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Influence of environmental variables on benthic algal associations from selected extreme environments in Slovenia in relation to the species identification

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Abstract

Background and Purpose: *Algal species composition, relative abundance and environmental factors were studied. The aim of the research was to identify indicator species and characteristic associations for specific environmental conditions.*

Materials and Methods: *Species composition and the distribution of benthic algal taxa were established at 30 sampling sites in selected extreme environments in Slovenia. Algal samples were collected two to four times at each sampling site during different seasons in 2005 and 2006.*

Results and Conclusions: *In total, 603 algal taxa were identified of 138 genera and 10 classis. Given the number of identified taxa, diatoms were prevailing at 29 sampling sites.* Achnanthes minutissima *was the most widespread species.* Nitzschia frustulum, Enteromorpha intestinalis, Diploneis didyma *and* Phormidium formosum *are the indicator species of the environments with a particularly high electric conductivity.* Gomphonema angustatum, Meridion circulare, Cocconeis placentula, Nitzschia palea, Gomphonema parvulum *and* Cymbella silesiaca *are the indicator species of the environment at alkaline pH and standing waters.* Eunotia bilunaris, E. exigua, E. implicata, Achnanthes flexella, Pinnularia subcapitata *and* Spirogyra *spp. are the indicator species of the environment at acidic pH. The canonical analysis was carried out for 27 sampling sites where algae were sampled and environmental variables assessed. We explained 21% of the variability of classis, 19% of the variability of genera. and 17% of the variability of species (taxa). In relation to the size of the explained variability of environmental variables, it was found out that the factor at the level of species (taxa), which had a decisive influence on the distribution of algae in selected habitats, was the geological substrate (silicate), the water pH at the level of genera and the velocity of water flow at the level of classis.*

INTRODUCTION

Algae inhabit widely different environments. Due to their undemanding nutritional habits, simple structure, fast growth and both sexual and asexual reproduction algae have a great capacity of adapting to extreme ecological conditions. Algae are often found in the environments where other organisms cannot survive *(1, 2)*. Cyanobacteria, in particular, have the ability to colonize a wide range of environments, including very extreme environments (e.g. thermal springs where the

water temperature reaches up to 80°C, stones in extremely hot or cold deserts, both in the Tropics and in the Antarctic, lakes and marshes with high salinity, biotopes in volcanic areas, etc.) Their survival capacity and species diversity can most probably be attributed to their ability to adapt to various ecological conditions *(3)*.

Owing to geographic diversity, a relatively lower level of pollution than elsewhere in Europe and fewer activities affecting the environment, Slovenia has a very large number of extreme environments (peat bogs, oxbows, springs, waterfalls, brackish waters); however, algae have been only partly researched in spite of their high biodiversity.

The distribution and species composition of algal communities and the relative abundance of individual algal taxa depend to a large extent on the physical and chemical factors of water that vary in relation to geological substrate *(4)*. Electrical conductivity, pH, calcium content and the carbonate-bicarbonate system have a major impact on the development and structure of algal communities, affecting particularly the development and structure of diatom and desmid communities *(5)*. Spatial and time changes of physical and chemical factors affect the occurrence and relative abundance of individual algal species and thus have an impact on the specific composition of algal communities *(6)*.

In this study, the algal species composition, relative abundance, and environmental factors were studied. The aim of the research was to identify indicator species and characteristic associations for specific environmental conditions. Direct gradient analysis allowed us to study a part of the variation in community composition at different species identification that can be explained by a particular set of environmental variables.

MATERIALS AND METHODS

Qualitative samples of benthic algae were taken in different seasons in 2005 and 2006 at 30 sampling sites (2–4 times at each sampling site) (Table 1). The samples were brushed from the surface of stones, rocks, macrophytes and squeezed out of water mosses. At the same time, the water temperature, pH, conductivity, dissolved oxygen, saturation and salinity were measured at 27 sampling sites by the WTW Multiline/F meters. At sampling sites 10, 15 and 21, physical and chemical parameters were not measured due to insufficient amount of water to perform measurements.

For identification we followed *(7-32)*. Most taxa were identified directly from living material. Some samples were first fixed with 4% formaldehyde and then analyzed for taxa identification. The diatoms were examined after preparation according to Schaumburg et al. *(33)*. Light microscopes Nikon Eclipse E400 and Nikon Eclipse TE300 and magnification 1000x were used to determine the taxa. The relative abundances of algal taxa were estimated by numbers 1, 3 and 5 (1-single, 3-customary, 5-dominant) *(34)*. The determination of algal taxa and estimation of relative abundances were performed by the same person.

A cluster analysis comparing sites (Bray-Curtis coefficient of similarity) and TWINSPAN analysis *(35)* were performed on the matrix of relative abundance estimations. Both analyses were performed on 106 samples from all 30 sampling sites. TWINSPAN analysis was performed for two reasons: (a) for the determination of sample groups and (b) for the description of groups by characteristic species.

Relative abundance estimations and environmental data (Table 1) were analyzed by canonical corresponding analysis (CCA) using the programme CANOCO for Windows 4.5 *(36)*. The CCA analysis was performed on 94 samples from 27 sampling sites. The CCA analysis was implemented at three levels: at the level of species (taxa matrix), at the level of genera (genera matrix) and at the level of classis (classis matrix). The matrix of environmental variables included ten variables (pH, electric conductivity, shading, water flow, saturation, salinity, water temperature, dissolved oxygen, silicate and limestone) (Table 1). We did not use any transformation of environmental and species data.

RESULTS

During the research, a total number of 603 algal taxa of 138 genera and 10 classis were identified; most of them belonged to diatoms (62%), followed by Cyanobacteria (14%). Diatoms prevailed at 29 of 30 sampling sites. For a detailed taxonomic result see *(37)*. *Achnanthes minutissima* Kützing was the most widespread species; it was present at 29 of 30 sampling sites.

The cluster analyses (Bray-Curtis coefficient of similarity) based on the relative abundance estimation of algal data resulted in 8 groups (data not shown) revealing spatial differences.

