS	Permanent	2	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GMIN	Intermitent	3	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GOLI	Intermitent	3	1	0	0	1	0	1	1	0	1	0	0	0	2	1
Gomphonem	GOLC	All	3	1	0	0	1	0	1	1	0	1	0	0	0	2	1
Gomphonem	GPAR	Ephemeral	3	1	0	0	1	0	1	0	1	1	0	0	0	4	3
Gomphonem	GPUM	All	2	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GPRI	Permanent	2	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GROS	Intermitent	4	1	0	0	1	0	1	0	1	1	0	0	0		
Gomphonem	GTER	Intermitent	4	1	0	0	1	0	1	0	1	1	0	0	0	1	3
Gomphonem	GUTA	Intermitent	4	1	0	0	1	0	1	0	1	1	0	0	0		
Karayevia cle	KCLE	Intermitent	3	1	0	0	1	1	0	0	1	0	1	0	0		
Mastogloia s	MSMI	Intermitent	4	1	0	0	0	0	0	0	1	0	0	1	0		3
Mayamaea a	MAAT	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Mayamaea a	MAPE	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Mayamaea p	MPMI	Permanent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Melosira vari	MVAR	All	5	0	0	0	0	0	0	1	0	1	0	0	0	3	2
Meridion circ	MCIR	All	4	0	0	0	1	1	0	1	0	0	1	0	0	2	1
Navicula ant	NANT	Intermitent	3	1	0	0	0	0	0	0	1	0	0	1	0		
Navicula cari	NCAR	Intermitent	4	1	0	0	0	0	0	0	1	0	0	1	0		
Navicula cinc	NCIN	Permanent	3	1	0	0	0	0	0	0	1	0	0	1	0	3	4
Navicula cryp	NCRY	Permanent	3	1	0	0	0	0	0	0	1	0	0	1	0	3	2
Navicula cryp	NCTE	All	3	1	0	0	0	0	0	0	1	0	0	1	0	3	2
Navicula cryp	NCTO	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Navicula greg	NGRE	All	3	1	0	0	0	0	0	0	1	0	0	1	0	4	3
Navicula lanc	NLAN	Permanent	4	1	0	0	0	0	0	0	1	0	0	1	0	3	3
Navicula radi	NRAD	Intermitent	5	1	0	0	0	0	0	0	1	0	0	1	0	2	3
Navicula reic	NRCH	All	2	1	0	0	0	0	0	0	1	0	0	1	0		
Navicula trip	NTPT	Intermitent	4	1	0	0	0	0	0	0	1	0	0	1	0	2	3
Navicula ven	NVEN	All	2	1	0	0	0	0	0	0	1	0	0	1	0		
NITZSCHIA A	NITZ	Intermitent	3	0	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia abb	NZAB	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia arc	NIAR	Intermitent	2	1	0	0	0	0	0	0	1	0	0	1	0	2	
Nitzschia den	NDEN	Intermitent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia dis	NDIS	Intermitent	4	1	0	0	0	0	0	0	1	0	0	1	0	2	3
Nitzschia fili	NFIC	Intermitent	2	1	0	0	0	0	0	0	1	0	0	1	0	3	3
Nitzschia for	NFON	Intermitent	3	1	0	0	0	0	0	0	1	0	0	1	0	2	1
Nitzschia gra	NIGR	Permanent	2	1	0	0	0	0	0	0	1	0	0	1	0	2	1
Nitzschia inc	NINC	All	1	1	0	0	0	0	0	0	1	0	0	1	0	3	3
Nitzschia lac	NILA	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0	1	
Nitzschia line	NLIN	Permanent	5	1	0	0	0	0	0	0	1	0	0	1	0	2	3
Nitzschia me	NIME	Intermitent	4	1	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia pal	NPAE	Intermitent	2	1	0	0	0	0	0	0	1	0	0	1	0	3	2
Nitzschia spe	NZSS	Intermitent	3	1	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia sup	NZSU	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Nitzschia tab	NTAB	Intermitent	2	1	0	0	0	0	0	0	1	0	0	1	0		
Parlibellus p	PPRO	Permanent	4	1	0	0	0	0	0	1	0	1	0	0	0		
Pinnularia m	PMIC	Intermitent	5	1	0	0	0	0	0	0	1	0	0	1	0	3	3
Pinnularia sc	PSHO	Permanent	5	1	0	0	0	0	0	0	1	0	0	1	0		
Planothidiur	PLFR	All	2	1	0	1	0	0	0	0	1	0	1	0	0		
Planothidiur	PLFT	Permanent	3	1	0	1	0	0	0	0	1	0	1	0	0		
Planothidiur	PTLA	All	3	1	0	1	0	0	0	0	1	0	1	0	0		
PLANOTHIDI	PLTD	Permanent	3	1	0	1	0	0	0	0	1	0	1	0	0		
Reimeria sin	RSIN	All	3	1	0	1	1	0	1	0	1	0	1	0	0		
Reimeria uni	RUNI	Intermitent	3	1	0	1	1	0	1	0	1	0	1	0	0		
Rhoicospher	RABB	All	3	0	0	0	1	0	1	1	0	0	1	0	0	2	2
Sellaphora p	SEPA	Intermitent	1	1	0	0	0	0	0	0	1	0	0	1	0		
Sellaphora se	SSEM	All	1	1	0	0	0	0	0	0	1	0	0	1	0		
Sellaphora st	SSTM	All	1	1	0	0	0	0	0	0	1	0	0	1	0		
Tabellaria fe	TFEN	Ephemeral	3	0	0	0	1	1	0	0	1	1	0	0	0	1	
Ulnaria acus	UACU	All	5	0	0	0	1	1	0	1	0	1	0	0	0		
Ulnaria bicep	UBIC	Permanent	5	0	0	0	1	1	0	1	0	1	0	0	0		
ULNARIA Cor	ULNA	All	5	0	0	0	1	1	0	1	0	1	0	0	0		
Ulnaria delic	UDEL	Permanent	5	0	0	0	1	1	0	1	0	1	0	0	0		
Ulnaria ulna	UULN	All	5	0	0	0	1	1	0	1	0	1	0	0	0		

