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Exploring periphyton unpredictability

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Abstract. Periphyton is so highly variable that the community resists modelling. To explore the unpredictability of this important resource, we studied: 1) alternative variables to the traditional trophic ones, 2) the spatial scale of periphyton variability, and 3) different levels of description of the community. For such an exercise, we partitioned the variability of epiphytic communities growing in Lake St. François (Québec) into various fractions explained by environmental variables, spatial structure, and covariation between environment and space. We described the epiphytic communities according to their fine (61 taxa) or coarse (6 classes) taxonomy, their size structure, and their total biomass to identify which of these state variables could be most successfully modelled. Our analysis suggests that periphyton modelling could be improved by: 1) the measurement of physical and biotic factors as well as nutrients, 2) the consideration of microscale variation, and 3) the division of periphyton into functional groups based on coarse taxonomy or size classes.

Key words: periphyton, epiphyton, spatial scale, description scale, size structure, canonical correspondence analysis, variation partitioning, St. Lawrence.

Rivers and lakes are increasingly threatened by anthropogenic development. To respond to the pressing demand to manage and monitor these resources, we need powerful models that can predict the response of the aquatic communities to environmental changes. Only a few quantitative models exist for periphyton (Horner and Welch 1981, Biggs 1988), despite the importance of this community as a food base for littoral invertebrates and fish, and also as a fouling agent on shorelines. There are various reasons why powerful predictive models for periphyton have proven elusive. Trophic variables, like phosphorus, have provided good predictions for phytoplankton (Dillon and Rigler 1974) and for other aquatic assemblages (Peters 1986), but have been less successful with periphyton data (Cattaneo 1987, Lalonde and Downing 1991). Because periphyton is attached, it may be affected by different biotic and abiotic variables. Variation in a system is related to the scale of the observations (Allen and Starr 1982, Levin 1992), and therefore the choice of distance between samples could be particularly critical for this spatially heterogeneous community (Morin and Cattaneo 1992). Variation on a fine spatial scale could just be unpredictable. Besides the spatial scale, the variability depends on the scale of the description of the community or "observing mode" (Lane 1986). For example, total periphyton biomass has proven difficult to predict, but more success has been obtained when focusing on a part of the community only. Filamentous green algae increased significantly with total phosphorus in a series of Québec lakes (Cattaneo 1987) while zygnematacean growth was correlated with acidity in Ontario lakes (France and Welbourn 1992). We hypothesise that periphyton models often fail to reach acceptable predictive power because the environmental variables chosen for analysis are not the correct ones for the sampling scale and taxonomic level used in a given study.

To improve our periphyton models it seems necessary to explore 1) new explanatory variables besides the traditional trophic ones, 2) the spatial scale of periphyton variability, 3) the level of periphyton description whose variability could be more effectively modelled. To this end, we performed an exploratory data analysis on samples of the epiphytic communities of Lake St. François, a fluvial lake of the St. Lawrence River (Québec). Following a method recently proposed by Borcard et al. (1992), we partitioned the heterogeneity exhibited by these communities into various fractions explained by the environmental variables, the spatial structure, and the covariation between these two sets of variables. Such an exercise

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shows the spatial scale at which we find variability not accounted for by the measured environmental variables and could suggest which additional biotic or abiotic variables are more likely to improve our models. To investigate which periphyton state variable may be more easily modelled, we compared the variabilities explained by the model when the total epiphyton biomass was considered, and when the community was subdivided into different groups based on taxonomy, at two different resolution levels (fine: 61 taxa, and coarse: 6 classes), or according to size.

Our findings should help design future periphyton studies by indicating the most appropriate choices of scale (i.e., distance between samples), of independent variables, and of the level of community resolution (taxonomy, size classes, or total biomass).

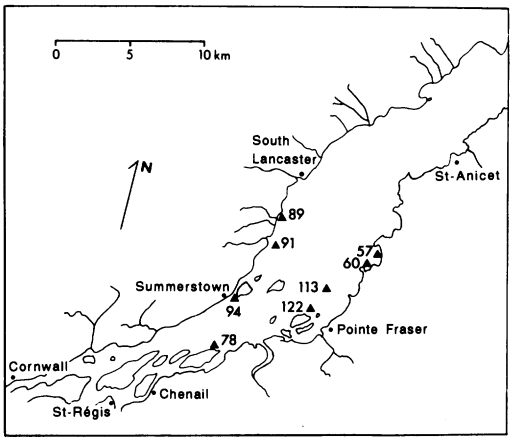

FIG. 1. Map of Lake St. François in southern Québec. Sampling sites are identified by numbers, and triangles indicate their location.

