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SYMBIOSIS BETWEEN DIATOMS AND CYANOBACTERIAL COLONIES

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BALTIC SEA
BRACKISH WATER
COMMUNITY ECOLOGY
DIATOMS
DIVERSITY
RIVULARIA
PRINCIPAL COMPONENT ANALYSIS
SYMBIOSIS

ABSTRACT. – Species-rich diatom communities were found to occur within colonies of the nitrogen-fixing cyanobacterium *Rivularia atra* Roth in the brackish Baltic Sea. These communities have never been reported before. To understand how the special conditions within the cyanobacterial colonies (limited light, presence of host mucilage, chemical excretions by the host) affected diatom community composition, comparisons were made with diatom communities epiphytic on macroalgae sampled from the same stones as the *Rivularia* colonies. Motile diatoms of the genera *Amphora*, *Berkeleya*, *Cymbella*, *Entomoneis*, *Epithemia*, *Lunella*, *Mastogloia*, *Nitzschia* and *Rhopalodia* dominated the *Rivularia*-associated communities whereas attached diatoms of the genera *Achnanthes*, *Cocconeis*, *Diatoma*, *Fragilaria*, *Gomphonema*, *Hyalosira*, *Licmophora*, *Rhoicosphenia* and *Tabularia* dominated the epiphytic communities on macroalgae. Diatom species richness, Shannon diversity and evenness were all significantly higher in the *Rivularia* communities. The diatoms probably profit from the symbiosis with *Rivularia* in several ways: (1) by protection against grazing (2) by protection against physical disturbances, (3) by using cyanobacterial mucilage as a substratum for motility and (4) by excretion of inorganic and organic nutrients from *Rivularia* cells. It is more difficult to identify advantages for *Rivularia* in this symbiosis, but nutritional advantages may exist for the cyanobacterium as well.

MER BALTIQUE
EAU SAUMATRE
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RÉSUMÉ. – Des communautés diatomiques riches en espèces ont été repérées au sein de colonies de *Rivularia atra* Roth, cyanobactéries fixatrices d'azote, en zone saumâtre de la mer Baltique. Ces communautés n'avaient pas été notées précédemment. Pour comprendre de quelle manière les conditions spécifiques rencontrées dans ces colonies cynanobactériennes pouvaient influer sur la composition de la communauté diatomique (lumière atténuée, présence de mucilage et d'excrétions chimiques en provenance de l'hôte), des comparaisons ont été établies avec les communautés de Diatomées épiphytes, rencontrées sur les macrophytes échantillonnés sur les mêmes roches que les colonies de *Rivularia.* Les Diatomées mobiles, appartenant aux genres *Amphora*, *Berkeleya*, *Cymbella*, *Entomoneis*, *Epithemia*, *Lunella*, *Mastogloia*, *Nitzschia* et *Rhopalodia* dominent les communautés associées à *Rivularia*, alors que les Diatomées fixées appartenant aux genres *Achnanthes*, *Cocconeis*, *Diatoma*, *Fragilaria*, *Gomphonema*, *Hyalosira*, *Licmophora*, *Rhoicosphenia* et *Tabularia* dominent les communautés épiphytes des macrophytes. La richesse spécifique, l'indice de diversité de Shannon et l'indice de similitude sont tous, et de manière significative, plus élevés dans les communautés de *Rivularia*. Les Diatomées profitent probablement de leur symbiose avec *Rivularia* de plusieurs manières : (1) en trouvant une protection contre le broutage, (2) un abri contre les perturbations physiques du milieu, (3) en utilisant le mucilage cyanobactérien comme substrat pour leur mobilité et (4) en profitant de l'excrétion de composés minéraux et organiques par les cellules de *Rivularia*. Il est plus difficile, dans cette symbiose, d'identifier les avantages pour la *Rivularia*, mais des avantages nutritionnels peuvent également être envisagés pour la cyanobactérie.

