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# Short-term colonization sequence of periphyton on glass slides in a large river (River Danube, near Budapest)

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With 16 figures and 3 tables in the text

**Abstract:** The colonization, structure and composition of the periphyton which developed on the artificial substratum (sand-blasted matglass-slides) positioned into current line were studied in the main arm of the River Danube at Göd (1669 riv. km) in the summer of 1997, during a low water period. Five replicates were taken on the first day in the 3rd, 6th, 9th and 24th hour, after that every day for a week, then every three days for another two weeks. Phytoplankton samples were taken four times during the study (on the 1st, 6th, 13th and 20th day) to compare the composition of benthic and planktic algae.

Altogether 222 taxa were identified 95 taxa from the phytoplankton and 176 from the periphyton. The number of common species was 50. After three hours from the immersion, only coccoid bacteria (mainly colineforms) were found on the substratum but after 6 hours the first algae. The first colonizer was *Diatoma vulgaris*, which adheres with on apical pad. In the first few hours only a few species formed the community and low diversity and low evenness was the consequence. After 24 hours the community was already diverse with a total of 35 species.

During the first week of colonization the periphyton was composed almost exclusively of quick reproduction rate R (ruderal strategy) selected species, the evenness showed an increase parallel to species richness. The basal-layer of the Danube periphyton developed at that time, where diatoms attached to the substratum mainly with on apical pad. From the second week there was a small decrease in the evenness, when the rate of slower multiplying C, C-S (competitive strategy, stress tolerant strategy) selected species increased. In the second week stalk forming species formed an intermediate layer adhering with shorter, non branching gelatinous stalks. In the third week an additional top layer developed, which consisted mainly of chain forming diatoms and diatoms adhering with long, branching gelatinous stalk. The thick periphyton cover filtered out planktic species from the water like a net, and more and more euplanktic Centrales species were found in the samples.

Key words: short term colonization, periphyton, phytoplankton, diatoms, artificial substratum, large river.

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## Introduction

For formation of the spatial structures of periphyton, the different adherence strategies of the algae have high importance. The architecture of the periphyton is complicated, and depends on many factors, for example: type of substratum, light circumstances, grazing, nutrient supply, current velocity in rivers, and/or strength of water motions caused by the wind in lakes.

The most compact review of the structure and morphology of river periphyton was made by ROSOWSKI et al. (1986). For two years, with monthly sampling, they examined the structure and seasonality of periphyton on glass-plates exposed in a braided eutrophic stream. The research was completed with scanning electron microscopic examinations. Concerning its structure, three types of the periphyton were identified. The first type consists of algae adhering parallel to the surface of the substratum, the second consists of perpendicularly standing algae, and the third one of algae forming filaments or having a basal stalk. With the thickening of the periphyton there is a nutrient limitation in the first and second layer, when the third layer starts its development. Some algae are capable of changing their adhesion mode (e.g. *Achnanthes minutissima* KÜTZ.) and they can get up to the third layer, adhering with long gelatinous stalk instead of short ones. ROSOWSKI et al. (1986) stated that in the first week, the role of the substratum is determinant for the development of the periphyton community, but from the second week the organic layer covering the surface cancels the original characteristics of the substratum. A few hours after the immersion, an organic filmlayer forms on the substratum, and in the first week the dominance of diatoms characterizes the periphyton.

MEULEMANS & ROOS (1985) studied the reed-periphyton of an artificial lake in the Netherlands. They analyzed to composition of the three layers formed by the differently adhering diatoms.

LUTTENTON et al. (1986) studied the effect of the turbulence on the architecture and the composition of the periphyton using artificial substratum placed into some pools of the Upper Mississippi River.

FAYOLLE et al. (1998) studied the response of epilithon (first of all the changes in the structure of epilithon) to the hydrodynamic disturbances in a regulated Mediterranean river (Lower-Durance, France).

Production of gelatinous stalks and tubes by attached diatoms has been well known for more than a century (SMITH 1856, CHOLNOKY 1927).

According to ROUND's classification (1981) we can distinguish between so called adnate and upright adhering organisms. The former adheres closely to the substratum, the latter rises up from the substratum. Diatoms secrete gelatinous material for adhesion, which has a changing chemical composition in relation to the strength of the adhesion.

Based on that which part of the diatom is adhered to the substrata, OTTEN & WILLEMSE (1988) distinguishes three basic forms of adhesion: 1) valval - the diamtoms adhere with whole cell surface (e.g. *Cocconeis* spp.); 2) pleural - the diatoms adhere with their girdle part (e. g. *Epithema zebra*); 3) terminal - diatoms adhere on the apical part, with a longer or shorter gelatinous stalk (e.g. *Gomphonema* spp.). Diatoms adhering with the apical part of cell can be divided into three additional groups (LAKATOS et al. 1992): 1) apical pad forming species (they secrete a small gelatinous pad at the end of the cell with which they adhere to the substratum, e.g. *Synedra* spp.); 2) tube forming species (the cells adhere to the substratum standing together in a gelatinous tube, e.g. *Cymbella lacustris*); 3) stalk forming species (the cells adhere with a longer or shorter gelatinous stalk, e.g. *Rhoicosphenia abbreviata*).

The most complete summary of the different adhesion mechanisms of diatoms is in the paper of HOAGLAND et al. (1993). Beside the above mentioned adhesion forms, he also details adhesion with adhering films, cell coatings and fibrils.

Certainly, we can find many marine studies which contain analysis of the adhesion mechanism of diatoms. Among others, KAWAMURA & HIRANO (1992) made difference between 7 types of growth forms of diatoms of the periphyton which developed in the Anuratsubo Bay on glass slides.

The immigration mechanism of diatoms to the substrata have been a subject of examination for a long time. PATRICK (1967) studied the immigration of diatoms and she found that the size of the area to be invaded affects the number of species and the diversity of the community. BLINN et al. (1980) studied the immigration process of algae on rocks of three different types of material in mountain rivers. JOHANSSON (1979) studied the colonization both on natural and artificial substrata in six Swedish rivers, among others, through the measurement of the chlorophyll *a* content of the periphyton.

EULIN & LE COHU (1998) investigated the process of colonization on artificial substrata in the River Garonne (in France), with weekly sampling during four weeks in a summer and a winter low water period. They compared the periphyton collected from artificial and natural substrata (pebbles).

We started to examine the colonization process of periphytic algae in the Danube in 1984 first (ÁCS & KISS 1993). The samples were taken in 2–4-day periods. Then in 1992 we repeated the study (samples taken daily, ÁCS 1998). That time the changes of current velocity among the substrata were relatively high and basically affected the process of colonization. Therefore, we repeated the examination in 1997 under constant current velocity and the samples were taken more frequently in the beginning of colonization.

