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Species richness and diversity of benthic diatom communities in tropical mountain streams of Mexico

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Abstract

We examined community structure of benthic diatoms and their substratum preferences (epilithic vs. macroalgae) by season in 4 tropical mountain streams in central Mexico. Of the 74 species compiled, *Cymbella silesiaca*, *Rhoicosphenia abbreviate*, and *Reimeria sinuata* were the most abundant and frequent. About 14% of species were exclusively epilithic, 13% were associated with macroalgae, and 73% had no clear preference. Environmental factors most closely related to spatial and temporal distribution of epilithic diatoms were changes in stream discharge and water temperature. For diatoms associated with macroalgae, the most important factors were changes in current velocity and the coverage and richness of macroalgae. The similarities in species richness and diversity in the 4 study sites suggest that the diatom community develops under conditions of moderate disturbance. The few differences found in species richness between epilithic and macroalgae-associated diatoms suggest that these diatoms do not have substratum preferences. The abundance of macroalgae-associated diatoms in all sites suggests a positive effect (facilitation) of macroalgae on diatoms.

Key words: epilithic diatoms, macroalgae-associated diatoms, mountain streams, spatial variation, temporal variation, tropical region

Introduction

Diatoms are the most frequent and abundant algal groups in lotic ecosystems; their abundance is related to their relative tolerance of hydrodynamic drag (Ní Chatháin and Harrington 2008, Hwang et al. 2011). Diatom species have several morphological features that may be interpreted as biomechanical adaptations for reducing drag, such as pennate forms with streamlined cell shapes, stalked or adnate growth forms with an extracellular secretion of mucilage that fastens them securely to the substratum, and the presence of a raphe, which permits gliding movement on diverse benthic surfaces (Anzola and Rondon 2005, Stevenson et al. 2010). Gliding locomotion allows diatoms to colonize various kinds of substrata when cells move out of epilithic habitats to avoid hydrodynamic stresses.

The spatial heterogeneity of stream beds offers a range of habitats that are likely refugia from stress for diatom species (Hildrew 1996). Roughness and dimensions of substrata have positive relationships with diatom species richness (Necchi and Moreira 1995, Schneck et al. 2011), and species abundances are related to substratum stability, substratum protection from drag, and the presence of dissolved nutrient concentrations (within macrophyte stands) higher than those in the surrounding water column (Burkholder 1996, Hart and Finelli 1999, Poulíčková et al. 2004).

In combination with hydrodynamics, the geological origin of substrata (e.g., chemical composition) and altitude are among the factors determining community structure of benthic algae (Weckström and Korhola 2001, Potapova and Charles 2003, Hwang et al. 2011). Mountain streams in tropical regions have reduced water temperatures associated with high altitudes (Jacobsen 2008) and seasonal cycles correlated with precipitation patterns (Martínez and Donato 2003). The algal communities in mountain streams in the Mexican Volcanic Belt (MVB) are subjected to moderate environmental disturbance; species experience alternating rainy and dry seasons and temperate or cold water in the winter (Bojorge-García and Cantoral-Uriza 2007, Bojorge-García et al. 2010). We predicted that the dynamics of diatom communities would be impacted by typical summer rains in tropical latitudes and by temperate to cold water in at least one season due to the high altitude, and that diverse diatom substratum colonization capabilities would also play a role in community dynamics.

The aims of this study were to determine features of community structure in the benthic diatoms of tropical mountain streams in Mexico and to identify possible ecological mechanisms influencing this structure. We also investigated whether the algal community was specific to this environment by (1) identifying the main environmental variables affecting algal spatial and temporal distributions; (2) determining species richness and diversity by site and season; and (3) investigating species' substratum preferences.

Material and methods

The study was conducted in mountain streams in the Valle de Bravo Basin (drainage basin area 546.9 km^2; Olvera-Viascan et al. 1998) located in the MVB. The 4 streams studied (Site 1 [S1], Amanalco; Site 2 [S2], Nacimiento González; Site 3 [S3] Carrizal; and Site 4 [S4], Borbollón) are located between 1890 and 2220 m a.s.l. and have abundant overhanging canopy cover (Fig. 1). Geomorphological and climatic conditions in the basin promote formation of coniferous forests, streams with relatively cold to warm waters 9 to 21°C (Ramírez and Cantoral-Uriza 2003), and a torrential rainy season during summer (Ferrusquía Villafranca 1998, García 2004).

We sampled epilithic and macroalgae-associated diatom communities every 3 months through 2 annual cycles at times of strongly contrasting weather conditions: warm dry season (D; Mar–May, $n = 3$), rainy season (R; Jun–Nov, $n = 2$), and cold dry season (CD; Dec–Feb, $n = 4$).

We measured the following physical and chemical parameters *in situ* at each site: water temperature, pH, specific conductivity (standardized to 25 °C, K_{25} with a conductivity meter: Conductronic PC-18), dissolved oxygen using an oxygen meter (YSI-85, YSI, Ohio, USA), percentage oxygen saturation calculated from dissolved oxygen data (taking into account altitude and water temperature; Wetzel and Likens 1991), and current velocity (v m s^{-1}), using a current velocity meter (Swoffer Instruments 3000, WA, USA). Discharge (Qm^3 s^{-1}) was calculated from current velocity date following Gore (1996).
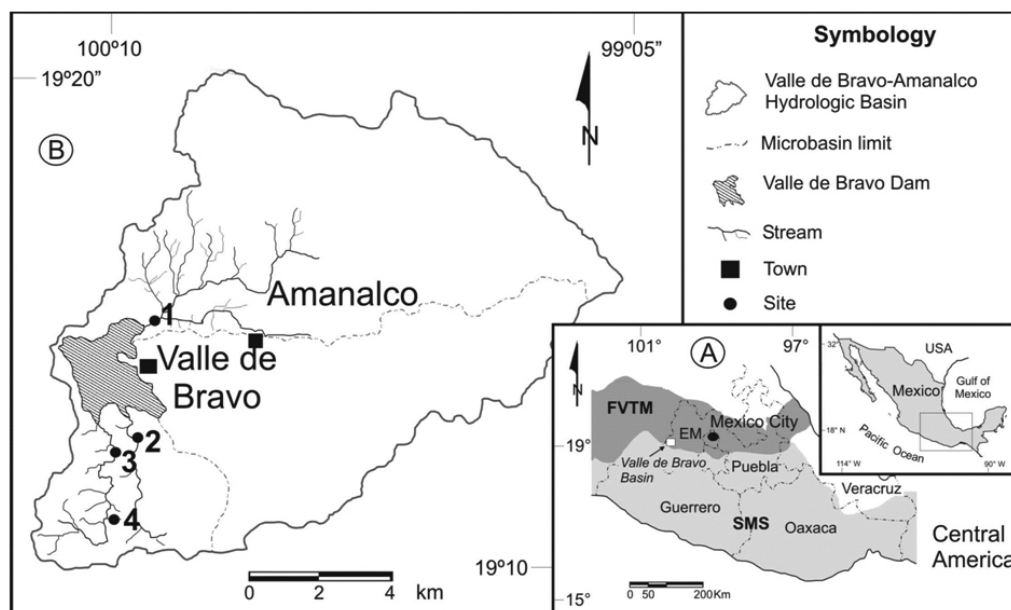
Fig. 1. Location of sampling sites in the Valle de Bravo Basin, Mexico. Site 1(S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón.