INTRODUCTION

The occurrence of unicellular nitrogen-fixing cyanobacterial endosymbionts in diatoms has frequently been reported (e.g. DeYoe *et al*. 1992, Villareal 1994, Carpenter & Janson 2000). Here we present an example of the opposite: diatoms living within multicellular colonies of the nitrogen-fixing cyanobacterium *Rivularia atra* Roth which occurs abundantly on rocky shores in the brackish Baltic Sea in autumn-winter. The maximum diameter of the *Rivularia* colonies is ca. 4 mm (Schmidt 1899, Snoeijs 1987) and the trichomes are tightly packed inside the colonies. Between the cyanobacterial trichomes, the diatoms form typical communities which to our knowledge never have been reported before. These diatom communities could be considered endophytic or epiphytic depending on the status one attaches to a colony versus a macroalgal thallus.

The relationship between microalgae and their hosts can be regarded as symbiotic, which is defined as a close association of two or more organisms of different species (Stiling 2002). The interaction may be advantageous to one or more parties (commensalism, mutualism), e.g. by supply of food, protection from enemies or provision of a favourable environment to grow and reproduce. The symbiosis between diatoms and *Rivularia* is not an obligate relationship in the sense that neither participant could exist without the other; *Rivularia* colonies without diatoms can be found and the diatom species living within *Rivularia* colonies also occur elsewhere. Similar symbioses occur between diatoms and kelps, e.g. *Navicula endophytica* Hasle and *Navicula fucicola* Taasen occur between the cells of *Fucus vesiculosus* (Taasen 1975, Baardseth & Cuesta 1983), and between diatoms and protozoans, e.g. diatom communities occur within colonies of the ciliate genus *Ophrydium* (Geitler 1975, Dute *et al.* 2000). In these studies the symbionts were identified as motile diatoms with the ability to traverse the host mucilage.

Our study presents a detailed description of the diatom communities in *Rivularia atra* in the northern Baltic Sea in comparison with epiphytic diatom communities sampled from the same stones. We also discuss why certain groups of diatom species may prefer the dark conditions within the *Rivularia* colonies.

MATERIAL AND METHODS

Samples were collected from six sites (Sites 1-6) at Forsmark (60º 25’ 80’’ N, 18º 11’ 14’’ E) in the southern Bothnian Sea (northern Baltic Sea) in early winter 1997. The area has a year-round stable salinity of 5 psu. The sampling sites were chosen according to the availability of *Rivularia atra* and were all shallow and little exposed to wave action. A ‘site’ was defined as a distance of ca. 10 m along the shore. One sampling site (Site 6) was situated inside the Forsmark Biotest basin, an artificial enclosure receiving thermal discharge from a nuclear power plant (Snoeijs 1994a) and had a temperature anomaly of +2 °C. This was the only site where *R. atra* was found inside the basin; it was absent from sites heated by 3-10 °C. Eight stones which visibly contained *R. atra* colonies were taken from 0.0-0.3 m of depth at each site. The stones were transported to the laboratory and stored in a cold room at 5 °C until further processing. Water temperature and salinity were measured at each site with an YSI MODEL 33, S-C-T Meter™ (Table I).

In the laboratory the epilithic biomass was separated from the stones by scraping with a sharp pointed knife and divided into two types of samples: (1) *Rivularia atra* samples consisting of ca. 50-100 cyanobacterial colonies 1-2 mm in diameter and (2) Macroalgal samples consisting of red, green and brown macroalgae. The macroalgal samples consisted mainly of *Cladophora glomerata* L., *Enteromorpha* spp. and *Ceramium gobii* Wærn. Living samples were studied by light microscopy. Altogether 96 samples (6 sites, 8 stones per site, 2 types of samples per stone) were preserved in 70% ethanol.

For the preparation of permanent diatom slides, the samples were treated with hydrogen peroxide and a few pinches of potassium dichromate to oxidise the organic matter, and then mounted in Naphrax™ (refraction index = 1.74) according to the method described in Snoeijs (1994b). Diatom species composition was assessed by counting all diatom valves in a radial transverse of the cover slip using a Nikon™ light microscope at ×1000 magnification under oil immersion. For each of the 96 samples 250 valves were counted. Community biovolumes were calculated using the cell volumes reported by Snoeijs *et al.* (2002). The majority of the studied species are illustrated in Snoeijs (1993), Snoeijs & Vilbaste (1994), Snoeijs & Potapova (1995), Snoeijs & Kasperoviciene (1996) and Snoeijs & Balashova (1998).

