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Substratum-associated microbiota

Nancy C. Tuchman, Christopher G. Peterson

METHODS

Jiang *et al.* compared the efficiency with which two Vortex Flow Filtration systems (the Benchmark and Pacesetter systems) concentrated particulate DNA, chlorophyll *a*, and bacteria from a variety of aquatic environments. The Benchmark system was recommended for quantitative studies of small-volume samples whereas concentration of material from large volumes of water was best accomplished with the Pacesetter system. A number of papers described methods for identifying and enumerating microorganisms from natural habitats. Direct microscopic counts of aquatic fungi stained with the fluorescent dye calcofluor white yielded more complete density estimates than traditional submerged-inoculation techniques (Terekhova *et al.*). Bacteria were isolated by Amy *et al.* from rock and water samples taken from a mined tunnel system in Nevada and classified using three identification systems (API-NFT strips, BIOLOG, and MIDI); each system identified only a small percentage of isolates, and substantial variation among systems was noted, but results showed that bacterial isolates from water samples differed considerably from endolithic isolates. Bacterial epiphytes on Eurasian watermilfoil were better characterized by growing them on nutrient-poor agar broth than on high-nutrient medium (Chand *et al.*); this method allowed seasonal changes in epiphytic bacterial community composition on this aquatic macrophyte to be followed. Amann *et al.* localized sulfate-reducing bacteria within sulfidogenic biofilms using fluorescent probes of 16S rRNA sequences characteristic of these microbes; ample quantities of rRNA were generated via polymerase chain reaction. Schmidt exposed microbial communities to a variety of growth substrates and calculated the biomass of different metabolic functional groups from the concentrations at which a given substrate elicited a growth response. Ganczarzyk *et al.* suggested glycol methacrylate resin as an embedding medium to stabilize microbial aggregates for analysis by light microscopy.

A number of procedures were described that quantified physiological processes, extracellular constituents, or microbial dynamics associated with attached biofilms. Toba *et al.* developed a colorimetric method for quantifying microbial extracellular polysaccharides that, unlike other methods, does not require laborious purification procedures. Actively respiring bacteria within a biofilm can be detected via epifluorescence microscopy after treating samples with 5-cyano-2,3-ditolyl tetrazolium chloride (CTC), which fluoresces when incorporated into cells and reduced by electron-transport activity (Rodriguez *et al.*). Tibbles *et al.* estimated bacterial productivity in marine sediments and water from a salt marsh lagoon using a dual-labeling technique that involved bacterial incorporation of [³H]-thymidine and [¹⁴C]-leucine into DNA and protein, respectively. Clavier and Boucher used dichlorophenyl-dimethylurea (DCMU) to inhibit photosynthesis in soft sediments during measurements of primary productivity, as a substitute for the more commonly used dark-incubation method. A DCMU concentration of 5×10^{-5}

moles/L inhibits photosynthesis without affecting metabolism of soft bottom sediments. A method for assessing metabolic potential of naturally occurring microbial populations by freezing and sectioning a *Pseudomonas aeruginosa* biofilm and quantifying distribution of ATP, ADP, and AMP was described by Kinniment and Wimpenny. They found that adenylate energy charge was lowest at the base of the biofilm. Rittmann *et al.* described a method for determining what fractions of bacterial biomass within a biofilm are actively respiring. These authors found that biofilm activity was directly related to the degree of substrate flux. Huang *et al.* devised a parallel-plate flow cell reactor for evaluation of cell adhesion and biofilm formation kinetics that allows growth under well-controlled fluid dynamics while providing continuous observation and direct sampling of biological or physical-chemical parameters. Lewandowski *et al.* found nuclear magnetic resonance imaging techniques to be excellent tools for quantifying fluid velocity changes near microbially colonized surfaces.

Several papers detailed statistical methods for examining relationships between microbiota and physical-chemical variables. A weighted-averaging regression model used by Hall and Smol to infer lake water total phosphorus concentrations from relative abundances of diatom taxa from surficial sediments of 37 Canadian lakes was identified as a powerful tool to assess eutrophication patterns. After comparing techniques for assessing lake trophic status from diatom assemblages, Agbeti concurred that weighted-averaging regression was superior to other methods of assessment. Kim *et al.* developed a convection-dispersion hydrologic transport model that incorporated transient-storage and biotic-uptake submodels to better understand nitrogen dynamics in a natural stream system. The model demonstrated how nitrate retention in stream ecosystems is dictated through interaction between physical and biotic processes. Valente *et al.* used sediment-profile photography and computer image analysis in conjunction with density measures of *Clostridium perfringens* spores to map patterns of benthic enrichment, identify "hot" spots of eutrophication, and provide information on the nature of nutrient sources in Narragansett Bay. By analyzing data from simulated communities in which species abundance distributions were the same or different and from natural epiphytic microbial assemblages, Kinkel *et al.* demonstrated that when sampling from independent communities with unknown species distributions standardization of sample size does not guarantee samples of equal species proportions to that of the sampled community. These constraints seriously limit the questions that can be adequately addressed in such systems. Morin and Cattaneo reanalyzed periphyton data published between 1975 and 1990 to assess the factors that impose variability on estimates of periphyton biomass. They concluded that sampling procedures and degree of replication typically used are adequate only for determining large differences with confidence.

