# Variable discharge alters habitat suitability for benthic algae and cyanobacteria in a forested Mediterranean stream

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**Abstract.** Large-scale algal community patterns can be understood by studying organisation within patches. Spatial heterogeneity in light and substratum type may affect the biomass and community composition of benthic algae and cyanobacteria. We compared the effects of these factors at the species level in two reaches differing in canopy cover in a forested Mediterranean stream in winter (high water flow) and late spring (low water flow). Partial redundancy analyses revealed that the major determinants of species distribution were strongly associated with variations in measured environmental variables. Light availability, the Reynolds number and substratum type were the main factors accounting for the algal and cyanobacterial distribution. Factors affecting algal distribution varied between hydrological periods, suggesting that some species had specific requirements whereas others had a wider tolerance to environmental conditions. Our results demonstrated that the hydraulic conditions (low velocity *v*. high velocity) influence small-scale heterogeneity in streams, and that this affects benthic community distribution.

Additional keywords: biovolume, Chlorophyll *a*, multivariate analysis.

# Introduction

The distributional patterns of biological communities are the result of a complex interplay of physical and biotic processes that operate over a wide range of spatial and temporal scales (Menge and Olson 1990). In stream ecosystems, water chemistry, light availability, variations in temperature, current velocity and/or substrata type induce spatial heterogeneity, as observed over a range of scales in the river system (Frissell et al. 1986). The variability of these environmental characteristics alters habitat suitability for stream algae, and this might be reflected in the algal community structure at the habitat scale (Walker et al. 1999; Cardinale et al. 2000). Light availability is the primary limiting factor for growth of the benthic algae in forested streams, whereas nutrients may be more relevant where the canopy cover is low (Hill and Knight 1988; Hill and Harvey 1990). Both in open and forested streams, water temperature and hydrological variation can modulate the metabolism of primary producers (Hill et al. 1995; Acuña et al. 2004; Uehlinger 2006). Because most streams have changing longitudinal patterns of canopy cover, stream-bed substratum or water velocities, algal communities are structured in mosaics of patches (Matthaei et al. 2003).

The variability of habitats and the implications for the structure of benthic algal communities have been reported in several studies. Variations in dissolved oxygen in a prairie

stream suggested spatial shifts across distances of decimetres or less (Kemp and Dodds 2001). Passy (2001) showed that the architecture of diatom patches on natural substrata depended on their location within the stream. Soininen (2003) reported significant spatial heterogeneity of diatom distribution at a scale of metres in a turbid Finnish river. At the patch scale, algae arrive from upstream reaches or from neighbouring patches as a result of continuous cell immigration. Hence, the algal community developing in a given patch is the result of cell settlement and attachment, the respective growth rates of the cells, the outcome of interaction with other algae and biota, and the response to random factors. However, the relative influence of environmental factors (that is, those that define the physical and chemical suitability of a given habitat for algal growth) on the spatial distribution of the taxa is not clearly established. The spatial distribution of communities within the stream is a result of the relative contribution of different factors (e.g. historical events, predation and competition) whose interaction often results in a complex spatial effect. Small-scale variation of environmental variables may be reflected by the spatial distribution of organisms (Pringle et al. 1988) and contributes to diversity maintenance in undisturbed natural systems.

Mediterranean streams are characterised by long periods of hydrological stability interrupted by floods or droughts (García et al. 2008; Sabater et al. 2008). Seasonality and variability in rainfall is the principal attribute of the Mediterraneantype climate (Gasith and Resh 1999). This climate is characterised by moderate to low rainfall, hot and dry summers and cool to cold winters. The seasonal patterns are relatively predictable (floods in late fall to winter, dry periods in summer), whereas interannual differences can be very large (Blondel and Aronson 1999; Gasith and Resh 1999; Sabater and Tockner in press). The Mediterranean hydrology is variable, with large floods in autumn and/or winter and severe droughts in summer (Butturini et al. 2003). As a result, streams may become intermittent or have intermittent reaches (Lake 2003). All these characteristics influence the stream biota and their interaction with the environment (Boulton 2003; Sabater and Tockner in press). Stream communities undergo an annual cycle where abiotic (environmental) forces dominate during high-discharge periods. When discharge declines, biotic (e.g. predation, competition) forces may become important; however, with drought or desiccation, abiotic regulation returns (Acuña et al. 2005).

In the present paper, we examined the distribution of algal communities in periods of higher discharge (winter) and lower discharge (late spring), two periods when light reaching the streambed also differed. We aimed to determine the factors affecting the microdistribution of biomass and the composition of benthic algal and cyanobacterial taxa under these different conditions. Because this was a field-based study, our underlying interest was to measure the fraction of species variation explained either by the environmental variables or by the spatial structure of the stream. We hypothesised that the physical heterogeneity in the stream (associated primarily with light availability and substratum type) affected the community composition of benthic algae and cyanobacteria, as well as their biomass distribution. Because of the hydrological variability of Mediterranean streams, we expected light and substratum type to be more important to algal community composition under conditions of higher water flow.