Community diversity was measured by species richness (number of species in 250 valves), Shannon index ($H' = \Sigma p_i \ln p_i$, where p_i is the proportion of individuals found in the ith species) and the evenness index ($E = H'/H'_{max}$) (Stiling 2002). To summarise community composition in relation to sampling site and host (*Rivularia* or macroalgae), principal component analysis (PCA, Jongman *et al.* 1987), implemented with the programme CANOCO, Version 4.5 (Ter Braak & Šmilauer 2002), was used on log-transformed relative abundance data.

Table I. – Summary of sampling sites, sampling dates and environmental data.

Site	Date (1997)	Salinity (psu)	Water temperature (°C)	Ice cover	Artificially heated
1	20 November	4.9	3.0	No	No
2	20 November	4.9	2.5	No	No
3	4 December	4.8	0.6	Yes	No
4	4 December	4.8	-0.05	Yes	No
5	4 December	4.9	2.5	No	No
6	4 December	4.8	4.5	No	Yes

RESULTS

Community structure

The relative abundances of diatoms with motile and epipsammic life forms were ca. 2.5 times higher in the communities within the *Rivularia* colonies (51.4/21.8 and 9.5/3.8%, respectively) while the relative abundance of the attached epiphytic life form was 2.2 times higher in the epiphytic communities (70.8/32.9%) (Table II). The same patterns were observed for all 35 abundant diatom species, except for *Navicula perminuta*, *Nitzschia paleacea* and *Cocconeis placentula*, which had similar abundances in both community types (Table II). Dominance (>50%) of motile diatom taxa was found at four of the six sampling sites in the *Rivularia* samples, both based on abundance and biovolume, but never in the macroalgal samples (Fig. 1). At all six sampling sites the occurrence of the motile life form was always much higher in the

Table II. – List of the 35 diatom taxa with total relative abundances (RA) > 0.4% in the 48 *Rivularia atra* samples and/or in the 48 macroalgal samples, sorted according to life form. Cell volumes *cf.* Snoeijs *et al.* (2002) or calculated from frustule measurements in the present study.

Abbreviation	Diatom taxon	Cell volume (µm^3)	RA *Rivularia* (%)	RA Macroalgae (%)
	Life form: motile			
Amp fleb	*Amphora* cf. *flebilis* Simonsen	87	2.9	0.1
Amp coff	*Amphora coffeaeformis* (C.A. Agardh) Kützing	639	0.6	0.2
Amp hybr	*Amphora hybrida* Grunow in Van Heurck	2789	0.5	0.0
Amp pedi	*Amphora pediculus* (Kützing) Grunow in A. Schmidt *et al.*	110	0.7	0.3
Ber fenn	*Berkeleya fennica* Juhlin-Dannfelt	123	6.4	1.3
Cym pusi	*Cymbella pusilla* Grunow in A. Schmidt *et al.*	263	0.5	0.0
Ent pseu	*Entomoneis pseudoduplex* Osada & Kobayasi	2353	1.1	0.0
Epi sore	*Epithemia sorex* Kützing	1866	7.2	3.7
Epi tuwe	*Epithemia turgida* var. *westermannii* (Ehrenberg) Grunow	22046	0.7	0.3
Lun bise	*Lunella bisecta* Snoeijs	35	0.5	0.1
Mas pumi	*Mastogloia pumila* (Cleve & Möller) Cleve	1110	2.7	0.3
Mas smit	*Mastogloia smithii* Thwaites	2402	6.0	1.0
Nav perm	*Navicula perminuta* Grunow in Van Heurck	74	3.7	4.4
Nit ardu	*Nitzschia ardua* Cholnoky	243	1.4	0.4
Nit frus	*Nitzschia frustulum* (Kützing) Grunow in Cleve & Grunow	61	6.8	4.0
Nit inco	*Nitzschia inconspicua* Grunow	21	2.8	1.4
Nit micr	*Nitzschia microcephala* Grunow in Cleve & Möller	55	3.0	1.0
Nit pace	*Nitzschia paleacea* (Grunow) Grunow in Van Heurck	43	2.1	3.3
Rhp gibb	*Rhopalodia gibba* (Ehrenberg) O. Müller	6216	1.9	0.0
	44 other taxa		4.0	1.7
	Total RA of motile taxa (63 taxa)		51.4	21.8
	Life form: epipsammic			
Fra sp.	*Fragilaria* sp.	150	3.5	1.3
Mar atom	*Martyana atomus* (Hustedt) Snoeijs	33	0.8	0.5
Mar mart	*Martyana martyi* (Héribaud) Round in Round *et al.*	673	1.3	0.3
Pla deli	*Planothidium delicatulum* (Kützing) Round & Bukhtiyarova	159	0.5	0.3
Pss zeil	*Pseudostaurosira zeillerii* (Héribaud) Williams & Round	90	3.4	1.4
	7 other taxa		0.9	0.4
	Total RA of epipsammic taxa (12 taxa)		9.5	3.8
	Life form: epiphytic			
Ach brin	*Achnanthes brevipes* var. *intermedia* (Kützing) Cleve	5290	0.6	0.9
Coc pedi	*Cocconeis pediculus* Ehrenberg	1722	2.6	7.9
Coc plac	*Cocconeis placentula* Ehrenberg	465	2.5	2.8
Dia moni	*Diatoma moniliformis* Kützing	269	2.8	5.5
Fra hyal	*Fragilaria hyalina* (Kützing) Grunow	793	0.1	1.0
Gom oliv	*Gomphonema olivaceum* (Hornemann) Brébisson	3156	9.2	13.9
Hya deli	*Hyalosira delicatula* Kützing	613	0.2	1.9
Lic debi	*Licmophora debilis* (Kützing) Grunow in Van Heurck	2234	0.6	2.6
Rho curv	*Rhoicosphenia curvata* (Kützing) Grunow	698	12.5	29.2
Tab laev	*Tabularia* cf. *laevis* Kützing*	696	1.2	3.6
Tab tabu	*Tabularia tabulata* (C.A. Agardh) Snoeijs	11967	0.7	1.6
	16 other taxa		1.4	1.4
	Total RA of epiphytic taxa (27 taxa)		32.9	70.8