The aim of this study was to examine the colonization process, the structure and composition of the periphyton developed on artificial substratum placed into the stream line of the main arm of the Danube. (The early phase of colonization

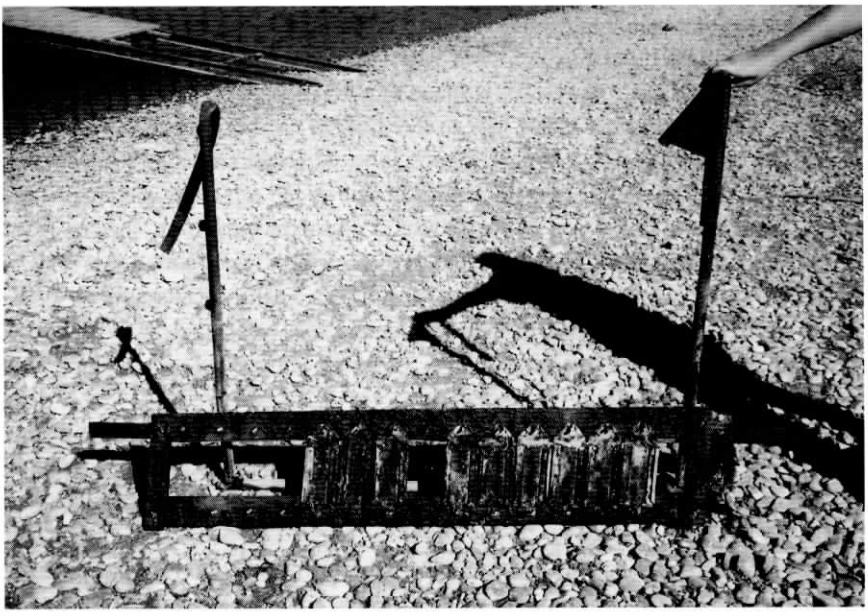


Fig. 1. The artificial substrata in their holders used in our study covered by periphyton.

process was never studied in large rivers). Further, we analyzed the composition of the phytoplankton, to compare it with periphyton.

## Material and methods

Sand-blasted matglass-slides were used as substratum. Five of them were placed into a holder, the holders were fastened onto a frame (Fig. 1) fixed to the shell of a boat anchored in the stream line of the Danube at Göd (1669 riv. km). The substrata were positioned on the 21$^{st}$ of August 1997, and samples in five replicates were taken first in the 3$^{rd}$, 6$^{th}$, 9$^{th}$ and 24$^{th}$ hour after the positioning, then every day for a week, then every three days for two more weeks. The algae were washed from the substratum into known-volume tap water, then the samples were divided into two. On part was used to determine chlorophyll *a* concentration by methanol (100%) extraction (Goodwin 1976) on the day of sampling, and the other one to count and determine algae by Utermöhl (1958) method according to Lund's statistical instructions (1958). To identify the diatoms, samples were sedimented, treated by $H_2O_2$ and washed with distilled water. The treated samples were mounted in Pleurax for light-microscopy. Pennales species were identified from clean mounts, since many frustules from the "Pennales" category could not be classified, according to the Utermöhl counting

method. Centrales taxa were identified in the cleaned samples with scanning and transmission electron microscope according to KISS (1986).

To examine the intact periphyton during the colonization, 0.5 × 0.5 cm mat-glass plates were sticked beside the slides onto the frame and they were taken one by one on the 4th, 6th, 12th, 18th and 21st day. Samples were immediately fixed by 5% glutaraldehyde in phosphate buffer. After washing with phosphate buffer, the samples were dehydrated in an acetone distilled water series (30, 50, 70, 80 90% one and 100% wice). They were loaded into the critical point drying apparatus after being unfiltrated with amyl-acetate, coated with gold and viewed on a scanning electron microscope (AMARY 1830 I/T6) at 20 kV acceleration voltage (GILMOUR et al. 1993).

Phytoplankton samples were collected weekly from the top 10 cm water body in the current line, 4 times during the study (22 August - 10 September). The discharge of the River Danube changed between 2214 $m^3 s^{-1}$ and 1686 $m^3 s^{-1}$ that means a low water period free of floods (the anual average of discharge near Budapest is 2300 $m^3 s^{-1}$. The chlorophyll *a* concentration of phytoplankton was determined by the same method the periphyton samples.

The species composition of phytoplankton and periphyton communities were compared using Sörensen similarity index (SÖRENSEN 1948), and the diversity (H) of samples, which was calculated according to the SHANNON and WEAVER index (SHANNON & WEAVER 1963). Evennes (J) was calculated as $H\ Hmax^{-1}$, were Hmax is the theoretical maximum of diversity (Hmax=lnS, S=number of species).

The colonization strategies of algae (R=ruderal, C=competitive, S=stress tolerant strategy) was reviewed by BIGGS et al. (1998).

## Results

Altogether 222 taxa were identified from the phytoplankton and the periphyton during the study (Table 1). The number of phytoplankton taxa was 95, that of the periphyton was 176, the number of common species was 50. Most phytoplankton species belonged to the Chlorophyceae class, and most periphyton species belonged to the Pennales order of Bacillariophyceae (Fig. 2).

Comparing the species of the phytoplankton and the periphyton, the value of similarity was 0.26. When this value was calculated only on the basis of species belonging to the Pennales order the similarity was smaller (0.12). When the calculation took place on the basis of all the others the value of similarity was 0.34.

The number of species of the phytoplankton changed between 41460 to 22430 ind. $ml^{-1}$ (Table 2). *Skeletonema potamos* had highest abundance, it comprised 24–42 percent of the phytoplankton, and 40–65 percent of Thalassiosiraceae. The water of the Danube is rich in plant nutrients (N, P) through the year and often hypertrophic in low water periods (KISS 1994). On the basis of the chlorophyll *a* contents of the phytoplankton the trophic level (based on OECD standards 1982) was hypertrophic in August and eutrophic in September.

Table 1. The list of taxa.

| Taxa | Phytoplankton | Periphyton |
|---|---|---|
| CYANOPHYTA | | |
| *Anabaena* sp. | | + |
| *Aphanocapsa* sp. | + | + |
| *Merismopedia glauca* (EHR.) NÄG. | + | |
| *Microcystis flos-aquae* (WITTR.) KIRCH. | + | |
| *Oscillatoria aghardii* GOM. | + | |
| *Oscillatoria redekei* VAN GOOR | + | |
| *Planctolyngbya limnetica* (LEMM.) ANAGN. et KOM. | + | + |
| EUGLENOPHYTA | | |
| *Euglena* sp. | + | + |
| CHRYSOPHYCEAE | | |
| *Chrysochromulina parva* LACKEY | + | |
| *Dynobrion sertularia* EHR. | | + |
| *Mallomonas tonsurata* TEILING et KRIEGER | | + |
| *Paraphysomonas vestita* (STOKES) DE SAEDELER | | + |
| BACILLARIOPHYCEAE / CENTRALES / | | |
| *Aulacoseira distans* (EHR.) SIM. | | + |
| *Aulacoseira granulata* (EHR.) SIM. | + | |
| *Aulacoseira granulata* var. *angustissima* (O. MÜLL.) SIM. | + | + |
| *Aulacoseira italica* var. *tenuissima* (GRUN.) SIM. AITAVT | + | + |
| *Cyclostephanos dubius* (FRICKE) ROUND | + | + |
| *Cyclotella atomus* HUST. | + | + |
| *Cyclotella atomus* var. *gracilis* GENKAL et KISS CATOVG | + | + |
| *Cyclotella meduane* GERMAIN | + | + |
| *Cyclotella meneghiniana* KÜTZ. | + | + |
| *Cyclotella pseudostelligera* HUST. | + | + |
| *Cyclotella radiosa* (GRUN.) LEMM. | + | + |
| *Cyclotella stelligera* CLEVE et GRUN. | + | + |
| *Melosira varians* AG. MELVAR | | + |
| *Skeletonema potamos* (WEBER) HASLE SKEPOT | + | + |
| *Skeletonema subsalsum* (CLEVE-EULER) BETHGE | | + |
| *Stephanodiscus alpinus* HUST. | + | + |
| *Stephanodiscus delicatus* GENKAL | + | + |
| *Stephanodiscus hantzschii* f. *hantzschii* GRUN. | + | + |
| *Stephanodiscus hantzschii* f. *tenuis* (HUST.) HAK. et STOER. | + | + |
| *Stephanodiscus invisitatus* HOHN et HELLERMAN STEINV | + | + |
| *Stephanodiscus minutulus* (KÜTZ.) CLEVE et MÖLLER | + | + |
| *Thalassiosira guillardii* HASLE | + | + |
| *Thalassiosira incerta* MAKAR | + | + |
| *Thalassiosira lacustris* (GRUN.) HASLE | + | + |
| *Thalassiosira pseudonana* HASLE et HEIMDAL | + | + |
| *Thalassiosira weissflogii* (GRUN.) FRYXELL et HASLE | + | + |
| BACILLARIOPHYCEAE / PENNALES / | | |
| *Achnanthes minutissima* KÜTZ. | | + |
| *Achnanthes exigua* GRUN. | | + |
| *Achnanthes lanceolata* (BRÉB) GRUN. | | + |
| *Achnanthes ploenensis* HUST. | | + |
| *Amphora inariensis* KRAMMER | | + |
| *Amphora lybica* EHR. | | + |
| *Amphora ovalis* KÜTZ. | | + |

