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HIERARCHICAL ANALYSIS OF COMMUNITY AND HABITAT STRUCTURE

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Abstract. The covariance structure of a freshwater mussel community and its habitat were analyzed using a hierarchical approach. Nested Analyses of Variance and Covariance were used to partition the variability and covariability of species abundances and habitat descriptors into two spatial scales differing by six orders of magnitude. Principal Component Analysis was then used to describe the community and habitat structure at each scale. For the mussel community, there was more of structure present at the site than the bay scale. Variation in *Lampsilis radiata* dominated the community structure at both spatial scales, but a second, independent gradient of *Anodonta grandis* and *Proptera alata* abundance was present at the bay scale. Secondary and tertiary gradients at the site scale described correlated variation in *Anodonta grandis* and *Ligumia nasuta*, and the ratio of the two species, respectively. The habitat structure at the bay scale was greater in magnitude than that at the site scale, and was defined by a "sand-mud" gradient in sediment quality, with associated variation in alkalinity and calcium. The structure of the habitat at the site scale was more complex, with three independent gradients of organic content of the sediment, se liment coarseness, and pH of the water. Canonical Correlation was applied to each spatial scale to quantify relationsh ɔs between the mussel community and its habitat, but no strong association was found.

Introduction

McIntosh (1985; Ch. 4) describes the study of communities as "one of the oldest of concerns that may be defined as ecological", yet the concept of *community structure* has historically been vague even to those purporting to model, describe, and quantify it. "Limited membership" (Elton 1966), or "what does occur together constitutes a limited subset of what might occur together" (Roughgarden and Diamond 1986) comes close to defining "structure" for the community ecologist. This definition is useful, but it lacks an explicit consideration of the spatial and temporal scale of the "structure". Specifically, the spatial and temporal extent of the pool of taxa which "might occur together" needs to be defined, as well as the scale at which we examine what "does occur together". The scale of "might" is greater than the scale of "does", since the structure of a community at a given spatial or temporal scale can only be described by collecting data from a smaller scale. Careful definition of scale is important because different processes may affect community structure at different scales, so structure at various scales needs to be determined and compared if we seek some general understanding of community dynamics (*e.g.* Wiens 1989, Ricklefs 1987, Addicott *et al.* 1987, Frost *et al.* 1988).

Scale has been accepted as an important component of community ecology, but there still exists a gap between its recognition (*e.g.* Wiens 1989) and specific approaches to observational or experimental research. Many theoretical ecologists construct theory using a community matrix or food web of some arbitrary, presumably uniform, but usually unspecified scale. Behavioural ecologists describe patterns or carry out experiments on particular elements of a community matrix (*i.e.* pairs or small sets of species potentially interacting in predator-prey or competitive relationships). They use specific, methodologically tractable spatial and temporal scales, often smaller than the usual range and shorter than the lifespan of the species involved. Statistical ecologists draw ordination plots or dendrograms based on a choice of one or an unproclaimed mixture of scales, usually constrained by sampling methods. All three groups (theoretical, behavioural, and statistical ecologists) seek accurate predictions about community trajectories, and most at least attempt speculative extrapolation of their data to a long temporal or a large spatial scale.

Recently, a variety of approaches have been developed to assess variation in community structure at different scales (*e.g.* Allen and Starr 1982, Hanski 1982, Fairweather 1988, Legendre and Fortin 1989, Rose and Leggett 1990, Collins and Glenn 1991). In the present study, I illustrate a new technique for explicitly partitioning both community and habitat structure into various spatial or temporal scales, and then comparing the nature of and the relationship between habitat and community structure among the scales of

interest. The method is derived from "pattern analysis", first developed by Greig-Smith (1952) and Kershaw (1960) for spatial analysis of plants sampled in contiguous quadrats (see Kershaw 1973; Ch.7). Greig-Smith's approach to deciphering spatial pattern has been combined with multivariate analysis by several plant ecologists (*e.g.* Noy-Meir and Anderson 1970, Walker *et al.* 1972, Bouxin and Le Boulengé 1983, Galiano 1983, Castro *et al.* 1986). However, the present approach is easily applied to multiple spatial and temporal scales and non-contiguous sampling points. It also describes independent aspects of structure at each scale rather than successively pooling variation and covariation of species and habitat descriptors at larger scales. I demonstrate this new method in examining the filter-feeding, freshwater mussel (Unionidae) community of Inner Long Point Bay, Lake Erie. Two spatial scales were described, the bay itself (about 100 x 10^6 m^2) and sampling sites within the bay (about 100 m^2). Variation and covariation among sites, within the bay, was used to describe "bay-scale" community and habitat structure, while variation and covariation among sub-sites, within sites, was examined to describe "site- scale" community structure.

