Helgol Mar Res (2003) 57:13–19
DOI 10.1007/s10152-002-0117-z

ORIGINAL ARTICLE

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The epizoic diatom community on four bryozoan species from Helgoland (German Bight, North Sea)

Received: 30 October 2001 / Accepted: 8 July 2002 / Published online: 28 September 2002

Abstract The composition of the diatom community on the bryozoans *Electra pilosa*, *Membranipora membranacea*, *Flustra foliacea*, and *Alcyonidium gelatinosum* from the German Bight was studied by light and scanning electron microscopy. In total, members of 26 diatom genera were found, with *Cocconeis*, *Tabularia*, *Licmophora*, *Amphora*, and *Navicula* being the most abundant. The amount and the composition of the diatom covering seem to be typical for single bryozoan species. *Electra pilosa* and *Membranipora membranacea* showed a rather dense covering with 71–547 cells/mm^2 and 77–110 cells/mm^2, respectively. The most prominent genus on *Electra pilosa* was *Cocconeis*, reaching up to 58% of all diatoms in one sample, followed by *Navicula*, *Tabularia* and *Amphora*. The most abundant genera on *Membranipora membranacea* were *Tabularia* and *Licmophora*, making up almost 70% of all diatoms in one sample, followed by *Navicula*, *Cocconeis* and *Amphora*. The diatom composition was very stable on all *Electra* samples, but varied on *Membranipora* samples. With <1–27 cells/mm^2, diatoms were much less abundant on *Alcyonidium gelatinosum*. Members of the genera *Tabularia* and *Navicula* were the most frequently found benthic diatoms, whereas the planktonic forms *Coscinodiscus*, *Cyclotella*, and *Thalassiosira* made up 35% of the diatoms. On *Flustra foliacea*, diatoms were virtually absent, with fewer than 5 cells/mm^2. The low diatom numbers are probably due to toxic metabolites produced by the host. The same may be true for *Alcyonidium gelatinosum*, but here they might also be a consequence of the surface properties of the bryozoan.

Keywords Biofilms · Bryozoa · Diatoms · Epizoic communities · Microbial mats

Communicated by K. Lüning

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Introduction

Bryozoan colonies are a favorable microenvironment for benthic microorganisms. Their often highly sculptured surface offers protection against predators and the feeding current generated by the polypids provides a permanent supply of nutrients (Scholz 1995). Accordingly, they often host extensive microbial mats and biofilms. It has been noticed that these microbial communities differ from those of the surrounding substratum, and that biofilms are morphologically different on the various bryozoan species (Scholz and Krumbein 1996). Therefore the occurrence of these epibionts cannot be regarded as microbial fouling but are rather the result of a specific interaction between bryozoans and microorganisms (Scholz and Krumbein 1996). As on other substrata, diatoms have been recognized as probably the most important mat-producing epibionts in photic areas (Scholz and Krumbein 1996). Diatom communities have been studied on many different surfaces, such as rocks, sediments, plants, and artificial substrata (see Hudon and Bourget 1981; Paterson et al. 1986; Underwood and Paterson 1993; Kelly et al. 2001); the growth form of diatom species is crucial for their distribution pattern under different environmental conditions (Hudon and Legendre 1987; Mazzella et al. 1994). Growth forms are defined as a group of morphologically similar, but not necessarily taxonomically related, taxa adapted to a particular mode of life in a specific environment (Hutchinson 1975).

Despite the importance of diatoms as bryozoan epibionts, no detailed comparative analysis of the diatom flora on different bryozoan species exists. For this communication we studied the diatom communities on four bryozoan species from the German Bight at Helgoland.

Membranipora membranacea and *Electra pilosa* are common epibionts of macroalgae on which the colonies form unilaminar sheets. *Flustra foliacea* and *Alcyonidium gelatinosum* grow as erect bush-like zoaria. The zooids of the cheilostomate genera *Membranipora*, *Electra*, and *Flustra* are distinguished by the occurrence of an operculum and of a calcified exoskeleton, whereas these features are missing in the ctenostomate genus *Alcyonidium*.

Our data indicate that each bryozoan species harbors a distinct diatom community even though there are no endemic diatom species here, or species that are obligate on bryozoans. Possible reasons for the different diatom patterns are discussed.