Methods

Site and sampling

Lake St. François (74°10′ to 74°40′W, 45°00′ to 45°16′N) is a fluvial lake along the St. Lawrence River, about 40 km upstream from Montréal (Québec). The lake is polluted by organic chemicals and metals from industries upstream, near Cornwall (Sloterdijk 1985), but remains relatively oligotrophic (total phosphorus around 10 μg/L). The lake is shallow (average depth = 6 m) and large macrophyte beds, mostly *Myriophyllum* and *Vallisneria*, extend over most of its western section. As part of a multidisciplinary survey on the effect of contamination on lake benthic communities, epiphyton was sampled at eight stations (Fig. 1) in the fall of 1989 (25 September–2 October). The stations were chosen to maximize the differences between levels of metal and organic contamination, based on previous studies (Sloterdijk 1985). As in all taxonomically based studies on epiphytes, the number of samples to be analysed had to be limited because of time constraints. The average distance between neighboring stations was 4 km and this can be taken as the "scale" at which our study was conducted. At each station, five replicate samples of macrophytes + epiphytes were collected along two parallel transects, the first one with three samples and the second one with two; the distance between each replicate was about 10 m. Macrophytes, whatever type was found at each 10-m location, were enclosed gently in a 6-L Plexiglas box without disturbing the epiphytes (Downing 1986). After the box was brought to the boat, epiphytes were detached from the plant by agitation. This treatment removes the loosely attached epiphytes but leaves the most tightly adhering algae on the plant. This tightly attached fraction, whose biovolume is apparently rather constant among samples (Cattaneo and Kalff 1980), was ignored in this study. Five 10-ml aliquots of epiphyte suspension were pooled and fixed with Lugol's solution for microscopic analysis. The macrophytes from which the epiphyton was detached were identified, frozen, and subsequently dried at 60°C.

Algal analysis

Algae were counted with an inverted microscope in randomly selected fields at 400×, 250×, and 100× magnification. Enough fields were counted to reach a precision of 30% (Lund et al. 1958). Large, rare algae were counted over the entire slide. Algae were classified by taxon and by size. Cell volumes were estimated by approximation to solids of known volume. When colonies or filaments were present, the whole volume was taken as algal size rather than the volume of a single cell. In the analysis, we excluded the rarest algae and retained the 61 taxa identified to the species or genus that represented more than 1% of the total community

TABLE 1. Algal taxa retained for the analysis of Lake St. François epiphyton, and their size and mean biovolume observed in this study. A detailed description of the assemblages observed at each station is published elsewhere (Pinel-Alloul et al. 1991)

Taxa	Size (μm^3)	Mean biovolume ($\mu m^3 \times 10^6$ per g macrophyte)
CYANOPHYCEAE		
Anabaena	280	49
Chroococcus	33	11
Dermocarpa	108	269
Homeothrix A	120	97
Homeothrix B	31,200	325
Oscillatoria A	840	2264
Oscillatoria B	7600	11,228
Phormidium	32	539
Rivularia	800	117
Synechococcus	12	46
Synechocystis	4	228
CHLOROPHYCEAE		
Bulbochaete	94,200	36
Characium	330	31
Cladophora	6,923,000	4767
Chlamydomonas	250	100
Chlorococcales (solitary)	65	284
Chlorococcales (colonies)	264	110
Closterium	15,000	116
Cosmarium	2400	84
Enteromorpha	1,330,000	5601
Geminella	23,400	10
Hydrodictyon	6,380,000	2109
Mougeotia A	282,600	389
Mougeotia B	11,755,000	1370
Oedogonium A	9000	166
Oedogonium B	630,000	4414
Pediastrum	2100	125
Protoderma	1260	105
Rhizoclonium	1,260,000	1814
Scenedesmus A	160	83
Scenedesmus quadricauda	1600	185
Spirogyra A	630,000	4164
Spirogyra B	16,956,000	13,920
Ulothrix	5040	9
Zygnema	15,700,000	4952
BACILLARIOPHYCEAE		
Acnananthes minutissima	40	701
Cocconeis pediculus	500	200
Cocconeis placentula	360	901
Cymbella A	300	436
Cymbella B	840	65
Diatoma vulgare var. *linearis*	1900	4617
Fragilaria capucina	6000	242
Fragilaria crotonensis	8400	137
Gomphonema A	140	873
Gomphonema B	800	232
Gyrosigma strigile	30,000	61
Melosira	13,500	477
Navicula A	70	560
Navicula gracilis	1400	472
Navicula rhyncocephala	300	444
Nitzschia A	100	420
Nitzschia obtusa	500	16
Rhoicosphenia curvata	120	48
Synedra pulchella	2000	168
CHRYSOPHYCEAE		
Chrysochromulina	33	59
Chrysophyceae (flagellate)	40	204
Chrysophyceae (solitary)	180	66
CHRYPTOPHYCEAE		
Chryptomonas	1200	91
Rhodomonas	180	333
EUGLENOPHYCEAE		
Euglenales	270	270
Phacus	1500	159

