

EFFECTS OF CHIRONOMID (INSECTA: DIPTERA) TUBE-BUILDING ACTIVITIES ON STREAM DIATOM COMMUNITIES^{1,2}

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ABSTRACT

Chironomid retreats, constructed out of sand grains upon submerged wood debris, increase the surface area available for diatom colonization. The three dimensional substratum afforded by chironomid tubes supports up to twelve times the diatom biovolume found upon adjacent, unmodified substratum in a northern Michigan stream. Diatom enumeration within scrapings from small defined areas on artificial substrata, combined with examination of intact natural substrata through scanning electron microscopy (SEM), reveals distinct microdistribution patterns. The larval retreats of two major taxa of tube-dwelling chironomids (Micropsectra sp. and Pseudodiamesa cf. pertinax Garrett) display significantly different diatom communities relative to adjacent masonite substratum. Substratum without chironomid tubes is primarily colonized by Achnanthes minutissima Kütz. and Cocconeis placentula Ehr., exhibiting the lowest species diversity of microhabitats examined. The diatom flora upon sand tubes of Micropsectra sp. is dominated by Opephora martyi Herib., as is the flora of sand grains collected from the stream sediment load. These two microhabitats exhibit a high community similarity (SIMI). The SIMI index also suggests that the flora of P. pertinax tubes is highly similar to that of sand grains. Diversity, however, is almost three times greater on P. pertinax tubes and SEM observations reveal that this microhabitat is characterized by a more spatially complex flora; Nitzschia and Navicula spp. dominate the upperstory, and O. martyi is located on underlying sand grains. Results indicate that tube-building chironomids in Carp Creek affect diatom microdistribution by: (1) stabilizing sand grains and associated flora within their retreats, (2) providing a 'refugium' for upperstory diatom taxa from the mayfly grazer, Baetis vagans McDunnough (Insecta: Ephemeroptera), and (3) through local nutrient enrichment.

Key index words: artificial substrata; chironomid tubes; diatoms; sand grains; SEM; streams

Factors underlying successional phenomena in terrestrial systems have received far more attention than their counterparts in aquatic systems. One of the fundamental principles of terrestrial plant ecology is that different species of plants are not distributed uniformly (Connell and Slayter 1977, Harper 1977, Huston 1979, Tilman 1982). Detailed

analysis of the distribution of individual taxa within microhabitats is prerequisite to the formulation of present-day concepts of habitat preference, competition and succession.

In aquatic environments, investigators have observed distinct microdistribution patterns of periphyton taxa on various natural substrata such as sand grains (Round 1965, Meadows and Anderson 1966), macrophytes (Whitford 1956, Jansson 1969, Eminson 1978, Siver 1980), and rocks (Blinn et al. 1980). The advent of scanning electron microscopy (SEM) has permitted even closer examination of the horizontal and vertical heterogeneity of intact communities, which conventional techniques of scraping, clearing and light microscope enumeration had precluded (Pringle 1979, Hoagland et al. 1982). Although SEM has revealed spatial relationships among periphytic diatoms that are now intrinsic to our understanding of periphyton communities (Allanson 1973, Perkins and Kaplan 1978, Hoagland et al. 1982, Hudon and Bourget 1981, Korte and Blinn 1983), the factors which determine observed microdistribution are poorly understood. Attention has been primarily focused upon the influence of physical factors such as current (Horner and Welch 1981, Muntenau and Maly 1981, Stevenson 1983) and light intensity (Stevenson and Stoermer 1981, Hudon and Bourget 1983). Investigations of the impacts of aquatic macroinvertebrates upon periphyton microdistribution have largely been confined to grazing studies (Nicotri 1977, Lubchenco 1978, Hunter 1980, Sumner and McIntire 1982).

Effects of nonherbivorous macroinvertebrates upon diatom microdistribution and community structure remain virtually unexplored. In aquatic environments, tube-dwelling chironomid larvae often completely cover submerged substrata, altering the nature of the substratum by forming tubes or cases. Given the extremely high densities of tube-dwelling Chironomidae in most aquatic environments (Hynes 1972, Wiley 1978) and their widespread occurrence as pioneer species on newly submerged substrata (Nilsen and Larimore 1973), it is hypothesized that chironomid tube-building activities exert a considerable effect on the periphytic diatom flora.

This investigation is designed to contribute to the understanding of the ecology of periphytic communities by: (1) presenting information concerning the distribution patterns of diatom taxa in several microhabitats, (2) examining the effects of tube-building activities of two taxa of Chironomidae: *Micropsectra* sp. and *Pseudodiamesa* cf. *pertinax* Garrett,

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² This paper is dedicated to Lawrence R. Blinks on the occasion of his 85th birthday.

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and (3) discussing some of the possible factors which interact to determine observed distribution patterns.

MATERIALS AND METHODS

Field portions of this study were conducted in Carp Creek, a 2nd to 3rd order nutrient-poor stream located on the University of Michigan Biological Station tract (45°33' N, 84°40' W) in Cheboygan County, Michigan, USA (Pringle 1979). This spring fed, sand-bottomed stream has a high sediment load which is fairly typical of many northern Michigan streams. It exhibits a relatively constant discharge and stable temperatures (10°C ± 3°C in July). Large numbers of coniferous trees (*Thuja occidentalis* L., *Pinus strobus* L., *Tsuga canadensis* (L.) Carr.) and shrubs overhang the stream, supplying abundant debris to the creek bed which serves as the primary substratum for benthic invertebrates. To simulate this wood substratum, masonite samplers were constructed according to methods published by Hester and Dendy (1962). Previous studies in Carp Creek have shown that diatom community assemblages on masonite samplers are similar to those on natural wood substrata (Pringle 1979). Eight artificial substrata were installed at a sunny site in Carp Creek in June. Each substratum was placed 10 cm below the water surface and anchored to the stream bottom by 2 rigid wire struts which were attached to the substratum's central axis and pushed into the sandy stream bottom. Artificial substrata were oriented so that the current flow was parallel to masonite plates. Current velocities were measured weekly in front of each substratum with a standard Pygmy Gurley meter and were between 25–35 cm·s⁻¹. After an 8 wk period, substrata were retrieved. Macroinvertebrate populations, consisting primarily of tube-dwelling Chironomidae (Diptera) and herbivorous Baetidae (Ephemeroptera), were abundant and similar to established populations on natural substrata (Pringle 1979). Direct underwater observations of macroinvertebrate communities were made using mask and snorkel at daily intervals throughout the 2 wk prior to substratum removal.