Table key

-Size class: one of these 5 values can be given to the taxon: 1: biovolume between 0-99 µm3, 2: 100-299 µm3, 3: 300-599 µm3, 4: 600-1499 µm3, 5: over 1500 µm3. (Rimet, 2012)

-Mobile: one of these 2 values can be given to the taxon: 0: immobile taxon, 1: mobile taxon (has a raphe). (Rimet, 2012)

-Pioneer: one of these 2 values can be given to the taxon: 0: non-pioneer taxon, 1: taxon considered as pioneer. (Rimet, 2012)

-Adnate: one of these 2 values can be given to the taxon: 0: non adnate taxon, 1: adnate taxon. (Rimet, 2012)

-Pedunculate (stalk or pad attached to substrate): one of these 2 values can be given to the taxon: 0: non pedunculate, 1: pedunculate. (Rimet, 2012)

-Pad (attached to substrate):one of these 2 values can be given to the taxon: 0: not producing a pad, 1: producing a pad. (Rimet, 2012)

-Stalk (attached to substrate): one of these 2 values can be given to the taxon: 0: not producing a stalk, 1: producing a stalk. (Rimet, 2012)

-Colonial: one of these 2 values can be given to the taxon: 0: not forming colonies, 1: can form colonies. (Rimet, 2012)

-**Non-colonial**: one of these 2 values can be given to the taxon: 0: can form colonies, 1: not forming colonies. (Rimet, 2012)

-Guilds(high profile, low profile, motile, planktonic): one of these 2 values can be given to the taxon: 0: do not belong to this guild, 1: belong to this guild. (Rimet, 2012)

-Oxygen requirements:1:continuously high (about 100% saturation),2:fairly high (above 75% saturation)**,** 3:moderate (above 50% saturation)**,** 4:low (above 30% saturation)**,** 5:very low (about 10% saturation). (Van Dam, 1994)

-Moisture: 1:never, or only very rarely, occurring outside water bodies**,** 2: mainly occurring in water bodies, sometimes on wet places**,** 3: mainly occurring in water bodies, also rather regularly on wetand moist places**,** 4: mainly occurring on wet and moist or temporarily dry places**,** 5 : nearly exclusively occurring outside water bodies. (Van Dam, 1994)

A.3 Matrix (C)