Samples for measuring water nutrient concentrations were collected in duplicate; each sample was filtered *in situ* through 0.22 µm pore size membranes (Millipore, MA, USA), preserved with a few drops of chloroform, and frozen for subsequent analysis in the laboratory with a SAN Plus Segmented Flow Analyzer (Skalar, GA, USA) following standard titration protocols. Soluble reactive phosphorus (in theory, mostly in the form of orthophosphate, PO_4^{3-}-P), nitrite nitrogen (NO_2^--N), nitrate nitrogen (NO_3^--N), ammonium nitrogen (NH_4^+-N), dissolved inorganic nitrogen (DIN), and silicon dioxide (SiO_2) were analyzed following Greenberg and Clesceri (1985), ASTM (1989), and APHA (1995).

Water samples for anion analysis of bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), chloride (Cl^-), and sulfate (SO_4^{2-}); total dissolved solids (TDS); and pH were frozen ($-20\ °C$) and held in darkness. Samples for cation analysis of calcium (Ca^{2+}), magnesium (Mg^{2+}), sodium (Na^+), and potassium (K^+) were preserved with 40% nitric acid to pH 2–3. Total hardness (TH) was calculated from the sum of calcium hardness and magnesium hardness. We determined carbonates by titration, chlorides by the selective electrode method, sulfates by turbidimetric procedures, and Na^+ and K^+ by the spectrophotometric atomic absorption method (APHA 1995).

Epilithic diatoms were collected by brushing pebbles located within the laminar flow layer of the stream bed; epiphytic and metaphytic diatoms (considered here as macroalgae-associated diatoms) were obtained by digesting the thalli of benthic algae with macroscopic forms (Sheath and Cole 1992), including free filaments, mats, and gelatinous and filamentous colonies. Each sampling site comprised a stream segment 10 m in length, divided into 5 equal segments from which we collected samples for each type of diatom from main stream microhabitats. In each segment, we collected 5 samples for epilithic diatoms and 5 samples for macroalgae-associated diatoms. Each diatom sample was collected from an area of 4.82 cm^2 (Soininen et al. 2004, Bojorge-García and Cantoral-Uriza 2007). Macroalgae abundance was evaluated using a circular sampling unit (10 cm radius, area of 157 cm^2; Necchi and Moreira 1995, Ramírez-Rodríguez et al. 2007, Bojorge-García et al. 2010).

Samples were cleaned following the oxidation technique of Rushforth et al. (1984); 3 permanent slides used for taxonomic identification and diatom counting were prepared for each sample using Naphrax resin (Brunel Microscopes, Chippenham, UK) as the mounting medium. Identification was mainly based on Krammer and Lange-Bertalot (1986, 1988, 1991a, 1991b); information on diatom growth forms was obtained from Cantoral-Uriza et al. 1997, Novelo 1998,

and Cantonati and Spitale 2009. We counted 400 valves per slide (Karthick et al. 2010) using an Olympus BX51 (Tokyo, Japan) light microscope. Abundance was calculated using a formula proposed by Battarbee (1986). Macroalgal data including species, morphological type, dominance, and species richness were obtained from previous studies at the site (Bojorge-García et al. 2010).

Spatial and seasonal differences in water physicochemistry and in the community structure of epilithic and macroalgae-associated diatoms were assessed using one-way analysis of variance (ANOVA) followed by Tukey's HSD tests (unequal for seasons) for multiple comparisons. We used 2-way ANOVA and Student's t-tests, respectively, to examine differences in structure and diversity between epilithic and macroalgae-associated diatoms in each site. Physical variables, chemical variables, and biological measures were transformed (log or square root) when necessary to satisfy ANOVA assumptions of normality and homogeneity of variance. Tests were performed with Statistica ver. 7.0 software.

To analyze differences in richness and species dominance among substrata among and within sites, we constructed dominance–diversity curves based on abundances. Species diversity was measured as the Shannon-Wiener $\log_2$ diversity index ($H'\ \log_2$) using Primer ver. 6 software. Relationships between spatial and temporal distributions of epilithic and macroalgae-associated diatoms and physical and chemical parameters were explored using canonical correspondence analysis (CCA), followed by Montecarlo tests (999 permutation, $\alpha = 0.05$); this analysis was performed with PC-ORD ver. 4 software.

Results

Diatom communities from the Valle de Bravo Basin were found in temperate waters with circumneutral pH, shallow depth, low to moderate specific conductivity, low to moderate current flow, and a high percentage of oxygen saturation. Physical and chemical parameters were relatively constant between seasons; there was no significant interaction between site and season (2-way ANOVA, $P > 0.05$), but the site effect was significant ($F = 37.88$, $P = 0.001$). Two groups, G1 and G2, were identified by Tukey's test ($P > 0.05$). Group 1 contained S1, and G2 contained S2, S3, and S4. Ionic concentration was higher in G1 (G1, 3–5 meq l^{-1}; G2, 1–3 meq l^{-1}), as was discharge (G1, 0.1–4 m^3 s^{-1}; G2, 0.01–0.9 m^3 s^{-1}). Spatiotemporal changes in physical and chemical parameters at the basin level were not reflected in the community dynamics on any of the substrata.