Table 1. (continued).

| Taxa | Phytoplankton | Periphyton |
|---|---|---|
| *Amphora pediculus* KÜTZ. | | + |
| *Amphora* sp. | | + |
| *Asterionella formosa* HASSAL | + | + |
| *Caloneis amphisbaena* (BORY) CLEVE | | |
| *Cocconeis pediculus* EHR. | | + |
| *Cocconeis placentula* EHR. | | + |
| *Cymatopleura solea* (BRÉB.) W. SMITH | | + |
| *Cymbella affinis* KÜTZ. | | + |
| *Cymbella cymbiformis* AG. | | + |
| *Cymbella helvetica* KÜTZ. | | + |
| *Cymbella minuta* HILSE | | + |
| *Cymbella silesiaca* BLEISCH | | + |
| *Cymbella sinuata* GREGORY | | + |
| *Cymbella tumida* GRUN. | | + |
| *Cymbella* sp. | | + |
| *Denticula tenuis* KÜTZ. | | + |
| *Diatoma mesodon* (EHR.) KÜTZ. | | + |
| *Diatoma moniliformis* KÜTZ. | | + |
| *Diatoma tenuis* AG. | | + |
| *Diatoma vulgaris* BORY DIAVUL | | + |
| *Fragilaria arcus* (EHR.) CLEVE | | + |
| *Fragilaria brevistriata* GRUN. | | + |
| *Fragilaria capucina* DESM. | | + |
| *Fragilaria capucina* var. *gracilis* (OESTRUP) HUST. | | + |
| *Fragilaria capucina* var. *mesolepta* (RAB.) RAB. | | + |
| *Fragilaria capucina* var. *rumpens* (KÜTZ.) LANGE-BERT. | | + |
| *Fragilaria capucina* var. *vaucheriae* (KÜTZ.) LANGE-BERT. | | + |
| *Fragilaria crotonensis* KITTON | | + |
| *Fragilaria famelica* (KÜTZ.) LANGE-BERT | | + |
| *Fragilaria fasciculata* (AG.) LANGE-BERT. | | + |
| *Fragilaria parasitica* (W. SMITH) GRUN. | | + |
| *Fragilaria pinnata* EHR. | | + |
| *Fragilaria pinnata* var. *intercedens* (GRUN.) HUST. | | + |
| *Fragilaria tenara* (W. SMITH) LANGE-BERTALOT | + | + |
| *Fragilaria ulna* (NITZSCH) LANGE-BERT. FRAULN | | + |
| *Fragilaria ulna* var. *acus* (KÜTZ.) LANGE-BERT. | + | + |
| *Fragilaria* sp. small | | + |
| *Gomphonema angustatum* (KÜTZ.) RAB. | | + |
| *Gomphonema angustum* AG. | | + |
| *Gomphonema gracile* EHR. | | + |
| *Gomphonema minutum* (AG.) AG. | | + |
| *Gomphonema olivaceum* (HORN.) BRÉB. | | + |
| *Gomphonema parvulum* (KÜTZ.) KÜTZ. | | + |
| *Gomphonema pumilum* (GRUN.) REICH et LANGE-BERT. | | + |
| *Gomphonema tergestinum* FRICKE | | + |
| *Gyrosigma acuminatum* (KÜTZ.) RAB. | | + |
| *Gyrosigma nodiferum* (GRUN.) REIMER | | + |
| *Gyrosigma scalproides* (RAB.) CLEVE | | + |
| *Navicula capitata* EHR. | | + |
| *Navicula capitatoradiata* GERMAIN NAVCAP | | + |
| *Navicula cari* EHR. | | + |
| *Navicula cincta* (EHR.) RALFS | | + |

Table 1. (continued).

| Taxa | Phytoplankton | Periphyton |
|---|---|---|
| *Navicula cryptocephala* KÜTZ. | | + |
| *Navicula erifuga* LANGE-BERT. | | + |
| *Navicula gregaria* DONKIN NAVGRE | | + |
| *Navicula laevissima* KÜTZ. | | + |
| *Navicula lanceolata* AG.) EHR. | | + |
| *Navicula menisculus* SCHUMANN | | + |
| *Navicula minima* GRUN. | | + |
| *Navicula mutica* KÜTZ. | | + |
| *Navicula perminuta* GRUN. | | + |
| *Navicula porifera* HUST. | | + |
| *Navicula protracta* (GRUN.) CLEVE | | + |
| *Navicula radiosa* KÜTZ. | | + |
| *Navicula saprophila* LANGE-BERT. | | + |
| *Navicula seminulum* GRUN. | | + |
| *Navicula subminuscula* MANGUIN | | + |
| *Navicula tenelloides* HUST. | | + |
| *Navicula tripunctata* (O.F. MÜLER) BORY NAVTRI | | + |
| *Navicula trivialis* LANGE-BERT. | | + |
| *Navicula viridula* var. *linearis* HUST. | | + |
| *Navicula* sp. | | + |
| *Navicula* sp. small | | + |
| *Nitzschia acicularis* (KÜTZ.) W.M. SMITH | + | + |
| *Nitzschia amphibia* GRUN. | | + |
| *Nitzschia angustata* GRUN. | | + |
| *Nitzschia angustatula* LANGE-BERT. | | + |
| *Nitzschia archibaldii* LANGE-BERT. | | + |
| *Nitzschia calida* GRUN. | | + |
| *Nitzschia capitellata* HUST. | | + |
| *Nitzschia constricta* (GREGORY) GRUN. | | + |
| *Nitzschia dissipata* (KÜTZ.) GRUN. NITDIS | | + |
| *Nitzschia dissipata* var. *media* (HANTZSCH) GRUN. | | + |
| *Nitzschia flexoides* GEITLER | | + |
| *Nitzschia fonticola* GRUN. | | + |
| *Nitzschia frustulum* (KÜTZ.) GRUN. | | + |
| *Nitzschia fruticosa* HUST. | + | + |
| *Nitzschia graciliformis* LANGE-BERT. et SIM. | | + |
| *Nitzschia gracilis* HANTZSCH | + | + |
| *Nitzschia heufleriana* GRUN. | | + |
| *Nitzschia hungarica* GRUN. | | + |
| *Nitzschia incognita* KRASSKE | | + |
| *Nitzschia intermedia* HANTZSCH | | + |
| *Nitzschia levidensis* (W. SMITH) GRUN. | | + |
| *Nitzschia linearis* (AG.) W. SMITH | | + |
| *Nitzschia linearis* var. *subtilis* (GRUN.) HUST. | | + |
| *Nitzschia linearis* var. *tenuis* (W. SMITH) GRUN. | | + |
| *Nitzschia palea* (KÜTZ.) W. SMITH NITPAL | + | + |
| *Nitzschia palea* var. *debilis* (KÜTZ.) GRUN. | | + |
| *Nitzschia paleacea* GRUN. | | + |
| *Nitzschia recta* HANTZSCH | | + |
| *Nitzschia sociabilis* HUST. | | + |
| *Nitzschia subacicularis* HUST. | | + |
| *Nitzschia sublinearis* HUST. | | + |

