Chapter 17

STRUCTURAL MORPHOLOGY OF DIATOM-DOMINATED STREAM BIOFILM COMMUNITIES UNDER THE IMPACT OF SOIL EROSION

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ABSTRACT

Diatom-dominated biofilm communities which developed in one-month periods over two years were monitored in tributaries of a small eutrophic prairie stream with agricultural watershed subject to extensive soil erosion. Site A, which was spring fed, had a year-round flow, the highest silica and nitrate-nitrogen levels, and a distinct diatom community regardless of the season with generally less trapped sediments in the early spring than sites downstream. All communities (Sites A-E) had at least two tiers existing side by side on the primary glass substrates: a prostrate tier of pennate diatoms, attached or motile, with their valve surfaces parallel to the substrate; and a second tier of pennate species attached by a proximal apical pole perpendicular to the primary substrate. At all sites, but particularly the downstream sites, the communities were surrounded and/or covered by sediments held by mucilages of dominant and codominant diatom species and bacteria of the first two tiers. Second tier (perpendicular) life-forms included rosettes of Surirella ovata, individual Navicula lanceolata, clumps or rows of Gomphonema parvulum, rosettes of Synedra ulna, clumps or rosettes of Eunotia curvata, and fan-like aggregates of Meridion circulare forming hemispherical colonies. Some diatoms of this tier were not attached directly to the artificial substrate but to other diatoms or to bound particulates. Filamentous bacteria were particularly important in tying together clumps of organisms and sediments in tiers 1 and 2, at sites C and D. A third tier consisted of filamentous organisms, e.g. Oedogonium sp. (Chlorophyceae), a stalked diatom Gomphonema sp., and protozoans including stalked peritrichs, which developed intermingled with the first two tiers and directly attached to the glass substrate. Secondary attachment of Gomphonema and Synedra to filaments of the third tier occurred, but this tier was never sufficiently populated or stable enough to trap and hold a layer of sediments. A species of diatom could occupy only one tier (Achnanthes lanceolata, tier 1; Synedra ulna, Synedra acus tier 2), or more than one tier if its growth habit included structural and/or functional heteromorphy. Diatom life-forms are illustrated, as are bacteria in their associations with the diatom-dominated communities.

17.1 INTRODUCTION

17.1.1 General

In studies of microbial biofilms, an understanding of algal attachment is now recognized as a prerequisite for developing effective means to control these

growths where they have serious economic consequences (Characklis and Cooksey, 1983). Regardless of the approach, it appears useful in both basic and applied studies to know what strategies attached algae employ to survive environmental perturbations, that is, what structural and perhaps behavioral adaptations they have evolved in response to natural selection within the biofilm. At present, it is difficult to assess such adaptations in freshwater periphyton communities from the information available.

Reviews on the ecology of attached freshwater algae (algal periphyton) suggest, from the paucity of references (Moss, 1980; Round, 1981), that freshwater algal periphyton has in the past received scant attention or has been ignored (Kalff and Hoagland, 1982) in comparison to freshwater phytoplankton which has received considerable attention with respect to life history form/function strategies (Margalef, 1978; Reynolds, 1984a), nutrient limitation and competition in structuring communities (Tilman et al., 1982; Tilman and Sterner, 1984; Kilham and Kilham, 1984), and has a depth and breadth of research in other areas which has provided the basis for book-length reviews (Fogg, 1975; Morris, 1980; Reynolds, 1984b). Indeed, attached eukaryotic photosynthesizers of the aquatic mileau have not received attention by terrestrial ecologists in developing ecological theory on herbivory and antiherbivore defenses (Rosenthal and Janzen, 1979), perhaps because until recently there were relatively few major algal/herbivore studies, and mostly from the marine environment (e.g., Vadas, 1977, 1986; Emerson and Zedler, 1978; Lubchenco, 1978; Sousa, 1979; Littler and Littler, 1980; Underwood, 1980; Hay, 1981a; Menge and Lubchenco, 1981; Underwood and Jernakoff, 1981; Robles, 1982; Littler et al., 1983a, b; Cubit, 1984; Dayton et al., 1984; Underwood, 1984a, b, c; Gaines, 1985; Harrold and Reed, 1985). This situation is changing rapidly with the stimulus for current work on attached algae coming from several directions.

17.1.2 Macroalgae

Among the macroalgae, an array of morphologies (Littler and Littler, 1980) and life history strategies (Hay, 1981b; Littler and Littler, 1983; Littler and Kauker, 1984) exist to increase fitness in the presence of environmental disturbances such as periodic desiccation at low tides, winter and summer temperature stresses, hydrodynamic shear forces created by waves and currents, sand-scouring abrasion or burial, and herbivory. Littler (1980), Littler and Littler (1980, 1983, 1984) and Littler et al. (1983a, b) have identified at least six functional-form groups that differ in external morphology, internal anatomy, and texture. They range, perhaps in a continuum, from the most herbivore resistant stony or tough crustose group to the soft, more herbivore susceptible sheet or filamentous groups. These morphological groups have shown a range in resistance to grazing from fish and sea urchins depending on their

texture and accessibility (Littler et al., 1983b). In specific cases where texture or accessibility does not predict the outcome of herbivory (e.g., Dictyota dichotoma, Littler and Littler, 1984), secondary metabolites in the tissues may explain herbivore avoidance. For example, where vegetative and sporophyllic tissues are only slightly different in toughness, the incorporation of secondary metabolites such as phenolic tannins in sporophyllic tissues may be of importance as a defense against grazing of these reproductive fronds under high herbivore density (Steinberg, 1984, 1985). However, in the red alga Iridaea (Rhodophyceae), nonfertile fronds, but not fertile fronds, possess a cuticle which deters the herbivore Idotea wosnesenskii (an isopod) although other herbivores are not deterred from either of these fronds (Gaines, 1985).

17.1.3 Microalgae

Allen (1977) suggests the use of microalgae for developing basic ecological theory and states that for studies of succession, "algae often offer the biological system of choice." Primary algal colonization and succession in freshwater suggest similarities to certain sequential events in terrestrial plant communities (Hoagland et al., 1982). However, the time interval between events is days or weeks for algae in contrast to months or years for plant communities (Brown and Austin, 1973; Hoagland et al., 1982; Roemer et al., 1984) thus making possible more rapid assessment of the basic attributes of primary substrate events.

Microalgae of the marine environment have received sporatic attention (Castenholz, 1961; Nicotri, 1977; Hunter and Russell-Hunter, 1983; Underwood, 1984a, b, c; Varela and Penas, 1985), but they may be more important than generally realized. As epiphytes, for example, they may equal the biomass of seagrass blades on which they are growing, and have a set of herbivores which seek them out even when they are in low abundance (Kitting et al., 1984). Biofouling is an area where the marine microalgae have received considerable attention in the past decade (Evans, 1981; Characklis and Cooksey, 1983).

Among the microalgae, diatoms (Bacillariophyceae) appear almost universally to be the first eukaryotic algae which colonize and dominate substrates of microcommunities in marine, brackish and fresh waters (Amspoker and McIntire, 1978; Gale et al., 1979; Lowe and Gale, 1980; Hudon and Bourget, 1981, 1983; Hoagland, 1983; Roemer et al., 1984), although diatoms and bacteria may be missing from turbulent marine waters (Sieburth et al., 1974). The increase in stature of developing biofilms, i.e., the increase in thickness of the periphyton fluff, has been suggested as reflecting competition for substrate surface, where thick communities may arise in response to gradients of CO_2, O_2, nutrients, or light (Hudon and Bourget, 1981; Hoagland et al., 1982; Sumner and McIntire, 1982). Hoagland et al. (1982) and Roemer et al. (1984) have speculated

that the formation of long stalks by diatoms may enable them to avoid this competition by elevating their frustules away from the accumulating sediment load, and that mucilaginous material of biofilms also stabilizes developing communities by aggregating potentially abrasive detrital particulates. It is the structuring of communities by diatoms and sediments that will be further considered here, on a morphological basis, using scanning electron microscopy (SEM).

17.1.4 Specific project

The Maple Creek Model Implementation Project provided the opportunity to examine seasonally the periphyton of a stream system within a watershed derived from cultivated agricultural land with extensive soil erosion. In the longer term, this project was designed to demonstrate ways in which nonpoint source pollution, specifically soil erosion, could be controlled. Land owners were encouraged to control soil erosion by such means as the establishment of permanent vegetative cover through terrace systems, sod waterways and diversions, windbreaks, conservation tillage, and to otherwise reduce sedimentation with water impoundments and other erosion or water-control structures (ACP, 1979; Schepers et al., 1985). The project area totaled 33,000 acres, with 85% planted to crops. Annual soil losses in the area prior to the project exceeded 100 tons/acre/year on 3% of the land, with an average loss of 22 tons/acre/year (Anonymous, 1982). The study sites for our work were impinged by watershed outside of the project area where implementation of the best soil conservation practices would be slow, as well as watershed in the project study area where 140 of 280 owner-operators of cropland established one or more soil conservation practices over a 3-year period (Anonymous, 1982). In the short term, our particular interest was in comparing the algal periphyton community of the headwaters of a stream without the full impact of soil erosion (Site A), with downstream communities where extensive soil erosion was occurring (Sites B-E).

17.2 MATERIALS AND METHODS

17.2.1 Study sites

The study sites (Fig. 1) were in Stanton and Colfax counties, Nebraska, U.S.A. Sites were chosen along the tributaries of Maple Creek to reflect a range of agricultural tillage practices. None of the sites had rock substrates and the stream bottom was mostly clay and silt. Site A is near the origin of the middle tributary (Fig. 1) and is spring fed. The spring flows continuously throughout the year at this site, which generally had the lowest turbidity for it does not reflect the impact of extensive soil erosion evident downstream. Site B is about 10 kilometers downstream from Site A, and is located below areas where soil

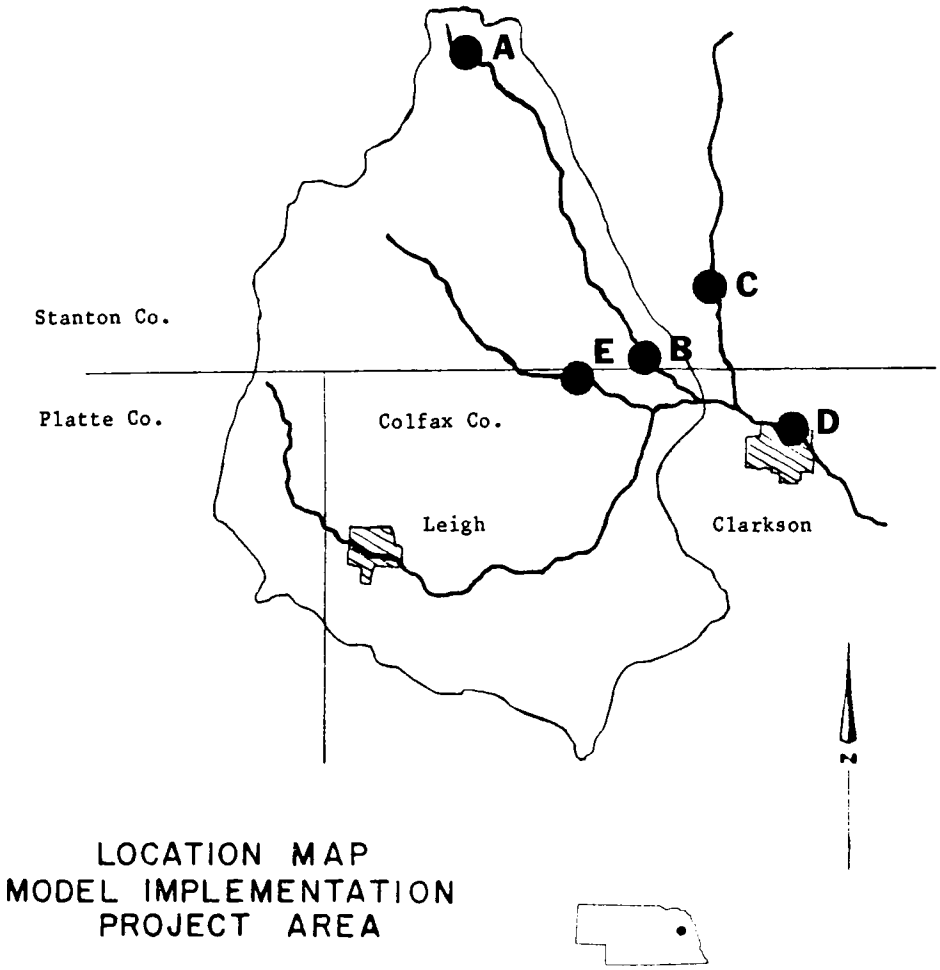


Fig. 1. Periphyton sampling sites A-E along tributaries of Maple Creek, in Stanton and Colfax counties, Nebraska, U.S.A.

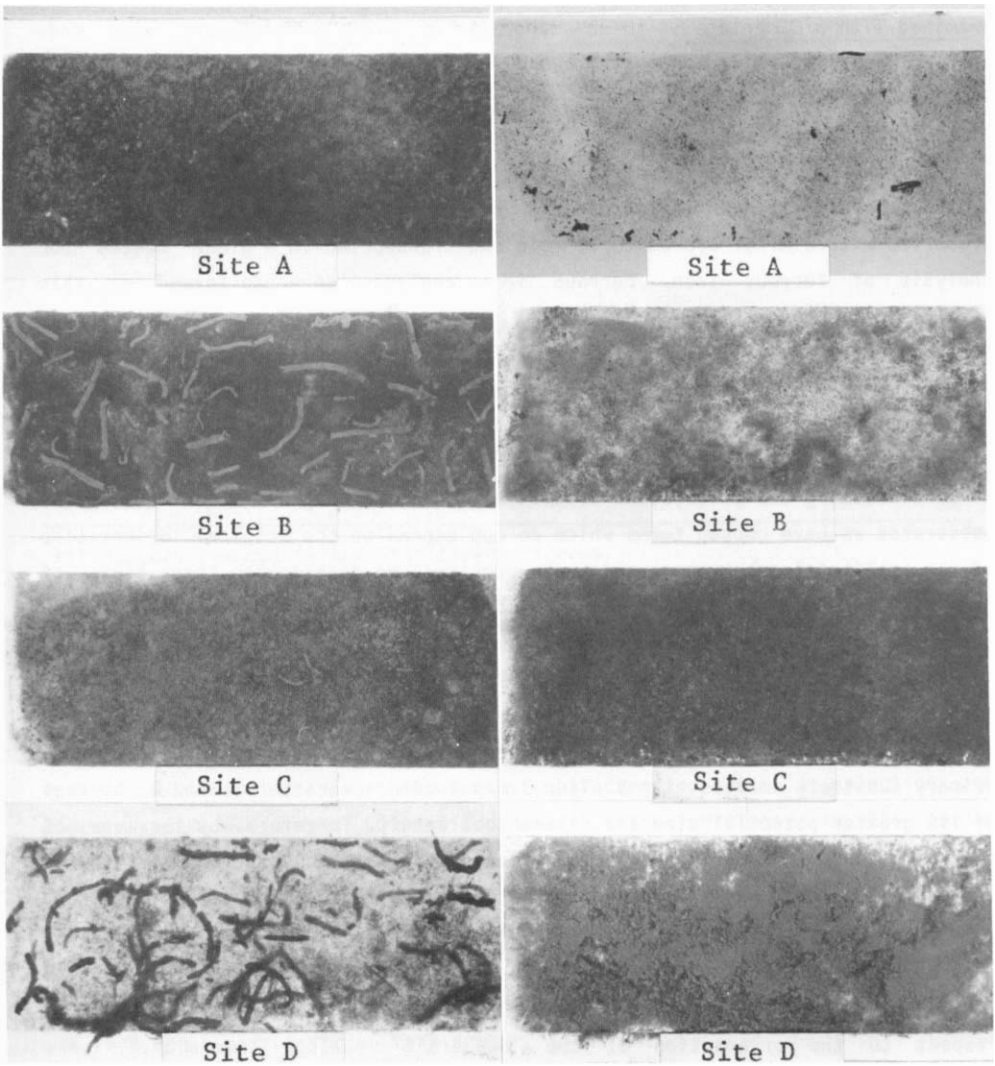
conservation practices were to be implemented. Low flow and high siltation rates are typical of this site, which is highly accessible to cattle. Site C is a potential future control since it is an eastern tributary which enters the creek below Site B, with watershed for this tributary located outside the Model Implementation Project area. Water flow at Site C was constant and intermittent shading occurred. Site D is below the point where the water from Sites B and C join, near the town of Clarkson, but above the sewage outflow from this town. This site would show the effects of dilution and addition from the mixing of water from Sites B, C, and E. Site E was added the second year of the study since it was below the watershed where soil conservation practices were to be implemented. However, this site was frequently dry and only three periphyton samples were collected. Samples in the winter months were not often collected at Sites B-D because the samplers became encased in or covered with ice.

