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Substratum-Associated Microbiota

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Stefan and Fang (1994a and b) reported formulating a deterministic, one-dimensional, unsteady-state DO model for regional lake analysis simulating DO under summer stratified conditions. The model was applied to a large number of lakes in the north central U.S. to study the potential effects of global climate changes. Calibration showed good predictions for DO and temperature.

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Substratum-associated microbiota

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METHODS

Methods for quantifying metabolic activity and cellular constituents in microbes were described in a number of papers. Boon (1994) described a rapid and inexpensive technique for discriminating between algal and bacterial alkaline phosphatase activity. This technique, which relies on differential inhibition of enzyme activity among microbial groups by eight different treatments, proved >90% accurate in detecting differences among bacteria and among algae. Phelps *et al.* (1994a) found that rates of organic carbon oxidation, sulfate reduction, and biomass production by bacteria in coastal sediments were overestimated by radiotracer timecourse experiments.

Concentrations of cellular and extracellular carbon in bacterial biofilms were estimated by Okabe *et al.* (1994) using two methods, an epifluorescence microscopic technique and a lipopolysaccharide assay. These methods yielded comparable results for suspended samples but differed when used on biofilms. Wallace *et al.* (1994) developed a broad-range *algD-lux* bioluminescent reporter plasmid to detect production of exopolysaccharides (EPS) within biofilms by measuring light output when the *algD*

promoter was activated. EPS production was sensitive to NaCl and ethanol concentrations, as well as carbon and nitrogren sources, in growth media. Napolitano *et al.* (1994) tested the effectiveness of fatty-acid biomarkers in the use of periphyton for water quality assessment. They found that chlorine-induced shifts in algal taxonomic structure could be detected by examining fatty acid profiles and suggested that use of algal signature fatty acid could evolve into a quantitative automated method for biomonitoring.

A fluorescently labeled nucleotide probe was used to determine that rRNA concentration in *Escherichia coli* cells was greatest just before initiation of active cell division (Ruimy *et al.*, 1994). Rochelle *et al.* (1994) reported that the manner in which marine sediment samples were handled before DNA extraction for analysis of microbial diversity greatly affected the outcome of such tests. These authors strongly recommended freezing sediment samples immediately if they are to be used to assess bacterial diversity by molecular methods. Kemp (1994) cautioned that emerging methodologies for studying microbial ecology, such as measurement of rRNA content, should be used as a complement to, not a replacement of, conventional methods.

Marzolf *et al.* (1994) modified a technique for measuring whole-stream metabolism using diurnal changes in dissolved oxygen concentration and found that respiration and primary production estimates using this method were 20–33% greater than *in situ* chamber incubations. A comparison of microcosm designs for copper toxicity bioassays by Balczon and Pratt (1994) showed that periphyton communities grown on artificial substrata of polyurethane foam were more sensitive to copper than communities grown in a simulated littoral zone.

Several descriptions of methods for collection and processing of substratum-associated microbiota were published in 1994. Kornijów and Kairesalo (1994) designed a collecting device for epiphyton on macrophyte stems that improved upon existing apparati by incorporating different-sized sieves, thus making sampling more precise and efficient. The use of 4′–6–diamidino–2-phenylindale dihydrochloride (DAPI) staining and epifluorescence microscopy greatly increased the probability of detection of *Cryptosporidium* oocysts in water samples (Grimason *et al.*, 1994). Rogerson *et al.* (1994) developed a method for estimating cell volume of naked amoebae using direct measurement of nuclear diameter. Their calculations indicated that most species of amoeba have very small biovolumes despite their large surface areas.

Methods for direct observation of intact biofilms were described in four papers. By incorporating episcopic differential interference contrast with ultraviolet (UV) fluorescence into a conventional light microscope, Walker *et al.* (1994) were able to view the heterogeneous surface topography of biofilms on copper pipes. Yu *et al.* (1994) described a rapid, minimally disruptive, cryosectioning technique for bacterial biofilms that allowed light-microscopic observation of surface protrusions, the biofilm-substratum interface, and water channels within the biofilm matrix. Freeze dehydration was suggested as an alternative to ethanol dehydration for preparation of epiphytic and epizoic communities for scanning electron microscopy (Veltkamp *et al.*, 1994). Glud *et al.* (1994) demonstrated that the use of microelectrodes to measure oxygen microgradients within aquatic sediments disrupted the diffusive boundary layer (DBL) if introduced from above. If the probes were introduced from below, however, no DBL disruption occurred.

ECOLOGY

Colonization and community development. Guezennec *et al.* (1994) found that bacterial attachment to steel interfered with cathodic protection, a mechanism used to control corrosion of submerged metals. Both flow velocity and nutrient concentration were found to influence attachment of marine bacteria to Pyrex® (Zheng *et al.*, 1994). Experimental and modeling results demonstrated that bacterial attachment rate was a direct function of laminar flow velocity (that is, delivery rate) but that mechanisms responsible for cell loss varied with nutrient regime. Abelson *et al.* (1994) suggested that larvae of suspension-feeding marine fouling organisms overcome hydrodynamic interference (to settle in areas of high food-particle flux and low sedimentation rate) by producing long mucous threads. The strength of initial temporary adhesion of barnacle larvae did not differ among surfaces of different wettability, whereas coverage of these surfaces by bacterial films had variable effects on larval adhesion, depending on larval age (Maki *et al.*, 1994). These authors hypothesized that bacterial inhibition of permanent barnacle attachment is regulated by larval chemoreception. An investigation of the life cycles of three species of the dinoflagellate, *Peridinium*, in an acid-sensitive lake showed that before zygote formation these species leave the water column and settle, preferentially, on specific substrata (Holt *et al.*, 1994).

