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Epilithic bacterial and algal colonization in a stream run, riffle, and pool: a test of biomass covariation

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Abstract

Epilithic bacterial and algal biomass were compared among a run, riffle, and pool along an open-canopy section of a third-order, temperate stream. Epilithic biofilms were sampled after 3, 7, 14, 21, 28, and 35 days colonization on unglazed ceramic tiles that were attached to plastic trays ($n = 3$) placed across each of the three habitats (i.e., run, riffle, pool). The diverse habitats and sampling regime were selected to provide a range in algal biomass so that potential covariation between epilithic bacterial and algal biomass could be assessed. There were significant differences among habitats and among trays within each habitat for both chlorophyll *a* and AFDM. Chlorophyll *a* and AFDM increased in the run and pool throughout the colonization period. In the riffle, chlorophyll *a* and AFDM increased rapidly early in colonization, then decreased. Epilithic bacterial biomass increased rapidly with no significant differences among the three habitats throughout colonization. Further, bacterial biomass did not correlate with either chlorophyll *a* or AFDM in any of the three habitats or on any of the sampling days. These results suggest that epilithic algal and bacterial biomass may be regulated by independent controls in some stream environments.

Introduction

Planktonic bacteria and algae frequently covary in freshwater and marine habitats (see reviews by Cole et al., 1988; White et al., 1991; Sander & Kalff, 1993), but covariation between epilithic bacteria and algae in stream biofilms is less certain (see review by Lock, 1993). Both phytoplankton biomass (e.g., chlorophyll *a*) and productivity are reliable predictors of bacterioplankton abundance and growth rates across planktonic systems. Phytoplankton are generally thought to function as a substrate for bacterioplankton growth, as opposed to simply covarying in response to a common environmental factor (Cole, 1982; Cole et al., 1988). Unlike planktonic bacteria, benthic bacteria in small lakes appear largely uncoupled to autochthonous carbon inputs (i.e., planktonic algal biomass); relying instead on allochthonous carbon inputs (i.e., terrestrial organic matter) (Schallenberg & Kalff, 1993). The relative contribution of autochthonous vs. allochthonous carbon in regulating epilithic bacteria in streams is unclear. Several studies have documented algal-bacterial linkages in epilithic biofilms in stream ecosystems (e.g., Haack & McFeters, 1982a; Kaplan & Bott, 1989; Stock & Ward, 1989), however the generality of such linkage remains debated (Couch & Meyer, 1992; Findlay et al., 1993; Lock, 1993).

Stream biofilms consist of a diverse assemblage of autotrophic and heterotrophic microorganisms incorporated into a polysaccharide and glyco-protein matrix on stream substrates (Lock, 1981; Lock et al., 1984). Epilithic biofilms play fundamental roles in stream primary production, secondary production, decomposition, and nutrient retention (see review by Lock, 1993). Epilithic biofilm colonization can vary considerably among habitats in which physical (Stevenson, 1983; Steinman & McIntire, 1986; Sinsabaugh et al., 1991),

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chemical (Mulholland et al., 1986; Pringle, 1990; Freeman et al. 1990), and biological (e.g., invertebrate grazing) (Rounik & Winterbourn, 1983; Mulholland et al., 1991; Hax & Golladay, 1993) conditions vary.

Two particularly important physical parameters in structuring the autotrophic component of epilithic biofilms are light availability and water velocity. Generally, declines in light availability will decrease algal biomass (Fuller et al., 1986) and alter algal assemblages (Stevenson & Stoermer, 1981). Differences in water velocity can also alter algal biomass accrual (Poff et al., 1990) and composition (Peterson & Stevenson, 1992), but relationships are less clear. Regardless, epilithic biofilms colonizing habitats that have different water depth and velocity regimes are predicted to have dissimilar algal assemblages (Korte & Blinn, 1983).