* See Snoeijs (1992)

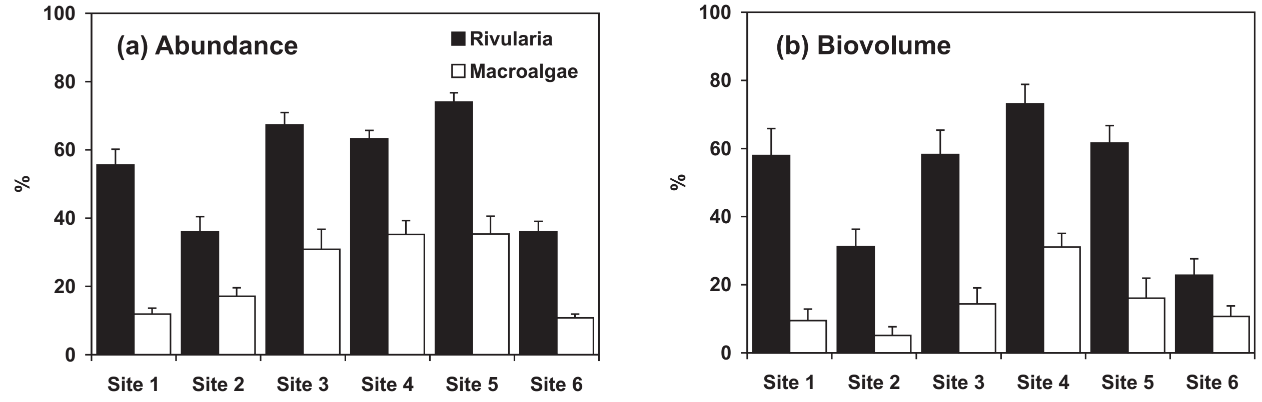

Fig. 1. – Occurrence of the motile life form in the diatoms of the *Rivularia* and macroalgal samples, expressed as (a) relative abundance and (b) relative biovolume.

Rivularia than in the macroalgal samples from the same site. Microscopic observations of living *Rivularia* colonies crushed between two microscopic slides showed that epiphytic species such as *Achnanthes brevipes*, *Cocconeis pediculus*, *Gomphonema olivaceum*, *Licmophora debilis* and *Tabularia tabulata* occurred attached to the outside of the colonies while the motile species occurred deeper down inside the colonies.

Community diversity

Species richness, Shannon diversity and evenness were significantly higher in the *Rivularia* samples than in the macroalgal samples at all sampling sites, except for species richness at Sites 4 and 5 (Table III).