Table 1. (continued).

| Taxa | Phytoplankton | Periphyton |
|---|---|---|
| *Nitzschia supralitorea* LANGE-BERT. | | + |
| *Nitzschia tubicola* GRUN. | | + |
| *Nitzschia* sp. | | + |
| *Nitzschia* sp. small | + | + |
| *Pinnularia* sp. | | + |
| *Rhoicosphenia abbreviata* (AG.) LANGE-BERT. | | + |
| *Surirella ovata* KÜTZ. | | + |
| *Surirella angusta* KÜTZ. | | + |
| *Surirella suecica* GRUN. | | + |
| CRYPTOPHYTA | | |
| *Chroomonas acuta* UTERM. | + | |
| *Chroomonas coerulea* (GEITL.) SKUJA | + | |
| *Cryptomonas erosa* var. *reflexa* MARSS. | + | |
| *Cryptomonas marssonii* SKUJA | + | |
| *Cryptomonas ovata* EHR. | + | + |
| *Cryptomonas rostratiformis* SKUJA | + | |
| DINOPHYTA | | |
| *Gymnodinium* sp. small | | + |
| *Peridinium* sp. | | + |
| CHLOROPHYTA | | |
| *Actinastrum hantzschii* LAGERH. | + | + |
| *Amphikrikos nanus* (FOTT et HEYNIG) HINDÁK | + | |
| *Chlamydomonas* sp. | | + |
| *Chlorella* sp. | + | |
| *Chlorogonium fusiforme* MATWIENKO | + | |
| *Chlorogonium maximum* SKUJA | + | |
| *Coelastrum microporum* NÄG. in A. BR. | + | + |
| *Coelastrum sphaericum* NÄG. | + | |
| *Crucigenia quadrata* MORR. | | + |
| *Crucigenia tetrapedia* (KIRCHN.) W. et G.S. WEST | + | + |
| *Crucigeniella apiculata* (LEMM.) KOM. | + | |
| *Dichotomococcus curvatus* KORŠ. | + | |
| *Dictyosphaerium anomalum* KORŠ. | + | |
| *Dictyosphaerium ehrenbergianum* NÄG. | + | |
| *Dictyosphaerium pulchellum* WOOD | + | |
| *Didymocystis inermis* (FOTT) FOTT | + | |
| *Diplochloris lunata* (FOTT) FOTT | + | |
| *Dunaliella* sp. | + | |
| *Kirchneriella contorta* (SCHMIDLE) BOHL. | + | + |
| *Kirchneriella lunaris* (KIRCHN.) MOET. | + | |
| *Kirchneriella obesa* (W. WEST) SCHMIDLE | + | |
| *Koliella longiseta* (KIRCHN.) HINDÁK | + | |
| *Lagerheimia balatonica* (SCHERFF.) HINDÁK | + | |
| *Micractinium crassisetum* HORTOB. | + | |
| *Micractinium pusillum* FRES. | + | + |
| *Monoraphidium arcuatum* (KORŠ.) HIND. | + | + |
| *Monoraphidium contortum* (THUR.) KOM. et LEGN. | + | + |
| *Neodesmus danubialis* HINDÁK | + | |
| *Nephroclamys subsolitaria* (G.S. WEST.) KORŠ. | + | |
| *Oedogonium* sp. | | + |

Table 1. (continued).

| Taxa | Phytoplankton | Periphyton |
|---|---|---|
| *Oocystis borgei* SNOW | + | |
| *Pachycladella komarekii* (FOTT et KOVÁČ.) REYM. | + | |
| *Pandorina morum* (O.F. MÜLLER) BORY | + | + |
| *Pediastrum boryanum* (TURP.) MENEGH. | + | |
| *Pediastrum duplex* MEYEN | + | + |
| *Pediastrum tetras* var. *tetraodon* (CORDA) HANSG. | | + |
| *Scenedesmus acuminatus* (LAGERH.) CHOD. | + | + |
| *Scenedesmus acutus* MEYEN | + | + |
| *Scenedesmus arnatus* CHOD. | + | |
| *Scenedesmus costato-granulatus* SKUJA | + | |
| *Scenedesmus denticulatus* LAGERH. | + | |
| *Scenedesmus ecornis* (EHR.) CHOD. | + | + |
| *Scenedesmus ellipsoideus* CHOD. | + | |
| *Scenedesmus intermedius* CHOD. | + | + |
| *Scenedesmus intermedius* var. *bicaudatus* HORTOB. | + | |
| *Scenedesmus nanus* CHOD. | + | |
| *Scenedesmus protuberans* FRITSCH | + | + |
| *Scenedesmus quadricauda* (TURP.) BRÉB. sensu CHOD. | + | + |
| *Scenedesmus spinosus* CHOD. | + | + |
| *Schroederia setigera* (SCHRÖD.) LEMM. | + | |
| *Scourfieldia cordiformis* TAKEDA | + | |
| *Siderocelis ornata* (FOTT) FOTT | + | |
| *Tetraedron caudatum* (CHOD.) HANSG. | + | |
| *Tetraedron minimum* (A. BR.) HANSG. | | + |
| *Tetrastrum staurogeniaeforme* (SCHRÖD.) LEMM. | + | |
| *Treubaria triappendiculata* BERN. | | + |

The proportion of diatoms varied between 94–100% of the total abundance of periphyton, so that this paper is reporting on the results of diatom investigations mainly.

Three hours after the positioning of the substrata only coccoid bacteria were found on. After 6 hours *Diatoma vulgaris* (11 cells $cm^{-2}$) and *Melosira varians* (1 cell $cm^{-2}$) appeared. After 9 hours, in addition, *Aulacoseira italica* var. *teniussima, Fragilaria ulna* and some Thalassiosiraceae species *(Cyclotella meduane* and *Stephanodiscus invisitatus)* were found. After 9 hours the total abundance was 38 cells $cm^{-2}$. After 24 hours the periphyton comprised more than 30 species, and the average (5 replicates) abundance was 8255 cells $cm^{-2}$ (Table 3). A definite increase was observed both in the abundance and in the chlorophyll *a* concentration from the second week on (Fig. 3).

The temporal change of diversity, evenness and the number of species showed similar trends during the whole colonization experiment (Fig. 4). Samples collected in the $6^{th}$ and $9^{th}$ hour showed small values and an increase was observed in the samples taken after 24 hours. A temporary decrease was noticed in the second week of colonization, then again an increase.