Methods

Sampling

Phylloids of *Laminaria digitata* covered with *Membranipora membranacea* were collected by divers of the Biologische Anstalt Helgoland (BAH) in the *Laminaria* belt around Helgoland from the upper sublittoral zone (0–1.5 m below mean low water) on 18 July 1998 (July sample) and 7 May 1999 (May sample). From the midsublittoral zone (1.5–4 m below mean low water) of the same locations the divers collected thalli of *Delesseria sanguinea* covered with *Electra pilosa* colonies on 18 July 1998 (July sample) and 7 May 1999 (May sample). Additional material was obtained by sampling with a dredge operated from the vessel "Senckenberg" from the lower sublittoral zone from a depth of 8–10 m at the Steingrund, 11 km north-northeast of Helgoland on 31 August and 1 September 1998 (September sample). *Flustra foliacea* and *Alcyonidium gelatinosum* were also collected at the Steingrund from a depth of 8–10 m, either by sampling with a dredge on 31 August and 1 September 1998 (September sample) or by divers on 31 March and 1 April 1999 (April sample).

Sample preparation and microscopy

The bryozoans were transferred to a seawater basin at the BAH or at the Terramare marine research station at Wilhelmshaven, Germany, from where samples were taken for further preparation within a few hours after sampling. The samples were rinsed with artificial seawater (28.13 g/l NaCl, 0.77 g/l KCl, 1.6 g/l $CaCl_2$ H_2O, 4.8 g/l $MgCl_2 \cdot 6$ H_2O, 0.11 g/l $NaHCO_3$, and 3.5 g/l $MgSO_4 \cdot 7$ H_2O) to remove loosely attached particles, and were fixed in artificial seawater containing 4% formaldehyde.

For scanning electron microscopy, fixed samples were passed through a dilution series of 70%, 50%, and 30% artificial seawater (2 h each), transferred into distilled water, and dehydrated by increasing concentrations of ethanol (30%, 50%, 70%, 90%, 96%, 1–2 h each). The samples were critical-point dried with a BAL-TEC critical point dryer 030, gold sputtered with a BAL-TEC sputter coater SCD 005 for 100 s at 30 mA and viewed in a Hitachi S-3200N scanning electron microscope.

For light microscopy, diatoms were prepared according to Round et al. (1990). Three pieces of 1 cm^2 each were excised from the centers of each fixed bryozoan colony with a scalpel. These were incubated separately in 2 ml concentrated HNO_3 for 24 h. Then 2 ml of a saturated $KMnO_4$ solution and 2 ml concentrated HCl were added and samples incubated at 60°C overnight. The frustules or pieces of exoskeleton with attached frustules were washed repeatedly with distilled water and allowed to sediment overnight until all traces of acid were removed. They were resuspended in a final volume of 4 ml distilled water and mixed well. Three aliquots of 100 µl of each suspension were dried on microscope glass slides and embedded in naphrax at 60°C for 24 h.

Quantification of diatoms

All embedded diatoms were analyzed. Due to the small size and orientation of many frustules it was not always possible to distinguish between closely related species and, therefore, the species were grouped. For each diatom genus, the mean ± standard deviation of the nine subsamples of each bryozoan sample was calculated and the results normalized to 1 mm^2 surface area, taking into account that each excised piece contained two bryozoan surfaces (this was true also for the epiphytic species investigated). Percentage values were calculated from the means. Cell numbers are the means ± standard deviations of the total cell numbers of the nine subsamples.

Results

The bryozoa investigated hosted a highly diverse diatom flora. In total, at least 33 species representing 26 genera were distinguished (Table 1). For the analysis of our findings we adopted the classification of growth forms as suggested by Mazzella et al. (1994). Growth form Group A consists of sessile species attached to the substratum with a mucopolysaccharide stalk or pad in an upright position. This group was represented by the genera *Grammatophora*, *Pteroncola*, *Tabularia*, *Licmophora*, *Rhohicosphenia*, *Gomphoseptatum*, *Raphoneis*, *Dimerogramma*, *Eunotogramma*, *Glyphodesmis*, and *Diatoma*. Group B contains sessile species attached prostate to the substratum. The genus *Cocconeis* was the only one which could be attributed to this group. The genus *Amphora* was the only representative of Group C, which is characterized by species living adherent to the substratum but having a good motility. All other pennate diatoms belong to Group D and are not adherent to the substratum but are highly motile like the genera *Navicula*, *Nitzschia*, *Trachyneis*, *Lyrella*, *Diploneis*, *Denticula*, and *Tryblionella* (Table 1).