This C Matrix includes the proportion of each trait per studied river

```
              Size    Mobile    Pioneer     Adnate Pedunculate
Brugent   2.266173 0.5430457 0.09649035 0.00000000  0.88811119
Portella  3.098310 0.5043504 0.07810781 0.00000000  0.93679368
Merles    1.544109 0.8578716 0.54550910 0.00000000  0.93168634
Major     2.448145 0.9347935 0.20802080 0.05360536  0.97219722
Osor      1.974892 0.9352806 0.00470141 0.26647994  0.09582875
Guilla    3.880148 0.9994002 0.03948421 0.94092363  0.05787685
Glorieta  1.329900 0.9666000 0.76820000 0.00000000  0.95420000
SantaCreu 1.396540 0.9903990 0.80168017 0.00240024  0.96859686
Guanta    2.376162 0.9800020 0.14168583 0.00739926  0.94280572
Avenco    2.137900 0.9779000 0.00250000 0.05420000  0.94580000
Daro      1.542717 0.9729892 0.69947979 0.02711084  0.86984794
Orlina    2.850570 0.8522705 0.06041208 0.46029206  0.25175035
Ridaura   1.377200 0.9448000 0.75740000 0.00000000  0.96880000
                   Pad      Stalk   Colonial Non.Colonial
Brugent   0.3934606539 0.49465053 0.46945305    0.4618538
Portella  0.5052505251 0.43154315 0.71747175    0.2825283
Merles    0.1517303461 0.77995599 0.26305261    0.7346469
Major     0.0513051305 0.92089209 0.05590559    0.9347935
Osor      0.0144043213 0.08142443 0.05741723    0.9282785
Guilla    0.0005997601 0.05727709 0.00019992    0.9994002
Glorieta  0.0334000000 0.92080000 0.07940000    0.9081000
SantaCreu 0.0362036204 0.93239324 0.00720072    0.9927993
Guanta    0.2366763324 0.70612939 0.02999700    0.9700030
Avenco    0.0148000000 0.93100000 0.02210000    0.9779000
Daro      0.0123049220 0.85754302 0.03211285    0.9555822
Orlina    0.0145029006 0.23724745 0.14772955    0.8522705
Ridaura   0.0456000000 0.92320000 0.04320000    0.9376000
          High.Profile_guild Low.Profile_guild Motile_guild
Brugent          0.439256074         0.4566543   0.00000000
Portella         0.734473447         0.2510251   0.01450145
Merles           0.170434087         0.6757351   0.02580516
Major            0.673167317         0.3152315   0.00230023
Osor             0.009302791         0.3528058   0.62358708
```

```
Guilla          0.017493003        0.9807077   0.00139944
Glorieta         0.092000000        0.8622000   0.02910000
SantaCreu        0.075007501        0.8935894   0.02660266
Guanta           0.174082592        0.7885211   0.03739626
Avenco           0.913800000        0.0813000   0.00490000
Daro            0.155662265        0.7537015   0.07833133
Orlina          0.019303861        0.6249250   0.35577115
Ridaura          0.180200000        0.7814000   0.00240000
          Planktonic_guild     Oxygen   Moisture
Brugent         0.03539646 0.04559544 0.01809819
Portella       0.00000000 0.03880388 0.11421142
Merles          0.12572515 0.21074215 0.07791558
Major          0.00000000 0.20252025 0.17931793
Osor           0.00000000 0.23847154 0.22636791
Guilla         0.00000000 2.79438225 1.88404638
Glorieta        0.00420000 0.12090000 0.07090000
SantaCreu        0.00480048 0.08470847 0.12341234
Guanta          0.00000000 0.14198580 0.19388061
Avenco          0.00000000 0.06900000 0.04190000
Daro           0.00000000 0.27581032 0.13735494
Orlina         0.00000000 1.34926985 1.23274655
Ridaura         0.01680000 0.06480000 0.04320000
```