Taxonomic composition

Of the 74 diatoms species identified in the study area, *Cymbella silesiaca*, *Reimeria sinuata*, and *Rhoicosphenia abbreviata* were the most frequent and abundant (Table 1; Fig. 2). Epilithic diatoms made up 14% of the total; 13% were macroalgae-associated and 73% were not preferentially distributed among substrata (Table 1). We found 24 species present on all substrata, with similar dominances in all sites (Fig. 2). Diversity was significantly different among substrata in S1 (t = 2.32, P = 0.03), S2 (t = 20.1, P = 0.01), and S4 (t = 8.9, P = 0.01), but not in S3 (P > 0.05). Macroalgae-associated diatoms had highest diversity values in all sites (Table 1).

The macroscopic algal community was composed of 13 species with heterogeneous distributions and diversities through 3 seasons of the year. The most abundant and frequent morphological forms were mucilaginous filaments, mucilaginous colonies, nonmucilaginous filaments, and tissue-like forms.

Species–physicochemical variable relationship

The differences in abundance between epilithic and macroalgae-associated diatoms were statistically significant in each site (Table 2). Macroalgae-associated diatoms were more abundant in S1, S3, and S4, while epilithic diatoms were most abundant in S2. Abundances of diatom communities in S2, S3, and S4 did not change significantly through the study period (P > 0.05). In S1, abundance varied by season (Table 2). Tukey's test identified 2 groups (P < 0.05); the lowest abundances
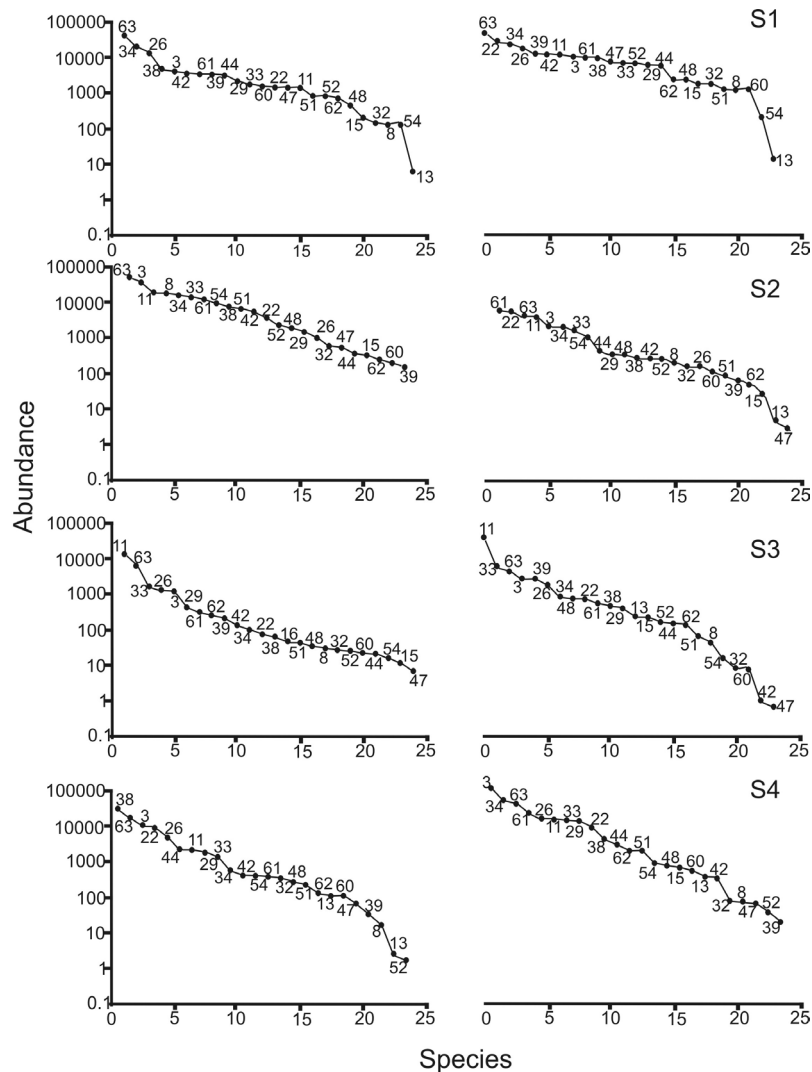
Fig. 2. Dominance–diversity curves based on diatom abundance (valves cm^{-2}) among sites and substrata. The left column of panels refers to epilithic diatoms and the right column to macroalgae-associated diatoms. Site 1 (S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón.
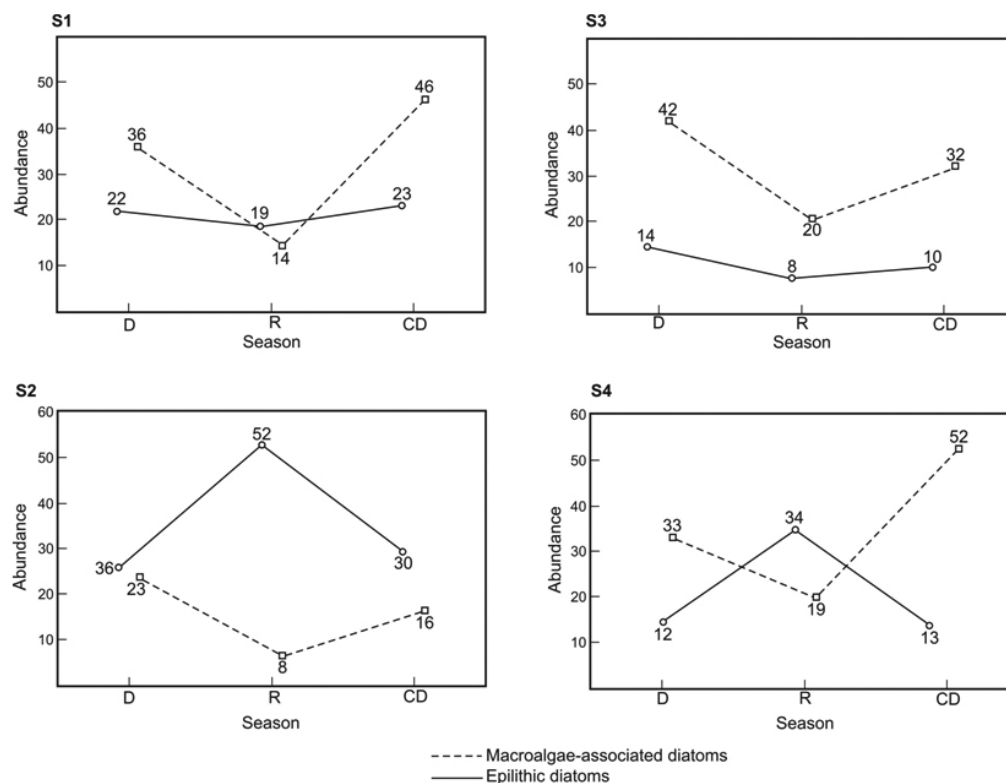
Fig. 3. Two-way ANOVA interaction plots shows changes in means abundance values (valves cm^{-2}) by substratum and season in each site. Site 1(S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón. D = warm dry season; R = rainy season; CD = cold dry season.