To analyze diatom microdistribution upon artificial substrata, eight substratum sections were removed from each of three microhabitats: (1) substratum without tube-dwelling Chironomidae, (2) substratum bearing the elongate tubular shelters of *Micropsectra*, and (3) substratum bearing the irregularly mounded retreats of *Pseudodiamesa pertinax*. Adjacent sections (1.0 cm²) of masonite substratum falling within these categories were carefully scored and then undercut with a razor blade for removal. Sections were only collected from the upper side of the top plate of each artificial substratum to further minimize variability caused by differences in micro-current regimes and light intensity. Three different microhabitat samples were collected from each of the eight masonite substrata upon retrieval. Larval Chironomidae within tubes were carefully extracted with watchmaker's forceps for identification and gut analysis. Head capsules were mounted ventrally and identified under immersion oil.

For quantitative analysis of diatom populations, four substratum sections per microhabitat were separately scraped with a fine brush. Scrapings were washed into a 50 mL beaker and diluted to 25 mL with distilled water. Each sample was mixed for 10 min with a magnetic stirrer to detach floral components from sand grains. Examination of substratum material before and after this process showed 92% removal. One half of the sample was then oxidized using a modification of the cleaning techniques described by Patrick et al. (1954) and Hohn and Hellerman (1963). Permanent slide mounts were prepared with Hyrax® from oxidized and unoxidized samples for species identification and the distinction and enumeration of live cells, respectively. Diatoms comprised at least 94% of the periphyton biovolume in all microhabitats and counts were restricted to diatom taxa. Seven hundred diatoms per sample were enumerated with a resulting count of 2800 frustules per habitat. Diatom cells were measured

with an ocular micrometer and substage adjustment to determine length, width, and thickness. A minimum of 25 cells per diatom taxon were used to determine mean dimensions (Pringle 1979). The cell volume of specific taxa was estimated by entering mean diatom dimensions into geometric equations that estimated volume of the frustule (Gruendling 1971). Comparisons of diatom community structure between microhabitats were made by calculating a similarity index (SIMI) as reported by McIntire and Moore (1977). Species diversity was calculated using the Shannon Wiener-informational index (Pielou 1966).

The diatom flora of sand grains suspended in the stream water column was similarly analyzed for purposes of comparison with the flora of the consolidated sand grain tubes of *P. pertinax* and *Micropsectra* sp. A small drift net (200 µm) was placed adjacent to artificial substrata and suspended 10 cm below the water surface. Sand grains representative of incoming grains 'hitting' artificial substrata were collected in four 20-min periods.

Scanning electron microscopy was used to qualitatively examine the fine, three-dimensional structure of intact periphyton communities upon the remaining four substratum sections. Sections were fixed in phosphate buffered glutaraldehyde and then dehydrated in a graded series of increasing concentrations of ethanol. Sections were ultimately air-dried after transfer to an absolute ethanol solution and then mounted with epoxy glue on aluminum stubs. Samples were pulse coated with 20 nm of gold palladium and observed with a scanning electron microscope. Distinct floral zones consistently observed in respective microhabitats were photographed. The diatom populations of chironomid tubes constructed on natural substrata in the stream were also qualitatively analyzed using SEM.

Fifteen larvae of both *Micropsectra* and *P. pertinax* were collected from artificial substrata for qualitative analysis of gut contents, using methods modified from Coffman et al. (1971). The substratum composition of chironomid retreats was also qualitatively examined. Five tubes of each taxon were placed separately onto microscope slides, dispersed into a fine slurry with a dissecting needle, diluted to 100 mL with distilled water, mixed with a magnetic stirrer and then filtered with a 0.45 µm Millipore® filter at low suction. The filter was subsequently cleared with immersion oil on a microscope slide for observation.

For chemical analyses, six tubes of *P. pertinax* were collected along with six control samples of unconsolidated, depositional sand from submerged wood substrata in Carp Creek. Sand was collected with a small cork borer. *Pseudodiamesa pertinax* larvae were removed from their retreats with watchmaker's forceps and identified. Substratum samples were subsequently weighed, diluted to 15 mL with distilled water in acid-cleaned glass beakers and dispersed for 10 min with a magnetic stirrer. Samples were analyzed for chloride, ammonia-N, nitrate-N, orthophosphate, and total phosphorus, utilizing standard methods (APHA 1975) with a Technicon II autoanalyzer.

RESULTS

Light microscopy. Forty-two diatom taxa were identified from microhabitats on artificial substrata in Carp Creek. The relative abundance and percentage biovolume of 12 major species were calculated in each of four microhabitats examined (Table 1). Total diatom densities and biovolumes supported per cm² of masonite substratum are included for the three microhabitats on artificial substrata. Diatom densities supported by the larval retreats of *Micropsectra* and *P. pertinax* were respectively 1.37 and 1.81 times greater than densities found upon substratum with no chironomid tubes. Differences in total diatom biovolumes between these microhabitats are

TABLE 1. Relative abundance (%) followed by percent volume in parentheses, for dominant^a diatom taxa found in four different microhabitats in Carp Creek. Mas = masonite substratum unmodified by chironomid retreats; Sand = bedload sand grains; Micro = *Micropsectra* tube; Pseudo = *Pseudodiamesa pertinax* retreat. (Values are averages of four light microscope counts.)