17.2.2 Periphyton sampling

The algal samplers (Design Alliance, Cincinatti, Ohio) were suspended in the creek between two 1.5 m long, 3.2 cm diameter galvanized pipes, driven 1 m into the creek bottom. Five microscope slides, including one spare, were placed in the samplers in a vertical position, with the long axis of the slides parallel to the water flow. For most months over a two-year period (May, 1979-May, 1981), four slides were removed from the sampler during the daylight hours, noon to mid-afternoon. Three slides were placed in Whirl-Pak bags; the fourth slide, in a plastic slide mailer, was fixed in 2% glutaraldehyde prepared in Alga-Gro medium (Carolina Biological Supply Co.). New microscope slides were then replaced in the sampler, which was immersed in the creek, to be removed the following month. All samples were placed on ice and returned to the laboratory. The glutaraldehyde-fixed samples were stored in a refrigerator for later dehydration, critical-point drying, and thermal coating with Au/Pd, for SEM.

Some slides were photographed in large finger bowls, for overall growth comparisons; examples are shown in Figure 2. Three slides from each sampler were processed to remove and clean the diatom frustules for identification and enumeration. Permanent slides were made for examination with light and scanning electron microscopy. The specific procedures were as follows. The slides for light microscopy were scraped and the frustules were treated with hydrogen peroxide and potassium dichromate (van der Werff, 1955). Permanent Hyrax slides were made to facilitate quantitative analysis using standard 22 mm^2 coverslips and known quantities of the diatom sample. A total of 600 valves per slide were counted and differentiated into the dominant and codominant species and all others.

The samples in glutaraldehyde were dehydrated in a 10% graded series of acetone and critical-point dried using liquid carbon dioxide as the transitional



May 23 - June 20 July 18 - August 15
1979

Maple Creek Model Implementation Project

Fig. 2. Glass microscope slides with periphyton, actual size.

fluid. The dried specimens were then coated by thermal evaporation with Au/Pd, and occasionally with additional coating by diode sputtering, using procedures which best stablize the specimens and protect them from thermal damage to their mucilage (Rosowski and Glider, 1977; Rosowski et al., 1981). Samples were examined with a Cambridge S4-10 SEM, operated at 20kV. Photographs were made with Polaroid 55 P/N or Kodak 4127 cut film.

17.2.3 Water chemical analyses

Water samples were collected in 1-liter polypropylene bottles and transported to the laboratory packed in ice and in the dark. A sample of 150 ml was preserved with 2 ml of hydrochloric acid and transported in a glass bottle for analysis of ferrous iron. Ferrous iron analyses were performed on this unfiltered water (APHA, 1976). Nitrate-nitrogen, ammonium-nitrogen, orthophosphate and silica were analyzed from filtered water samples (Millipore filter type HA, 0.45 µm porosity), following the procedures of APHA (1976).

17.2.4 Terminology

In discussing the orientation of diatoms and other organisms on the glass substrates we have chosen terms which do not depend on the original orientation of the artificial substrates, which was vertical. We distinguish three tiers of community structure but do not mean to imply that it is always possible to view these tiers, for in many cases sediments obscure the relative position of the community members. The terms prostrate or low profile are used for tier 1 and perpendicular or upright for tier 2 rather than lowerstorey and upperstorey, or vertical and horizontal. Tiers 1 and 2 develop alongside each other on the primary substrate as does tier 3. Tier 3 may develop over tiers 1 and 2 because of its greater potential size and filamentous nature. Therefore, by the use of the term tier we do not imply that one tier develops attached to or on top of another. Organisms which attach to members of the three tiers would be epiphytes, not additional tiers. The original position of the communities is how they appear when the plates of this paper are viewed with the pages held vertically. Second tier communities thus develop in a lateral fashion with respect to the orientation of the substrate during immersion, i.e., perpendicular to the vertically oriented substrate.

17.3 RESULTS

The dominant and codominant diatoms for the spring and summer months of the first year of the study (1979) are presented in Table 1. The mean number of genera for all sites was 9.2 and the range was 3-15. In the two-year study period, 17 species occurred as dominants or codominants (Tables 1-5). For purposes of illustrating the three dimensionality of the communities at Sites A,

TABLE 1

Spring and summer diatom periphyton of Maple Creek, on glass substrates, 1979.

	Total* Diatoms/mm^2	Dominant Species/mm^2	Codominant Species/mm^2	Other Diatoms/mm^2
Site A**				
June	1,500	630[a]	270[g]	600
July	100	68[a]	16[b]	23
August	7	4[a]	1[b]	2
Site B				
June	1,500	900[c]	380[b]	290
August	470	180[d]	180[b]	160
Site C				
June	1,200	450[b]	77[c]	600
July	3,700	2,300[e]	820[b]	550
August	5,600	4,300[e]	880[b]	360
Site D				
June	720	230[d]	190[c]	280
July	2,800	1,000[d]	890[e]	900
August	1,600	500[d]	590[f]	510

*All numbers rounded to two significant figures.

**Immersion periods: June = May 23-June 20; July = June 20-July 18; August = July 18-August 15. Key: a. = Achnanthes lanceolata (Bréb.) Grun., b. = Gomphonema intricatum Kütz., c. = G. parvulum (Kütz.) Grun., d. = Navicula lanceolata (Ag.) Kütz., e. = Nitzschia amphibia Grun., f. = Nitzschia spp., g. = Synedra ulna (Nitz.) Ehr.

B, C, and D, but to limit the number of electron micrographs as documentation, these communities are morphologically characterized with a selection of photographs from a single collection period which developed in the spring (May/June, 1979, Figs. 3-28).

Figure 2 illustrates the relative density and low profile of the communities which develop in one month. Midge fly (Chironomidae) pupal cases were clearly evident at Sites B and D in the spring but not in the summer. The only other obvious detail discernible without magnification is that the community at Site A was less dense in the spring than summer. This was because angiosperm growth along the banks of the stream screened out a significant portion of the light during the transition from spring to summer. During the following year, black plastic was used effectively to inhibit angiosperm growth. Shading due to vascular plant growth at the other sites was apparently not as significant when total numbers of cells are compared for both years of the study (cf. Tables 1, 3, 4). This was perhaps due to the grazing and trampling by cattle, and, because the stream was much wider at these sites, placing of samplers in the middle reduced the likelihood of shading.

TABLE 2

Fall and winter diatom periphyton of Maple Creek, on glass substrates, 1979/1980.

	Total Diatoms/mm^2	Dominant Species/mm^2	Codominant Species/mm^2	Other Diatoms/mm^2
Site A				
September*	27	7[d]	5[a]	15
December	4,499	2,677[g]	872[a]	950
February	83	52[a]	11[c]	20
Site B				
September	1,041	383[d]	248[e]	410
Site C				
September	16,336	5,733[e]	3,569[d]	7,034
October	10,302	3,538[b]	2,965[f]	3,799
November	10,989	5,101[c]	1,706[d]	4,182
December	801	309[h]	172[d]	320
Site D				
September	8,771	2,477[d]	2,249[e]	4,045
October	7,765	3,721[b]	1,945[f]	2,100
November	537	217[h]	200[c]	120

*Immersion periods: September = August 15-September 11; October = September 11-October 9; November = October 9-November 8; December = November 8-December 4; February = December 4, 1979-February 23, 1980.
Key: a. = Achnanthes lanceolata (Bréb.) Grun., b. = Gomphonema intricatum Kutz., c. = G. parvulum (Kütz.) Grun, d. = Navicula lanceolata (Ag.) Kütz., e. = Nitzschia amphibia Grun., f. = Nitz. fonticola Grun., g. = Meridion circulare (Grev.) Ag. , h. = Nitz. apiculata (Greg.) Grun.

17.3.1 Spring and summer growth (1979)

In the first three months of this study we found 17 different genera of diatoms; only those which were dominant or codominant were identified to the species level. These dominant and codominant diatoms were found at all sites with the exception of Cymatopleura solea (Bréb.) Wm. Smith and Meridion circulare, which occurred only at Site A. Six species of diatoms were dominant or codominant. At Site A, the dominant diatom in June and July was Achnanthes lanceolata, a species not found at the other sites and one known to colonize new streams and to disappear under conditions of high organic enrichment (Lowe, 1974). It is perhaps significant that Gomphonema parvulum did not occur as a dominant at Site A whereas it occurred at all other sites. This species has been suggested as an indicator of organic water pollution (Lowe, 1974; Patrick and Reimer, 1975). The dominant diatoms at Site C were Navicula lanceolata and Gomphonema intricatum, species generally characteristic of eutrophic waters (Lowe, 1974; Patrick and Reimer, 1975).

TABLE 3

Spring diatom periphyton of Maple Creek, on glass substrates, 1980.

	Total Diatoms/mm^2	Dominant Species/mm^2	Codominant Species/mm^2	Other Diatoms/mm^2
Site A				
March*	460	375[d]	53[a]	32
April**	2,518	1,512[d]	743[f]	263
May	552	234[a]	208[b]	110
Site B				
March	644	377[g]	212[c]	55
April	1,087	563[c]	380[g]	154
May	306	221[d]	40[e]	45
June	32	22[d]	5[e]	5
Site C				
March	99	38[g]	33[c]	28
April	829	510[g]	225[c]	94
May	849	441[e]	161[c]	248
June	307	210[h]	51[c]	46
Site D				
March	229	106[g]	105[c]	18
April	995	665[g]	157[c]	123
May	383	124[c]	110[e]	149
Site E***				
May	1,002	713[c]	70[e]	219
June	889	600[h]	169[d]	120

*Immersion periods: March = February 23-March 22; April = March 22-April 19; May = April 19-May 19; June = May 19-June 18. Key: a. = Achnanthes lanceolata (Bréb.) Grun. , b. = Fragilaria vaucheriae (Kütz.) Peter., c. = Gomphonema intricatum Kütz., d. = G. parvulum (Kütz.) Grun., e. = Navicula lanceolata (Ag.) Kütz., f. = Meridion circulare (Grev.) Ag., g. = Surirella ovata Kütz., h. = Nitzschia amphibia Grun.

**On April 19 sheets of heavy black plastic were placed along the stream banks to inhibit angiosperm growth which had caused severe sampler shading.

***Added on April 19, since soil conservation practices were to be implemented upstream from this location.

SEM has provided a useful perspective of the organisms and associated particulates which developed in the creek periphyton. The morphological effect of soil particle build-up is illustrated by comparing Sites A and B (cf. Figs. 3-7 & 8-14). Although the total number of diatoms at each site was similar (1,500/mm^2; see Table 1, footnote*), the dominant species were different, and whereas diatoms were clearly evident at Site A (Fig. 3) and were still trapping considerable quantities of particulates (Figs. 4-7), they were almost obscured

TABLE 4

Summer and fall diatom periphyton of Maple Creek, on glass substrates, 1980.

	Total Diatoms/mm^2	Dominant Species/mm^2	Codominant Species/mm^2	Other Diatoms/mm^2
Site A *				
July	613	459[a]	79[b]	74
August	131	58[b]	52[a]	21
September	693	392[a]	153[b]	148
October	4,220	2,844[a]	532[e]	844
November	8,932	6,457[h]	1,027[a]	1,447
Site B				
July	948	400[f]	387[d]	152
August	55	26[f]	17[e]	12
Site C				
July	1,006	410[f]	323[c]	273
August	1,692	804[c]	614[f]	274
September	920	403[f]	294[e]	223
October	6,990	3,691[f]	2,146[c]	1,063
November	3,898	1,902[i]	896[c]	1,099
Site D				
July	1,631	841[f]	388[e]	415
September	185	98[e]	47[f]	39
October	2,315	1,581[f]	259[e]	475
November	5,227	2,990[d]	1,531[g]	706
Site E				
August	301	99[f]	94[e]	109

* Immersion periods: July = June 18-July 23; August = July 23-August 21; September = August 21-September 22; October = September 22-October 20; November = October 20-November 20. Key: a. = Achnanthes lanceolata (Bréb.) Grun., b. = Eunotia curvata (Kütz.) Lagerst., c. = Gomphonema intricatum Kütz., d. = G. parvulum (Kütz.) Grun., e. = Navicula lanceolata (Ag.) Kütz., f. = Nitzschia amphibia Grun., g. = Nitz. augustata (Wm. Smith) Grun., h. = Nitz. linearis Wm. Smith, i. = Surirella ovata Kütz.

by particulates at Site B (Figs. 8 & 9). SEM also shows the relative importance of the size of various diatoms. For example, although Achnanthes lanceolata (tier 1) was the numerical dominant for Site A in June, it was Synedra ulna (tier 2) which was the biovolume dominant when scanning electron micrographs are examined (cf. Figs. 3 & 4).

The striking feature of Site B (cf. Figs. 6 & 10, at the same magnification) was the difficulty in finding any diatoms because of the debris which covered them. Some spherical cells (unidentified, Fig. 12) were able to keep debris at a distance, perhaps from slime which they secrete, which then shrinks or is lost in specimen preparation leaving a space around them. This flocculant material not only collects between the diatoms (Figs. 9-11) but may also occur on their surface (Figs. 13 & 14). It was not determined if the diatoms secreted this material or if it was deposited on the diatoms from the stream water.

TABLE 5

Spring diatom periphyton of Maple Creek, on glass substrates, 1981.

	Total Diatoms/mm^2	Dominant Species/mm^2	Codominant Species/mm^2	Other Diatoms/mm^2
Site A *				
March	9,917	6,505^d	1,388^f	2,023
April	1,279	568^b	409^a	302
May	7,582	7,537^a	30^d	16
Site B				
April	1,462	619^c	483^f	361
Site C				
March	260	93^d	36^f	130
April	5,810	2,034^e	843^b	2,934
May	908	218^g	87^a	603
Site D				
March	10,447	6,456^b	2,633^d	1,358
April	13,939	7,318^c	3,136^b	3,485
May	3,833	1,782^b	1,428^f	623

*Immersion periods: March = November 20-March 14; April = March 14-April 14; May = April 14-May 12. Key: a. = Achnanthes lanceolata (Breb.) Grun., b. = Gomphonema parvulum (Kütz.) Grun., c. = Navicula lanceolata (Ag.) Kütz., d. = Nitzschia hungarica Grun., e. = Nitz. linearis Wm. Smith, f. = Nitz. subcapitellata Hustedt, g. = Rhoicosphenia curvata (Kütz.) Grun.