A.4 Kruskal-Wallis Tests for the three river types per each trait

```
Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 3.7692, df = 2, p-value = 0.1519

NULL

            Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 2.6593, df = 2, p-value = 0.2646

NULL

            Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 2.2198, df = 2, p-value = 0.3296

NULL

            Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1.3023, df = 2, p-value = 0.5214

NULL
```

```
        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 2.4505, df = 2, p-value = 0.2937

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1, df = 2, p-value = 0.6065

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 3.8022, df = 2, p-value = 0.1494

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 2.0549, df = 2, p-value = 0.3579

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 2.0549, df = 2, p-value = 0.3579

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 0.37363, df = 2, p-value = 0.8296

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1.3626, df = 2, p-value = 0.5059

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 3.5495, df = 2, p-value = 0.1695
```

```
NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1.7429, df = 2, p-value = 0.4184

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1.1648, df = 2, p-value = 0.5585

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp1
Kruskal-Wallis chi-squared = 1.1648, df = 2, p-value = 0.5585
no hi ha diferències en lloc per 3 categories

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 2.9388, df = 1, p-value = 0.08648

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 2.4694, df = 1, p-value = 0.1161

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 1.6531, df = 1, p-value = 0.1985

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0, df = 1, p-value = 1

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
```

```
Kruskal-Wallis chi-squared = 1.3061, df = 1, p-value = 0.2531

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0.73469, df = 1, p-value = 0.3914

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 3.449, df = 1, p-value = 0.06329

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 2.0408, df = 1, p-value = 0.1531

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 2.0408, df = 1, p-value = 0.1531

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0.020408, df = 1, p-value = 0.8864

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 1.3061, df = 1, p-value = 0.2531

NULL

        Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 2.0408, df = 1, p-value = 0.1531

NULL

        Kruskal-Wallis rank sum test
```

```
data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0.026531, df = 1, p-value = 0.8706

NULL

            Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0.020408, df = 1, p-value = 0.8864

NULL

            Kruskal-Wallis rank sum test

data:  matriuC[, i] and temp2
Kruskal-Wallis chi-squared = 0.18367, df = 1, p-value = 0.6682
```

A.5 Herbarium for the identified species (Objective 1)

Làmina 1

X1500

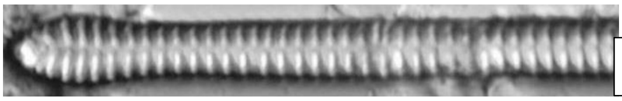
Figura 1*: **Fragilaria cf radians***

Figura 2*: **Fragilaria dilatata***

Figura 3-4*: **Fragilaria ulna***

Figura 5-7*: **Rhopalodia parallela***

Figura 8*: **Gyrosigma cf attenuatum***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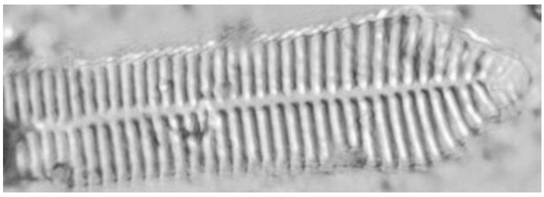
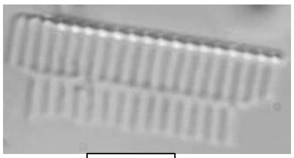

2

3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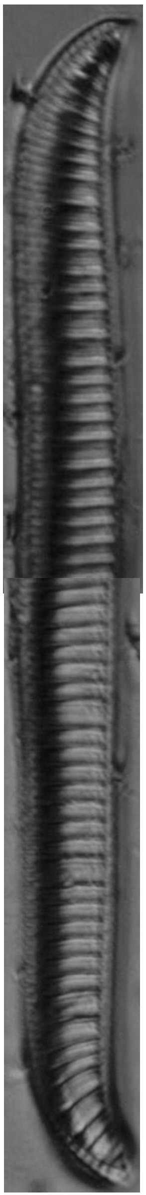
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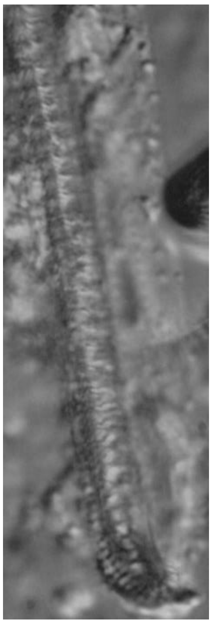
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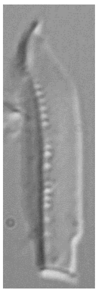
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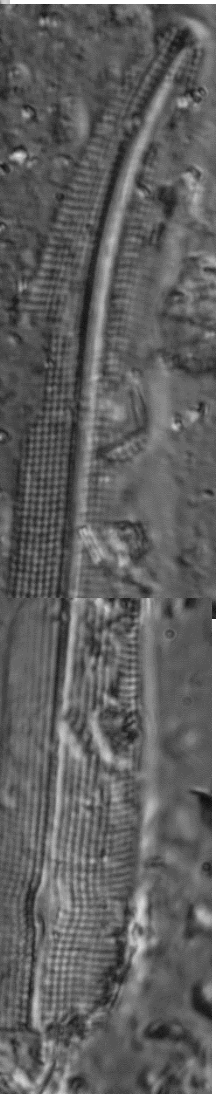
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Làmina 2