Periphyton response to variation in hydraulic regime and/or scour disturbance was examined in several studies. Biggs and Hickey (1994) characterized lotic periphyton communities from a wide range of flow regimes in a nutrient-poor river. Gross primary production did not differ among flow regimes, whereas ash-free dry mass (but not chlorophyll) was significantly greater in high current, principally because of copious mucilage production by diatoms in these habitats. Light- and dark-grown riverine biofilms were subjected to scour by a simulated spate and the effects quantified using transmission electron microscopy to directly observe changes in vertical structure of the communities; scanning electron microscopy was used to observe surficial changes in the biofilms (Blenkinsopp and Lock, 1994). Perkins and Jones (1994) demonstrated rapid increases and subsequent decrease of nutrients and suspended chlorophyll (from scoured periphyton) in response to four spring spates in a headwater Missouri stream. Peterson *et al.* (1994) compared the response of epilithic algal communities in a desert stream to a simulated spate (scour and short-term nutrient enrichment) with response to a natural spate to determine the mechanisms that drive algal recovery from disturbance. Algal recovery rates were strongly influenced by the extent of scour-induced biomass removal, but recovery patterns were also affected by length of post-spate enrichment and taxonomic composition of the community. Algal biomass and distribution (exposed surfaces versus crevices) on cases of larval caddisflies varied among caddisfly species that differed in burrowing activity (Bergey and Resh, 1994).

Rodriguez (1994) transferred artificial substrata between stations of an oligotrophic lake at different intervals to investigate the influence of environmental fluctuations and community age on periphyton succession and community stability. Frequent transfers slowed succession, and recovery from these manipulations to a convergence with controls was slower for taxonomic structure than for biomass. Norrman and Andersson (1994) tracked community development in sea-ice algal communities in the northern Baltic Sea and noted considerable successional

change in algal species composition and establishment of a diverse assemblage of heterotrophic organisms.

Cells within a population of *Gyrosigma balticum*, a large motile epipelic diatom, were observed to orient their long axis perpendicular to the sediment surface, instead of lying flat as was typically assumed (Jönsson *et al.*, 1994). The authors suggested that such behavior, which is facilitated by production of a short mucilaginous stalk at one end of the cell, may be common among epipelic diatoms. Sandjensen *et al.* (1994) described developmental changes during colony formation in *Ophrydium versatile*, a freshwater ciliate that contains symbiotic zoochlorellae.

Temporal and spatial distribution. *Seasonal variation in microbiota.* Guasch and Sabater (1994) found differences in seasonal trends in metabolic parameters of the epilithic algal communities of two Mediterranean streams, one calcareous and open and the other siliceous and highly shaded. Shamsudin and Sleigh (1994) investigated seasonal change in epilithic algal abundance and species composition in two streams originating from different geological strata (chalk versus sand/gravel) and differing in pH (8.2 versus 7.0). Although periphyton communities in both systems showed marked seasonal change and were dominated by diatoms, they differed significantly in species composition and algal densities (both as cell numbers and chlorophyll *a* concentrations). In contrast, Rosemond (1994) observed very little seasonal change in periphyton biomass and primary productivity in a temperate forest stream in Tennessee. She suggested that high snail densities and, to a lesser extent, asynchrony in patterns of variation in nutrient supply and irradiance combined to constrain periphyton biomass. Epilithic algal biomass and species composition varied considerably with seasonal change in environmental conditions, particularly flow rate, in a pristine forest stream in India (Rout and Gaur, 1994). LaPerriere (1994) described seasonal changes in algal and invertebrate communities in a large spring-fed river in the Alaskan interior. Algal standing crop in this system peaked in spring and autumn and was an order of magnitude higher than a nearby stream fed by surface water.

Freeman *et al.* (1994) used a field manipulation of longitudinally connected peat wetlands to investigate the influence of drought-induced changes in water chemistry on algae and bacteria in streams draining these systems. Stream water diverted from drought-impacted wetlands contained more nitrate, had cooler temperatures, and supported 145% more chlorophyll than stream water drained from "control" peat wetlands.

Two studies investigated seasonal variation in epiphytic algae growing on macrophytes. Seasonal changes in biomass production and algae successional patterns (diatom dominance giving rise to chlorophyte dominance during periods of high light availability) on *Phragmites australis* in an eutropic lake were very consistent over the course of a 3-year study (Muller, 1994). Enzyme activity of epiphyton on *P. australis* stems varied seasonally, with summer maxima, and appeared to be dependent on bacterial activity and abundance, as well as pH and temperature (Chappell and Goulder, 1994). In contrast, epiphyton on *Elodea canadensis* showed no seasonal variation and was most influenced by surrounding water quality.

Spatial variation within systems. Goldsborough (1994) quantified vertical and horizontal microheterogeneity in diatom distribution on vertically oriented artificial substrata placed in a duckweed covered canal and the littoral zone of a prairie lake. He used refined nearest-neighbor analyses to demonstrate differences in aggregation patterns among taxa that reflected differences in dispersal abilities from initial immigration sites. Two studies examined spatial distribution of macroalgae in mangrove forests. Phillips *et al.* (1994) used correspondence analysis to conclude that gradients in salinity and tidal inundation (that is, wetting frequency) were the key forces in generating observed algal distributional patterns on mangrove pneumatophores in a South African estuary. In a mangrove forest in Malaysia, Aikanathan and Sasekumar (1994) found significant differences in algal distribution associated with four substratum types, mangrove pneumatophores, sediment surface, and two height zones on mangrove trunks.