A comparison of Sites B and C at the same magnification shows that Site C (Fig. 15) also trapped a dense silt load, but it was possible to distinguish individual diatoms in this community (Figs. 15 & 16), unlike Site B in most specimen areas. On many of the diatoms at this site, an organic skin was noted (Figs. 18 & 19).

The silt load that the substrates could hold at Sites B and C appeared to be that which occurred between the perpendicular diatoms of the community which meant that the prostrate forms were mostly buried, i.e., not observed with SEM. A third tier developed in certain areas of the substrate and consisted of filaments of unknown identity (Fig. 17), initiated perpendicular to the substrate but which then developed over the adjacent sediment-loaded double tier paralleling the surface; these filaments were not stalks of peritrichs (Vorticellidae) which were readily identifiable (Fig. 19) because they extended away from the second tier by their coiled stalks.

The most interesting tier of the one-month old substrates was at Site D (Figs. 20 & 21). As at Sites B and C, the two-tiered community was completely buried with sediments (Figs. 25-28), and certain diatoms were noted to have an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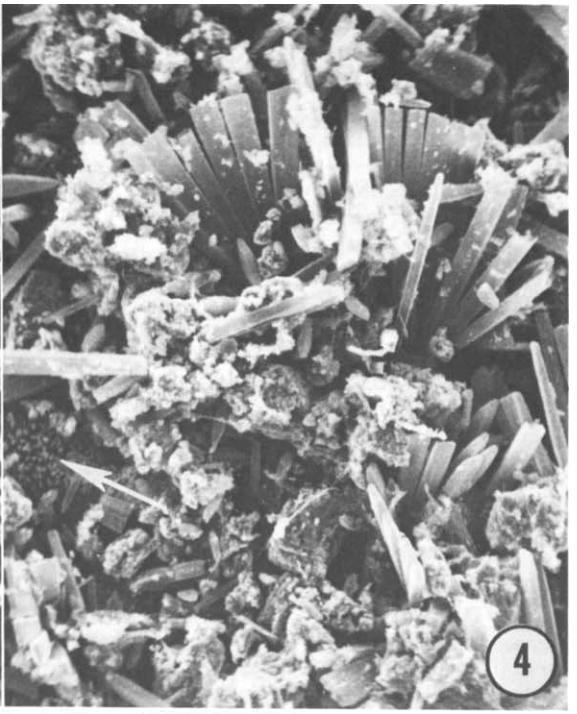
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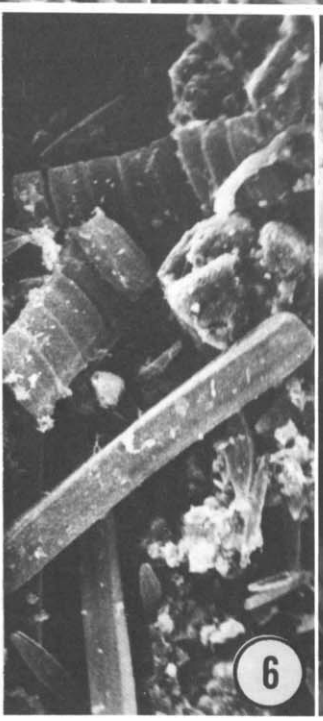
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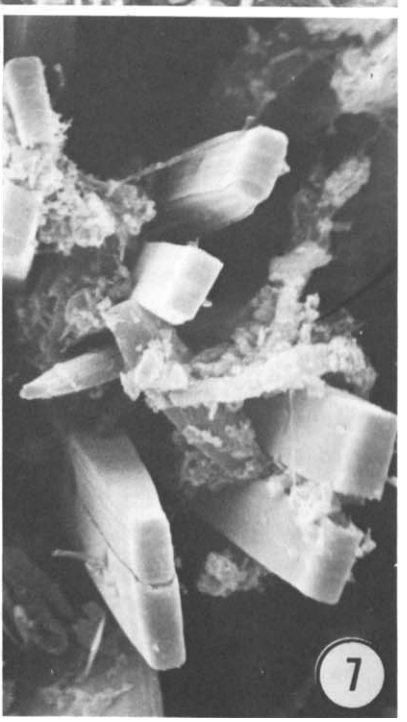
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intricate organic coating (Figs. 22-24); certain nondiatom members of the community, loricate peritrichs (Vaginicolidae), were conspicuous within the two-tier level of the community but are not illustrated here. A filamentous third tier also developed, attached to the glass but with the bulk of this tier composed of filaments parallel to the buried substrate and colonized by diatoms like Synedra ulna and Gomphonema parvulum (Figs. 20 & 21). Because of the loose network of this third tier of filaments, and the ability of the Peritrichida to expand and contract in and out of the second and third tier levels (Figs. 20, 25, 28), this third-tier community did not appear sufficiently stable to be important in holding seston.

17.3.2 Fall and winter growth, 1979.

The fall collections generally showed an increase in cell density over those in the summer (Table 2). Site D showed a four-fold increase in cell numbers in monthly collections from Sept.-Nov., while at Site C densities were two to three times greater than in the summer period. Overgrowth of Typha at Site A prevented development of a diatom periphyton. At Site B (Oct. 9th) the stream had dried up and sediment was within 5 cm of the top of the pipe holding the sampler, suggesting a deposition of sediment over the preceeding months to a depth of 30 cm.

A new dominant, Nitzschia amphibia, occurred at Sites C and D in early fall along with Navicula lanceolata. These taxa were later replaced by Gomphonema intricatum and Nitzschia fonticola, followed by G. parvulum and N. lanceolata at Site C in the late fall.

Meridion circulare was an early winter dominant, occurring only at Site A (water temp. 3°C), followed by Achnanthes lanceolata and Gomphonema intricatum in late winter. At Site C (Dec. 4th.), Nitzschia apiculata and Navicula lanceolata were codominants. An ice cover or encasement of the sampler in the ice prevented the development and/or collection of samples at Sites B and D during the winter months.

Figures 3-7 of periphyton communities at Site A, immersed May 23-June 20, 1979.

Fig. 3. Light sediment load with second tier of Synedra ulna dominant in this area of the substrate. 130 X.

Fig. 4. First tier with bacteria evident at white arrow; second tier Synedra ulna with particulates clumped near their apices. 260 X.

Fig. 5. Tier 1 with Achnanthes lanceolata and Navicula lanceolata in center. Sediment particulates aggregated and attached to tier 1. 260 X.

Fig. 6. Mixed diatom species of great range in size, and several not attached directly to the glass substrate. 650 X.

Fig. 7. Particles trapped within the perpendicular colony of Synedra ulna. 1,300 X.

17.3.3 Spring, 1980

Relatively low levels of growth developed at all stations in the spring (Table 3), with the highest density occurring at Site A in April (2,518 cells/mm^2). At Sites B-D, Surirella ovata was dominant in early spring, a taxon characteristic of cool running water (Lowe, 1974). Gomphonema intricatum, G. parvulum and Navicula lanceolata constituted most of the other diatoms present in the spring flora. In late spring at Site A, Fragilaria vaucheriae appeared as a new codominant; this taxon is indicative of eutrophic waters (Lowe, 1974).

17.3.4 Summer and fall, 1980

Data for this period is found in Table 4. The heavy rains and high winds which occurred on June 14 altered the entire stream morphometry as the stream bank was eroded and the bank vegetation destroyed. Consequently, all slides at Sites A and D were lost and those at the remaining sites had undoubtedly undergone extreme abrasion. Although June was a month of dense algal growth the previous year, the growth for samples from Sites B, C, and E fell well below those of the previous year.

Water flow was down substantially by midsummer at all sites except A. Site A was dominated by A. lanceolata and a new codominant Eunotia curvata, while Sites B, C, and D were again dominated mainly by Nitzschia amphibia. The water level at Site E was negligible and the sampler was destroyed (presumably by cattle).

By late summer, water levels as well as diatom densities were low at Sites A, B, and E. Samplers at Sites B and E were densely shaded and partially encased in mud, while at Site D the sampler was destroyed. Only Site C exhibited appreciable diatom growth, with Gomphonema intricatum and Nitzschia amphibia the dominant species.

In the early fall, Sites B and E (Sept. 22) were dry and water flow was low at Sites C and D. Achnanthes lanceolata and Eunotia curvata were again dominant at Site A and Navicula lanceolata and Nitzschia amphibia were the dominants at Sites C and D. By late fall the sampler at Site A was damanged but intact, with evidence of heavy silting. Low water flow occurred at Sites C and D, with turbid and/or stained waters. Maximum cell densities occurred at Site C, with Nitzschia amphibia dominant.

In the later fall, a new diatom dominant for Site A occurred, Nitzschia linearis, generally indicative of oxygen rich springs and streams (Lowe, 1974). Lower densities were found at Sites C and D beneath 1-2 cm of ice (with extremely low water flow), including a new dominant at Site D, Nitzschia angustata. Interestingly, this diatom is noted as being characteristic of standing water (Lowe, 1974).

17.3.5 Spring, 1981

Slides immersed on Nov. 20, 1980, were harvested on March 14 (Table 5). It should be noted that this sample represented almost a 4-month immersion period, unlike most other samples which were harvested after a one-month immersion period. Site A was dominated by Nitzschia linearis and Nitzschia subcapitellata, with many of the subdominants being large diatoms (greater than 100 µm in length), such as Navicula cuspidata, Stauroneis phoenicenteron, and Pinnularia gentilis (Donk.) Cl. This dominance by large species of diatoms was not observed at any sampling site prior to this sample.

A spring sample at Site C (Table 5) was dominated by Nitzschia linearis and Gomphonema parvulum, both species indicators of very high nitrogen levels (Lowe, 1974). The slides at Site A (May 12th) were covered with a nearly unialgal population of Achnanthes lanceolata. Pure stands of one species had not been encountered at any site up to this time.

17.3.6 Community structure

Seasonal differences were evident in the periphyton community at Site A (Figs. 29-32). A distinct two-tiered community developed in late spring, 1979, consisting of a dense growth of prostrately attached Achnanthes lanceolata and perpendicularly oriented (in respect to the substrate) Synedra ulna associated with sediment particulates. In contrast, the early fall, 1979, sample showed sparse development of diatoms (only 10 frustules observed after scanning most of a 1 cm^2 glass chip), but bacteria predominated, forming small clumps of mucilaginous strands on the substrate. In addition, some particulate matter overlaid the glass surface. It should be noted that the overgrowth of angiosperms causing shading probably favored this development of heterotrophs over autotrophs.

The periphyton community collected at Site A in early spring, 1980, consisted of many clumps of diatoms with little accumulation of sediment particulates. Portions of the glass substrate between the clumps were uncolonized by diatoms, but higher magnification showed the substrate to be covered with a film of bacteria and their associated mucilage strands. The early fall, 1980, community consisted of a heavy accumulation of sediment particulates, with diatoms only occasionally viewed within this material (Fig. 32). On areas of the substrate where sediment build-up was not evident, isolated patches of Achnanthes lanceolata were found. Although the prostrate A. lanceolata was the numerical dominant at Site A on Oct. 20, 1980 (Table 4), it was mostly buried by sediments (Fig. 32), i.e., not observed with SEM except in isolated patches. Perhaps the placement of the black plastic along the banks of the stream, in the spring of 1980, to control shading of the sampler from vegetation, contributed to runoff and sedimentation in the immediate area of Site A.

In communities from Sites B, C, and D, where extensive sediment build-up was evident, diatoms were often found attached to and dividing within the sediments, thus likely contributing to the stabilization of the particulate matter on the artificial substrate. In addition, sessile diatoms were commonly found either partially or fully buried in the sediments (Figs. 33-34), evidence that particulates were continuously accumulating in the periphyton stream community.

Further increase in the thickness of the periphyton beyond the two tiers created by prostrate and perpendicular forms was observed in samples collected from Sites C and D. Large erect algal filaments (Oedogonium sp.) were basally attached, forming a partial canopy over the substrate, with the greatest density at the edge of the glass slide (Fig. 36).

Bacterial mucilages are important in the binding of sediment particles in the periphyton of Maple Creek. Unicellular and colonial bacteria were found attached, via mucilage secretions, directly to the glass substrate (Figs. 10 & 42), to surfaces of inorganic and organic particles (Figs. 37-41), and to diatom frustules (Figs. 39 & 40). Bacteria and their mucilages were found in all communities sampled, regardless of the season. Clumps of bacterial mucilage were occasionally found covering the glass surface (Fig. 37). A more common form of bacterial mucilage was sheet-like webs (Fig. 38) which often collected particulates. In Fig. 44, bacteria beneath the mucilage are visualized as the electron beam of the SEM penetrated the delicate mucilage webs. Furthermore, diatoms on the substrate surface or elevated away from the surface were sometimes found either partially of fully overgrown with strands of bacterial mucilage (Fig. 40). In addition to the bacteria, protozoa and fungi were common, although they never were dominants in the community.

Figures 8-14 of periphyton communities at Site B, immersed May 23-June 20, 1979.

Fig. 8. Substrate densely packed with sediments entirely obscuring tier 1 and tier 2 communities. 260 X.

Fig. 9. A few diatoms barely visible; diatom at black arrow not attached to the glass and with frustule damage. 650 X.