#### Material and methods

#### Sampling

Temporal and spatial patterns of benthic algae and cyanobacteria distribution were studied in winter (December) 2005 and late spring (May) 2006 in Fuirosos, a forested Mediterranean stream on the north-eastern Iberian Peninsula. During these periods, there were no sudden variations of water flow. Most of the watershed is forested with coniferous and some deciduous tree species. The streambed consists of alternating riffles and pools. Boulders and cobbles are the dominant substrata in riffles ( $\sim$ 60–70%), whereas sand accumulates in pools and littoral areas ( $\sim$ 30–40%). Branches and leaves are scattered on the streambed and accumulate mainly in riffle areas during periods of low water flow. The riparian vegetation is Platanus acerifolia, Populus nigra and Alnus glutinosa. Light incidence is modulated by the leaf canopy and the slope of the banks. Higher irradiance values occur in spring and winter (leafless period); minimum values are characteristic of summer  $(\sim 5-10 \,\mu\text{mol photons m}^{-2} \,\text{s}^{-1})$ , Acuña *et al.* 2004). Water flow was above the base-flow average in winter 2005  $(23.5 \text{ L s}^{-1})$  and extremely low  $(2.4 \text{ Ls}^{-1})$  in late spring 2006 (Sabater *et al.* 2008). Sampling was conducted in two reaches, differing in riparian cover, located  $\sim$ 200 m apart. The proportion of benthic substrata in these reaches is similar, comprising boulders and cobbles overlying sand and gravel.

Physicochemical variables were measured along three perpendicular transects in each of the two reaches. Transects were  $\sim 6 \text{ m}$ apart. Water depth, water velocity, incident light, pH, conductivity, percentage oxygen saturation, water temperature, chlorophyll fluorescence (F0), and substratum type were measured every 10 cm along each transect at a position as close as possible to the substrata (from 0.5 to 1 cm). The number of measurements in each transect ranged from 20 to 40, depending on its length. Conductivity, water temperature, percentage oxygen saturation and pH were measured with WTW meters (Wissenschaftlich-Technische Werkstätten, Weilheim, Germany). Incident light was measured with a Li-Cor quantum sensor (Li-192SB, Lincoln, NB, USA). Water velocity readings were taken with a current meter (MiniAir2 Schiltknecht 43221, Gossau, Switzerland) and depth at each position was measured with a ruler. Reynolds and Froude numbers were calculated from water velocity and depth. The Reynolds number quantifies the ratio of inertial to viscous forces within a fluid, and can be used to distinguish between less turbulent to laminar regimes (low Reynolds number) and turbulent flow (high Reynolds number). The Froude number represents the ratio of inertial forces to gravitational forces, and differentiates steady flow from turbulent flow, affecting the capacity of an organism to remain attached to a given substratum (Allan 1995). Substratum type was measured as a categorical variable according to the relative abundance of the different substratum types (rocks, sand and leaves) present in each 10 cm of the six transects, as follows: 1 = 100% rocks, 2 = 70% rocks and 30% sand, 3 = 70% rocks and 30% leaves, 4 = 100% sand, and 5 = 70% sand and 30% leaves.

Fluorescence in situ along each transect was measured with a pulse amplitude modulation (PAM) fluorometer (MINI-PAM, WALZ, Effeltrich, Germany). The PAM method determines chlorophyll fluorescence, which may vary between a quasi-dark level (F0), when all Photosystem II reaction centres are open, and a maximal level (Fm), when all these centres are closed (Schreiber et al. 2002). Therefore, F0 gives an estimate of Chlorophyll a (Chl a) content (Geel 1997). Fifteen periphyton samples were selected from the six transects on the basis of the F0 range of values recorded previously every 10 cm along each transect, and used to extract Chl a in the laboratory. Chl a samples were collected following Stockner and Armstrong (1971), rinsed in distilled water and transported to the laboratory. Suspended material was retained in GF/F filters (0.7-µm pore size), which were then wrapped in aluminium foil and frozen until analysis. Chl a was estimated from spectrophotometric readings (U-2000, Spectrophotometer; Hitachi, Japan) following Jeffrey and Humphrey (1975). These measurements were compared with their respective F0 values, and the calibration curve between the two parameters was used to transform the values for F0 measures along the transects to Chl a (n = 15,  $r^2 = 0.64, P < 0.001$ ) for the final estimates of algal biomass.

Because it was not feasible to sample algal community composition for all identified spots (177 in winter and 141 in late spring), the physical variables (light, temperature, water depth) and the F0 measured in the field in each transect were used to stratify areas to be sampled in every transect. Within those areas, different spots were selected randomly, and benthic algae and cyanobacteria were collected in up to seven spots per transect, with a total of 42 samples per sampling period.