Several studies quantified patterns of periphyton zonation associated with hydrologic fluctuations. Rott and Pernegger (1994) identified four distinctive cyanophyte assemblages associated with different depths in soft-water mountain lakes in Bulgaria and Austria. Cronk and Mitsch (1994) compared algal biomass and productivity on artificial substrata and on five species of macrophyte in constructed wetlands subjected to two different hydrologic regimes. High-flow wetlands (41 cm water depth inflow/wk) supported higher epiphyte productivity than low-flow wetlands (6–9 cm water depth inflow/wk), likely because of higher nutrient availability in the former. Primary productivity and biomass of microphytobenthos in a southwestern Netherlands estuary was greatly increased by construction of a storm-surge barrier that reduced tidal range to 88% and current velocities to 70% of their preconstruction levels (Dejong *et al.*, 1994). Smol *et al.* (1994) examined distribution of the nematode-dominated meiofauna in this same estuary and predicted that changes associated with construction of the storm-surge barrier will significantly alter meiofaunal community structure. Asmus and Bauerfeind (1994) quantified marked differences in diatom assemblages at three stations of similar substratum characteristics, but differing in tidal inundation regimes, on a tidal flat in the northern Wadden Sea. Buczkó and Ács (1994) characterized the periphyton communities from fast-flowing, slow-flowing, and stagnant sites within a branch-system of the Danube in Hungary, as well as the epiphytic communities on several different macrophytes within the same system. They reported 241 taxa, nine of which were constant species and the majority of which were accidental. Spatial variation in benthic algal standing crop in gravel-bottomed reaches of a desert stream were linked to differences in hydrologic exchange patterns (Valett *et al.*, 1994). Localized areas of upwelling where nitrate-rich hyporheic water entered the surface stream supported higher algal biomass and recovered more rapidly from substratum-mobilizing spates than downwelling zones.

Variation in bacterial standing stock and organic carbon from marine sediments along a depth gradient (258–4 427 m) across the deep Arctic Eurasian Basins was reported by Kroncke *et al.* (1994). Fabiano and Danovaro (1994) investigated relationships between biochemical characteristics of sediment organic matter and bacterial and microphytobenthic biomass in sediments in an estuarine outlet. Their results suggested that specific organic compounds should be measured rather than bulk carbon and nitrogen to accurately relate microbial biomass to quality of organic matter. Zheng and Kellogg (1994) sampled and characterized bacteria from a basalt aquifer and concurrently measured eight physicochemical variables. Gram-negative mesophilic heterotrophs dominated these samples, but the authors were able to discern, with cluster analysis, 14 assemblages containing representatives from several genera.

The influence of meiobenthic copepod emergence on copepod densities in pelagic and phytal habitats was measured by Walters and Bell (1994) and found to be inconsequential. Schmidaraya (1994) tracked densities of heterotrophic flagellates and three size classes of ciliated protozoa in surface sediments and hyporheic habitats in a gravel-bed brook over a year. Both ciliates and flagellates occurred in distinct zones of highest density within the hyporheic but were differentially affected by a spring spate, with flagellates exhibiting higher resilience than ciliates.

Three papers addressed spatial variation in distribution of substratum-associated microbiota tied to longitudinal displacement. Stoyneva (1994) suggested that benthic microalgae in river arms of the Bulgarian Danube, and in shallow midriver sections, represent an important source pool for recruitment into the potamoplankton assemblage. Leff *et al.* (1994) tested the hypothesis that dislodgement of attached bacteria by benthic macroinvertebrates was a primary mechanism for bacterial dispersal in aquatic systems. Results of experiments using four different types of invertebrates did not support this hypothesis. Influence of upstream activity of algal herbivores on algal colonization and growth downstream was investigated by McCormick *et al.* (1994). Rates of algal accrual on newly introduced substrata downstream of active snail grazing were significantly higher than below ungrazed sections of the channel, but these differences could not be attributed to differences in the flux of algal propagules or in nutrient supply rates.

Spatial variation among systems. Robinson *et al.* (1994) conducted a 5-year study of diatom communities at 14 stream sites in and around Yellowstone National Park in catchments that had been burned to different extents during the 1988 wildfires in that area. Diatom assemblages in streams in extensively burned catchments showed the greatest amount of structural change from year to year and differed from less-disturbed sites in identity of dominant taxa. A survey of diatoms, bryophytes, macroinvertebrates, and fish in 18 Napalese stream systems ranging in elevation from 600 to 3 750 m showed pronounced altitudinal transitions in each of these groups, reflecting influence of a wide range of physical and chemical factors (Ormerod *et al.*, 1994). Species richness and abundance of freshwater macroalgae in 22 stream segments in the Preto River Basin, Brazil, were correlated with a suite of physicochemical variables, and results were compared with predictions of the River Continuum Concept (Necchi *et al.*, 1994).

Niederhauser and Schanz (1994) characterized six remote high-mountain lakes in Switzerland on the basis of water chemistry and epilithic diatom community composition. These authors used both cluster analysis and the Index B system of pH classification for diatoms developed by Hustedt to interpret these data and found the Index B system to be unsatisfactory. Distribution and abudance of the filamentous bluegreen alga, *Lyngbya wollei*, at 15 sites in a central Florida river/estuarine system was most influenced by variations in conductivity and alkalinity, with nutrient concentrations having little effect (Cowell and Botts, 1994). Laboratory studies corroborated field observations with low salinities, slightly alkaline pH, and addition of Ca^{2+} yielding best growth in *L. wollei* cultures. High salinities in laboratory culture experiments were also found to limit growth of the filamentous green alga, *Ctenocladius circinnatus* (Herbst and Castenholz, 1994). These authors varied salinity and monitored changes in growth rate, cell form, chlorophyll *a*, and water content in clones isolated from Mono Lake, California, and Abert Lake, Oregon, systems that are both alkaline, sodium chlorocarbonate-type lakes but differ in salinity.

Distribution of ice algae. Diatom assemblages collected from fast ice in Prydz Bay, Antarctica, differed considerably from those taken from pack ice in the same area (Scott *et al.*, 1994). Factors important in generating these differences included ice crystal type, ice salinity, and time of year of ice formation. Smith *et al.* (1994) found that a common psychrophilic ice diatom, *Nitzschia seriata*, is able to thrive at the low temperature of its natural habitat by optimizing efficiency and compensating for physiological changes induced under these conditions. Robineau *et al.* (1994) observed, for the first time, ultra-algae (0.4–5 μm) in sea ice in southeastern Hudson Bay. Ice-bottom-ice-water interface and water-column habitats supported different taxonomic assemblages; variation in abundance and species composition was tied to gradients in salinity and light and ice structure and particle load. Arrigo and Sullivan (1994) developed a two-dimensional time-dependent model for microalgal growth in sea-ice habitats that incorporated effects of temperature, spectral irradiance, nutrient concentration, and salinity. Model results showed excellent agreement with field measurements of sea-ice microalgal bloom dynamics.