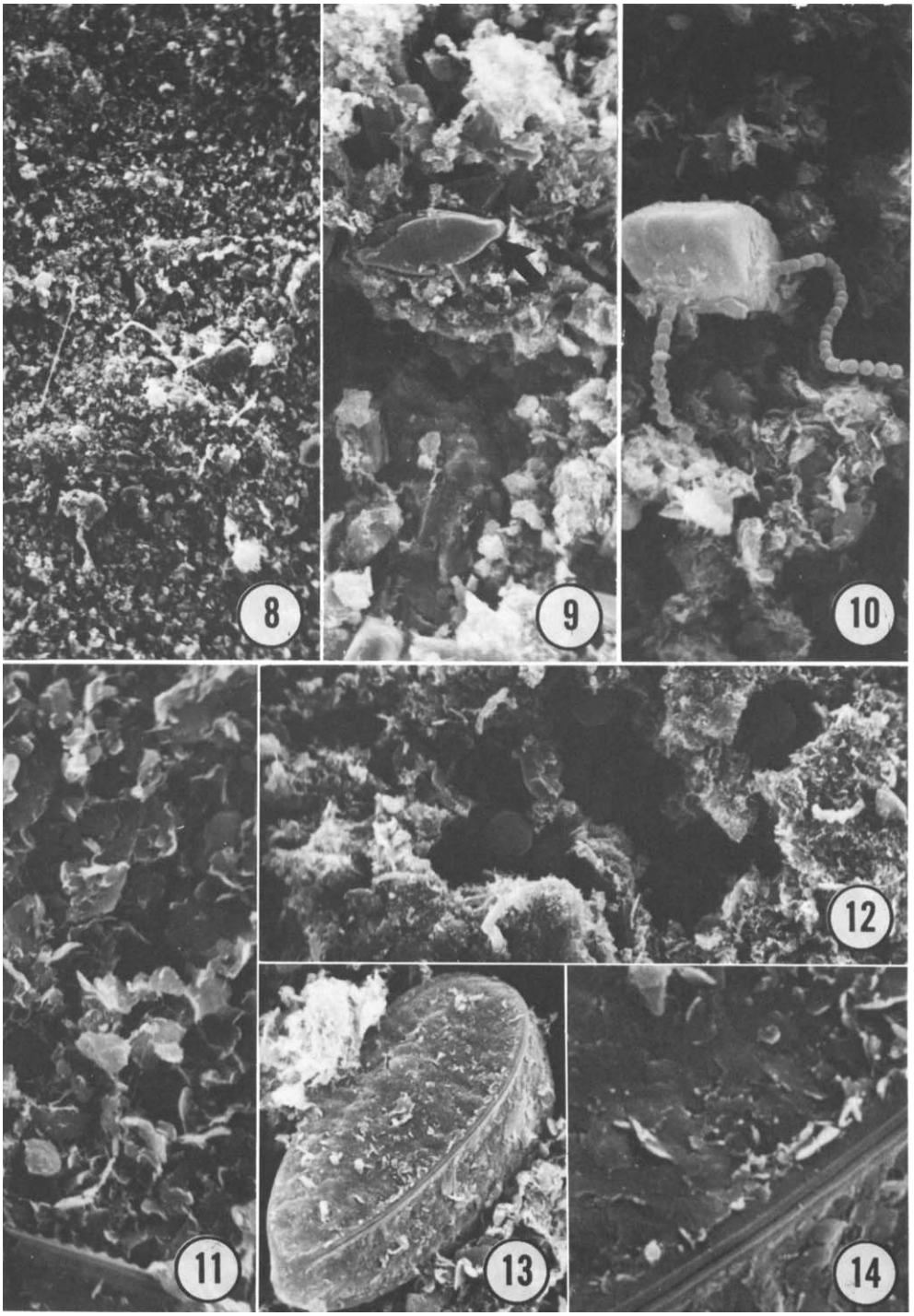
Fig. 10. Two prokaryotic filaments attached to diatom of tier 2 with flocculant debris in the vicinity. 2,600 X.

Fig. 11. Higher magnification of the flocculant debris shown in Fig. 10. 6,000 X.

Fig. 12. Some spherical cells of tier 1 surrounded by debris. The clear areas may represent where highly hydrated mucilage occurred and collapsed to the substrate with critical-point drying. 1,300 X.

Fig. 13. Surirella ovata on cells and debris of tier 2. 2,600 X.

Fig. 14. Flaky particles bound to Surirella ovata of Fig. 13 resemble the small particles found on the glass substrate in Fig. 11; raphe on edge is evident. 13,000 X.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Occasionally, rod-shaped bacteria adhered directly to the glass surface with few attachment strands (Fig. 42). Generally, however, bacteria were attached to the glass substrate via many extracellular mucilage strands (Figs. 37-40, 43). Figures 43-48 illustrate bacteria with their associated mucilage strands attached to the surface of the periphyton or the glass substrate. Some bacteria secreted large numbers of strands from their cell surface with only a few interconnections (Figs. 43 & 47), whereas other bacteria formed colonies with fine, densely woven slime threads (Fig. 44). Bacteria were commonly associated with the surfaces of diatoms. Rod-shaped bacteria were found attached apically to the valves of Gomphonema intricatum (Fig. 45), and were in the process of budding at the free end (Fig. 46). Other rod-shaped bacteria with mucilage threads were seen prostrately attached to the girdle region of Nitzschia sp. (Fig. 47) and to the valves and girdle bands of Meridion circulare (Fig. 48).

The most important organisms associated with the surface of the trapped sediments were filamentous types, similiar to those illustrated in Fig. 55. These presumptive bacteria were present at Sites A-D, but appeared most important at Sites C and D. Indeed, these filaments, occasionally branching, were the conspicuous feature of the outer surface of the tier 2 communities at Site C (10/20/80) and D (8/11/79), for example. In all communities, similar thin filaments developed, connecting aggregates of organisms together. Most of the filaments were about 1 micrometer in diameter but others were up to 4 micrometers, indistinguishable as bacteria based on their morphology.

Diatoms were the most conspicuous eukaryotic members of the one-month old periphyton. A variety of growth habits and attachment mechanisms were exhibited by the diatoms. Achnanthes lanceolata colonized large expanses of the glass surface at Site A, and was prostrately attached by an adhesive pad produced between the raphid valve and the substrate. The attachment was so secure that even the raphid valves of dead cells remained attached (Fig. 49). The attachment structures were less evident in Amphora ovalis var. pediculus (Kütz). V.H. ex

Figures 15-19 of periphyton communities of Site C, immersed May 23-June 20, 1979.

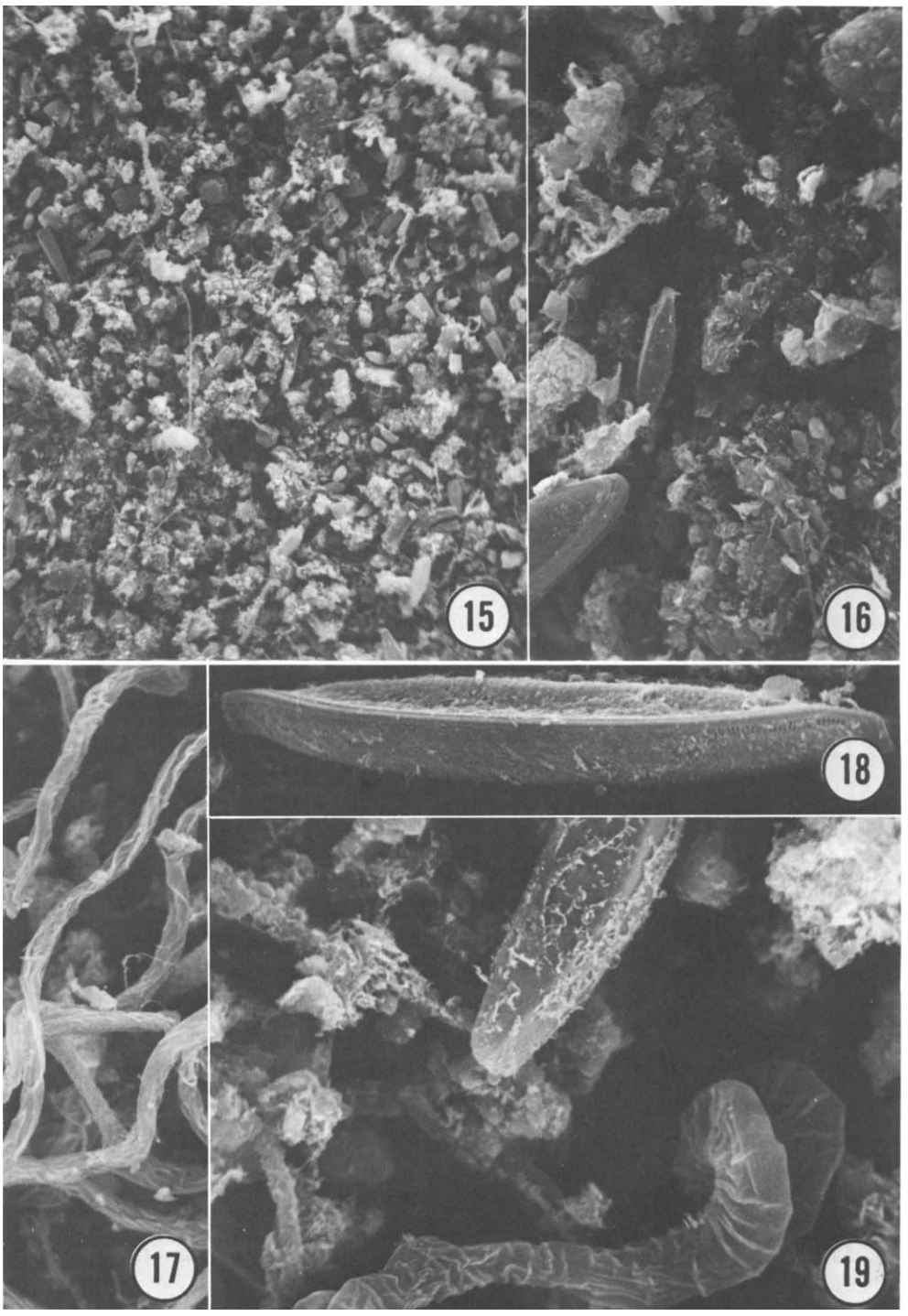
Fig. 15. Debris not tightly packed and diatoms evident. 260 X.

Fig. 16. Diatom apically attached to the glass substrate and surrounded by debris; another diatom, lower left on tier 2. 1,300 X.

Fig. 17. Unidentified filaments of tier 3 community. Filaments originated from the glass surface. 260 X.

Fig. 18. Nitzschia sp. on the tier 2 community with mucilage adhering to the valve face and girdle regions. 2,600 X.

Fig. 19. Diatom with mucilage strands on valve face and girdle regions; coiled stalk of peritrich evident at lower right. 2,600 X.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DeT. (Fig. 50) and Navicula lanceolata (Fig. 52), species commonly found embedded in detrital particulates. In contrast, Synedra acus, Meridion circulare, Eunotia curvata, Surirella ovata and Gomphonema parvulum formed perpendicular colonies which were attached to the substrate by adhesive pads. The attachment pad of Eunotia curvata was connected to the proximal cell apex near the vestigial raphe (Fig. 56), whereas Gomphonema parvulum produced a short mucilaginous stalk (Fig. 58). Long-stalked diatoms were, however, uncommon in the Maple Creek periphyton although the early spring 1980 community at Site B showed several patches of Gomphonema sp. with very long stalks forming a third tier (Fig. 59).

17.3.7 Water chemistry

The water chemistry data is presented in Tables 6 and 7. Site A represents nutrient input primarily from ground water while the downstream sites (B-E) include contributions from soil runoff. The highest nitrate level (mean 1.43 mg/l) was at Site A, with levels reduced downstream (means below 0.58 mg/l). Ammonia on the other hand was lowest at Site A; cattle and wildlife active in the stream watershed presumably account for the high ammonia levels determined for Sites C-E. The highest mean concentration for orthophosphate, a form associated with soil particulates in runoff situations, occurred at Site C, the site with watershed that will be least likely to be impacted by soil conservation practices. Iron, implicated in the crash of planktonic diatom communities in certain situations (Bringmann and Kuhn, 1971; Lund et al., 1975), remained at high levels for every collection period (Table 6). Silica, shown when at low levels to cause the wane of diatoms, particularly planktonic species (Jorgensen, 1957; Heron, 1961; Kilham, 1971), was found at very high mean levels (9.21-27.51 mg/l) and would not have been limiting to growth on any of the days

Figures 20-24 of periphyton communities of Site D, incubated May 23-June 20, 1979.

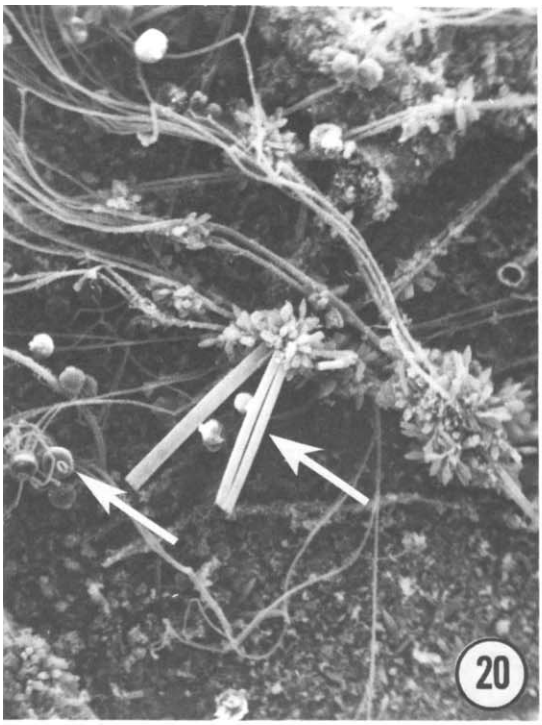
Fig. 20. Synedra ulna (right white arrow) and Gomphonema sp. colonies (the clumps of cells) on unidentified filaments of tier 3; stalked peritrichs evident at the left white arrow and above. Tiers 1 and 2 buried in sediments, lower right.
132 X.

Fig. 21. Cluster of Gomphonema sp. on filaments of tier 3; a few diatoms evident in the debris of tiers 1 and 2. 330 X.

Fig. 22. Valve (V) and girdle view (G) of Nitzschia sp. on surface of tier 2 showing a few clumps of mucilage. 2,650 X.

Fig. 23. Mantle edge of specimen in Fig. 22; valve face (right) and girdle (left) region with mucilage strands. 13,300 X.

Fig. 24. Girdle of specimen in Fig. 22 showing minute papillae of mucilage of unknown origin. 26,500 X.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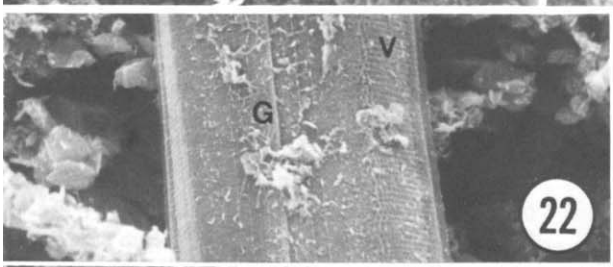
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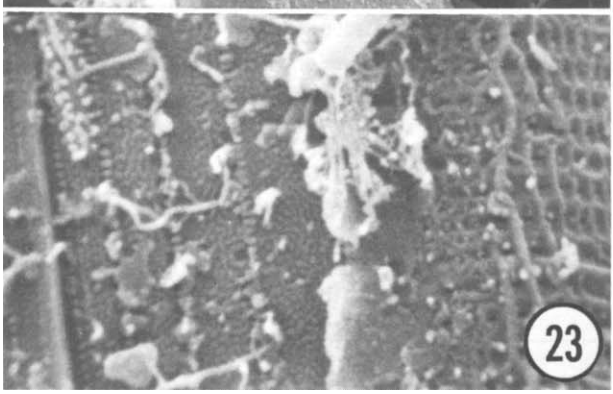
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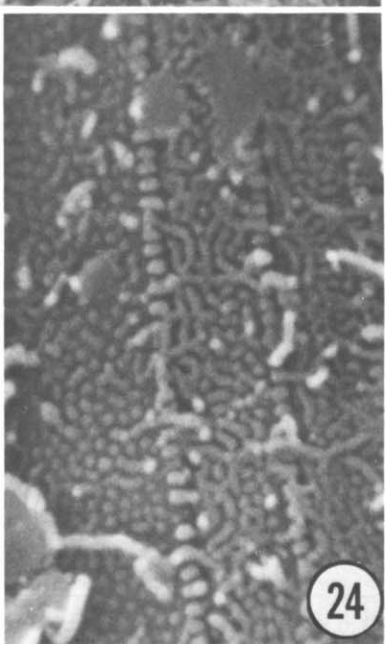
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TABLE 6

Maple Creek water chemistry (mg/l)

		NH_4-N	NO_3-N	PO_4-P	SiO_2	Fe^{++}
Site	A	0.28	1.29	0.05	24.16	0.22
	B	0.86	0.90	0.05	14.48	0.28
5/19	C	0.47	0.73	0.22	15.92	0.26
1980	D	1.24	0.75	0.22	16.08	0.28
	E	0.75	0.87	0.12	18.72	0.34
	A	0.30	1.35	0.05	27.94	0.26
	B	0.62	0.65	0.05	23.17	0.68
6/18	C	0.57	1.40	0.51	24.33	0.72
	D	0.57	0.91	0.16	19.28	0.56
	E	0.80	0.67	0.08	23.56	1.04
	A	0.04	2.03	0.07	26.50	0.15
	B	0.08	0.05	0.06	2.13	0.30
7/23	C	0.38	0.98	0.15	16.10	0.15
	D	0.10	0.32	0.09	12.10	0.45
	E	0.19	0.01	0.07	7.90	0.41
	A	0.17	1.15	0.07	46.53	0.09
	B	0.15	0.24	0.18	10.25	0.32
8/21	C	1.39	0.45	0.43	39.35	1.10
	D	1.48	0.52	0.24	12.36	0.49
	E	0.87	BLD	0.08	6.60	0.24
	A	BLD	1.42	0.52	30.55	0.35
9/22	C	0.06	0.05	0.15	20.04	0.23
	D	0.50	BLD	0.02	1.93	0.36
	A	0.03	2.04	0.03	28.72	0.32
10/20	C	5.92	0.62	1.60	24.61	1.25
	D	0.32	0.95	0.29	15.12	0.83
	A	0.05	1.44	0.08	21.90	0.30
11/20	C	0.20	1.31	0.23	18.67	0.15
	D	0.08	0.65	0.22	7.90	0.13
	A	0.07	1.25	0.03	21.67	1.14
	B	BLD	BLD	0.02	0.96	0.12
3/14	C	0.06	0.13	0.02	7.49	0.20
1981	D	0.63	0.61	0.12	2.37	0.15
	A	0.04	1.31	0.04	17.11	0.23
	B	0.02	BLD	0.05	4.25	0.68
4/14	C	0.08	BLD	0.17	1.93	0.43
	D	0.02	0.05	0.16	0.14	0.47
	A	BLD	0.98	0.04	30.04	0.20
5/12	C	0.09	BLD	0.19	14.32	0.28
	D	0.83	0.75	0.58	3.45	0.41

BLD = below level of detection

TABLE 7

Mean and range values of the water chemistry of Maple Creek (mg/l) May, 1980 to May, 1981.