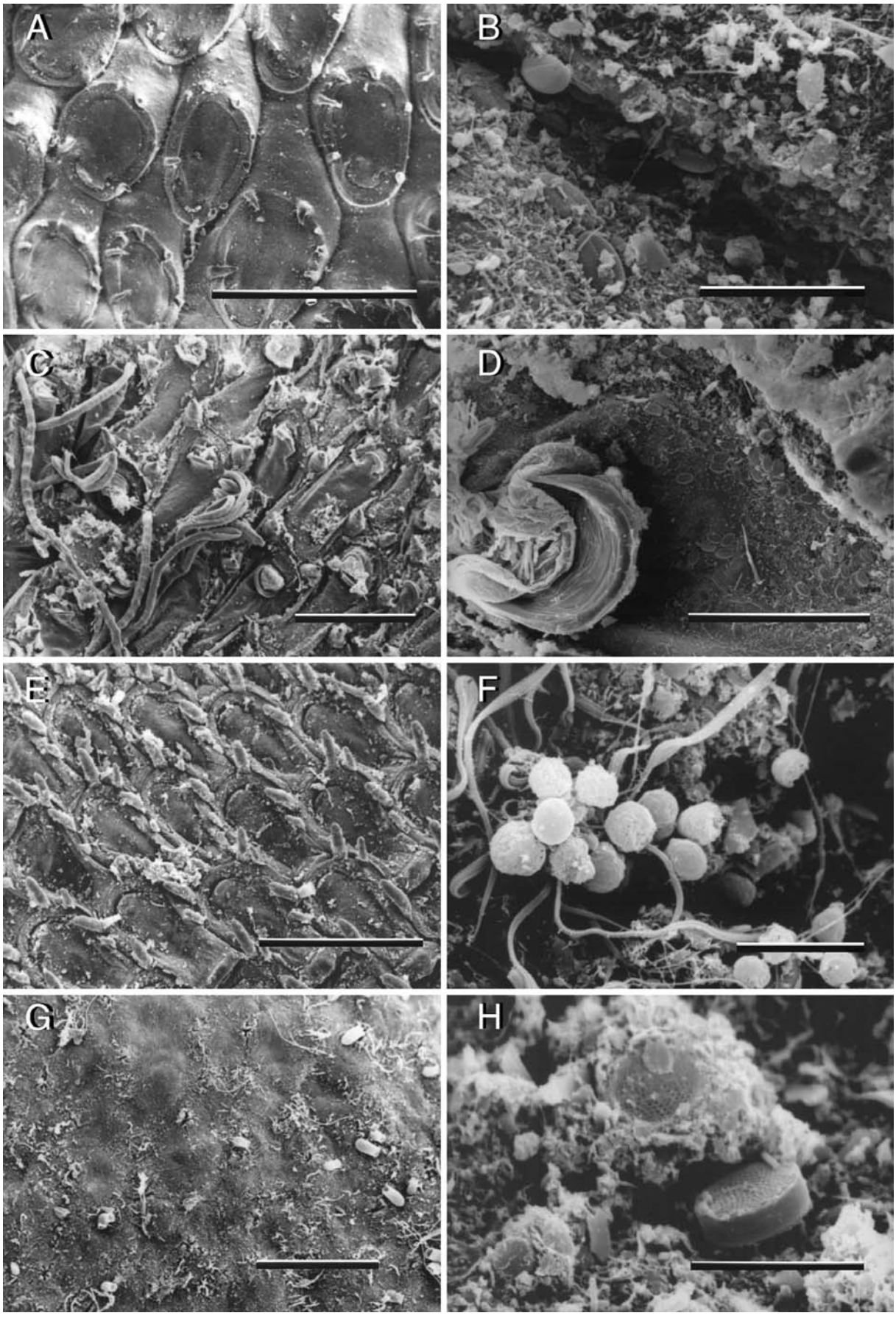
The total number of cells and the diversity of the diatom community differed significantly between the bryozoan species. *Electra pilosa* showed a complex surface structure with deep grooves at the margins of the single zooids and prominent spines surrounding the opercula (Fig. 1A). In the scanning electron microscope, these regions were identified as the preferred habitats of the epizoic diatom community. The cells were embedded in a microbial mat consisting of coccoid bacteria, filamentous cyanobacteria, coccoid algae, and possible fungal hyphae (Fig. 1B). Of the three samples examined, July and May samples hosted the lowest (70.9±30.0) and the highest (547.3±157.9) cell number/mm^2, respectively, even though collected at the same site (Fig. 2A). The September sample showed an intermediate value (242.2±61.7). Despite the different total cell numbers, all three samples showed a strikingly similar composition of the diatom flora. This is dominated by a single genus, *Cocconeis*, with 95% represented by the species *Cocconeis scutellum var. stauroneiformis*, constituting 35–58% of all diatoms. Other prominent genera are *Tabularia*, *Amphora*, and *Navicula*. Centric diatoms are insignificant.