Diatom taxon	Microhabitat			
	Mas	Sand	Micro	Pseudo
<i>Achnanthes exigua</i> Grun.	1.35 (2.57)	4.74 (2.73)	5.58 (2.52)	1.71 (0.55)
<i>Achnanthes minutissima</i> Kütz.	88.53 (43.16)	3.99 (0.50)	7.17 (0.70)	6.94 (0.48)
<i>Cocconeis placentula</i> Ehr.	3.03 (25.41)	2.59 (5.55)	2.09 (3.53)	1.43 (1.72)
<i>Cymbella microcephala</i> Grun.	3.06 (7.38)	—	0.10 (0.05)	0.07 (0.02)
<i>Frustulia rhomboides</i> (Ehr.) De T.	—	—	0.10 (1.13)	3.76 (4.48)
<i>Gyrosigma acuminatum</i> (Kütz.) Rabh.	—	—	1.35 (9.04)	1.54 (7.34)
<i>Navicula cryptocephala</i> Kütz.	—	—	0.50 (0.75)	5.43 (5.91)
<i>Navicula tripunctata</i> (O. G. Mull.) Bory	0.23 (5.64)	—	2.65 (13.19)	4.15 (17.72)
<i>Nitzschia dissipata</i> (Kütz.) Grun.	0.13 (0.39)	—	0.97 (0.59)	12.04 (5.17)
<i>Nitzschia linearis</i> W. Sm.	—	—	0.14 (0.61)	1.71 (5.18)
<i>Nitzschia palea</i> (Kütz.) W. Sm.	—	—	—	2.89 (4.50)
<i>Opephora martyi</i> ^b Herib.	1.28 (5.40)	80.47 (86.45)	64.78 (54.76)	37.64 (22.66)
Percent of total diatoms	97.61 (89.95)	91.79 (95.23)	85.43 (86.87)	79.31 (75.73)
Total diatom density ($\times 10^6$ cells \cdot cm ⁻²) \pm SD	1.49 \pm 0.05	—	2.04 \pm 0.04	2.70 \pm 0.12
Total diatom biovolume ($\times 10^8$ μ m ³ \cdot cm ⁻²) \pm SD	0.90 \pm 0.04	—	6.08 \pm 0.23	11.29 \pm 0.58

^a Dominant taxa defined as comprising 4% of total number or volume in any one of the microhabitats.

^b *Fragilaria pinnata* (Ehr.) was included in this taxon because of difficulties encountered in distinguishing these two taxa morphologically.

much greater, due to the large size of many biraphid diatom taxa colonizing chironomid tubes, particularly those of *P. pertinax*. *Micropsectra* and *P. pertinax* retreats respectively support 6.7 and 12.6 times more diatom volume than substratum unmodified by chironomid tubes. Multiple comparisons indicate that microhabitat effects were highly significant; all three microhabitats are significantly different from one another with respect to total diatom density and biovolume ($P < 0.01$, Student-Newman-Keuls test).

Numerically, *Achnanthes minutissima* Kütz. was the dominant species upon substratum unmodified by chironomid tubes (88.5% no., 43.2% vol.). *Achnanthes minutissima* and *Cocconeis placentula* Ehr. were the dominant taxa in this microhabitat (92.6% no., 68.6% vol.). To assess taxa specific, microhabitat effects, multiple comparisons of species density means were made (Student-Newman-Keuls test). *Achnanthes minutissima* densities on unmodified masonite substratum were significantly higher than densities of this species on *P. pertinax* or *Micropsectra* tubes ($P < 0.01$), exceeding densities by seven and ninefold, respectively. *Cocconeis placentula* densities were not significantly different between microhabitats. *Micropsectra* tubes were dominated by *Opephora martyi* Herib. (64.8% no., 54.8% vol.), supporting significantly greater densities of this taxon relative to unmodified masonite substratum ($P < 0.01$) and *P. pertinax* tubes ($P < 0.05$). Densities of *O. martyi* upon *Micropsectra* tubes were almost seventy times greater than upon substratum unmodified by chironomid tubes. *Opephora martyi* was also the dominant species on sand grains in the stream sediment-load (80.5% no., 86.5% vol.). Tubes of *P. pertinax* were similarly dominated by *O. martyi* (37.6% no., 22.7% vol.), along with high numbers of motile biraphid diatoms in the genera *Navicula* (13.6% no., 27.8% vol.) and *Nitzschia* (17.8%

no., 16.8% vol.). Densities of these two taxa were significantly greater upon *P. pertinax* tubes relative to *Micropsectra* tubes and masonite substratum ($P < 0.01$).

Values of the similarity index (SIMI), comparing diatom community structure between microhabitats, are presented in Table 2. Assuming that SIMI values of < 0.50 suggest a low similarity in species composition and apportionment (Sullivan 1975), values indicate a dissimilarity between substratum unmodified by chironomid tubes and all other microhabitats examined (all < 0.20). Highest similarity exists between *Micropsectra* tube flora and sediment load, sand grain communities (SIMI = 0.995).

Species diversity values were averaged for the four collections made per microhabitat (Table 3). Multiple comparisons showed that mean species number was greatest for communities established upon *P. pertinax* tubes, lowest on masonite and sand substratum and intermediate on *Micropsectra* tubes ($P < 0.01$).

Scanning electron microscopy. Observations made through SEM confirmed data obtained with light microscopy and yielded additional information regarding the vertical and spatial distribution of taxa. The monoraphid taxa, *A. minutissima* and *C. placentula*, were observed as the dominant species growing on masonite substratum unmodified by tubes. Their sites of attachment, however, differed. The former species was consistently observed within crevices between compressed wood fibers of masonite substratum (Fig. 1), while the latter predominated on adjacent, 'smooth' areas (Fig. 2). *Opephora martyi*, the dominant species on sand grains, was attached by a thick mucilaginous stalk at the narrow extremity of its valve face (Fig. 3). This species infrequently grew directly on masonite substratum, though it was often

TABLE 2. SIMI indices for comparisons of diatom communities in different microhabitats. (See Table 1 for microhabitat explanation code.)