Our understanding of controls on the heterotrophic component of epilithic biofilms is less developed. Heterotrophic bacteria are often carbon limited, thus growth responses are frequently attributed to the availability of algal exudates during algal growth or lysis (Cole et al., 1988). Epilithic (heterotrophic) bacterial growth in streams can be supported by a variety of carbon sources: algal exudates in the water column (Kaplan & Bott, 1989), algal exudates within biofilms (Stock & Ward, 1989), algal lysis (i.e., senescent cells) (Haack & McFeters, 1982), allochthonous dissolved organic carbon (DOC) (Findlay et al., 1993), and the biofilm's polysaccharide matrix (Freeman & Lock, 1995). The physical proximity of algal and bacterial cells within epilithic biofilms suggests that algal biomass and bacterial biomass should covary if there is a trophic linkage between the two (Lock, 1981). Although a positive relationship between algal biomass and bacterial biomass is well documented in planktonic systems, evidence for a similar relationship in stream biofilms is limited.

We examined epilithic biofilm colonization in an adjacent stream run, riffle, and pool in which water depth and velocity significantly differed. Specifically, we examined bacterial biomass and algal biomass and composition among the three habitats throughout a five week colonization period. Studies investigating algal-bacterial linkages in aquatic ecosystems frequently establish a range in algal biomass by surveying a large number of systems (e.g., Cole et al., 1988) or relying on annual variance within a single system (e.g., Haack et al., 1988). This study was designed to provide a range in algal biomass within a single stretch of stream during a single colonization period, thus enabling us to evaluate covariation between epilithic algal and bacterial biomass in the absence of confounding stream-specific and seasonal environmental factors. We hypothesized that epilithic bacterial biomass would positively covary with epilithic algal biomass, regardless of habitat or colonization time, due to a trophic linkage.

Materials and methods

Study area and sampling procedure

Field work was conducted at a third-order, open-canopy section of the Ford River (Michigan, USA) in July and August 1991. The Ford River arises in northern Dickinson and southern Marquette Counties and enters the Michigan portion of Green Bay south of Escanaba, Michigan. The majority of the watershed contains deciduous forests that are dominated by balsam poplar (*Populus balsamifera*) and speckled tag alder (*Alnus rugosa*). The Ford is a hardwater river with a summer discharge of 1.8 $m^3 s^{-1}$ and moderately low concentrations of nitrate (78 $\mu g\ l^{-1}$) and soluble reactive phosphorus (4.9 $\mu g\ l^{-1}$) (see Eggert & Burton, 1994). Unglazed ceramic tiles (6.5 cm^2) attached to plastic trays with silicon served as the substrate for biofilm colonization. Epilithic algal assemblages which colonize ceramic tiles have been shown to be representative of assemblages which colonize natural substrates (Tuchman & Stevenson, 1980; Lamberti & Resh, 1985). Each tray was secured to a partially-buried cinder block. Trays were arranged perpendicular to flow across an adjacent run, riffle, and pool within a 10 m section of stream. Three trays were placed across each habitat (see Figure 1). Tiles were randomly removed from each of the nine trays after 3, 7, 14, 21, 28, and 35 days of colonization for ash-free dry mass (AFDM) ($n=3$), chlorophyll *a* ($n=3$), bacterial biomass ($n=3$), and diatom relative abundance ($n=3$) estimates. Tiles were transported to the laboratory in individual Whirl-Pak Bags® that were wrapped in foil and placed on ice. Current velocity (using a Marsh-McBirney Model 2000 portable flowmeter) and depth were measured at each tray on each sampling day. The three habitats had contrasting depths (run, mean = 23 cm; riffle, mean = 10 cm; pool, mean = 50 cm) and flow velocities (run, mean = 8 cm s^{-1}; riffle, mean = 50 cm s^{-1}; pool, mean = 2 cm s^{-1}) throughout the study. Trays within each habitat had similar depths (run, CV = 5.2%; riffle CV = 14%;