ECOLOGY

Colonization and community development. The nature of colonizing substrates and the colonization mechanisms used by algae were investigated by several authors. Clifford *et al.* examined the importance of substratum texture (rough versus smooth) on the colonization of algae (chlorophyll *a*) and macroinvertebrates in two streams. They found rough-textured tiles enhanced the colonization rates of both algae and macroinver-

tebrates. In a review of the 1975–1990 literature that presented both quantitative and qualitative data of periphyton on natural and artificial substrata, Cattaneo and Amireault found that although natural diatom assemblages were often accurately represented on artificial substrata, green and blue-green algae were severely underrepresented. Wigglesworth-Cooksey and Cooksey examined the means by which surfaces may be sensed by diatoms. They suggest that specific receptors and a Ca^{2+} flux mechanism control the secretion of an adhesive polymer by *Amphora coffeaeformis*. Barnese and Lowe suggested the diel emigration periodicities of lotic benthic diatoms were species specific, were under autogenic regulation, and were influenced by light, substrate type, and invertebrates.

Colonization of various substrates by meiofauna and invertebrates was investigated by several authors. Holström *et al.* isolated five marine epilithic bacteria that inhibited colonization by barnacle (*Balanus amphitrite*) and ascidian (*Ciona intestinalis*) larvae and attempted to isolate and characterize the chemical inhibitory compounds. Suren and Winterbourn found that invertebrate colonization rates on artificial bryophytes in shaded and unshaded New Zealand streams were related to associated periphyton and detrital biomasses and were unrelated to shelter provided by the bryophytes at each site. Thiéry and Cazaubon described the colonization of epizootic algae and protozoans on branchipod exoskeletons in temporary ponds. They suggested that algal colonization is related to water turbidity, as algae tend to colonize the upper surfaces of crustaceans that remain in surface waters, whereas protozoans that attach to the appendages of deeper water notostracans appear to benefit from the nutrient- and O_2 -rich water created by the host.

Several authors analyzed bacterial colonization of different substrata. McCarter *et al.* used a variety of genetic tools to describe the ability of the bacterium *Vibrio parahaemolyticus* to sense surfaces and transform from free-swimming to “swarmer” cells upon contact with a surface. Makemson *et al.* found that luminous bacteria (*Vibrio harveyi*) in seawater have the ability to adhere to artificial surfaces. Although phytoplankton did not appear to be associated with the bacteria, macroalgae were shown to support an enhanced concentration of the luminous bacteria. The adhesion of spores of 10 different species of *Bacillus* to hydrophobic and hydrophilic glass was investigated by Husmark and Rönner. All spores tested adhered more easily to hydrophobic surfaces; appendages were suggested to promote adhesion in at least three of the species. Couch and Meyer looked at the development and composition of an epixylic biofilm in a black-water river and found bacterial colonization was not related to algal abundance. Seston appeared to be the source of material accumulating in the biofilm, and at least nine times more carbon was contained in extracellular polysaccharides than in bacterial biomass.

Factors influencing succession in protozoan and microalgal communities were investigated. McCormick and Cairns studied the relative roles of internal (species interactions) and external (for example, abiotic parameters and transport processes) forces on protistan and metazoan community development in mature (4-year-old) and immature artificial aquatic islands. They suggested that transport of new species into the community greatly influenced taxonomic structure even in relatively stable (mature) communities. Rodríguez examined development of initially different attached microalgal assemblages in an oligotrophic lake. Convergence of a control and two experimental communities

indicated that community structure was regulated toward a single, highly dynamic equilibrium.

Temporal and spatial distribution. Metaxas and Lewis examined variation in diatom communities among marine tidepools; although some discernable zonation patterns were related to gradients of temperature, salinity, and tidal height, results suggested that frequency of pool flushing was most influential in generating taxonomic differences. Garcia-Gil and Abella reported that spatial distribution and seasonal changes in the taxonomic composition of phototrophic bacterial assemblages in Lake Banyoles were tied to changes in light availability. Rajendran *et al.* examined distribution of phospholipid ester-linked fatty acid in the sediments of two eutrophic bays in Japan and found that microbial biomass, community structure, and nutritional status varied as a function of environmental conditions and pollution. Tidal creeks draining into Chesapeake Bay supported greater bacterial biomass, abundance, and productivity than seaside creeks; this interhabitat variation may have stemmed from differences in dissolved organic carbon (DOC) sources, grazing pressure, or bacterial community structure (MacMillin *et al.*).

A number of studies documented variation in microbial communities along environmental gradients. Periphyton collected from three physically similar sites that differed in distance from a point source of industrial discharge did not differ in either cell densities or uptake of radiolabeled bicarbonate or amino acids but did differ in the ratio of membrane lipids to storage lipids synthesized (an indicator of physiological stress) (Guckert *et al.*). Karner *et al.* noted marked changes in bacterial production and extracellular activity along a trophic gradient and among seasons in the Northern Adriatic Sea. Hansson found a curvilinear relationship between periphyton biomass and lake productivity among Swedish and Antarctic lakes of varying trophic status and suggested this pattern was generated by a shift from nutrient limitation to light limitation as phytoplankton standing crops increased. Diatom species composition varied among 21 Antarctic lakes as a function of nutrient and light availability (Hansson and Håkansson). In comparing microbial leaf decomposition among Adirondack streams of differing pH, Osgood and Boylen observed that maple leaves were degraded more slowly at low pH not because of differences in bacterial numbers but because of lower bacterial productivity (as measured by thymidine incorporation) in more acid waters. Hudson *et al.* reported bacterial productivity and biomass in stream sites with open canopies was greater than at shaded sites; this difference was more pronounced in water-column samples than in sediment samples. Sabater and Sabater used principal components analysis to assess longitudinal variation in benthic algal biomass (chlorophyll *a*) in the river Ter during a spring and summer and reported that differences among sites were greater in the summer than in the spring. Molloy examined longitudinal changes in diatom colonization patterns in three tributaries to the Kentucky River and documented variation in community composition and accumulation rates associated with stream order and current regime. Composition and abundance of diatom epiphytes of *Cladophora glomerata* exhibited longitudinal change over a 340-km stretch of the Colorado River; vertical variation associated with river depth and flow fluctuations were also noted (Hardwick *et al.*).