Patterns and processes within biofilms. Meyerreil (1994) reviewed aspects of microbial life within biofilms, including discussion of colonization processes, functions of extracellular polysaccharides, spatial heterogeneity in microbial distribution and activity, and distribution and availability of organic carbon. Wolfaardt *et al.* (1994) used scanning confocal laser microscopy and mass spectroscopic analysis to determine that the herbicide diclofop methyl was accumulated within the exopolysaccharide matrix of a bacterial biofilm where this chemical was eventually mineralized to degradation products. This extracellular material was directly, and nonselectively, ingested by grazing protozoa, indicating that microbial exopolymers likely play an important role in bioaccumulation of contaminants in natural systems.

Biofilms were found to be very spatially heterogeneous, and this variation in physical structure greatly influenced the transport and processing of material entering from the water column. Considerable variation in vertical structure was observed within a heterotrophic biofilm by Zhang and Bishop (1994a). Relative to the upper surface, the base of the biofilm contained higher cell densities, a lower percentage of live cells per unit biomass, and fewer pores with smaller pore diameters. These same authors (1994b) used biofilm porosity data and two models to determine effective diffusivities and tortuosity within biofilms. Modeling of biofilm processes in conjunction with empirical data also demonstrated that heterogeneity in biofilm thickness greatly influenced substrate-inhibited kinetics (Jih and Huang, 1994). de Beer *et al.* (1994) reported that flow-velocity gradients within bacteria biofilms were 50% of those measured adjacent to surfaces not supporting microbial growth. Tracking the transport of fluorescent latex spheres within these biofilms showed that liquid flowed freely through interstitial voids but was stagnant within microbial cell clusters.

Temporal and spatial variations in physiological activity within biofilms were studied by a number of authors. The processes of nitrification and denitrification in algal-colonized limnetic and estuarine sediments were found to be coupled during periods of illumination, whereas during dark periods, denitrification activity was driven primarily by nitrate supplied from the water column (Risgaardpedersen *et al.*, 1994). Joye and Paerl

(1994) noted significant seasonal and diel variation in nitrogen fixation and denitrification in sediments from exposed estuarine mudflats and vegetated marsh habitats. They emphasized the importance of determining integrated diel rates for both of these processes when constructing ecosystem nitrogen budgets. Prosperi (1994) determined that *Nostoc cordubensis*, a colonial cyanobacterium, was able to maintain nitrogen-fixation capabilities under high oxygen concentrations by virtue of copious mucilage produced by heterocysts.

Emerson and Revsbech conducted field (1994a) and laboratory (1994b) studies on microbial mats from natural iron seeps. Field studies quantified vertical changes in community structure and cell densities, oxygen profiles, and distribution of iron oxides. Laboratory studies quantified iron oxidation rates and growth stimulation by $FeCl_2$. Caumette *et al.* (1994) analyzed vertical changes in microbial composition and microprofiles of oxygen and sulfide in microbial mats from hypersaline ponds. Rates of sulfate reduction in these mats, which supported two new halophilic species of purple sulfur-oxidizing bacteria, were among the highest reported.

Lemmer *et al.* (1994) compared population density, community composition, and enzyme activities of sewer biofilms and activated sludges. Sewer biofilms exhibited high population densities and high enzyme activity. Electron transport system activity and biomass of a microbial community developing on aluminum plates in a marine bay increased with immersion time (Bhosle *et al.*, 1994).

Activity and distribution of attached bacteria. Bacterial activity and distribution in sediments were investigated by several authors. Kazumi and Capone (1994) measured bacterial activity (as glucose uptake and thymidine incorporation rates) in sediments of shallow sandy aquifers of Long Island, New York. Although overall bacterial activities were orders of magnitude lower than values in soil or surface sediment of marine and estuarine systems, the authors reported higher bacterial activity in shallow oxic sediments than in deep anoxic sediments. Rusterholtz and Mallory (1994) measured density, activity, and diversity of indigenous bacteria at two sites 100 m below the surface in Mammoth Cave National Park, Kentucky, and reported that the communities in the karstic sediments exhibited a high degree of diversity. The abundance and metabolic activity of microorganisms from four boreholes in Atlantic Coastal Plain sediments were examined (Phelps *et al.* 1994b). Regardless of depth, low permeability sediments that contained >20% clay particles exhibited much lower activities and biomasses than higher permeability sandy sediments.

In comparing the activity and distribution of free-living bacteria with particle-associated bacteria in the Chesapeake Bay, Griffith *et al.* (1994) demonstrated that free-living bacteria were responsible for most of the total bacterial production, whereas bacteria attached to degrading phytoplankton cells in the bottom waters demonstrated much higher metabolic activities. Alber and Valiela (1994) were able to produce organic aggregates containing large numbers of rod-shaped bacteria in the laboratory by bubbling dissolved organic material (DOC) derived from macrophytes. Size of the aggregates was related to the amount of DOC initially present, and large aggregates ingested by consumers could be a potentially important route for the flow of labile organic C in aquatic systems.

The degradation properties of bacteria in sediments were addressed by several authors. Arnosti and Repeta (1994) tested the degradation rates of structurally related oligosaccharides by anaerobic marine bacteria and found that substrate structural features can have a significant effect on degradation rates, even at molecular weights below the direct transport size limit. On investigating the enzymatic response of a natural deep sea (4 500 m depth) microbial community to input of organic matter, Boetius and Lochte (1994) found enzyme production to be proportional to the supply of organic matter for enzymes degrading structural polysaccharides (beta-glucosidase, chitobiase), whereas aminopeptidase activity was inhibited and no clear effect was found for enzymes degrading storage compounds (alpha-glucosidase and lipase). Toth *et al.* (1994) measured terminal electron transport system (ETS) activity in the sediment of Lake Balaton, Hungary, and demonstrated that at low temperatures, ETS can remain active days after death of microorganisms. These authors suggested that the high respiratory potential in the upper 3–5 cm of sediments in springs may contribute to the rapid oxidation of the lake.