The TWINSPAN analysis between the sites based on the relative abundance estimations of algal data resulted in 7 groups and 16 indicator species (Figure 1). Group I includes the samples from the constructed wetland; Groups II and III cover brackish sampling sites; Group IV incorporates all sampling sites with running water on limestone substrate; the sampling sites with still or slow running water on limestone and silicate substrate belong to Group V; the sampling sites on silicate substrate at acidic pH fall within Group VI and the sampling sites on limestone substrate at acidic pH and standing water belong to Group VII. In the first stage of division, Groups I, II and III were separated from other sample groups; they are characterized by greatly increased electric conductivity (brackish or polluted water). The indicator species of environments with a particularly high electric conductivity are *Nitzschia frustulum* (Kützing) Grunow and *Enteromorpha* intestinalis (L.) Nees. In the second stage of division, Group I was separated from Groups II and III; the indicator species of organic pollution and high electric conductivity (constructed wetland – CW) is *Phormidium* formosum (Bory) Anagnostidis & Komárek. The

separation of Groups IV and V (alkaline pH) from Groups VI and VII (acidic pH) also took place in the second stage of division. The indicator species of environments at alkaline pH and running water are *Gomphonema angustatum* (Kützing) Rabenhorst, *Meridion circulare* (Greville) C.A. Agardh and *Cocconeis placentula* Ehrenberg, while *Eunotia bilunaris* (Ehrenberg) Mills, *E. exigua* (Brébisson ex Kützing) Rabenhorst and *Pinnularia subcapitata* Gregory specify environments at acidic pH. In the third stage of division, the separation of Groups II and III, IV and V and VI and VII took place. *Diploneis didyma* (Ehrenberg) Ehrenberg is the indicator species of samples taken at sampling sites 28 and 29 (Group II) where electric conductivity values were much higher than at sampling sites 26 and 27 (Group III). *Nitzschia palea* (Kützing) W. Smith, *Gomphonema parvulum* (Kützing) Kützing and *Cymbella silesiaca* Bleisch are the indicator taxa of Group V (low velocity of water flow, alkaline pH), *Pinnularia subcapitata* and *Eunotia implicata* Nörpel are the indicator species of Group VI (silicate substrate, acidic pH) and *Spirogyra* Link and *Achnanthes flexella* (Kützing) Brun are the indicator taxa of Group VII (limestone substrate, acidic pH, standing water).

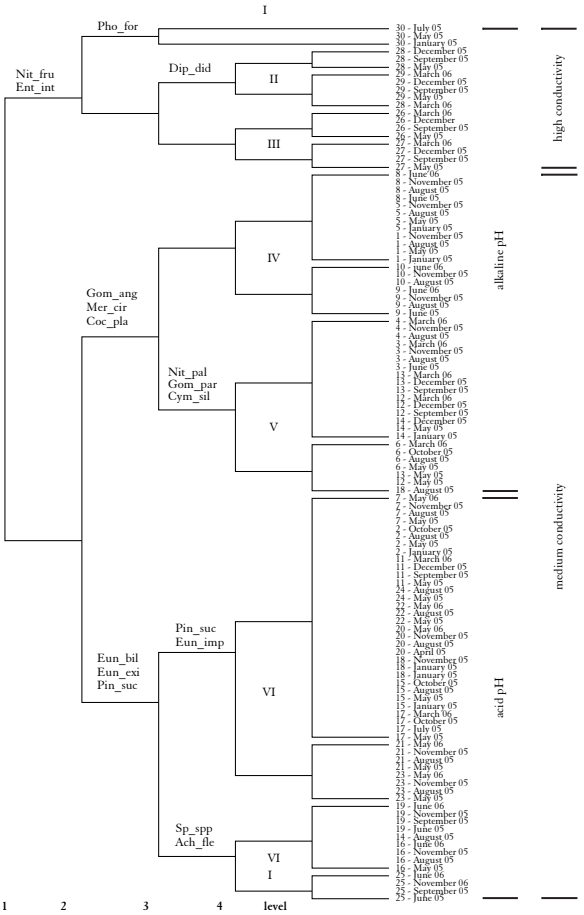

Figure 1. *TWINSPAN dendrogram based on the relative abundance estimation of algal data with presented indicator taxa of algae. Taxa abbreviations are explained in Table 2.*

By the number of identified taxa, diatoms prevailed in all TWINSPAN groups of sampling sites (Figure 2). Their share was the highest in Groups II and III (>90%) comprising the brackish sampling sites, while the lowest share (<50%) was recorded in Group VII covering sampling sites at bogs and marshes on limestone substrate at acidic pH. Cyanobacteria reached their highest share (>15%) in Group IV incorporating sampling sites with fast running water on limestone substrate at alkaline pH. Cyanobacteria had a high share also in Groups I (constructed wetland), VI (silicate substrate, acidic pH) and VII (limestone substrate, acidic pH). Chlorophyceae, Zygnematophyceae and Euglenophyceae reached their highest shares in Groups VI and VII which mainly represent bogs and marshes at acidic pH. Representatives of class Xanthophyceae were not present in Groups I (constructed wetland), II and III (brackish sampling sites). A representative of class Florideophyceae (*Audouinella chalybea* (Lyngbye) Fries) was present at sampling sites with fast running water (Groups IV and VI).

Canonical Corresponding Analysis (CCA)

Taxa level

Seven variables (silicate, pH, limestone, shading, water flow, saturation and conductivity) were chosen by the forward selection method (within the CCA) from the matrix of environmental variables (Table 1). Forward selected variables ($P \leq 005$) explained 17.42% of the variance of the taxa matrix or the variability of communities at the species level. The environmental variable, which was selected first and was the most explanatory one, was the silicate (3.64 %). The pH variable explained 3.18% of the variance, the variable limestone 3.11% and the variable shading 2.50%. Each of the other variables explained less than 2% of algal variance at the species level. The other variables of the environmental data-set did not explain significant additional variation in the species data.