Table 1 Diatom species found on the bryozoan samples and their attribution to certain growth form groups according to Mazzella et al. (1994) and genus numbers in Fig. 2. Genera without numbers were too rare to be included in Fig. 2

Order/Family	Species	Growth form group	No. in Figure 2
Pennales			
Araphidineae			
Diatomaceae	*Tabularia fasciculata*	A	1
	Licmophora communis	A	2
	Grammatophora marina	A	3
	Diatoma sp.	A	
	Raphoneis surirella	A	4
	R. amphiceros	A	4
	Eunotogramma weissei	A	5
	Pterocola sp.	A	6
	Dimerogramma minor	A	
	Glyphodesmis distans	A	
Raphidineae			
Naviculaceae	*Rhoicosphenia marina*	A	7
	R. genuflexa	A	7
	Gomphoseptatum aestuarii	A	8
	Amphora sp.	C	10
	A. marina	C	10
	A. pusio	C	10
	Trachyneis aspera	D	12
	Navicula sp.	D	13
	Lyrella lyra	D	
	Diploneis littoralis	D	15
Achnantaceae	*Cocconeis scutellum*	B	9
	C. scutellum var. stauroneiformis	B	9
	C. molesta	B	9
Bacillariaceae	*Denticula* sp.	D	11
	Nitzschia pellucida	D	14
	N. navicularis	D	14
	N. valdestriata	D	14
	Tryblionella panduriformis	D	
Centrales			
Heliopeltaceae	*Actinoptychus undulatus*		16
Thallassiosiraceae	*Thalassiosira* sp.		17
	Thalassiosira decipiens		17
	Cyclotella littoralis		18
Coscinodiscaceae	*Coscinodiscus radiatus*		19
Biddulphiaceae	*Biddulphia alternans*		
Lithodesmiaceae	*Lithodesmium undulatum*		

Membranipora membranacea was collected as an epibiont on *Laminaria digitata*. In contrast to *Membranipora*, *Laminaria* hosted no diatoms, as revealed by scanning electron microscopy. *Memranipora membranacea* showed a heavily structured surface similar to that of *Electra pilosa* (Fig. 1C). A rich epiflora with bacteria, filamentous cyanobacteria and sprouting macroalgae was detected. Diatoms were found all over the zooids (Fig. 1D). The cell numbers were similar to those in *Electra pilosa*, with 76.7±23.4 cells/mm^2 in the summer sample and 110.36±16.0 cells/mm^2 in the spring sample. The composition of the diatom community, however, was rather different, though the samples were collected at the same time and at the same site as the *Electra* specimens (Fig. 2B). The genus composition seems to be less stable than on *Electra*. *Cocconeis* is much less abundant and contributes only 13–17% to the total cell number. The spring sample is dominated by Group A diatoms, with *Licmophora communis* being the most prominent species, making up 45% of all diatoms. This species was not found in summer, pointing to a seasonal fluctuation of species. Here, Group D diatoms, especially *Navicula*, which made up 21%, play a more prominent role. As with *Electra*, *Membranipora* showed the lowest diatom numbers in the July sample, pointing to a seasonal fluctuation pattern with summer minima.