Patterns of longitudinal or temporal variation in benthic bacterial assemblages were investigated by several authors. McArthur

et al. investigated genetic diversity and genetic similarity among bacterial isolates collected along a stream continuum and found that diversity did not change longitudinally, but the degree of dissimilarity among isolates was directly related to distance between collection sites, suggesting localized adaptation. Leff *et al.* discussed mechanisms by which bacteria cells or their DNA might be translocated between stream habitats and likened these patterns to those described for spiraling of nutrients and DOC. Fluxes of bacterial cells and particulate and dissolved organic matter into the Ogeechee River from river sediments and floodplain soil were documented by Wainright *et al.*; these previously unmeasured fluxes help to explain high concentrations of suspended bacteria in this system. Abundance and physiological activity of free-living and attached bacteria in a coastal marine ecosystem were compared by Unanue *et al.* over a year. Attached bacteria, which accounted for only 6.8% of total standing crop, responded to different environmental factors than free-living cells and were more physiologically active, incorporating radiolabeled substrates two to five times more rapidly on a per cell basis.

Sabater and Roca identified mineral content of spring water as key in determining diatom distribution among springs on the Spanish side of the Pyrenees Mountains. Nechhi tracked percent cover and relative abundance of four macroalgal species in a spring in southeastern Brazil over a year. Although highly dynamic, changes in this assemblage were not related to changes in physical-chemical parameters but, instead, were ascribed to a combination of competition for space and differences in species reproductive strategies. Sheath and Cole surveyed macroalgal distribution in 1 000 20-m-long stream segments ranging in latitude from northern Baffin Island (73°N) to central Costa Rica (10°N); they reported differences in percent cover, taxonomic structure, and species richness among seven biomes and summarized occurrence of common taxa with respect to current velocity, pH, specific conductance, and temperature. Current knowledge on the ecology of the ubiquitous macroalga *Cladophora* was reviewed by Dodds and Gudder. This review included discussion of taxonomic considerations, reproduction, variation in epiphyte loads, and distribution as related to current and nutrient regimes, competition with other algae, and herbivory by aquatic invertebrates. Vyverman (a) surveyed the distribution of desmid and diatom taxa along an altitudinal gradient in Papua New Guinea. Of the 383 diatom taxa and 357 desmids for which he collected distributional data, 80 and 73% of the taxa within these groups, respectively, were cosmopolitan, whereas the remaining taxa were confined to a specific biogeographical area. Multivariate analyses performed on diatom data from the previously mentioned survey revealed that conductivity, water temperature, and altitude were the main factors explaining variation in the data (Vyverman, b). A 2-year study of the epiphytic algal community on water hyacinth in coastal lagoons and creeks of southwestern Nigeria demonstrated that community composition varied seasonally and was dependent on whether host plants were collected in the middle of a water body or at the margins (Nwankwo and Akinsoji). Joo *et al.* documented seasonal growth patterns and substratum preference of the freshwater bryozoan *Pectinatella magnifica* in an oxbow lake in Alabama. Surfaces supporting bryozoan colonies were dominated by cyanobacteria whereas diatoms dominated bryozoan-free substrata.

Distribution of interstitial microfauna. Dole-Olivier and Marmonier (a) examined the distribution of interstitial microfauna

within two gravel bars in the Rhône River. In the first, which exhibited hydrologic downwelling at the head of the reach and upwelling at the tail, epigeal microfauna dominated at the downwelling zone whereas the upwelling area was dominated by stygofauna. In the second reach, hydrologic conditions were reversed (upwelling at the head) and no pattern of interstitial assemblage structure was found. The same authors (b) described distribution and ecological requirements of individual taxa from these two reaches. Marmonier *et al.* sampled interstitial assemblages from stations spanning the entire alluvial plain of the Rhône River and determined that both groundwater characteristics and habitat position relative to the floodplain margin influence spatial distribution of interstitial fauna. Species richness of microfauna beneath a regulated section of the River Rhine was positively related to oxygenation of interstitial water and was unrelated to hydrologic characteristics; unlike other large European rivers, stygofauna were absent from these collections (Creuzé des Châtelliers *et al.*). Chafiq *et al.* examined spatial heterogeneity in interstitial fauna across transverse transects of two tributaries of the Rhône River that originated from a karst area and described the influence of groundwater circulation on community structure. Boulton *et al.* surveyed the hyporheic zones of five desert streams, in Arizona, found a species-rich interstitial assemblage, and described four physicochemically and biologically distinct biotopes that they suggested could be viewed as functional subunits of desert stream ecosystems. A study of meiofaunal assemblages in shaded and unshaded New Zealand streams showed that meiofaunal densities were highest in unshaded sites and higher in bryophyte habitats than within gravel; assemblages in these two habitats were taxonomically distinct (Suren). Santangelo and Lucchesi described the dynamics of an interstitial ciliate community from coastal sands of the Mediterranean Sea and noted seasonal variation in density. Webb and Parsons collected harpacticoid copepods from seagrass and from underlying sediment on Roberts Bank, British Columbia and found that, unlike sediment-dwelling assemblages that display stable successional patterns, copepod abundance on seagrass exhibited significant year-to-year variation.

Dole-Olivier and Marmonier (c) studied dynamics of an interstitial assemblage in the Rhône River during a 480-day period that included nine spates and found a strong relationship between spate intensity and changes in vertical distribution of fauna. Spates displaced epigeal fauna into interstitial layers; rates of recovery to prespate conditions varied with disturbance intensity, disturbance history, and season. Palmer *et al.* used a combination of field and flume experiments to test whether the hyporheic zone could serve as a refuge for meiofauna during spates. They concluded that, even though increased flow can stimulate vertical descent of several centimeters in some taxa, these movements are not adequate to prevent significant reduction of meiofaunal density during flooding events.