abundance or biovolume and were present in at least two of the 40 samples (Table 1). We also grouped these 61 taxa into six classes (Chlorophyceae, Bacillariophyceae, Chrysophyceae, Cyanophyceae, Cryptophyceae, and Euglenophyceae), and, alternatively, into five logarithmically increasing size classes ($<10^2$ μm^3, 10^2–10^3 μm^3, 10^3–10^4 μm^3, 10^4–10^5 μm^3, and $>10^5$ μm^3). Algal biovolume, either for single taxa, large groups, or total, is expressed as $\mu m^3 \times 10^6$/g macrophyte dry weight.

Environmental and spatial variables

At each site, several physical and chemical characteristics of the water and sediment were measured in the field or analysed in the laboratory (Table 2). We collected subsurface water samples and sediments by Ekman dredge. Both water and sediment samples were obtained as composite samples from the five replicates and were analysed following the standard methods

TABLE 2. The range of values of the environmental variables measured in the water and sediments at eight stations of Lake St. François.

Water		Sediment	
Depth (m)	1–2.5	As (μg/g)	0.5–3.2
Temperature (°C)	14–18	Cu (μg/g)	3–13
Color (Hazen units)	4–24	Mn (μg/g)	35–183
Turbidity (Jackson units)	0.2–1.4	Ni (μg/g)	2–9
pH	8.05–8.85	Pb (μg/g)	2–13
Alkalinity (mg $CaCO_3$/L)	76–89.2	Se (μg/g)	0.2–1.4
Hardness (mg $CaCO_3$/L)	106.2–123.9	Zn (μg/g)	7–96
Conductivity (μS/cm)	156–298		
Anion sum (meq/L)	2.55–3		
Cation sum (meq/L)	2.57–3.02		
Ionic balance (%)	0.1–0.9		
Ca (mg/L)	31–36.3		
Mg (mg/L)	7–8.2		
Na (mg/L)	9.4–11.7		
K (mg/L)	1.29–1.52		
SO_4 (mg/L)	24.2–28.2		
Cl (mg/L)	18.5–22.2		
NO_3 + NO_2 (mg/L)	0.02–0.15		
Total P (mg/L)	0.008–0.014		
Al (μg/L)	26–96		
Ba (μg/L)	20.2–22.7		
Cr (μg/L)	0.4–0.9		
Cu (μg/L)	1.1–7.6		
Fe (μg/L)	12.8–124		
Li (μg/L)	2.5–2.8		
Mn (μg/L)	1.5–6.3		
Mo (μg/L)	0.9–1.3		
Ni (μg/L)	0.7–1.2		
Sr (μg/L)	149–177		
V (μg/L)	0.3–0.6		
Zn (μg/L)	0.8–6.2		

proposed by Environment Canada (Environment Canada 1979).

Geographic coordinates for each site were measured with a Loran® system. Prior to analysis, the latitudes and longitudes of the sites, expressed in degrees-minutes-seconds, were transformed into x, y coordinates on a Cartesian plane. The sequence of monomials x, y, x^2, xy, y^2, x^3, x^2y, xy^2, y^3, etc., was used in canonical analysis (Legendre 1990) in much the same way as in trend surface regression, which is a classical method for describing the shape of a geographical surface (Student 1914, Ripley 1981). Because the five replicates at each station were close to one another, given the total area surveyed in this study, we assumed that the geographic coordinates of their center point could adequately describe all the replicates. Consequently, our data table contains 40 data rows, but these are attributed to only eight geographical locations. Comparing the unexplained variability of these 40 data rows to that of an 8-row data table, obtained by averaging the epiphytic data of the various replicates of each station, allowed us, later in the analysis, to quantify the among-replicate within-station variability of the epiphytic community.

Statistical analyses

As a preliminary exploratory analysis, we performed a principal component analysis (PCA) on the environmental variable matrix to identify the most important environmental variables that separated the various stations. The first two PCA axes produced a diagram in which

the five replicates of station 78 were separated from all the other samples, which were grouped together.