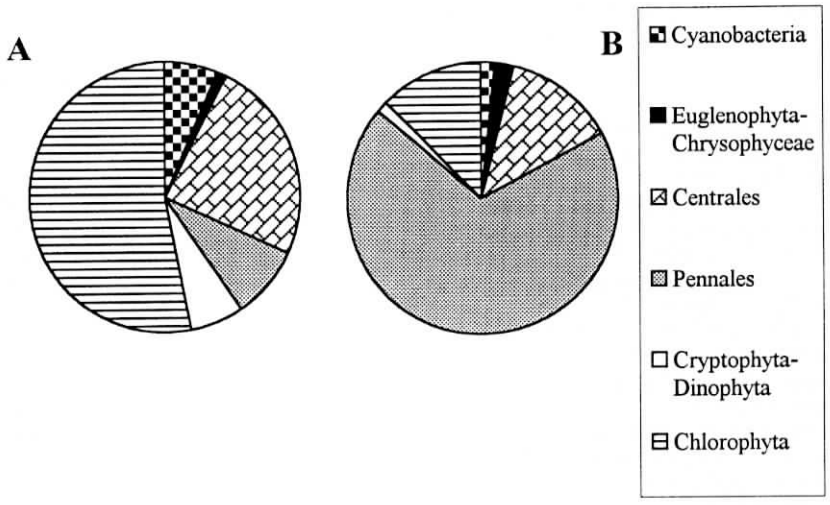



Fig. 2. The total taxonomical composition of the phytoplankton (**A**) and the periphyton (**B**).

In the beginning of colonization phytoplankton forms an important portion of the periphyton (Fig. 5). Planktic Centrales species occurred in relatively high numbers, mainly *Aulacoseira italica* var. *tenuissima, Cyclotella atomus* var. *gracilis, C. meduane* and *Skeletonema potamos*, but also euperiphytic species *Melosira varians* was found in high numbers. During the second week of colonization, with thickening of the periphyton, the planktic diatoms were gradually replaced by euperiphytic ones.

In the first week of the colonization the periphyton was characterised by the strong dominance of *Diatoma vulgaris*, which adheres with apical pads. This is gradually replaced by the dominance of *Melosira varians* and *Nitzschia dissipata* from the second week (Fig. 6).

In the beginning of the colonization the periphyton was characterized by the dominance of araphid diatoms, continuously giving place to biraphid species (Fig. 5). Within the attached organisms, the rate of C and C-S selected species was increasing (Fig. 7). As it is well seen on several micrographs, the basal layer of the periphyton developed in the first week of colonization, diatoms attached to

Table 2. The abundance and chlorophyll *a* content of phytoplankton during the study.

| | 22 Aug. | 27 Aug. | 03 Sept. | 10 Sept. |
|---|---|---|---|---|
| Abundance [ind. $ml^{-1}$] | 41460 | 40370 | 37250 | 22430 |
| Chl *a* [$\mu g\ l^{-1}$] | 89 | 85 | 66 | 38 |

Table 3. List of taxa (and their abundance in ind. $cm^{-2}$) found on the substratum after 3, 6, 9 and 24 hours respectively.

| | 3 hours | 6 hours | 9 hours | 24 hours |
|---|---|---|---|---|
| BACILLARIOPHYCEAE-CENTRALES | | | | 0 |
| *Aulacoseira granulata* var. *angustissima* (O. MÜLL.) SIM. | | | | 520 |
| *A. italica* var. *tenuissima* (GRUN.) SIM. | | | 7 | 130 |
| *Cyclostephanos dubius* (FRICKE) ROUND | | | | 195 |
| *Cyclotella atomus* HUST. | | | | 130 |
| *C. a.* var. *gracilis* GENKAL et KISS | | | | 325 |
| *C. meduane* GERMAIN | | | 1 | 390 |
| *C. meneghiniana* KÜTZ. | | | | 260 |
| *C. pseudostelligera* HUST. | | | | 65 |
| *C. radiosa* (GRUN.) LEMM. | | | | 65 |
| *Melosira varians* AG. | | 1 | 3 | 65 |
| *Skeletonema potamos* (WEBER) HASLE | | | | 2665 |
| *Stephanodiscus alpinus* HUST. | | | | 130 |
| *S. delicatus* GENKAL | | | | 65 |
| *S. hantzschii* GRUN. | | | | 130 |
| *S. invisitatus* HOHN et HELLERMAN | | | 1 | 325 |
| *S. minutulus* (KÜTZ.) CLEVE et MÖLLER | | | | 195 |
| *S. hantzschii* f. *tenuis* (HUST.) HÅK. et STOER. | | | | 195 |
| *Thalassiosira lacustris* (GRUN.) HASLE | | | | 65 |
| *T. pseudonana* HASLE et HEIMDAL | | | | 65 |
| BACILLARIOPHYCEAE-PENNALES | | | | |
| *Achnanthes minutissima* KÜTZ. | | | | 195 |
| *Diatoma tenuis* AG. | | | | 65 |
| *D. vulgaris* BORY | | 11 | 25 | 780 |
| *Fragilaria capucina* var. *gracilis* (OESTRUP) HUST. | | | | 65 |
| *F. ulna* (NITZSCH) LANGE-BERT. | | | 1 | 65 |
| *Nitzschia acicularis* (KÜTZ.) W.M. SMITH | | | | 195 |
| *N. amphibia* GRUN. | | | | 65 |
| *N. dissipata* (KÜTZ.) GRUN. | | | | 65 |
| *N. fonticola* GRUN. | | | | 65 |
| *N. frustulum* (KÜTZ.) GRUN. | | | | 65 |
| *N. gracilis* HANTZSCH | | | | 65 |
| *N. palea* (KÜTZ.) W. SMITH | | | | 65 |
| *N. sublinearis* HUST. | | | | 65 |
| *N. tubicola* GRUN. | | | | 65 |

the substratum without stalk, mainly with apical pad (Fig. 8). On the fourth day species capable of stalk formation (e.g. *Gomphonema* species) adhered to the substratum directly, but without stalk (Fig. 9). Many euplanktic Centrales species settled out onto the substratum from the phytoplankton (Fig. 10). In the second week the intermediate layer developed, where diatoms adhered with a little bit longer but not branching gelatinous stalks (Fig. 11). In the third week the top layer developed, where diatoms attached with a long, branching stalk (Fig. 12). Chain forming species (first of all *Melosira varians*) appeared and became domi-

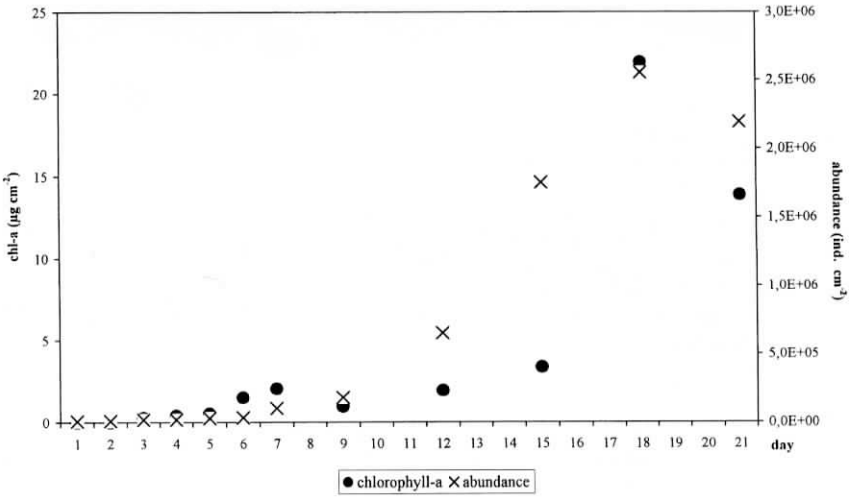



Fig. 3. Temporal changes of average abundance and average chlorophyll *a* concentration.

