

RIVER RESEARCH AND APPLICATIONS

*River Res. Applic.* **30**: 1216–1232 (2014)Published online 15 August 2014 in Wiley Online Library  
(wileyonlinelibrary.com) DOI: 10.1002/rra.2818

## DIATOMS OF TEMPORARY AND PERMANENT WATERCOURSES IN SOUTHERN EUROPE (PORTUGAL)

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## ABSTRACT

The potential importance of benthic diatoms in Mediterranean watercourses has received limited academic attention historically. This study sought to provide baseline information for this poorly studied group. Temporary and permanent watercourses in Portugal differ in catchment characteristics, climatic variables and water chemistry. The benthic diatom communities were characterized in terms of ecological preferences and conservation status for taxa with relative abundance above 1% in at least one site covering 39 temporary sites (109 taxa) and 53 permanent sites (130 taxa). The low-profile guild dominated both temporary and permanent watercourses, followed by the high-profile and motile guilds. Indicator value analysis indicated that *Amphora copulata*, *Cocconeis placentula*, *Diploneis separanda*, *Encyonopsis subminuta*, *Fragilaria radians*, *Gomphonema olivaceum*, *Gomphonema truncatum*, *Halamphora veneta*, *Navicula radiosa*, *Navicula veneta*, *Sellaphora seminulum* and *Ulnaria acus* were indicators of temporary watercourses, whereas *Encyonema minutum*, *Eunotia minor*, *Fragilaria rumpens*, *Fragilaria cf. socia* and *Navicula rhynchocephala* were characteristic of permanent watercourses. Ecological preferences of indicator taxa were inferred on the basis of environmental variables that differed significantly between temporary and permanent watercourses. The importance of temporary watercourses for the maintenance of diatom biodiversity is discussed and explored. Copyright © 2014 John Wiley & Sons, Ltd.

KEY WORDS: diatoms; ecological guilds; ecological preferences; indicator taxa; seasonality

Received 19 November 2013; Revised 11 July 2014; Accepted 14 July 2014

## INTRODUCTION

Rivers that periodically cease to flow comprise a substantial proportion of the total number, length and discharge of the world's rivers (Tooth, 2000). Temporary rivers are not restricted to arid regions; they occur in most terrestrial biomes between 84°N and S latitudes (Larned *et al.*, 2010). During the next century, the number and length of rivers that become temporary may increase in regions experiencing drying trends as a result of climate change and water abstraction for socio-economic uses (Rosado *et al.*, 2012). An increase of 50% in the use of water for agriculture and industry is also predicted by 2025 (Tockner and Stanford, 2002). Furthermore, it is assumed that climate change will result in significant aquatic biodiversity losses due to changes in population dynamics resulting from an increasingly harsh environment.

The Mediterranean Region is predicted to experience greater flood frequency, punctuated by warmer, drier conditions that will lead to more frequent and prolonged droughts

during the summer months, on the basis of most climate change models (Barceló and Sabater, 2010; IPCC, 2014) and represents a prominent 'hot spot' for potential change in water availability (Giorgi and Lionello, 2008). In Portugal, for instance, current estimates indicate that the total surface area drained by temporary rivers represents more than 80% of the Portuguese territory. Furthermore, in the south-east of the country, the driest region, the only permanent watercourses are the large rivers Guadiana, Sado and Mira, and ~90% of watercourses are temporary in character (Morais, unpublished data).

The extension and vulnerability of these aquatic systems have led to an increase in research on temporary rivers in the Mediterranean Region (e.g. Morais *et al.*, 2004; Feio *et al.*, 2010; Dodkins *et al.*, 2012). Nevertheless, phytobenthos has generally been overlooked in temporary rivers, and until recently, research undertaken on the use of diatoms as indicators of ecological status in Mediterranean temporary streams (e.g. diatom metrics and indices) has been limited (e.g. Martín *et al.*, 2010; Delgado *et al.*, 2012).

Despite the importance of temporary rivers in the Mediterranean region, the European Union Water Framework Directive (Directive 2000/60/EC) does not explicitly recognize their value or importance, probably because intermittency

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is a naturally occurring phenomena. Nevertheless, the effects of a temporary flow regime and measures to address this (where appropriate) should be included in any update of river basin management plans. However, to propose appropriate measures, a detailed knowledge of the biotic components of temporary watercourses is crucial.

This topic requires specific attention because the implementation of the Water Framework Directive (Directive 2000/60/EC) requires European countries to assess lotic ecosystem quality using diatoms in addition to other biological elements. Diatoms are considered excellent environmental indicators because they represent a large part of the freshwater algal diversity, occur in almost all aquatic habitats and respond directly to many physical, chemical and biological changes in aquatic ecosystems. Furthermore, the value of diatoms as ecological indicators has been demonstrated in a variety of surface waters, primarily lakes and reservoirs (e.g. Novais *et al.*, 2012). A biological indicator approach based on diatom growth forms, capacity to tolerate nutrient limitation and physical disturbance was proposed by Passy (2007) and is currently being widely tested across Europe (Berthon *et al.*, 2011; Gottschalk and Kahlert, 2012).

The aim of this study is to enhance the baseline knowledge available concerning benthic diatoms in Mediterranean watercourses. The objectives of this research were as follows: (i) to provide an abiotic characterization of watercourses in the South of Portugal; (ii) to characterize benthic diatoms in temporary and permanent watercourses in Southern Portugal by assessing several indicators including ecological guilds, species richness, diversity and conservation status; and (iii) to determine ecological preferences of taxa that are characteristic of temporary and permanent watercourses.

## METHODS

### Sampling sites

A total of 92 sites were sampled in southern and central Portugal during spring 2006, when differences in the flow regime were already apparent but prior to temporary watercourses drying during late spring. The sites comprised 39 temporary and 53 permanent watercourses, according to the hydrological regime determined using a surface runoff model within a geographic information system (INAG, 2008a), and were located within the following watersheds: Ribeiras do Algarve (17), Guadiana (12), Mira and Sado (13) and Tejo (50) (Figure 1). The sites selected were subject to low anthropogenic pressure in accordance with the objectives of the study. The site selection was initially based on the REFCOND (2003) criteria developed by the National Water Institute. The environmental characterization of each site was intended to be comprehensive and addressed watershed characteristics, climatological, hydromorphological and

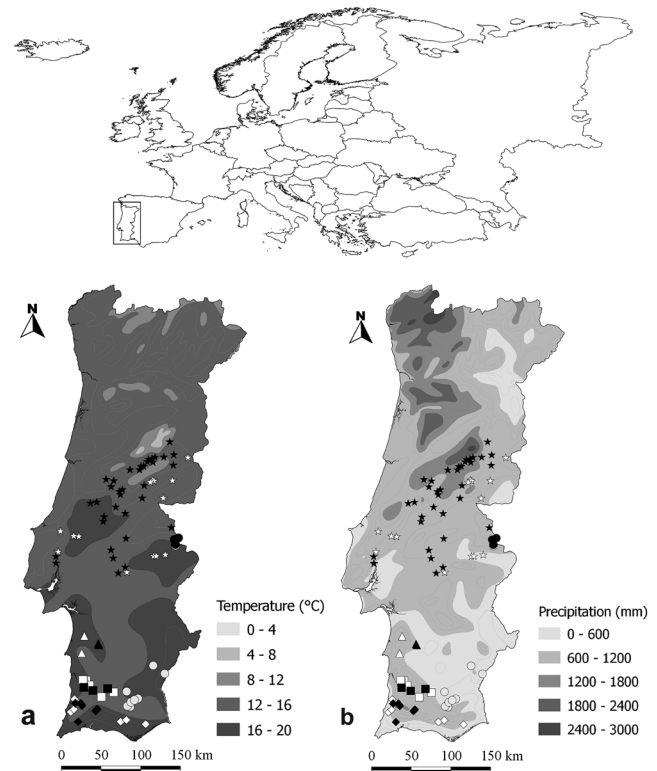


Figure 1. Map of Europe indicating the location of Portugal. Map of Portugal indicating (a) average annual temperature and (b) average annual precipitation (source: Atlas do Ambiente Digital—IA). Symbols on the maps indicate the catchments examined in this study: circle = Guadiana; triangle = Sado; square = Mira; diamond = Ribeiras do Algarve; and star = Tejo. Solid/black = permanent watercourses and open/white = temporary watercourses

water chemistry parameters. For each site, elevation, catchment area upstream of the sample site, distance to source, average annual runoff, thermal amplitude, coefficient of variation of annual precipitation, and mean annual temperature and precipitation were derived from the National Water Institute database. In addition, land use within the watershed, urban area, presence and characteristics of the riparian vegetation, sediment loads, level of hydromorphological alteration and changes to river connectivity caused by the presence of dams were recorded. The potential effects of toxicity, acidification and organic contamination were identified and explored by collecting water quality samples and analysis of the following parameters: dissolved oxygen  $\geq 5 \text{ mg O}_2 \text{ L}^{-1}$ ,  $6 \leq \text{pH} \leq 9$ , ammonium  $\leq 1 \text{ mg NH}_4^+ \text{ L}^{-1}$ , nitrates  $\leq 25 \text{ mg NO}_3^- \text{ L}^{-1}$ , total phosphorus  $\leq 0.13 \text{ mg PL}^{-1}$  and biological oxygen demand  $\leq 6 \text{ mg O}_2 \text{ L}^{-1}$  (INAG, 2009).

Hydromorphological characterization was undertaken simultaneously with diatom community and water quality sample collection; water temperature, pH, oxygen saturation and conductivity were measured *in situ* with portable meters calibrated in the field. Additional field measurements of

flow velocity, percentage of channel shaded, channel depth, channel width and wetted width and the presence or absence and type of riparian vegetation were recorded. Environmental standard methods for water chemical analyses were carried out according to APHA (1995), and all variables examined are summarized in Tables I and II.