The surface of *Flustra foliacea* resembles those of *Electra* and *Membranipora*, having prominent spines and deep grooves between the single zooides (Fig. 1E). However, the epiflora differed significantly. The colony was covered with detritus aggregates containing broken diatom valves, but virtually no intact diatoms were found. The epizoic community consisted mainly of filamentous and coccoid microorganisms (Fig. 1F). The dia-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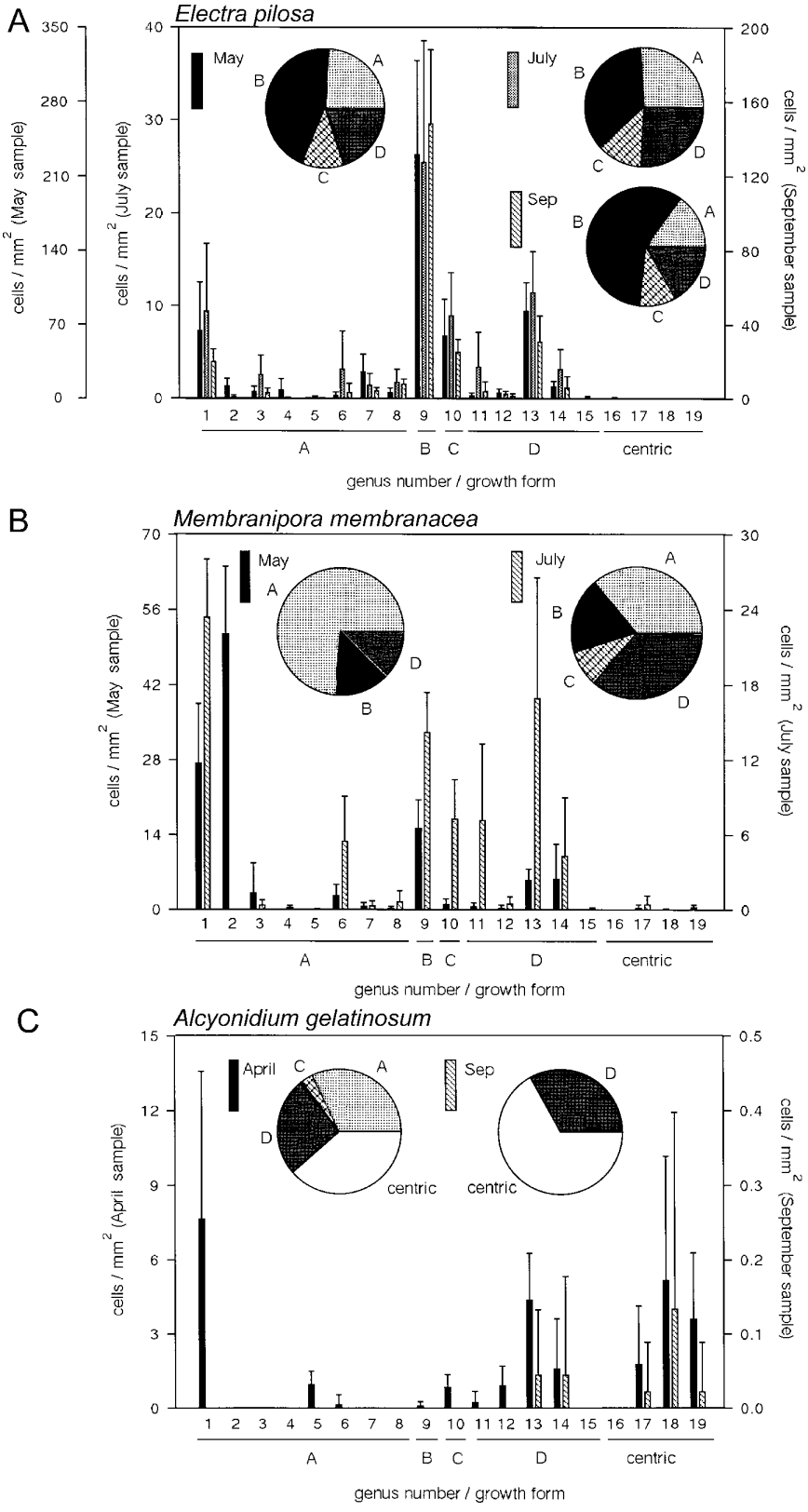

Fig. 2 Cell numbers of diatom genera/mm^2 bryozoan surface on *Electra pilosa* (**A**), *Membranipora membranacea* (**B**), and *Alcyonidium gelatinosum* (**C**) samples. The genera are *numbered* as outlined in Table 1. The *pie charts* show the proportion of each growth form group