	Microhabitat			
	Mas	Sand	Micro	Pseudo
Mas	—	0.066	0.127	0.183
Sand	—	—	0.995	0.916
Micro	—	—	—	0.933
Pseudo	—	—	—	—

abundant upon sand grains adherent to the substratum. Another diatom associated with sand grains in lesser numbers was *Achnanthes exigua* Grun., a relatively sessile monoraphid species attached by one valve face to smooth surfaces of grains (Fig. 4).

Larval retreats of *Micropsectra* were dominated by the sessile, araphid *O. martyi*, although species of motile biraphids were also present (Figs. 5, 6). Dense patches composed almost exclusively of *Nitzschia linearis* W. Sm. and smaller numbers of *Navicula tripunctata* (O. G. Mull.) Bory, covered the decomposing exuviae of a mayfly (*Baetis vagans*) nymph lodged on masonite adjacent to a *Micropsectra* tube (Figs. 7, 8). The upperstory flora covering retreats of *P. pertinax* larvae was similarly dominated by monotypic patches of motile pennate diatoms, such as *Nitzschia linearis* and *Navicula tripunctata* (Figs. 9, 10). The flora associated with underlying sand grains was *O. martyi* (Fig. 11).

Macroinvertebrate observations. Numbers of *Baetis vagans*, enumerated from the top exposed surface of masonite substrata upon retrieval, ranged from 0.14–0.71 nymphs·cm⁻² ($\bar{x} = 0.37 \pm 0.19$). *Baetis vagans* was frequently observed to feed in close proximity to chironomid tubes but never directly upon inhabited tubes. No direct interactions were observed between *Baetis* and fixed tube-dwelling chironomids. However, gut analysis of *P. pertinax* revealed that this chironomid is partially carnivorous, feeding upon small instars of *Baetis*, immature Chironomidae and detritus. Gut contents of nine out of fifteen larvae contained body parts of *B. vagans*. In contrast, all *Micropsectra* larvae examined consumed detritus mixed with small numbers of *A. minutissima* and *C. placentula*.

Micropsectra retreats were elongate tubular structures (≈ 3.0 mm wide) of varying lengths (5–40 mm) which formed a crisscrossing pattern, often inter-

secting *P. pertinax* retreats. The shelters of *P. pertinax* were asymmetrical and irregularly mounded structures covering from 1.6–2.7 cm² of masonite and frequently containing more than one individual larva. *Micropsectra* tubes were almost exclusively composed of sand grains cemented together with salivary secretions, while *P. pertinax* retreats were comprised of sand grains and almost equal amounts of dark brown material in compact aggregates, which appeared to be fecal pellets of the organism. Such aggregates were incorporated into the mound and were visually similar to the fecal material excreted from *P. pertinax* larvae, as they were mounted alive under immersion oil. At the end of the 8 wk colonization period, chironomid tubes cumulatively covered from 22–48% of the surface area on artificial substrata.

Chemical analyses. Chemical analyses of *P. pertinax* tubes and control, sand substrata indicated that the former substratum contained significantly greater amounts of ammonia-N, ortho-phosphate, and total phosphorus ($P < 0.005$, Student-*t*-test). Average amounts of these nutrients, for both substratum types, are presented in Table 4.