	Site	A	B	C	D	E
NH_4-N	low	BLD	BLD	0.06	0.02	0.19
	mean	0.10	0.29	0.92	0.58	0.65
	high	0.30	0.86	5.92	1.48	0.87
NO_3-N	low	0.98	0.05	BLD	BLD	BLD
	mean	1.43	0.38	0.58	0.55	0.39
	high	2.04	0.90	1.40	0.95	0.87
PO_4-P	low	0.03	0.02	0.02	0.02	0.07
	mean	0.10	0.07	0.33	0.21	0.09
	high	0.52	0.18	1.60	0.58	0.12
SiO_2	low	17.11	0.96	1.93	0.14	6.60
	mean	27.51	9.21	18.28	9.08	14.20
	high	46.53	23.17	39.35	19.28	23.56
Fe^{++}	low	0.09	0.12	0.15	0.13	0.24
	mean	0.33	0.40	0.48	0.41	0.51
	high	1.14	0.68	1.25	0.83	1.04

BLD = below level of detection

water samples were taken. The limited number of water samples (10) makes it difficult to determine any seasonal trends (Table 6), although regeneration of certain nutrients over the one-month span between samples is suggested from the data.

17.4 DISCUSSION

17.4.1 Water chemistry

The data from the water chemical analyses (Tables 6 and 7) make it clear that Maple Creek is highly eutrophic, based on inorganic nitrogen and phosphorus concentrations. Silica was always 10-100 times more abundant that necessary for diatom growth, with other macronutrients at sufficient levels to support active growth.

17.4.2 SEM methodology

Studies which assess a particular aspect of periphyton *in situ* without removing and minimally disturbing the substrate, for example, for carbon production (Rodgers et al., 1978; Pennak and LaVelle, 1979; Loeb, 1981), would appear to least interfere with the functioning of natural communities once the measuring apparatus is in place (although container effects must always be considered). Studies which vary a physical parameter of natural communities, for example such as light by shading half of stream channels with a plastic cover

(Rounick and Winterbourn, 1983), leave the water itself unaltered and other parameters (e.g., wind, insects, debris) are minimally affected.

Direct observation of some community aspects are possible underwater (Vadas, 1977; Protasov et al., 1982). However, direct study of freshwater microcommunity structural morphology or development in situ usually is not possible because of the minute size of many of the members; such communities must be removed from their environment for microscopic observations of detailed community organization and morphological features (but see Kennelly and Underwood, 1984).

The removal of artificial or natural substrates may result in data with limited applications in assessing community dynamics and total community components, for the following reasons. First, the grazers, by definition species which move over and through the community, are not likely to remain attached when substrates are removed. If they are sometimes attached, their attachment may be tenuous or short in duration so that they are dislodged or leave as the sample is collected. Or, they may be fast movers in low abundance on a microscale (e.g., insect larvae or gastropods), and perhaps nocturnal in their activities as well, and thus would be unobserved if the samples were small (sections of microscope slides) or if the collections were made in daylight hours (as in this study).

Even approaching an aquatic site for collection purposes may frighten off certain grazers just as it would in a terrestrial community. It is well known that zooplankters may avoid nets that are used to collect them, if the nets are not moved rapidly enough. Clearly then, the herbivores of a microcommunity are not likely to be directly assessed by SEM of substrates since they are not permanently attached and/or abundant components of such substrates. In 10 years of studying periphyton microcommunities we have yet to find any typically motile herbivores on SEM substrates from stream or reservoir samples collected on artificial substrates in the daytime (Hoagland, Rosowski, Roemer, unpublished

Figures 25-28 of periphyton communities of Site D, immersed May 23-June 20, 1979. Cracks in Figures 25-27 are believed to be artifacts from specimen preparation, i.e, shrinkage from critical-point drying.

Fig. 25. Diatoms obscured by sediments; two peritrichs (Peritrichida) attached to glass substrate and feeding at the level of tier 3. 265 X.

Fig. 26. Lone apically attached Navicula lanceolata of tier 2 surrounded by debris. 1,350 X.

Fig. 27. Gomphonema parvulum (right) on debris which has buried tiers 1 and 2. 660 X.

Fig. 28. Same specimen and magnification as in Fig. 27, but in an area with diatoms and peritrichs of the family Vorticellidae. Several diatoms dispersed within the second tier rather than attached directly to the glass substrate. 660 X.


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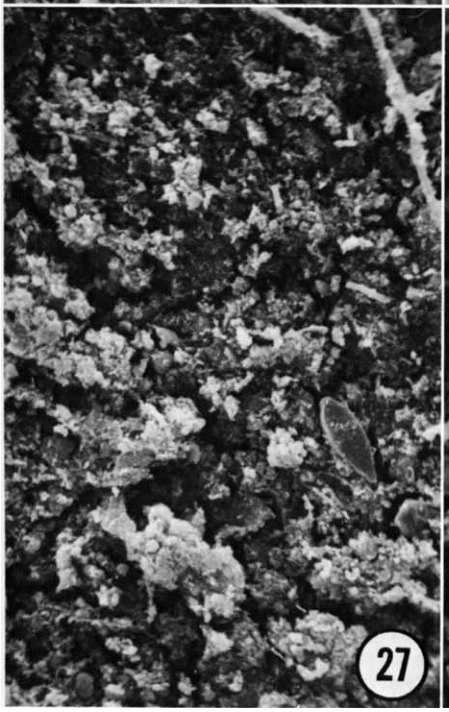
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observations). Thus, in considering the data of the present stream study, we are aware that we are not observing a major component of the community, the herbivores, and that the dominant diatom life-forms of the community have developed under selection pressure from this component.

In face of these limitations, there is nevertheless value in SEM studies which utilize collections from artificial or natural substrates. Those members of the community which are firmly attached, including bacteria, algae, fungi, and protozoans, usually do survive collection and processing without being moved from their original point of attachment. Still, there are problems which must be addressed. Once a sample is collected for SEM, many changes of fluids are used to fix and dehydrate the samples. These changes of fluids tend to dislodge loose components (e.g., pseudoperiphytic or motile members) of the community. In addition, coating procedures to make dried specimens electrically conductive to reduce specimen charging so that they can be viewed with SEM may drastically alter or destroy particularly delicate mucilaginous and flagellar features of cells (Rosowski and Glider, 1977). The highly hydrated mucilage of diatoms and bacteria is largely artifactual with respect to specific morphology (e.g., strand diameters, surface features, and interconnections), although we believe that the sites of attachment (origin) are representative. Moving specimens in and out of the vacuum system of the SEM can result in gross displacement of loosely associated community members (Rosowski et al., 1981), even though the sample has supposedly been structurally stabilized with a metal coating. Finally there is the problem that in periphyton communities that are well developed (Roemer et al., 1984), samples may be difficult to view internally or to coat evenly with a heavy metal since the communities are so dense (Rosowski et al. 1981).

On the positive side, critical-point drying procedures have been developed which minimize the artifacts of specimen preparation for SEM (Cohen, 1979 ; Rosowski et al., 1981; Hoagland et al. 1982; Boyde and Tamarin, 1984); and

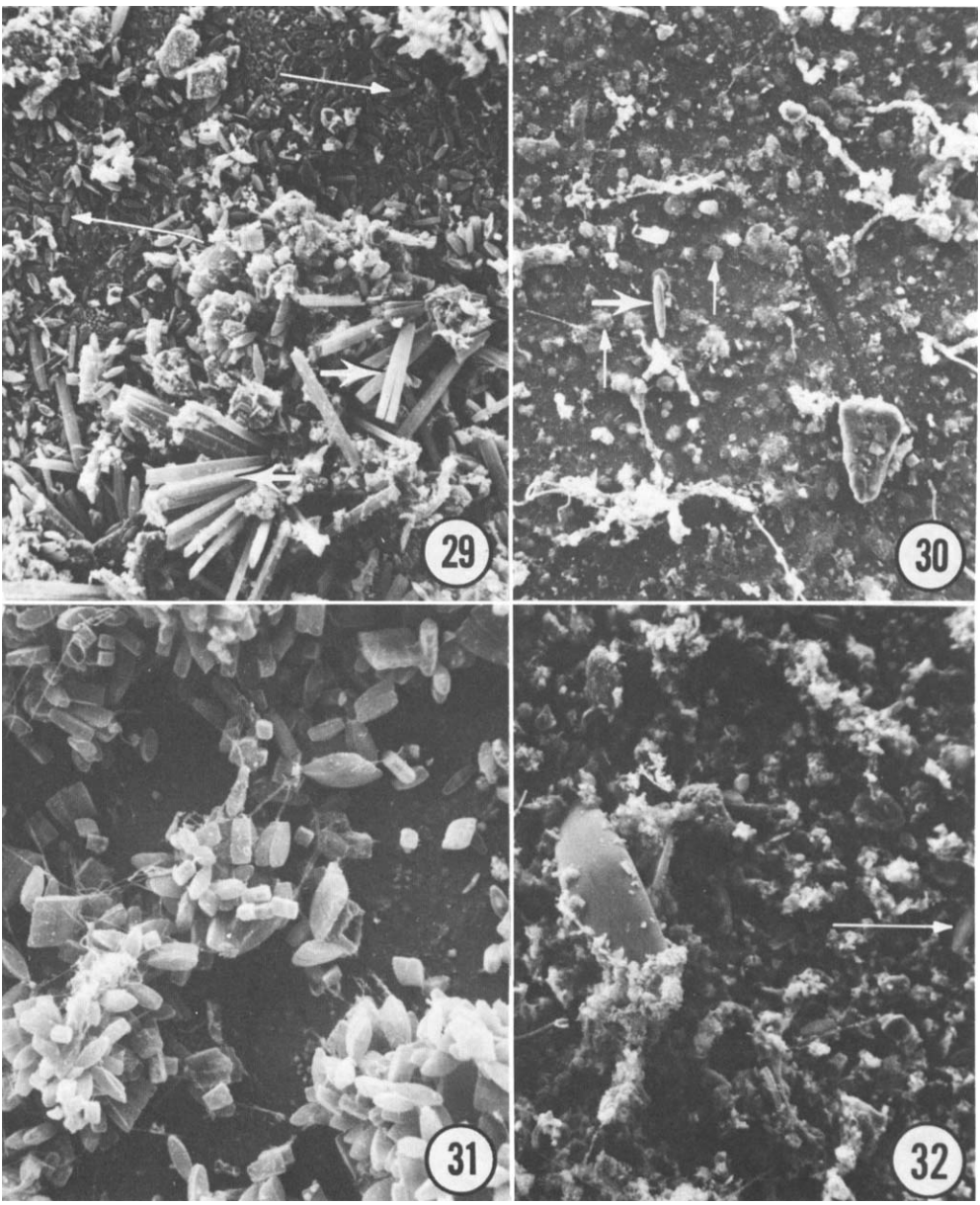
Figures 29-32 of seasonal differences in community structure at Site A.

Fig. 29. Late spring, 1979, two-tiered commmunity showing prostrate layer of Achnanthes lanceolata (small arrows), and laterally attached second storey of Synedra ulna. May 23-June 20, 1979. 140 X.

Fig. 30. Early fall, 1979, microcommunity with numerous clumps of bacterial mucilage (small arrows) and one diatom (large arrow). Severe shading of sampler by tracheophytes at this time. Sept. 11-Oct. 9, 1979. 280 X.

Fig. 31. Early spring, 1980, four-celled chains of Gomphonema sp. and other diatoms on the glass substrate, with sparse accumulation of sediments; before placement of black plastic on the stream banks. March 22-April 19, 1980. 280 X.

Fig. 32. Early fall, 1980, a large diatom surrounded by sediments and smaller diatoms (arrow). Sept 22-Oct. 20, 1980. 290 X.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fractured walls of diatoms observed in SEM samples (Fig. 9) can thus be attributed to damage which occurred prior to the sampling. Furthermore, SEM studies have shown that particulates which impinge on aquatic communities and that are bound to it by bacteria and algae can be assessed visually and very informatively in a qualitative manner (Chamberlain, 1976; Daniel et al., 1980; Hudon and Bourget, 1981, 1983; Rounick and Winterbourn, 1983; Hoagland et al., 1982; Roemer et al., 1984).

17.4.3 Immersion period, substrate and methods

The choice of the immersion period of the samples was based on our previous experience in lentic environments in which four weeks appeared to produce communities stable in cell density except as sloughing occurred (Hoagland et al., 1982; Roemer et al. 1984). Others have also found that four weeks is a suitable period in streams and rivers (Cattaneo and Ghittori, 1975; Blinn et al., 1980), but perhaps more complex or diverse communities develop with longer periods, as noted in two of our samples that were immersed more than 3 months (Tables 3 & 5). Brown and Austin (1973) found that station differences were least between stations for substrates that were immersed for monthly intervals and greatest for those immersed for a four-month period.

Clay tiles are considered by several investigators to be superior to rocks with repect to reduced sample variability (Tuchman and Stevenson, 1980; Lamberti and Resh, 1985), and although glass slides have not accurately reflected the periphyton of some communities in biomass accural or species composition (Siver, 1977), they apparently have in others (Cattaneo and Ghittori, 1975). We defend our use of glass because of its highly uniform and chemically inert surface, which reduces within- and between-sample variation.