◀ **Fig. 1a–h** Scanning electron micrographs of bryozoan colonies. **A** Zooids of *Electra pilosa*; *bar* 600 µm. **B** Detail of the groove between two zooids at higher magnification with a diatom-rich microbial mat; *bar* 30 µm. **C** Zooids of *Membranipora membranacea* partly covered with filaments of a small macroalga, probably *Polysiphonia* sp.; *bar* 600 µm. **D** Close-up of a zooid with a frontal membrane surface covered with *Cocconeis* sp.; *bar* 150 µm. **E** Zooids of *Flustra foliacea* covered with detritus aggregates; *bar* 600 µm. **F** Close-up of the surface with filamentous and coccoid structures. The detritus aggregate in the background contains broken diatom frustules; *bar* 12 µm. **G** Zooids of *Alcyonidium gelatinosum.* The surface of the colony is less structured than the surfaces of the other bryozoans investigated; *bar* 300 µm. **H** Detritus aggregate on the surface with embedded centric diatoms at higher magnification; *bar* 12 µm

tom cell numbers/mm^2 were below 5 for the spring as well as the fall sample, although the September sample of *Electra pilosa*, which was collected at the same sampling site, hosted a substantial diatom community. Among the few diatoms found, Group A representatives dominated, with more than 50% of all genera. Centric diatoms, virtually absent from *Electra* and *Membranipora*, were relatively abundant.

Alcyonidium gelatinosum was the only member of the Ctenostomata examined. In the scanning electron microscope it showed a smooth surface quite different from the other bryozoans investigated (Fig. 1G). Only few diatoms could be observed. Most of them were centric species, which were included in clusters of debris sticking to the surface (Fig. 1H). The September sample was virtually devoid of diatoms. The cell number was less than 1 cell/mm^2. In the April sample 26.5±9.9 cells/mm^2 were found. As on *Flustra*, centric diatoms were quite abundant. Among the pennate diatoms only a few genera dominated, of which *Tabularia* (Group A) and *Navicula* (Group D) were the most prominent (Fig. 2C). Group B and C diatoms were of no importance.

Discussion

We studied the diatom flora on four bryozoan species by scanning electron microscopy and by quantifying the diatom frustules after treatment with HNO_3, $KMnO_4$, and HCl. This acid treatment was best for removing all organic substances of the bryozoan. This method had a much better effect than treatment with H_2SO_4. However, in the case of *Electra*, *Membranipora*, and *Flustra* it was not possible to dissolve the entire calcareous exoskeleton. Diatoms often stuck to these calcareous clusters and could not be removed by mixing or ultrasonic treatment. The relatively high standard deviations shown in Fig. 2 may be due to these clusters, but they might also be caused by an uneven distribution of diatoms on the colony surfaces. For some diatoms, identification was not possible beyond the genus level because the frustules were partly covered by the calcareous exoskeleton of the bryozoan, or broken or only visible in girdle view. However, a more detailed identification was not necessary. In order to examine bryozoans as a habitat for diatoms and identify factors that affect their epiflora, we classified the diatoms according to their growth forms as suggested by Mazzella et al. (1994), and for this purpose an identification at the genus level was sufficient.

We were able to reveal a characteristic pattern of the diatom epiflora for each bryozoan species. *Electra* was characterized by the dominance of a single genus, *Cocconeis*, and a large variation in the total cell numbers found in the three samples examined. The dominance of *Cocconeis* is probably caused by the impact of herbivores on other diatoms. Many grazers avoid *Cocconeis* spp. (Hudon 1983). These diatoms are less susceptible to predation due to their prostate adherent growth form, and consequently they show an enhanced relative abundance under high grazing pressure (Hoagland et al. 1993). Furthermore, the variation in the cell numbers/mm^2 might reflect a seasonal change, with a summer minimum and a spring and fall maximum. The relatively low values for the September sample may be caused by the fact that this sample was collected at a deeper site where the light climate was less favorable (see Hudon and Bourget 1983).