Factors influencing distribution of ice algae. Hsiao compared seasonal dynamics of ice algae and phytoplankton in Frobisher Bay, Canadian Arctic, reporting that microalgal biomass and taxonomic structure in sea ice varied both vertically and seasonally, whereas biomass of phytoplankton in the underlying water column was lower and less variable. Meguro *et al.* described the floristic composition of two distinct ice diatom communities in Lützow Holm Bay, Antarctica: one associated with outer pack ice and the second from a narrow band of "fast ice" near the ice shelf. Analyses of ice-algal assemblages collected from the

Barents Sea over a 2-year period showed distinct seasonal changes in taxonomic composition, little evidence for nutrient limitation, and strong evidence for control of distribution by variation in light intensity. Ice algae were strongly shade adapted, were inhibited by high irradiances, and exhibited significant interspecific variation in their ability to adapt to changing light regimes (Hegseth). Photosynthetic capacities of microalgae in Antarctic pack ice, a habitat that comprises 90% of the ice cover in Antarctic seas but that has not typically been included in calculations of ice-algal production, were nearly an order of magnitude greater than that of the more-frequently quantified fast-ice assemblage, suggesting that the contribution of sea-ice algae to primary production in the southern ocean has been underestimated (Lizotte and Sullivan). Aletsee and Jahnke documented the ability of the psychrophilic diatoms *Thalassiosira antarctica* and *Nitzschia frigida* to survive and grow at extremely low temperatures and described changes in cellular chlorophyll content and light saturation characteristics with variations in temperature and salinity. Arrigo and Sullivan measured responses of ice algae to varying temperature, irradiance, and salinity to determine whether these parameters acted independently or interactively to control rates of photosynthesis. Temperature and salinity exerted both multiplicative and independent effects on photosynthetic rate under light-limiting conditions. Legendre *et al.* determined, via culture experiments, that variation in ice-algal biomass associated with a strong salinity gradient in Hudson Bay (Canadian Arctic) was generated primarily by differences in salinity not nutrient availability. Nelson and Tréguer noted depletion of silicic acid, nitrate, and phosphate associated with an ice-algal bloom in the Ross Sea and conducted silicon-uptake experiments to assess the possibility of silica limitation to ice-algal growth. Results provided evidence of weak substrate limitation of silicic acid in naturally occurring ice diatom assemblages.

Effects of disturbance and patterns of recovery. Ritzrau and Graf documented that benthic bacteria suspended into the water column during storm events in Kjel Bight remain within 40 cm of the sediment-water interface; such occurrences enhance production of microbial biomass and likely serve as an important source of energy to the benthic community. Periphyton colonization of diatometers suspended at different depths within a shallow eutrophic lake was examined before and after implementation of artificial aeration as a means of destratification (Choi *et al.*). Aeration increased cell densities in upper strata, yielded greater homogeneity in algal distribution among strata, and shifted the periphyton from dominance by diatoms to cyanobacterial dominance.

Rao Bhamidimarri and See examined the relationship between biofilm growth and substrate utilization rates under varying degrees of shear stress in a phenol-using biofilm. Net biomass accrual and shear stress were curvilinearly related, with maximal biomass attained at $9 \text{ N} \cdot \text{m}^{-2}$; substrate removal rates increased exponentially with increasing shear stress, and maintained a maximum beyond $3.5 \text{ N} \cdot \text{m}^{-2}$. Biofilms developed in the North Wales River under light or dark conditions were transported to laboratory streams and subjected to a simulated spate to examine the influence of storm flow on electron transport activity (ETS) (Blenkinsopp and Lock). Cell-specific ETS activity increased significantly following storm flow in light- but not in dark-grown biofilms and returned to predisturbance levels within 2 days. Humphrey and Stevenson varied nutrient concentrations and current velocities in artificial stream channels to levels charac-

teristic of subscouring spates to assess individual and interactive effects of these parameters on benthic algal dynamics. Their results suggested that subscouring spates can inhibit algal growth in nutrient-poor systems but may have a stimulatory effect in nutrient-rich streams. In a manipulative experiment designed to determine the influence of current regime and successional stage on resistance and recovery of benthic algal communities after spates, Peterson and Stevenson found that communities that developed in fast currents were generally more resistant to biomass removal than communities that developed in slow currents, whereas slow-current communities recovered more rapidly from disturbance. Resistance of slow-current communities varied during community development and appeared to be influenced by disturbance history. Power presented data suggesting that year-to-year variation in *Cladophora* dynamics during the summer months in northern California's Eel River are tied to winter flood activity.

Recovery after different periods of atmospheric exposure of cyanobacterial mats inhabiting Antarctic ponds and streams was investigated by Hawes *et al.* Mats dominated by *Nostoc* remained wet 5 hours after exposure and returned to predesiccation rates of photosynthesis and respiration within 10 minutes; *Phormidium* was less tolerant to desiccation, yet viable diaspores of this taxon were found in cyanobacterial mats that had been exposed for 3 years.