X1500

Figura 1-4: ***Cymbopleura amphicephala***

Figura 5-7: ***Eucocconeis flexella***

Figura 8: ***Diploneis elliptica***

Figura 9-10: ***Eunotia bidens***

Figura 11-13 ***Eunotia denticulata***

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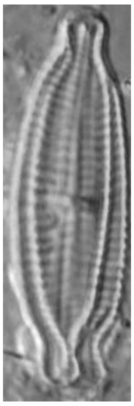

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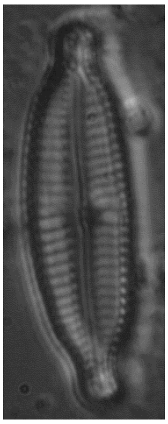

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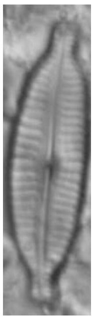

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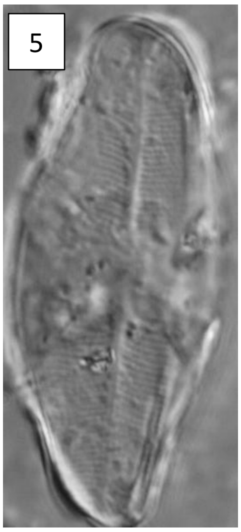

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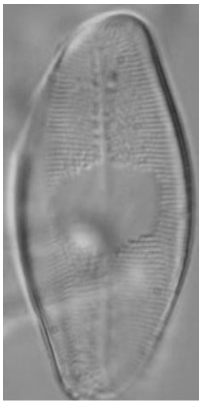

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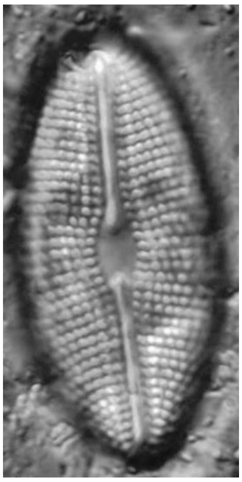

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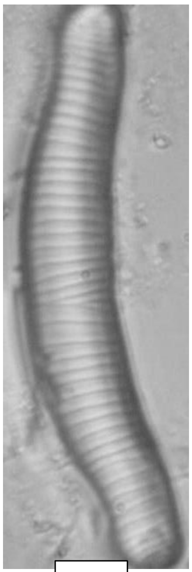

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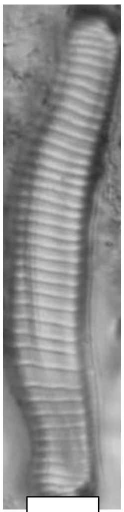

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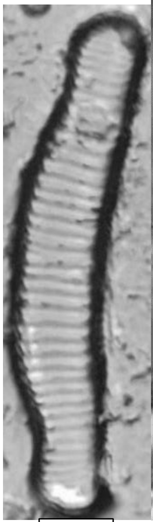

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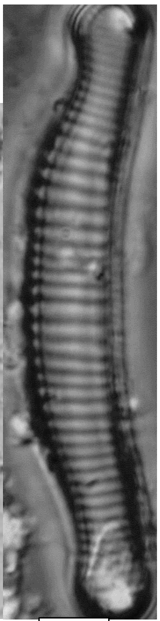

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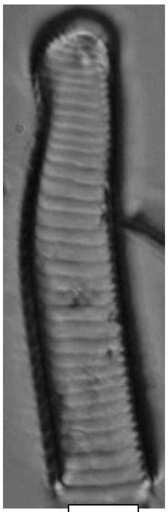

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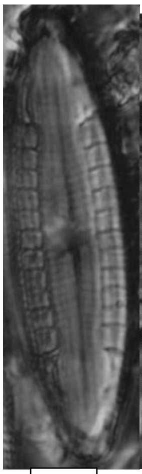
Làmina 3

X1500

Figura 1-7: ***Mastogloia smithii***

Figura 8-10: ***Mastogloia lacustris***



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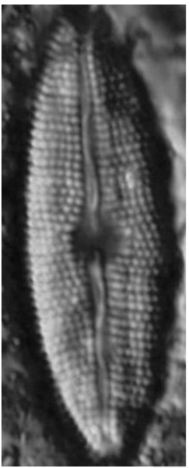