The maximum eigenvalue is the value of the first canonical axis (0.652), which indicates a strong gradient in this direction (Table 4). The first axis statistically significantly explained 4.9% of the variance of the taxa matrix ($P = 0.002$). The eigenvalues of the following canonical axes were lower, which implies a weaker gradient and a smaller percentage of variance explained by an individual axis. The first four axes together explain 12.9% of the

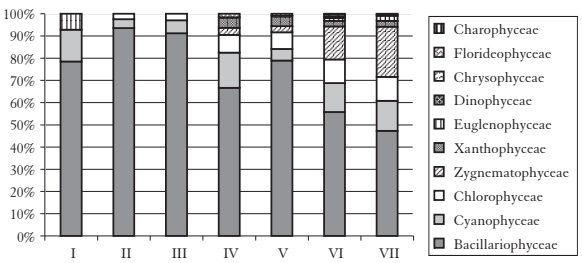

Figure 2. *Composition of algal flora in different TWINSPAN groups of samples in 2005 and 2006.*

TABLE 1

Caracteristics of the sampling sites studied. Shading: 1-no shade; 2-partly shaded; 3-intensive shade; water flow: 1-standing water; 2-running water, 3-fast running water.

	Sampling site	Gauss-krueger coordinates	pH	T [°C]	χ [µS/cm]	O_2 [mg/L]	Saturation [%]	Salinity [‰]	Bedrock	Shading	Water flow	substrate	*Dates of sampling
springs	1	X=5477863 Y=5084792	7.0-7.5	9.5-10.5	506-539	9.53-11.70	86.2-106.5	/	limestone	3	1	concrete, wood, moss	7.1.05 30.5.05 19.8.05 3.11.05
	2	X=5502251 Y=5156699	6.4-7.2	7.3-8.8	66-72	10.30-11.77	96.5-108.9	/	silicate	3	2	wood, moss, stones	9.1.05 8.5.05 21.8.05 31.10.05
	3	X=5476731 Y=5083645	7.1-7.7	8.2-12.4	433-509	4.09-10.87	39.4-97.7	/	limestone	3	1	stones	14.6.05 19.8.05 3.11.05 19.3.06
	4	X=547675, Y=5083672	7.2-7.8	6.5-12.0	438-509	4.85-10.14	40.1-86.9	/	limestone	3	2	stones, wood, macrophytes	19.8.05 3.11.05 19.3.06
	5	X=5434913 Y=5092355	7.4-7.9	7.9-9.6	376-473	9.88-13.24	90.7-123.0	/	limestone	2	2	moss	7.1.05 13.5.05 19.8.05 9.11.05
waterfalls	6	X=5497819 Y=5154729	6.6-7.1	4.8-12.8	82-118	10.05-12.62	91.2-106.2	/	silicate	3	3	stones, moss	7.5.05 21.8.05 31.10.05 26.3.06
	7	X=5539018 Y=5145207	6.8-7.1	6.8-10.1	43-50	10.02-10.65	97.1-99.2	/	silicate	3	3	moss	21.5.05 6.8.05 4.11.05 28.5.06
	8	X=5453329 Y=5082343	8.1-8.5	7.3-10.9	370-412	10.3-11.60	105.2-113.8	/	limestone	3	3	moss	3.6.05 10.8.05 2.11.05 21.6.06
	9	X=5453074 Y=5082522	8.0-8.7	9.2-11.2	389-430	11.02-11.55	98.2-109.6	/	limestone	2	3	stones	3.6.05 10.8.05 2.11.05 21.6.06
	10	X=5453194 Y=5081848	/	/	/	/	/	/	limestone	2	3	stones	10.8.05 2.11.05 21.6.06
oxbows	11	X=5580870 Y=5168070	6.2-7.0	0.2-22.8	280-507	0.12-8.70	0.9-81.7	/	silicate	1	1	wood, duckweed	14.5.05 16.9.05 16.12.05 23.3.06
	12	X=5580690 Y=5168100	6.0-7.2	1.8-15.9	548-732	0.22-4.04	5.2-27.0	/	silicate	3	1	wood	14.5.05 16.9.05 16.12.05 23.3.06
	13	X=5585970 Y=5163716	7.0-8.8	1.2-14.9	427-514	2.67-11.65	12.5-108.0	/	silicate	3	1	macrophytes, wood	14.5.05 16.9.05 16.12.05 23.3.06
mires, bogs	14	X=5476720 Y=5087020	7.0-8.5	1.4-26.2	407-552	7.47-11.47	57.1-143.4	/	limestone	1	1	macrophytes	22.1.05 30.5.05 19.8.05 18.12.05
	15	X=5502390 Y=5156150	/	/	/	/	/	/	silicate	1	1	grass	9.1.05 8.5.05 21.8.05 31.10.05

	Sampling site	Gauss-krueger coordinates	pH	T [°C]	χ [µS/cm]	O_2 [mg/L]	Saturation [%]	Salinity [‰]	Bedrock	Shading	Water flow	substrate	*Dates of sampling
	16	X=5435660 Y=5089110	7.0-7.9	9.3-14.2	188-441	6.84-8.38	61.4-101.0	/	limestone	1	1	moss	13.5.05 19.8.05 9.11.05 16.6.06
	17	X=5491240 Y=5156900	5.1-5.6	3.0-10.6	58-110	0.19-9.53	5.7-80.2	/	silicate	2	1	moss, macrophytes	8.5.05 24.7.05 31.10.05 25.3.06
	18	X=5452400 Y=5094400	6.5-6.8	0.9-22.2	115-194	1.05-2.22	9.1-17.7	/	limestone	3	1	wood, macrophytes	23.1.05 26.5.05 19.8.05 9.11.05
	19	X=5431535 Y=5124542	5.5-6.7	4.6-25.0	65-211	0.45-2.69	6.5-24.3	/	limestone	1	1	moss, macrophytes	28.6.05 9.9.05 16.11.05 22.6.06
	20	X=5537800 Y=5148400	7.0-7.1	7.3-13.9	53-60	2.71-8.07	32.1-75.8	/	silicate	3	1	macrophytes	27.4.05 6.8.05 4.11.05 28.5.06
	21	X=5535715 Y=5144006	/	/	/	/	/	/	silicate	2	1	moss	21.5.05 6.8.05 4.11.05 28.5.06
	22	X=5535746 Y=5143880	6.4-7.6	10.2-13.4	131-174	5.52-6.63	59.0-70.8	/	silicate	2	1	moss	21.5.05 6.8.05 28.5.06
	23	X=5535290 Y=5144800	5.1-6.2	9.4-20.5	24-36	7.27-9.14	90.2-97.1	/	silicate	1	1	moss, wood, macrophytes	21.5.05 6.8.05 4.11.05 28.5.06
ht	24	X=5496700 Y=5153724	7.0-7.3	9.8-15.2	98-127	5.30-7.80	49.2-82.0	/	silicate	3	1	wood, silt	7.5.05 21.8.05
	25	X=5431415 Y=5125342	6.6-8.1	7.2-28.4	150-220	3.78-8.34	38.0-117.5	/	limestone	1	1	wood, stones	28.6.05 9.9.05 16.11.05 22.6.06
brackish waters	26	X=5391070 Y=5041129	7.7-7.8	9.8-20.2	748-30.700	3.06-13.6	34.6-120.2	0.1-21.2	flysch	1	2	concrete, stones, macrophytes	20.5.05 7.9.05 14.12.05 17.3.06
	27	X=5405327 Y=5046686	8.1-8.2	9.1-17.5	391-5.080	6.44-13.4	66.8-118.8	0.0-2.7	flysch	3	2	stones, concrete, macrophytes	20.5.05 7.9.05 14.12.05 17.3.06
	28	X=5391808 Y=5043288	7.7-7.9	7.7-23.3	1737-55.000	6.99-12.96	59.8-111.0	0.7-36.3	flysch	1	2	wood, macroscopic algae	20.5.05 7.9.05 14.12.05 17.3.06
	29	X=5392606 Y=5043346	7.5-7.9	6.0-21.6	934-51.500	3.1-12.82	37.6-102.8	0.2-30.8	flysch	2	2	macrophytes	20.5.05 7.9.05 14.12.05 17.3.06
constructed wetland	30	X=5587800 Y=5141700	8.0-8.1	16.0-25.0	7100- 10900	0.13-2.94	1.2-28.0	3.9-5.7	silicate	2	1	macrophytes	17.1.05 25.5.05 25.7.05

