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ORIGINAL ARTICLE

Synchrony in aquatic microbial community dynamics

Angela D Kent[1,2,5], Anthony C Yannarell[3,6], James A Rusak[1], Eric W Triplett[4] and Katherine D McMahon[2]

[1]*Center for Limnology, University of Wisconsin-Madison, Madison, WI, USA;* [2]*Department of Civil and Environmental Engineering, University of Wisconsin-Madison, Madison, WI, USA;* [3]*Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC, USA and* [4]*Department of Microbiology and Cell Science, University of Florida, Gainesville, FL, USA*

Population dynamics are influenced by drivers acting from outside and from within an ecosystem. Extrinsic forces operating over broad spatial scales can impart synchronous behavior to separate populations, while internal, system-specific drivers often lead to idiosyncratic behavior. Here, we demonstrate synchrony in community-level dynamics among phytoplankton and bacteria in six north temperate humic lakes. The influence of regional meteorological factors explained much of the temporal variability in the phytoplankton community, and resulted in synchronous patterns of community change among lakes. Bacterial dynamics, in contrast, were driven by system-specific interactions with phytoplankton. Despite the importance of intrinsic factors for determining bacterial community composition and dynamics, we demonstrated that biological interactions transmitted the signal of the regional extrinsic drivers to the bacterial communities, ultimately resulting in synchronous community phenologies for bacterioplankton communities as well. This demonstrates how linkages between the components of a complex biological system can work to simplify the dynamics of the system and implies that it may be possible to predict the behavior of microbial communities responsible for important biogeochemical services in the landscape.
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Introduction

Microbial communities regulate the flow of nutrients and energy in the Earth's biosphere, but little is known about the forces that govern their structures and functions. Quantifying the influence of these forces is essential to understanding microbially mediated processes. Ecologically, these drivers can be separated into intrinsic (site-specific) and extrinsic (regional) categories and the relative importance of each is a topic of much debate (Grenfell *et al.*, 1998; Hudson and Cattadori, 1999; Rusak *et al.*, 1999; Bjørnstad and Grenfell, 2001; Liebhold *et al.*, 2004; Hessen *et al.*, 2006). Lakes provide an excellent system to explore the influence of intrinsic vs extrinsic drivers of microbial communities, since the shoreline boundaries enable us to distinguish forces acting from within and from outside the system. Extrinsic factors operating at a regional scale can be observed as they impose synchrony on the dynamics of various ecosystem parameters (Liebhold *et al.*, 2004). Abiotic variables such as temperature and major ion concentrations, for example, exhibit strong interannual synchrony across lakes in a region (Magnuson *et al.*, 1990; Kratz *et al.*, 1998). Lake-specific intrinsic drivers, such as food-web interactions and stochastic population dynamics, typically dampen such patterns in plankton (Baines *et al.*, 2000; Magnuson *et al.*, 2005).

Previous studies exploring the relative importance of extrinsic and intrinsic factors in population ecology have typically examined synchrony among populations of a single species (Grenfell *et al.*, 1998; Hudson and Cattadori, 1999; Rusak *et al.*, 1999; Liebhold *et al.*, 2004; Hessen *et al.*, 2006). Spatial synchrony (or temporal coherence) refers to correlated temporal variability in the abundance of distinct taxa, usually within regions (Liebhold *et al.*, 2004). In the absence of dispersal, spatial synchrony among populations is often attributed to the 'Moran effect' (extrinsic drivers) or to trophic

Correspondence: Dr KD McMahon, Department of Civil and Environmental Engineering, University of Wisconsin-Madison, 1415 Engineering Drive, Madison, WI 53706, USA.
E-mail: tmcmahon@engr.wisc.edu
[5]Current address: Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA
[6]Current address: Department of Animal Sciences, University of Illinois at Urbana-Champaign, Urbana, IL 61801, USA
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interactions with populations that exhibit spatial synchrony (Grenfell *et al.*, 1998; Hudson and Cattadori, 1999; Liebhold *et al.*, 2004). Concordance is an analogous concept, applied to communities rather than a single taxon, that quantifies the degree to which spatial patterns in community structure are similar among locations or co-occurring taxonomic groups (Paszkowski and Tonn, 2000; Peres-Neto and Jackson, 2001). The notion of 'temporal concordance' implies that compositional shifts among communities occur at the same time and pace, thus providing an invaluable approach to quantifying synchrony from a community perspective.

Annual patterns of succession have been described for the zooplankton and phytoplankton (Sommer, 1989; Anneville *et al.*, 2002), but the predictability and pace of succession varies among lakes owing to local, lake-specific conditions (Rusak *et al.*, 1999; Baines *et al.*, 2000; Bronmark and Hansson, 2005). Predicting population dynamics would appear to be even more challenging for aquatic bacterial populations given their inherent diversity, rapid generation times, and the wide array of factors that can influence their activity and dynamics (Yannarell *et al.*, 2003; Kent *et al.*, 2004; Yannarell and Triplett, 2005). Additionally, defining appropriate taxonomic units for cross-system comparisons of microbial populations is exceedingly difficult. Rather than focusing on the fluctuations of individual populations, we therefore examined seasonal patterns in the composition of planktonic microbial *communities* and the factors responsible for community dynamics. Synchrony at the community level is virtually unexplored. While some recent studies have examined synchrony in bacterial dynamics across multiple sites, these communities were very similar in composition, and were sampled at a coarser level of temporal resolution (monthly or seasonally) (Stepanauskas *et al.*, 2003; Crump and Hobbie, 2005). Demonstration of concordant community dynamics among lakes over time would indicate that communities also respond in predictable ways to regional extrinsic drivers. Sorting out the relative influence of drivers creating regional patterns in community dynamics and those creating system-specific, idiosyncratic behavior can provide a predictive framework for understanding future environmental change and its effect on microbial communities.