Community composition

The data set used in the PCA contained 96 samples and 102 diatom taxa. The PCA yielded the eigenvalues 0.20, 0.12, 0.08 and 0.05 for the first four ordination axes, respectively, indicating that Axis 1 explained most of the variation in the data. The sample scores had relative positions in the ordination with respect to host and sampling site (Fig. 2a). Along Axis 1 the sample scores of the *Rivularia* samples (to the left) were clearly separated from those of the macroalgal samples (to the right). Along Axis 2 a separation was found according to sampling date and site, suggesting that environmental variables explained part of the variation in the data as well, but much less than host because of the lower eigenvalue of axis 2 compared with axis1. When temperature, salinity and ice-cover were tested passively in the PCA, i.e. not used as constraints, but later tested on the ordination by multiple regression analysis, they appeared to have no significant effects on the variation in community composition.

The patterns shown by the taxon scores in the ordination summarised the distribution of the diatom taxa by host and site (Fig. 2b). Diatom taxa typical of epiphytic communities were found to the right of the ordination. These are mainly typical epiphytes (e.g. *Cocconeis pediculus*, *Diatoma moniliformis*, *Gomphonema olivaceum*, *Fragilaria hyalina*, *Hyalosira delicatula*, *Licmophora debilis*, *Rhoicosphenia curvata*, *Tabularia tabulata*). The

Table III. – Mean diversity measures (± STD) in 250 diatom valves from the *Rivularia atra* samples (n=8) and in 250 diatom valves from the macroalgal samples (n=8) at each sampling site. The results of pairwise comparisons of the means (t-tests) are shown as the significance levels: *** = p<0.001, ** = p<0.01, * = p<0.05, n.s. = no significant difference (p ⩾ 0.05).

	Species richness			Shannon index			Evenness index		
Site	*Rivularia*	Macroalgae	t-test	*Rivularia*	Macroalgae	t-test	*Rivularia*	Macroalgae	t-test
Site 1	30.5 ± 1.8	20.6 ± 3.6	***	2.90 ± 0.12	2.22 ± 0.07	***	0.85 ± 0.03	0.74 ± 0.04	***
Site 2	27.9 ± 2.7	18.1 ± 3.6	***	2.74 ± 0.13	2.05 ± 0.21	***	0.83 ± 0.04	0.71 ± 0.06	***
Site 3	27.5 ± 2.6	22.0 ± 4.4	**	2.80 ± 0.17	2.40 ± 0.34	**	0.84 ± 0.05	0.78 ± 0.07	*
Site 4	23.9 ± 2.8	23.8 ± 3.2	n.s.	2.61 ± 0.12	2.38 ± 0.23	*	0.82 ± 0.03	0.75 ± 0.06	**
Site 5	22.5 ± 1.8	19.6 ± 5.8	n.s.	2.64 ± 0.10	2.24 ± 0.25	**	0.85 ± 0.03	0.77 ± 0.05	**
Site 6	26.1 ± 2.7	16.9 ± 3.0	***	2.70 ± 0.13	1.91 ± 0.22	***	0.83 ± 0.02	0.68 ± 0.05	***