Drawing dispersion diagrams of the species versus the principal components allowed us to check whether the species had a unimodal or a linear response to the principal components derived from the environmental variables (ter Braak 1987). Because the response of most species was not linear, we used the canonical form of correspondence analysis (CA) rather than the canonical form of PCA in the remainder of our analysis, as explained below.

To partition the total variation into purely environmental, purely spatial, covariation between environmental and spatial, and unexplained variation, we followed the method of Borcard et al. (1992). In this method, canonical ordination techniques, called "constrained ordination analysis methods" by ter Braak (1987), are used to analyze the relation between a table of dependent variables (here the periphyton species) and a table of independent or explanatory variables (here, the environmental or spatial variables). The better-known equivalent of canonical ordination is regression analysis, which can be used when modelling a single dependent variable. Two forms of constrained ordination methods are available: 1) redundancy analysis (RDA) is to be used in the linear context, when the Euclidean distance appropriately represents the among-point relationships; this is the canonical equivalent of PCA; 2) canonical correspondence analysis (CCA) is used in the unimodal context, when the chi-square distance appropriately describes the relationships among samples, as is often the case with species presence/absence or abundance data. The CCA is the canonical form of CA, selected for our analysis to allow for nonlinear response. Partial forms of RDA and CCA are available which allow computation of the canonical correlation between two data tables while controlling for the influence of a third data table. For the partition of periphyton variability, we first used CCA to compute the fraction of variability of the species data that can be explained either by the environmental variables (called "fraction a + b" in our results), or by the spatial structure (called "fraction b + c"), as expressed by the spatial coordinate polynomial described above. We also used partial CCA to compute a fraction of the species variability, called "fraction a", which is the part that can be explained by the environmental variables while controlling for the influence of the spatial structure, and another part of the species variability, called "fraction c", which is the part that can be explained by the spatial variables while controlling for the influence of environmental variables.

Canonical correspondence analysis (CCA) and partial CCA were computed on the three matrices of algal data (61 taxa, 6 large taxonomic groups, 5 size classes) and on the total epiphytic biomass using the program CANOCO (ter Braak 1988) release 3.11 (ter Braak 1990). Before analysis, the data in the fine taxonomy matrix were normalised by log transformation ($y = \ln(x + 1)$). No transformation was necessary for the other matrices. A forward selection procedure, like the one used in regression analysis to select the best subset of explanatory variables, was used to determine spatial and environmental variables which are more important in explaining the variation in the epiphyte matrices. For each variable entered, a permutation test was performed to assess the significance of its additional contribution to the explanation of variability ($\alpha = 5\%$).

Because station 78 is sharply separated from the others in the PCA ordination based upon the environmental variables, we wanted to test whether the patterns we obtained had been biased by the presence of this outlier station. Therefore, the variation partitioning was first performed on all 40 samples (8 sites × 5 replicates) and then repeated after omitting the five replicates of station 78.

To represent the spatial structure of the different fractions of variation of the epiphyton data, we separately mapped their first canonical axes. The contour maps and the clipping contours of the lake were produced using the contour mapping program MacGridzo 3.30. The interpolation algorithm used for gridding employs the inverse-distance-weighting method (Ripley 1981).

Results

Environmental and spatial variables

The most important environmental and spatial variables selected by the forward selection procedure for the 61 epiphyton taxa, the 6 larger

TABLE 3. Environmental variables selected by the forward selection procedure for the fine taxonomy (61 taxa), coarse taxonomy (6 groups), size classes (5 classes), and total biovolume epiphyte data. The selection was repeated after omitting station 78. The partial contributions of the variables to the total variance are listed in parentheses.

Fine taxonomy	Coarse taxonomy	Size classes	Total biovolume
All stations			
Chara (12%)	Colour (19%)	Colour (25%)	*Vallisneria* (18%)
K_{water} (8%)	*Chara* (15%)	Cu_{water} (10%)	K_{water} (15%)
Zn_{water} (6%)	K_{water} (5%)	*Vallisneria* (6%)	Cu_{water} (9%)
Fe_{water} (6%)			
Colour[a] (3%)			
Temperature[a] (3%)			
Ceratophyllum[a] (3%)			
Station 78 omitted			
Chara (13%)	*Chara* (18%)	*Ceratophyllum* (24%)	Depth (16%)
K_{water} (11%)	K_{water} (14%)	Depth (15%)	N_{water} (11%)
Zn_{water} (9%)	Zn_{water} (9%)	N_{water} (9%)	Turbidity (8%)
Fe_{water}[a] (4%)		P_{water} (5%)	
Ceratophyllum[a] (4%)			
Temperature[a] (4%)			

[a] Variables omitted when performing partial CCA because of collinearity caused by the inclusion of the spatial variables.

taxonomic groups, the 5 size classes, and the total biomass are reported in Tables 3 and 4. Because several of the environmental variables are highly correlated, forward selection yields only a small subset of significant variables. The subsets selected by the analysis are not unique because many variables contribute similarly to the total variation (Montgomery and Peck 1982). Moreover, some environmental and spatial variables retained by the forward selection procedure were later discarded because collinearity was observed when both sets of variables were included in the partial canonical correspondence analysis (Tables 3 and 4).