Samples for water chemistry were collected following the same criteria as for the algal samples. Water samples were passed through Whatman Nylon membrane filters with a pore diameter of  $0.2 \,\mu\text{m}$  in the field. Samples were then stored at 4°C and frozen in the laboratory until analysis. Nitrate was analysed by ion-chromatography (Metrohm Ltd, Herisau, Switzerland). Phosphate concentration was measured by the method described by Murphy and Riley (1962). Ammonium was analysed following HACH (1992).

#### Algae collection and analysis

Benthic algae and cyanobacteria were sampled only from hard substrata, rocks and sand. Leaves were not sampled because they never were an abundant substratum in any of the spots. Rocks were sampled using a brush-syringe system adapted from Stockner and Armstrong (1971). Sandy samples were collected by coring an area of  $\sim$ 2-cm depth with a syringe. Sand surface area was estimated after applying a conversion factor obtained by granulometry (Artigas *et al.* 2004). These methods allowed the collection of the samples without alteration of the stream bottom. The sample retained in the brush or in the syringe was rinsed in 5 mL of river water (not filtered) and preserved in 4% formaldehyde until analysis.

Each algal sample was partitioned for the taxonomic analysis of diatom and non-diatom algae, and cyanobacteria. Diatom frustules were cleaned from organic material with sulfuric acid, dichromate potassium, and hydrogen peroxide. Quantitative slides were prepared using Naphrax (r.i. 1.74; Brunel Microscopes Ltd, Chippenham, Wiltshire, UK). At least 400 valves were counted on each slide by using random fields under light microscopy. A Nikon Eclipse E600W light microscope (Nikon, Tokyo, Japan) equipped with Nomarski differential interference contrast optics at a magnification of ×1000 was used for diatom counts. Taxa were identified following mainly Krammer and Lange-Bertalot (1991–1997), and Lange-Bertalot (2001). By using Kann (1978) and Sabater (1987), non-diatom algae and cyanobacteria were identified under light microscopy (Nikon Eclipse E600W) at a magnification of ×1000. However, large algal species were counted at lower magnification. This algal fraction was determined after counting 50 random microscope fields per aliquot.

#### Biovolume calculation

Algal and cyanobacterial biovolume was calculated following Hillebrand *et al.* (1999), after measuring at least 10 randomly selected individuals of each taxon. The biovolumes of species not included in Hillebrand *et al.* (1999) were calculated by the best fit of the cells to geometrical models. In the case of the red alga *Lemanea* sp., cell counts were not possible and the volume was calculated for the entire thalli at ×40. For *Cladophora glomerata* mats, the extended filaments present in microscopic fields at ×40 were used to calculate the biovolume. In all cases, biovolume was expressed as  $\mu m^3 cm^{-2}$ .

#### Data analysis

Model II linear regression (geometric mean regression) using SPSS for Windows (version 14.0.1, SPSS, Chicago, IL, USA) was conducted to analyse the relationship between F0 and Chl *a* because both variables were measurements with errors (Sokal and Rohlf 1995). Environmental data (water depth, water velocity, Reynolds number, Froude number, conductivity, incident light, percent oxygen saturation, water temperature, ammonium concentration, phosphate concentration and nitrate concentration) and Chl *a* were analysed with analysis of variance (MANOVA, SPSS for Windows, version 14.0.1, SPSS, Chicago, IL, USA) to test for significant differences between seasons (sampling period), shading (reach) and substrata types.

Biovolume data of the algae and cyanobacteria were analysed by detrended correspondence analysis (DCA) (Hill and Gauch 1980) to determine the length of the gradient for the first two axes. DCA revealed that the gradient length was shorter than 3 standard deviation units; therefore, linear ordination techniques were more appropriate (Lepš and Šmilauer 2003). Consequently, redundancy analysis (RDA) was used to select predictors that best explained the variance in the algal data in each sampling period (ter Braak and Šmilauer 2002). Partial RDAs were then used to examine the relative importance of two groups of explanatory variables for the species data. Two groups of explanatory variables (environmental data and spatial data) were used for the constrained analyses (Borcard et al. 1992). Environmental data included in the analyses were substratum type, water depth, water velocity, Reynolds number, Froude number, conductivity, incident light, percentage oxygen saturation, water temperature, ammonium concentration, phosphate concentration and nitrate concentration.

Spatial data were generated by a polynomial trend surface regression equation on the x (along the stream) and y (across the stream) coordinates of the position in the space occupied by the samples within each transect (Borcard *et al.* 1992; Legendre and Legendre 1998). A third-order polynomial regression was applied to ensure not only the extraction of the linear gradient patterns in species data, but also more complex features such as patches or gaps, which require correct description of the quadratic and cubic terms of the coordinates, and their interactions (Borcard *et al.* 1992).