Materials and methods

Study sites

Bacterioplankton and phytoplankton communities were examined in six shallow humic lakes located in northern Wisconsin, USA. Physical and chemical limnological characteristics of the lakes are provided in Table 1. These lakes are hydrologically isolated, with no stream or river connections between them. The extensive *Sphagnum* mat surrounding each lake is responsible for the high concentration of humic substances found in these waters.

Field sampling

Integrated epilimnion samples were collected twice weekly from May 28 to August 22, 2003, as described previously (Kent *et al.*, 2004). Briefly, epilimnion depth was determined by temperature and dissolved oxygen profiles. Integrated epilimnetic samples were collected at the deepest point in each lake using an integrated water column sampler. Bacteria present in these samples were concentrated onto 0.2-μm filters (Supor-200; Pall Gelman, East Hills, NY, USA). Filters were frozen immediately, and stored at -80°C awaiting DNA extraction using the FastPrep DNA purification kit (MPBiomedicals, Solon, OH, USA). Aliquots were preserved in 2% glutaraldehyde for determination of phytoplankton identification and abundance, and also for enumeration of bacterioplankton, zooplankton and heterotrophic nanoflagellates (HNF). Samples were also collected for water chemistry analyses.

Planktonic community composition

Abundance of bacteria, phytoplankton, zooplankton and HNF. To determine bacterial abundance, cells were stained with 4′,6′-diamidino-2-phenylindole (DAPI) and counted on black 0.2 μm polycarbonate track etched filter membranes (PCTE) filters using

Table 1 Lake characteristics

Lake	*Latitude (N)*	*Longitude (W)*	*Surface area (Ha)*	*Maximum depth (m)*	*DOC (mg/l)*	*pH*	*Total P (μg/l)*	*Total N (μg/l)*	*Chl a (μg/l)*
Crystal Bog	46°00′26.8″N	89°36′22.5″W	0.56	2.5	9.5	5.1 (0.8)	22.3 (7)	629.0 (261)	22.4 (44.2)
Forestry Bog	46°02′51.4″N	89°39′04.8″W	0.13	2.5	10.4	5.5 (0.4)	27.2 (13)	830.5 (369)	28.1 (43.3)
N. Sparkling Bog	46°00′16.0″N	89°42′18.6″W	0.47	4.5	9.5	5.2 (1.2)	25.4 (11)	691.9 (206)	27.4 (71.3)
S. Sparkling Bog	46°00′13.6″N	89°42′19.9″W	0.44	8.0	11.2	5.1 (0.9)	21.8 (20)	642.0 (161)	22.3 (34.7)
Trout Bog	46°02′27.5″N	89°41′09.6″W	1.01	7.9	28.0	4.8 (0.7)	31.6 (22)	815.2 (237)	31.5 (59.5)
Why Not Bog	46°00′17.0″N	89°37′30.9″W	1.23	6.5	6.6	5.7 (1.1)	18.9 (23)	492.9 (279)	8.17 (15.9)

Abbreviations: DOC, dissolved organic carbon; total N, total nitrogen; total P, total phosphorus; Chl a, chlorophyll a.
Numbers in parentheses represent the range of observed values (maximum value−minimum value).

epifluorescence microscopy (Porter and Feig, 1980), as described previously (Kent *et al.*, 2004). HNF were visualized with DAPI and enumerated on black 0.8 μm PCTE filters using epifluorescence microscopy (Kent *et al.*, 2004). Detailed information on bacterial and HNF enumeration is also contained in the on-line methods manual for the Microbial Observatory for the North Temperate Lakes Long Term Ecological Research (NTL-LTER) site, which may be accessed at http://microbes.limnology.wisc.edu/methods.htm.

Phytoplankton populations were identified and enumerated microscopically as described previously (Kent *et al.*, 2004). Volumes ranging from 10 to 25 ml of preserved sample were settled in chambers for at least 24 h before counting. Identification of dominant phytoplankton species was based on Smith (1950), Prescott (1954) and Patterson (1998). Microscopic counts of phytoplankton populations were transformed using biovolume estimates previously generated for species common to these lakes (Graham *et al.*, 2004), before analysis.

Zooplankton populations were identified and enumerated using standard methods (Frost and Montz, 1988).