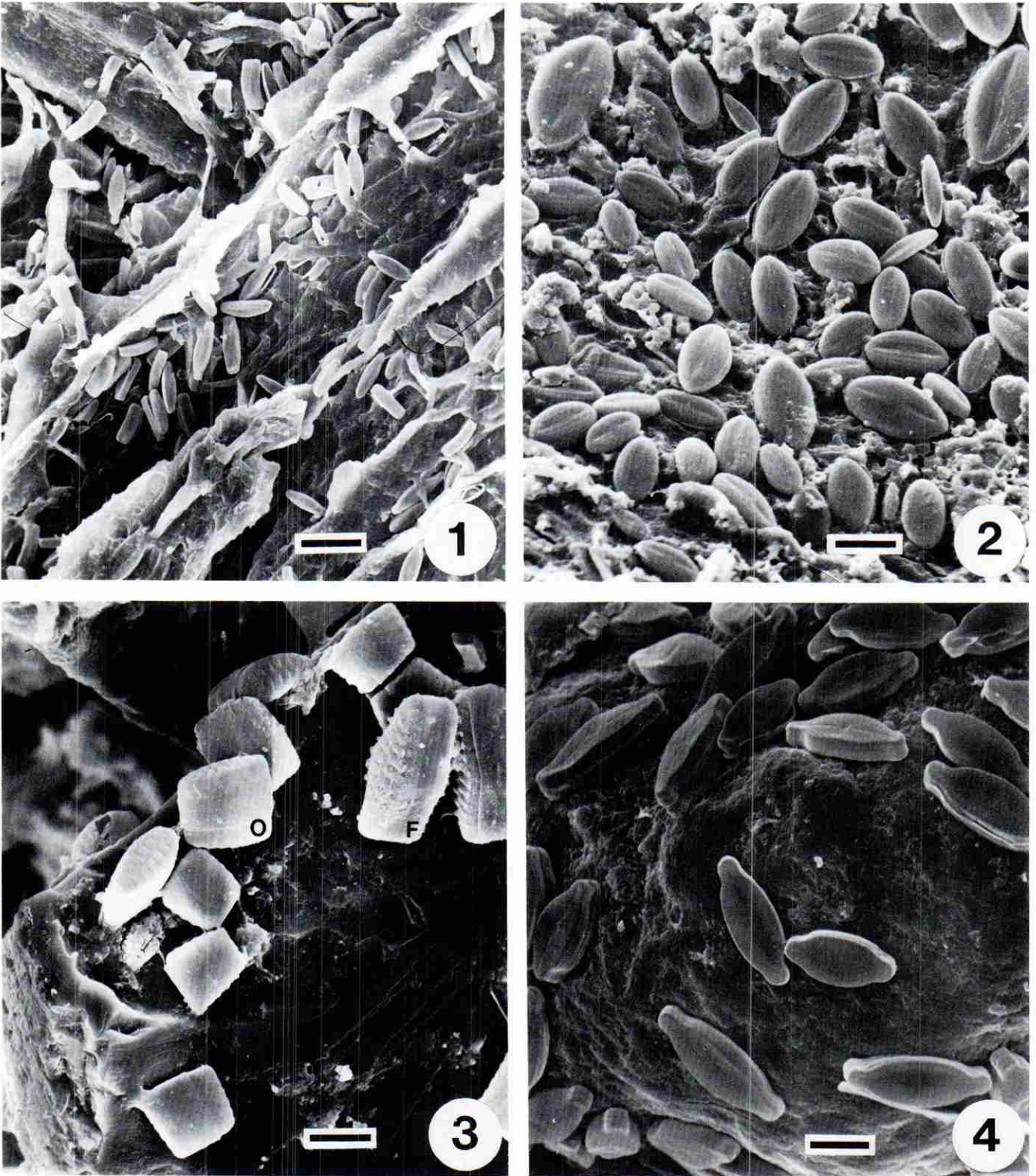
DISCUSSION

Tube-building activities of the Chironomidae produce distinct modifications of the diatom flora, providing a more three dimensional habitat with a correspondingly greater habitat complexity (micro-current, light regime, etc.) and a greater surface area for diatom colonization relative to underlying masonite substratum. These factors may partially explain the significantly greater diatom species diversity and biovolumes supported by tubes relative to adjacent substratum.

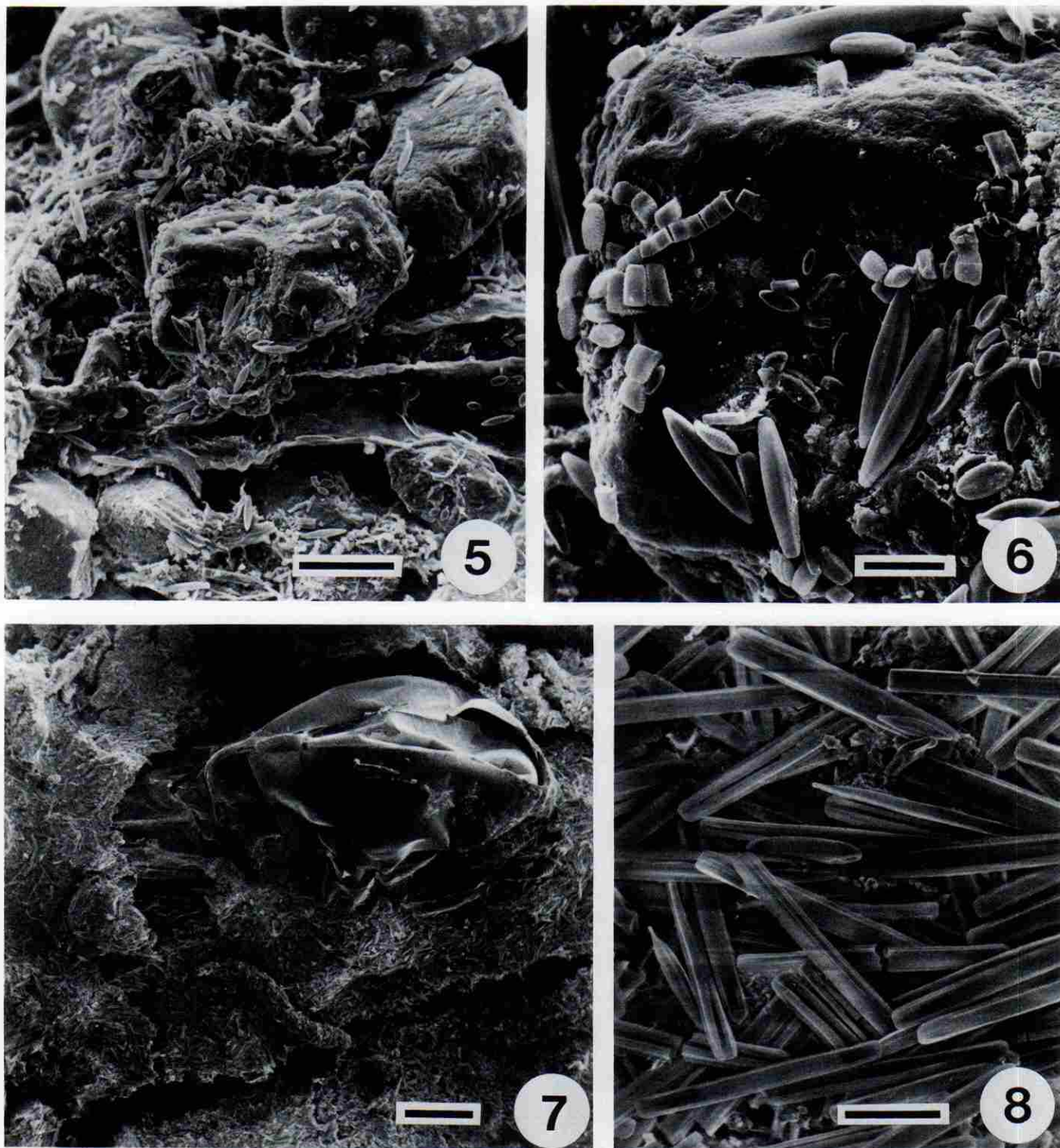
Sand grains as vehicles for diatom colonization. The SIMI index suggests that both chironomid tube microhabitats share a similar flora with that of unconsolidated sand grains. The very high similarity between *Micropsectra* tubes and sand grains (SIMI = 0.995) can be explained by the fact that sand grains are the principle building blocks of these retreats. The sand grains carried along in the stream sediment load appear to be important vehicles for periphyton colonization of submerged substrata in Carp Creek (Pringle 1979). Korte and Blinn (1983) similarly observed the importance of 'detrital micro-

TABLE 3. The mean species diversity (H'), number of species (S) and their range of values for each microhabitat (See Table 1 for microhabitat explanation code.)