Materials and Methods

Sampling Strategy

Sets of three, circular (i.d.=1m) benthic samples were taken at each of 41 sites in Inner Long Bay, Lake Erie (42°38'N; 80°24'W) in June 1984 (for details of sampling see Bailey 1988). At each subsite, depth, %sand (%material by weight not passing through a 74 μm sieve), % Loss on Ignition (LOI), alkalinity, calcium, and pH were determined as described in Bailey (1988). Mussels were hand-collected with SCUBA from the top 10-15cm of sediment in each subsite.

Neglecting the time period over which the samples were taken (see Discussion), these data represent three

Table 1. Sample calculations of Nested ANOVA/ANCOVA for a) variance of *Proptera alata* and b) covariance of *P. alata* and *Lampsilis radiata*. a) Components of Variance of the abundance of *Proptera alata* ($\log_{10}$ transformed).

a) Components of Variance of the abundance of *Proptera alata* ($\log_{10}$-transformed).

Source	df	Sum of Squares (SS)	Mean Square (MS)	Expected MS
Sites	n-1=40	0.09898197	0.002475494*	$\hat{\sigma}^2_{SITE} + m_o \hat{\sigma}^2_{BAY}$
Sub-sites	$\sum_{i=1}^{n}(m_i-1) = 80$	0.16613494	0.002076687	$\hat{\sigma}^2_{SITE}$
Total	$\sum_{i=1}^{n} m_i - 1 = 120$	0.26511691		

* Calculated variance in "typical" study (multiplied by m_o ; see text) if data from sub-sites were averaged for each site.

$\hat{\sigma}^2_{SITE} = 0.002076687$; $\hat{\sigma}^2_{BAY} = \frac{MS(Sites) - MS(Sub\text{-}sites)}{m_o}$, where $m_o = \frac{\sum_{i=1}^{n} m_i - \frac{\sum_{i=1}^{n} m_i^2}{\sum_{i=1}^{n} m_i}}{n-1}$, or just "m" if there are an equal number of sub-sites (m) at all sites. In this study, $m_o = 2.95$, so :

$$\hat{\sigma}^2_{BAY} = \frac{0.002475494 - 0.002076687}{2.95} = 0.00013483091$$

spatial scales in the benthic ecosystem of Inner Long Point Bay . The largest scale is the entire bay (about 100 x 10^6 m^2), or at least the part of it within my sampling frame, while the middle scale is the approximately 100 m^2 area of each of the 41 sampling sites, and the smallest scale is the area of the sub- sites, the benthic samples themselves. For any community sampled at **s** scales (**s** = 2 in this case), we may define **s+1** spatial or temporal scales, which includes one scale *above* that which was sampled. I define the *community structure* of scale **i** as the variation and covariation of member species *among* units at scale **i-1**, *within* units at scale **i**. Thus, all the species occurring within the **i-1** sampling units determine the size of scale **i**'s covariance matrix. The size of this matrix may be considered representative of "what might occur together", while the magnitude and sign of its elements describe "what does (or does not) occur together" in the areas of scale **i-1** actually sampled.

Habitat structure is defined exactly the same way, but variation and covariation of habitat descriptors rather than species abundances are described. This definition of community and habitat structure limits analysis to the **s** largest scales, since no data concerning *structure* at the smallest scale (*e.g.* variation and covariation of the community and the habitat *within* sub-sites in the present study) are collected. Therefore, the present analysis examines and compares community and habitat structure at the "bay" and "site" spatial scales.

Statistical Analyses

The dataset consisted of three sets (m=3 sub-sites) of mussel abundances and habitat descriptors from each of the n=41 sites, with the exception of two sub-sites with missing LOI determinations. The total variance and covariance of the ($\log_{10}(x+1)$-transformed) abundance of the ten Unionidae species collected were partitioned between "within-site" (*i.e.* site scale) and "among-site" (*i.e.* bay scale) components using Model II ANOVA/ANCOVA (Bailey and Byrnes 1990). SAS Proc Nested (SAS Institute Inc. 1985) was used for this procedure. Sample calculations of both nested variation (Table 1a) and covariation (Table 1b)

b) Components of Covariance of the abundance of *Proptera alata* and *Lampsilis radiata* ($\log_{10}$-transformed).