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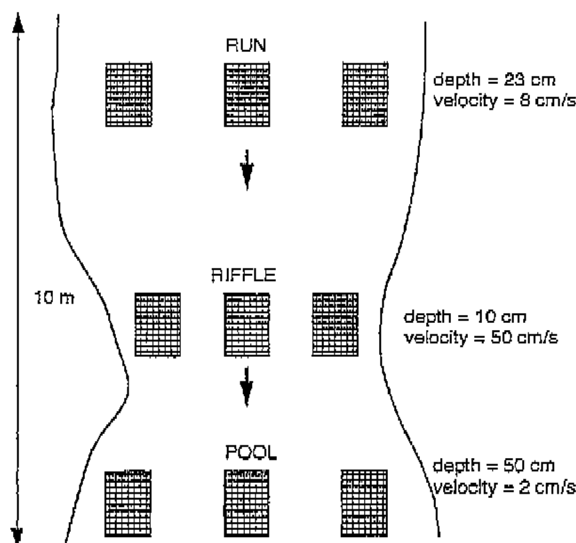

Figure 1. Schematic diagram of study site on Ford River which highlights the spatial proximity of the three habitats (i.e., run, riffle, pool). Checkered squares represent trays lined with sampling tiles. Mean depth and velocity for each habitat is presented ($n = 6$ sampling dates).

pool = 7.2%) and water velocities (run, CV = 10%; riffle, CV = 11%; pool, CV = 30%).

Laboratory protocol

Chlorophyll *a* – Upon returning to the laboratory Whirl-Pak Bags® containing tiles were removed from ice and frozen for 24 h. Buffered 90% acetone was added to each Whirl-Pak Bag® to extract pigments and filtered for fluorometric analysis. Chlorophyll *a* was then determined by the procedures outlined in Methods 1003C and 1002G in *Standard Methods* (APHA 1985) and converted to μg cm^{-2}.

AFDM – Tiles were stored frozen within individual Whirl-Pak Bags®. The difference between dry weight (24 h at 60 °C) and ashed weight (1 h at 450 °C) was measured.

Diatom relative abundance – Tiles were scraped with a razor blade and rinsed with filtered water (pore size = 0.22 μm). Samples were homogenized and preserved in 5% formalin. 1 ml sub-samples were pipetted onto 22 mm^2 glass coverslips. The coverslips were air dried and permanently mounted on glass slides using Hyrax medium. Tiles from each tray were pooled and >250 valves per tray were counted for colonization days 7, 21, and 35.

Bacterial biomass – Field-preserved (5% formalin) samples were scraped with a sterile razor blade, homogenized with a tissue grinder, and returned to Whirl-Pak Bags®. Sub-samples were stained with DAPI (4'6-diamidino-2-phenylindole, 20 μg ml^{-1}; to yield a final concentration of 2 μg ml^{-1}). Stained subsamples were filtered onto polycarbonate membrane filters (pore size = 0.2 μm). Bacteria were observed with a Leitz Laborlux II microscope, equipped with an HBO 50W mercury light source. Two sub-samples from each tile were counted for days 3 and 7. On subsequent days (14, 21, 28, and 353, one sample was counted per tile. At least 20 cells were counted/field; 10 fields were counted for each sample. Biomass estimates were made by dividing cells into ten size classes (2 cocci, 4 narrow rods, and 4 wide rods) using a micrometer (Haack et al., 1988). Cell volumes were calculated using simple geometric shapes. Volumes of cocci were calculated as spheres, and rods were assumed to be cylinders capped with half spheres. Bacterial biomass was estimated as μg C cm^{-2} by multiplying mean number of cells cm^{-2} × mean weighted-cell volume of all cells of that sample × (5.6×10^{-13} g C μm^{-3}) (Bratbak, 1985; Haack et al., 1988).