Bacterioplankton community analysis. Bacterial community composition and diversity were assessed using automated ribosomal intergenic spacer analysis (ARISA) (Fisher and Triplett, 1999), as described previously (Kent *et al.*, 2004; Yannarell and Triplett, 2005). Polymerase chain reactions (PCRs) contained 1 μl of lake-extracted DNA and primers typically used for ARISA 1406f, 5′-TGYACACACCGCCCGT-3′ (universal, 16S rRNA gene), and 23Sr, 5′-GGGTTBCCCCATTCRG-3′ (bacteria-specific, 23S rRNA gene). The 1406f primer was labeled at the 5' end with the phosphoramidite dye 6-FAM. PCR was carried out in an Eppendorf MasterCycler Gradient (Eppendorf AG, Hamburg, Germany) with an initial denaturation at 94°C for 2 min, followed by 30 cycles of 94°C for 35 s, 55°C for 45 s, and 72°C for 2 min, with a final extension carried out at 72°C for 2 min. Denaturing capillary electrophoresis was carried out for each PCR using an ABI PRISM 3700 DNA Analyzer (Applied Biosystems, Foster City, CA, USA) as described previously (Kent *et al.*, 2004; Yannarell and Triplett, 2004). Size-calling was carried out using GeneScan 3.1.2 (Applied Biosystems). Capillary electrophoresis results in minor run-to-run variations in observed vs actual fragment length that were resolved using the allele-calling features in Genotyper 2.5 (Applied Biosystems) before analysis. To include the maximum number of peaks while excluding background fluorescence, a threshold of 100 fluorescence units was used. The signal strength (i.e. peak area) of each peak was normalized to account for run-to-run variations in signal detection by dividing the area of individual peaks by the total fluorescence (area) detected in each profile, expressing each peak as a proportion of the observed community (Rees *et al.*, 2004; Yannarell and Triplett, 2005).

Environmental data
Chemical analyses were conducted as outlined by the North Temperate Lakes Long-Term Ecological Research (NTL-LTER) site (http://lterquery.limnology. wisc.edu) (Stanley, 2003). The environmental dataset includes water temperature and dissolved oxygen profiles, total phosphorus (total P), total nitrogen (total N), and dissolved organic carbon (DOC) concentrations, pH and chlorophyll a (Chl a) concentrations. Total P, total N, DOC and Chl a measures were $\log_{10}$-transformed before analysis. The transformed data were confirmed to exhibit normal distributions.

Meteorological data
A meteorological dataset was included to examine external factors acting at a regional scale. This data set included a 3-day moving average of mean daily air temperature, photosynthetically active radiation (PAR), and precipitation measured at the municipal airport in nearby Woodruff, WI. Meteorological data for these study sites are available through the NTL-LTER's on-line data sets (http://lterquery.limnology.wisc.edu) (Rusak and Kratz, 2003).

Data analysis
Correspondence analysis was carried out using bacterial community composition data generated by ARISA, and separately for phytoplankton community composition based on biovolume estimates for algal populations present on each date. All correspondence analyses were carried out using Canoco 4.5.1 (Biometris-Plant Research International, Wageningen, The Netherlands) (ter Braak and Smilauer, 2002).

The Bray–Curtis similarity coefficient (Legendre and Legendre, 1998) was calculated using the ARISA data generated from each sample to assess the degree of similarity between bacterial communities obtained from different samples:

$$S_{jk} = 1 - \sum \frac{|y_{ij} - y_{ik}|}{(y_{ij} + y_{ik})}$$

where y_{ij} is the normalized peak area of the ith population in the jth sample and y_{ik} is the normalized peak area of the ith population in the kth sample. A similarity matrix was generated for all possible pairs of samples. This similarity matrix was used to generate analysis of similarity (ANOSIM) statistics (Clarke and Green, 1988) to test the hypothesis that bacterial communities from the same lake were more similar in composition to each other than to communities in different lakes. ANOSIM generates a test statistic, R. The magnitude

of R indicates the degree of separation between groups of samples, with a score of 1 indicating complete separation and 0 indicating no separation. Calculation of similarity coefficients and ANOSIM analyses were carried out using PRIMER 5 for Windows v. 5.2.7 (PRIMER-E Ltd, Plymouth, UK).

Procrustean matrix superimposition was used to assess the degree of association, or concordance, between the temporal patterns in phytoplankton and bacterial community composition within each lake, and for bacterial and phytoplankton communities separately among lakes using the first three axes from correspondence analyses (Jackson, 1995; Legendre and Legendre, 1998; Peres-Neto and Jackson, 2001). The sum of squared residuals between scaled and rotated configurations of each ordination solution is used as a metric of association (m^2) (Peres-Neto and Jackson, 2001). The m^2 metric varies between 0 and 1, and smaller values of m^2 indicate stronger concordance between data sets. Significance was assessed by permutation tests (999 permutations) using the PROTEST package (Jackson, 1995).

Variance partitioning using partial canonical correspondence analysis distinguished the relative importance of different sets of variables for explaining the temporal patterns of bacteria or phytoplankton community composition in each lake (ter Braak and Smilauer, 2002). Three sets of potential explanatory variables were used: environmental (pH, total P, total N, DOC and water temperature), meteorological (described above), and biotic variables (chl a, phytoplankton populations and HNF were included as biotic explanatory variables for the bacterioplankton data set, while cladoceran zooplankton populations were included as biotic explanatory variables for the phytoplankton data set). The unique contribution of individual groups of variables was determined by removing the influence of two of the groups of variables (covariables) and using the remaining group as the explanatory set of variables. These partial ordinations were then compared to the total variance explained when all categories are included in the analysis.