Distribution and function of aquatic fungi. Several authors investigated decay rates of leaves submerged in aquatic ecosystems and the associated fungal communities. Rates of leaf litter decay on seven leaf species of different lignin, tannin, nitrogen, and phosphorus content were assessed in a soft-water mountain stream (Gessner and Chauvet, 1994). The initial lignin content of leaves was most strongly correlated to leaf litter breakdown rate, whereas nitrogen and phosphorus were poor predictors of litter decomposability. Griffith and Perry (1994) investigated fungal biomass and leaf litter processing in four streams of differing pH and alkalinity. Processing rates were highest at pH 6.0, lowest at pH 4.3, and intermediate at pH 7.5. Submerged red, black, and white mangrove leaves were collected and treated so that oomycotes could be isolated (Newell and Fell, 1994). *Halophytophthora spinosa* and *H. vesicula* were the dominant species found on white and red mangroves, whereas an undescribed species of *Halophytophthora* was commonly found on black mangrove leaves. Essafi *et al.* (1994) compared breakdown rates of leaves buried 20 cm in the sediment with leaves at the sediment surface within a Morrocan stream. Buried leaves decomposed at rates similar to surface leaves in invertebrate-poor reaches of the stream, whereas shredder-rich stream sites produced higher surficial decay rates. Howe and Suberkropp (1994) analyzed the effects of Isopoda (*Lirceus* sp.) shredding on the species richness and sporulation rates of aquatic hyphomycetes that colonized tulip poplar leaves by placing leaves in fine- (shredder excluded) and coarse-meshed (shredder included) bags. Although overall leaf decay rates were enhanced in the presence of *Lirceus*, species richness and respiration rates of the microbial communities were not significantly different.

Viability of aquatic hyphomycete conidia in foam was estimated to be 76–91% in fresh foam and 20–43% in old foam (Sridhar and Bärlocher 1994). Sugiura *et al.* (1994) reported two isolates of *Streptomyces* spp. that can effectively use the cyanobacteria *Microcystis aeruginosa* and *Anabaena spiroides* and the diatom *Synedra acus* as carbon sources to produce a musty-smelling 2-methylisoborneol byproduct.

Interactions between nutrients and microbenthos. The nutritional interaction of microorganisms associated with plants or animals was explored by several researchers. Jackson *et al.* (1994) estimated the bioaccumulation factors of essential and nonessential elements being transferred from sediments by *Myriophyllum spicatum* to epiphytic algae. Accumulation of both types

of elements was not significantly different between epiphytes and macrophyte shoots, suggesting that buried nonessential elements may be reintroduced to the littoral food web by epiphyte grazing. Neely (1994) reported that the presence of epiphytes enhanced bacterial decomposition rates of senescent *Typha latifolia* by autotrophic oxygen and/or dissolved organic carbon release. Carman (1994) suggested that the amino acids and ammonia excreted by high density copepod aggregates may significantly stimulate bacterial activity, and epibiotic bacteria living on copepods may be optimally positioned to exploit these resources. The nutritional interaction in an alga-barnacle association was studied by Williamson and Rees (1994), who suggested that the barnacle is an important source of nitrogen for algae in midintertidal reefs of northeastern New Zealand.

Effects of nutrient amendments to aquatic habitats were assessed in a number of papers. Gabor *et al.* (1994) studied the effects of a single application of either high, low, or organic nitrogen and phosphorus to plankton, periphyton, and invertebrates in a series of experimental wetland enclosures in Manitoba. Phytoplankton biomass increased in all fertilized enclosures, epipelon increased in the organic treatment, metaphyton standing crops were highest in the inorganic treatments, and epiphytic periphyton exhibited only minor responses in all treatments. In a similar study conducted in the same interlake region of central Manitoba, Murkin *et al.* (1994) fertilized wetland enclosures biweekly for 4 months using low, intermediate, and high inorganic nitrogen and phosphorus. Although these wetlands were relatively unproductive, the addition of nutrients stimulated only phytoplankton, epiphytic periphyton, and metaphyton community biomasses but did not affect epipelon biomass, algal productivity, or invertebrates. Nutrient-diffusing clay pots containing different combinations of nitrogen, phosphorus, silicon, and carbon were used to investigate nutrient limitation of algal abundance in a softwater oligotrophic lake in Florida (Barnese and Schelske, 1994). Results suggested that nitrogen and carbon were the limiting factors to algal growth; however, treatments with combined nitrogen and carbon amendments resulted in lower algal diversity and dominance by coccoid green algae and *Scenedesmus*. Hepinstall and Fuller (1994) manipulated light and nutrients in a second-order stream and determined that bacterial abundance was positively correlated with algal abundance, suggesting that bacteria within the biofilm may rely on algal exudates for growth.

In a water column nitrate enrichment study of epiphytic microalgae on eelgrass in experimental mesocosms, Coleman and Burkholder (1994) demonstrated a stimulation of blue-green algae after 3 weeks in moderate nitrate levels and a stimulation of community productivity at low and moderate nitrate levels after 6 weeks, a response produced mostly by larger diatoms. Biggs and Lowe (1994) conducted a benthic survey and two experiments at eight sites in the Kakanui River, New Zealand, to investigate the interaction between nutrients, periphyton, and macrograzers. Nutrient enrichment generally stimulated macrograzer production while leaving chlorophyll *a* levels unchanged, suggesting a tight coupling between first and second trophic levels and strong grazer control of periphyton in this river. Lijklema (1994) discussed the potential for fluxes of nutrient pools between water bodies, sediments, and soils to impact long- and short-term productivity of aquatic systems. Ghosh and Gaur (1994) used nutrient-diffusing clay pots to study the effect of periphytic algal colonization at low, moderate, and high current velocities in an unshaded Indian stream. Phosphorus enrichment enhanced filamentous green algal biomass but only at low flows. Nutrient-diffusing clay pots were also used by Nord and Toetz (1994) to assess nutrient limitation in a stream impacted by agriculture and silviculture. Although the biofilms on clay pots indicated nitrogen limitation, nitrogen:phosphorus supply ratios indicated phosphorus limitations during 1 year. The authors suggested that high turbidity and high discharge fluctuations in impacted streams can influence nutrient limitation factors.