#### Diatom sampling and processing

Benthic epilithic diatoms were sampled following a standard methodology (European Committee for Standardization, 2003; INAG, 2008b), which consisted in brushing at least five well-illuminated stones (cobbles if available) occurring in the main flow under stable conditions. All samples were preserved with a formaldehyde solution (4% v/v) immediately after sampling. Samples were treated using hydrogen peroxide (35%) and HCl (37%) in order to obtain a suspension of clean frustules. Permanent slides were mounted with Naphrax® (Brunel Microscopes Ltd, Wiltshire, UK). Diatoms were identified to a specific or sub-specific level using light microscopy (Leica DMRX with 100x oil immersion objective, Leica Microsystems, Wetzlar, Germany). At least 400 valves were identified and counted from each slide to estimate the relative abundance of each taxon. Identification was based on diatom reference floras (e.g. Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b), as well as recent bibliographic sources, including the series 'Diatoms of Europe', 'Iconographia Diatomologica', 'Bibliotheca Diatomologica' and relevant taxonomic papers.

#### Data analysis—environmental variables

Environmental variables were standardized and log transformed prior to analysis. The Shapiro–Wilk normality test was conducted using SigmaPlot 12.0 (Systat Software Inc., Chicago, IL). To verify which variables differed significantly between temporary and permanent watercourses, the non-parametric Mann–Whitney *U* test was used. Subsequently,

a comparison between climatological, hydromorphological and water chemistry variables was undertaken by means of non-parametric Spearman rank correlations. Both Mann–Whitney *U* tests and Spearman rank correlations were undertaken using STATISTICA 6.0 (StatSoft, Inc., Tulsa, OK).

#### Data analysis—diatoms

Diatom taxa were characterized in terms of habitat, flow velocity (when flowing), moisture content, pH, trophic state, ecology and conservation status according to the diatom 'Red List' compiled by Lange-Bertalot and Steindorf (1996) for German watercourses (based on Denys, 1991; Van Dam *et al.*, 1994; Lange-Bertalot and Steindorf, 1996) and the 2012 OMNIDIA v. 5.3 (Omnis Software, Inc.) database (Lecointe *et al.*, 1993). Ecological guilds were assigned to all taxa identified following the classification of Passy (2007) and Berthon *et al.* (2011): low-profile, high-profile and motile guilds. To examine the influence of environmental variables on ecological guilds' relative abundance and to compare information provided by the Specific Pollution Sensitivity Index (SPI) and ecological guilds, Spearman rank correlations were calculated using STATISTICA 6.0 (StatSoft, Inc.).

The indicator value (IndVal) method was used to identify the key species (indicators) of temporary and permanent watercourses (Dufrene and Legendre, 1997), using PC-Ord 6.0 (MjM Software Ltd., 217-219 Hamstel Road, Southend on Sea Essex SS2 4LB). This provides IndVals for each species, based on the combination of information on the specificity and fidelity of occurrence of a taxon in a group. The statistical significance of the species IndVal was evaluated using Monte Carlo random permutation tests. Ecological preferences of indicator species were inferred on the basis of the environmental variables that differed significantly between temporary and permanent watercourses.

For each sample, taxa richness (*S*), Shannon index of diversity (*H'*) and Pielou's evenness index (*J'*) were determined.

Table I. Catchment and climatological characteristics of the temporary and permanent watercourses examined in the southern Portugal study area

Variable	Temporary		Permanent	
	Median	Interquartile range	Median	Interquartile range
Elevation (m above sea level)	138.91	61.03–214.46	129.80	66.00–342.18
Catchment area upstream** (km <sup>2</sup> )	57.34	33.32–150.81	127.36	66.36–984.55
Distance to source** (m)	18999.26	12282.53–28865.43	29920.60	16849.90–72644.10
Average annual runoff* (mm)	175.00	175.00–250.00	350.00	175.00–700.00
Thermal amplitude (°C)	10.34	9.99–11.30	10.39	9.70–11.23
Average annual temperature** (°C)	15.62	15.11–15.99	15.18	13.70–15.35
Average annual precipitation** (mm)	668.00	633.75–763.50	804.00	686.00–1042.00
Coefficient of variation of annual precipitation	0.31	0.29–0.32	0.30	0.29–0.31

Variables that differ between temporary and permanent watercourses are indicated by

\**p* < 0.05 and \*\**p* < 0.001 using the Mann–Whitney *U* test.

Table II. Physical and water chemistry characteristics of the temporary and permanent watercourses examined in the study area.

Variable	Temporary		Permanent	
	Median	Interquartile range	Median	Interquartile range
Current velocity** (m s <sup>-1</sup> )	0.32	0.00–0.58	0.67	0.41–0.91
Water temperature* (°C)	19.36	15.85–20.94	23.52	17.70–26.19
Conductivity (Cond)** (µS cm <sup>-1</sup> )	392.50	223.75–586.50	143.00	109.00–333.00
pH*	7.49	6.94–7.85	7.12	6.64–7.48
Oxygen (O <sub>2</sub> )** (%)	72.95	67.78–81.60	84.60	73.20–99.20
Alkalinity** (mg L <sup>-1</sup> )	62.50	46.50–167.50	40.00	34.00–61.00
Hardness** (mg L <sup>-1</sup> )	96.50	51.75–173.50	32.00	10.00–85.00
Phosphate (PO <sub>4</sub> <sup>3-</sup> ) (µg L <sup>-1</sup> )	24.00	11.25–49.00	32.00	9.00–52.00
Total phosphorus (P <sub>tot</sub> ) (µg L <sup>-1</sup> )	19.50	8.75–29.75	21.00	9.00–32.00
Soluble reactive phosphorus (SRP) (µg L <sup>-1</sup> )	8.00	3.75–16.00	10.00	3.00–17.00
Total organic carbon (TOC) (mg L <sup>-1</sup> )	2.96	1.70–6.13	2.90	1.40–4.70
Chemical oxygen demand (COD) (mg L <sup>-1</sup> )	12.00	6.00–18.00	9.00	4.00–13.00
Biological oxygen demand (BOD <sub>5</sub> ) (mg L <sup>-1</sup> )	1.00	0.00–4.00	2.00	0.00–4.00
Ammonium (NH <sub>4</sub> <sup>+</sup> ) (µg L <sup>-1</sup> )	2.00	2.00–23.75	2.00	2.00–20.00
Kjeldahl nitrogen (µg L <sup>-1</sup> )	1120.00	560.00–1680.00	1120.00	560.00–1120.00
Nitrate (NO <sub>3</sub> <sup>-</sup> ) (µg L <sup>-1</sup> )	275.50	159.75–487.25	315.00	220.00–386.00
Nitrite (NO <sub>2</sub> <sup>-</sup> ) (µg L <sup>-1</sup> )	1.00	0.00–10.00	10.00	0.00–20.00
Total nitrogen (mg L <sup>-1</sup> )	1335.00	985.86–1979.00	1355.00	898.00–1795.00
Chloride (Cl <sup>-</sup> )* (mg L <sup>-1</sup> )	40.45	23.80–88.68	19.40	17.40–31.30
Sulfate (SO <sub>4</sub> <sup>2-</sup> ) (m L <sup>-1</sup> )	22.40	9.98–29.73	13.60	9.33–18.10
Sodium (Na <sup>+</sup> )* (mg L <sup>-1</sup> )	3.70	2.33–6.03	2.70	1.10–5.20
Manganese (Mn <sup>2+</sup> ) (mg L <sup>-1</sup> )	0.01	0.01–0.05	0.02	0.01–0.08
Magnesium (Mg <sup>2+</sup> )* (mg L <sup>-1</sup> )	8.02	4.37–13.55	4.86	3.16–7.05
Calcium (Ca <sup>2+</sup> )* (mg L <sup>-1</sup> )	19.50	11.25–33.93	12.40	8.00–22.00

Variables that significantly differ between temporary and permanent watercourses are indicated by \* $p < 0.05$  and \*\* $p < 0.001$  using the Mann–Whitney  $U$  test.

The SPI was also calculated from diatom abundances (Coste in Cemagref, 1982), using the OMNIDIA v. 5.3 software (Lecoite *et al.*, 1993). OMNIDIA was selected because it has been developed for assessing the quality of running waters and has been recommended as reference index for several Iberian basins (Gomà *et al.*, 2005; Blanco *et al.*, 2008).

The relationship between taxa richness ( $S$ ), Shannon index of diversity ( $H'$ ), Pielou's evenness index ( $J'$ ), SPI and the 11 environmental variables that varied significantly between temporary and permanent watercourses was investigated by least squares stepwise multiple linear regression with experiment-wise type I error rates of 0.05 for coefficients calculated using the Dunn–Šidák method (Ury, 1976). The complete candidate model included one qualitative variable, namely the watercourse regime (which was binary coded as 0 or 1), 11 environmental variables and all interactions between watercourse regime and environmental variables. Variance inflation factors and Durbin–Watson  $d$  were examined to evaluate multicollinearity and serial correlation. Equations were fitted using Statgraphics 4.2 (STCS, Inc., Rockville, MD). Only taxa with relative abundances over 1% from at least one site were considered in the analyses in order to reduce the influence of rare taxa.

## RESULTS

### *Environmental characterization of temporary and permanent streams*

Descriptive statistics of the environmental parameters recorded from the temporary and permanent watercourses are presented in Tables I and II. On the basis of the Mann–Whitney  $U$  test, temporary and permanent watercourses differ in catchment characteristics ( $p < 0.001$ ), climatological variables (average annual temperature and precipitation, both  $p < 0.001$ , and average annual runoff,  $p < 0.05$ ), current velocity ( $p < 0.001$ ) and several water chemistry variables (Table II). A detailed examination of the data indicated that catchment area upstream of the sample point, distance to source, average annual precipitation, average annual runoff, current velocity, dissolved oxygen saturation and water temperature were higher in permanent watercourses. In contrast, average annual temperature, conductivity, alkalinity, hardness, pH, chloride, magnesium, sodium and calcium were higher in temporary watercourses.