The two groups of explanatory variables (environmental and spatial) were submitted to a stepwise forward selection procedure in which the statistical significance of each variable was tested by the Monte Carlo permutation test (999 permutations) at a cut-off point of P = 0.05. Probabilities for multiple comparisons were corrected using Bonferroni correction. Collinear variables were identified on the basis of inspection of variance inflation factors (VIF < 20) (ter Braak and Verdonschot 1995). After that, variation partitioning was conducted in several steps, as follows: (1) RDA of the species matrix constrained by the environmental matrix; (2) RDA of the species matrix constrained by the spatial matrix; (3) partial RDA of the species matrix constrained by the environmental matrix and with the spatial matrix as covariables; and (4) partial RDA of the species matrix constrained by the spatial matrix and with the environmental matrix as covariables.

Taxa biovolumes with a relative proportion > 3% occurring in more than one sample were included in the analyses. Taxa biovolumes were logarithmically transformed before analyses. Environmental data (except pH, percentage oxygen saturation and substratum type, expressed as a dummy variable) were logarithmically transformed before analyses to reduce skewed distributions. Analyses of biovolume were performed on algae (diatom and non-diatom algae) and cyanobacteria. PCA, RDA and partial RDA were undertaken using CANOCO for Windows (Version 4.5, Microcomputer Power, Ithaca, NY, USA).

#### Results

#### Site characterisation

The environmental variables (Table 1) differed significantly in winter and in late spring, except for water velocity and Froude number (respectively, ANOVA,  $F_{1,302} = 0.211$ , P = 0.639; and  $F_{1,302} = 0.280, P = 0.597$ ). These findings showed that the data required separate analysis per period. Variables were tested separately in each sampling period for significant differences between reach and substrata type (Table 2). In winter, differences between the shaded and the unshaded reaches were due to light availability, water temperature, and ammonium and phosphate concentrations. In late spring, significant differences between the reaches were detected in water depth, incident light, Reynolds number, percentage oxygen saturation and ammonium concentration. Incident light, percentage oxygen saturation and Reynolds number differed with respect to substratum type in winter, although only depth was significantly different between the substratum types in late spring (Table 2).

### Chlorophyll distribution

The Chl *a* (surrogate of F0) values significantly differed between the substratum types only in winter (Table 2). Estimated Chl *a* ranged from 0 to 2.8  $\mu$ g cm<sup>-2</sup> in the unshaded reach, and from 0 to 2.6  $\mu$ g cm<sup>-2</sup> in the shaded one during winter. In late spring, Chl *a* ranged from 0 to 2.9  $\mu$ g cm<sup>-2</sup> in the unshaded reach, and from 0 to 2.3  $\mu$ g cm<sup>-2</sup> in the shaded one (Fig. 1*a*). Chl *a* in winter ranged from 0 to 2.8  $\mu$ g cm<sup>-2</sup> on sand and from 0 to 2.6  $\mu$ g cm<sup>-2</sup> on rock. In late spring, maximum Chl *a* reached 0.6  $\mu$ g cm<sup>-2</sup> on sand and 2.9  $\mu$ g cm<sup>-2</sup> on rock (Fig. 1*b*).

## Spatial distribution of taxa biovolume

Dermocarpa kerneri, Nitzschia dissipata and Chantransia stage made up  $\sim 60\%$  of total algal biovolume in winter, whereas Lemanea sp., Spirogyra sp. and Cladophora glomerata accounted for 81% of the total algal biovolume in late spring. Most of the winter biovolume comprised *N. dissipata*, *Melosira varians* and *Fragilaria ulna* in the unshaded reach, and *D. kerneri* and *Chantransia* in the shaded reach. In late spring, *Spirogyra* sp. and *C. glomerata* prevailed in the unshaded reach, whereas *Lemanea* sp. alone contributed 91% of the biovolume in the shaded reach.

The maximum biovolumes for most of the species occurred in the unshaded reach. F. ulna, Navicula gregaria, M. varians, Nitzschia palea and N. dissipata characterised the unshaded habitats in winter, whereas Fragilaria ulna var. acus, F. ulna, Cocconeis pediculus and N. dissipata dominated these spots in late spring. D. kerneri typified shaded habitats in winter, whereas Lemanea sp. accounted for most of the biovolume in late spring. D. kerneri, Gongrosira debaryana and Nitzschia linearis accounted for the highest biovolume in rocky habitats, whereas Cocconeis placentula, C. pediculus, Fragilaria biceps and Phormidium sp. were the most abundant in sandy habitats in winter. In late spring, G. debaryana, Homoeothrix sp., Pleurocapsa minor and Oedogonium sp. occupied rocky habitats, whereas F. biceps was typical of the communities in sandy habitats.