Statistical analysis

Repeated measures, nested ANOVAs (nested ANOVARs) were conducted to test the main effects of habitat (i.e., run vs. riffle. vs. pool) and trays within habitat, throughout colonization for three separate dependent variables: AFDM, chlorophyll *a*, and bacterial biomass. For the nested ANOVARs, tiles ($n = 3$) were 'nested' into trays ($n = 3$), and trays were 'nested' into habitat ($n = 3$). Post-hoc tests on pairs of means using Tukey's HSD procedure were conducted when significant ($p < 0.05$) main effects for habitat were detected. Regressions were performed for individual sampling days ($n = 6$) and habitats ($n = 3$) in which bacterial biomass was the dependent variable and either chlorophyll *a* or AFDM served as the independent variable. Data were natural-log transformed in the analysis of habitats due to increased variance through colonization time. Statistical analyses were performed with SYSTAT 5.12 (Wilkinson, 1989).

Table 1. Results of nested ANOVARs for the following dependent variables: chlorophyll *a* (Chl. *a*), AFDM, and bacterial biomass (BB). Tiles ($n = 3$) are nested into tray. Trays ($n = 3$) are nested into habitat (i.e., run, riffle, pool). Repeated measures combine sampling days ($n = 6$). A decomposition of the source of variance 'trays' is provided to illustrate variance within each habitat. Statistics designated by * = $p < 0.05$; ** = $p < 0.01$.

Source of variation	(df)	Nested ANOVAR *p* value		
		Chl. *a*	AFDM	BB
Between subjects				
Tray(run)	2	0.012*	0.001**	0.998
Tray(rime)	2	0.007**	0.005**	0.489
Tray(pool)	2	0.002**	0.013*	0.095
Habitat	2	0.031*	<0.001**	0.471
Error	18			
Within Subjects				
Time	5	<0.001**	<0.001**	0.003**
Tray(run) × Time	10	0.022*	0.005**	0.956
Tray(riffle) × Time	10	0.001**	0.010**	0.202
Tray(pool) × Time	10	<0.001**	<0.001**	<0.001**
Habitat × Time	10	<0.001**	<0.001**	0.006**
Error	90			

Table 2. Post-hoc tests on pairs of means using Tukey's HSD procedure for habitats from nested ANOVARs in which a significant ($p < 0.05$) habitat main effect was detected. NS denotes $p > 0.05$.

Dependent Variable	Comparison	*p* value
Chlorophyll *a*	run vs. riffle	NS
	run vs. pool	NS
	riffle vs. pool	<0.05
AFDM	run vs. riffle	<0.01
	run vs. pool	<0.05
	riffle vs. pool	NS