occurred in R. There was an inverse relationship between abundance and water discharge in S2 and S4, depending on the substratum occupied by diatoms (hence, the significant season × substratum interaction; Table 2; Fig. 3). Abundance of macroalgae-associated diatoms decreased (65→42%) between D and R in S2 and S4; epilithic diatom abundance increased (50→58%) between D and R in S4 and S2. In S1, macroalgae-associated and epilithic diatoms declined between D and R (61→14%).

The importance of the relationship between physico-chemical parameters and species distribution varied by site and substratum. CCA indicated that in all sites the distribution of macroalgae-associated diatoms was related mainly to changes in current velocity and macroscopic algal coverage (MC) or richness (MR); the distribution of epilithic diatoms was related mainly to discharge and temperature (Table 3; Fig. 4 and 5). In S1, the first 3 ordination axes were significant ($P = 0.001$) and explained 78.4% of total variation for epilithic diatoms and 75% of total variation for macroalgae-associated diatoms.

The variation in epilithic diatom abundance was related to ionic concentration, nutrients, v m s^{-1}, Qm^3 s^{-1}, and temperature; variation in macroalgae-associated diatom abundance was related to ionic concentration,

nutrients, v m s^{-1}, Qm^3 s^{-1}, and MR (Fig 4). The species–environment relationship in S2 for both diatom substratum categories was based on nutrients and ionic concentration ($P = 0.02$), with the first 3 ordination axes explaining 75.9% of total variation for epilithic species and 89.3% for macroalgae-associated species. The distribution of epilithic diatoms was also related to Qm^3 s^{-1}; the distribution of macroalgae-associated diatoms was related to MC, Qm^3 s^{-1}, and depth (cm; Fig. 4).

According to the CCA for S3, ionic and nutrient concentration strongly influenced abundances of both groups of diatoms, with the first 3 axes explaining 93.6% and 92.3% of total variation for epilithic ($P = 0.01$) and macroalgae-associated diatoms ($P = 0.02$), respectively. The variation in epilithic diatom abundance was also related to Qm^3 s^{-1} and T, and the variation in macroalgae-associated diatoms was related to MR, v m s^{-1}, and depth in cm (Fig 5). The first 3 CCA axes of S4 explained 91.9% of total variation for epilithic diatoms and 88.2% of total variation for macroalgae-associated diatoms ($P = 0.01$). As at the other sites, the distributions of epilithic and macroalgae-associated species were related to ion and nutrient concentrations; epilithic diatom parameters were also related to Qm^3 s^{-1} and macroalgae-associated diatom parameters to MR and v m s^{-1}.

Table 1. Mean abundance values (valves cm^{-2}), diversity values (*H´*) and species richness of benthic diatoms (E = epilithic, A = macroalgae-associates) at study sites in the Valle de Bravo Basin. Bold numbers refer to species found in 3 or fewer sites.

	Species	S1		S2		S3		S4	
		E	A	E	A	E	A	E	A
	Pennate Diatoms								
1	*Achnathidium exiguum* (Grunow) Czarneki	3	2	25	6	3	0.1	4	1
2	*Achnanhtes inflata* (Kützing) Grunow	—	0.6	10	4	30	—	—	—
3	*Achnanthidium minutissimum* (Kützing) Czarnecki	53	53	110	37	1	1	66	110
4	*Amphipleura lindheimerii* Grunow	5	12	11	10	2	—	5	2
5	*Amphora montana* Krasske	8	5	1	2	2	—	2	—
6	*Amphora pediculus* Ehrenberg	9	17	19	7	3	—	2	0.5
7	*Berkella linearis* Ross y Sims	9	13	11	17	—	7	8	6
8	*Caloneis* sp1	8	12	78	11	4	5	3	2
9	*Caloneis* sp2	—	**2**	**18**	**8**	—	—	—	—
10	*Cocconeis pediculus* Ehrenberg[a]	—	**3**	—	—	—	—	—	—
11	*Cocconeis placentula* Ehrenberg	32	43	97	41	75	193	40	69
12	*Cymbella mexicana* (Ehrenberg) Cleve	**1**	**0.5**	**1**	—	—	—	—	—
13	*Cymbella naviculiformis* (Auerswald) Cleve	1	0.4	1	2	3	12	1	10
14	*Cymbella norvergica* Grunow[a]	—	—	—	**1**	—	—	—	**0.5**
15	*Cymbella silesiaca* Bleisch	9	14	6	4	2	15	7	13
16	*Cymbella tumida* (Brébisson) van Heurck*	—	—	—	—	—	—	—	**0.1**
17	*Denticula elegant* Kützing	**1**	**6**	**1**	—	—	—	—	—
18	*Diploneis elliptica* (Kützing) Cleve[e]	**2**	—	**2**	—	—	—	—	—
19	*Epithemia turgida* (Ehrenberg) Kützing[a]	—	0.4	—	0.3	—	2	—	78
20	*Eunotia* sp1	2	1	2	1	—	3	1	2
21	*Eunotia* sp2[a]	—	—	—	**1**	—	—	—	**2**
22	*Fragilaria capucina* Desmazières	31	69	39	38	7	31	39	0.1
23	*Fragilaria construens* (Ehrenberg) Grunow	3	6	4	6	—	—	—	2
24	*Gomphonema acuminatum* Ehrenberg	2	—	2	2	2	0.5	1	—
25	*Gomphonema* cf *affine* Kützing	—	1	—	2	—	—	1	1
26	*Gomphonema angustum* Agardh	46	65	24	9	24	39	51	2
27	*Gomphonema clevei* Fricke	2	4	15	2	—	—	—	47
28	*Gomphonema gracile* Ehrenberg[e]	—	—	—	—	**3**	—	—	—
29	*Gomphonema parvulum* Kützing	35	37	23	12	12	22	25	67
30	*Gomphonema truncatum* Ehrenberg	1	1	1	—	—	1	2	1
31	*Gyrosigma* sp.	4	9	9	9	2	3	1	—
32	*Luticula mutica* (Kützing) Mann	7	13	10	8	3	61	9	3
33	*Navicula capitatoradiata* Germain	33	36	54	28	20	59	30	75
34	*Navicula cryptotenella* Lange-Bertalot	54	73	63	33	7	20	17	85
35	*Navicula minuscula* Grunow	6	5	1	2	2	4	5	10
36	*Navicula radiosa* Kützing[a]	—	**2**	—	—	—	—	—	—
37	*Navicula rynchocephala* Kützing	5	4	4	11	2	6	8	11
38	*Navicula shroeterii* Meister	53	42	47	12	5	16	62	29