Results

Different bacterial communities were observed in each lake (ANOSIM $R = 0.604$, $P < 0.001$), and much of this difference was related to water chemistry parameters such as total nitrogen, total phosphorus, DOC and pH (Figure 1). Within each lake, bacterial and phytoplankton community composition were highly variable over the study period, particularly in the month of June (Figure 2). Bray–Curtis similarity coefficients indicated that bacterial communities observed on the last day of sampling were, on average, only 30% similar to those observed on the first day; phytoplankton communities observed at the end of the sampling period were, on average,

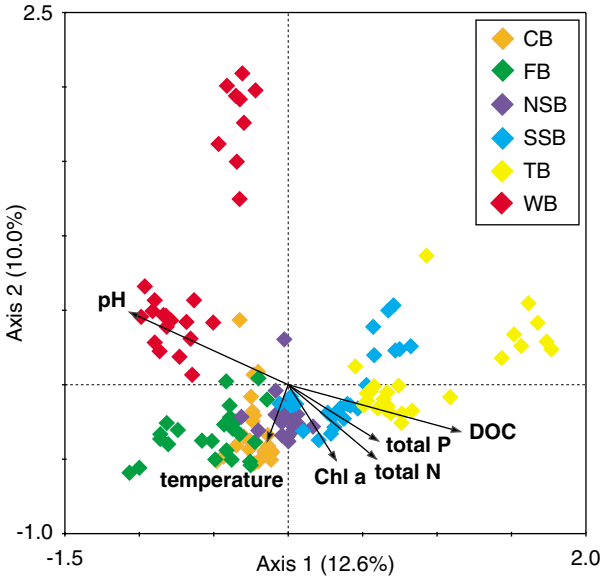

Figure 1 Correspondence analysis biplot of bacterial community composition. Bacterial communities were compared using ARISA relative fluorescence in a suite of six humic lakes in northern Wisconsin (CB, Crystal Bog; FB, Forestry Bog; NSB, N. Sparkling Bog; SSB, S. Sparkling Bog; TB, Trout Bog; WB, Why Not Bog). Points represent bacterial community samples collected twice weekly between May 28 and August 22 2003, from each lake. Arrows for the supplemental chemical and physical variables included in this analysis show the direction of increase for each variable, and the length of each arrow indicates the degree of correlation with the ordination axes. Total N, total nitrogen; total P, total phosphorus; Chl a, chlorophyll a; surface temp, surface water temperature; DOC, dissolved organic carbon. Percentage of community variance explained by each axis is indicated in parentheses. The first two CA axes explain 55.8% of the relationship between the bacterial community and environment (the 'species–environment relationship' from Canoco). This plot indicates that TB and WB differ the most in bacterial community composition, and also in water chemistry parameters.

only 27% similar to those observed in May. However, phytoplankton and bacterial community dynamics within each lake were strongly concordant (Table 2), indicating that synchronous shifts occurred in both communities. This temporal concordance was particularly strong in Crystal Bog (CB), Forestry Bog and South Sparkling Bog. We also detected significant community concordance *among* lakes (Table 3), indicating that synchronous changes occurred in the planktonic microbial assemblages across the region despite the hydrologic isolation of these lakes and the lake-specific community composition.

Because synchrony in population dynamics is often attributed to the influence of extrinsic forcing (Grenfell *et al.*, 1998; Liebhold *et al.*, 2004), we used canonical multivariate analyses to investigate whether similar drivers are responsible for community-level synchrony. We explored the dependence of bacterial and phytoplankton community dynamics on meteorological factors and physical/chemical factors that have shown synchrony (or temporal coherence) in previous studies (Magnuson *et al.*,