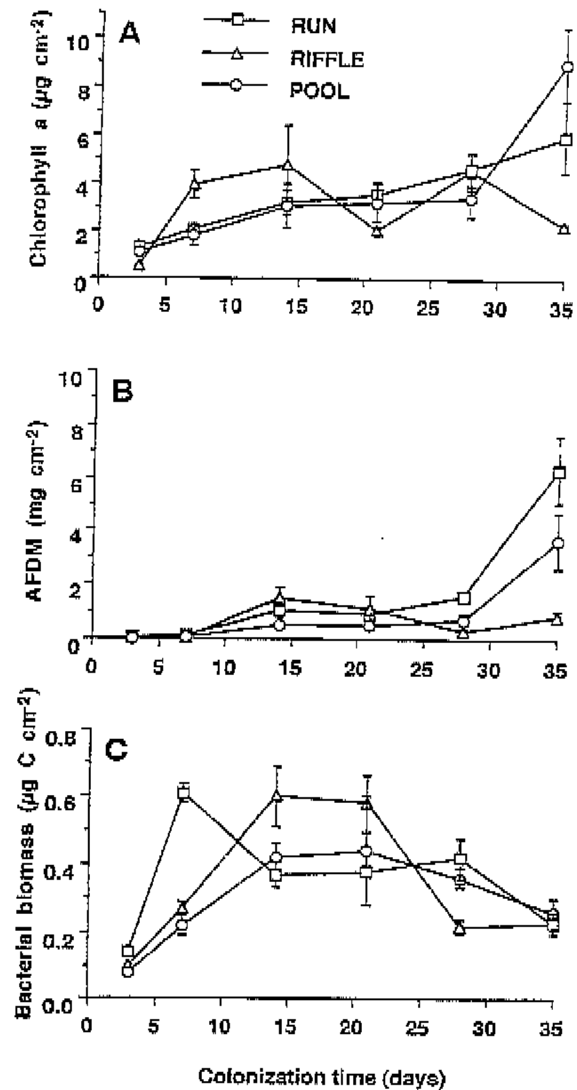

Figure 2. Chlorophyll *a* (A), AFDM (B), and bacterial biomass (C) in the run, riffle, and pool habitats through colonization time. Symbols represent means of trays within each habitat ($n = 3$) ± 1 SE.

Results

Chlorophyll *a* increased significantly ($p<0.05$) throughout colonization in all three habitats (Table 1, Figure 2A). Chlorophyll *a* increased steadily through colonization in both the run and pool, and increased rapidly and oscillated in the riffle (Figure 2A). Significant differences ($p<0.05$) were found among trays within all three habitats (Table 1). A significant ($p<0.05$) habitat main effect was detected as well (Table 1). Post-hoc tests on pairs of overall means from the habitats using Tukey's HSD revealed a significant ($p<0.05$) difference between riffle vs. pool (Table 2), however this significant difference is due to differences on day 35.

The epilithic algal community was dominated by diatoms throughout colonization, except on day 35 in the run and pool. Diatom composition varied among habitats, and within habitats through colonization time (Figure 3). *Achnanthes minutissima* and *Cocconeis placentula* dominated diatom relative abundance in all

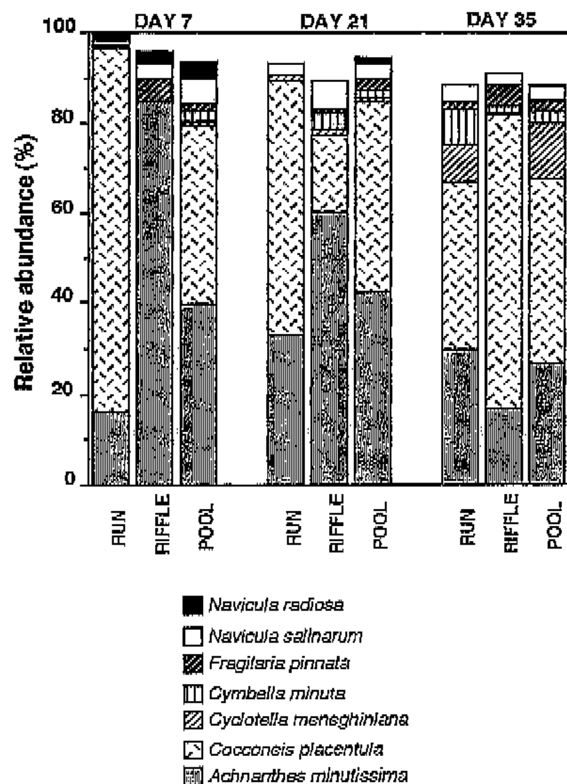

Figure 3. Diatom relative abundance of dominant species in the run, riffle, and pool habitats on colonization days 7, 21, and 35.

habitats throughout colonization time (Figure 3). On day 35 the pool and run habitats also contained an unidentified filamentous alga.

AFDM increased significantly ($p<0.05$) throughout colonization time in the run and pool habitats (Table 1, Figure 2B). Sudden increases occurred on colonization day 35 in both habitats. In the riffle, AFDM increased rapidly early in colonization and then decreased later in colonization (Figure 2B). Significant differences ($p<0.05$) were found among trays within all three habitats (Table 1). A significant ($p<0.05$) habitat main effect was detected as well (Table 1). Post-hoc tests on pairs of overall means from the habitats using Tukey's HSD revealed significant differences between run vs. pool ($p<0.05$) and run vs. riffle ($p<0.01$) (Table 2). As with chlorophyll *a*, these significant differences are due to the differences on day 35.