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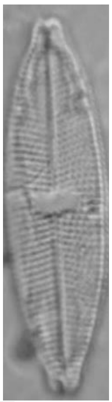

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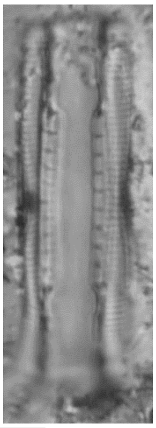

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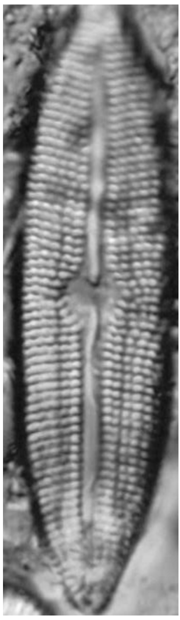

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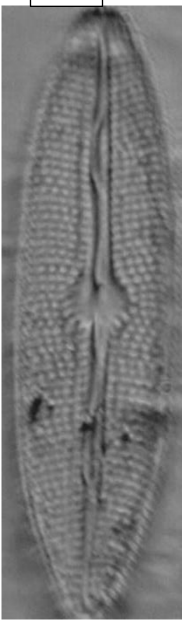


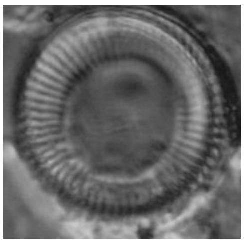
Làmina 4

X1500

Figura 1: ***Cyclotella meneguiniana***

Figura 2: ***Stephanodiscus minutulus***

Figura 3: ***Cyclostephanos dubius***



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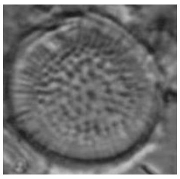

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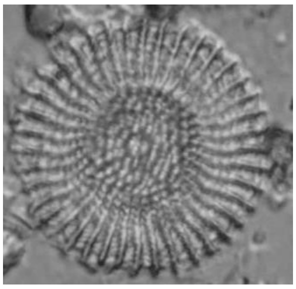

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Làmina 5

X1500

Figura 1-3: ***Cymbella excisa***

Figura 4-5: ***Cymbella cf compacta***

Figura 6: ***Cymbella cf laevis***

Figura 7-8***: Encyonema silesiacum***

Figura 9-10: ***Cymbella cymbiformes***

Figura 11: ***Cymbella cf lancettula***


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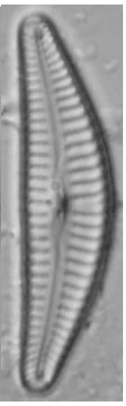
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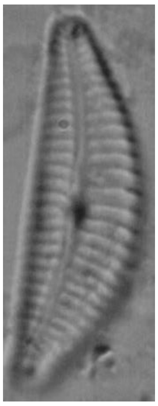
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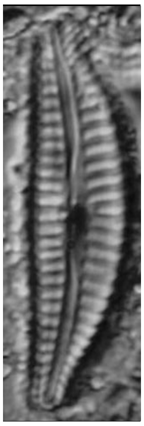
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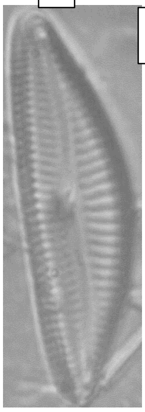
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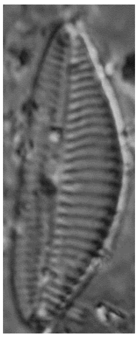
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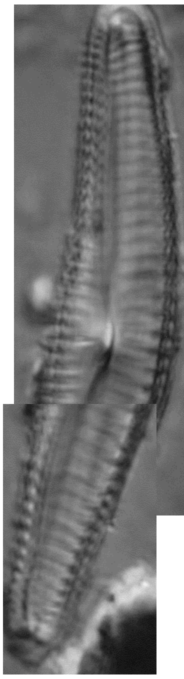
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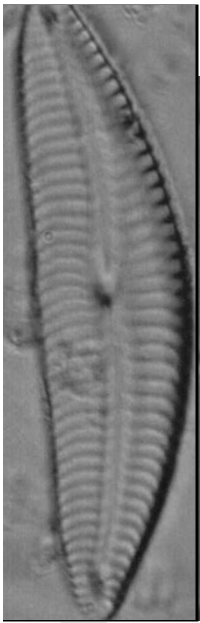
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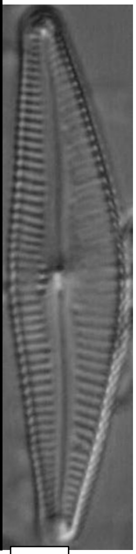
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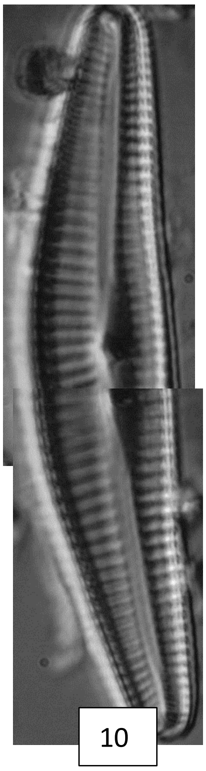
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Làmina 6