Nutrient uptake dynamics of algae were addressed by a few authors. Portielje and Lijklema (1994) described how the luxury uptake of phosphate by algae-dominated benthic communities demonstrated first-order kinetics with respect to the intracellular phosphorus-deficit. The maximal storage capacity of phosphorus per unit dry weight was positively correlated to the level of external nutrient loading. Fong *et al.* (1994) constructed a useful simulation model to explore the importance of resource competition among three algal community functional forms: phytoplankton, foliose algae, and cyanobacterial mats. Analysis of model behavior indicated that a two-step model uncoupling nutrient uptake and growth (using a nutrient storage term) provided most accurate results when the model was validated with three field experiments from published literature. Kjeldsen (1994) used a database from the Danish Nationwide Research Programme on Nitrogen, Phosphorus, and Organic matter to determine the relationship between phosphorus and peak biomass of benthic algae in small lowland streams. He reported that phosphorous played a major role in algal regulation on fine-grained sediments but that other regulatory factors were of greater importance on stony substrata. Upon examination of the inorganic phosphorus uptake kinetics of *Spirogyra fluviatilis* as a function of current velocity, Borchardt *et al.* (1994) described a complex relationship where the effects of current velocity on phosphorus uptake were varied and not always beneficial. Similarly, Borchardt (1994) published the effects of flowing water on nitrogen and phosphorus-limited photosynthesis and optimum nitrogen:phosphorus ratios by *S. fluviatilis* and suggested that flowing water is physiologically costly for nitrogen- or phosphorus-limited *S. fluviatilis*, whereas growth was not diminished at high velocities when phosphorus was available.

Several authors investigated the role of aquatic microbiota in nutrient cycling. Alongi (1994) stressed the significance of the role of bacteria in tropical mangrove ecosystems as mineralizers and recyclers of essential nutrients. Whereas in most benthic aquatic ecosystems bacteria have a large trophic role as food for protists and invertebrates, in mangrove and other tropical coastal benthic ecosystems, bacterial death by consumption seems to be less common than natural mortality. Mulholland *et al.* (1994) investigated the effect of periphyton biomass (high biomass, without snail grazers; low biomass, with snails) on hydraulic characteristics and nutrient cycling in laboratory streams. High biomass communities altered the hydraulic characteristics of streams by increasing zones of stationary water, thereby decreasing diffusion of nutrients to cells that resulted in overall lower phosphorus uptake than in low density communities.

Photosynthesis and the effects of irradiance. A group of scientists developing a fiber-optics microprobe for measuring irradiance within sediments and microbial mats published some of their work. The manufacture of a new fiber-optic irradiance microsensor for use in sediments and microbial mats was dis-

cussed by Lassen and Jörgensen (1994). These authors stressed the importance of measuring the appropriate light parameter when photobiological processes in sediments are investigated and when the application of scalar irradiance and irradiance as a quantitative measure of available light for photosynthesis are studied. Similarly, Kuhl *et al.* (1994) used this fiber-optic microprobe to determine irradiance and scalar irradiance in sandy sediments of different particle size. Intense scattering caused a maximum integral light intensity at the sediment surface ranging from 180% of incident light in the coarsest sediment to 280% in the finest sediment; light penetration into the sediments was greater for larger particles. Kuhl and Jorgenssen (1994) further described the radiance distribution and microscale optics of sandy coastal sediments.

The effects of light on sponge-algal interactions were discussed in two papers. Gaino and Sara (1994) suggested that the sponge *Tethya seychellensis* could use its siliceous spicules as a natural pipeline for light, similar to fiber-optic systems, to support the growth of filamentous green algae deep within the sponge body. Alternately, Sandjensen and Pedersen (1994) described the strong light attenuation within the sponge tissue of *Spongilla lacustris* that limits photosynthesis of symbiotic zoochlorellae unless exposed to very high light intensities. These authors suggested that filtration of particles from these light-limited streams was probably needed to support the prolific growth of *S. lacustris* observed.

Friberg and Kjeldsen (1994) described the light-limiting effects of terrestrial leaf canopies on small forest streams in Denmark. Although light was less limiting to periphyton of deciduous forest streams before leaves emerged in the spring, light was consistently limiting throughout spring and summer in coniferous forest streams. Photosynthesis-irradiance parameters were estimated for microphytobenthos at the sediment-air interface of an intertidal mudflat during low tide (Blanchard and Cariou-Le Gall, 1994). There was no indication of a photo-inhibitory effect *in situ*, which, the authors suggest, could be due to the strong attenuation of light within the sediment, self-shading within algal mats, motility of microalgae, and bioturbation.

Bothwell *et al.* (1994) conducted an eloquent study assessing the effects of UVB radiation on benthic stream trophic-level interactions. Although UV radiation can reduce the growth of benthic diatom communities in shallow freshwater systems, greater biomasses of algae tend to accumulate in UV-exposed habitats than in UV-protected environments because UVB radiation inhibits algal consumers (Diptera: Chironomidae).

Napolitano (1994) demonstrated changes in chlorophyll *a*, triacylglycerols, and phospholipids but stability of sterol concentrations in *Chladophora* and *Spirogyra* in response to changes in irradiance, demonstrating the usefulness of sterol measurements as a predictor of eukaryote biomass. Further, light-induced changes in algal lipids and fatty acids have important implications for grazer food quality.