#### Variation partitioning of biovolume

Redundancy analysis with forward selection showed that Reynolds number, incident light, water temperature and substratum type were the environmental variables most associated with the winter biovolume of the taxa. Partial RDA showed that these environmental variables accounted for 15.7% of the total variation (Fig. 2*a*). In late spring, Reynolds number, percentage oxygen saturation, incident light and conductivity were statistically significant in RDA, accounting for 14.6% of the total variation in partial RDA (Fig. 2*b*). The spatial position of the taxa (spatial variation, not shared by the environmental variation) accounted for 6.4% of total variation in winter and 4.3% in late spring in partial RDA. Up to 6.1% of the variation in algal data was shared between the environmental and spatial variables in winter, whereas in late spring, the percentage shared increased to 9.8%.

#### Environmental preferences of the species

The RDA indicated that the biovolume distribution of several taxa was related mostly to the environmental variables

Table 1.	Mean values (s.e.) of physica	l and chemical variables fo	or the reaches studied each	sampling period
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Environmental variable	W	inter	Late	spring
	Unshaded reach	Shaded reach	Unshaded reach	Shaded reach
Water depth (cm)	22.39 (0.67)	18.57 (0.81)	5.95 (0.47)	9.08 (0.55)
Water velocity $(m s^{-1})$	0.02 (0.00)	0.07 (0.01)	0.02 (0.00)	0.02 (0.00)
Conductivity ( $\mu$ S cm <sup>-1</sup> )	187.52 (0.04)	198.39 (0.75)	231.17 (0.10)	229.23 (0.09)
Oxygen (%)	112.17 (1.38)	107.48 (1.04)	96.76 (0.43)	89.36 (0.45)
Water temperature (°C)	5.07 (0.12)	2.87 (0.03)	15.92 (0.16)	15.84 (0.12)
$NH_{4}^{+}-N(\mu g L^{-1})$	224.78 (10.73)	154.01 (21.49)	11.27 (2.36)	18.52 (3.57)
$PO_4^{3-}-P(\mu g L^{-1})$	7.72 (0.32)	11.92 (0.69)	5.35 (0.17)	5.92 (0.27)
$NO_{3}^{-}-N(\mu g L^{-1})$	259.69 (31.46)	364.30 (22.71)	33.31 (1.68)	41.34 (1.67)
Chl $a (\mu g \text{ cm}^{-2})$	0.53 (0.07)	0.69 (0.08)	0.56 (0.07)	0.44 (0.06)
Light ( $\mu$ mol photons m <sup>-2</sup> s <sup>-1</sup> )	45.31 (2.02)	27.30 (0.49)	957.15 (57.08)	79.05 (7.49)
Reynolds number	3747.51 (405.66)	9197.99 (1869.55)	914.52 (102.23)	1756.31 (453.46)