39	*Navicula tripunctata* (O.F. Müller) Bory	47	53	8	5	11	34	3	0.5
40	*Navicula* sp. 1	3	4	19	7	3	1	2	3
41	*Navicula* sp. 2[a]	—	—	—	3	—	—	—	—
42	*Nitzschia amphibia* Grunow	46	61	30	12	7	0.4	13	10
43	*Nitzschia clausii* Hantzsch	7	3	1	—	2	1	—	1
44	*Nitzschia dissipata* (Kützing) Grunow	37	31	13	15	3	10	21	32
45	*Nitzschia flexoides* Geitler[e]	**2**	—	**1**	—	**2**	—	—	—
46	*Nitzschia* cf. *homburgiensis* Lange-Bertalot[e]	**2**	—	**1**	—	—	—	—	—
47	*Nitzschia incospicua* Grunow	32	38	9	2	2	0.5	3	0.3
48	*Nitzschia linearis* (Kützing) W. Smith	17	22	15	13	4	17	9	—
49	*Nitzschia microcephala* Grunow[e]	**7**	—	**1**	—	**3**	—	—	—
50	*Nitzschia ovalis* Arnott ex Grunow	2	1	1	—	—	—	1	—
51	*Nitzschia palea* (Kützing) W. Smith	22	9	14	6	4	5	8	17
52	*Nitzschia sinuata* var. delognei (Grunow) Lange-Bertalot	20	36	22	12	3	9	1	1
53	*Nitzschia* cf *umbonata* (Ehrenberg) Lange-Bertalot[e]	**2**	—	**1**	—	—	—	—	—
54	*Nupela* sp.	7	3	53	26	14	2	10	17
55	*Pinnularia borealis* Ehrenberg[e]	**2**	—	**1**	—	**12**	—	—	—
56	*Pinnularia microestauron* (Ehrenberg) Cleve[e]	—	—	—	—	—	—	**2**	—
57	*Pinnularia* sp. 1	2	7	2	5	—	2	4	—
58	*Pinnularia* sp. 2[e]	**2**	—	**1**	—	—	—	—	—
59	*Pinnularia* sp. 3[e]	—	—	—	—	—	—	**2**	—
60	*Planothidium frecuentissimum* (Lange-Bertalot) Round and L. Bukhtiyarova	26	18	7	5	15	0.5	6	9
61	*Planothidium lanceolatum* (Brébisson) Round and Bukhtiyarova	47	48	67	52	11	27	15	71
62	*Reimeria sinuata* (Gregory) Kociolek and Stoermer	18	21	6	5	2	12	7	21
63	*Rhoicosphenia abbreviata* (Agardh) Lange-Bertalot	96	102	137	47	—	50	109	100
64	*Rhopalodia gibberula* (Ehrenberg) O. Müller	6	1	1	—	—	—	—	7
65	*Rhopalodia* sp1[a]	—	—	—	—	—	—	—	**1**
66	*Sellaphora pupula*[a]	—	**1**	—	—	—	—	—	—
67	*Staurosirella pinnata* (Ehrenberg) William and Round	7	6	24	8	57	0.1	—	0.3
68	*Surirella angusta* Kützing	4	7	2	4	—	—	2	1
69	*Ulnaria ulna* (Nitzsch) Compère	12	31	16	13	—	36	9	22
	Centric Diatoms								
70	*Aulacoseira granulata* (Ehrenberg) Simonsen	**2**	**4**	**1**	—	—	—	—	—
71	*Melosira varians* Agardh	17	61	52	60	—	88	5	21
72	*Cyclotella menenghiniana* Kützing	3	10	1	2	—	27	1	0.5
73	*Cyclotella pseudostelligera* Husted	5	13	1	1	—	—	1	—
74	*Stephanodiscus* sp.[a]	—	**0.2**	—	—	—	—	—	—
	Species richness	57	58	59	51	39	40	47	47
	Diversity index (H' $\log_2$)	2.8	2.9	2.2	3.1	2.7	2.7	1.5	2.1