When all the stations were included in the analysis, most of the significant variables were those that discriminated station 78 from the others in the PCA (colour, Fe, Cu, *Vallisneria*). With station 78 omitted, the variables that explained most of the variance for the fine and coarse taxonomy were very similar: *Chara*, K, and Zn. Depth and nitrate are more important in explaining the variance of the total biomass and of the size classes. For size classes, *Ceratophyllum* presence was also important.

One or two monomials were sufficient to explain the spatial variation of all the matrices, except in the case of the fine taxonomy where the situation was more complex (Table 4); even in that case, a third degree polynomial was sufficient to describe spatial variation. The omission of station 78 appeared to have little influence on the monomials chosen by forward selection.

Partition of the variance

Partial canonical ordinations partitioned the epiphyton variation in four parts: a) variation explained by the environmental variables independently of their spatial structure; b) variation explained by the spatially structured component of the environmental variables (covariation between environmental variables and spatial coordinates); c) strictly spatial community variation; d) unexplained variation. The relative importance of these fractions for the epiphyton, at different resolution levels, is illustrated in Figure 2. Environmental factors (fraction a + b) always explained a substantial portion of the total variation (32 to 54%); a large part of this variation (50 to 80%) resided, however, in the spatial structure of the environmental variables (fraction b).

The periphyton community structure, as explained by the environmental variables, is mapped in Figures 3 (fine taxonomy) and 4 (size classés); only canonical axis I of each fraction is

TABLE 4. The spatial monomials retained by the forward selection procedure for the fine taxonomy (61 taxa), coarse taxonomy (6 groups), size classes (5 classes), and total biovolume epiphyte data. The analysis was repeated after omitting station 78. The partial contributions of the variables to the total variance are listed in parentheses.

Fine taxonomy		Coarse taxonomy		Size classes		Total biovolume	
All stations							
y^3	(10%)	x^2	(20%)	x^2	(27%)	xy	(19%)
y	(8%)	xy	(8%)	xy	(9%)		
x^2	(7%)						
x^3 [a]	(7%)						
x^2y [a]	(5%)						
Station 78 omitted							
y^3	(10%)	x^2	(25%)	x^2	(31%)	xy	(20%)
y	(10%)						
x^2	(10%)						
x [a]	(6%)						
xy^2 [a]	(4%)						

[a] Variables omitted when performing partial CCA because of collinearity caused by the inclusion of the environmental variables.

represented here. Both figures show that the effects of environmental variables (a + b) consisted of a spatially well-structured fraction (b) plus a spatially unstructured component (a). When representing fraction (a), one faces the inherent contradiction of mapping a structure whose spatial component has been removed; since an interpolation algorithm would always produce an impression of continuity between the observation points, we chose to represent the non-spatially-structured fraction (a) in the form of plateau polygons, where each point of the map is estimated to have the same value as the closest observed value (Isaaks and Srivastava 1989). It became obvious then that there was no continuity among sampling stations on the maps of fraction (a): each sampling location produced a value that was different and independent from the other locations. Figures 3 and 4 show clearly that the environmentally explained variation (a + b) was largely spatial (b). In both cases, there was a gradient in the periphyton structure, with canonical axis values increasing from south to north. In Figures 3 and 4, this general trend is valley-shaped in the west-to-east direction, with higher values on both sides of a central channel.

Strictly spatial variation (fraction c) accounted for only a small and insignificant portion of the variation (Fig. 2), with the exception of epiphyton expressed through fine taxonomy; it appears that most of the spatially structured processes occurring at the scale of this study (average of 4 km between neighboring stations) were accounted for by our environmental variables.