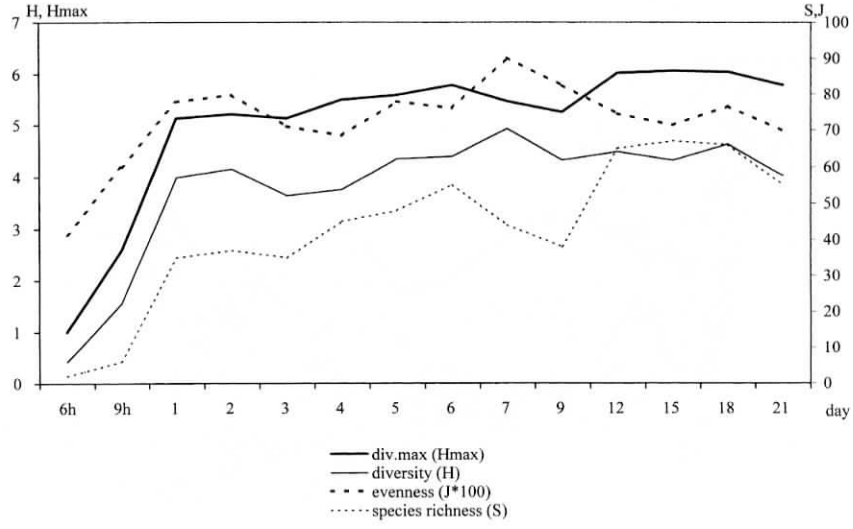



Fig. 4. Temporal changes of diversity, diversity maximum, evenness and species number during the experiment (**h** = hour).

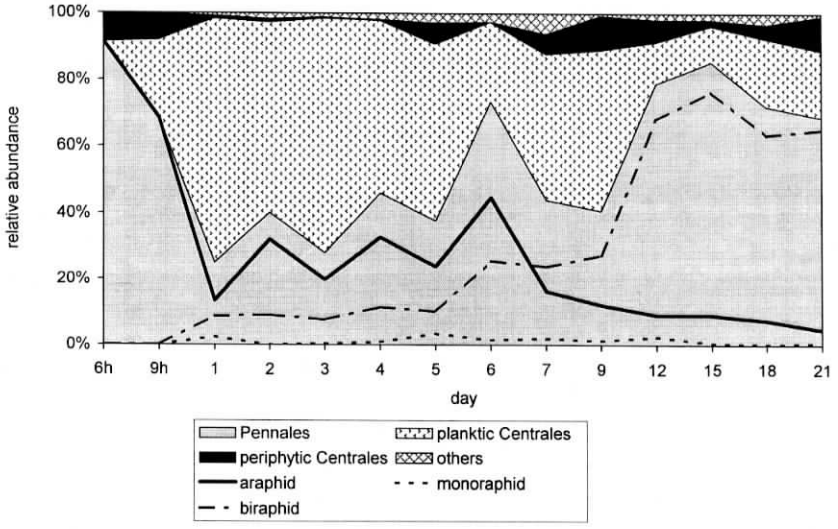



Fig. 5. Temporal changes of average relative abundance of the different groups of algae and araphid, monoraphid and biraphid pennates during the study (**h** = hour).

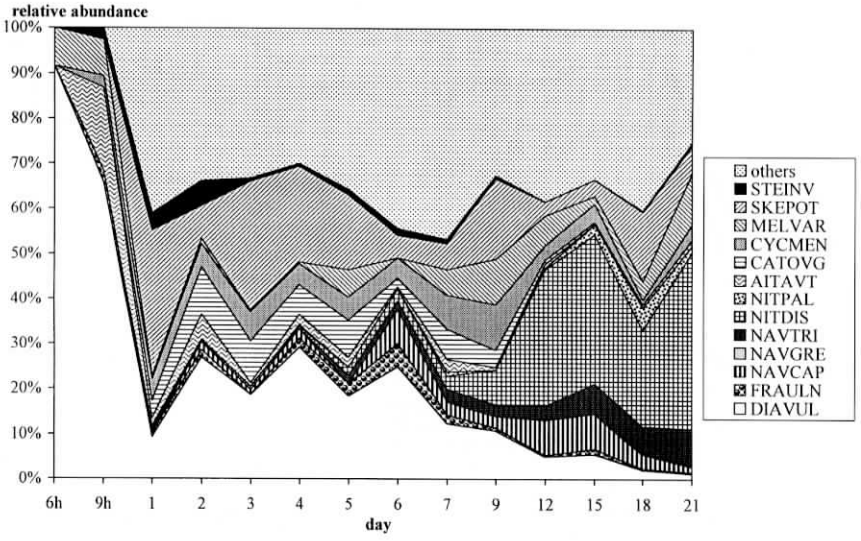



Fig. 6. Temporal changes of average relative abundance of dominant algae during the study (**h** = hour). Abbreviation in the Table 1.

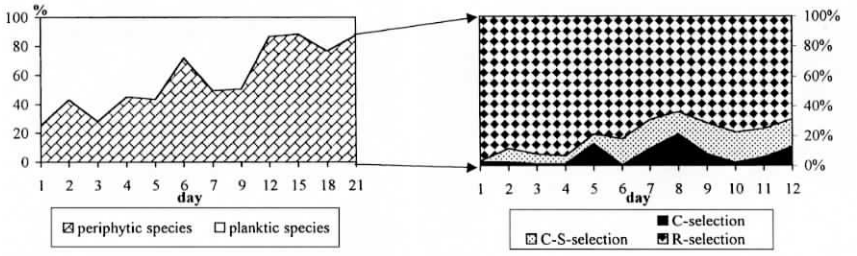


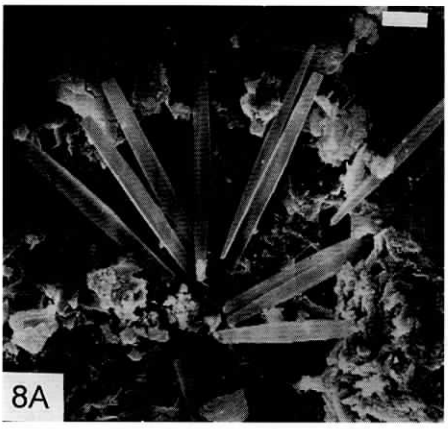

Fig. 7. Temporal changes of proportions of periphyton and plankton species on total phytobenthos counts (left) and the portions of C-, C-S- and R-selected species of periphyton taxa (right) during the colonization experiment.

nant in the periphyton for the 21st day (Fig. 13). At that time *Diatoma vulgaris* formed long chains. The basal layer of the periphyton was very rich in species by then, more and more euplanktic Centrales species "filtered" out from the phytoplankton (Fig. 14). Diatoms were sporadically thickly covered with bacteria (Fig. 15). Among the euplanktic Thalassiosiraceae species *Cyclotella meduane* (Fig. 16) appeared first and also reached the highest abundance (on the 21st day of colonization we counted 74000 cells $cm^{-2}$).