[a] species restricted to macroalgae-associated condition
[e] species restricted to epilithic condition
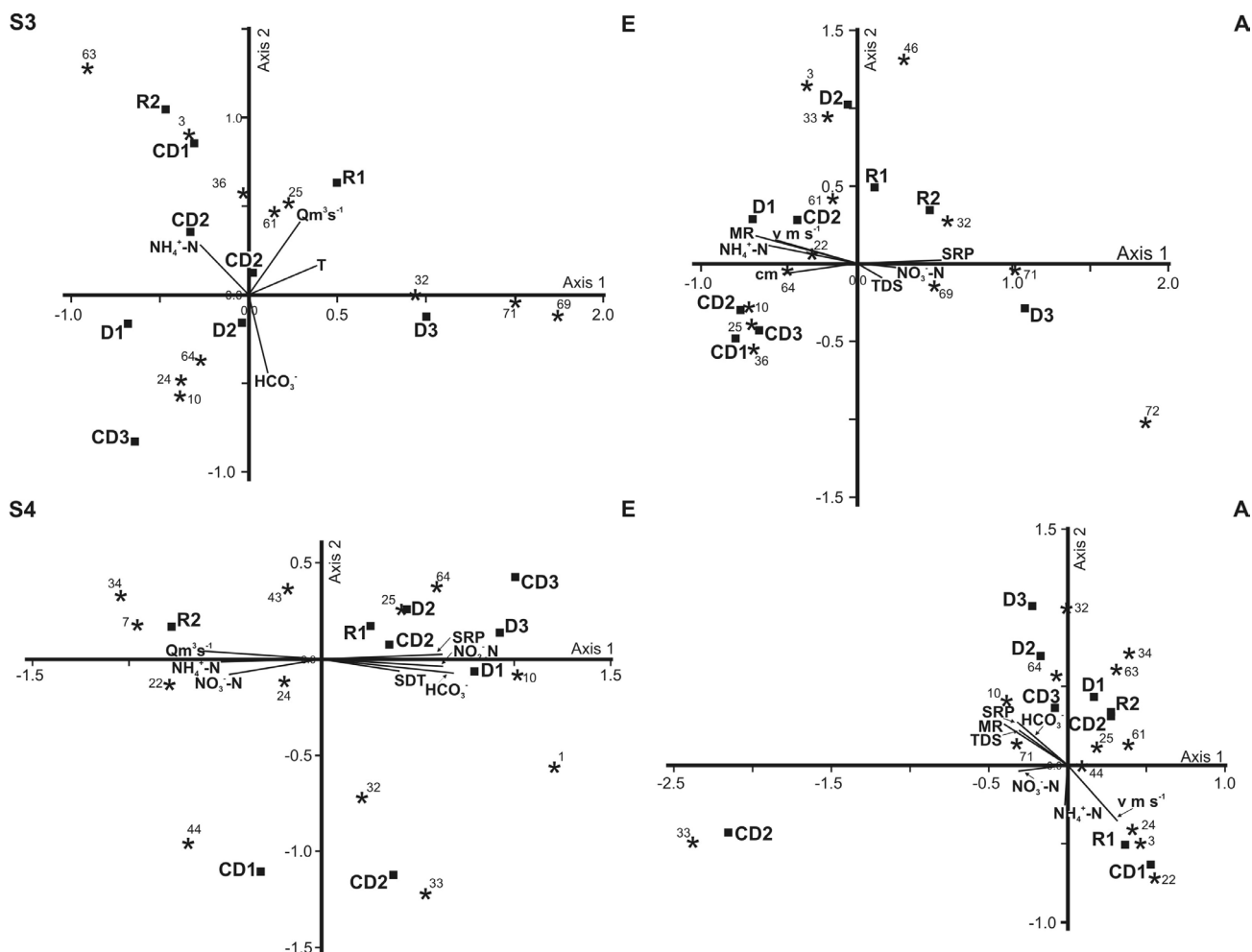— not recorded
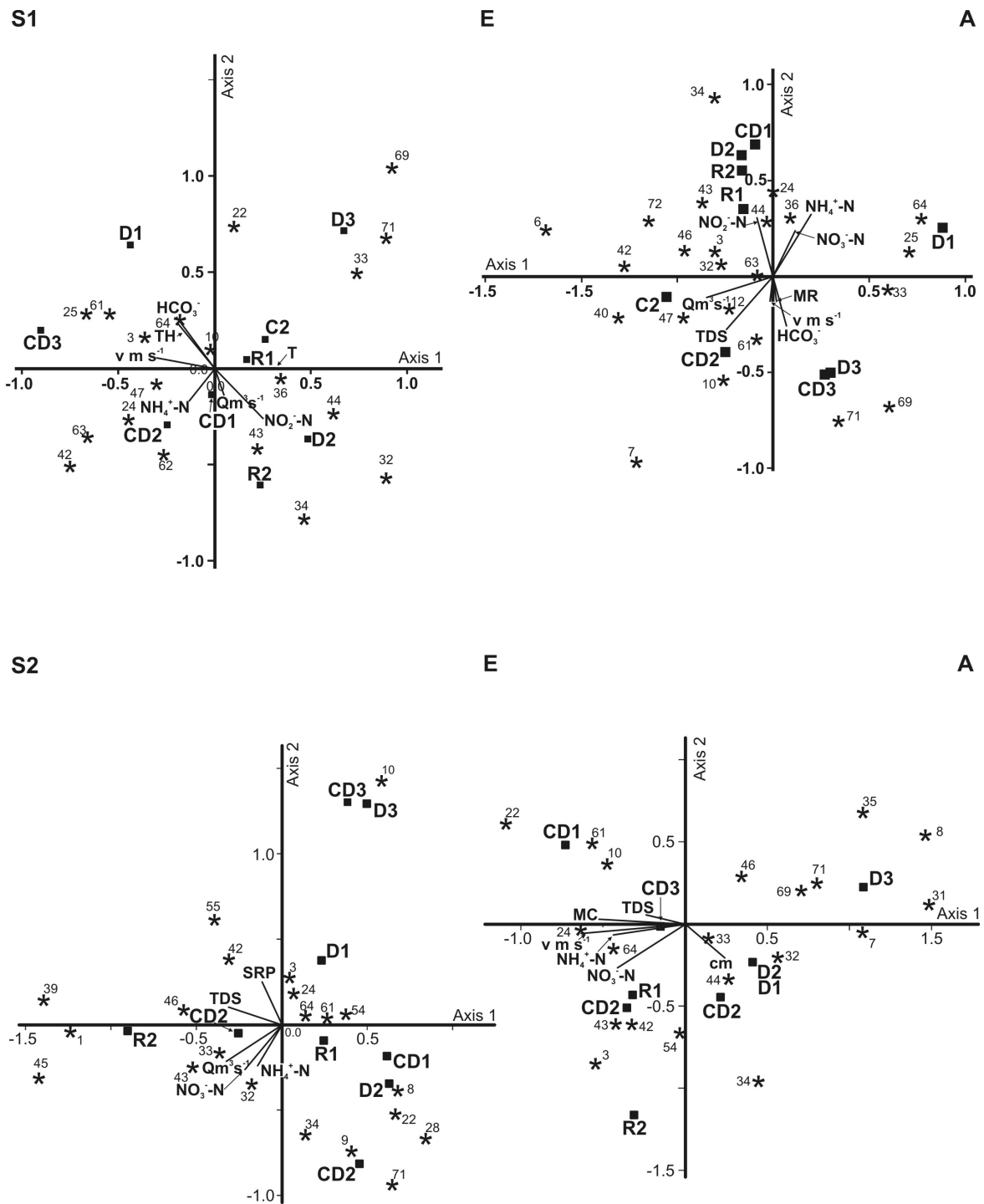
Fig. 4. CCA biplot showing the general distribution of diatoms in relation to physical and chemical parameters recorded in S1 and S2. The number of asterisks corresponds to the number of species in Table 2. The number after each seasonal abbreviation is the number of collections. The left column refers to epilithic diatoms and the right column to macroalgae-associated diatoms. Site 1 (S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón. D = warm dry season; R = rainy season; CD = cold dry season.