X1500

Figura 1-6: ***Brachisyra vitrea***

Figura 7: ***Brachisyra liliana***

Figura 8-9: ***Navicula vandamii***

Figura 10: ***Navicula criptotenella***

Figura 11-16: ***Encyonopsis cesatii***

Figura 17-18: ***Encyonopsis minuta***

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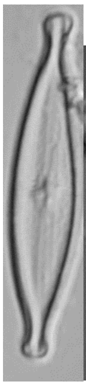

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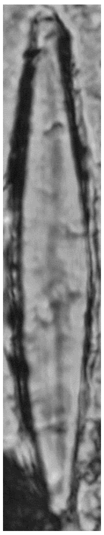

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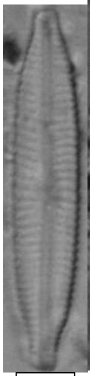

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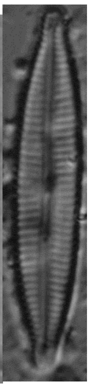

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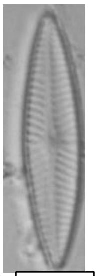

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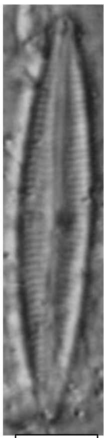

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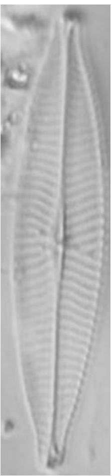

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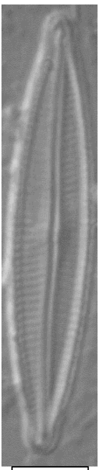

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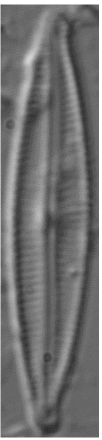

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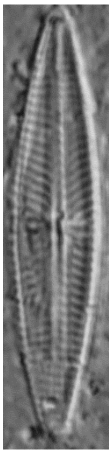

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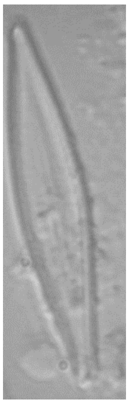

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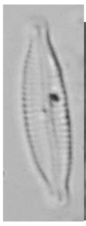

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Làmina 7

X1500

Figura 1: ***Pinnularia cf subcapita***

Figura 2-3: ***Pinnularia cf sinistra***

Figura 4: ***Pinnularia nobilis***

Figura 5: ***Denticula tenuis***

Figura 6-7: ***Nitzschia denticula***

Figura 8: ***Hantschia abundans***

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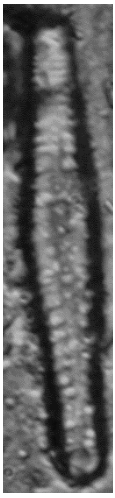

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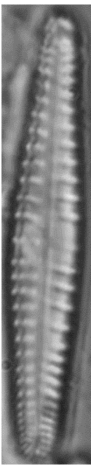

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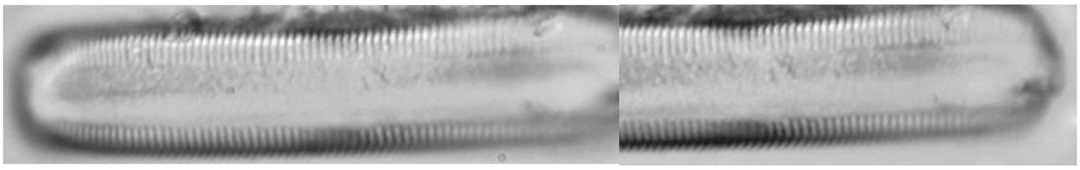