Methods for sampling periphyton have been the focus of specific studies (Weitzel, 1979; Austin et al., 1981). Glass rods were used to simulate Typha

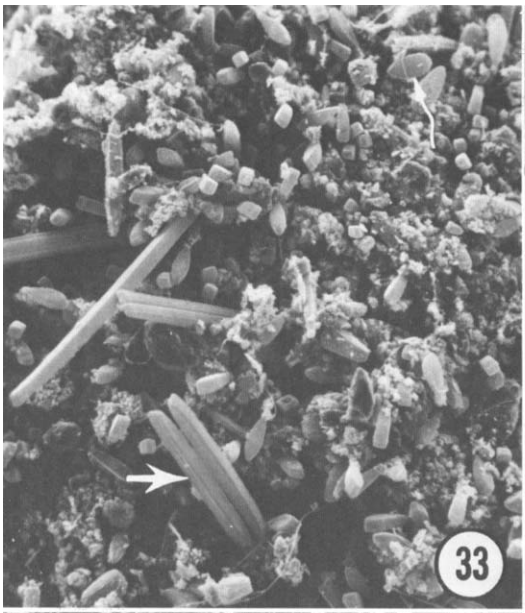
Figures 33-36 of special structural features of the periphyton of communities of Sites B, C, and D.

Fig. 33. Dense accumulation of sediments at Site B associated with diatoms. Note Synedra ulna (large arrow) and Surirella ovata (small arrow). Mar. 22-Apr. 19, 1980. 290 X.

Fig. 34. Diatom (arrow) attached apically to the glass surface and surrounded by sediments; upper right a diatom with a cracked frustule attached on the second tier; lower left of diatoms secondarily attached to sediments of tier 2. May 22-June 21, 1979. Site B. 2,800 X.

Fig. 35. Basal attachment to glass substrate of Oedogonium sp. which becomes a component of tier 3. Oct. 9-Nov. 8, 1980. Site D. 145 X.

Fig. 36. Filaments of Oedogonium sp. concentrated on edge of the glass substrate. June 20-July 18, 1979. Site C. 29 X.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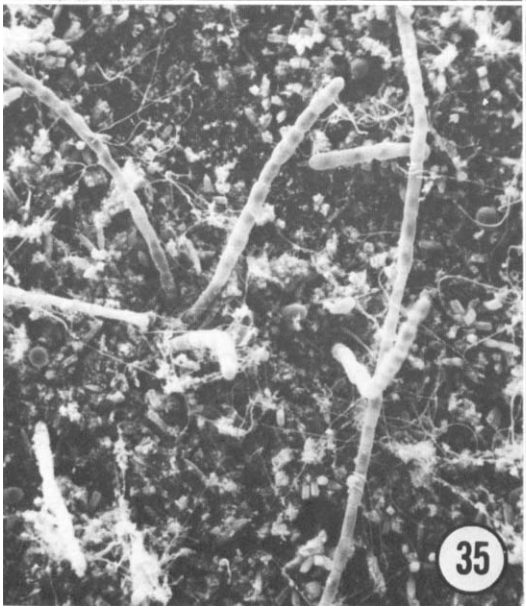
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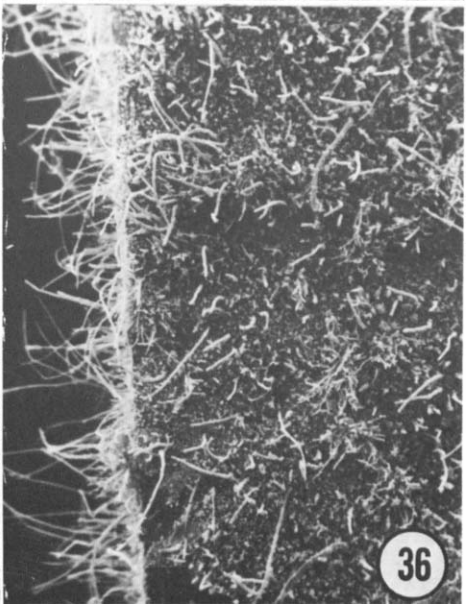
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stems in a study of chironomid grazing (Mason and Bryant, 1975). Although periphytic algae grew well on the 0.5 cm glass rods, with similar species diversity as on the Typha, chironomids did not occur on the glass rods presumably because they could not find a suitable surface on which to attach (Mason and Bryant, 1975). The higher density of periphyton on the glass rods than on the Typha was suggested to be due to the lack of feeding by the chironomids on the periphyton of the glass-rods. On our glass-slide substrates chironomid pupal cases did develop (Fig. 2, Sites B and D, spring). Perhaps the larger flat surface of the 2 cm wide slide oriented in the direction of stream flow provided a broader and more protective boundary layer for attachment to occur in which local shear forces would be reduced sufficiently below that of the main stream (Silvester and Sleigh, 1985).

Although there are many examples of interesting and diverse attachment structures illustrated for bacteria associated with diatom dominated communities (Hoagland et al., 1982; Roemer et al., 1984), Marshall (1980) has suggested that "definitive evidence for permanent adhesion of microorganisms to soil and sediment particulates is lacking," with evidence for permanent attachment the demonstration of polymer bridges between the microorganisms and the substrate, so that they would not be dislodged "when substantial shear forces are applied." Marshall (1980) cautions that "especially with SEM, it is dangerous to assume that all microorganisms seen on solid surfaces were firmly adhering to the surfaces prior to specimen drying. Many of the organisms may have been in the bulk aquaeous phase or superficially attracted to the surfaces and merely deposited on the surfaces during the drying process." This statement bears consideration.

Figures 37-42 of extracellular bacterial mucilages and/or of bacterial attachment modes.

Fig. 37. Clumps of bacterial mucilage (with bacteria beneath) from a sample with sparse autotrophic growth. Sept. 11-Oct. 9, 1979. Site A. 1,400 X.

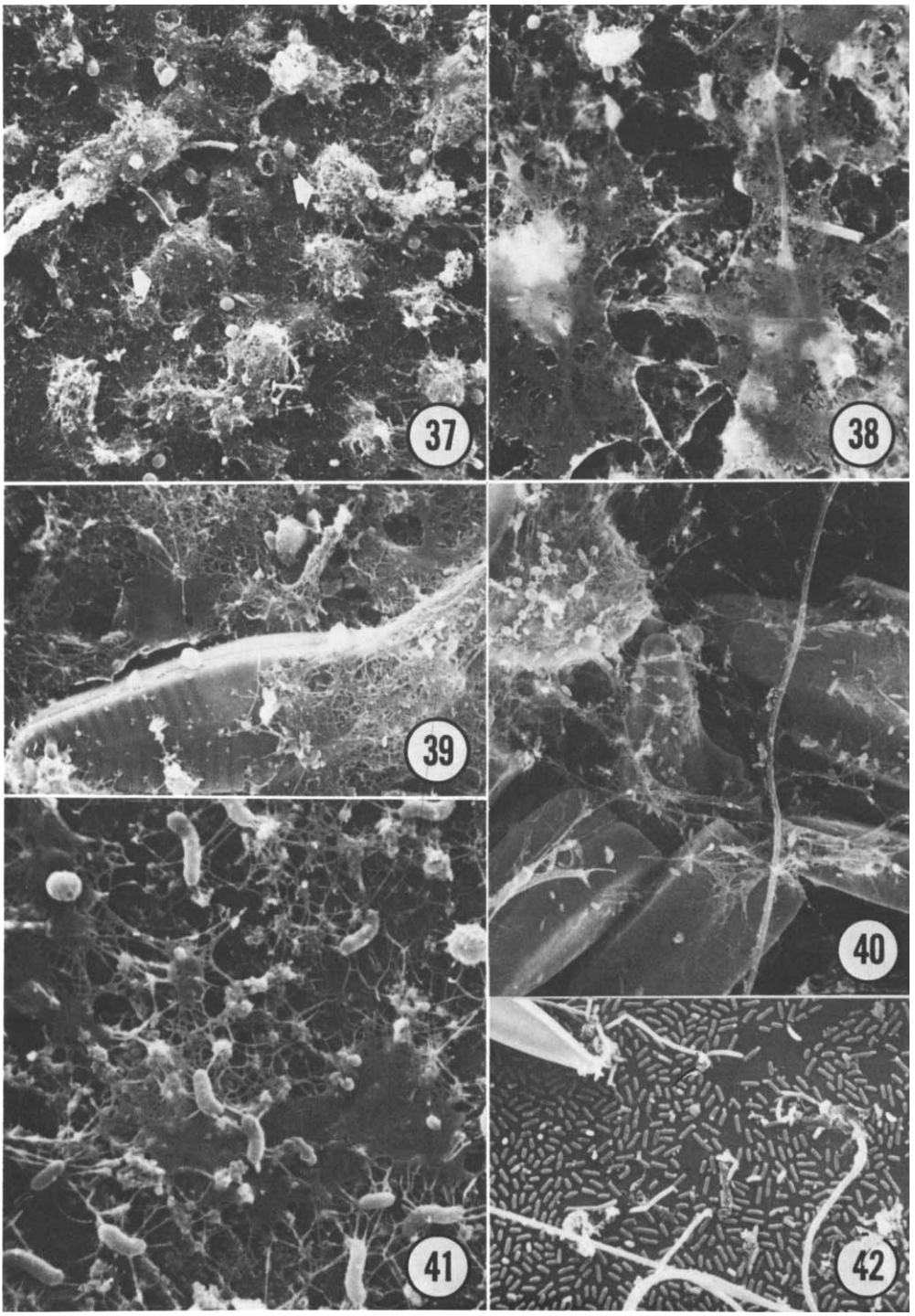
Fig. 38. Sheet-like webs of bacterial mucilage adhering to the glass substrate from a sample with sparse autotrophic growth. June 18-July 23, 1979. Site A. 2,800 X.

Fig. 39. Bacterial mucilage strands partially covering a cell of Achnanthes lanceolata extending from the pseudoraphe valve face to the substrate surface (right). June 20-July 18, 1979. Site A. 2,850 X.

Fig. 40. Bacterial mucilage strands in a loose network over cells of Gomphonema sp. Mar. 22-Apr. 19, 1980. Site A. 1,400 X.

Fig. 41. Apically attached bacteria with mucilage strands adhering them to the glass substrate. June 20-July 18, 1979. Site A. 7,200 X.

Fig. 42. Prostrately attached bacteria lacking conspicuous mucilage attachment strands. Mar. 22-April 19, 1980. Site D. 1,400 X.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It was our procedure in previous studies (Hoagland et al., 1982; Roemer et al., 1984) to fix natural collections in fixative made up in reservoir water so that the concentration of the suspended organisms of these samples were those of the original reservoir water. In the present study our fixative was made up in Alga-Gro medium from tap water which was forced from a squeeze bottle under pressure into open slide containers; the density of suspended cells in this case would be less than originally occurred in the stream samples.

The purpose of positioning slides vertically when immersed in the stream is so that organisms that appear are more likely to have actively attached. Sediments that are present are firmly attached or they would come off during removal for fixation or in transfer of liquids in subsequent specimen dehydration. And although clean glass slides which are fixed with one-month old communities on slides do not collect organisms during fixation (Rosowski, unpublished), it cannot be denied that suspended organisms of the bulk aquaeous phase could become entangled in the periphyton of well developed communities, as undoubtably occurs in the natural environment as well. However, given the specificity of attachment sites of the bacteria (Figs. 37-42; 45-47), the specific sites of origin of attachment strands on the bacteria (Figs. 41, 43, 47), the specific orientation of certain bacteria species when attached (Figs. 41, 43, 45-48), and the paucity of bacteria that appear to be only casually attached, we believe that contributions of unattached cells from the water column which would firmly adhere to the substrate during fixation comprise an insignificant component of the communities we have observed in this study. The low density of bacteria on one-week old samples during colonization also

Figures 43-48 of extracellular bacterial mucilages and/or of attachment modes and bacterial morphology.

Fig. 43. Bacterial mucilages with strands radiating apically and laterally from the apically attached bacterial cells. May 23-June 22, 1979. Site A. 14,200 X.

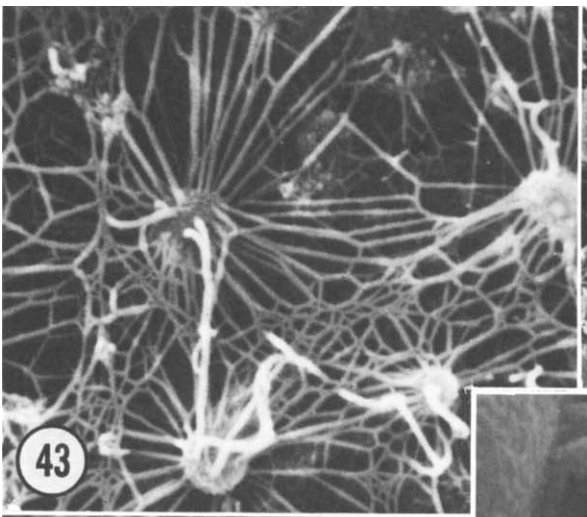
Fig. 44. Fused mucilage strands forming webs over the bacteria attached to the glass substrate. Sept. 11-Oct. 9, 1979. Site A. 7,200 X.

Fig. 45. Bacteria apically attached to the Gomphonema intricatum. Note budding (arrows). May 12-June 21., 1979. Site C. 2,900 X.

Fig. 46. Detail of Fig. 45--bacteria showing papillae of cell surface (arrow). May 12-June 21, 1979. Site C. 14,500 X.

Fig. 47. Fusiform bacteria, one in the process of division but not separated (left), attached to girdle band surfaces of Nitzschia sp. Mar. 22-Apr. 19, 1980. Site C. 14,250 X.