	Microhabitat				
	Mas	Sand	Micro	Pseudo	
H'	$\bar{x} \pm SE$ (min.–max.)	0.835 ± 0.099 (0.753–0.946)	1.255 ± 0.192 (1.112–1.473)	2.232 ± 0.113 (2.242–2.271)	3.495 ± 0.286 (3.165–3.665)
S	$\bar{x} \pm SE$ (min.–max.)	9.3 ± 0.5 (9–10)	9.5 ± 0.6 (9–10)	28.3 ± 2.5 (26–31)	39.5 ± 2.4 (37–42)



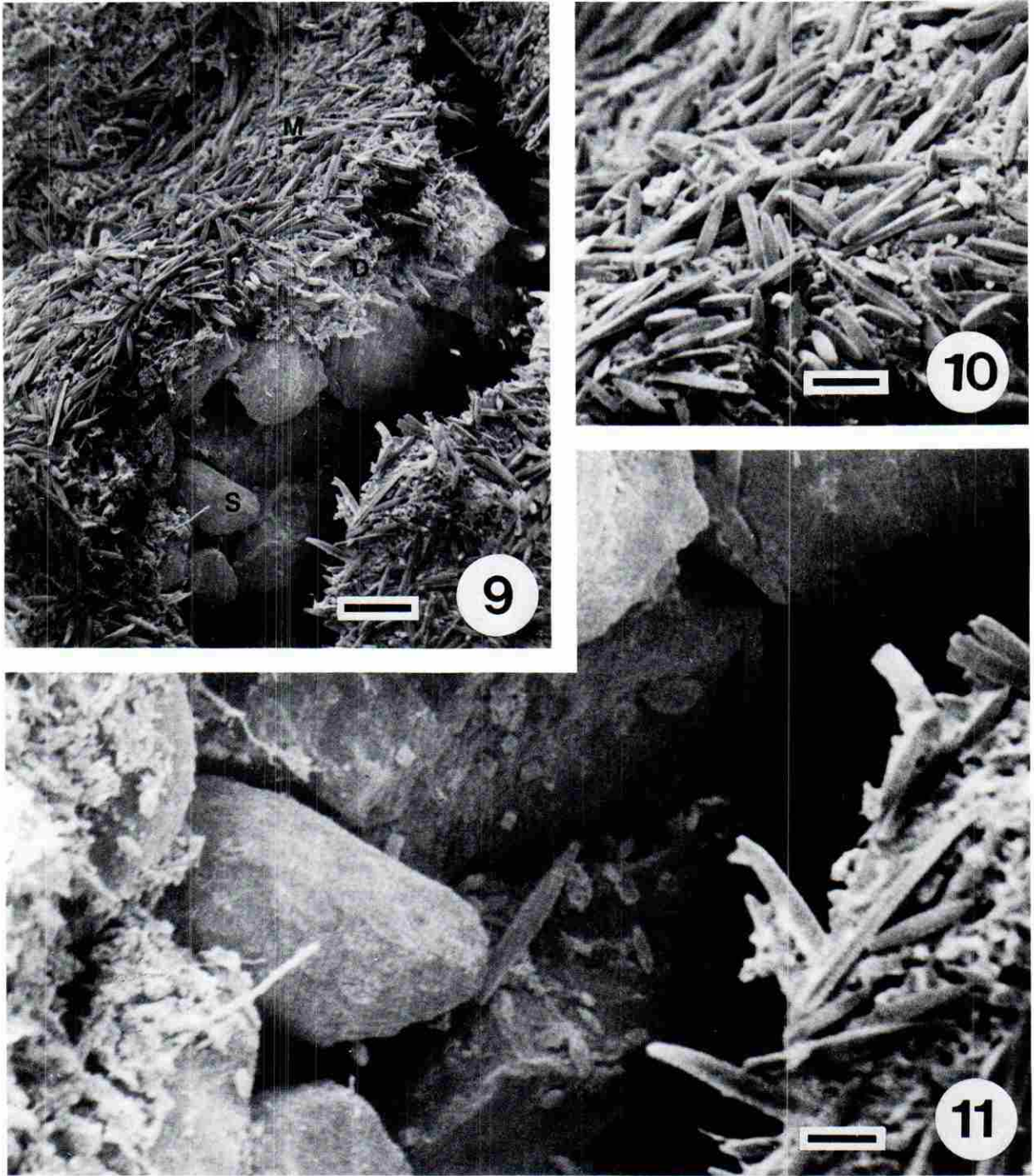
FIGS. 1-4. Diatom flora associated with masonite substratum unmodified by chironomid tubes (Figs. 1-2), and associated with sand grains (Figs. 3-4). FIG. 1. *Achnanthes minutissima*, commonly observed growing on short mucilage stalks within crevices upon masonite substratum. Scale bar = 10 μ m. FIG. 2. *Cocconeis placentula* typically observed upon smooth portions of the masonite substratum. Scale bar = 10 μ m. FIG. 3. *Opephora martyi* (O) and *Fragilaria pinnata* (F) dominant upon sand grains within the stream sediment load. Scale bar = 10 μ m. FIG. 4. Micro-colonies of *Achnanthes exigua*, frequently observed upon smooth portions of sand grains. Scale bar = 5 μ m.