The application of the Mann–Whitney  $U$  test to the hydromorphological variables only detected significant differences for water current between the two groups (with

$p < 0.001$ ; Table II). Because statistical differences were not observed for other hydromorphological variables, a series of charts were plotted to explore the variability of hydromorphological parameters among the groups (Figure 2). Temporary watercourses were typically less shaded, with a greater proportion of sites with no shade or <30% of the river channel shaded. Temporary and permanent watercourses had similar proportions of sites >60% shaded, and there was a higher percentage of permanent sites with 30–60% of the channel shaded. These results were reinforced by examination of the type of riparian vegetation (Figure 2e). Temporary watercourses were generally narrower and had smaller channels, as illustrated by a higher percentage of low-river-width (between 1–5 and 5–10 m) and lower-channel-width (<1 m) sites. Permanent sites had a greater percentage of sites that were >20 m wide (Figure 2b, c), although they also had relatively high proportions of sites with low channel width (1–5 m being the most common). Both temporary and permanent watercourses had high percentages of shallow sites (<0.25 m); temporary systems were dominated by the 0.25- to 0.5-m

depth class and permanent rivers by the 0.5- to 1- and >1-m classes. The absence of sites in temporary watercourses with >1-m depth is noticeable (Figure 2d).

Climatological variables were clearly different between groups with temporary watercourses typically located in areas with higher average annual temperature and lower average annual runoff and annual precipitation (Table I and Figure 1). In the south-east of the country, the driest region, the majority of watercourses were temporary (Figure 1), whereas precipitation and average annual runoff were higher and more variable in permanent watercourses typical of the central region (Table I and Figure 1).

Spearman correlation coefficients between catchment characteristics and climatological and hydromorphological variables indicated that elevation was positively correlated ( $p < 0.001$ ) with climatological variables including average annual runoff ( $r = 0.56$ ) and average annual precipitation ( $r = 0.53$ ). Elevation was also negatively correlated with the average annual temperature ( $r = -0.59$ ). Catchment area and distance to source were strongly correlated ( $p < 0.001$ )

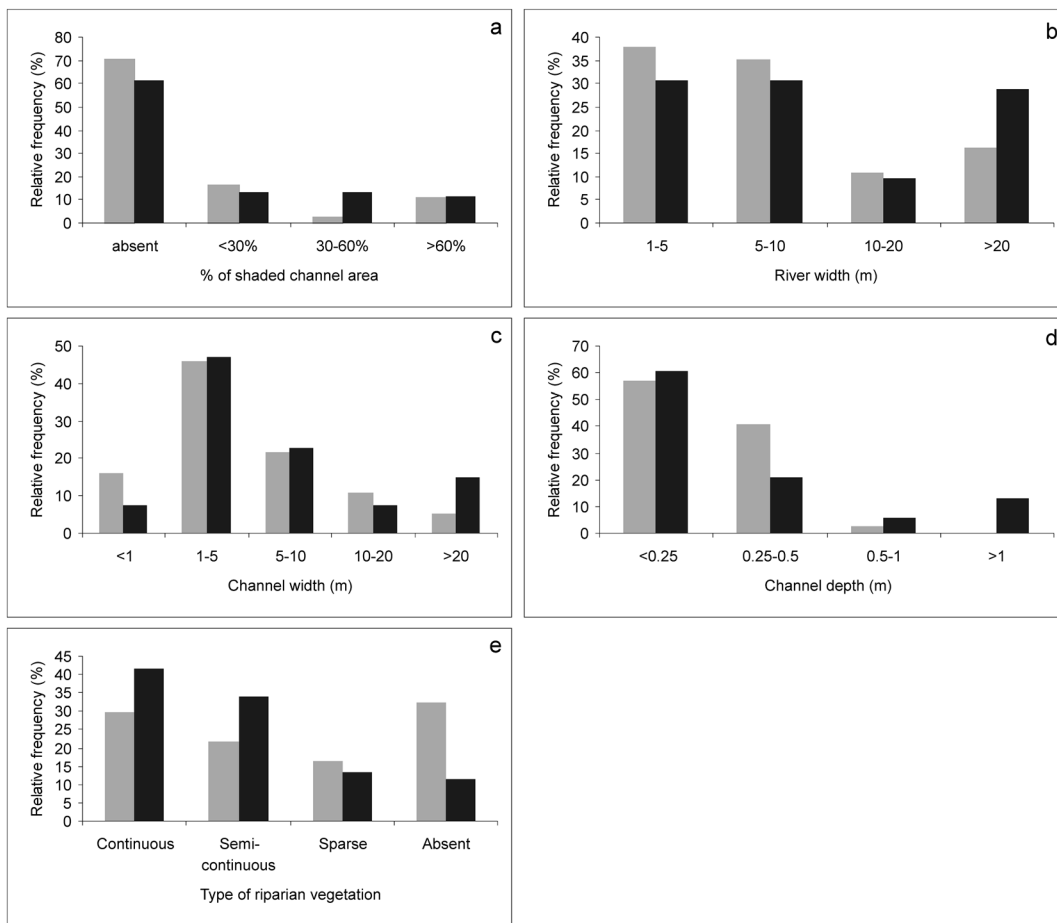


Figure 2. Comparison of mean values of characteristics of temporary (grey) and permanent (black) watercourses within the study area expressed as frequencies for: (a) percentage of channel area shaded; (b) river width; (c) channel width; (d) channel depth; and (e) type of riparian vegetation

with hydromorphological variables such as river width ( $r=0.56$  and  $r=0.61$ , respectively) and channel width ( $r=0.48$  and  $r=0.56$ , respectively).

The Spearman correlations between catchment characteristics, climatological and hydromorphological variables and water chemistry were used to explore the contribution of each of these variables to the changes in water chemistry observed. The only catchment characteristic correlated with water chemistry was elevation, which is negatively correlated ( $p < 0.001$ ) with conductivity ( $r = -0.61$ ), calcium ( $r = -0.57$ ), chloride ( $r = -0.62$ ), hardness ( $r = -0.56$ ) and sodium ( $r = -0.52$ ). For the climatological variables, negative correlations ( $p < 0.001$ ) were observed between the average annual runoff and conductivity ( $r = -0.55$ ), alkalinity ( $r = -0.52$ ), calcium ( $r = -0.57$ ), chloride ( $r = -0.63$ ), hardness ( $r = -0.55$ ) and magnesium ( $r = -0.49$ ). Average annual precipitation was negatively correlated ( $p < 0.001$ ) with conductivity ( $r = -0.50$ ), chloride ( $r = -0.56$ ), chemical oxygen demand ( $r = -0.50$ ) and hardness ( $r = -0.52$ ) and positively correlated with water temperature ( $r = 0.50$ ) and nitrite ( $r = 0.53$ ). It was interesting to note that neither riparian vegetation nor current velocity was correlated with any water chemistry parameters.

#### Diatom communities' characterization

A total of 322 diatom taxa were identified in the dataset; from these, 229 were recorded in temporary watercourses and 250 from permanent systems. Only 109 taxa were present with a relative abundance above 1% from at least one temporary watercourse and 130 taxa from permanent water bodies. Within temporary watercourses, taxa with relative abundance above 1% comprised 34 genera: *Gomphonema* (15 taxa) and *Achnantheidium* (11 taxa); and from perennial flowing sites, the most frequently sampled genera comprised *Achnantheidium* (16 taxa), *Fragilaria* (14 taxa), *Gomphonema* (13 taxa), *Nitzschia* (14 taxa) and *Navicula* (13 taxa). Appendix A includes the taxa with relative abundances above 1% from at least one site, their ecological preferences and conservation status (based on published literature), maximum relative abundance and frequency of occurrence within each group. *Achnantheidium minutissimum*, *Amphora pediculus*, *Cocconeis euglypta*, *Gomphonema rosenstockianum*, *Planothidium frequentissimum*, *Nitzschia inconspicua* and *Reimeria sinuata* were among the most abundant taxa and occurred at more than 50% of sites in temporary watercourses. Within permanent watercourses, the most abundant and frequently recorded taxa were *A. minutissimum*, *Eolimna minima*, *Karayevia oblongella*, *P. frequentissimum* and *R. sinuata*.

The Red List status (Lange-Bertalot and Steindorf, 1996) was available for ~70% of the taxa (Appendix A). From these, ~12.5% are classified as endangered to varying degrees. Among the diatoms recorded, *Achnantheidium lineare*

and *Stauroforma exiguiiformis* have been classified as 'endangered' (category 3); *S. exiguiiformis* only occurs in permanent watercourses, whereas *A. lineare* also occurs in temporary waterbodies infrequently. *Gomphonema lagenula* and *Navicula cataracta-rheni* are classified as 'extremely rare' (R). *Gomphonema lagenula* was found in low abundances in both temporary and permanent watercourses, whereas *N. cataracta-rheni* was typically present in low abundance within temporary watercourses. *Achnantheidium subatomoides*, *Fragilaria nanana*, *Gomphonema exilissimum*, *Karayevia oblongella* and *Pinnularia microstauron* are classified as 'decreasing' (V). Among these taxa, *G. exilissimum* and *K. oblongella* were present in more than 10% of both temporary and permanent watercourses, and *K. oblongella* was also abundant in both groups (>40% maximum relative abundance). In contrast, *A. subatomoides*, *F. nanana* and *P. microstauron* were only recorded from permanent watercourses in low abundances. For *Eunotia implicata*, *Eunotia soleirolii*, *Navicula notha* and *Ulnaria biceps*, threats to their long-term conservation exist (category G). All were recorded from both groups, although *E. soleirolii* and *N. notha* were more abundant and occurred more frequently in permanent watercourses.

Information regarding trophic preferences (for ~70% of the taxa) and pH (for ~75% of the taxa) was available for the majority of the taxa. Nevertheless, 48.5% of the taxa lacked information regarding their habitat preferences; 51.5% had no details regarding current velocity, and 38.6% lacked details regarding moisture preferences (Appendix A).