The amount of unexplained variation (fraction d) was fairly high (43 to 64%) especially when the community was described by the total biomass or the fine taxonomy. A large part of this fraction was represented by the variance among replicates within stations; this was shown by the fact that the unexplained variance was greatly reduced (75 to 85% reduction) when site

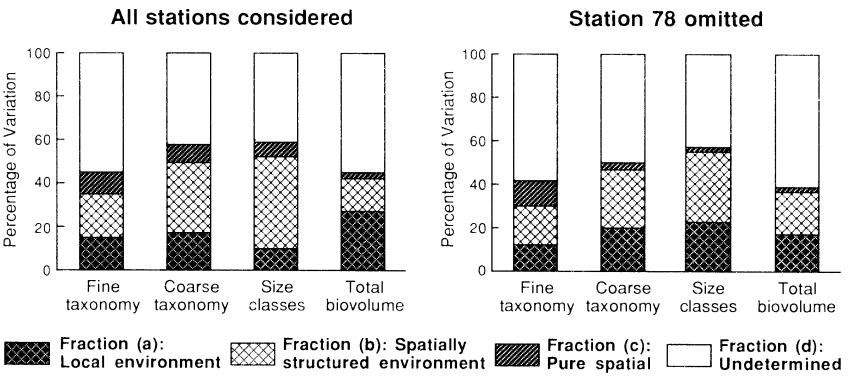

FIG. 2. Variation partitioning of the epiphyton fine taxonomy (61 taxa), coarse taxonomy (6 classes), size classes (5 classes), and total biovolume. Analyses were performed considering all stations and then repeated after omitting station 78.

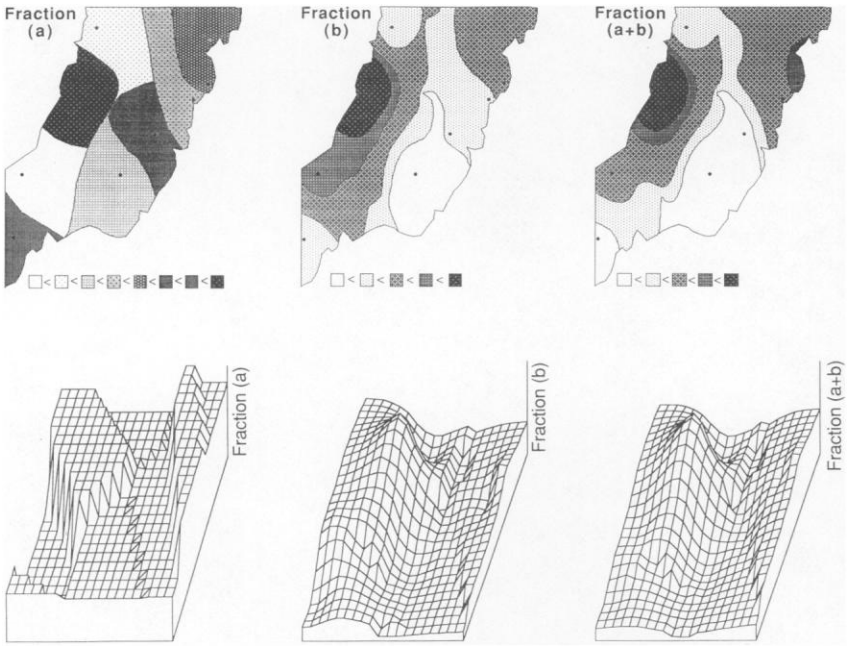

FIG. 3. Epiphyton described through 61 taxa. Maps of the first canonical axes of fractions a (environmental variation not spatially structured), b (covariation between environment and space), and a + b (total environmental variation). Station 78 is included. The 3-D maps (on the bottom) represent the same areas as the contour maps (on the top) that show the position of the sampling stations. In the three panels, shadings represent different scales, but values increase with the density of shading everywhere. The vertical scale on the 3-D maps varies among panels.

averages (8-line data sets) were substituted for single measurements (40-line data sets) in the analyses (Table 5). This variance was not accounted for by our environmental variable measurements, which were averages over each site.

The omission of outlier station 78 from our analysis did not change the patterns observed when all stations were considered.

Discussion

The role of the environmental variables is rather important in explaining epiphytic variation, even if their range of variation is limited in the present study (Table 2). Besides chemical variables (nutrients and metals), our analysis suggests the importance of physical factors (depth and colour) on epiphyton distribution and abundance. The only biotic variable that we tested was the macrophyte type, which also was important. This effect, however, could be related to some other unmeasured physical or chemical variables because a single type of plant was predominant at each station. The importance of the macrophyte host is a subject of debate (Lalonde and Downing 1991, Cattaneo and Kalff 1980). Depth (Lalonde and Downing 1991), nutrients (Ennis 1975, Cattaneo and Kalff 1980, Lalonde and Downing 1991) and metals (Genter et al. 1987, Crossey and La Point 1988, Cattaneo 1992) have all been shown previously to affect periphyton biomass or taxonomy. It is more difficult to interpret the importance of potassium in the analysis, considering its narrow range of variation (Table 2). Potassium could, however, be associated with some other measured or unmeasured variable whose interpretation would be more ecologically meaningful. It should also be kept in mind that the forward selection procedure could lead to different subsets because of high correlations among factors, as stated above, so that single factors should be interpreted cautiously.