FIGS. 5–8. Flora of *Micropsectra* larval retreat (Figs. 5–6), and the decomposing nymphal exuviae of *Baetis vagans* (Figs. 7–8). FIG. 5. Sand grains and associated flora incorporated into tube of *Micropsectra*. (A strand of filamentous algae is positioned horizontally along the lower half of the photo.) Scale bar = 100 μm . FIG. 6. Enlargement of central sand grain in Fig. 5. *Opephora martyi* abundant on left face of grain. Elongate frustules of *Navicula tripunctata* in center. Scale bar = 25 μm . FIG. 7. Gross view of nymphal *Baetis* exuviae. Scale bar = 200 μm . FIG. 8. Enlargement of diatom mat upon exuviae illustrated in Fig. 7, consisting primarily of *Nitzschia linearis*. Scale bar = 25 μm .

cosms' (chunks of material containing algae and decomposers as 'seeds' for recolonization in streams). *Opephora martyi* is the dominant species on sand grains transported in the stream flow of Carp Creek. This

taxon can maintain its dominance upon artificial substrata in those microhabitats where sand grains have been incorporated into the fixed tube dwellings of *Micropsectra*.



FIGS. 9–11. Flora of *Pseudodiamesa pertinax* larval retreats. FIG. 9. Cross-sectional view of retreat showing layers; periphyton mat (M), detrital layer (D), and underlying sand grains (S). Scale bar = 50 μm . FIG. 10. Enlargement of upperstony periphyton mat dominated by *Navicula tripunctata*. Scale bar = 20 μm . FIG. 11. Enlargement of underlying sand grains with attached *O. martyi*. Scale bar = 15 μm .

Although SIMI values also indicate that the flora of *P. pertinax* retreats is similar to that of sand grains (SIMI = 0.916), the high index value is somewhat misleading. Because SIMI gives most weight to dominant taxa it does not reflect important and major differences in community structure. The high index value obtained is due, in part, to the numerical abundance of *O. martyi* in both microhabitats; however, the proportional contribution of this species to total

diatom numbers is almost twice as great on sand grains as on *P. pertinax* tubes. *Pseudodiamesa pertinax* tubes also support a much greater species diversity and some four times the number of species relative to unconsolidated sand grains. Furthermore, SEM observations reveal that *O. martyi* communities on *P. pertinax* retreats are associated with sand grains (Fig. 11) which are typically overlain by a detrital layer and thick mats of large motile biraphid diatoms

TABLE 4. Mean levels of chloride (Cl), ammonia-nitrogen (NH_4-N), nitrate-nitrogen (NO_3-N), ortho-phosphate (PO_4-P) and total phosphorus (TP), in *P. pertinax* tubes and sand substrata collected from submerged wood debris in Carp Creek ($\mu\text{g}\cdot\text{g}^{-1}$ substratum \pm SD).

	Microhabitat	
	<i>P. pertinax</i> tube	Sand (control)
Cl	0.10 \pm 0.25	0.01 \pm 0.02
NH_4-N	234.54 \pm 151.40	7.02 \pm 2.85
NO_3-N	0.01 \pm 0.01	0.00 \pm 0.00
PO_4-P	8.91 \pm 5.15	0.36 \pm 0.10
TP	305.95 \pm 68.62	6.20 \pm 3.65

(Fig. 10). Such observations suggest that *O. martyi* is unable to maintain itself in the upperstory of this community due to its lack of motility and overgrowth by motile biraphid taxa such as *Navicula* and *Nitzschia*. Therefore, despite its occurrence in high numbers on underlying sand grains, as revealed by light microscope enumeration, *O. martyi* does not constitute a spatially dominant member of the upperstory community as it does on sand grains and *Micropsectra* tubes. This observation further illustrates the value of SEM as a qualitative tool to clarify data obtained through light microscope techniques.

Diatom growth habits and Baetis grazing behavior. It is suggested that the closely adherent growth forms of *C. placentula* and *A. minutissima* allow these taxa to maintain themselves as dominants on masonite substratum despite intense grazing activities. Densities of *B. vagans* (0.37 ± 0.19 nymphs \cdot cm $^{-2}$) upon the substrata are interpreted as a general indication of high grazing activity, since grazer density on a given surface can vary significantly on a time scale of hours (Wiley and Kohler 1981). Coincident grazing/colonization studies (Pringle 1979) revealed high *Baetis* densities upon artificial substrata after 2.5 wk, with peak densities up to 1.3 nymphs \cdot cm $^{-2}$. In light of observed diatom microdistribution patterns, and the observation that *B. vagans* feeding was generally confined to masonite substratum unmodified by chironomid tubes, it is suggested that the activities of this highly mobile grazer resulted in removal of upperstory periphyton. The sweeping action of *Baetis*'s labrum combined with the activity of other mouthparts and legs may dislodge loosely attached periphyton. Though *C. placentula* and *A. minutissima* contribute to the diet of *B. vagans* (Pringle 1979), they maintain their dominance in the grazed community via those segments of the population which escape predation by: (1) occupying 'low-lying' areas of the masonite microtopography (e.g. *A. minutissima* frustules in crevices), or (2) closely adhering to the substratum (e.g. *C. placentula*, which is horizontally attached along one valve face with mucilage). Several studies have similarly inferred that the activities of various herbivores result in removal of loosely attached upperstory periphyton and the maintenance

of adherent taxa (Moore 1975, Nicotri 1977, Hunter 1980, Kesler 1981, Sumner and McIntire 1982).