#### Ecological guilds

The majority of the taxa identified within temporary watercourses belonged to the low-profile guild (44.0%) followed by the high-profile (31.2%) and motile (24.8%) guilds. Permanent sites were dominated by low-profile taxa (35.4%); nevertheless, there was a higher percentage of high-profile and motile taxa (33.8% and 30.8%, respectively). Although there were no significant differences among the number of taxa assigned to each guild per group, it is clear that the low-profile guild dominated the relative abundance in both groups (77.5% temporary and 75.8% permanent watercourses), followed by high-profile (12.3% in both groups) and motile guilds (10.2% temporary and 11.9% permanent watercourses). No strong Spearman rank correlations ( $\rho > 0.5$ ,  $p < 0.05$ ) were observed between any ecological guilds' relative abundance and environmental variables. Significant correlations were recorded between low-profile and motile guilds and the SPI index, although these were not strong ( $\rho = 0.39$  and  $\rho = -0.38$ , respectively,  $p < 0.05$ ).

#### Characteristic diatom taxa and their ecological preferences

Indicator value analysis undertaken to identify diatom taxa that are characteristic of temporary or permanent watercourses

demonstrated that *Amphora copulata*, *Cocconeis placentula*, *Diploneis separanda*, *Encyonopsis subminuta*, *Fragilaria radians*, *Gomphonema olivaceum*, *Gomphonema truncatum*, *Halamphora veneta*, *Navicula radiosa*, *Navicula veneta*, *Sellaphora seminulum* and *Ulnaria acus* were indicators of temporary watercourses, whereas *Encyonema minutum*, *Eunotia minor*, *Fragilaria rumpens*, *Fragilaria cf. socia* and *Navicula rhynchocephala* were characteristic of permanent watercourses (Table III). The taxa characteristic of temporary watercourses were also common in highly intermittent, water-logged (wet subaerial—four taxa) and moist soils (moist subaerial—three taxa); only two taxa were considered aquatic, although data were not available for three taxa. Most taxa indicative of temporary waterbodies were indifferent to the current velocity (eight taxa; Appendix A). As for the pH preferences, five taxa were classified as alkaliphilous (class 4), four as neutrophilous and two as alkalibiontic, and there was no information available for *D. separanda*. Regarding the trophic preferences, five taxa were classified as eutrphentic, two as meso-eutrphentic and one as oligotrphentic (*E. subminuta*),

and *D. separanda* and *F. radians* were not classified. Three of these taxa were not present in the Red List classification (Appendix A).

The five taxa indicative of permanent watercourses were also commonly present in non-permanent water bodies; they were largely indifferent regarding current velocity preferences. Three taxa lack information regarding moisture preferences, whereas *E. minutum* is strictly aerophilous and *N. rhynchocephala* is occasionally aerophilous. Their pH preferences were quite diverse, as *E. minor* is acidophilous, *E. minutum* and *F. rumpens* are neutrophilous and *N. rhynchocephala* is alkaliphilous. Data on trophic preferences were only available for *F. rumpens* (eutrphentic) and *N. rhynchocephala* (indifferent). *Fragilaria cf. socia* was not classified in the Red List (Appendix A). Because these were taxa characteristic of both types of watercourses, their ecological preferences are highlighted for the environmental variables that statistically separate temporary and permanent watercourses (Table IV). Taxa characteristic of temporary watercourses have a clear preference for sites with lower current velocity and higher conductivity and pH

Table III. Indicator values for the characteristic taxa of temporary or permanent watercourses examined in this study

Code	Taxon name	Temporary			Permanent		
		F	S	IndVal	F	S	IndVal
ACOP	<i>Amphora copulata</i> (Kützing) Schoeman & R.E.M. Archibald 1986	23	83	19	8	17	1
CPLA	<i>Cocconeis placentula</i> Ehrenberg 1838	10	99	10	2	1	0
DSEP	<i>Diploneis separanda</i> Lange-Bertalot 2004	31	92	28	8	8	1
ENMI	<i>Encyonema minutum</i> (Hilse in Rabenhorst) D.G. Mann 1990	13	18	2	38	82	31
ESUM	<i>Encyonopsis subminuta</i> Krammer & E. Reichardt 1997	10	100	10	0	0	0
EMIN	<i>Eunotia minor</i> (Kützing) Grunow 1881	5	2	0	23	98	22
FRAD	<i>Fragilaria radians</i> (Kützing) D.M. Williams & Round 1987	13	100	13	0	0	0
FRUM	<i>Fragilaria rumpens</i> (Kützing) G.W.F. Carlson 1913	21	29	6	43	71	31
FSOC	<i>Fragilaria cf. socia</i> (N.M. Wallace) Lange-Bertalot 1980	0	0	0	25	100	25
GOLI	<i>Gomphonema olivaceum</i> (Hornemann) Brébisson 1838	13	100	13	0	0	0
GTRU	<i>Gomphonema truncatum</i> Ehrenberg 1832	18	89	16	4	11	0
HVEN	<i>Halamphora veneta</i> (Kützing) Levkov 2009	33	93	31	6	7	0
NRAD	<i>Navicula radiosa</i> Kützing 1844	18	90	16	8	10	1
NRHY	<i>Navicula rhynchocephala</i> Kützing 1844	5	16	1	21	84	17
NVEN	<i>Navicula veneta</i> Kützing 1844	67	72	48	42	28	12
SSEM	<i>Sellaphora seminulum</i> (Grunow) D.G. Mann 1989	36	81	29	23	19	4
UACU	<i>Ulnaria acus</i> (Kützing) Aboal 2003	18	100	18	0	0	0

Monte Carlo random permutations tests were used to assess the significance of each taxon as a group-specific indicator ( $p < 0.05$ ). Fidelity (F) and specificity (S) values are also presented.

Table IV. Abundance-weighted averages (WA) and range for the 11 environmental variables that were significantly different between temporary and permanent watercourses

		ACOP	CPLA	DSEP	EMIN	ENMI	ESUM	FRAD	FRUM
Current velocity (m s <sup>-1</sup> )	WA	0.12	0.02	0.27	0.44	0.53	0.88	0.87	0.67
	Range	1–0.73	0–0.64	0–0.80	0–0.85	0–0.97	0.61–1.18	0.61–1.18	0–1.41
T (°C)	WA	22.2	25.9	20	24.6	24.1	17.5	19.7	20.8
	Range	13.0–29.4	21.0–28.7	9.4–28.7	14.1–28.2	13.0–32.6	13.3–20.1	13.3–20.1	11.8–28.0
Conductivity (mS cm <sup>-1</sup> )	WA	663	365	606	162	125	189	223	157
	Range	109–860	98–409	98–1393	55–428	55–543	124–230	124–230	55–637
pH	WA	8.0	6.9	7.3	6.4	6.9	6.9	6.8	7.1
	Range	6.6–8.6	6.7–8.2	6.6–8.6	5.7–8.2	5.7–8.9	6.3–7.7	6.3–7.7	6.3–8.5
DO (%)	WA	109.9	79.5	78.4	83.7	80.9	74.8	84.6	77.9
	Range	38.3–128.6	66.3–98.6	42.9–128.6	31.5–116.8	31.5–148.2	59.8–91.9	59.8–91.9	42.9–116.8
Alkalinity (mg L <sup>-1</sup> )	WA	222	130	167	46	42	43	49	42
	Range	28–274	46–172	31–386	26–157	25–225	31–53	31–53	24–110
Calcium (mg L <sup>-1</sup> )	WA	62.2	30.8	44.3	22.9	10.5	15.2	10.7	10.1
	Range	8.0–107.0	4.8–43.3	4.8–144.0	6.0–58.0	4.6–87.0	10.0–24.0	10.0–24.0	5.6–24.0
Chloride (mg L <sup>-1</sup> )	WA	88.2	50.6	72.3	27.8	17.2	25.6	28.3	27.9
	Range	16.4–148.9	13.9–57.1	13.9–163.8	7.7–37.7	5.0–99.3	20.8–29.8	20.8–29.8	5.9–163.8
Hardness (mg L <sup>-1</sup> )	WA	251	110	208	27	27	69	52	34
	Range	10–312	10–182	10–528	6–182	10–242	46–100	46–100	10–160
Magnesium (mg L <sup>-1</sup> )	WA	20.9	8.2	25.5	3.8	5.8	7.5	5.9	5.9
	Range	2.7–28.2	2.9–23.8	1.9–85.5	0.7–23.8	0.4–28.2	4.4–9.7	4.4–9.7	0.5–25.2
Sodium (mg L <sup>-1</sup> )	WA	7.7	4.9	7	2.3	2.2	6	3.1	3.2
	Range	0.7–11.8	0.7–5.8	0.7–15.8	0.7–9.8	0.7–9.8	2.4–11.2	2.4–11.2	0.7–13.1

The taxa reflect a spectrum of taxa from temporary and permanent watercourses. The names of the taxa corresponding to the codes (in four letters) are provided in Table III.

(except for *Encyonopsis minuta*). Similar preferences were detected for alkalinity, chloride, hardness, magnesium and sodium, which were generally higher for taxa characteristic of temporary watercourses. When considering the percentage oxygen saturation, with the exception of *A. copulata*, there were no significant differences detected among the groups, probably because all sites were not subject to strong anthropogenic pressures.

#### Diatom metrics and environmental variables

The mean values, standard deviation, median and interquartile range for taxa richness (*S*), Shannon index of diversity (*H'*), Pielou's evenness index (*J'*) and the SPI are presented in Table V. Results of regressions between environmental parameters that differed significantly between temporary and permanent watercourses and taxa richness (*S*), Shannon index of diversity (*H'*), Pielou's evenness index (*J'*) or SPI are presented in Table VI. There was no evidence of multicollinearity, and no positive or negative serial correlations were recorded at  $p = 0.05$ , except a slightly positive autocorrelation in evenness (*J'*). There were significant differences for taxa richness (*S*) between temporary and permanent watercourses because of an interaction between average annual runoff and the qualitative variable (temporary/permanent). The qualitative variable (temporary or permanent) explained 47.3% of the variation of taxa richness, whereas oxygen

explained 35.4% and calcium 17.3%. No significant differences were recorded between watercourses for *H'* and *J'* with pH explaining 98.9% and 99.2% of their variation or for the SPI, where average annual runoff explained 44.1%, alkalinity 21.6%, current velocity 18.8% and oxygen 15.5% of the variance in the data.