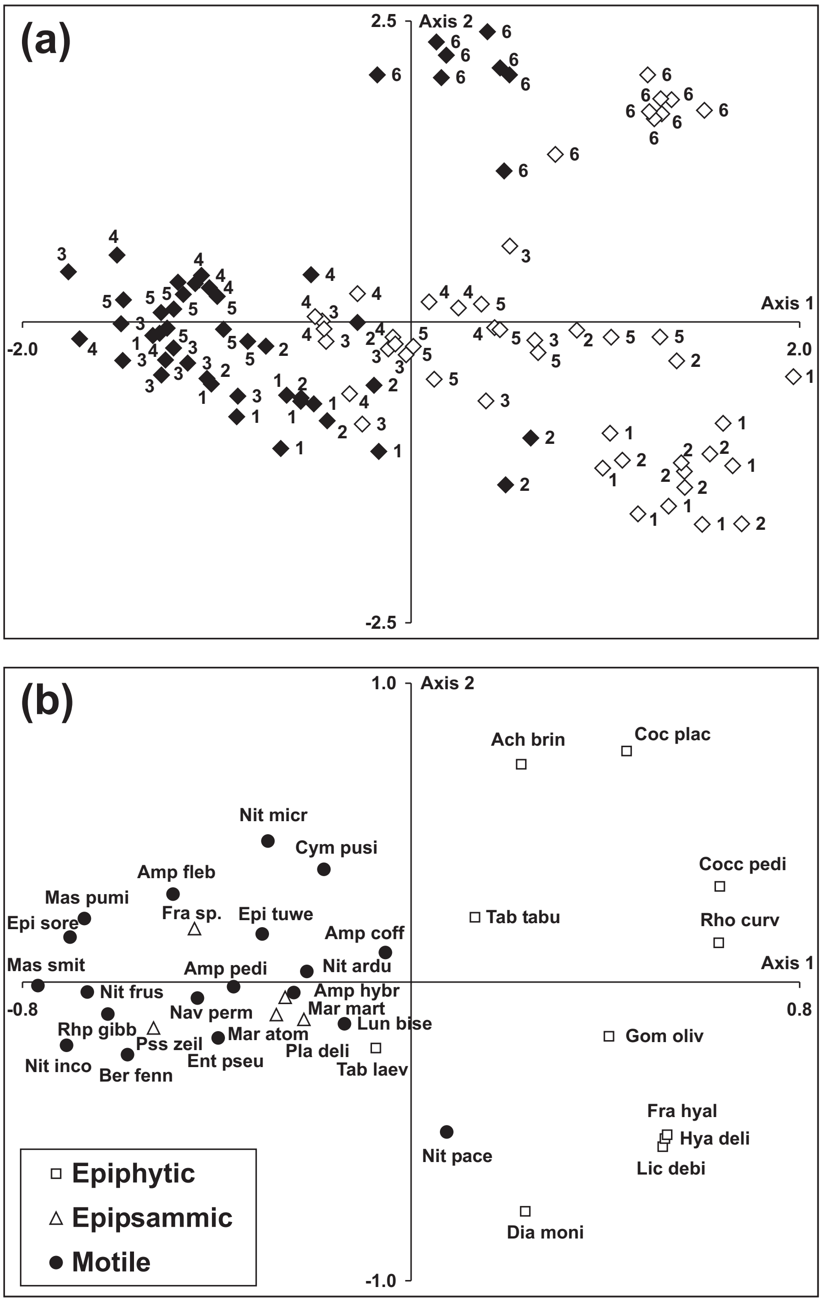

Fig. 2. – PCA ordination diagrams based on 96 samples and 102 diatom taxa. a, Sample scores with black diamonds representing the 48 *Rivularia* samples and white diamonds representing the 48 macroalgal samples. b, Taxon scores of the 35 diatom taxa with relative abundances >0.4% in the data set, abbreviations *cf.* Table II.

diatom composition in the communities found to the left of the ordination are mainly motile taxa typical of the *Rivularia* samples. These include *Amphora* spp., *Berkeleya fennica*, *Cymbella pusilla*, *Entomoneis pseudoduplex*, *Epithemia* spp., *Mastogloia* spp., *Nitzschia* spp. and *Rhopalodia gibba.* Also the importance of small epipsammic Fragilariaceae is shown by the ordination. Small epipsammic diatom taxa *Fragilaria* sp., *Martyana* spp., *Planothidium delicatulum* and *Pseudostaurosira zeillerii* were also placed in the left half of the ordination, indicating that also these taxa were more abundant in the *Rivularia* samples than in the macroalgal samples. In the upper-right of the ordination where the sample scores of the artificially heated Site 6 were situated (Fig. 2a), the taxon scores of *Cocconeis placentula* and *Achnanthes brevipes* were found.

DISCUSSION

Host-specificity

The diatom communities associated with *Rivularia* and macroalgae consisted of species that are known to occur in the northern Baltic Sea (Rönnberg & Lax 1980, Hällfors & Niemi 1989, Snoeijs 1988, 1994b, 1995). The quantitative composition of epiphytic diatom communities is usually highly host-specific (Ramm 1977, Medlin 1983, Snoeijs 1994b). In the present comparison between *Rivularia* and macroalgae, diatom species with particular life forms were shown to be strongly host-specificity with motile species predominating in the *Rivularia* colonies and (attached) epiphytic on the macroalgae. Generally, life-form strategies, such as attached (epiphytic, epilithic, epipsammic) or motile (metaphytic, epipelic), are key aspects to niche differentiation in diatoms and determine their responses to environmental conditions (Round 1981, Snoeijs 1995, Snoeijs *et al.* 2002). In our study host-specificity was more important than the environmental conditions at the different sampling sites because the separation according to host was along the first (most important) PCA axis. This was probably at least partly related to the low variation in environmental variables in our data set although the heated sampling site was separated from the others along the second (less important) PCA axis.