## Discussion

The high number of taxa and the high abundance of euplanktic Centrales in the periphyton was surprising in some respect (Table 3, Fig. 5). Based on SÖRENSSEN index, little similarity was observed between phytoplankton and periphyton species (Table 1), especially when only the pennates were compared, because most of them are sessile and time to time they detach, drift and attach again on an appropriate surface. Higher similarity was found comparing other species, as they are settled from the phytoplankton (e.g. Thalassiosiraceae, Chlorococcales). CAZAUBON (1988) observed the species spectrum that in the drift and on artificial substratum was strongly linked, because the artificial substrate collected the drift flora which have become detached from the different natural habitats. Although this study was carried out in a karstic spring (in South-East France) where no euplanktic assemblage is formes. CHO (1991) found a clear separation of the planktic and periphytic diatom assemblages in Naktong River Estuary (Korea).

During the first few hours the periphyton was characterized by small diversity, low number of species and small evenness. On the second day there was already a diverse community with great evenness containing 35 species. The number of species had been rising more or less steadily during the study. The composition of the periphyton had changed remarkably the monoraphid species was replaced by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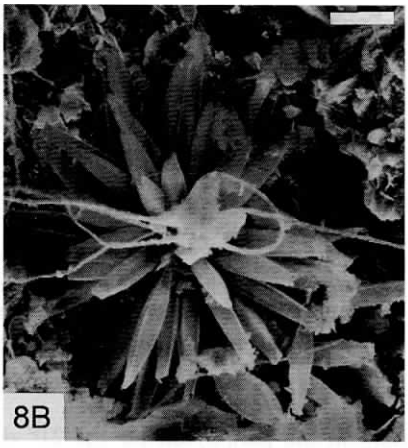
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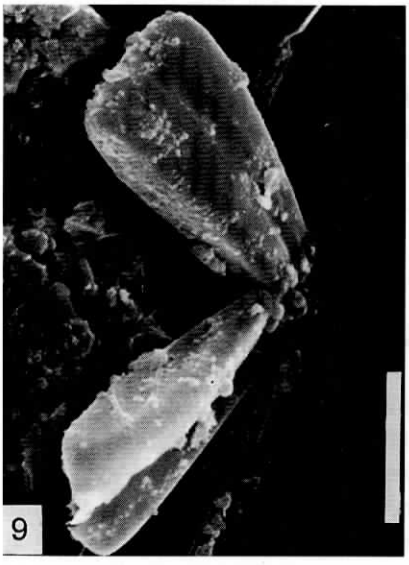
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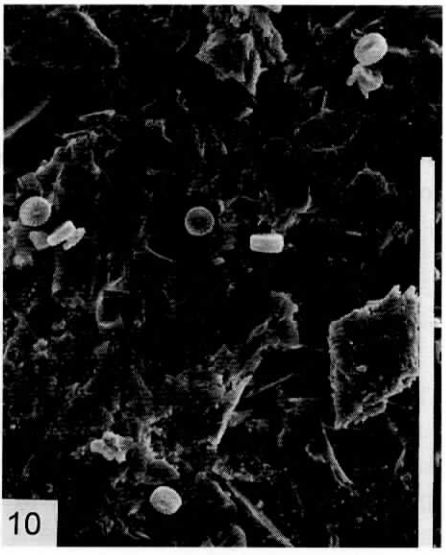
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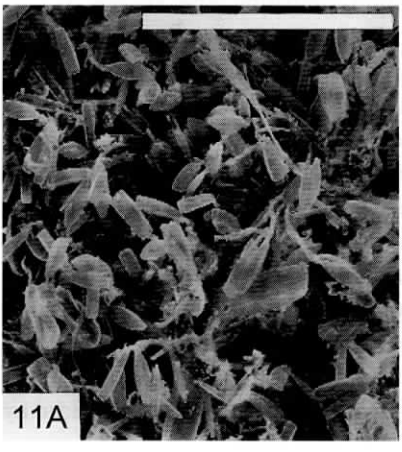
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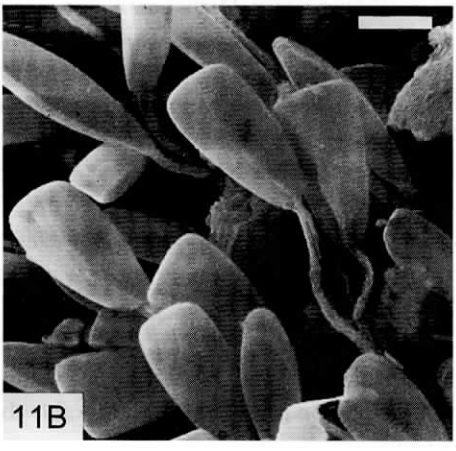
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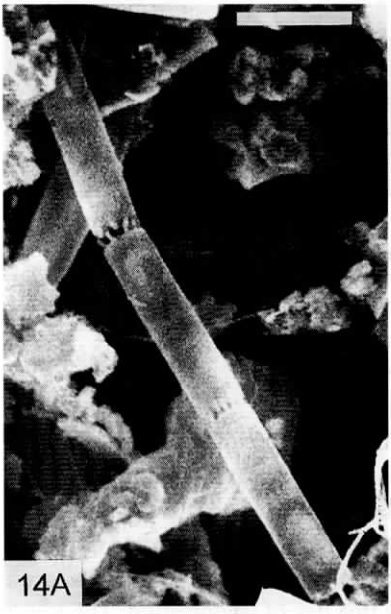
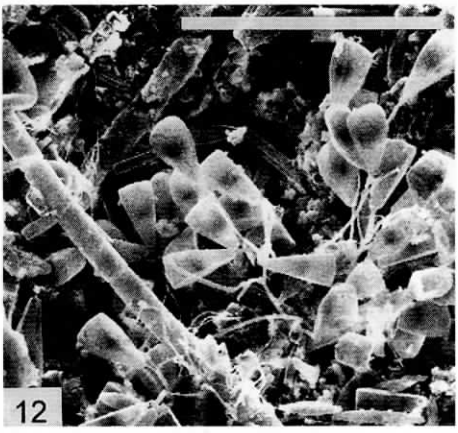
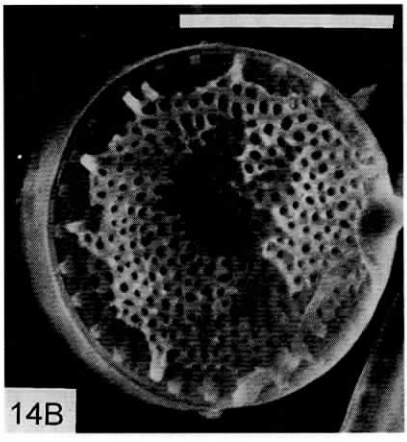
◁ Fig. 8. 6 days periphyton (**A**: *Fragilaria* sp., **B**: *Nitzschia* sp.). Diatoms attached to the substratum mainly with apical pad. [Bar: 10 μm]
Fig. 9. 4 days periphyton. The stalk forming species (*Gomphonema* sp.) attached to the substratum still without stalk. [Bar: 10 μm]
Fig. 10. 4 days periphyton. In the early stage of colonization many euplanktic Centrales species settled out onto the substratum from the phytoplankton. [Bar: 100 μm]
Fig. 11. 12 days periphyton (**A**: "total" view, **B**: mainly *Gomphonema olivaceum*). Diatoms attached with short, non branching stalks. [Bar: A = 100 μm, B = 10 μm]