#### DISCUSSION AND CONCLUSIONS

The environmental characterization of watercourses in the south of Portugal clearly differentiated temporary and permanent sites on the basis of catchment characteristics and climatological variables. Among the hydromorphological variables, only current velocity was statistically different between the two stream types, whereas other variables only differed slightly between the temporary and permanent waterbodies. The lack of significant hydromorphological differences reflects the characteristics of Mediterranean watercourses generally, independent of the hydrologic regime. It is important that further research is undertaken on headwater temporary watercourses, characterized by short distances to source and small catchment area, and especially their role in the supply, transport and fate of water resources and solutes (including pollutants; Barceló and Sabater, 2010). Temporary watercourses experience greater variation in annual precipitation (Lillebø *et al.*, 2007). This fact, coupled with their smaller watersheds,



Table IV. (Continued)

FSOC	GOLI	GTRU	HVEN	NRAD	NRHY	NVEN	SSEM	UACU
0.27	0.28	0.12	0.23	0.41	0.57	0.35	0.4	0.35
0.02–1.41	0–1.19	0–0.87	0–1.06	0–0.97	0.17–0.97	0–1.63	0–1.63	0–1.18
23.3	19.3	17.8	20.7	18.8	24.4	19.4	17.4	18.6
16.3–32.6	17.2–20.1	13.0–29.2	11.8–28.7	13.0–26.8	11.8–29.2	9.4–29.2	9.4–29.4	17.1–20.0
101	460	300	411	241	210	396	441	426
69–200	223–543	78–411	98–1361	55–472	65–616	55–1393	76–1361	223–1348
7.3	7.3	7.7	7.7	7	6.7	7.4	7.6	7.1
6.3–8.9	6.3–7.9	6.2–8.6	6.2–8.8	6.2–8.6	5.7–7.7	5.7–8.8	5.7–8.9	6.2–8.9
72.8	77.3	84.2	83.8	76.3	82.3	74.0	74.8	74.3
66.1–148.2	75.3–91.9	69.0–99.0	67.5–103.7	51.4–115.3	31.5–106.5	31.5–128.6	31.5–121.0	49.7–84.6
51	171	98	100	57	43	93	71	94
24–56	48–225	36–174	25–225	28–174	25–157	25–386	25–268	46–270
8.9	63.3	15.4	26.9	11.5	14.3	27.7	19.9	28.1
5.6–18.4	10.0–87.0	4.6–22.0	4.8–87.0	5.6–19	5.6–58.0	5.6–144.0	4.6–92.0	10.0–107.0
8.1	29	40.8	64.3	48.7	34.1	70.8	100.8	80.9
5.9–31.3	23.8–93.5	8.9–66.5	8.4–292.8	7.7–140	9.9–163.8	2.8–292.8	8.4–421.8	26.3–421.8
12	185	114	98	54	40	106	79	92
11963	46–242	44835	10–242	10–224	10–165	7–528	7–282	50–257
4.8	6.7	14.4	8.2	7.9	4.6	11	9	5.6
0.7–7.1	4.4–10.5	0.4–28.2	1.7–28.2	1.0–28.2	0.7–11.9	0.7–85.5	0.4–24.5	2.7–10.5
1.3	1.8	3.4	4.2	3.4	4.3	4.9	4.7	3.4
0.7–9.8	1.1–3.7	0.7–8.9	0.7–13.1	0.7–9.8	0.7–13.1	0.7–15.8	0.7–13.1	2.4–8.6

helps explain the high inter-annual and intra-annual variability of the flow regime and their unpredictability.

Water chemistry parameters and indicators of anthropogenic contamination did not differ between temporary and permanent watercourses. This reflects the sample design focussed on relatively unimpaired sites. Nevertheless, indicators of organic enrichment were more abundant in permanent watercourses (Table II) and reflect the greater catchment area and agricultural/pastoral practices (Hlúbiková *et al.*, 2014). However, it was interesting to note that contrary to the findings of authors such as Moore *et al.* (2005) and Studinski *et al.* (2012), the percentage of riparian vegetation did not have a significant effect on stream temperature and may reflect the sclerophyllous and evergreen riparian vegetation typical of southern Portugal and the wider Mediterranean region (Gasith and Resh, 1999).

The low-profile guild dominated the relative abundance of both temporary and permanent watercourses, reflecting the frequent disturbance and low nutrient content. These environmental conditions favour small taxa that are able to persist in low-nutrient environments, withstand extreme flow events and recolonize sites rapidly. These results support observations of Berthon *et al.* (2011) and Hlúbiková *et al.* (2014), who reported a dominance of low-profile diatoms in nutrient-poor environments. Even though the temporary and permanent watercourses studied differed significantly with regard to a number of environmental parameters, such as watershed characteristics, climatological variables, current velocity and water chemistry, diatom guilds did not reflect these differences. In addition, light availability and shading did not appear to influence the diatom ecological guilds, probably because of the riparian vegetation associated with

Table V. Mean values, standard deviation, median and interquartile range for the taxa richness ( $S$ ), Shannon index of diversity ( $H'$ ), Pielou's evenness index ( $J'$ ) and Specific Pollution Sensitivity Index for the temporary and permanent watercourses examined in this study

	Temporary			Permanent		
	Mean $\pm$ SD	Median	Interquartile range	Mean $\pm$ SD	Median	Interquartile range
Taxa richness	26.87 $\pm$ 8.83	28.00	19.00–33.00	25.91 $\pm$ 1.00	23.00	19.00–33.00
Shannon index of diversity ( $H'$ )	2.72 $\pm$ 0.91	2.93	2.08–3.49	2.64 $\pm$ 0.85	2.78	2.06–3.16
Pielou's evenness index ( $J'$ )	0.57 $\pm$ 0.15	0.60	0.48–0.70	0.56 $\pm$ 0.14	0.58	0.50–0.65
Specific Pollution Sensitivity Index	15.93 $\pm$ 1.86	15.70	14.45–17.45	16.76 $\pm$ 1.99	17.50	15.0–18.5

Table VI. Regression coefficients for equations fitted to taxa richness ( $S$ ), Shannon index of diversity ( $H'$ ), Pielou's evenness index ( $J'$ ) and Specific Pollution Sensitivity Index of temporary and permanent watercourses examined in this study

Variable	Watercourses	Y intercept	Average annual runoff (mm)	Current velocity (m s <sup>-1</sup> )	pH	Oxygen (%)	Alkalinity (mg L <sup>-1</sup> )	Calcium (mg L <sup>-1</sup> )	Coefficients (p)	F	Significance of Model	R <sup>2</sup> <sub>adj</sub>	VIFs	d
Taxa richness ( $S$ )	Temporary	16.401	0			0.190		-0.102	≤0.0025	8.15 (3.88)	10 <sup>-4</sup>	0.191	≤1.1	1.89
	Permanent	16.401	-0.013			0.190		-0.102						
Shannon index of diversity ( $H'$ )	Temporary				0.406			-0.010	≤0.0009	522.10 (2.90)	<10 <sup>-5</sup>	0.920	1.0	1.55
	Permanent													
Pielou's evenness index ( $J'$ )	Temporary				0.085			-0.002	≤0.0007	820.59 (2.90)	<10 <sup>-5</sup>	0.947	1.0	1.42
	Permanent													
Specific Pollution Sensitivity Index	Temporary	17.607	0.003	1.182		-0.024	-0.008		≤0.0097	15.28 (4.87)	<10 <sup>-5</sup>	0.386	≤1.3	2.04
	Permanent													

The greater significance level of coefficients,  $F$ -values (with degrees of freedom within parentheses), significance levels of models, adjusted  $R^2$  values ( $R^2_{adj}$ ), the variance inflation factors (VIFs) and Durbin-Watson statistics ( $d$ )

Mediterranean rivers. Therefore, nutrient content appears to be the primary main factor driving ecological guild abundance in the rivers examined. This is in marked contrast to Swedish low-acidity lakes, where grazing and light levels might play an important role in determining their distribution (Gottschalk and Kahlert, 2012). In addition, current velocity did not appear to influence ecological guild abundance, suggesting that under nutrient-deficient conditions, flow plays a secondary role (Larson and Passy, 2012).

Even though only a few taxa were classified as threatened, a number of other taxa had conservation designations independently of being temporary or permanent water specialists, highlighting the need to manage and conserve 'unimpacted' watercourses, independently of their hydrological regime. Additionally, ~30% of the identified taxa were not recorded on the Red List of Lange-Bertalot and Steindorf (1996), and little or no information was available regarding the ecological preferences of several taxa indicative of both permanent and temporary watercourses. This may also reflect the fact that some taxa have only recently been described, such as *Pseudostaurosira alvareziae* or *Geissleria lusitanica* (Cejudo-Figueiras *et al.*, 2011; Novais *et al.*, 2013).

The importance of temporary watercourses for the maintenance of diatom biodiversity has been clearly demonstrated by the results of this study, as the variation in diatom taxa richness (higher in temporary watercourses) was directly linked with the average annual runoff. Diatom species richness increased with natural hydrological disturbance (drying), in accordance with the intermediate disturbance theories. Williams *et al.* (2003) also reported an increase in aquatic diversity in association with disturbance (physical habitat complexity), although their field observations suggested that seasonality reduced the richness of some ponds compared with species-rich river sites. Further studies are therefore required to explore the wider applicability of the results reported, as the relationship between species richness and connectivity is determined by a series of complex factors, with species richness maxima for different faunal and floral elements occurring at different positions along hydrological connectivity and permanence gradients (Ward *et al.*, 2002).

Further studies centred on phytobenthos in temporary Mediterranean watercourses are required, not only for biodiversity conservation purposes but also for the determination of diatom richness along the riverine connectivity gradient and to provide a greater understanding of physiological aspects of diatom adaptation to drought.