Diversity

Diatom community diversity was higher in the *Rivularia* samples than in the macroalgal samples. The reason for this is probably that the *Rivularia* colonies provided a larger variety of microhabitats than the macroalgae. The same diatom species with typical attached life forms were observed attached to the surface area of the *Rivularia* colonies as well as to the macroalgae. Besides this, the internal part of the *Rivularia* colonies were obviously attractive to motile diatoms for reasons discussed below. Higher abundances of epipsammic species suggest that more sand grains were trapped by the *Rivularia* colonies than by the macroalgae.

Protection

Diatoms associated with rocky substrates are attractive food items, in the Forsmark area especially for snails and crustaceans (Snoeijs 1989). These grazers are effectively closed off from the diatoms living inside the *Rivularia* colonies by the colony size. The colonies are also very tough; they can be crushed between two diatom slides, but not between a diatom slide and a cover slip. The diatoms are also protected from exposure to wave action and other physical disturbance inside the *Rivularia* colonies.

Mucilage

When living in association with *Rivularia*, the diatoms may benefit from the cyanobacterial mucilage for their motility so that they do not have to invest in own mucilage production. Motile diatoms need a surface to move on, and they use either secretions from their own raphe-system or mucilage from other organisms (Edgar & Pickett-Heaps 1984). The motile diatoms living inside the *Rivularia* colonies belonged to species that in the area have been observed to occur on stones in mucilage matrixes, e.g. *Epithemia* spp., *Mastogloia* spp. and *Nitzschia* spp. (Snoeijs pers observ). They did not belong to the group of epipelic species (motile sediment-associated species).

Nutritional relationships

No previous reports were found of symbiotic relationships with large cyanobacteria and diatoms as in the *Rivularia*-diatoms case. However, a well-investigated symbiotic relationship is that where a large marine planktonic diatom is the host and numerous small cyanobacteria are the endophytes (DeYoe *et al.* 1992). For large diatoms of the family Epithemiaceae (*Epithemia turgida* and *Rhopalodia gibba*) it was shown that the nature of the relationship was determined by the nitrogen-fixing ability of the unicellular cyanobacterial endosymbionts. The number of endosymbionts per diatom increased or decreased depending on the ambient nitrogen supply in the water. This suggests that nitrogen in the environment was a limiting factor for diatom growth, and that this nutrient was provided by the cyanobacteria instead. The flexibility of the endosymbiont load in the diatoms may reduce the metabolic cost for the diatoms and offers *Epithemia* and *Rhopalodia* a competitive advantage in nutrient-poor habitats. The cyanobacteria, in turn, receive nutrition and protection in this mutualistic relationship. In our case the same genera (*Epithemia* and *Rhopalodia*) belonged to the group of diatoms typical of *Rivularia* colonies, and possibly a similar relationship occurs. Many studies have shown that heterocystous cyanobacteria, such as *Rivularia*, can actively fix atmospheric nitrogen (Stewart 1981, Livingstone *et al.* 1984). Inside the *Rivularia* colonies the diatoms may profit from the nitrogen-fixing ability of the cyanobacterium. However, inorganic nitrogen limitation does not occur in the Forsmark in winter (Snoeijs 1994a). It is possible that organic substances excreted by *Rivularia* can be used as food source by the diatoms. Many diatom species are mixotrophic (Werner 1977), thus having different nutritional options. From the occurrence of species-rich diatom communities with high numbers of cells inside *Rivularia* it may be concluded that low light availability is not a disadvantage. Diatoms can tolerate low light regimes (Hudon & Bourget 1983) and if necessary the motile diatoms are able to migrate to the surface of the colonies to obtain better light conditions. It is more difficult to identify advantages for *Rivularia* in the symbiosis, but nutritional advantages may exist for the cyanobacterium as well.

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