Herbivory. Several authors addressed methods for measuring protist grazing rates on bacteria. Salat and Marrase (1994) developed a method to calculate grazing on bacteria determined by the disappearance of marked cells or particulates. In comparing an exponential model with two linear approaches, the authors concluded that the exponential model based on population dynamics demonstrated the strongest fit. The relative importance of methodology, temperature, bacterial abundance, and protist abundance in determining the rates of protist grazing on bacteria was examined by Vaque *et al.* (1994). Multiple datasets extracted from the literature that used different measurement techniques under different ecological parameters were compared, and each of these variables was found to affect the grazing rates that were estimated. Starink *et al.* (1994) described a new method using 5-(4,6-dichlorotriazin-2-yl)-aminofluorescein-stained sediment to measure *in situ* bacterivory by benthic protists and reported that their method produced grazing rates about twofold higher than the widely used monodispersed fluorescently labeled bacteria method.

Bacterial grazing by macroinvertebrates was addressed in two papers. Bacterial production in surficial sediments was enhanced in microcosm experiments at high amphipod, oligochaete, or chironomid densities because of increased oxygen penetration into the sediments resulting from deposit-feeder activities (van de Bund *et al.*, 1994). Although *Tubifex tubifex* feeding activities negatively affected bacterial abundance, the surficial feeding activities of *Monoporeia affinis* and *Chironomus riparius* resulted in a compensation of bacterial cell losses. The capacity of a bryozoan to feed on bacteria was demonstrated for the first time by Richelle *et al.* (1994).

Selective herbivory by macroinvertebrates was assessed by a number of authors. Feeding selectivity on periphyton, detritus, nettle broth, and periphyton with moss by five epilithic case-building trichopteran species was examined (Becker, 1994). Resource partitioning was demonstrated by these trichopteran species; three species preferred periphyton and one of these preferred to graze on epiphytes on moss, two species selected detritus, and all but one species avoided the nettle broth. Gresens and Lowe (1994) generated four algal patch types using nutrient diffusing clay pots and determined the feeding preference of the chironomid *Paratanytarsus dubius* by observing dispersal of larvae among patches of differing periphyton composition. Patch preference of larva was negatively correlated with *Stigeoclonium* abundance, chlorophyll *a*, and algal biovolume and positively correlated with algal diversity. The feeding of amphipods on the brown macroalga *Zonaria angustata* demonstrated a selective preference for the meristematic tissue at the apex of each branch of the macroalga over the abundant microalgal epiphytes (Poore, 1994). Creed (1994) demonstrated the complex role of keystone consumers that large crayfish play in a small Michigan stream. Crayfish, which tend to prefer deeper waters, feed on the filamentous alga *Cladophora glomerata*, thereby indirectly facilitating epilithic diatoms and sessile grazing insects there, a community not found in the shallower waters where *Cladophora* remains ungrazed. McCormick (1994) evaluated the multiple mechanisms that underlie herbivore-algal interactions in streams and suggested that ambient environmental conditions (for example, nutrient concentrations and physical disturbance histories) can greatly affect the outcome of algal-herbivore interactions in ecosystems with pronounced temporal and spatial variation in biotic and abiotic conditions. Pan and Lowe (1994) investigated the independent and interactive effects of phosphorus addition and grazing by *Helicopsyche* and *Baetis*. Nutrient amendment alone stimulated diatom growth and produced a dominance of the erect diatom *Synedra ulna*, which was most vulnerable to grazer impact when herbivores were introduced.

Although densities of the deposit-feeding gastropod *Rhinoclavis aspera* did not affect biomass of microalgae in coral-reef-flat sediments of the Great Barrier Reef, bacterial productivity was significantly correlated with *R. aspera* densities (Hansen and Skilleter, 1994). Hentschel and Jumars (1994) selectively

eliminated diatoms from benthic sediments by using an herbicide to demonstrate that the meiofaunal oligochaete *Amphichaeta leydigii* and juveniles of the polychaete *Hobsonia florida* (whose adults deposit feed) share benthic diatoms as a limiting resource during recruitment. To test whether plant litter in freshwater marshes served mainly as cover for invertebrates and a substrate for algal growth rather than as a direct source of invertebrate nutrition, Campeau *et al.* (1994) replaced hardstem bulrush litter with a nonnutritive artificial substrate and fertilized within the enclosures. Epiphytic herbivores-detritivores responded to changes in both detritus and algal food sources, with longer term enhancement effects exemplified by increased chironomid emergence. Goedkoop and Johnson (1994) measured the exploitation of sediment bacterial carbon by juveniles of the amphipod *Monoporeia affinis* and determined that bacterial carbon was not quantitatively important to the amphipod, accounting for only 1.7–5.2% of overall amphipod carbon demand; low amphipod ingestion rates are suggested to limit absorption of this carbon resource. Snail grazers demonstrated density-dependent reductions in grazing rate at densities above 16 individuals/m^2 (Brown *et al.*, 1994). Radioisotope experiments suggested that both assimilation efficiency and respiratory costs increased in the snails at higher densities. Carman and Guckert (1994) determined that ^{14}C-bicarbonate assimilated by periphytic algae was a reliable tracer for determining grazing activity on the algal component of periphytion, whereas tritiated amino acids tend to differentially adsorb to components of the periphyton and detritus, resulting in a less optimal method for determining grazing activity on microbes.

Ecological and taxonomic surveys. Studies of morphological variability and ecological requirements of diatom flora in four different regions were published in 1994. Pipp and Rott (1994) performed a cluster analysis on periphyton data from 137 reaches of 54 streams from the western mountainous part of Austria. Algal species were grouped by altitude, disturbance to the stream site, and water chemistry. Fifty-six diatom species from aquatic and subaerial habitats in the Papaloapan basin, Mexico, were reported and described by Tavera *et al.* (1994). Vinocur *et al.* (1994) reported the distribution of diatom flora (173 taxa) from the Saldo River and associated shallow lakes, including illustrations of 15 new records for Argentina. Alhandal (1994) reported 116 diatom species containing a mixture of fresh- and brackish-water taxa from Sawa Lake, a brackish water basin in south Iraq. Coute and Therezien (1994) used a large number of scanning electron micrographs and photographic plates to describe 23 species of Euglenophytes collected from the Bolivan Amazon.