#### ACKNOWLEDGEMENTS

This project was supported by Fundação para a Ciência e a Tecnologia—Portugal (PhD grant SFRH/BD/21625/2005), by the Fonds National de la Recherche du Luxembourg

(grant AFR, PHD-09-120) and by the Public Research Centre—Gabriel Lippmann (Luxembourg). The National Water Institute is thanked for the data on watershed characteristics and the climate. Vanessa Peardon is gratefully acknowledged for English grammar revisions of the manuscript.

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APPENDIX A

List of taxa recorded with relative abundance above 1% from at least one site and a summary of their ecological preferences and distribution. H = habitat (Denys, 1991), 0 = unknown, 2 = aquatic, 3 = also commonly in periodic water or wet subaerial, 4 = also commonly moist subaerial, 5 = also commonly dry subaerial; C = current (Denys, 1991), 0 = unknown, 1 = irrelevant, 2 = rheophilous, 3 = rheophilous, 4 = indifferent, 5 = limnophilous. Ecological preferences according to Van Dam *et al.* (1994). M = moisture, 1 = strictly aquatic, 2 = occasional aerophilous, 3 = aquatic to subaerial, 4 = aerophilous strict, 5 = terrestrial; pH, 1 = acidobiont, 2 = acidophilous, 3 = neutrophilous, 4 = alkaliphilous, 5 = alkalibionts, 6 = indifferent; T = trophic state, 1 = oligotraphentic, 2 = oligo-mesotraphentic, 3 = mesotraphentic, 4 = meso-eutraphentic, 5 = eutraphentic, 7 = indifferent. E = Ecological preferences according to Lange-Bertalot and Steindorf (1996). AE = aerophilous, OK = oligotraphentic alkaliphilous, OD = oligotraphentic acidophilous, OG = oligotraphentic, HP = halophilous, EU = meso to eutraphentic, ww = not listed. RL = Red List species (Lange-Bertalot and Steindorf, 1996), 3 = endangered, G = presumed endangered, R = extremely rare, V = decreasing, \* = not estimated, ◊ = not threatened, D = insufficient data, • = widespread, z = not listed. MRA = maximum relative abundance in each group. FREQ = percentage of sites in which the taxon was recorded. Bold = characteristic/indicative taxa of temporary or permanent watercourses based on IndVal analysis (see details presented in Table III).

Code	Taxon name	Temporary							Permanent			
		H	C	M	pH	T	E	RL	MRA	FREQ	MRA	FREQ
	<i>Achnanthydium</i> aff. <i>saprophilum</i> (H. Kobayasi & Mayama) Round & Bukhtiyarova 1996	0	0	0	0	0	0		16.3	5.1	84.65	7.55
ADCV	<i>Achnanthydium caravelense</i> Novais & Ector 2011	0	0	0	0	0	ww	z	9.5	5.1	17.00	7.55
ADCT	<i>Achnanthydium catenatum</i> (J. Bily & Marvan) Lange-Bertalot 1999	0	0	0	0	0	EU	*	2.2	12.8	5.78	18.87
ADEU	<i>Achnanthydium eutrophilum</i> (Lange-Bertalot) Lange-Bertalot 1999	0	0	3	3	5	ww	z	4.0	28.2	3.76	43.40
ADEG	<i>Achnanthydium exiguum</i> (Grunow) Czamecki 1994	3	4	3	4	7	EU	◊	1.7	5.1	1.48	13.21
ADJK	<i>Achnanthydium jacksonii</i> Rabenhorst 1861	0	0	0	3	0	ww	D	3.9	15.4		
ADLI	<i>Achnanthydium lineare</i> W. Smith 1855	0	0	0	3	0	O	3	1.23	2.56	16.26	5.66
ADMA	<i>Achnanthydium macrocephalum</i> (Hustedt) Round & Bukhtiyarova 1996	5	4	0	0	0	ww	D	1.23	7.69	1.21	5.66
ADMI	<i>Achnanthydium minutissimum</i> (Kützing) Czamecki 1994	5	4	3	3	7	TOL	◊	75.6	82.1	72.21	69.81
	<i>Achnanthydium minutissimum</i> (Kützing) Czamecki 1994 s.l.								34.9	10.3	70.44	30.19
ADPY	<i>Achnanthydium pyrenaicum</i> (Hustedt) H. Kobayasi 1997	0	0	0	4	3	TOL	◊	23.8	28.2	57.34	24.53
	<i>Achnanthydium</i> sp. 1										29.16	1.89
	<i>Achnanthydium</i> sp. 2										24.34	3.77
	<i>Achnanthydium</i> sp. 3										10.84	1.89
	<i>Achnanthydium</i> sp. 4										98.06	3.77
ADSB	<i>Achnanthydium straubianum</i> (Lange-Bertalot) Lange-Bertalot 1999	0	0	3	3	4	ww	z			1.23	5.66
ADSO	<i>Achnanthydium subatomoides</i> (Hustedt) O. Monnier, Lange-Bertalot & Ector 2007	0	0	1	2	2	ww	V			2.46	7.55
ADSH	<i>Achnanthydium subhudsonis</i> (Hustedt) H. Kobayasi 2006	0	0	0	4	3	ww	z	18.8	12.8	38.33	43.40
ADMS	<i>Adlafia minuscula</i> (Grunow) Lange-Bertalot 1999	0	0	4	4	1	TOL	*			0.97	9.43
ACOP	<b><i>Amphora copulata</i></b> (Kützing) Schoeman & R.E.M. Archibald 1986	3	4	1	4	5	TOL	◊	14.6	23.1	1.22	7.55
AMID	<i>Amphora indistincta</i> Levkov 2009	0	0	0	0	0	ww	z	4.5	17.9		
APED	<i>Amphora pediculus</i> (Kützing) Grunow 1875	3	4	3	4	5	TOL	◊	83.2	71.8	33.01	47.17
AAMB	<i>Aulacoseira ambigua</i> (Grunow) Simonisen 1979	2	4	1	4	5	EU	◊			1.24	3.77
AUPU	<i>Aulacoseira pusilla</i> (F. Meister) Tuji & Houki 2004	0	0	0	0	0	ww	z			8.70	1.89

(Continues)

Table. (Continued)

Code	Taxon name	H	C	M	pH	T	E	RL	Temporary			Permanent	
									MRA	FREQ	MRA	FREQ	
AUTL	<i>Aulacoseira tenella</i> (Nygaard) Simonsen 1979	0	0	0	2	0	ww	z				1.45	3.77
BBRE	<i>Brachysira brebissonii</i> R. Ross 1986	0	0	3	2	1	OD	*		1.0	5.1		
BNEG	<i>Brachysira neglectissima</i> Lange-Bertalot 2004	0	0	0	0	0	ww	z		3.4	2.6		
CLCT	<i>Caloneis lanceolata</i> (Schulz) Lange-Bertalot & Witkowski 1996	0	0	0	0	0	ww	z		2.7	17.9	8.63	16.98
CHSP	<i>Chamaepinnularia</i> sp.	0	0	4	3	3	ww	*		8.0	2.6		
CEUG	<i>Cocconeis euglypta</i> Ehrenberg 1854	3	4	2	4	5	TOL	◇		78.6	61.5	68.81	37.74
CPLI	<i>Cocconeis lineata</i> Ehrenberg 1854	3	4	2	4	5	ww	◇		7.9	28.2	56.10	22.64
CPED	<i>Cocconeis pediculus</i> Ehrenberg 1838	3	4	1	4	5	EU	◇		9.6	20.5	8.19	9.43
CPLA	<i>Cocconeis placentula</i> Ehrenberg 1838	4	3	2	4	5	TOL	◇		32.4	7.7		
CPPL	<i>Cocconeis pseudolineata</i> (Geitler) Lange-Bertalot 2004	3	4	0	4	0	ww	D		29.8	41.0	45.81	32.08
COC5	<i>Cocconeis</i> sp.	0	0	0	0	0	ww	z		23.9	28.2	25.78	22.64
CTPU	<i>Ctenophora pulchella</i> (Ralfs ex Kützing) D.M. Williams & Round 1986	4	4	3	4	5	HAL	◇		1.0	2.6		
CDUB	<i>Cyclostephanos dubius</i> (Fricke) Round in Theriot <i>et al.</i> 1987	2	5	1	5	5	EU	◇		1.23	2.56		
CMEN	<i>Cyclotella meneghiniana</i> Kützing 1844	3	4	2	4	5	EU	◇		1.7	12.8	1.20	20.75
CAFF	<i>Cymbella affinis</i> Kützing 1844	3	4	2	4	5	ww	*		13.7	5.1		
CAEX	<i>Cymbella excisa</i> Kützing 1844	3	4	2	4	5	ww	z		4.2	2.6	2.20	7.55
CPPV	<i>Cymbella perparva</i> Krammer 2002	0	0	0	4	0	ww	z		1.7	7.7		
CTUM	<i>Cymbella tumida</i> (Brébisson in Kützing) Van Heurck 1882–1885	2	4	1	4	4	EU	z		2.4	10.3	3.48	13.21
CBNA	<i>Cymbopleura naviculiformis</i> (Auerswald ex Heiberg) Krammer 2003	3	4	2	3	5	TOL	*				2.41	18.87
DTEN	<i>Denticula tenuis</i> Kützing 1844	3	4	3	4	3	ww	*				1.00	1.89
DCOT	<i>Diademsis contenta</i> (Grunow ex Van Heurck) D.G. Mann 1990	5	4	4	4	7	ww	◇		1.0	2.6		
DELL	<i>Diploneis elliptica</i> (Kützing) Cleve 1894	4	5	3	4	3	ww	*		1.47	10.26		
DSEP	<i>Diploneis separanda</i> Lange-Bertalot 2004	0	0	0	0	0	ww	z		2.2	28.2		
DSTE	<i>Discostella stelligera</i> (Cleve & Grunow) Houk & Klee 2004	2	4	1	0	0	ww	*				3.47	9.43
ENLB	<i>Encyonema</i> cf. <i>silesiacum</i> (Bleisch in Rabenhorst) D.G. Mann 1990											2.23	3.77
ENMI	<i>Encyonema lange-bertalotii</i> Krammer 1997	0	0	0	3	0	ww	z		2.5	7.7	1.20	5.66
EPRO	<i>Encyonema minutum</i> (Hilse in Rabenhorst) D.G. Mann 1990	3	4	0	3	0	ww	*		3.0	12.8	16.13	37.74
ESLE	<i>Encyonema prostratum</i> (Berkeley) Ralfs 1845	0	0	1	4	5	ww	z				1.71	5.66
ESLB	<i>Encyonema silesiacum</i> (Bleisch in Rabenhorst) D.G. Mann	3	4	1	3	7	ww	*		3.7	12.8	5.06	20.75
ENVE	<i>Encyonema sublangebertalotii</i> Lange-Bertalot & Cantonati 2010	0	0	0	0	0	ww	z		10.6	12.9	10.45	33.96
ESUM	<i>Encyonema ventricosum</i> (C. Agardh) Grunow 1875	3	4	0	3	0	ww	*		2.2	28.2	4.43	37.74
EOMI	<i>Encyonopsis subminuta</i> Krammer & E. Reichardt 1997	0	0	0	3	1	ww	z		1.0	10.3		
EADN	<i>Eolimna minima</i> (Grunow in Van Heurck) Lange-Bertalot 1998	4	4	3	4	5	TOL	◇		9.1	61.5	43.42	64.15
ESOR	<i>Epithemia adnata</i> (Kützing) Brébisson 1838	3	4	2	5	4	EU	◇		29.4	10.3		
ETUR	<i>Epithemia sores</i> Kützing 1844	3	4	2	5	5	EU	◇				1.22	3.77
ETGR	<i>Epithemia turgida</i> (Ehrenberg) Kützing 1844	0	0	3	5	4	EU	*		1.0	2.6		
EBIL	<i>Epithemia turgida</i> var. <i>granulata</i> (Ehrenberg) Brun 1880	3	4	3	5	4	ww	*				0.98	1.89
EIMP	<i>Eunotia bilunaris</i> (Ehrenberg) Mills 1934	3	4	3	6	7	TOL	◇				0.99	1.89
EMIN	<i>Eunotia implicata</i> Nöpel-Schempp, Alles & Lange-Bertalot 1991	0	0	3	2	0	OD	G		15.3	10.3	17.32	9.43
ESOL	<i>Eunotia minor</i> (Kützing) Grunow 1881	4	4	4	2	0	TOL	*				17.56	20.75
FSAP	<i>Eunotia soleirolii</i> (Kützing) Rabenhorst 1864	0	0	3	3	1	OD	G		1.0	5.1	2.68	11.32
	<i>Fistulifera saprophila</i> (Lange-Bertalot & Bonik) Lange-Bertalot 1997	0	0	3	3	5	EU	◇				5.84	7.55