Herbivory. Several studies investigated the impact of multiple trophic interactions on benthic microbial assemblages. For example, Hart described how complex interactions between current regime and herbivore activity dictated whether a *Cladophora*-dominated assemblage or a low-lying epiphytic algal assemblage became established in a headwater stream and how establishment of these algal patch types generated different assemblages of macroinvertebrates. Brönmark *et al.* conducted an enclosure/exclosure experiment in Wisconsin lakes and demonstrated that periphyton biomass increased and filamentous and stalk-forming algae became more prevalent when high densities of a molluscivorous fish (pumpkinseeds) reduced snail grazers. A similar study by Bechara *et al.* found that when brook trout reduced the number of large macroinvertebrates in a boreal forest stream, densities of chironomids and, in some cases, periphyton increased. They demonstrated that size-selective predation of invertebrates by brook trout can cause profound changes in the structure of epibenthic communities at multiple trophic levels. Holomuzki and Stevenson found that the presence of predatory fish (*Lepomis*) in an ephemeral stream did not affect the composition of lower trophic levels (including benthic algae) before or after stream intermittence.

The relationship between epiphytes, epiphyte grazers, and host plants was investigated by several authors. Dudley examined how invertebrate epiphyte grazers (*Baetis* and *Agapetus*) affected biomass of the host macroalga (*Cladophora*). He found that although grazers can inhibit early establishment of *Cladophora* tufts, they can stimulate growth of established tufts by removing epiphytic algal cells. A similar study by Underwood *et al.* demonstrated mutualistic interactions between snails, epiphytes, and the host plant (*Ceratophyllum demersum*). Selective epiphyte removal by snails enhanced growth of the host plant while reducing epiphyte competition for the adnate diatom *Cocconeis placentula*. Klumpp *et al.* estimated that epifaunal grazers (mainly snails) consume between 20 and 62% of the epiphytic periphyton in tropical seagrass beds.

Hill *et al.* (a) were able to stimulate both primary production (periphyton chlorophyll *a*) as well as secondary production of grazing snails (*Elimia*) by enriching with nutrients. In another study, Hill *et al.* (b) demonstrated that growth and lipid accumulation by two grazers were strongly food limited. By augmenting the diets of these grazers with periphyton and leaves, they were able to stimulate growth rates two to seven times. Madsen investigated the diets of several species of freshwater snails and concluded that, in general, detritus was the largest dietary component, followed by epiphytic algae and decaying macrophytes. Apart from avoidance of blue-green algae, snails did not selectively feed on other algal taxa.

The influence of grazers on spatial and temporal distribution of benthic periphyton was investigated in several papers. Steinman manipulated both light and snail grazer densities in a stream and found that periphyton carbon fixation rates increased with higher light levels and with reduced grazers; upright and large diatoms dominated under these conditions. Under low-light or high-grazer conditions, basal cells of *Stigeoclonium* dominated periphyton communities. Page *et al.* indicated that the random distribution of a deposit-feeding bivalve (*Macoma nasuta*) contributed to small-scale patchiness of benthic algae. Lamberti *et al.* reported that the effects of two large benthic herbivores, tadpoles (*Ascaphus truei*) and caddisfly larvae (*Dicosmoecus gilvipes*), on benthic algal biomass of streams near Mount St. Helens varied spatially in relation to stream disturbance history, local environmental factors, and herbivore distributional patterns and abundance. Karouna and Fuller examined the influence of four insect grazers on periphyton communities growing on leaves and clay tiles. Periphyton communities on leaves differed from those on tiles, and grazers with different mouth-part morphologies had varying effects on both algal and heterotrophic microbial community structure. France and Welbourn found that softwater lakes in Ontario with pH less than 6 contained extensive accumulations of metaphytic Zygnematacean algae and that crayfish and tadpole grazers could reduce the abundance of the alga.

Two papers detailed the influences of periphyton patchiness on the distribution of invertebrate grazers. Poff and Ward described the importance of algal patchiness in mediating grazer foraging activity and distribution. They also documented the significance of near-bed currents to the patterns of resource use by grazers. In experimentally shaded areas of a Hong Kong stream, which grew lower biomasses of benthic algae, the abundance of grazing invertebrates declined compared with unshaded patches (Dudgeon and Chan).

Bacterivory by meiofauna in different benthic habitats was described by several authors. Bernhard and Bowser observed the use of pseudopodia and pseudopodial networks by benthic foraminifera to ingest up to 80% of the bacteria in marine intertidal biofilms. Rates of microbenthic and meiobenthic bacterivory in a muddy tidal flat community were measured using a fluorescence-labeled bacteria (FLB) technique (Epstein and Shiaris). Although the rates of bacterivory for individual grazers were high (up to 169 FLB/individual·h) grazer densities were low so that the major bacterial grazers (microflagellates, ciliates, and nematodes) could only potentially consume up to 0.2% of the bacterial standing stock. McGuinness and Johnson described bacterivory by a flagellated protozoan that is capable of growing in acidic drainage streams (pH 1.8–4.5) with high iron levels.

Interactions between nutrients and microbenthos. Several pa-

pers addressed the physiological utilization of nitrogen by algae; phosphorus dynamics were discussed in a few of these studies. Reuter and Axler reported differences in the physiological nitrogen uptake mechanisms in epipelagic periphyton and sublittoral and splash zone epilithic periphyton in a nitrogen-deficient lake. Sublittoral algae depended on nitrogen fixation for their nitrogen supply, eulittoral algae used dissolved inorganic nitrogen, whereas epipelagic algae (living in an NH_4 -rich environment) showed no physiological adaptation for surviving in a nitrogen-deficient environment. Lohman and Priscu investigated physiological indicators of nutrient deficiency in river *Cladophora*, and found that cellular nitrogen levels were at or below the critical minimum for maximal growth during the summer and early fall (when ambient dissolved inorganic nitrogen levels were also low), while cellular phosphorous levels increased throughout the season. The number of endosymbiotic nitrogen-fixing cyanobacteria in diatoms of the family Epithemiaceae increased under nitrogen-limiting conditions (DeYoe *et al.*). Nitrogen-fixation capacity of a benthic freshwater cyanobacterium, *Lyngbya wollei*, was reduced under aerobic conditions, promoted under exposures to light/dark cycles, and also varied with irradiance intensity (Phlips *et al.*). Jones reported a higher nitrogen-fixation rate for heterocystous tropical marine cyanobacteria (*Calothrix*) than for nonheterocystous *Lyngbya* during daylight hours, whereas *Lyngbya* fixed nitrogen at a rate three times higher than *Calothrix* at night. Mulholland and Rosemond showed that periphyton uptake of nutrients introduced into a Tennessee stream from localized sources of enriched groundwater reduced nutrient concentrations downstream and thereby influenced the structure and functioning of downstream periphyton communities. Kuwabara measured diel fluctuation in a South Dakota stream of two chemically similar anions (orthophosphate and arsenate) that have similar abiotic adsorption properties but differ in biological use. Diel patterns in arsenate were tied to variation in physicochemical parameters affecting abiotic sorption, but phosphate dynamics indicated the importance of uptake and rerelease by benthic microbiota.