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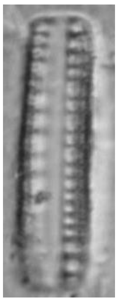

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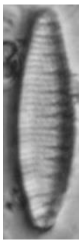

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Làmina 8

X1500

Figura 1-7: ***Gomphonema lateripunctatum***

Figura 8-11: ***Gomphonema micropus***

Figura 12-13 : ***Gomphonema gracile***

Figura 14: ***Gomphonema vibrio***

Figura 15-20: ***Gomphonema parvulis***

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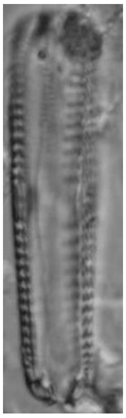

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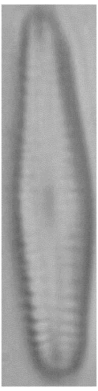

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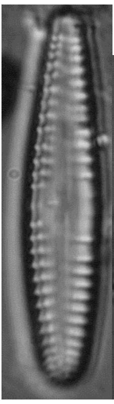

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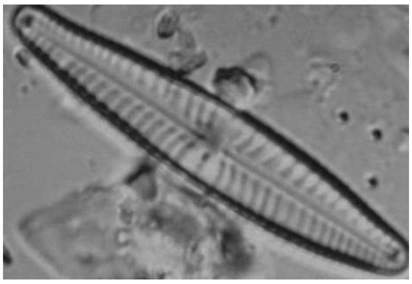

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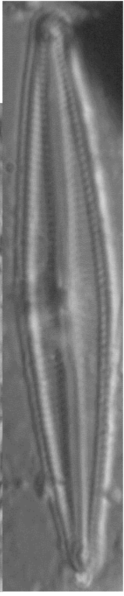

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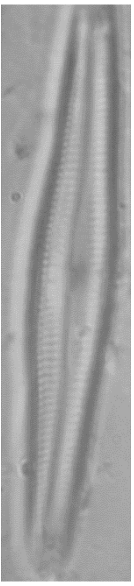

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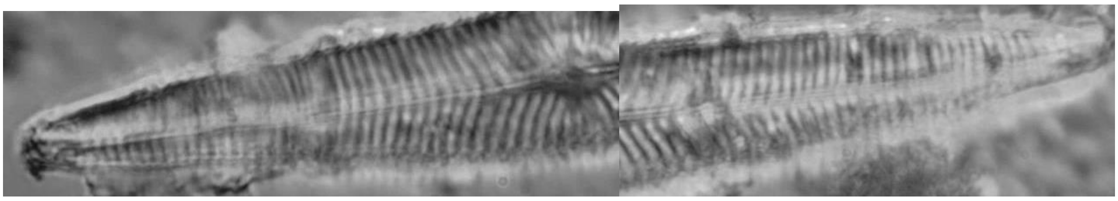

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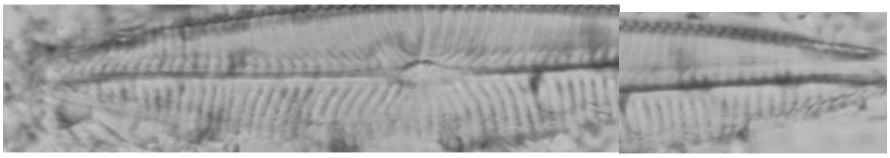

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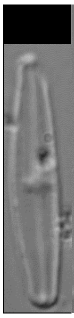

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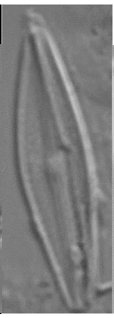

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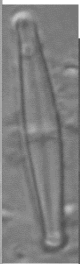

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Làmina 9

X1500

Figura 1-7: ***Achnantidium minutissimum***

Figura 8: ***Achnantes cf trinoidis***

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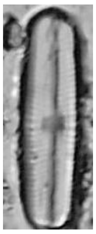

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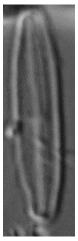

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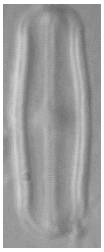

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