Table 2. Effects of season (S), substratum (DSB), and their interaction (S × DSB) on diatom abundance at 4 sites analyzed by 2-way ANOVA. Site 1(S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón.

Site	DSB		S		S × DSB	
	F	P	F	P	F	P
S1	18.73	0.00	16.8	0.00	9.5	0.00
S2	48.55	0.00	2.2	0.1	18.7	0.00
S3	16.3	0.00	2.2	0.1	0.54	0.6
S4	10.96	0.001	1.9	0.1	11.74	0.00

Fig. 5. CCA biplot showing the general distribution of diatoms in relation to physical and chemical parameters recorded in S3 and S4. The number of asterisks corresponds to the number of species in Table 2. The number after each seasonal abbreviation is the number of collections. The left column refers to epilithic diatoms and the right column refers to macroalgae-associated diatoms. Site 1(S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón. D = warm dry season; R = rainy season; CD = cold dry season.

Table 3. Correlation CCA results for epilithic (E) and macroalgae-associated diatoms (A). The bold numbers indicate the most important variables for each axis. Site 1(S1) Amanalco; Site 2 (S2) Nacimiento González; Site 3 (S3) Carrizal; and Site 4 (S4) Borbollón.

Physical and Chemical Variables	S1 E 1	S1 E 2	S1 E 3	S1 A 1	S1 A 2	S1 A 3	S2 E 1	S2 E 2	S2 E 3	S2 A 1	S2 A 2	S2 A 3	S3 E 1	S3 E 2	S3 E 3	S3 A 1	S3 A 2	S3 A 3	S4 E 1	S4 E 2	S4 E 3	S4 A 1	S4 A 2	S4 A 3
NH_4^+-N	−0.27	−0.40	**0.64**	0.40	**0.75**	−0.34	−0.24	**−0.44**	0.13	**−0.64**	−0.13	−0.58	−0.42	**0.50**	−0.06	**0.75**	0.22	−0.28	**−0.71**	−0.02	−0.03	−0.02	**−0.48**	−0.17
NO_2^--N	0.50	**−0.62**	0.37	−0.16	**0.72**	0.07	**0.46**	−0.16	0.34	—	—	—	0.27	0.13	**−0.60**	0.28	**0.40**	−0.12	**0.86**	−0.08	0.003	—	—	—
NO_3^--N	—	—	—	0.24	**0.56**	−0.29	−0.36	**−0.48**	0.45	**−0.60**	−0.57	−0.45	**0.44**	−0.25	−0.02	0.33	−0.04	0.06	**−0.65**	−0.17	0.19	−0.40	−0.07	0.01
SRP	—	—	—	—	—	—	−0.20	**0.46**	−0.10	0.53	−0.19	**0.60**	**0.66**	−0.10	0.14	**0.72**	0.03	−0.015	**0.86**	0.05	−0.08	−0.39	0.49	−0.08
TDS	—	—	—	−0.49	**−0.66**	0.09	−0.52	0.19	0.42	−0.34	0.12	**0.86**	0.44	0.55	−0.15	0.21	−0.18	−0.22	0.55	−0.13	0.02	−0.39	**0.44**	0.27
TH	−0.39	**0.51**	−0.34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
HCO_3^-	−0.40	**0.63**	−0.40	0.14	**−0.61**	0.002	**0.43**	−0.01	−0.04	**0.72**	0.25	0.11	0.16	**−0.78**	−0.38	—	—	—	**0.93**	−0.15	−0.05	−0.41	0.51	**0.65**
Temp	**0.63**	0.007	0.04	—	—	—	0.01	−0.13	**0.84**	—	—	—	0.60	0.29	−0.62	—	—	—	**0.29**	0.16	−0.18	—	—	—
Depth (cm)	—	—	—	—	—	—	—	—	—	0.34	−0.43	−0.29	—	—	—	**−0.64**	−0.13	−0.15	—	—	—	—	—	—
Q ($m^3 s^{-1}$)	0.09	−0.32	**−0.84**	**−0.70**	−0.27	0.12	−0.54	−0.39	**0.66**	—	—	—	0.45	**0.73**	−0.46	—	—	—	**−0.83**	0.09	−0.18	—	—	—
Current velocity ($m s^{-1}$)	**−0.60**	0.13	−0.27	−0.02	−0.31	−0.81	—	—	—	**−0.92**	−0.12	0.21	—	—	—	**−0.70**	0.29	−0.23	—	—	—	0.41	**−0.67**	−0.44
MR	—	—	—	0.03	**−0.3**	0.09	—	—	—	—	—	—	—	—	—	**0.87**	0.34	−0.12	—	—	—	**−0.52**	0.49	−0.03
MC	—	—	—	—	—	—	—	—	—	**−0.77**	0.06	0.56	—	—	—	—	—	—	—	—	—	—	—	—
% of variance	40.4	20.0	17.9	37.9	20.8	16.2	33.5	22.9	19.6	65.6	14.1	9.7	54.8	30.4	8.4	70.5	15.5	6.3	73.5	12.5	6.0	62.7	13.7	11.8
% total of variance	78.4			75			75.9			89.3			93.6			92.3			91.9			88.2		

Discussion

The relative seasonal pattern stability and homogeneity of ionic concentrations in the Valle de Bravo Basin may explain the similarity in species richness among the streams studied. According to Soininen et al. (2004), the most important variable explaining the differences among regions is the chemical composition of water, demonstrated in several diatom communities in fluvial systems (Winter and Duthie 2000, Soininen and Eloranta 2004, Cantonati and Spitale 2009). Our measured chemical compositions, water temperatures, and diatom richness were similar to those reported for other basins with headwaters in the MVB (Ramírez-Vázquez et al. 2001, Ramírez and Cantoral-Uriza 2003, Bojorge-García and Cantoral-Uriza 2007), which suggests a common flora for mountain streams of central Mexico.