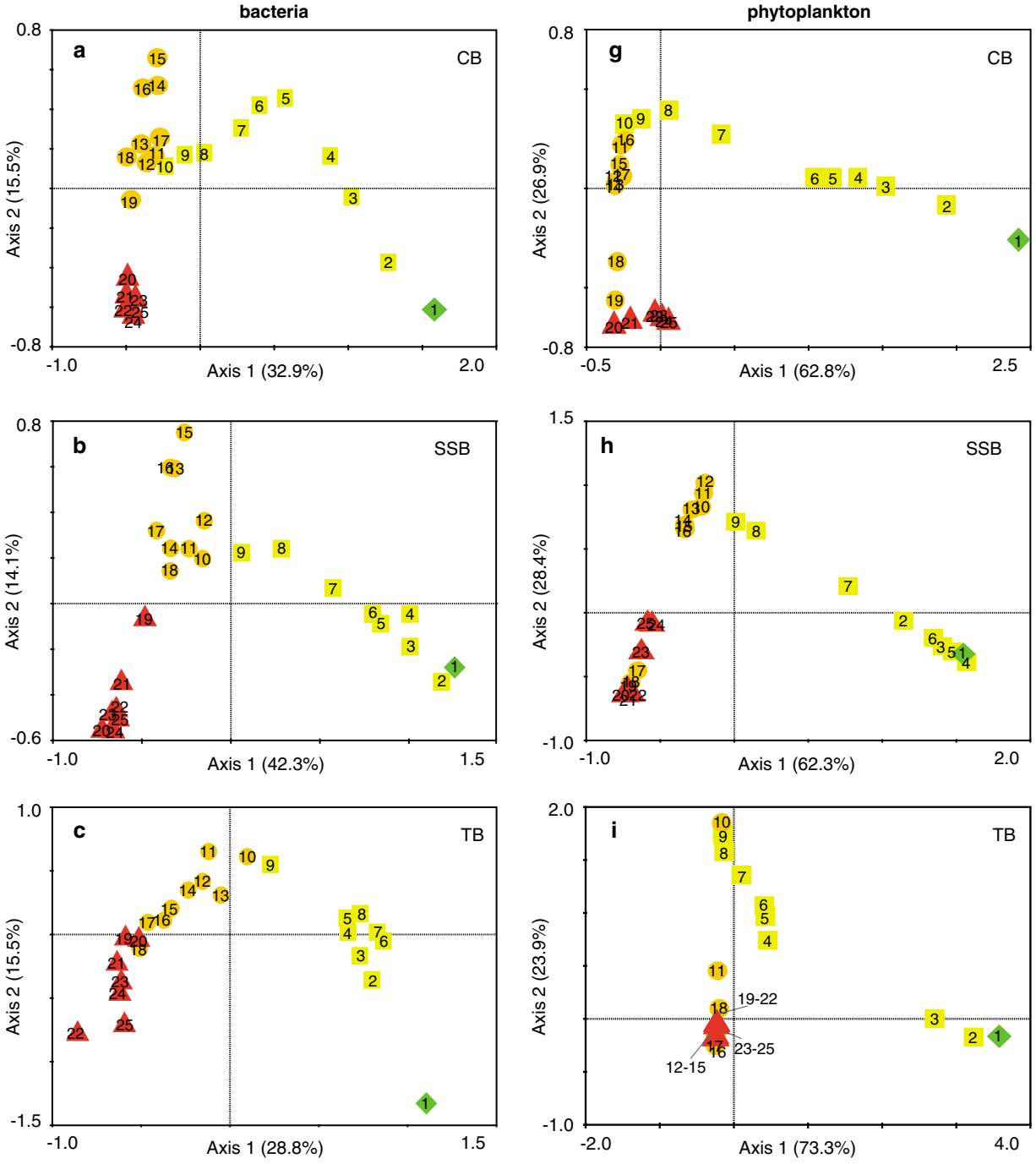

Figure 2 Correspondence analysis of planktonic microbial communities. Bacterial community composition (**a–f**) and phytoplankton community composition (**g–l**) in samples collected twice weekly between May 28 and August 22, 2003, from each lake. Points representing sample dates are numbered consecutively, and the color indicates the month in which the sample was collected (green, May; yellow, June; orange, July; red, August). Percentage of community variance explained by each axis is indicated in parentheses. See Figure 1 legend for lake acronym definitions.

2005). In addition, we examined the impacts of biological interactions within each lake by assessing the influence of zooplankton communities on phytoplankton and the influence of phytoplankton and nanoflagellate grazers on bacteria.

Extrinsic meteorological and local environmental variables explained 46% of within-lake phytoplankton variability (Figures 3a and 4), while biotic interactions accounted for very little. On average, 37% of variance in lake chemical and physical parameters could be attributed to regional meteorological factors, with water temperature being most strongly correlated (81% of variance in water temperature among lakes was explained by the meteorological factors). Thus,