Two papers looked at the contribution of animals to benthic nutrient supply. Murphy and Kremer suggest that activities of callinassid shrimps can contribute up to 5% of the nutrients required to support the benthic algal community in a tropical ecosystem, whereas the entire benthic macroinvertebrate community could support up to 21% of the needed nutrients. Rand *et al.* examined the potential of decaying carcasses of migratory salmon to stimulate primary production of stream periphyton by releasing phosphorous. Their results indicate that these streams are already nutrient rich and productive and, whereas light could be limiting, salmon migrations are unlikely to substantially increase rates of primary productivity.

Studies investigating the effects of nutrient enrichment on benthic algae often suggested that additional factors also limited growth. Bowden *et al.* found that epilithic algae in an arctic tundra stream responded more to nitrogen than phosphorous enrichment, and that total biomass and productivity was higher in pools than riffles because of the scouring effects of stream flow. Welch *et al.* found that stream periphyton biomass greatly increased in response to point-source phosphorous enrichment unless the sites below the input were associated with high grazer densities, riparian shading, or unsuitable attachment surfaces. A review of data describing the effects of phosphorous enrichment on algal and macroinvertebrate communities in the Ev-

erglades was compared with preliminary data collected by Rader and Richardson. Although phosphorous enrichment changed species composition and increased productivity of thick cyanobacterial mats, algal diversity was not changed. Klotz reported an increase in alkaline phosphatase activity for stream epilithon that were shaded and enriched with nitrogen, but not for phosphorous-enriched treatments. Fairchild and Sherman showed that epilithic algal production in lakes with low alkalinity (less than 100 $\mu\text{eq/L}$) was strongly limited by inorganic carbon as well as phosphorous and nitrogen, whereas epilithon in lakes having higher alkalinities responded less to inorganic carbon enrichment. Peterson and Grimm found that the effects of nitrogen enrichment on periphyton succession in a nitrogen-limited desert stream diminished as communities developed. Enrichment favored establishment of non-nitrogen-fixing taxa early in community development, but in unenriched early-successional communities and in thick late-successional mats (regardless of treatment), nitrogen-fixing algae dominated. Lohman *et al.* studied the effects of nutrient enrichment and flood frequency on periphyton biomass in Ozark streams and found that periphyton in nitrogen- and phosphorous-enriched streams recover more quickly to catastrophic floods than periphyton in streams with low concentrations of water column nutrients.

Photosynthesis, production, and the effects of irradiance. Microsensors were used in several studies to investigate changes in productivity and irradiance from the surface to the base of periphyton mats. Photosynthetic rates of littoral epilithic algal communities in Lake Thingvallavatn were higher at the surface of the mat, and decreased with depth. Up to 79% of the variation in photosynthetic rate was explained by irradiance: 0.4–8% by temperature and 2–5% by biomass (St. Jónsson). Glud *et al.* used an O_2 microsensor to quantify photosynthesis and photosynthesis-coupled respiration in two types of biofilms: one dominated by diatoms and one dominated by cyanobacteria. They observed high $\text{O}_2:\text{CO}_2$ ratios, especially within the diatom biofilm, and suggested that these conditions could indicate that photorespiration was a dominant O_2 -consuming process. A modified fiber-optic light probe and an O_2 microelectrode were employed by Dodds to document photosynthesis-irradiance patterns in *Ulothrix*- and diatom-dominated periphyton communities; these communities differed in the degree of light attenuation with depth and in the intensity at which photosynthetic saturation occurred. Lassen *et al.* measured scalar irradiance and photosynthesis within an epipelagic microbial mat using scalar irradiance microsensors and oxygen microelectrodes spaced 120- μm apart. They described a 10-fold increase in photosynthetic efficiency at 1.0 mm depth in the mat under high light (740 $\mu\text{E}/\text{m}^2 \cdot \text{s}$), as compared with the mat surface and defined the lower boundary of the euphotic zone (detectable gross photosynthesis) to occur at less than 7.5 $\mu\text{E}/\text{m}^2 \cdot \text{s}$.

The effects of irradiance on primary production and photosynthesis was investigated. DeNicola *et al.* examined the influences of canopy cover on spectral irradiance and periphyton assemblages at four sites with varying degrees of terrestrial canopy cover in a prairie stream. The degree of temporal variability in the underwater spectral distribution at a site was often greater than differences between sites because of the relationship of solar path to canopy structure and orientation. Periphyton assemblage structure was related to the degree of canopy cover at the sites. Blanchard and Montagna found that benthic microalgae in shallow marine systems were sensitive to hourly change in ir-

radiance generated by wind-induced currents; unlike open-ocean phytoplankton, the photosynthetic potential of microphytobenthos showed no diel periodicity. Kuehn *et al.* documented 21 species of viable photosynthetic microalgae that occurred in groundwater samples from a subterranean aquifer. They suggested groundwater recharge zones are the possible source of the algae to the aquifer and that resting stages and facultative heterotrophy are possible mechanisms for their survival in an aphotic environment. Pentecost described four species of endolithic algae in North Yorkshire streams and discussed the ability of these algae to penetrate the rocks up to 1.3 mm. The rates of carbon fixation for these encrusting algal communities were comparable to those obtained for pure cultures.