Table 2.	<b>ANOVA</b> results	s for each of the	e variables tested	after the MAN	OVA analysis, c	considering singl	e source effect:	s and interacti	ions of the two f	actors, reach (	R) and substr	atum type (S)
P-values <	<0.05 are indicate	ed in boldface ty	ype. The results con	me from all the n were measured	neasurements ma l in only seven sa	ide for each varial impled spots per	ole in each of tra transect (see tex	ansects (20–40) «t for details)	), except for nutri	ients (nitrate, pł	tosphate and ar	nmonium) that
Source	Depth	Velocity	Conductivity	Light	Oxygen	Temperature	Reynolds	Froude	Chl a	NH <sup>+</sup> <sub>4</sub> -N	$PO_4^{3-}$ -P	NO <sup>-</sup> -N
Winter												
R	$F_{1,171} = 0.647$ P = 0.427	$F_{1,171} = 0.933$ $P = 0.335$	$F_{1,171} = 154.587$	$F_{1,171} = 27.128$	$F_{1,171} = 0.743$ P = 0.390	$F_{1,171} = 99.590$	$F_{1,171} = 0.128$ P-0771	$F_{1,171} = 0.922$	$F_{1,171} = 0.315$ P = 0.575	$F_{1,38} = 5.304$ P = 0.027	$F_{1,38} = 18.281$	$F_{1,38} = 2.648$ P = 0.112
$\mathbf{N}$	$F_{3,171} = 1.077$	$F_{3,171} = 3.783$	$F_{3,171} = 3.913$	$F_{3,171} = 15.788$	$F_{3,171} = 3.962$	$F_{3,171} = 4.820$	$F_{3,171} = 8.067$	$F_{3,171} = 2.809$	$F_{3,171} = 25.104$	$F_{1,38} = 0.106$ $B_{-0.746}$	$F_{1,38} = 2.142$	$F_{1,38} = 0.001$ $B_{-0.077}$
$\mathbf{R}\times\mathbf{S}$	F = 0.500 $F_{2,171} = 2.646$ P = 0.074	$F_{2,171} = 2.595$ P = 0.078	F = 0.010 $F_{2,171} = 5.285$ P = 0.006	$F_{2,171} = 1.142$ P = 0.322	$F_{2,171} = 1.272$ P = 0.283	$F_{2,171} = 0.016$ P = 0.984	$F_{2,171} = 0.981$ P = 0.377	F = 0.041 $F_{2,171} = 2.453$ P = 0.089	$F_{2,171} = 0.461$ P = 0.631	$F_{1,38} = 0.740$ $F_{1,38} = 0.014$ P = 0.907	F = 0.152 $F_{1,38} = 0.029$ P = 0.866	F = 0.977 $F_{1,38} = 0.975$ P = 0.330
Late spring												
К	$F_{1,131} = 10.467$ P = 0.002	$F_{1,131} = 0.635$ P = 0.427	$F_{1,131} = 50.356$ <b>P &gt; 0.001</b>	$F_{1,131} = 79.528$ P > 0.001	$F_{1,131} = 52.016$ <b>P &gt; 0.001</b>	$F_{1,131} = 5.423$ P = 0.021	$F_{1,131} = 9.873$ P = 0.002	$F_{1,131} = 0.003$ P = 0.958	$F_{1,131} = 1.660$ P = 0.200	$F_{1,38} = 8.392$ P = 0.006	$F_{1,38} = 2.746$ P = 0.106	$F_{1,38} = 2.020$ P = 0.163
S	$F_{4,131} = 4.506$ P = 0.002	$F_{4,131} = 0.468$ P = 0.759	$F_{4,131} = 3.793$ P = 0.006	$F_{4,131} = 0.428$ P = 0.788	$F_{4,131} = 1.253$ P = 0.292	$F_{4,131} = 2.269$ P = 0.065	$F_{4,131} = 1.980$ P = 0.101	$F_{4,131} = 0.809$ P = 0.522	$F_{4,131} = 1.895$ P = 0.115	$F_{1,38} = 0.677$ P = 0.416	$F_{1,38} = 5.945$ P = 0.020	$F_{1,38} = 0.118$ P = 0.733
$\mathbf{R}\times\mathbf{S}$	$F_{4,131} = 1.153$ P = 0.335	$F_{4,131} = 0.446$ P = 0.775	$F_{4,131} = 2.748$ P = 0.031	$F_{4,131} = 3.909$ P = 0.005	$F_{4,131} = 1.638$ P = 0.169	$F_{4,131} = 5.918$ <b>P &gt; 0.001</b>	$F_{4,131} = 1.359$ $P = 0.252$	$F_{4,131} = 0.637$ P = 0.637	$F_{4,131} = 0.437$ P = 0.782	$F_{1,38} = 3.743$ P = 0.061	$F_{1,38} = 0.168$ $P = 0.685$	$F_{1,38} = 1.706$ P = 0.199



**Fig. 1.** (*a*) Chl *a* values in winter (W) and late spring (S) for the two reaches, unshaded (U) and shaded (S). (*b*) Chl *a* values of winter (W) and late spring (S) for the two substratum types, sand (Sd) and rocks (R). Boxes represent the median, and 25th and 75th quartiles.

(Table 3). Amongst these, Navicula gregaria, Gongrosira debaryana, Cymbella tumida, Achnanthes biasolettiana, Diatoma vulgaris, Nitzschia recta, Melosira varians and Achnanthes minutissima had their distributions mostly explained by environmental variables in winter. Fragilaria biceps, Cocconeis pediculus, Pleurocapsa minor, Lemanea sp. and Cladophora glomerata were the species most related to the environmental variables in late spring (Table 3). In contrast, the biovolume variation of Amphipleura pellucida, Chantransia stage, Cocconeis placentula, Fragilaria ulna, Gomphonema pumilum and Lyngbya sp. was explained both by the environmental and spatial variables in winter (Table 3). A. minutissima, Gomphonema clavatum, M. varians and Oedogonium sp. were species affected by both the environment and space in late spring. None of these taxa was related only to the spatial variables.

# Discussion

# *Relative contribution of environmental variables to stream habitat heterogeneity*

Several environmental variables (i.e. temperature, substratum type, light, local hydraulic conditions) explained most of the variation of the biovolume distribution in the stream in the two



**Fig. 2.** Partial redundancy analysis results in the ordination space of the first and second axes. Ordination of the biovolumes of algae and cyanobacteria in (*a*) winter and (*b*) late spring. Taxa codes are given in Table 3.

different hydrological periods. The position of samples (expressed in the spatial matrix in our study) indicates unmeasured underlying processes that contribute to contagious distribution. These include the settlement of the cells and/or stochastic factors that do not have a direct relationship with the environmental variables included in the analyses. The spatial distribution of the algal and cyanobacterial taxa in the stream was only weakly related to the factors associated to dispersion in the reach and settlement on the substrata. Even so, the amount of unexplained variation was high, probably owing to the local effects of unmeasured (biotic and abiotic) variables or to spatial structures that were overlooked because they require the description of more complex functions (Borcard *et al.* 1992).