Fig. 48. Rod-shaped bacteria prostrately attached and interconnected with sparsely produced mucilage strands, on Meridion circulare. Note Caulobacterium sp. attached at girdle band suture (see minute arrow). Mar. 22-Apr. 19, 1980. 7,100 X.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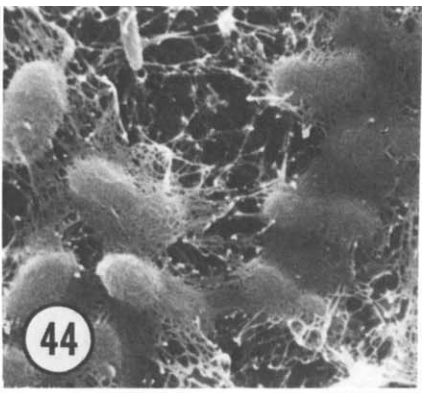
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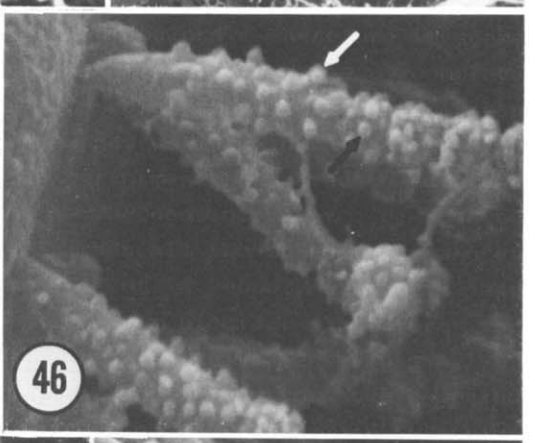
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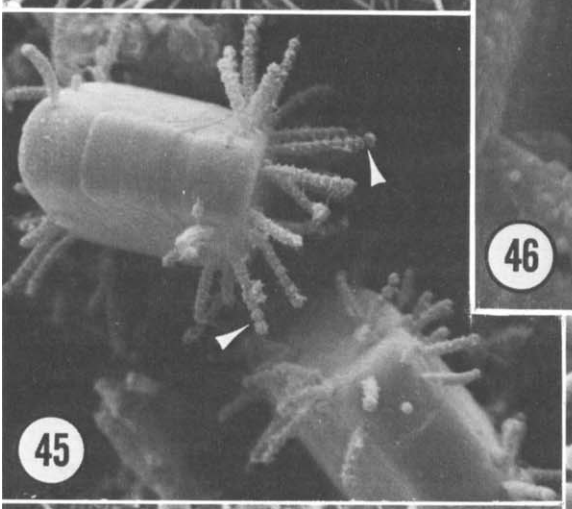
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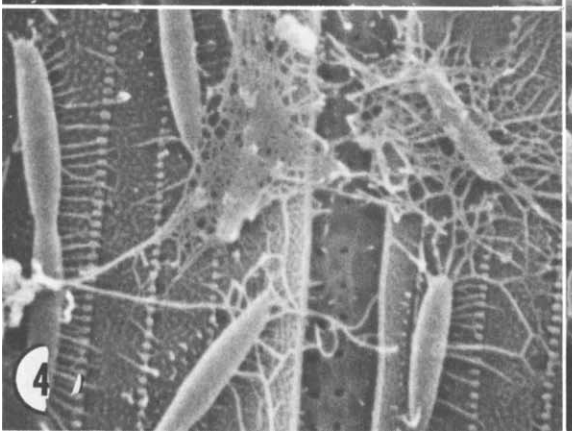
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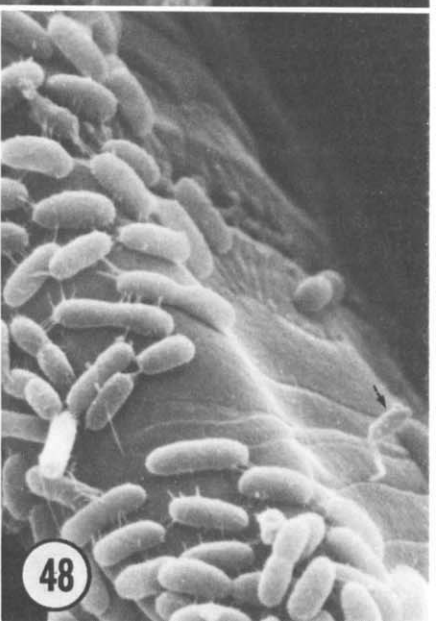
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suggests that artifactual settling on substrates during fixation is low (Hoagland et al., 1982; Hoagland, 1983; Roemer, et al., 1984). Still, settling could be important in bodies of water where there are many suspended organisms at the time of sample fixation.

17.4.4 Periphytic diatom life forms--Structural and functional heteromorphy

How attached diatoms cope with physical and biological disturbances is mostly conjecture based on forms viewed as analogous to those of the benthic macroalgae. Experimental work has verified the extent of the antiherbivore defenses of certain morphologies and/or life history strategies (Littler and Littler, 1984). As yet, functional-form models have not been proposed for the diatoms or for attached microalgae. A recent study considers the adaptive morphological aspects of Achnanthes lanceolata in resisting grazing and stream hydrodynamic forces, based on material from Site A in Maple Creek (Rosowski et al., 1986). In this case, being small, prostrate, sessile, and particularly well adhered to the substrate are important adaptive features for a stream environment, whereas being free-living and small are not (Kondratieff and Simmons, 1985). In another study, life-form strategies of diatoms which were strictly periphytic, or periphytic and tychoplanktonic, were noted for particular species (Kuhn et al., 1981). The water current velocity which will best support the growth of periphytic diatoms and other algae has been documented for a number of species (Antoine and Benson-Evans, 1982). In the following discussion, in considering the adaptive potentialities of the

Figures 49-54 of growth habits and attachment modes of selected diatom taxa.

Fig. 49. Achnanthes lanceolata attached prostrately to glass surface. Raphe valves of dead cells remain attached (arrows). May 23-June 20, 1979. Site A. 720 X.

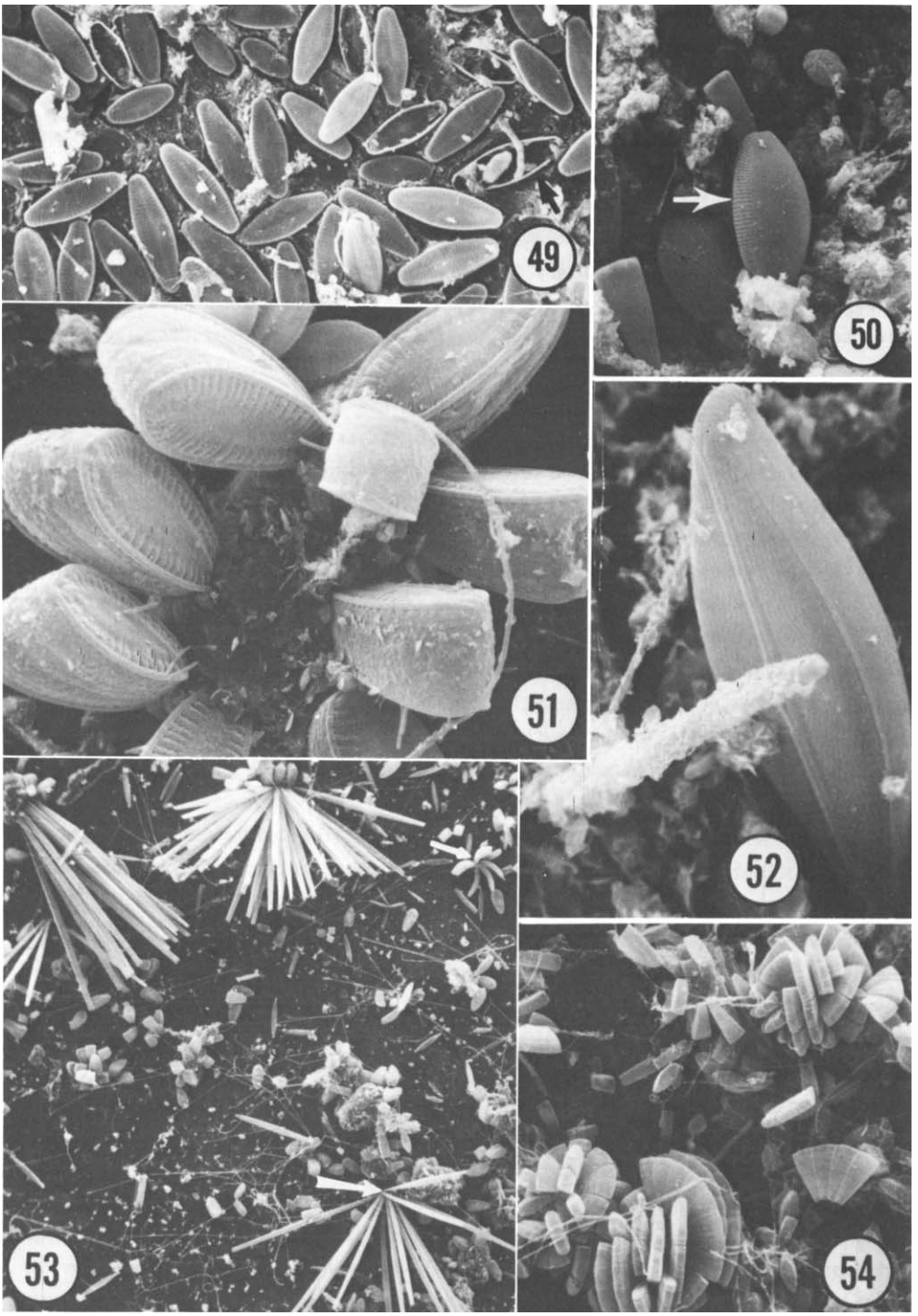
Fig. 50. Amphora ovalis var. pediculus attached to the glass substrate (below arrow) and above this substrate (arrow) on sediment. May 23-June 20, 1979. Site C. 725 X.

Fig. 51. A circular nine-celled colony of Surirella ovata attached apically at the tapered end by a confluent pad of mucilage. Mar. 22-Apr. 19, 1980. Site D. 1,400 X.

Fig. 52. Navicula lanceolata surrounded toward the base by particulates. May 23-June 20, 1979. Site A. 2,800 X.

Fig. 53. Rosettes of Synedra acus Kütz. (large arrow) attached to glass surface; note small rosette of Eunotia curvata (small arrow). Note fine filaments on substrate. Mar. 22-Apr. 19, 1980. Site D. 140 X.

Fig. 54. Fan-shaped arrays of Meridion circulare forming hemispherical colonies. Mar. 22-Apr. 19, 1980. Site D. 280 X.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periphytic microalgae, it is useful to keep in mind the life history strategies elucidated for certain macrobenthic marine algae: e.g., heterotrichy (Littler and Kauker, 1984) and heteromorphy (Littler and Littler, 1983).

Hoagland et al. (1982) and Roemer et al. (1984) showed a range in stature of lentic periphyton, with early invading prostrate forms having the least stature. However, both monoraphid and biraphid diatoms which have part of their life history in a prostrate mode may increase their stature with respect to the community by secreting an apical attachment pad and elevating themselves on their proximal end at right angles to the substrate (Hudon and Bourget, 1981, 1983; Hoagland et al., 1982; Korte and Blinn, 1983; Roemer et al., 1984). Diatoms which take the best advantage of this strategy are those with the longest apical axis, such as Synedra. Such genera, which have no raphes, arrive passively at the substrate surface where they presumably are unable to move except to adjust their angle of attachment. However, certain smaller species may attain even greater perpendicular stature by secreting stalks of mucilage which elevate them in the canopy several orders of magnitude higher than they would be if they could only elevate their sessile frustule on their proximal end, from prostrate to perpendicular.

These changes in life-form may be viewed as functional heteromorphy since there is no increase in the biovolume of the organism when a prostrate cell elevates itself on its proximal apex and increases the distance from its distal apex to the substrate without a cell-size increase and without stalk formation (e.g., araphid rosette formers such as Meridion circulare, Synedra ulna, and Fragilaria vaucheriae). Structural heteromorphy would be when such an elevation is followed by the development of a stalk, which may become dichotomous and extensive if sibling progeny continue to produce stalks and maintain the colony continuity (as in many monoraphid and biraphid species). In this case there is also an increase in the biovolume of the organism, with the stalks often occupying a much greater volume than the cells which produced them (Drum, 1963; Roemer et al., 1984). Such an increase in size is not viewed here as heterotrichy, since the particular diatoms which form the perpendicular tier 2 growth form are no longer prostrate and thus are not members of the prostrate tier 1 community.

The two-tiered nature of stream periphyton was not discussed in an earlier (Hynes, 1970) or in a more recent review (Moss, 1980); it has, in fact, only been mentioned briefly for streams. Patrick and Roberts (1979) described the mature stream periphyton as a "miniature complex forest." It has been suggested that filamentous overgrowth which creates an upperstorey is brought about by nutrient deficiency at the substrate level in the understorey (Sumner and McIntire, 1982). Other studies suggest that nutrients may affect development of specific diatom communities in the face of equal sources of primary colonizers

but unequal nutrient availability. For example, in a study of lentic periphyton on artificial substrates which released single nutrients, Epithemia danata and Rhopalodia gibba were found to be stimulated in growth with phosphate addition, while growth of Achnanthes minutissima was slightly depressed (Fairchild and Lowe, 1984). In another study, substrates with nitrate and phosphate together favored naviculoid diatoms (Fairchild et al., 1985). In a lotic study using sand/agar substrates which released nitrate and phosphate, singly or together, it was found that phosphate alone or nitrate and phosphate together stimulated the growth of Navicula and Nitzschia whereas the substrates of the control and nitrate treatments alone were dominated by Cocconeis placentula and Achnanthes minutissima (Pringle and Bowers, 1984).

It has been proposed (Blinn et al., 1980) that periphyton development in streams is influenced by microsurface features and substrate solubilization in the first week in particular, but that after two weeks aggregated organic matter is sufficiently dense to mask the influence of the original substrate surface. The evidence in support of this hypothesis was the failure of development of different diatom communities in the same stream on Verde limestone, Supai sandstone and Andesitic basalt substrata after three weeks, the period in which maximum diatom densities developed. In a study of bacterial colonization, Mills and Maubrey (1981) found that bacteria more heavily colonized quartz (chemical analog of sandstone) than calcite artificial substrates (chemical analog of limestone) at two different sites at 10 and 20 day periods; a third site had more bacteria than the other two, but there was no difference in bacterial numbers on the two different substrates suggesting that "the composition of the mineral substrate, in concert with the immersion environment, controls the formation of primary slime layers in aquatic systems." Differential colonization into microzones occurs as a result of current direction, as conceptualized in models illustrated by Korte and Blinn (1983).

17.4.5 Herbivory and periphyton

It has been suggested by Kesler (1981a) that "the impact of grazer organisms upon freshwater periphyton communities has been assumed by most workers to be insignificant. However, without quantification of material removed by grazers, and comparison of this amount to the periphyton standing crop, these assumptions are unfounded." Perhaps such an assumption could explain why Moore (1977a, b, 1978) found grazing in streams to have little effect on the standing crop, whereas other studies of streams show a decrease in abundance and/or diversity of taxa with grazing (Dickman, 1968; Elwood and Nelson, 1972; Doremus and Harman, 1977; Hunter, 1980; Mulholland et al., 1983), or a slight decrease in abundance with no effect on species diversity (Kehde and Wilhm, 1972). In any case, a factor in obscuring the importance or role of herbivory would be rapid

turnover rates of the periphyton (McIntire and Colby, 1978). Even the relatively low standing crops we report here in respect to those for reservoir communities (Hoagland et al., 1982; Hoagland, 1983; Roemer et al., 1984) might be supporting a high consumer biomass with a rapid turnover of the algal periphyton (Lamberti and Resh, 1983). And, in diverse aquatic systems, high nutrient regeneration rates from grazing and other activities have been shown to be responsible for increased algal (Cooper, 1973; Flint and Goldman, 1975; Porter, 1976; Graneli, 1979; Robles and Cubit, 1981; Osborne and McLachlan, 1985; Power et al., 1985) and bacterial production (Lopez et al., 1977; Sierszen and Brooks, 1982). However, recycling can be so tight as to occur within the microcommunities themselves without transfer into the water (Haack and McFeters, 1982; Cuker, 1983) and thus this exchange could easily go undetected.

In enclosure-exclosure experiments, Kesler (1981b) showed a reduction in the periphyton standing crop when the gastropod Amnicola limosa was included, while Cattaneo (1983) showed that a sudden decline in epiphyte biomass was due to intense grazing from oligochaetes and chironomids. There is apparently discriminatory herbivory with respect to the microalgae (Bowker et al., 1983, 1985), with an example of removal of unwanted species to perhaps provide room for growth of desired species (Hart, 1985). We do not here consider the invertebrate fauna of Maple Creek, some features of which have been studied by Pitcairn (1981) and Shadle (1984).