Primary production of benthic marine littoral zones was investigated in two studies. Daehnick *et al.* measured primary production of the sand microflora under seagrass beds and found that water temperature, tidal range, and light energy were the best environmental predictors of sand microfloral production rates. Cahoon and Cooke compared benthic microalgal production to planktonic production on a North Carolina continental shelf and found that production of the two components was similar and that biomass of the benthos always exceeded the plankton. These results counter the traditional view that open sandy-bottom habitats are relatively barren.

Steinman *et al.* suggested that phosphorous uptake, carbon fixation, and susceptibility to grazing were related to growth form (surface area:volume; SA:V) of some benthic algae. They reported positive relationships between SA:V and phosphorous uptake and SA:V and carbon fixation and found grazers preferred unbranched filamentous diatoms > prostrate algae > unbranched filamentous green algae.

Physiological processes within biofilms. Chappell and Goulder compared extracellular enzyme (glycosidase, sulphatase, and phosphatase) activities within epilithic biofilms from acid and calcareous streams and demonstrated that variation in activity was influenced by both water quality and microbial variables but not by physical factors such as current velocity, depth, and stone size. Recalcitrant, high-molecular-weight materials inhibit metabolic activity in river biofilms through occlusion by biofilm surfaces (Freeman and Lock). McKinley and Vestal tested microbial assemblages in arctic sediments from four sources (littoral and profundal lake sediment, thaw pond sediment, and peat from an eroding river bank) for differences in microbial biomass, capacity to mineralize simple and complex carbohydrates, and the influence of nutrient enrichment on mineralization capacity. Profundal sediments supported the lowest microbial biomass and showed evidence of nitrogen limitation, whereas communities from the other three sediment types were phosphorus limited and, although initial mineralization rates were low, ultimately exhibited the highest capacity to mineralize lignocellulose.

Vandevivere and Baveye (a–c) examined characteristics of aerobic bacteria that influence the hydraulic conductivity of sand filters. Clogging of sand filters containing the bacterium *Arthrobacter* sp. occurred when large, unattached cell aggregates plugged pore spaces not via attachment of uniform biofilms as is generally assumed (Vandevivere and Baveye, a). Differences in clogging efficiency of two non-slime-producing bacterial strains were related to differences in the propensity to form large cell aggregates (Vandevivere and Baveye, b). In a third paper the clogging efficiency of four bacterial strains, one slime producer, one encapsulated strain, and two strains that did not produce exo-

polymers, was investigated; all strains induced severe clogging when they colonized the inlet chambers of sand columns, but only the slime producer significantly reduced hydraulic conductivity under other circumstances (Vandevivere and Bayve, c).

Peyton and Characklis determined the relationship between detachment rate of cells within a *Pseudomonas aeruginosa* biofilm and both biofilm thickness and glucose utilization rate. Diffusion of acetate and lithium salt (a nonreactive tracer) was measured in anaerobic methanogenic biofilms of varying thicknesses (Kitsos *et al.*); effective diffusivity of the tracer through biofilms ranging from 200–1200 μm in thickness was 7% of that through pure water. Acetate consumption was linearly proportional to biofilm thickness in biofilms of up to 800 μm . Kugaprasatham *et al.* investigated the influence of five levels of turbulence on ammonium flux, areal biomass, and physiognomy within nitrifying biofilms under nonlimiting substrate conditions. Higher turbulence resulted in higher $\text{NH}_4\text{-N}$ flux, higher areal biomass, and a more uniform community physiognomy. Microzonation of denitrification activity in trickling filter biofilms was documented by Dalsgaard and Revsbech using a combined $\text{O}_2/\text{N}_2\text{O}$ microsensors. Denitrification activity increased with addition of NO_3^- , ceased under high photosynthesis-generated O_2 concentrations, and resumed quickly to the previous steady-state rate upon return of anoxic conditions. Kühl and Jørgensen used microsensors to measure concentration profiles of O_2 , S^{2-} , and pH at high spatial resolution (25–100 μm) within an aerobic trickling filter biofilm. They documented spatial patterns of sulfate reduction, oxygen respiration, calculated turnover times of H_2S and O_2 , and examined effects of SO_4^{2-} and NO_3^- on biochemical conversion rates. Visscher *et al.* investigated sulfur dynamics in a marine microbial mat by examining vertical distribution and densities of three functional groups of sulfur bacteria, measuring sulfate reduction rates, and assessing vertical distribution of thiosulfate consumption.

Lyngbya birgei, a large mat-forming cyanophyte, is capable of efficient utilization of HCO_3^- under alkaline conditions (Beer *et al.*). Further, this cyanophyte has the ability to concentrate inorganic carbon internally, thus suppressing photorespiration and making it a superior competitor in alkaline waters. Hollocher and Kristjánsson surveyed Icelandic hot springs for thermophilic bacteria capable of denitrification. Denitrifiers were lacking from acidic springs, but neutral hot springs yielded both nitrate-reducing and denitrifying bacteria; the latter appeared to be *Bacillus*, two strains of which exhibited an unusual denitrification phenotype.