Species common in tropical and subtropical streams of central Mexico, such as *Achnanthes inflata*, *Amphipleura lindehimeri*, *Cocconeis pediculus*, *Cymbella mexicana*, *Gomphonema angustum*, *Gyrosigma* sp., and *Navicula schroeterii* (Cantoral-Uriza et al. 1997, Montejano et al. 2000) also occurred in our study area. These occurrences may be related to (1) warmer waters in the streams studied than in other flowing waters of the MVB and (2) the presence of carbonates derived from Lower Cretaceous calcareous sediments and meta-sedimentary rocks formed of limestone, calcareous phyllite, carbonaceous phyllite, sercite phyllite, chlorite phyllite, and meta-graywacke, (Olvera-Viascan et al. 1998, Fitz-Díaz et al. 2008). These characteristics suggest that the Valle de Bravo Basin may represent a transition zone between a flora with temperate water/siliceous substratum affinities and a flora with warm water/carbonate substratum affinities.

We observed seasonal variations in some physical (substratum size, discharge, and temperature) and biological factors (richness and percent cover of macroscopic algae), which were related to community changes in epilithic and macroalgae-associated diatoms (Cantonati and Spitale 2009). A relationship between physical factors and diatom community structure has been described previously; relevant factors are substratum stability, discharge rate, and temperature, which act as significant environmental disturbance agents through yearly seasons. Nevertheless, in some cases, seasonal fluctuations in physical characteristics of a river may have only limited or no effect on the community (O'Quinn and Sullivan 1983, Rothfritz et al. 1997, Nautiyal and Singh 2000).

The small differences we found between the richness of epilithic and macroalgae-associated diatoms species suggest that these groups do not have substratum preferences; any observed differences may relate more to the varying abilities of individual species (e.g., *Rhoicosphenia abbreviata*, *Cocconeis placentula*, *Melosira varians*, and *Navicula shroeterii* in this study) to colonize different microhabitats. Differing colonization abilities may stem from different species physiological requirements, dependencies on habitat characteristics provided by macrophytes, and susceptibilities to dislodgement by rapid currents (Marker et al. 1986, Winter and Duthie 2000, Passy 2001, Antoniades and Douglas 2002, Soininen and Eloranta 2004).

Species particular to one type of substratum accounted for 25% of richness, were infrequent, and occurred at low abundances, such as *Epithemia turgida* whose distribution was restricted to the macroalgae-associated condition, and *Nitzschia microcephala*, which occurred only epilithically. Limitation of some species to a specific substratum may be determined by a differentiation in microenvironmental conditions that promotes higher nutrient concentrations in the preferred habitat than in surrounding waters (Burkholder 1996, Poulíčková et al. 2004).

Previous studies report *Achnanthidium minutissimum*, *Gophonema parvulum*, and *Navicula cryptotenella* as epilithic species occurring preferentially in waters with high current velocities (0.4–0.6 m s^{-1}; Rolland et al. 1997, Passy 2001). We found *Gophonema parvulum* and *Navicula cryptotenella* growing preferentially in high current velocities (up to 1.06 m s^{-1}), and these were most abundant in the macroalgae-associated condition. The same pattern was observed for other species, such as *Planothidium lanceolatum*, *Cocconeis placentula*, *Navicula capitatoradiata*, and *Reimeria sinuata*, suggesting that current velocity influences habitat preferences of species that move out of epilithic benthic environments to reduce the effects of hydrodynamic drag (Passy 2001, Cantonati and Spitale 2009). Macroalgae are ecosystem engineers that provide protection against drag and maintain a nutrient-rich environment around their leaf surfaces, which facilitates development of greater abundances of species (in comparison with epilithic abundances).

Interspecific facilitation, a process of positive interactions between species whereby one obtains benefits without harming the other (McCormick and Stevenson 1991, Bruno et al. 2003), is the likely mechanism that favors enhanced abundances of macroalgae-associated diatoms. The pattern we observed suggests a positive interaction between diatoms and macroalgae, with the diatom species acting as beneficiaries. This benefit may be generated by improved microenvironmental conditions in the habitats formed by macroalgal thalli (Burkholder 1996) and by elevated species diversity in these habitats. According to Cardinale et al. (2002), high diversity, leads to interspecific facilitation, which may promote efficiency of resource use and persistence under stressful conditions.

Diatoms and macroalgal communities are to some extent under the control of the same environmental factors in the Valle de Bravo Basin (Bojorge-García et al. 2010). The diversity of macroalgae-associated diatoms was related to macroscopic algal coverage; this effect was modified by disturbance caused by increased water flow. The abundance of macroalgae-associated species in all sites decreased during the rainy season, as is the case for benthic diatoms in other regions of the world (Aboal et al. 1996, Rolland et al. 1997, Comte and Cazaubon 2002, Cantonati and Spitale 2009). The increased abundance of epilithic diatoms in the rainy season at sites with low rates of flow may be explained by the submergence of otherwise emergent stone surfaces as the water column deepens; however, a low rate of flow ensures reduced water drag so that diatoms and stone surfaces are not likely to be swept away.

Although this combination of circumstances favors development of the epilithic community, seasonal changes in specific richness were not significant, suggesting that diatom communities in the Valle de Bravo Basin are adapted to grow under moderate disturbance. The low preferences for the epilithic versus macroalgae-associated condition may result from the ability of diatoms to move from one substratum to another over short distances (centimeters to meters) due to (1) current transport (Vannote et al. 1980), (2) an increment in macroscopic algal coverage comprising diverse morphological types that may provide refugia (Bojorge-García et al. 2010), and (3) potential dispersal by aquatic macroinvertebrates or vertebrates (Kristiansen 1996).

The diatom community of the Valle de Bravo basin is subjected to moderate environmental disturbance conditions, and it may represent a transitional community between warm and cold waters that is regulated primarily by changes in water volume and temperature. There was no clear substratum preference, possibly because species have had the capacity to colonize different substrata; however, the growth of macroalgae seems to enhance nutrient availability and reduce hydrodynamic disturbance, thus promoting greater abundances of diatom species. The proposed ecological mechanisms need to be confirmed through experimental work and field records in a shorter time scale

Acknowledgements

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