# Environmental determinants of the distribution of stream benthic algae and cyanobacteria

As there was a relatively homogenous chemical environment in the Fuirosos stream, physical variables (temperature, light, flow, substrata type) were those varying spatially and thus primarily determined the distribution and abundance of the benthic algae. Physical variations were more marked than chemical variations at the habitat scale. Chemical water quality varies slightly within a stream reach (Soininen 2004), and may govern the distribution of algae and cyanobacteria mostly at the largest spatial scales (e.g. Tornés *et al.* 2007).

In terms of hydraulic conditions, most of the species were associated with the least turbulent habitats (lower Reynolds number) in the two periods. The optimum current in lownutrient habitats is probably lower than that in high-nutrient habitats (Stevenson 1996). However, some of the algal taxa (Cladophora, Lemanea) were more abundant in turbulent flow (higher Reynolds number) habitats. These taxa withstand the drag of current (Stevenson 1996; Sheath 2003), their growth being favoured by turbulent flow. Filamentous algae (e.g. Spirogyra) not having basal attachment cells are not able to maintain filaments in fast currents. However, Cladophora and Lemanea are tightly attached and can withstand drag and accumulate great biomass in fast currents (Stevenson 1996). The drag of current mostly affects larger algae, because small cells may be within the boundary layer where frictional forces between water and substratum slow the flow (Silvester and Sleigh 1985). However, algal mats can modify local current regimes and slow down near-substratum velocities as a function of the community growth form and architecture (Dodds and Biggs 2002). The substratum roughness may also lessen the current effects on algal detachment (Biggs et al. 1998).

Accordingly, the importance of substratum type in algal distribution in the Fuirosos was higher during the period of high flow (winter). The physical properties of substrata affect the development of benthic algae (Burkholder 1996; Bergey 2005; Murdock and Dodds 2007); however, this mostly occurs because the higher flow is associated with higher hydraulic heterogeneity in the system (Brown 2007). The higher occurrence of Cocconeis pediculus and C. placentula on sand grains is related to their prostrate growth form. Prostrate taxa are nonmotile forms that adhere tightly in spite of the constant movement of the sand grains (Miller et al. 1987). Rosette-forming diatoms such as F. biceps use flexible mucilage pads to adhere strongly to the substrata and can colonise sand grains. The growth form of mucilage pads provides elongate shapes with a relatively large surface area available for attachment (Steinman and McIntire 1986). Taxa found on sand grains are mostly pioneer species, typically observed during early stages of succession (Miller et al. 1987; Sekar et al. 2004). Diatom taxa such as Nitzschia linearis, filamentous green algae (e.g. Gongrosira debaryana and Oedogonium sp.) and cyanobacteria (e.g. Homoeothrix sp. and Pleurocapsa minor) comprise late-phase communities (Sabater 1989; Sekar et al. 2004). Large stable substrata such as rocks, resisting even fast-flowing conditions, seem to be important for the establishment of mature benthic communities. Conversely, sand is easily moved by the current and taxa living on this substratum must be tightly fastened and capable of rapid colonisation.

Light governs photosynthesis (Hill 1996), and in the Fuirosos this factor determines changes in algal biomass and taxonomic composition between seasons (Veraart *et al.* 2008). Our study revealed that during the period of low flow (late spring), light was one of the most important factors determining the

#### Table 3. Results of the partial redundancy analyses (RDA) with forward selection of the variables

The table shows the percentage of variance explained by environmental and spatial variables with respect to the total variance and the percentage of total biovolume of each taxa