Several authors investigated the influence of benthic microbiota in controlling material flux between the benthos and water column of aquatic systems. Sinke *et al.* conducted a diffusion-chamber experiment to investigate the influence of activity by methanotrophic bacteria on phosphate flux from lake sediments. Although methane oxidation reduced O_2 concentrations in sediment, a condition typically associated with release of phosphate, growth of methanotrophs contributed to phosphate uptake by aerobic sediments. Occurrence of the mucilaginous cyanobacterium *Microcystis* in sediments of a hypereutrophic Swedish lake stimulated activity of bacteria associated with the mucilage, which in turn altered patterns of phosphorus release from lake sediments (Brunberg and Boström). Meiofaunal activity (primarily nematodes, juvenile bivalves, and polychaetes) in marine sediments greatly facilitates the flux of solutes from sediments

to water column via both biologically induced fluid motion and through altering the distribution of oxic zones that alter chemical release properties (Aller and Aller).

Fenchel described the physiological, taxonomic, and chemical complexity of benthic microbial communities and argued that these communities provide special opportunities for experimental manipulation and are excellent and appropriate systems for addressing a wide array of ecological questions. Schönborn presented production and energy budgets for protozoan communities in lakes, streams, mosses, and soils and pointed out the importance of this group to ecosystem function. In many systems, protozoan communities are second only to bacteria in terms of biomass turnover, and nutrients released upon death provided an important nutrient source to other microbiota. Corliss detailed the potential benefits of interfacing the fields of ecology and taxonomy for studying protists and suggested specific steps through which these benefits could be realized.

Fungal distribution and function. Several papers described the colonization and distribution of aquatic fungi or their interactions with leaf litter in lakes and streams. Thomas *et al.* examined the preferences of aquatic fungi for eight different terrestrial vegetative tissues. The fungi showed significant substrate preferences (mostly for eucalypt twigs and sedge leaves), although no species was confined to a single substrate. Chauvet sampled natural foam and incubated leaf litter in four streams along an altitudinal gradient and found seasonal differences in the occurrence of aquatic hyphomycete conidia. Conidia densities showed peaks in late spring and during November and December; successional change in species composition was evident at all sites. Suberkropp and Wallace compared the aquatic hyphomycetes in an insecticide-treated stream where shredders had been greatly reduced with two untreated reference streams and found conidia densities in the water column and sporulation frequency on leaf litter were both greater in the treated stream. Bengtsson studied the dynamics of immigration and colonization of stream bacteria and hyphomycetes onto beech leaves and found that fungi were faster immigrants, especially on new leaves, and that bacteria grew faster in the water column than on the leaves. He described a synergistic relationship between fungi and bacteria in which each group grew significantly faster in the presence of the other. A phenolic acid fraction (2500 D) of beech leaf leachate seemed to inhibit both fungal and bacterial growth. Bergbauer *et al.* investigated the decomposition of lignocellulose from a freshwater sedge by five fungal taxa and found that the lignin component was mineralized less than the polysaccharide component and that the extent of mineralization of both moieties was less in mixed culture than in pure cultures. Bärlocher showed that freezing or drying autumn-shed leaves increased the leaching of soluble substances, and these leaves supported more species of aquatic hyphomycetes during early decay, and conidium production from these fungi was higher.

Miscellaneous. Maki *et al.* investigated the effects of films produced by two strains of a marine bacterium (*Deleya marina*) on the attachment of barnacle larvae. These films either had no effect or inhibited attachment of 0–4-day-old larvae, but not through alteration of surface free energy of the films. Weller *et al.* found, through DNA sequencing, several new inhabitants of a hot spring microbial mat, including two cyanobacteria, a green nonsulfur bacteria, and two spirochete-like bacteria. Karlson stated that an evaluation of the size-dependent variation in statoblast numbers in a freshwater bryozoan (*Plumatella repens*)

indicated that this organism uses divergent strategies in dispersing its asexual offspring in space and time. Large ramets produced disproportionately more floatoblasts than did small ramets. Strycek *et al.* studied the ability of freshwater algae and cyanobacteria to form extracellular fibrils by screening 28 species with ruthenium red staining. Algae with high proportions of stained cells produced high levels of slime-like material and distinct fibrils that were often seen attached to the cell surface. Vagnoli *et al.* studied the main morphological and physiological characters of several symbiotic cyanobacterial strains isolated from plant-cyanobacteria associations. The strains showed heterocystous immotile filaments typical of the genus *Nostoc*, and some had a marked tendency to produce hormonogonia, synthesize C-phycoerythrin, and produce small akinetes; these characteristics were generally host specific. Bertrand looked at 135 raphid diatom species and categorized them based on their movement abilities and behaviors.

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Nonpoint sources

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Nonpoint source (NPS) pollution originates from generally diffuse land areas that intermittently contribute pollutants to surface and groundwater. This article is a review of literature on several aspects of NPS pollution including policy, economics, and management issues; effects of NPS pollution on surface and groundwater; best management practices (BMPs) for NPS pollution control; and modeling and monitoring NPS pollution.

Several proceedings or compilations of NPS pollution control research and recommendations were published. Lessons learned from the 10-year experimental U. S. Department of Agriculture (USDA)-sponsored Rural Clean Water Program (RCWP) were addressed by numerous authors in the proceedings of the National Rural Clean Water Program Symposium (U. S. EPA, a). The U. S. Environmental Protection Agency (EPA) published a special journal issue addressing the problem of NPS pollution, NPS and policy, and case studies from Colorado and Wisconsin (U. S. EPA, 1991). Agricultural production, its impact on the environment, risk/benefit considerations, and current and future approaches to protecting water quality from agricultural contaminants were analyzed by the Council for Agricultural Science and Technology. Proceedings of the North Dakota Water Quality