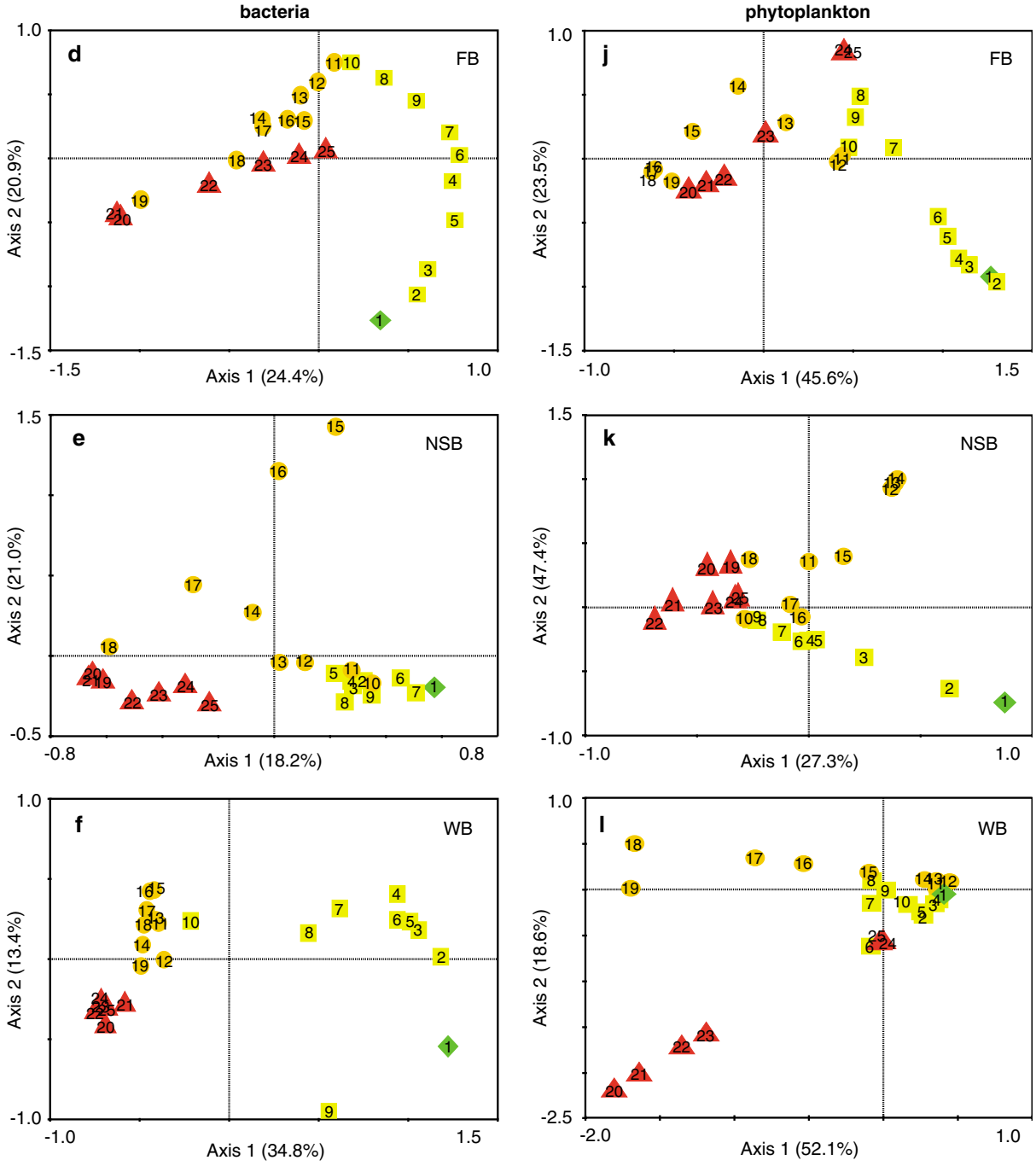

Figure 2 Continued.

patterns in phytoplankton communities were largely explained by extrinsic and abiotic variables acting across the region (e.g. trends in water temperature). In contrast, these parameters explained very little of the within-lake patterns for bacteria (Figures 3b and 5). While the combination of meteorology, biotic interactions and local environmental variables accounted for 94% of the bacterial variation, much of the explanatory power (40%) was attributable to biotic interactions with phytoplankton acting independently of other factors. A further 25% of bacterial variation was attributable to covariation of phytoplankton with local environmental and meteorological factors.

Discussion

Significance of synchrony and temporal concordance
Cross-system differences in community composition and strong biological interactions within each system would be expected to impart distinct dynamics to communities in different lakes. Sur-

Table 2 Temporal concordance between bacterioplankton and phytoplankton communities in each lake

Lake	m^2
Crystal Bog	0.25
Forestry Bog	0.37
N. Sparkling Bog	0.66
S. Sparkling Bog	0.28
Trout Bog	0.51
Why Not Bog	0.68

Concordance was determined by Procrustean matrix superimposition of correspondence analysis results from bacterial and phytoplankton communities in each lake (Paszkowski and Tonn, 2000; Peres-Neto and Jackson, 2001). A smaller value of m^2 implies a stronger concordance. Mean $m^2 = 0.46$, $P < 0.001$ for all within-lake comparisons.

Table 3 Community concordance among lakes

	CB	*FB*	*NSB*	*SSB*	*TB*	*WB*
Crystal Bog	0	0.35	0.40	0.26	0.33	0.76
Forestry Bog	0.32	0	0.53	0.26	0.56	0.65
N. Sparkling Bog	0.29	0.39	0	0.54	0.56	0.66
S. Sparkling Bog	0.14	0.30	0.38	0	0.60	0.57
Trout Bog	0.24	0.38	0.46	0.27	0	0.86*
Why Not Bog	0.46	0.58	0.52	0.31	0.51	0

Concordance was determined by Procrustean matrix superimposition of correspondence analysis results from bacterial or phytoplankton communities among lakes (Paszkowski and Tonn, 2000; Peres-Neto and Jackson, 2001). Phytoplankton comparisons are displayed in the upper right portion of the table (mean $m^2 = 0.53$), and bacterial comparisons are displayed in the lower left portion of the table (mean $m^2 = 0.37$). A smaller value of m^2 implies a stronger concordance. $P < 0.001$ for all between-lake comparisons except some comparisons involving WB (* not significant, $P > 0.05$).