Although 30–55% of the epiphytic variability could be accounted for by a few environmental variables, the part of that variability (50 to 80%)

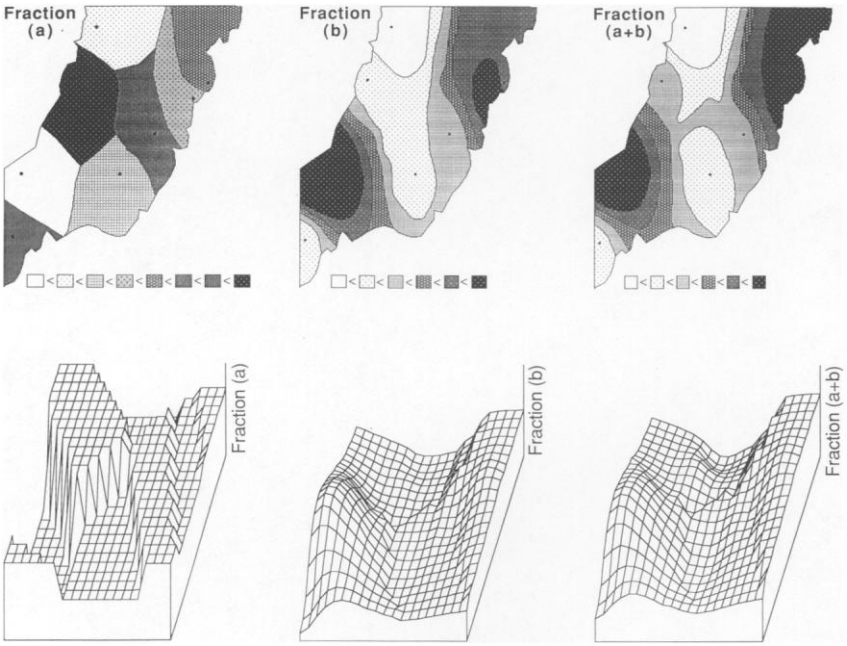

FIG. 4. Epiphyton described through five size classes. Maps of the first canonical axes of fraction a (environmental variation not spatially structured), b (covariation between environment and space), and a + b (total environment variation). Station 78 is included. The 3-D maps (on the bottom) represent the same areas as the contour maps (on the top) which show the position of the sampling stations. In the three panels, shadings represent different scales, but values increase with the density of shading everywhere. The vertical scale on the 3-D maps varies among panels.

that could be attributed to the spatial component of these environmental variables was not negligible. That part of the variability, in particular, may be related to the measured environmental variables, but it may also be confounded with other spatially structured environmental factors (or by historical events) not included in the analysis. Such factors may influence both the environmental variables in the analysis (or covary with them) and the community spatial structure (Borcard and Legendre 1993). In the lake section that we studied, industrial discharges come mostly from the south shore; the channel-like structure in periphyton community structure may well be a response to these pollutants transported by currents or to the currents themselves (Figs. 3 and 4). The city of Cornwall, further upstream (west), is a significant source of metal pollution (Sloterdijk 1985), so that the water entering our map from the most southwestern station (78) is also heavily polluted. There is an apparent response (low canonical axis value) by the periphyton community at this station. The peaks on the northwestern shore probably reflect the effect on periphyton of the inflow of several tributaries draining a mostly agricultural watershed. In our example, therefore, the location of industrial and agricultural discharges appears to control the spatial distribution of periphyton. Because of this sharing of variance between spatial and

TABLE 5. Percentages of unexplained variance (fraction d) observed when analyses were performed using all replicates (40-line data sets) and site averages (8-line data sets). The difference between the two percentages indicates the portion of variance attributable to replicates.

	Unexplained variance (%)		
	Replicates	Averages	Difference
Fine taxonomy	58.3	19.9	38.4
Coarse taxonomy	46.6	9.6	37.0
Size classes	44.4	6.8	37.6
Total biovolume	56.5	13.4	43.1

environmental variables, one has to be careful when extrapolating the resulting models to other locations.