* These are also dates of measuring physical and chemical parameters. At sampling sites 10, 15 and 21, physical and chemical parameters were not measured due to insufficient amount of water to perform measurements.

total variance of the taxa matrix. The correlation coefficients between the first three axes of the taxa matrix and the environmental matrix were larger than 0.9; the correlation coefficient of the first axis amounts even to 0.98,

while the value of the correlation coefficient of the fourth axis was slightly lower (0.82). This means that the distribution of taxa in the direction of the first three axes was explained very well by the forward selected environmental variables, but somewhat worse in the direction of the fourth axis.

The first CCA axis is in negative correlation with silicate ($r = –0.44$), limestone ($r = –0.34$) and shading ($r = –0.14$) and in positive correlation with conductivity ($r = 0.66$), water flow ($r = 0.37$), pH ($r = 0.48$) and saturation ($r = 0.11$). Only the correlation of the first axis with conductivity is stronger ($r = 0.66$), while the correlation of other environmental variables with the first axis is weaker. The second ordination axis explains less variance that the first one and it is in weaker correlation with the selected variables. The strongest negative correlation is with pH ($r = –0.61$) and shading ($r = –0.55$). It is in positive correlation with electric conductivity ($r = 0.19$) and silicate ($r = 0.37$). The third ordination axis is in strong positive correlation with limestone ($r = 0.72$), and in strong negative correlation with silicate ($r = –0.72$) and shading ($r = –0.67$). The correlation of variables with the fourth axis is very weak.

Figure 3 shows the TWINSPAN indicator taxa in relation to environmental variables. The indicator species of brackish waters are shown on the right-hand side of the top of ordination diagram: *Nitzschia frustulum*, *Enteromorpha intestinalis* and *Diploneis didyma*. It is characteristic of them to live on flysch substrate in high-conductivity environments at alkaline pH and low velocity of water flow. The indicator species of acidic waters are shown on the left-hand side of the top of ordination diagram: *Eunotia bilunaris, E. exigua*, *Pinnularia subcapitata, E. implicata*, *Spirogyra* spp. and *Achnanthes flexella*. The listed taxa are characteristic of waters on limestone or silicate substrates at acidic pH, low electric conductivity and generally lower saturation values (bogs, marshes). The indicator species of running waters at alkaline pH are shown in the lower part of the ordination diagram: *Gomphonema angustatum, Meridion circulare, Cocconeis placentula, Cymbella silesiaca* and *Nitzschia palea*. The aforementioned taxa are characteristic of running waters at alkaline pH, with good oxygen saturation level, medium conductivity value and fully or partly shaded by riparian vegetation (waterfalls, springs, oxbows).

TABLE 2

TWINSPAN indicator species and their abbreviations used in TWINSPAN and CCA analyses.

Taxa	Abbreviation
Achnanthes flexella	Ach_fle
Cocconeis placentula	Coc_pla
Cymbella silesiaca	Cym_sil
Diploneis didyma	Dip_did
Enteromorpha intestinalis	Ent_int
Eunotia bilunaris	Eun_bil
Eunotia exigua	Eun_exi
Eunotia implicata	Eun_imp
Gomphonema angustatum	Gom_ang
Gomphonema parvulum	Gom_par
Meridion circulare	Mer_cir
Nitzschia frustulum	Nit_fru
Nitzschia palea	Nit_pal
Phormidium formosum	Pho_for
Pinnularia subcapitata	Pin_suc
Spirogyra spp.	Sp_spp

Genera level

Six variables (pH, silicate, shading, limestone, water flow and saturation) were chosen by the forward selection method from the environmental matrix (Table 1). These variables statistically significantly ($P \leq 0.05$) explain the variance of the genera matrix and hence the variability of communities at the genera level. The selected variables explained 18.54% of the variance of the genera matrix. The first selected variable, which explained most of the variance (4.82%), was the pH. The silicate variable explained 3.71% of the variance, the shading variable 3.34% and the limestone variable 3.15%. The variables of water flow and saturation explained less than 3% of the community variance at the genera level. The other variables of the environmental data-set did not explain significant additional variation in the genera data.