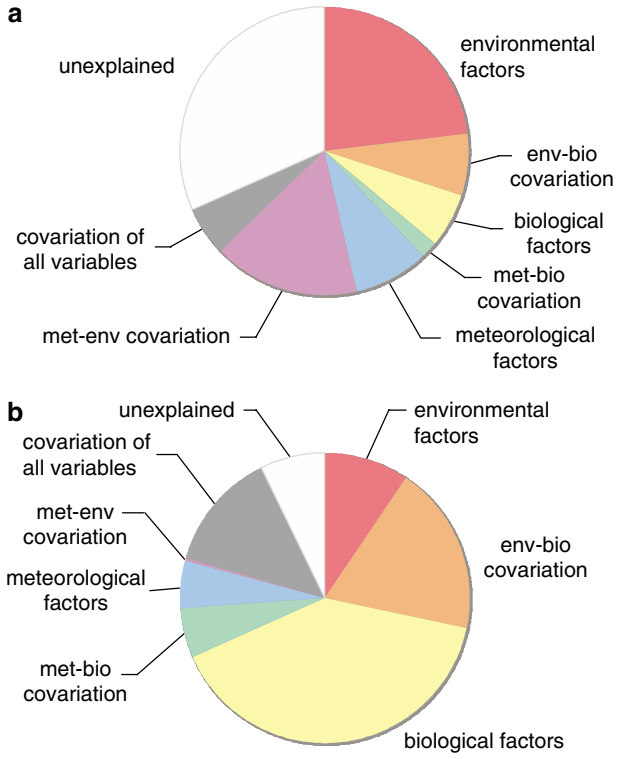

Figure 3 Partitioning microbial community variance among intrinsic and extrinsic variables. (**a**) Phytoplankton or (**b**) bacterioplankton community temporal variance was partitioned among meteorological (met), environmental (env) and biological (bio) sets of variables for each lake and variance partitioning results were averaged among lakes. The sets of potential explanatory variables were defined as follows: environmental – pH, total P, total N, DOC and water temperature; meteorological – 3-day moving average of mean daily air temperature, PAR and precipitation; biological – Chl a, phytoplankton populations and HNF were used as biotic explanatory variables for the bacterioplankton data set, cladoceran zooplankton populations were used as biotic explanatory variables for the phytoplankton data set.

prisingly, the planktonic communities in this study displayed concordant dynamics among lakes, despite lake-specific differences in microbial community composition (Figures 1 and 2, Table 3). This concordance, or synchrony, implies a predictability to community dynamics and can help delineate the relative influence of deterministic vs stochastic events on ecological systems (Sugihara, 1995; Grenfell *et al.*, 1998).

Synchronous change is ultimately the footprint of environmental factors acting at a regional scale to influence chemical, physical or biological lake variables (Magnuson *et al.*, 2005). The signal may be obscured as it is filtered through intrinsic, or site-specific, regulators of lake parameters. Synchrony depends, in part, on the directness of a variable's connection to the regional-scale drivers, and on the number of intrinsic, lake-specific factors with the potential to influence the dynamics of a variable (Magnuson *et al.*, 2005). We limited the gradient of local environmental variables by looking only at small humic lakes. Across lake types, with wider ranges of nutrients, depth and size, we might expect that local factors play a stronger role. This is true for phytoplankton communities in temperate lakes across a trophic gradient (Anneville *et al.*, 2002). Indeed, humic lakes exhibit the strongest levels of synchrony in abiotic variables, compared to other lake types (Jarvinen *et al.*, 2002). In addition, the simple food webs found in these lakes (no planktivorous fishes) may also reduce the number of intrinsic factors with the potential to influence phytoplankton and bacterioplankton community composition.

Spatial synchrony is generally attributed to the influence of regional meteorological factors on the dynamics of discrete populations (Hudson and Cattadori, 1999; Liebhold *et al.*, 2004). Here, we demonstrated that synchronous patterns of succession were robust enough to be detected both in different taxa (phytoplankton and bacterioplankton) and in communities of differing composition, arguing that strong regional environmental drivers are ultimately responsible for determining the

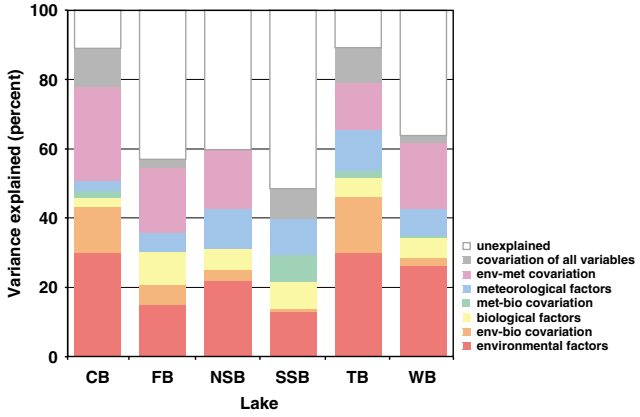

Figure 4 Results of phytoplankton variance partitioning for each lake. Variance in phytoplankton community composition over time (assessed by biovolume) was partitioned among meteorological (met), environmental (env) and biological (bio) sets of variables using partial canonical correspondence analyses. The sets of potential explanatory variables were defined as follows: environmental – pH, total P, total N, DOC and water temperature; meteorological, 3-day moving average of mean daily air temperature, PAR and precipitation; biological – chl a, phytoplankton populations and HNF were used as biotic explanatory variables for the bacterioplankton data set, cladoceran zooplankton populations were used as biotic explanatory variables for the phytoplankton data set. Abiotic factors included in the meteorological and environmental data sets explain more of the variance in phytoplankton community composition in each lake than do biotic variables. See Figure 1 legend for lake acronym definitions.