(Continues)

Table. (Continued)

Code	Taxon name	H	C	M	pH	T	E	RL	Temporary			Permanent		
									MRA	FREQ	FREQ	MRA	FREQ	FREQ
FCAP	<i>Fragilaria capucina</i> Desmazières 1825	3	4	0	3	3	EU	◇	1.0	2.6	1.72	33.96		
FCRO	<i>Fragilaria crotonensis</i> Kitton 1869	0	0	1	4	3	TOL	◇	5.2	5.1	2.21	7.55		
FGRA	<i>Fragilaria gracilis</i> Østrup 1910	0	0	0	3	2	TOL	*	25.2	23.1	2.66	24.53		
FNAN	<i>Fragilaria nanana</i> Lange-Bertalot 1991	0	0	2	3	2	ww	V			1.99	30.19		
FPAV	<i>Fragilaria parva</i> Tuji & D.M. Williams 2008	0	0	0	0	0	ww	z			4.43	7.55		
FPEM	<i>Fragilaria perminuta</i> (Grunow) Lange-Bertalot 2004	0	0	0	3	0	EU	*			13.58	15.09		
FRAD	<i>Fragilaria radians</i> (Kützing) D.M. Williams & Round 1987	0	0	0	3	0	ww	z	6.4	12.8	4.34	43.40		
FRUM	<i>Fragilaria rumpens</i> (Kützing) G.W.F. Carlson 1913	0	0	0	3	5	TOL	*	2.0	20.5	40.69	24.53		
FSOC	<i>Fragilaria cf. socia</i> (N.M. Wallace) Lange-Bertalot 1980	0	0	0	0	0	ww	z	2.9	10.3	13.08	16.98		
FRAS	<i>Fragilaria</i> sp.	0	0	0	4	7	ww	z			2.73	1.89		
FUAN	<i>Fragilaria ulna</i> Sippen <i>angustissima</i> (Grunow) Lange-Bertalot 1991	0	0	1	4	5	EU	◇	2.1	38.5	2.41	1.89		
FVAU	<i>Fragilaria vaucheriae</i> (Kützing) J.B. Petersen 1938	4	4	3	4	4	EU	◇			1.17	3.77		
GDEC	<i>Geissleria decussis</i> (Østrup) Lange-Bertalot & Metzeltin 1996	0	0	3	4	4	EU	◇			1.73	9.43		
—	<i>Geissleria lusitanica</i> Novais & Ector 2013										1.21	3.77		
GANG	<i>Gomphonema angustatum</i> (Kützing) Rabenhorst 1864	3	4	0	3	4	TOL	*			7.07	1.89		
GCOM	<i>Gomphonema commutatum</i> Grunow 1880	0	0	0	0	0	ww	z	1.49	12.82				
GELG	<i>Gomphonema elegantissimum</i> E. Reichardt & Lange-Bertalot 2011	0	0	0	0	0	ww	z	9.9	2.6				
GEXL	<i>Gomphonema exilissimum</i> (Grunow) Lange-Bertalot & E. Reichardt 1996	0	0	3	3	1	ww	V	4.4	12.8	8.19	15.09		
GGRA	<i>Gomphonema gracile</i> Ehrenberg 1838	3	4	3	3	3	ww	D	1.23	17.95	1.99	30.19		
GISF	<i>Gomphonema insigniforme</i> E. Reichardt & Lange-Bertalot 1999	0	0	0	0	0	ww	z	1.42	5.13				
GLGN	<i>Gomphonema lagenula</i> Kützing 1844	3	4	0	0	0	ww	R	2.7	2.6	1.98	7.55		
GLTC	<i>Gomphonema laticollum</i> E. Reichardt 2001	0	0	0	0	0	ww	z	1.23	2.56				
GMIN	<i>Gomphonema minutum</i> (C. Agardh) C. Agardh 1831	0	0	0	3	5	EU	◇	3.7	12.8	2.66	13.21		
GOLI	<i>Gomphonema olivaceum</i> (Hornemann) Brébisson 1838	3	4	1	5	5	EU	◇	2.5	12.8				
GPAR	<i>Gomphonema parvulum</i> Kützing 1849	3	4	3	3	5	TOL	◇	3.2	56.4	19.55	67.92		
GPAS	<i>Gomphonema parvulum</i> var. <i>parvulum</i> f. <i>saprophilum</i> Lange-Bertalot & E. Reichardt 1993	3	4	0	3	6	EU	◇			3.97	3.77		
GPUM	<i>Gomphonema pumilum</i> (Grunow) E. Reichardt & Lange-Bertalot 1991	0	0	0	0	7	EU	*	3.9	10.3	1.94	9.43		
GPRI	<i>Gomphonema pumilum</i> var. <i>rigidum</i> E. Reichardt & Lange-Bertalot 1997	0	0	0	0	0	ww	z	20.0	33.3	10.37	26.42		
GRHB	<i>Gomphonema rhombicum</i> M. Schmidt 1904	0	0	0	0	0	ww	•	18.9	25.6	32.51	26.42		
GROS	<i>Gomphonema rosenstockianum</i> Lange-Bertalot & E. Reichardt 1993	0	0	0	0	0	ww	z	31.5	69.2	4.46	37.74		
GTRU	<i>Gomphonema truncatum</i> Ehrenberg 1832	2	4	2	4	4	TOL	*	2.2	17.9				
GURH	<i>Gomphonema uniserhombicum</i> E. Reichardt 2005	0	0	0	0	0	ww	z	4.2	7.7	4.93	15.09		
HVEN	<i>Halamphora veneta</i> (Kützing) Levkov 2009	3	4	3	5	5	EU	◇	1.23	30.77				
HHUN	<i>Hippodontia hungarica</i> (Grunow) Lange-Bertalot, Metzeltin & Witkowski 1996	3	4	3	4	4	EU	*	1.21	10.26				
KCLE	<i>Karayevia clevei</i> (Grunow) Bukhtiyarova 2006	3	4	1	4	4	ww	*	1.24	10.26	2.44	15.09		
KOBG	<i>Karayevia oblongella</i> (Østrup) Aboal 2003	0	0	3	3	1	O	V	41.1	28.2	77.15	56.60		
LGOE	<i>Luticola goeppertiana</i> (Bleisch in Rabenhorst) D.G. Mann 1990	0	0	3	4	5	EU	◇			2.23	3.77		
LMUT	<i>Luticola mutica</i> (Kützing) D.G. Mann 1990	5	4	4	3	5	TOL	◇			6.52	1.89		
MVAR	<i>Melosira varians</i> C. Agardh 1827	3	4	2	4	5	ww	◇	5.8	33.3	1.72	33.96		
NAGI	<i>Navicula agnita</i> Hustedt 1955	2	1	0	0	0	ww	z	1.33	2.56				

(Continues)

Table. (Continued)