The maximum eigenvalue is the value of the first canonical axis (0.372), which indicates a strong gradient in this direction (Table 5). The first axis explains also the highest percentage of the genera matrix variance (6.9%). The eigenvalues of the following canonical axes are lower, which implies a weaker gradient and a smaller per-

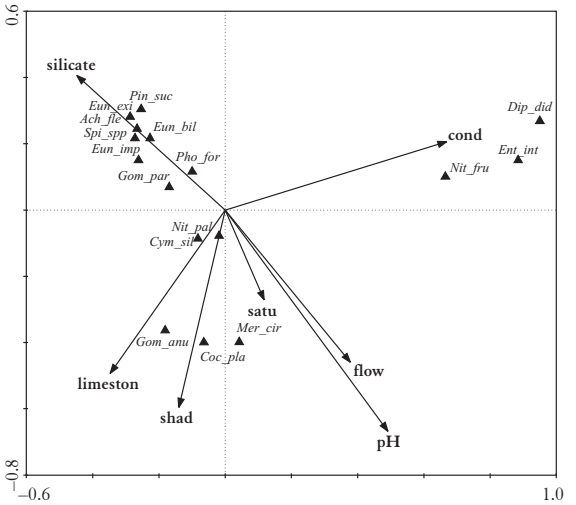

Figure 3. *Results of the Canonical Corresponding Analysis (CCA) carried out in CANOCO shown as a biplot environmental variables and 16 TWINSPAN indicator taxa. Cond--conductivity, limeston-limestone, shad-shading, satu-saturation. Taxa abbreviations are explained in Table 2.*

TABLE 3

Genera and their abbreviations used in CCA analysis.

Anabaena	Anabaena
Aphanocapsa	Aphanoca
Aphanothece	Aphanoth
Borzia	Borzia
Calothrix	Calothri
Chamaesiphon	Chamaesi
Chroococcus	Chroococ
Coelomoron	Coelomor
Cyanothece	Cyanothe
Cylindrospermum	Cylindro
Geitlerinema	Geitleri
Gloeocapsa	Gloeocap
Gloeocapsopsis	Gloeocap
Gomphosphaeria	Gomphosp
Heterolebleinia	Heterole
Homoeothrix	Homoeoth
Leptolyngbya	Leptolyn
Limnothrix	Limnothr
Merismopedia	Merismop
Microcystis	Microcys
Nostoc	Nostoc
Oscillatoria	Oscillat
Phormidium	Phormidi
Plectonema	Plectone
Pleurocapsa	Pleuroca
Pseudanabaena	Pseudana
Schizothrix	Schizoth
Scytonema	Scytonem
Spirulina	Spirulin
Tolypothrix	Tolypoth
Tychonema	Tychonem
Woronichinia	Woronich
Euglena	Euglena
Colacium	Colacium
Phacus	Phacus
Amphidinium	Amphidin
Gymnodinium	Gymnodin
Peridinium	Peridini
Botryochloris	Botryoch
Bumilleria	Bumiller
Characiopsis	Characio
Gloeobotrys	Gloeobot
Heterodendron	Heterode
Heterothrix	Heteroth
Ophiocytium	Ophiocyt
Peroniella	Peroniel
Tribonema	Tribonem
Vaucheria	Vaucheri
Dinobryon	Dinobryo
Stylopyxis	Stylopyx
Synura	Synura
Achnanthes	Achnanth
Amphipleura	Amphiple
Amphora	Amphora
Anomoeoneis	Anomoeon
Aulacoseira	Aulacose
Bacillaria	Bacillar
Caloneis	Caloneis
Cocconeis	Cocconei
Cyclotella	Cyclotel
Cymatopleura	Cymatopl
Cymbella	Cymbella
Denticula	Denticul
Diatoma	Diatoma
Didymosphenia	Didymosp
Diploneis	Diplonei
Entomoneis	Entomone
Epithemia	Epithemi
Eunotia	Eunotia
Fragilaria	Fragilar
Frustulia	Frustuli
Gomphonema	Gomphone
Gyrosigma	Gyrosigm
Hantzschia	Hantzsch
Licmophora	Licmopho
Mastogloia	Mastoglo
Melosira	Melosira
Meridion	Meridion
Navicula	Navicula
Neidium	Neidium
Nitzschia	Nitzschi
Pinnularia	Pinnular
Pleurosigma	Pleurosi
Rhoicosphenia	Rhoicosp
Rhopalodia	Rhopalod
Stauroneis	Staurone
Stenopterobia	Stenopte
Surirella	Surirell
Tabellaria	Tabellar
Ankistrodesmus	Ankistro
Asterococcus	Asteroco
Carteria	Carteria
Chaetophora	Chaetoph
Characium	Characiu
Chlamydomonas	Chlamydo
Chlorella	Chlorell
Chlorococcum	Chloroco
Chlorophysema	Chloroph
Cladophora	Cladopho
Coleochaete	Coleocha
Draparnaldia	Draparna
Enteromorpha	Enteromo

Gloeocystis	Gloeocys
Keratococcus	Keratoco
Klebsormidium	Klebsorm
Koliella	Koliella
Microspora	Microspo
Microthamnion	Microtha
Oedogonium	Oedogoni
Oocystis	Oocystis
Palmodictyon	Palmodic
Pandorina	Pandorin
Pediastrum	Pediastr
Scenedesmus	Scenedes
Stigeoclonium	Stigeocl
Trentepohlia	Trentepo
Ulothrix	Ulothrix
Actinotaenium	Actinota
Closterium	Closteri
Cosmarium	Cosmariu
Cylindrocystis	Cylindro
Desmidium	Desmidiu
Euastrum	Euastrum
Hyalotheca	Hyalothe
Micrasterias	Micraste
Mougeotia	Mougeoti
Netrium	Netrium
Penium	Penium
Pleurotaenium	Pleurota
Spirogyra	Spirogyr
Spondylosium	Spondylo
Staurastrum	Staurast
Staurodesmus	Staurode
Teilingia	Teilingi
Tetmemorus	Tetmemor
Zygnema	Zygnema
Chara	Chara
Audouinella	Audouine

centage of the variance explained by an individual axis. The first four axes together explain 15.8% of the total variance of the genera matrix. The correlation coefficients between the first two canonical axes of the genera matrix and the environmental matrix are larger than or equal to 0.9; the correlation coefficient of the third axis is slightly lower (0.86), while the value of the correlation coefficient of the fourth axis is the lowest (0.74).