Wong and Beebee (1994) described a new species of nonpigmented unicellular Chlorophyte within the genus *Prototheca* isolated from the feces of a British anuran tadpole. This species, which is associated with growth inhibition in the tadpole, was compared antigenically with the five previously recognized species of *Prototheca*. Three diatom species, formerly of the genus *Navicula* (*N. ulvacea*, *N. subinflata*, and *N. expecta*), were placed into a reestablished genus, *Dickieia*, by Mann (1994), who discussed the evolutionary relationship of this genus and described auxospore formation, reproductive plasticity, and cell structure.

Miscellaneous. Cell motility was discussed in two papers. The effects of pH, osmolarity, and presence of the chelating agent, EDTA, on motility in the diatoms *Craticula cuspidata*, *Nitzschia* spp., and *Stauroneis* spp. were studied by Cohn and Disparti (1994). In contrast to published reports on marine diatoms, these freshwater taxa do not require calcium in the external media for motility, but these authors suggested that regulation of internal calcium stores may be important in motility. Beatson and Marshall (1994) used phase-contrast microscopy and videotaping to gather evidence that a rotational gliding pattern observed in strains of *Cytophaga* bacteria is produced by machinery oriented helically on the cell surface and likely involves interaction with the substratum via an adhesive polymer network.

Goodman *et al.* (1994) summarized the evidence for the occurrence of gene transfer by conjugation, transformation, and transduction among nongrowing bacteria in nutrient depleted environments. The occurrence of this phenomenon has only been generally accepted for cells in nutrient-rich media. Different morphotypes of bacteria collected in the Adriatic Sea differed substantially in their propensity for infection by bacteriophage viruses, with rods, cocci, and spirillae showing infection percentages of 27%, 79%, and 100%, respectively (Weinbauer and Peduzzi, 1994).

Hollow balls, composed of monospecific or multispecies assemblages of algae, were described by Ballantine *et al.* (1994) from the Caribbean Sea off Venezuela. These structures contained, and perhaps imprisoned, a large variety of invertebrates, including polychaetes, sipunculans, molluscs, and crustaceans. Crystalline evaporites from the shore of an evaporation pond in Baja California, a habitat typically considered too hostile to support life, contained metabolically active cyanobacteria (Rothschild *et al.*, 1994). Srikanth and Berk (1994) discovered that amoebae-inhabiting cooling towers developed resistance to four different biocides when exposed to subinhibitory concentrations of these chemicals. Moreover, these authors documented the phenomenon of cross-resistance, in which exposure to one biocide generates resistance to other biocides.

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Effects of pollutants on freshwater organisms

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A myriad of "pollutants" enter freshwaters from innumerable sources, and their effects on aquatic life are exhibited from the cellular to ecosystem levels. Much research has been published in these areas. This paper reviews some of the published research on the effects of chemicals on freshwater organisms.

METALS

Both growth inhibition and bioaccumulation of aluminum in the green alga *Chlorella pyrenoidosa* was studied by Parent and Campbell (1994) in soft water media. The results of these studies showed that aluminum bioavailability was predictably a function of the free aluminum ion in systems containing only inorganic monomeric aluminum, and the effect of aluminum on algal growth is highly pH dependent. *Hydrilla verticillata* was used to evaluate the usefulness of peroxidase activity as an indicator of rooted plant exposure to metabolic and organic contaminants (Byl *et al.*, 1994). Significant increases in this endpoint were observed as a result of exposure to 0.01 mg/L cadmium, copper, and chromium; 0.1 mg/L selenium; and 1.0 mg/L manganese. Tubbing *et al.* (1994) tested the hypothesis that the concentration of free copper metal ions is the main determinant of metal toxicity by adding different concentrations of copper to water from the River Rhine and measuring the effect on the photosynthetic rate of the alga *Selenastrum capricornutum*. Addition of 5 μM copper to the medium with 5 or 10 μm of EDTA inhibited algal photosynthesis, although copper was not voltametrically detectable (<0.005 μM). *Lemna minor* (duckweed) was grown in treated domestic wastewater containing added copper to study the relationship between complexation and bioavailability of copper (Buckley, 1994a). Measurement of the copper Complexing Capacity (CC) of the wastewater gave values of 0.26 to 0.29 mg/L. Growth was not inhibited until total copper exceeded 0.079 to 0.119 mg/L. Effective Concentrations (ECs) based on tissue concentration of copper rather than solution concentration are more sensitive and have been proposed as an alternative for work in complex solutions like wastewater. A particular effect of copper on duckweed was observed by Buckley (1994b) in the activity inhibition of the enzyme superoxide dismutase (SOD) in *Lemna minor* containing 408 μg Cu/g (dry wt) but not in plants containing 215 μg Cu/g (dry wt) or less. The presence of copper in a planktonic community caused a reduction in the dry-weight biomass of zooplankton, ciliates, flagellates, and phytoplankton (Havens, 1994a). Copper also reduced the effectiveness of the food web in transporting carbon to the surviving zooplankton.

Water hyacinths exposed to water containing 2μg Cd^{2+}/mL bioconcentrated the element mainly in the roots and in proportion to the increase of the thiol group content (Ding *et al.*, 1994). This suggests the possibility of using the thiol group content to assess the bioconcentration of heavy metal ions in water hyacinths and as a general parameter for monitoring heavy metal pollution. Dirilgen and Inel (1994) investigated the effects of combined zinc and copper concentrations on the growth and degree of metal accumulation in duckweed, *Lemna minor*, under laboratory conditions. Duckweed was selected for study because of its rapid growth and ability to adapt to aquatic conditions. The effects of increased concentrations of zinc and copper in combination were correlated with the corresponding relative growth rates (RGR), dry to fresh weight ratios (DFR), and concentrations of metal accumulated by the duckweed. The level of zinc accumulated in the plant was higher than the copper concentration accumulated in every concentration tested. At the concentrations of 0.10 to 2.00 ppm, zinc suppressed the