Bacterial biomass increased rapidly early in colonization and generally decreased late in colonization (Figure 2C), however a significant ($p<0.05$) change throughout colonization was only found in the pool habitat (Table 1). Bacterial biomass did not significantly ($p>0.05$) differ among habitats or among trays within habitats (Table 1). There were no significant ($p<0.05$) correlations between either bacterial biomass and chlorophyll *a* or bacterial biomass and AFDM in any of the three habitats or on any of the individual sampling days.

Discussion

Differences in chlorophyll *a* and AFDM among the three habitats (i.e., run, riffle, pool) were expected to be much greater than differences among trays within the habitats. The small-scale differences (i.e., variance among trays within the same habitat) that we observed support the idea that a stream habitat is frequently heterogeneous and contains a 'mosaic' of microhabitats (Pringle et al., 1988). In addition, much greater differences among habitats were predicted. The absence of clear differences suggests that the positive effect of increased light availability with decreased water depth may be counter-balanced by the deleterious effect of increased shear stress due to increased water velocity. This is most evident on day 35 when the riffle habitat had lower chlorophyll *a* and AFDM than the pool and run habitats (Figure 2). Decreases in chlorophyll *a* and AFDM late in colonization in the riffle may be related to biofilm sloughing.

Although chlorophyll *a* and AFDM varied significantly among and within habitats, bacterial biomass did not vary either among or within habitats (Table 1) and failed to correlate with either chlorophyll *a* or AFDM. Hence, bacterial biomass does not covary with algal biomass in the epilithic biofilms examined. These results suggest that epilithic algal and bacterial biomass may be regulated by independent controls. While several studies have documented epilithic bacterial-algal covariation in streams (Haack & McFeters, 1982a; 1982b; Kaplan & Bott, 1989; Stock & Ward, 1989), general conditions in which such a relationship can be predicted remain unclear.

Our results do not provide evidence for an epilithic bacterial-algal linkage. Several reasons can be postulated for why a potential epilithic bacterial-algal linkage may not have been detected in this study: (1) bacterial-algal linkages may be strongest in fully developed biofilms, (2) density-dependent grazing by microorganisms within biofilms may regulate bacterial biomass, (3) only a small percentage of the bacteria in

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a stream biofilm may be viable, (4) productivity measures, rather than biomass estimates, may be more sensitive for detecting algal-bacterial relationships, (5) the small spatial and temporal scales used in this study may not have provided an adequate range in algal biomass, and (6) bacterial biomass may be regulated by DOC in the water column.

(1) Bacterial-algal linkages may be strongest in fully developed biofilms. Epilithic bacteria and algae may colonize bare substrates at different rates, hence a trophic coupling between epilithic bacteria and algae may have a time-lag. It is likely that mature biofilm communities were established during this study's 35 day colonization period since Oemke & Burton (1986) found that mature diatom communities were established after a 28 day colonization period in both pools and riffles in a fourth-order section of the Ford River. In addition, major disturbance events (e.g., storm-flow) were not observed during the course of the study. However, chlorophyll *a* and AFDM increased throughout the course of the study in both the run and pool suggesting that the biofilms in these habitats had not reached a steady state.

(2) Density-dependent grazing by microorganisms within biofilms may regulate bacterial biomass. The importance of the 'microbial loop' in structuring marine and freshwater foodwebs has become well established in the two decades following Pomeroy's (1974) proposed conceptual model (see special issue of Microbial Ecology, 1994). Lotic ecologists have realized the potential importance of bacteria in stream food webs (Cummins, 1974; Findlay et al., 1984; Edwards & Meyer, 1987; Meyer, 1994), but documented examples of bacterivory by meiofauna are conspicuously rare. We know that grazing by stream meiofauna can remove a significant portion of bacteria associated with detritus (Perlmutter & Meyer, 1991) and the water column (Carlough & Meyer, 1990; 1991) and may keep biomass cropped at a set density in streambed sediments (Bott & Kaplan, 1990). Density-dependent grazing by meiofauna within biofilms may have resulted in similar bacterial biomass among habitats, but we have no evidence to suggest density-dependent grazing.