The first axis is in a weak negative correlation with silicate ($r = –0.37$) and limestone ($r = –0.14$) and in positive correlation with pH ($r = 0.65$), saturation ($r = 0.25$), water flow ($r = 0.61$) and shading ($r = 0.33$). The correlations of the first axis with pH and water flow are stronger, while other correlations are weaker. The second axis is in positive correlation with all forward selected environmental variables, but the correlations are weaker. However, the correlations of the second axis with shading ($r = 0.54$) and limestone ($r = 0.42$) are stronger.

The genera are distinctly distributed along the gradient of water flow (Figure 4). The representatives of genera *Coelomoron* Buell, *Closterium* Nitzsch ex Ralfs, *Aulacoseira* Thwaites, *Coleochaete* Brébisson, *Amphidinium* Claparède & Lachmann, *Cosmarium* Corda ex Ralfs, *Microthamnion* Nägeli, *Pediastrum* Meyen, *Chroococcus* Nägeli, *Gomphosphaeria* Kützing, *Mougeotia* Agardh, *Pseudanabaena* Lauterborn, *Spondylosium* Brébisson, *Peridinium* Ehrenberg, *Chaetophora* Schrank, *Penium* Brébisson ex Ralfs, *Characiopsis* Borzi, *Aphanocapsa* Nägeli, *Calothrix* Agardh, *Tolypothrix* Kützing, *Gloeocystis* Nägeli, *Gymnodinium* Stein, *Spirogyra*, *Scenedesmus* Meyen, *Ankistrodesmus* Corda, *Zygnema* Agardh, *Nostoc* Adanson, *Tychonema* Anagnostidis & Komárek, *Teilingia* Bourrelly, *Ophiocytium* Nägeli, *Characium* A.Braun, *Chlamydomonas* Ehrenberg, *Euastrum* Ehrenberg ex Ralfs, *Rhopalodia* O.Müller, *Anabaena* Bory, *Aphanothece* Nägeli, *Draparnaldia* Bory, *Oocystis* Nägeli, *Pandorina* Bory, *Tabellaria* Ehrenberg, *Carteria* Diesing, *Pleurotaenium* Nägeli, *Netrium* (Nägeli) Itzigsohn & Rothe, *Staurastrum* Meyen ex Ralfs, *Palmodictyon* Kützing, *Actinotaenium* Teiling, *Dinobryon* Ehrenberg, *Chlorella* Beye-

TABLE 4

Summary statistics of the canonical corresponding analysis (CCA) at taxa level.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.652	0.427	0.354	0.269	13.201
Species-environment correlations	0.978	0.920	0.952	0.823	
Cumulative percentage variance of species data	4.9	8.2	10.9	12.9	
of species-environment relation	28.4	46.9	62.3	74.0	
Sum of all canonical eigenvalues					2.300
Monte Carlo test					Test of significance of first canonical axis
Eigenvalue					0.652
F-ratio					4.471
P-value					0.002

TABLE 5

Summary statistics of the canonical corresponding analysis (CCA) at genera level.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.372	0.209	0.166	0.103	5.396
Species-environment correlations	0.909	0.892	0.855	0.736	
Cumulative percentage variance of species data	6.9	10.8	13.9	15.8	
of species-environment relation	37.1	58.0	74.5	84.8	
Sum of all canonical eigenvalues					1.003
Monte Carlo test					Test of significance of first canonical axis
Eigenvalue					0.372
F-ratio					6.444
P-value					0.001

rink, *Merismopedia* Meyen, *Hyalotheca* Ehrenberg, *Gloeobotrys* Pascher, *Desmidium* Agardh, *Asterococcus* Scherffel, *Cylindrospermum* Kützing, *Micrasterias* Agardh ex Ralfs, *Staurodesmus* Teiling, *Woronichinia* Elenkin, *Borzia* Cohn and *Phacus* Nitzsch are typical for standing waters. The listed genera were present mostly at sampling sites with acidic pH, low dissolved oxygen, low saturation, and in sunny locations. The species belonging to the genera *Homoeothrix* (Thuret) Kirchner, *Meridion* Agardh, *Cocconeis* Ehrenberg, *Denticula* Kützing, *Schizothrix* Kützing ex Gomont, *Scytonema* C.A. Agardh, *Heterodendron* Steinecke, *Audouinella* Bory, *Chamaesiphon* A. Braun & Grunow, *Cladophora* Kützing, *Gloeocapsa* Kützing, *Pleurocapsa* Thuret, *Diatoma* Bory and *Plectonema* Thuret were present at sampling sites with running water, alkaline or neutral pH, shaded by riparian vegetation and in general, with high saturation values. The genera shown in the right lower part of the ordination diagram are characteristic of brackish waters: *Licmophora* Agardh, *Spirulina* Turpin, *Pleurosigma* W. Smith, *Entomoneis* Ehrenberg, *Bacillaria* Gmelin and *Enteromorpha* (Link) Harvey. The genera located near the middle of the ordination diagram are present at the mean values of the measured parameters. Some of these genera are: *Didymosphenia* M. Schmidt, *Stauroneis* Ehrenberg, *Hantzschia* Grunow, *Gomphonema* Ehrenberg, *Achnanthes* Bory, *Frustulia* Rabenhorst, *Fragilaria* Lyngbye, *Phormidium* Kützing ex Gomont, *Navicula* Bory, *Nitzschia* Hassall.

Classis level

Five variables (water flow, pH, silicate, limestone and saturation) were chosen by the forward selection method from the environmental matrix (Tab. 1). Forward selected variables statistically significantly ($P \leq 0.05$) explain 21.13% variance of the classis matrix and hence the variability of communities at the classis level. The first selected environmental variable, which explained most of the variance (9.54%), was the water flow. Each of the other variables, i.e. pH, silicate and limestone, explained 3.14% of the variance, while the saturation variable explained 1.36% of the variance of communities at the classis level. The other variables of the environmental data-set did not explain significant additional variation in the classis data.