17.4.6 Community development

It has been suggested that a primary seral stage in aquatic habitats is the establishment of organic-rich detrital materials on surfaces which develop no further if they fail to receive light, e.g., the undersides of submerged stones or in shaded areas (Calow, 1975). Such organic films may develop in only a few hours (Korte and Blinn, 1983). The accumulation of organic carbon on rocks may reach its peak in the dark after one month and maintain that level for up to three months (Rounick and Winterbourn, 1983). Surface organic layers of hard substrata are potential sites for the uptake of dissolved organic matter which could be transferred to the benthos (Winterbourn et al., 1985). Illuminated microcommunities in lotic and lentic systems usually are dominated by diatoms within the first week of immersion and maintain that dominance for up to four-five weeks (Hoagland et al., 1982, Hoagland, 1983; Roemer et al., 1984), with more diverse diatom communities requiring months for development (Brown and Austin, 1973) and even years in the case of long-lived macroalgae of the marine environment (Kay and Butler, 1983).

We found a great reduction in the standing crop of diatoms when a community was shaded (1,500 diatoms/mm^2 to 7/mm^2, Table 1). Similarly, Moore (1977b) found that "the flora developed at only 1-2% of the rate exhibited by a similar

community in unshaded conditions"; reduction in gross primary production was also noted by Sumner and McIntire (1982) in shaded laboratory streams. Recently it was shown that certain nutrient requirements and species interrelationships are affected by light which bring about these effects by altering the optimum cellular N:P ratios (Wynne and Rhee, 1986). We found the highest cell density in a nearly 4-month old community, with Nitzschia linearis a dominant at Site C and N. subcapitellata as a codominant at three different sites (Table 5), species which did not occur as the dominant or codominant species in any of 15 one-month immersion periods over 2 years (cf. Tables 1-5).

17.4.7 Bacteria, diatoms, and sediment associations

Previous reviews have dealt with the interactions of microorganisms, soils, and sediments (Corpe, 1980; Paerl, 1980). Stabilization of sediments by diatom mucilages is known (Holland et al., 1974). There is accumulating evidence that algae and bacteria interact in stimulatory and inhibitory manners (Cole, 1982). It is now appreciated that bacteria are important as major producer organisms utilizing dissolved organic carbon and that grazing by bacteriovores is significant in the release of bacterial-bound nutrients that contribute to algal growth (Ducklow, 1983). In epilithic stream communities, the nutritional relationship between algae and bacteria may result in "a direct flux of soluble algal products to the bacterial population, with little heterotrophic utilization of dissolved organics from the overlying steam water" (Haack and McFeters, 1982). This stimulation of bacteria by algae appears to occur best in daylight hours in some situations (Nalewajko et al., 1984).

There is a close association of unicellular, colonial and filamentous bacteria with diatoms and sediments in the stream community of Maple Creek. Certain bacteria attach with fibrous webs near and sometimes over diatoms with apical or prostrate attachment at specific sites on the valves or girdle bands. These sites are presumably where the diatoms are secreting metabolites, and these associations provide morphological evidence of the close proximity that might be necessary for nutrient exchanges to occur without detection in the water column (Haack and McFeters, 1982; Cuker, 1983). Although we have found bacteria in the tier 2 communities attached to diatoms (Figs. 45-48), it is the primary substrate where most unicellular and colonial bacteria occur when one-month old substrates are examined (Figs. 37-42). With sediment trapping, it is impossible to view the diatoms or bacteria regardless of the magnification because they appear "covered" with reflected type of viewing (SEM) although the transmitted light of the natural community is probably still adequate for photosynthesis at the tier 1 substrate level.

Paerl (1980), in reviewing the literature, has noted that bacteria will colonize inert substrates as well as those which provide nutrients, and that the

mere presence of a surface for colonization, even if inert, allows for microbial growth. Glass slide substrates are initially inert, but it is widely reported that colonization by bacteria quickly follows, and there may be successional bacterial events as well, for example with nonbranching bacteria followed by branching bacteria (Aumen, 1980). The evidence presented by Hamilton and Duthie (1984) for the absence of a preconditioning organic film and a paucity of bacteria in early colonization of a boreal forest stream is six scanning electron micrographs of substrates of the first five days at ca. 140 X, a magnification at which bacteria and tight organic films would be impossible to distinguish even when the substrate colonizers are sparse (see our Fig. 53). Their highest magnification electron micrograph (Fig. 11 at 1,300 X) reveals only the upper tier of a nine-day old community, as evidence that bacteria were "noticeably absent and were not important components of colonization initiation." At this magnification it is difficult to definitively identify bacteria by SEM (see our Fig. 42). Similarly, Perkins and Kaplan (1978) also reported that SEM failed to reveal a "heterotrophic biomass" in a subalpine stream. However, since only extant epilithic samples were examined in which the periphyton was already well developed it might be difficult to determine (as their electron micrographs suggest) if bacteria attached directly to the natural substrates. We would expect oligotrophic stream substrates to have a lower bacterial density than eutrophic, particularly when the water is acidic (Hamilton and Duthie, 1984). However, although their conclusions (Perkins and Kaplan, 1978; Hamilton and Duthie, 1984) may be correct, failure to show bacteria with SEM in these cases is not nearly so convincing as would have been their demonstration.

It is the period during and after the appearance of the tier 1 and tier 2 diatoms that most of the silt and detritus is trapped. However, in the case where only heterotrophic growth was significant (shaded samples), particulates accumulated but did not develop beyond about the tier 1 level. Diatoms thus appear to be essential in the Maple Creek community for the trapping of sediments that compose the tier 2 level which then buries the tier 1 level. The particles provide potentially new sources of nutrients for the microcommunities, but they do not appear to provide a particularly suitable surface for further attachment of diatoms. We noted high densities of diatoms within silt laden communities, but these diatoms appeared to be largely attached to the primary substrate (the glass slides) presumably attaining that position before most of the particulates accumulated over and around them. But some diatoms do manage to attach within their own developing clumps, or on debris (e.g., Gomphonema parvulum, Nitzschia sp., Synedra ulna), and this ability to exist without direct attachment to the primary substrate may be a species attribute. Further observations on the attachment habit of specific species in silt laden

communities is needed.

Although diatom buildup on substrates has been considered a layering process (Pryfogle and Lowe, 1979), we must emphasize that the increase in thickness of periphyton in one-month old communities is primarily due to the progression of the community to larger life-forms attached to the primary substrate (Hoagland et al. 1982; Roemer et al. 1984), not to the build up of one community by attachment on the top of another. Although the accumulation of debris over the tier 1 and around the tier 2 communities would appear to have a stabilizing factor and protect the members of these communities from dislodgement, these communities may still be sufficiently unstable or otherwise unsuitable for further colonization by diatoms. Alternatively, one-month old substrates may not have been old enough for other sediment colonizing tier species to have invaded. The third tier community (largest life-forms attached to the primary substrate) does develop its own diatom epiphytes. These epiphytes move indirectly, unlike the diatoms of tiers 1 and 2, as the filaments of the third tier with their epiphytes shift position with changing currents.

We have assumed in the present study, and in the past (Hoagland et al., 1982; Roemer et al., 1984), that the material which binds sediments is mucilage from diatoms and bacteria. Such material is destroyed by organic acids (cf. Rosowski, 1980 and Rosowski et al., 1983). However, Lewin et al. (1980) have noted that clay particles bound to the marine diatom Chaetoceros armatum remain attached after prolonged hot acid treatment which suggests that the binding material of this diatom is not a typical mucilage. Therefore, the assumption here that mucilage of diatoms is responsible for the binding of sediments should be considered tentative. Diatom mucilage could have the opposite effect, of course, that of keeping off the rain of particulates; evidence for this in our study was in the 10/20/80 sample, Site C, in which clumps of Gomphonema intricatum had copious quantities of surface mucilage (fuzzy surfaces) with no attached debris.

Does the silt of these silt-laden communities affect tiering structure? Unfortunately, we had no way of separating the effects of stream flow from that of the silt load carried by that flow, which had reported ranges in dry weight of 0.23-12.72 g/l in 1979, 0.38-8.08 in 1980, and 0.42-121.40 g/l in 1982 (Schepers et al., 1985). Compared with shallow reservoirs in Nebraska (Hoagland et al., 1982; Hoagland, 1983), the Maple Creek periphyton did not develop as thick of a layer in one month, but binding of sediments (quantity trapped as judged by apparent density) appeared with SEM to be greater. The silt load of Maple Creek did not destroy the periphyton by scouring as might have been expected, but it would take experimental work at erosion prone sites (B through E) to demonstrate community structure without the impact of particles from this erosion-prone watershed.

It should be noted that in our bright-field microscopy assessment of

diversity and dominance we did not distinguish between living and dead cells, which were distinguishable with SEM to the extent that intact frustules could be distinguished from damaged frustules; inclusion of dead cells in cell enumerations may have either increased or decreased sample diversity (Pryfogle and Lowe, 1979). A study of hourly, daily and weekly development of silt laden communities which eventually slough would be a logical extension of the present work, which was confined primarily to a comparison of one-month old communities. Attention in future studies could then be directed to defining diversity and structure of mature communities, perhaps defined as communities which exhibit mass sloughing, rather than studying communities of a specific age which may or may not be mature depending on the season and period of immersion.

17.4.8 Implications of soil erosion to the stream biofilm

The highly erosion-prone watershed of the tributaries of the prairie stream of the present study (Sites B-D) showed that substrate colonization and dominance by diatoms at one month immersion intervals was not prevented by scouring from the silt load. Indeed, tier 1 and tier 2 diatom life-forms trapped and held sediments. These two tiers were present in all one month samples over a two-year period, with the exception of a shaded sample which had mostly bacteria and had trapped only a modicum of debris. Thus the diatoms themselves provide for the accumulation and increase in the thickness of the sediment layer. The final thickness of attached debris was determined largely by the level of the distal apices of the diatoms forming the second tier, the debris generally not extending beyond this level. The occurrence of tier 2 diatoms appears to provide the means by which prostrate diatom species of tier 1 are often covered by sediments. These buried species may be dominant or codominant species, as was the case for Achnanthes lanceolata at Site A in the summer and fall. However, at the other sites (B-D) during most seasons, much higher diatom densities

Figures 55-59 of growth habits and of attachment profiles of selected diatom taxa.

Fig. 55. Rosette of Eunotia curvata with associated prokaryotic filaments. Sept. 22-Oct. 20, 1980. Site A. 1,350 X.

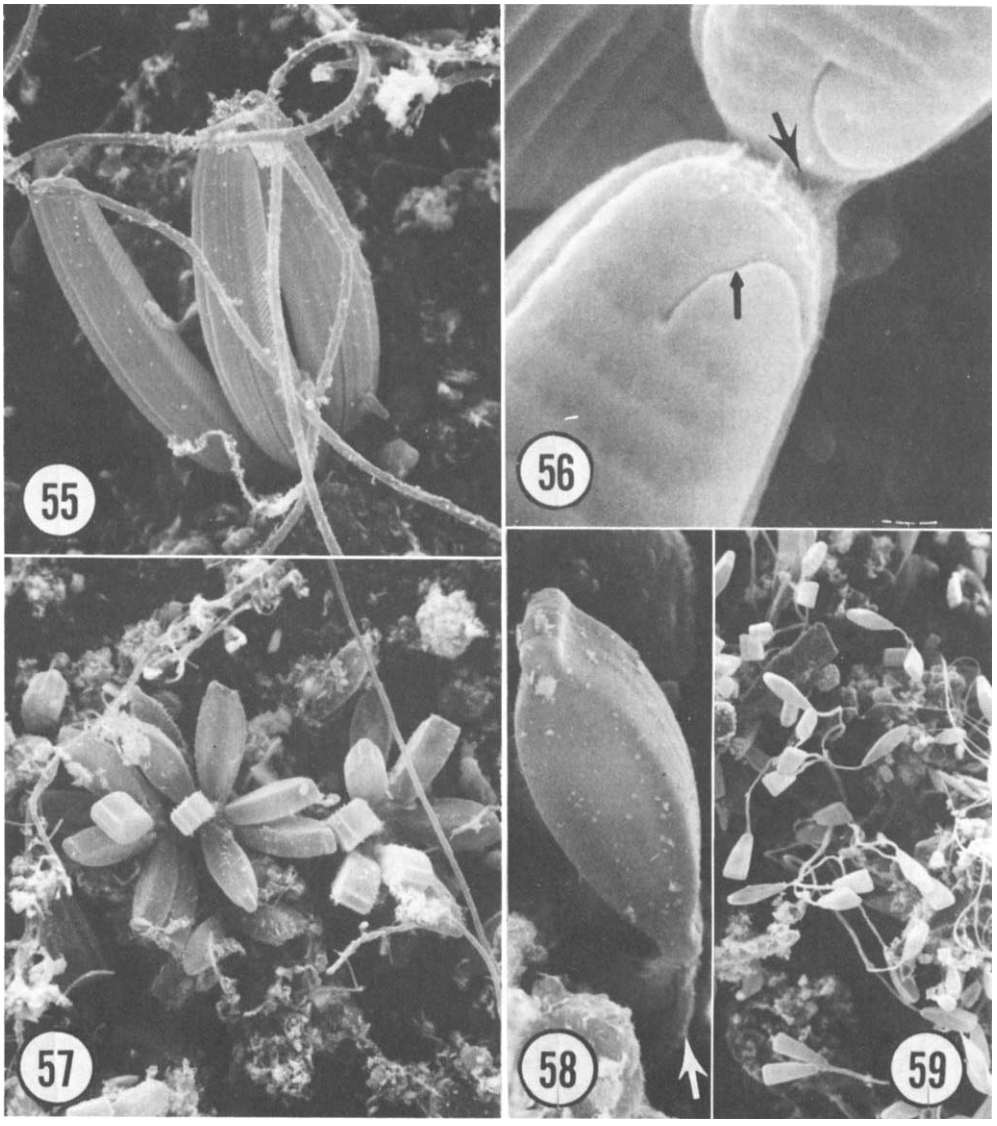
Fig. 56. Cells of Eunotia curvata produce mucilage (large arrow) at the cell apex near the vestigial raphe (small arrow). Mar. 22-Apr. 19, 1980. Site A. 14,000 X.

Fig. 57. Tier 2 rosettes of Gomphonema parvulum surrounded by debris. Oct. 9-Nov. 8, 1979. Site D. 725 X.

Fig. 58. Short mucilaginous stalk (arrow) of Gomphonema parvulum. Sept. 22-Oct. 20, 1980. Site A. 2,800 X.

Fig. 59. Long mucilaginous stalks of Gomphonema sp. forming a third tier community. Mar. 22-Apr. 19, 1980. Site B. 280 X.

occurred. Here the dominant or codominant species was one that perhaps arrived as a tier 1 species but ultimately became a member of a tier 2 community. Once established as tier 2 members, many of these colony formers appear able to multiply and to add their offspring directly to this tier without going through the tier 1 phase, through perpendicular colony formation (Figs. 51, 53, 54).



Since stalk and colony forming diatoms usually exhibit their typical life-form morphologies in cultures where impingement of silt from moving water is not taking place (Roemer, Hoagland, Rosowski, unpublished), the tiering reported here is probably not the ontogenetic result of a turbid environment. Rather, the silt particles appear to be passively collected by the diatoms and bacteria, by life-forms that would have presented themselves anyway. The specific role, if any, of the silt in structuring or even stabilizing microcommunities thus remains undocumented. It is clear however that soil erosion from the watershed does not inhibit biofilm formation on artificial substrates in this highly eutrophic stream. Through the interactions of diatoms, bacteria and other microspecies, a stable sediment laden periphyton community develops and persists, trapping debris that would be likely absent without this community.

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