Taxon	Code		Winter			Late sprin	ng
		Fraction of varianc	total e	Fraction of total biovolume	Fraction of varianc	total e	Fraction of total biovolume
		Environment	Space		Environment	Space	
Achnanthes biasolettiana Grunow	abia	20.82	1.46	0.19			
Achnanthes minutissima Kützing	amin	15.67	1.49	0.75	15.31	16.66	0.65
Amphipleura pellucida Kützing	apel	16.66	14.93	0.41			
Amphora ovalis (Kützing) Kützing	aova	34.87	20.69	0.08			
Chantransia stage	chan	3.81	2.88	11.69			
Cladophora glomerata (Linnaeus) Kützing	cglo				15.39	1.58	7.97
Cocconeis pediculus Ehrenberg	cped	25.19	6.68	0.78	39.55	0.91	0.31
Cocconeis placentula Ehrenberg	cpla	12.11	10.44	1.06	14.87	4.74	0.29
Cymbella tumida (Brébisson) Van Heurck	ctum	29.64	1.79	0.37	14.61	6.70	0.15
Dermocarpa kerneri (Hansgirg) Bourrelly	dker	25.52	7.25	27.77	8.07	4.75	0.75
Diatoma vulgaris Bory	dvul	6.39	0.48	0.08			
Fragilaria biceps (Kützing) Lange-Bertalot	fbcp	6.97	2.11	3.87	33.45	0.63	3.06
<i>Fragilaria capucina</i> Desmazières var. <i>capitellata</i> (Grunow) Lange-Bertalot	fccp				27.41	4.27	0.30
Fragilaria ulna (Nitzsch) Lange-Bertalot	fuln	8.15	10.59	4.25	7.77	12.51	2.95
Fragilaria ulna (Nitzsch) Lange-Bertalot var. acus (Kützing) Lange-Bertalot	fuac	0.110	10107	1120	34.91	6.49	1.03
Gomphonema clavatum Ehrenberg	gela				8 58	6 78	0.10
Gomphonema pumilum (Grunow)	gnum	12.76	12.14	0.08	12.48	2.61	0.16
Reichardt & Lange-Bertalot	Spuill	12170	12111	0100	12.10	2101	0110
Gomphonema truncatum Ehrenberg	gtru	1.05	3.10	0.09			
Gongrosira debaryana Rabenhorst	gdeb	22.36	1.17	2.24	7.87	0.94	0.19
Homoeothrix sp.	homo				2.50	4.06	0.02
Lemanea sp.	lema				7.48	0.68	41.64
Lyngbya sp.	lyng	6.28	6.01	1.06			
Melosira varians Agardh	mvar	14.57	1.14	5.76	8.35	11.95	2.97
Navicula gregaria Donkin	ngre	20.14	0.94	0.58			
Nitzschia dissipata (Kützing) Grunow	ndis	10.40	4.57	19.78	12.93	4.10	0.58
Nitzschia linearis (Agardh) W. Smith	nlin	13.52	8.55	0.73	6.14	2.88	0.12
Nitzschia palea (Kützing) W. Smith	npal	15.25	2.35	0.44			
Nitzschia recta Hantzsch in Rabenhorst	nrec	15.28	1.19	1.93			
Oedogonium sp.	oedo	11.06	7.31	4.04	5.16	7.24	2.34
Phormidium sp.	phor	7.80	13.44	0.19			
Pleurocapsa minor Hansgirg	pmin	19.88	2.90	0.72	4.60	0.32	0.26
Rhoicosphenia abbreviata (C. Agardh) Lange-Bertalot	rabb	7.11	3.35	0.45			
Spirogyra sp.	spir				19.32	7.44	31.51

distribution of algal biovolume. Diatoms, which contributed most of the biovolume in winter and late spring, were more abundant in the unshaded sectors. Light limitation inhibits the development of diatoms (Kawecka 1986; Lowe *et al.* 1986; Robinson and Rushforth 1987). Filamentous green algae (e.g. *Cladophora glomerata* and *Spirogyra* sp.) also became abundant in unshaded habitats, whereas red algae (e.g. *Lemanea* sp.) and colonial cyanobacteria (e.g. *Dermocarpa kerneri*) proliferated at low-light conditions. Filamentous green algae increase in stream sections with high incident light (Shortreed and Stockner 1983; Lowe *et al.* 1986) whereas cyanobacteria grow best under irradiances of  $< 50-100 \,\mu$ mol photons m<sup>-2</sup> s<sup>-1</sup> (Steinman *et al.* 1989). However, the relative proportion of filamentous taxa increases when light energy is elevated (Duncan and Blinn

1989). Prostrate cyanobacteria (predominant in the Fuirosos stream) may have physiological mechanisms that allow them to persist under low-light conditions below benthic algal mats (Hill 1996). Freshwater Rhodophyta are adapted to low light and most exhibit low saturation levels of illumination for photosynthesis ( $35-400 \mu$ mol photons m<sup>-2</sup> s<sup>-1</sup>) (Sheath 2003). Likewise, members of Lemaneaceae occur more frequently at low irradiance (Mullahy 1952; Thirb and Benson-Evans 1983).

The relative importance of environmental factors on the distribution of stream periphyton shifted seasonally as observed by Rosemond *et al.* (2000). As an example, *Achnanthes minu-tissima* and *Melosira varians* were ubiquitous in late spring during the homogenous hydraulic conditions governing the period of low flow. However, in winter (when the hydraulic

heterogeneity was higher), their abundance was explained mostly by light incidence. Our results suggest that some taxa have specific requirements and occur only under certain environmental conditions, whereas others are more tolerant. This assertion is made with caution because only two time periods were available for analysis.

## Conclusions

Habitat heterogeneity associated with environmental variability is likely the major driver of community diversity in lotic systems and is expressed at the substrata scale (Bergey 2005; Murdock and Dodds 2007) and the reach scale (Passy 2001; Matthaei *et al.* 2003). Our results also demonstrated that the hydrological condition (low flow v. high flow) is a factor controlling the effects of small-scale heterogeneity in streams (Ledger *et al.* 2008). A consequence from our study is that the increased homogenisation of natural habitats (mostly related to human intervention) is directly related to lower diversity of algal communities. Although the findings of the present study cannot be directly extrapolated to large-scale algal and cyanobacterial community patterns (Wilson and Dodds 2009), joint analyses at the small and large scale can provide further insights into algal distribution.

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