The maximum eigenvalue is the value of the first canonical axis (0.149), which indicates the maximum gradient in this direction (Table 6). The first axis explains also the highest percentage of the classis matrix variance (10.1%). The eigenvalues of the following canonical axes are lower, which implies a weaker gradient and a smaller percentage of the variance explained by an individual axis. The first four axes together explain 20.8% of the total variance of the classis matrix. The correlation coefficients between the first canonical axis of the classis matrix and the environmental matrix amounts to 0.71. The

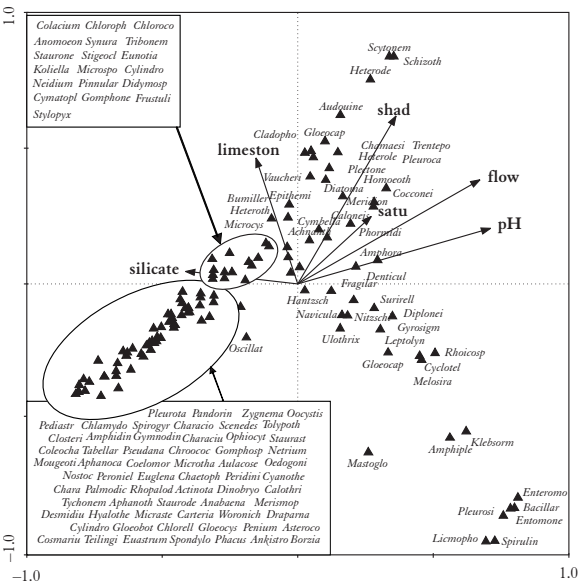

Figure 4. *Results of the Canonical Corresponding Analysis (CCA) carried out in CANOCO shown as a biplot environmental variables and algal genera. Limeston-limestone, shad--shading. Genera abbreviations are explained in Table 3.*

TABLE 6

Summary statistics of the canonical corresponding analysis (CCA) at classis level.

	Axes				Total inertia
	1	2	3	4	
Eigenvalues	0.149	0.083	0.052	0.022	1.468
Species-environment correlations	0.706	0.599	0.539	0.372	
Cumulative percentage variance of species data	10.1	15.8	19.3	20.8	
of species-environment relation	48.0	74.6	91.3	98.3	
Sum of all canonical eigenvalues					0.310
Monte Carlo test					Test of significance of first canonical axis
Eigenvalue					0.149
F-ratio					9.939
P-value					0.001

distribution of classis in the direction of the first axis was explained fairly well by the forward selected environmental variables. The distribution of classis in the direction of the second axis was explained to a lesser extent (0.60) and even less in the direction of the third and the fourth axes. The correlation coefficients are 0.54 (third axis) and 0.38 (fourth axis).

The first axis is in positive correlation with water flow ($r = 0.68$), saturation ($r = 0.34$) and pH ($r = 0.39$) and in a weak negative correlation with silicate ($r = –0.21$) and limestone ($r = –0.06$). The second ordination axis is in a relatively weak correlation with the forward selected variables.

It is evident from the ordination diagram (Figure 5) that the first axis separates the algal classis particularly in relation to the velocity of water flow and, to a lesser extent, in respect to the pH, dissolved oxygen saturation and geological substratum. The representatives of classis Euglenophyceae, Charophyceae, Xanthophyceae, Zygnematophyceae, Dinophyceae and Chrysophyceae were common at the sampling sites with standing water, while the representative of class Florideophyceae (*Audouinella chalybea*) was present at the sampling sites with higher water flow velocity. The species of class Euglenophyceae were present at the sampling sites with extremely low saturation, and the species of classis Dinophyceae and Chrysophyceae were present in a large number at the sampling sites with low (acidic) pH values. All classis were represented both on the silicate and limestone substrata, with the exception of class Charophyceae which was present only at the sampling site 16 (limestone). Only the species of classis Cyanobacteria, Bacillariophyceae and Chlorophyceae were recorded on flysch substrate.

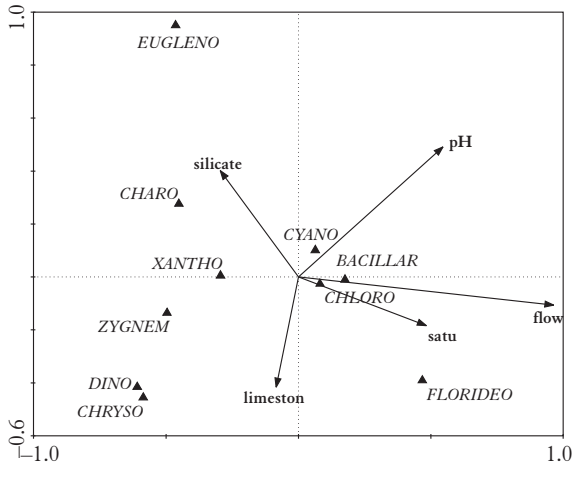

Figure 5. *Results of the Canonical Corresponding Analysis (CCA) carried out in CANOCO shown as a biplot environmental variables and algal classis. Limeston-limestone, satu--saturation, EUGLENO-Euglenophyceae CHARO-Charophyceae, XANTHO-Xanthophyceae, ZYGNEM-Zygnematophyceae, DINO-Dinophyceae, CHRYSO-Chrysophyceae, FLORIDEO-Florideophyceae, CHLORO-Chlorophyceae, BACILLAR-Bacillariophyceae, CYANO-Cyanophyceae.*

The representatives of classis Cyanobacteria, Bacillariophyceae and Chlorophyceae were present at most sampling sites (at different values of measured parameters) and are located near the centre of the ordination diagram.

DISCUSSION

The TWINSPAN analysis was used to determine the sample groups with similar species composition of algal communities and indicator algal taxa for individual sample groups. A number of authors *(38, 39, 40, 41)* applied the TWINSPAN analysis to classify algal samples and determine the indicator species. In Slovenia, the TWINSPAN analysis for algal communities was used for the first time within our research. By the TWINSPAN analysis, the samples were classified in four stages; however, for reasons of rationality, the results are explained only up to the third stage of classification. In the first stage of classification, the sampling sites with high electrical conductivity (brackish waters, CW) were separated from other sampling sites. The second stage of classification involved the separation of sampling sites at acidic pH from the ones at alkaline pH and the separation of CW samples from brackish samples. In the third stage of classification, the sampling sites at acidic pH were divided into those

on limestone substrate and those on silicate substrate. The sampling sites at alkaline pH were divided into those with running water and those with standing water. According to the measured electric conductivity values, the brackish sampling sites were divided into those with high conductivity and those with low conductivity. We determined 16 TWINSPAN indicator algal taxa.