Code	Taxon name	H	C	M	pH	T	E	RL	Temporary			Permanent	
									MRA	FREQ	MRA	FREQ	
NANT	<i>Navicula antonii</i> Lange-Bertalot 2000	3	4	0	4	5	EU	◇	1.24	20.51			
NCTT	<i>Navicula cataracta-rheni</i> Lange-Bertalot 1993	0	0	0	0	0	OC	R	2.2	5.1	1.97	13.21	
NCRY	<i>Navicula cryptocephala</i> Kützing 1844	4	4	2	3	7	EU	◇	5.2	10.3	12.56	32.08	
NCTE	<i>Navicula cryptotenella</i> Lange-Bertalot 1985	3	4	2	4	7	TOL	◇	1.48	20.51	3.95	54.72	
NGRE	<i>Navicula gregaria</i> Donkin 1861	3	4	3	4	5	HAL	◇	14.9	48.7	3.86	9.43	
NLAN	<i>Navicula lanceolata</i> (C. Agardh) Kützing 1844	3	4	3	4	5	EU	◇	3.0	7.7	6.90	22.64	
NNOT	<i>Navicula notha</i> J.H. Wallace 1960	0	0	0	2	2	O	G	4.2	20.5	0.99	5.66	
NRAD	<i>Navicula radiosa</i> Kützing 1844	3	4	3	3	4	TOL	◇			2.47	18.87	
NRCH	<i>Navicula reichardtiana</i> Lange-Bertalot 1989	0	0	0	4	0	EU	◇			2.47	13.21	
NRHY	<i>Navicula rhynchocephala</i> Kützing 1844	3	4	2	4	7	TOL	◇	1.22	2.56			
NROS	<i>Navicula rostellata</i> Kützing 1844	2	0	2	4	5	EU	◇	0.99	2.56			
NSLU	<i>Navicula subclidula</i> Hustedt 1950	0	0	0	0	0	EU	*	1.42	10.26			
NSYM	<i>Navicula symmetrica</i> R.M. Patrick 1944	3	4	3	4	5	EU	◇	3.2	12.8	1.23	1.89	
NTPT	<i>Navicula tripunctata</i> (O.F. Müller) Bory 1827	3	4	3	4	5	EU	◇	3.7	66.7	25.23	16.98	
NVEN	<i>Navicula veneta</i> Kützing 1844	4	4	3	4	5	EU	◇	1.0	12.8	3.60	41.51	
NACD	<i>Nitzschia acidoclinata</i> Lange-Bertalot 1976	0	0	3	3	3	TOL	*	1.6	25.6	2.67	24.53	
NAMP	<i>Nitzschia amphibia</i> Grunow 1862	4	4	3	4	5	TOL	*			2.17	3.77	
NBRE	<i>Nitzschia brevisstima</i> Grunow 1881	3	4	3	3	5	HAL	◇			1.86	9.43	
NCPL	<i>Nitzschia capitellata</i> Hustedt 1922	3	0	3	4	6	EU	◇	1.23	5.13			
NCLA	<i>Nitzschia clausii</i> Hantzsch 1860	3	0	3	4	5	EU	◇			2.56	20.75	
NDIS	<i>Nitzschia dissipata</i> (Kützing) Grunow 1862	3	4	3	4	4	EU	◇	2.7	10.3	8.94	15.09	
NFON	<i>Nitzschia fonticola</i> (Grunow) Grunow 1881	3	4	1	4	4	EU	◇			1.24	5.66	
NIFR	<i>Nitzschia frustulum</i> (Kützing) Grunow 1880	4	4	3	4	5	EU	◇			5.58	3.77	
NHAN	<i>Nitzschia hantzschiana</i> Rabenhorst 1860	3	4	4	3	3	TOL	*	32.8	69.2	21.21	41.51	
NINC	<i>Nitzschia inconspicua</i> Grunow 1862	0	0	3	4	5	EU	◇	3.2	17.9	1.49	11.32	
NMIC	<i>Nitzschia microcephala</i> Grunow 1880	4	4	3	3	6	EU	◇			1.46	13.21	
NPAL	<i>Nitzschia palea</i> (Kützing) W. Smith 1856	3	4	1	4	5	HAL	◇	3.2	5.1	0.99	13.21	
NPAE	<i>Nitzschia paleacea</i> Grunow in Van Heurck 1881	3	4	2	4	5	EU	◇					
NIPM	<i>Nitzschia perminuta</i> (Grunow in Van Heurck) M. Peragallo 1903	0	0	3	3	7	EU	◇	1.22	25.64	0.99	1.89	
NIPU	<i>Nitzschia pusilla</i> (Kützing) Grunow emend. Lange-Bertalot 1976	0	0	4	3	5	EU	◇			1.20	16.98	
NZSU	<i>Nitzschia supralitorea</i> Lange-Bertalot 1979	3	4	2	3	7	EU	◇			0.98	1.89	
PGIB	<i>Pinnularia gibba</i> Ehrenberg 1843	0	0	1	3	7	OD	V			1.23	7.55	
PMIC	<i>Pinnularia microstauron</i> (Ehrenberg) Cleve 1891	4	4	3	3	7	OD	V			0.98	3.77	
PNCO	<i>Planothidium conspicuum</i> (A. Mayer) Aboal 2003	0	0	1	3	7	ww	z			2.44	5.66	
PTDE	<i>Planothidium delicatulum</i> (Kützing) Round & Bukhtiyarova 1996	3	4	3	5	3	ww	*	2.0	7.7			
PLFR	<i>Planothidium engelbrechii</i> (Cholnoky) Round & Bukhtiyarova 1996	0	0	0	5	0	ww	*	76.9	84.6	37.16	71.70	
PLFN	<i>Planothidium frequentissimum</i> (Lange-Bertalot) Lange-Bertalot 1999	0	0	0	4	7	EU	◇			0.98	3.77	
PGRN	<i>Planothidium granum</i> (M.H. Hohn & Hellerman) Lange-Bertalot 1999	0	0	3	2	2	ww	•			4.19	3.77	
PHAY	<i>Planothidium haynaldii</i> (Schaarschmidt) Lange-Bertalot 1999	0	0	3	4	7	ww	D			6.67	35.85	
PTLA	<i>Planothidium lanceolatum</i> (Brébisson ex Kützing) Lange-Bertalot 1999	4	4	3	4	5	TOL	◇	13.4	43.6			
PLMN	<i>Planothidium minutissimum</i> (Krasske) Lange-Bertalot 1999	0	0	0	0	0	ww	z	20.2	2.6			
PLEV	<i>Pleurosira laevis</i> (Ehrenberg) Compère 1982	3	0	3	5	5	HAL	◇			2.72	1.89	

(Continues)



Table. (Continued)

Code	Taxon name	H	C	M	pH	T	E	RL	Temporary			Permanent		
									MRA	FREQ	FREQ	MRA	FREQ	FREQ
PALV	<i>Pseudostausosira abvareziae</i> Cejudo-Figuera, E. Morales & Ector 2011	0	0	0	0	0	ww	z	5.7	20.5	31.01	16.98		
PSBR	<i>Pseudostausosira brevisiriata</i> (Grunow) D.M. Williams & Round 1987	3	4	2	4	7	TOL	∅			15.14	1.89		
PSSE	<i>Pseudostausosira elliptica</i> (Schumann) Edlund, E. Morales & S.A. Spaulding 2006	0	0	1	4	4	ww	*			5.54	9.43		
RSIN	<i>Reimeria sinuata</i> (W. Gregory) Kociolek & Stoermer emend. S.E. Sala, J.M. Guerrero & Ferrario 1993	3	4	3	3	3	TOL	∅	26.6	61.5	60.00	60.38		
RUNI	<i>Reimeria uniseriata</i> S.E. Sala, J.M. Guerrero & Ferrario 1993	0	0	0	0	0	ww	z	12.5	33.3	2.72	18.87		
RABB	<i>Rhoicosphenia abbreviata</i> (C. Agardh) Lange-Bertalot 1980	3	3	2	4	5	EU	∅	4.5	28.2	9.36	18.87		
RADT	<i>Rhoicosphenia adriatica</i> Caput Mihalic & Levkov 2010	0	0	0	0	0	ww	z			42.64	1.89		
RGIB	<i>Rhopalodia gibba</i> (Ehrenberg) O. Müller 1895	3	4	3	5	5	EU	*	2.7	2.6				
SPUP	<i>Sellaphora pupula</i> (Kützing) Mereschkowsky 1902	3	4	2	3	4	EU	∅	1.0	7.7				
SSEM	<i>Sellaphora seminulum</i> (Grunow) D.G. Mann 1989	4	4	3	3	5	EU	∅	4.5	33.3	1.24	24.53		
SEXG	<i>Stauroforma exiguiformis</i> (Lange-Bertalot) Flower, Jones & Round 1996	0	0	2	3	1	ww	3			6.01	1.89		
SBND	<i>Staurosira binodis</i> (Ehrenberg) Lange-Bertalot 2011	3	4	2	4	4	ww	*	2.5	2.6	0.96	7.55		
SSPE	<i>Staurosira</i> sp.	0	0	0	0	0	ww	z	2.2	7.7				
SSVE	<i>Staurosira venter</i> (Ehrenberg) H. Kobayasi 2002	3	4	1	4	4	TOL	∅	29.7	28.2	36.30	26.42		
SPIN	<i>Staurosirella pinnata</i> (Ehrenberg) D.M. Williams & Round 1987	4	4	3	4	7	TOL	∅	3.4	10.3	2.64	7.55		
TFLO	<i>Tabellaria flocculosa</i> (Roth) Kützing 1844	3	4	3	2	3	TOL	∅	0.99	2.56				
THUN	<i>Tryblionella hungarica</i> (Grunow) D.G. Mann 1990	3	4	1	4	5	EU	∅			1.40	11.32		
UACU	<i>Ulnaria acus</i> (Kützing) Aboal 2003	2	4	2	4	5	ww	*	1.0	17.9				
UBIC	<i>Ulnaria biceps</i> (Kützing) Compère 2001	0	0	0	4	5	O	G	2.6	23.1	3.47	28.30		
UDEL	<i>Ulnaria delicatissima</i> (W. Smith) Aboal & P.C. Silva 2004	0	0	0	0	0	ww	z	13.6	2.6				
UULN	<i>Ulnaria ulna</i> (Nitzsch) Compère 2001	3	4	2	4	7	ww	*	8.6	20.5	1.72	35.85		