Membranipora showed a higher variability of the diatom flora than *Electra*. This might be caused by the less stable physicochemical parameters in their environment. *Laminaria digitata*, the host of *Membranipora*, grows higher on the shore than *Delesseria sanguinea* (Lüning 1970), and thus is more influenced by tidal fluctuations. As in case of *Electra*, variation in the cell numbers/mm^2 point to a seasonal change with a summer minimum in cell abundance. This may be caused by the seasonal fluctuations of the nutrient concentration in the water column. However, in a microbial mat on the bryozoan surface, nutrients are probably not a limiting factor, given the permanent feeding current by the polypids and the high number of bacteria. Therefore the decrease in diatom numbers might rather be due to an increase in grazers, since Group A diatoms, which are most vulnerable to grazing pressure (e.g. Lowe and Hunter 1988), are most dramatically reduced on *Membranipora*, while the absolute number of *Cocconeis* cells remains unchanged.

It is noteworthy that diatoms were absent on *Laminaria*, the host of *Membranipora*. This might be caused by the smooth slimy surface of the algae which gives little protection against grazers and abrasion and/or by the antimicrobial substances produced by the alga (Al-ogily and Knight-Jones 1977; Lobban and Harrison 1994). Thus, *Membranipora* offers the diatoms a habitat in an otherwise unfavorable environment.

In contrast to *Electra* and *Membranipora*, *Flustra* harbored only few diatoms. In this case the low diatom number is almost certainly due to the production of antimicrobial substances by the bryozoan (Al-ogily and Knight-Jones 1977; Anthoni et al. 1990), since *Flustra* had a surface structure similar to that of *Electra* and *Membranipora* and was collected at the same site as some *Electra* samples. Accordingly, most of the few pennate diatoms found on the bryozoan belong to growth form A. Group A growth form diatoms have an extension vertical to the boundary layers (Blunn and Evans 1981) and because of their raised position they are less susceptible to anti-fouling substances. The centric diatoms found on *Flustra* might have been deposited on the bryozoan colony as a component of “marine snow” (see Jackson 1990), and may not have been alive.

Alcyonidium is also characterized by a low diatom number, indicating that this bryozoan is not favorable for diatoms, too. As in the case of *Flustra*, this cannot be attributed to the bryozoan's habitat since it was collected at the same site as the September sample of *Electra pilosa*. Group A and Group D provided the most prominent pennate diatoms on *Alcyonidium*. Since the highly motile Group D diatoms are most easily removed from their substratum and re-suspended in the water column as

tychoplankton they are among the most probable early colonizers of empty surfaces (Hudon and Bourget 1983; Becker 1997). However, as in the case of the predominant centric diatoms, it remains unclear whether they were still alive. In addition, Group A diatoms might be more common in the water column than Group B and Group C taxa, since prostate attached diatoms adhere 5–15 times more strongly to their substrate than stalk-producing species (Woods and Fletcher 1991).

The low overall cell numbers might be due to the smooth surface of the bryozoan. Scholz and Hillmer (1995) observed that bryozoan species with smooth frontal walls were rarely colonized by microorganisms. They attributed this to the reduced turbulence in the bryozoan–water interface, which is less favorable regarding nutrient availability. In addition, a smooth surface might offer less protection against grazers and abrasion. It is also possible that *Alcyonidium,* like *Flustra foliacea*, produces antimicrobial substances to control its epizoic community. To date, no toxins are known from this organism, but the low abundance of Group B and C diatoms in combination with the relatively high number of Group A genera suggest that this possibility should not be excluded.

In summary, our data show that each bryozoan species harbors a specific diatom community. The extent and the composition of the diatom flora obviously depend on factors intrinsic to the bryozoans (surface structure, antimicrobial substances) as well as on extrinsic factors such as physicochemical parameters and grazing pressure. Some bryozoans are an unfavorable substratum for epibionts, but others may offer a habitat for diatoms in environments where they otherwise could not grow.

Acknowledgements We are indebted to Drs. R.M. Crawford and O.E. Romero (Alfred Wegener Institute, Bremerhaven and University of Bremen, Germany) for their valuable assistance in the identification of diatom species. We also like to thank Ms. Renate Kort for technical assistance and the crew of the *Senckenberg* and the staff of the Terramare marine research station at Wilhelmshaven and of the Biologische Anstalt Helgoland for their help in harvesting and storing the bryozoan samples. The financial support of the state of Niedersachsen for the project "Biotechnologie des Meeres" is gratefully acknowledged. The experiments comply with the current laws of the Federal Republic of Germany.

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