(3) Only a small percentage of the bacteria in a stream biofilm may be viable. Hence, bacterial biomass estimates based on direct microscopic counts may not be conducive for examining bacterial-algal linkages in stream biofilms. Direct microscopic counts do not readily distinguish between viable and non-viable bacterial cells, so if only a small percentage of the bacterial cells counted are viable then it may be difficult to detect if the viable bacteria are covarying with algal biomass. In other words, when bacterial cells in the water column passively accumulate in biofilms during colonization, it is difficult to discriminate between a trophic and spurious relationship with algal biomass. However, relationships between bacterial abundance and algal biomass have been observed in biofilms and attributed to trophic linkage (Haack & McFeters, 1978; Haack et al., 1988).

(4) Productivity estimates, rather than biomass estimates, may be more sensitive in detecting covariation between bacteria and algae. Kaplan & Bott (1989) documented diel fluctuations in bacterial productivity during vernal algal blooms, but did not show any concomitant changes in bacterial abundance. In addition, Haack & McFeters (1982a) attributed increases in heterotrophic activity to algal senescence within epilithic biofilms, but did not detect shifts in either bacterial biomass or abundance. However, Hudson et al. (1992) document significantly greater bacterial biomass and productivity in open streams than in forested streams. Biomass estimates coupled with estimates of algal productivity (e.g., ^{14}C incorporation) and bacterial productivity (e.g., ^{3}H-thymidine incorporation into bacterial DNA) may enhance the detection of bacterial-algal linkages and increase confidence in non-significant results.

(5) The small spatial (ten m stream section) and temporal (five weeks) scales of this study may not have provided an adequate range in algal biomass in order to detect covariation between algal and bacterial biomass. The study was designed to provide a range in algal biomass, however a one order of magnitude range in algal biomass may not be adequate for detecting covariation with bacterial biomass. Cole et al. (1988) and Sander & Kalff (1993) used data sets with three orders of magnitude in algal biomass to demonstrate cross-system covariation with bacterial biomass.

(6) Bacterial biomass may be regulated by DOC in the water column (i.e., allochthonous DOC or autochthonous DOC released from upstream sources). Previous studies have documented the availability of streamwater DOC to benthic bacteria (Bott et al., 1984; Ford & Lock, 1987; Findlay et al., 1993; see Kaplan & Newbold, 1993). A portion of this DOC pool may contain algal-released DOC from upstream sources (Kaplan & Bott, 1982; Kaplan & Bott, 1989). However, Findlay et al. (1993) failed to find an epilithic bacterial-algal linkage in streams at the Hubbard Brook Experimental Forest even though a relationship was postulated and both activity and biomass linkages were

examined. They concluded that a bacterial-algal linkage may be difficult to detect due to the relatively large allochthonous DOC inputs (relative to autochthonous carbon production) in the Hubbard Brook streams. They suggest that bacterial-algal covariation is unlikely in oligotrophic streams and more likely in eutrophic streams. The Ford River has much greater epilithic chlorophyll *a* than the streams studied by Findlay et al. (1993), yet its chlorophyll *a* concentrations fall within the middle of the range of temperate streams (Lock, 1981). The similarity in bacterial biomass among and within habitats suggests that allochthonous DOC may be an important control on the epilithic bacterial community in the Ford River, however the bioavailability of the Ford River's DOC has not been examined.

Although several factors potentially mask a bacterial-algal linkage, our results indicate that bacterial and algal biomass do not covary in the habitats investigated throughout a five week colonization period. The generality of these findings is difficult to assess due to the dearth of studies that examine epilithic bacteria and algae across a range of streams in which autochthonous and allochthonous carbon inputs vary.

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