Several processes could account for the small-scale (10-m) heterogeneity that we observed between replicates and that is often reported in periphyton studies (Weitzel et al. 1979, Morin and Cattaneo 1992). Substratum age influences colonization time and consequently epiphyton biomass (Sand-Jensen and Sondergaard 1981). A macrophyte bed contains many microenvironments where current, and consequently water renewal, and light conditions are different. A similar or higher amount of heterogeneity could be expected on the stony bed of a lake or stream. The nutrient regime measured in water could be very different from that of the periphytic algae which can use nutrient released by the sediment (Hansson 1988) or the plant substratum (Burkholder and Wetzel 1990). Grazers, which are important in regulating the quantity and quality of periphyton (Lamberti and Resh 1983, Cattaneo 1983), have a patchy distribution (Downing 1979) and probably a patchy impact on the algae. To improve periphyton models we should concentrate on these variables that are likely to vary at smaller scales. Microelectrodes, able to measure the fine grain of the environment around the periphyton, appear promising (Revsbech and Jørgensen 1986), but are unlikely to become standard tools in large environmental surveys. A significant amount of variability associated with periphyton estimates, both at the subsampling (Biggs 1987) and at the counting levels (Willén 1976), could be reduced by improved methods. However, models at a small spatial scale have to contend with the variability introduced by stochastic events, such as the sloughing of part of the periphyton when the layer close to the substratum in a thick community dies. This stochasticity may fatally weaken predictions at a fine spatial scale. Besides, predictions at such scale are rarely meaningful for most questions of water management and monitoring. Nevertheless, this local variability should be considered in designing large-scale surveys so that enough replicates are collected to detect significant differences among sites (Morin and Cattaneo 1992).

Even though the partitioning of the variation was similar whatever state variables were used to describe the periphyton, some interesting differences were found (Fig. 2). The purely spatial portion (c) was significant only when the epiphyton was described at fine taxonomic level. This suggests that some unmeasured spatially structured processes are significant for the distribution of particular species. When more aggregate groups were considered, the importance of these processes waned, probably because species with similar taxonomy or size substituted for each other along the gradient. For similar reasons, the unexplained variation (fraction d) was larger when the community was described at a fine taxonomic level than when species were pooled in coarser taxonomic groups or size classes (Fig. 2). As Rigler (1982) suggested, community models based on species have low predictive power. In fisheries, coarser models also outperform highly detailed ones (Ludwig and Walters 1985). However, a complete lack of detail was equally unfruitful in this study. When the taxa were further grouped to obtain the total biomass, the fraction of unexplained variation increased to its largest value. This further pooling of different epiphyton fractions appeared to obscure part of the structure brought out by CCA and partial CCA analyses. This structure reflected differences among components of the community that may have balanced each other when we totalled the fractions to obtain total biomass. Differences in phosphorus uptake, carbon fixation, and susceptibility to grazing have been observed for different growth forms of stream algae (Steinman et al. 1992). Different benthic algae may respond differently to the environmental variables; and hence acidification (France and Welbourn 1992), metal contamination (Leland and Carter 1984, Cattaneo 1992), and eutrophication (Cattaneo 1987) have been observed to affect periphyton size structure and taxonomy, but not total biomass. Division of the community into functional groups defined by coarse taxonomy, size classes, or growth forms seems to be the most efficient basis for modelling. This division also could address the different contributions of these algal groups to the food base and to fouling. A thick diatom mat used by invertebrates (Lamberti and Moore 1984) and fish is ecologically and aesthetically different from a large mass of green filamentous algae that accumulates and decays on shorelines. The main appeal of total biomass is that it can be assessed rapidly by simple measurements of chlorophyll or dry weight. Recent technical ad-

vances could, however, facilitate the measurement of different periphyton fractions and their subsequent use in large-scale surveys. Complete pigment absorbance spectra are now more easily available, and their study could provide information on the taxonomic composition of algal assemblages (Eloranta 1983, Wilhelm et al. 1991). Video image analyses (Porter 1988) can also speed up the measurement of periphyton size structure. An overly detailed taxonomic analysis does not seem warranted for such a purpose.

In conclusion, our exploratory analysis suggests that 1) physical and biotic variables, as well as nutrients, should be measured and used as explanatory variables in models; 2) small-scale variability (10-m scale or less) is large and mostly unpredictable; larger-scale sampling programs should be designed to account for this heterogeneity; 3) for modelling, periphyton should be divided into functional groups based on coarse taxonomy or size classes; fine taxonomic description and total biomass appear to be less amenable to modelling. A judicious choice of the spatial scale of the observations and of the detail at which we describe the community is likely to improve our capacity to predict periphyton for lake and river management and biomonitoring purposes.

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