Nitzschia frustulum, *Enteromorpha intestinalis*, *Diploneis didyma* and *Phormidium formosum* are the indicator species of environments with highly increased electric conductivity. *Gomphonema angustatum, Meridion circulare, Cocconeis placentula, Nitzschia palea, Gomphonema parvulum* and *Cymbella silesiaca* are the indicator species of environments at alkaline pH with running water. *Eunotia bilunaris, E. exigua E. implicata, Achnanthes flexella, Pinnularia subcapitata* and *Spirogyra* spp. are the indicator taxa of environments at acidic pH. *Spirogyra* sp. and *Achnanthes flexella* are the taxa typical of acidic standing waters on limestone substrate, while *Pinnularia subcapitata* and *Eunotia implicata* are species characteristic of acidic waters on silicate substrate.

General ecology of TWINSPAN indicator taxa *(17, 19-22, 30, 31):*

Achnanthes flexella	standing and slowly running waters, wide ecological amplitude regarding pH and conductivity
Cocconeis placentula	standing and running waters, cosmopolitan
Cymbella silesiaca	standing and running waters, cosmopolitan
Diploneis didyma	cosmopolitan sea species
Enteromorpha intestinalis	brackish waters near sea coasts
Eunotia bilunaris	standing and running waters with low values of conductivity
Eunotia exigua	acid waters with low values of conductivity
Eunotia implicata	waters with low values of conductivity
Gomphonema angustatum	smaller standing and running waters with different values of conductivity
Gomphonema parvulum	different types of waters, cosmopolitan
Meridion circulare	cosmopolitan, mass occurrence in karst waters
Nitzschia frustulum	cosmopolitan, mass occurrence in waters near sea coasts
Nitzschia palea	cosmopolitan, typical for alfa-mesosaprobic to polysaprobic waters
Phormidium formosum	standing waters, lakes, pools and also in brackish and sewage polluted waters
Pinnularia subcapitata	cosmopolitan, waters with low values of conductivity
Spirogyra sp.	smaller standing and slowly running waters

Canonical corresponding analysis (CCA)

Environmental variables explained a certain percentage of the variation of algal communities in selected aquatic environments. This means that we tried to explain the distribution of algae in selected extreme environments in Slovenia on the basis of environmental variables. The unexplained percentage of variance (from 83% to 79%) could have been reduced by including additional biotic and abiotic environmental variables; however, Palmer *(42)* states that the size of correlation between the taxa matrix and the environmental matrix is more important than the size of the explained percentage of variability. In cases of high correlation, the variables were determined that, directly or indirectly, significantly affect the distribution of organisms.

We established that the species identification affects the share of explained variance (the higher the level, the higher the percentage of explained variance). Urbanič *(43)* came to a similar conclusion in his research of Trichoptera in some watercourses in Slovenia. Moreover, we found out that the species identification influences the order of variables which explain the maximum share of the variability of algal communities. Urbanič *(43)* discovered just the opposite, namely that the species identification had not affected the order of variables with which he explained the maximum share of the variance of Trichoptera communities.

Various authors *(38, 41, 44, 45, 46)* explained the variability of algal communities by the combination of several environmental variables. We came to a similar conclusion that a significant share of the variability of algal communities can be explained by environmental variables. However, the findings as to which environmental variables are critical differ. Many authors *(6, 38, 44, 46, 47)* state that the water pH is a crucial factor affecting the distribution of algal communities. The water temperature most essentially affected the distribution of diatom communities in the Grand River in Ontario *(39),* while the velocity of water flow was most important physical factor affecting diatom communities in mountain watercourses in Himalaya *(40)*. We explained the major part of the variability of algal communities at the species (taxa) level by silicate variable, by pH variable at the genera level and by water flow variable at the classis level. The other variables which explained the largest share of the variability of algal communities at the taxa level and at the classis level were the pH variable and silicate variable at genera level.

The variable found to have a relatively small influence on the distribution of algal communities at the levels of species and genera is water flow; however, it is crucial at the classis level. This is probably because of the selection of sampling sites, as the majority of sampling sites were

selected in standing water habitats and only a few in running or fast running waters. Velocity of water flow was the most important factor affecting the communities of benthic algae in fast-running mountain watercourses *(48)*. We established that the representatives of classis Euglenophyceae, Charophyceae, Xanthophyceae, Zygnematophyceae, Dinophyceae and Chrysophyceae are frequent at standing water sampling sites, which is common knowledge from literature *(17, 23, 32)*. *Audouinella chalybea*, the representative of class Florideophyceae, is characteristic of environments with higher velocities of water flow *(17),* which was further confirmed by our findings.

Different lighting conditions in shaded and unshaded parts of rivers have a strong effect on changes in the structure of benthic algal associations *(49)*. Shading was the second most important factor (the first being pH) affecting the distribution of algal communities in the research of algae in peat bogs of the Czech Republic *(47)*. According to our results, the factor significantly affecting the distribution of algal communities is also shading by riparian vegetation.

Electric conductivity is an important factor influencing the distribution of algal communities *(4, 6),* it is a crucial factor affecting the distribution of benthic diatoms in rivers *(41)*. However, in our research, the conductivity variable was not statistically significant and was not included in ecological research.

In some studies *(39, 45),* water temperature during the sampling period was stated as an important factor affecting the distribution of algal communities. In our research, water temperature during the sampling period was not statistically significant and therefore not included in ecological research.

Nitzschia frustulum, *Enteromorpha intestinalis*, *Diploneis didyma* and *Phormidium formosum* are the indicator species of environments with a particularly high electric conductivity. *Gomphonema angustatum, Meridion circulare, Cocconeis placentula, Nitzschia palea, Gomphonema parvulum* and *Cymbella silesiaca* are the indicator species of environment at alkaline pH and standing waters. *Eunotia bilunaris, E. exigua, E. implicata, Achnanthes flexella, Pinnularia subcapitata* and *Spirogyra* spp. are the indicator species of environment at acidic pH. With CCA analysis. 21% of the variability of classis, 19% of the variability of genera and 17% of the variability of species (taxa) were explained. In relation to the size of the explained variability of environmental variables, it was found that the factor at the level of species (taxa), which had a decisive influence on the distribution of algae in selected habitats, was geological substrate (silicate), water pH at the level of genera and the velocity of water flow at the level of classis.

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