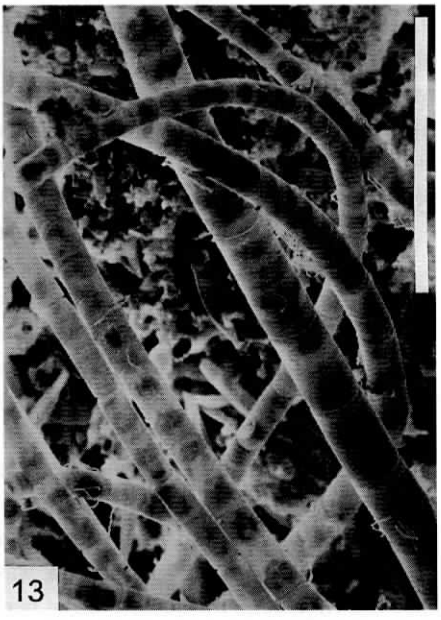
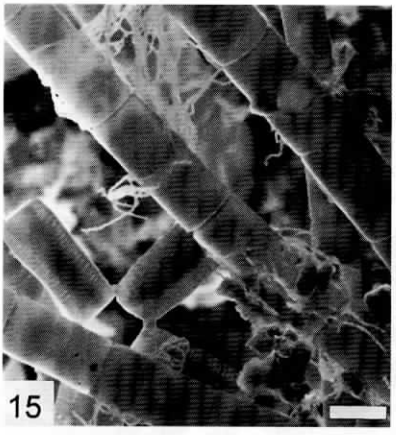




Fig. 12. 18 days periphyton. Diatoms attached with long, branching stalk. [Bar: 100 μm]
Fig. 13. 21 days periphyton. Chain forming diatoms (first of all *Melosira varians*) appeared and became dominant in the periphyton. [Bar: 100 μm]
Fig. 14. 18 days periphyton (**A**: *Skeletonema potamos*, **B**: *Thalassiosira lacustris*). More and more euplanktic species "filtered" out from the phytoplankton. [Bar: 10 μm]



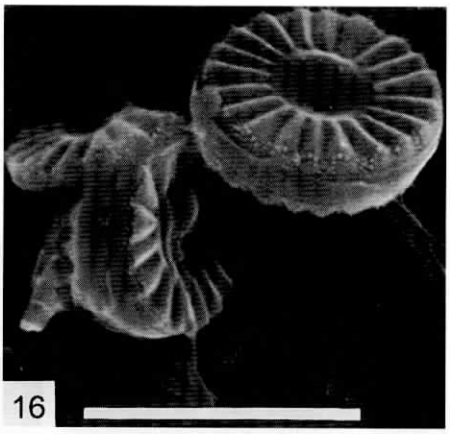




Fig. 15. 21 days periphyton. Different bacteria are attached to the surface of *Melosira* valves. *Melosira varians* and *Diatoma vulgaris* formed chain. [Bar: 10 μm]
Fig. 16. 4 days periphyton. Among the euplanktic Thalassiosiraceae taxa, *Cyclotella meduane* appeared most quickly and also reached the highest abundance on the substratum. [Bar: 10 μm]

the dominance of biraphid ones and the formation of the intermediate layer had started. After that, more and more new species appeared periphyton, thus diversity increased, but the evenness significantly decreased. We took similar results during an earlier colonization study in the River Danube (Ács 1998). Stevenson (1984) also found a diverse community with high evenness on artificial substratum in Fleming Creek on the first day of colonization. The result of his 32-day-study was that the number of species increased all the time, but the evenness (and also the diversity) decreased remarkably.

The changes of the number of species and evenness in periphyton depends on the immigration and reproduction rate of algae. Immigration causes an increase in the number of species. Reproduction, on the one hand, maintains species richness by reducing the losses deriving from death, emigration and grazing, although reducing evenness on the other hand, by higher reproduction rate can of growing species. During this study the periphyton was mainly composed by quick growing R-selected species in the first week of colonization, the evenness increased parallel with the increase in species richness. From the second week a small decrease occurred in evenness when the rate of C, C-S selected species increased (although the periphyton was still mainly composed of R-selected species). In general the succession of periphyton community should be seen as a community developing towards a "climax" community composed of S, C-S or C taxa (Biggs et al. 1998). Certainly, during the 21 days of our study the periphyton did not reach the "climax" stage, since it was characterized by the dominance of R-selected species. Barry et al. (1996) demonstrated that the R-selected diatoms

are clearly good colonizers and usually colonize before C- and S-selected taxa in a disturbed system (as large rivers generally). According to STEVENSON & PETERSON (1989) there are some differences within the R-selected group such as araphid species being much better immigrants than mono- and biraphid ones. Our studies clearly showed that the dominance of araphid species characterized the periphyton in the beginning of colonization and was replaced by the dominance of biraphid algae from the second week.

*Skeletonema potamos* is a characteristically dominant species of the phytoplankton of the River Danube in warm water periods (KISS et al. 1994). It is not surprising that we found it in the periphyton in relatively high numbers, as it settles out, gets caught by the periphyton cover on the substratum. For these reasons we can also find other Thalassiosiraceae species on the substratum only after a few hours (after 9 hours) as they composed half of the phytoplankton. In the first week of colonization (when the periphyton is thin, it has only a basal layer with low algal abundances) the periphyton was characterized by the dominance of euplanktic species and *Diatoma vulgaris*. In spite of this, euperiphytic diatoms appeared soon, from the 6$^{th}$ hour, but became dominant only from the second week on.

During colonization experiments carried out in the sea it was clearly proved that the first colonizers were bacteria followed by sessile diatoms and fungi (MARSHALL 1988). During our study we found only coccoid bacteria (mainly colineform ones, VARGA et al. 2000) on the substratum after 3 hours of its immersion, but we found already algae after 6 hours. The first colonizer alga was *Diatoma vulgaris* adhering with apical pads. This species attach to the substratum very quickly and efficiently with secreted material through its apical pore-field. The first cells of apical pad forming *Fragilaria ulna* and that of *Melosira varians*, which later formed long chains and became dominant, also quickly appeared. It is remarkable, that all three species do not appear frequently in the phytoplankton at the Göd section of River Danube.

The basal layer of the periphyton of River Danube develops in the first week of colonization in summer. At this time diatoms adhere to the substratum directly with apical pad. In the second week stalk forming species form the intermediate layer with non branching gelatinous stalk. In the third week the top layer forms out already. This consists mainly of chain forming diatoms, and diatoms adhering with long, branching gelatinous stalk. There is a better nutrient supply and light conditions for the quick development. The thick periphyton filters out euplanktic organisms from the water like a net, therefore more and more euplanktic Centrales species can be found in the periphyton. PATRICK (1976), during her river studies also found first a "two dimensional" community on the substratum, then stalk form species appear gradually, and finally a three dimensional periphyton is draped by different chain forming diatoms (e.g. *Melosira*).

It frequently occurs that the surface of diatoms living in the periphyton is covered by bacteria. COOKSEY (1992) found that diatoms are not only a substratum for the bacteria but they have metabolic interaction. The bacteria take up certain extracellular products (e.g. amino-acids and sugars) of diatoms as a nutrient source. The high rate of primary production of the attached algae and cyanobacteria is only possible because of the internal recycling of nutrients within the so called biofilm, including carbon and gases within the attached microcommunities (WETZEL & SÖNDERGAARD 1998).

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