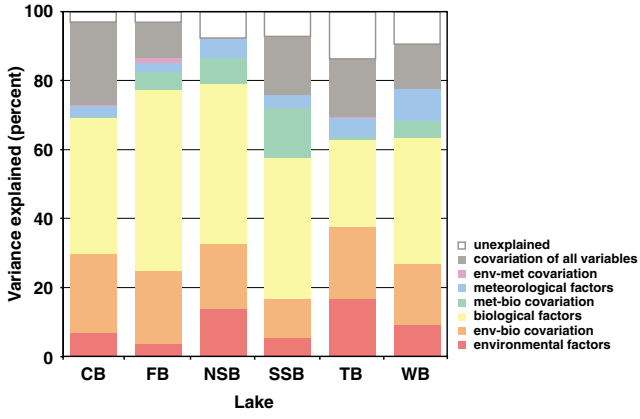

Figure 5 Results of bacterioplankton variance partitioning for each lake. Variance in bacterial community composition over time (assessed by ARISA relative fluorescence) was partitioned among meteorological (met), environmental (env) and biological (bio) sets of variables using partial canonical correspondence analyses. The sets of potential explanatory variables were defined as follows: environmental – pH, total P, total N, DOC and water temperature; meteorological – 3-day moving average of mean daily air temperature, PAR and precipitation; biological – chl a, phytoplankton populations and HNF were used as biotic explanatory variables for the bacterioplankton data set, cladoceran zooplankton populations were used as biotic explanatory variables for the phytoplankton data set. The suite of biotic variables explains much of the variance in bacterial community composition over time in each lake. See Figure 1 legend for lake acronym definitions.

structure of planktonic populations in humic lakes. The variance partitioning results indicated strong correlations between regional factors and phytoplankton community dynamics (Figures 3 and 4), suggesting regional control of phytoplankton in these systems. Although we also observed synchrony in community succession for the bacteria in these lakes, this temporal concordance did not appear to be due to the direct influence of extrinsic drivers (Figures 3 and 5). Intrinsic factors, notably the interactions with other planktonic populations, are likely to be the proximate drivers of bacterial community dynamics within each lake. Because the phytoplankton communities are themselves exhibiting temporal concordance (synchrony), we propose that these biotic interactions are transmitting the regional signal to the bacteria (i.e. covariation of biological variables with meteorology and environment, Figures 3 and 5), producing the observed temporal concordance among lakes (Table 3).

Resource-mediated (bottom-up) control may be the mechanism by which the regional environmental signal is passed along from the phytoplankton to the bacterial communities. While these humic lakes are consistently high in DOC, a large fraction of this is presumed to be comprised of recalcitrant humic compounds (Malcolm, 1990; Wetzel *et al.*, 1995). Succession in the phytoplankton community (driven by regional environmental factors) likely affects the concentration and biochemical composition of autochthonous organic matter available to bacteria (van Hannen *et al.*, 1999; Arrieta and Herndl, 2002; Pinhassi *et al.*, 2004). Mesocosm and field studies have demonstrated that dissolved organic matter of differing quality will enrich different bacterial populations, thus influencing the composition of bacterial communities (van Hannen *et al.*, 1999; Crump *et al.*, 2003). We have previously noted within-lake concordance between bacterial and phytoplankton communities (in CB) and proposed that phytoplankton community composition provides a useful proxy for evaluating diversity and abundance of labile organic carbon resources available to aquatic bacteria (Kent *et al.*, 2006). The within-lake concordance between bacterial and phytoplankton communities observed in these systems (Table 2) may therefore be due to the evolving resource base of autochthonous carbon (van Hannen *et al.*, 1999; Kisand and Tammert, 2000; Arrieta and Herndl, 2002). The among-lake concordance observed for bacterial communities (Table 3), as noted above, is likely due to the effects of regional drivers acting to synchronize the dynamics of the phytoplankton communities. Although we cannot rule out the possibility that the bacteria are also synchronizing phytoplankton community dynamics through mechanisms such as competition, allelopathy and nutrient recycling, the evidence presented here taken together with the previous studies described above supports the hypothesis that synchronization of bacterial community dynamics is driven most

directly by phytoplankton–bacteria interactions. Notably, the weakest concordance values observed within or among lakes involved comparisons with Why Not Bog (WB) (Tables 2 and 3), which had significantly lower phytoplankton biovolume than the other lakes in this study (Table 1). These results suggest that phytoplankton communities are an important link between aquatic bacterial communities and regional environmental drivers.

Conclusion

The concordant dynamics observed in this study demonstrate how general patterns may emerge in microbial systems despite the immense diversity and complexity of their communities. Conceptual and mechanistic models are needed to predict the behavior of microbial communities, given their integral role in ecosystem function. The results of this study identify important environmental drivers that should be included in such models. Although indirectly linked to regional climate via phytoplankton dynamics, the existence of concordance suggests that bacterial community composition and dynamics in humic lake ecosystems (and by extension, the ecological processes mediated by these microbial communities) are strongly influenced by extrinsic drivers. Recognition of such general organizing forces suggests that dynamics of microbial communities are less idiosyncratic than expected and that the regular patterns imposed by these environmental drivers may have predictive power in other ecosystems. This has important implications for macroscale research challenges ranging from the cycling of nutrients and matter at landscape levels to regional ecosystem management and the forecasting of ecosystem responses to global change.

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