It is likewise proposed that tubes inhabited by chironomids represent ungrazed microcosms, acting as 'refugia' for upperstory elements of the periphyton which might otherwise be removed by *Baetis* activities. This is supported by the observation that *B. vagans* did not feed directly on chironomid tubes. The predatory behavior of *P. pertinax* on *B. vagans* would be expected to discourage feeding upon retreats of this chironomid. Diatom taxa which formed a significant component of the flora on chironomid tubes were correspondingly not found to predominate in *Baetis* guts (Pringle 1979).

Spatial heterogeneity of nutrients. As elegantly demonstrated by Lehman and Scavia (1982), phytoplankton taxa in natural waters have differential abilities to exploit short-lived nutrient patches excreted by zooplankton herbivores. Tube-dwelling Chironomidae may likewise be important in creating nutrient micropatches which determine the nature and distribution patterns of attached periphyton. Although data do not exist for *Micropsectra* tubes, given the significantly greater amounts of ammonia-N, ortho-phosphate and total phosphorus in *P. pertinax* tubes relative to unconsolidated sand substrata, it is suggested that the metabolic and excretory activities of chironomid larvae provide nutrients for the microorganisms attached to their tubes. The location of fecal material in the matrix of *P. pertinax* retreats would impede its dispersal by stream currents and enhance its potential usefulness to local microorganisms. Jansson (1980) found that benthic algae assimilated a large amount of the ammonia-nitrogen in the interstitial water of sediments. The biomass of epipelagic algae has likewise been found to increase as the organic carbon, nitrogen and phosphorus content of the sediment increases (Skorik et al. 1972).

The occurrence of monotypic patches of *Nitzschia linearis* and *Navicula tripunctata* in the upperstory of *P. pertinax* retreats may be a function of their motility relative to underlying sessile forms and/or respective uptake abilities for dissolved nutrients and organic matter. *Nitzschia linearis* and *Navicula tripunctata* also were observed, via SEM, in dense patches upon the decomposing exuviae of *B. vagans* (Figs. 7, 8). Recent studies in Carp Creek reveal similar patterns of diatom community composition upon nutrient-enriched artificial substrata composed of agar-consolidated sand (Pringle and Bowers 1984). Enrichment with PO_4 triggered a fourfold increase in *Navicula* and a threefold increase in *Nitzschia* relative to unenriched controls. Addition of both $NO_3 + PO_4$ (25:1) resulted in a greater than tenfold increase in *Navicula* and *Nitzschia*, with *A. minutissima* and *C. placentula* displaying significantly lower biovolumes relative to controls. These two latter taxa were likewise predominant on control

and NO₃ treatments. Such distribution patterns are also interesting in light of taxa specific autecological information in the literature. Members of the genus *Nitzschia* usually reach greatest abundance in eutrophic waters (Benecke 1900, Butcher 1946, 1947) and also show the most pronounced development of heterotrophic capabilities among diatoms (Hellebust and Lewin 1977).

Periphyton distribution patterns are clearly determined by many complex and yet to be elucidated interactions between physical parameters and both grazing and nongrazing components of the invertebrate fauna. This study demonstrates that the distribution and behavior of tube-building Chironomidae can play a major role in the spatial heterogeneity of periphyton communities. The overall potential effects of tube-building chironomids and associated meiofauna should not be underestimated; Wiley (1976) notes that populations of *Micropsectra* and *P. pertinax* are large and striking components of the wood substratum invertebrate community in a northern Michigan stream similar to Carp Creek, reaching peak densities of 120 000 m⁻² and 24 000 m⁻², respectively. Chironomidae constitute the most numerically abundant taxon of organisms in a variety of aquatic systems, frequently contributing from 50–100% of the benthic fauna (Saether 1968, Kownacki and Kownacka 1971, Hynes 1972). Likewise, Chironomidae are commonly observed as the first invaders of new substrata (McLachlan 1970, Glime and Clemons 1972, Nilsen and Larimore 1973, Cover and Harrel 1978). Results of this study indicate that chironomid tube-building activities can affect diatom microdistribution by direct substratum modification, local nutrient enrichment, and by providing a 'refugium' from grazing herbivores.

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INTERACTIONS BETWEEN LIGHT, NH_4^+ , AND CO_2 IN BUOYANCY REGULATION OF *ANABAENA FLOS-AQUAE* (CYANOPHYCEAE)¹

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ABSTRACT

Buoyancy of the gas-vacuolate alga Anabaena flos-aquae Brébisson was measured under various levels of light, NH_4^+ , and CO_2 . At high irradiance ($50 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) the alga was non-buoyant regardless of the availability of CO_2 and NH_4^+ . At low irradiance ($\leq 10 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) buoyancy was controlled by the availability of NH_4^+ and CO_2 . When NH_4^+ was abundant, algal buoyancy was high over a wide range of CO_2 concentrations. In the absence of NH_4^+ algal buoyancy was reduced at high CO_2 concentrations, however as the CO_2 concentration declined below about $5 \mu\text{mol} \cdot \text{L}^{-1}$, algal buoyancy increased. These results help explain why gas vacuolate, nitrogen-fixing blue-green algae often form surface blooms in eutrophic lakes.

Key index words: blue-green algae; buoyancy; light; nitrogen; carbon dioxide; surface blooms

Bloom-forming blue-green algae are distinct from other phytoplankton because they possess gas vacuoles which allow considerable buoyancy regulation. A growing body of literature has appeared recently which suggests that alterations in various environmental parameters may result in changes in blue-green algal buoyancy. Walsby and co-workers have shown that reduced light intensities tend to increase the buoyancy of *Anabaena flos-aquae* and other blue-green algae (Walsby 1969, Dinsdale and Walsby 1972, Walsby and Booker 1980, Walsby et al. 1983). Addition of NH_4^+ appears to increase the buoyancy of *Oscillatoria* spp. (Walsby and Klemer 1974, Klemer et al. 1982, Van Rijn and Shilo 1983). Finally, reduced CO_2 availability appears to increase the buoyancy of *A. flos-aquae* and other blue-green algae

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