Source	df	Sum of Products (SP)	Mean Product (MP)	Expected MP
Sites	n-1=40	-0.033264432	-0.000831611**	$\hat{\sigma}_{Pala \cdot Lrad(SITE)} + m_0\hat{\sigma}_{Pala \cdot Lrad(BAY)}$
Sub-sites	$\sum_{i=1}^{n}(m_i-1) = 80$	0.105722235	0.001321528	$\hat{\sigma}_{Pala \cdot Lrad(SITE)}$
Total	$\sum_{i=1}^{n} m_i - 1 = 120$	0.072457803		

** Calculated covariance in "typical" study (multiplied by m_0 ; see text) if data from sub-sites were averaged for each site.

$\hat{\sigma}_{Pala \cdot Lrad(SITE)} = 0.001321528$; $\hat{\sigma}_{Pala \cdot Lrad(BAY)} = \frac{MS(Sites) - MS(Sub\text{-}sites)}{m_0}$, $m_0 = 2.95$ (as above), so

$$\hat{\sigma}_{Pala \cdot Lrad(BAY)} = \frac{-0.000831611 - 0.001321528}{2.95} = -0.0007296731$$

illustrate the approach used and distinguish it from the "typical" analysis of such data (*e.g.* Bailey 1988), where means from sub-sites are calculated prior to univariate or multivariate analysis. As shown in the table, such an analysis is really carried out on "among-site" squares and products divided by m_o. The factor m_o is more or less the average number of sub-sites sampled at each site (see Table 1). The "typical analysis" will be more and more similar to the "among-site" analysis as m_o gets larger.

Variances and covariances were generated for each of the ten species and each of the 0.5 x 10(10-1)=45 pairs of species respectively at both scales. The resulting covariance matrices represented the "community structure" for the two spatial scales considered. Such a matrix is the "raw material" for various "R-analyses" of multivariate data such as cluster analysis or ordination (Legendre and Legendre 1983). I used Principal Component Analysis (PCA) to describe the community structure at each scale, as programmed in SAS Proc Factor (SAS Institute Inc. 1985). The same approach was used to partition and describe the habitat structure after $\log_{10}$-transforming all habitat descriptors except pH.

The usefulness of linear covariances for analyzing community structure with R-analyses like PCA has been challenged in the past. Legendre and Legendre (1983; pp. 211-215) argue convincingly that the joint absence of two rare species should not contribute to their positive covariance, since "the absence of a rare species in a given sample constitutes a stochastic phenomenon which does not necessarily indicate that the environment where it comes from is unfavorable to this species." There are three rationales I would offer for using linear covariances in the present context:

i) Joint absence of rare species contributes little to their calculated correlation. If 50 sites are sampled and neither of two rare species occur at 48 of them, while a single individual of each appears alone at the other two sites, the Pearson correlation between the species is −0.02 (non-significant!). If they are jointly absent at 48 sites, together at one, and only one appears at the fiftieth site, the correlation is +0.70. Rare species have means close to zero, and since covariances and correlations are computed by summing the products of deviations from the means of each species, joint presence actually affects the value and sign of the correlation far more than joint absences or individual presences.

ii) There is a stochastic element to joint *presence*, and it is only the coincident absence and presence of two species, above that expected by chance, which leads to a high observed correlation. The stochastic aspect of joint presence makes it desirable to weight similarity coefficients by the actual *abundance* of the two species (cf. Legendre and Legendre 1983).

iii) Applying the hierarchical approach to presence/absence (p/a) data, or similarity measures derived from such data, is unsatisfactory. Suppose p/a data from the 123 sub-sites in the present study were used to calculate a similarity measure such as Jaccard's coefficient, which does not count joint absences of species (Legendre and Legendre 1983). A similar approach could be taken with the 41 sites, counting each species as "present" if it occurred at any of the three sub-sites at a particular site. But ordinations from these two R matrices would confound the structure of the larger scale in the ordination of the smaller. This hierarchical confounding is a major limitation of other "multi-scale" analyses, where the data is analyzed separately for each of the several "block sizes" (*i.e.* spatial scales) sampled (*e.g.* Walker *et al.* 1972). The nested approach described here limits analysis at each scale to the structure present at that scale. Using linear covariances does limit the detection of structure at different scales to mutlivariate linear patterns. Although this was not a severe constraint with the present dataset, an alternative ordination technique such as non-metric multidimensional scaling may better retrieve structure of non-linear community patterns at the different scales.

Pearson correlations within and between mussel abundances and habitat descriptors were also generated using the technique described above, again at each of the two spatial scales. These were obtained using the estimated variance of variables **x** and **y**, $(\hat{\sigma}_x^2, \hat{\sigma}_y^2)$, as well as their covariance, $\hat{\sigma}_{x \cdot y}$, for either the bay or site scale:

$$r_{xy} = \frac{\hat{\sigma}_{x \cdot y}}{\hat{\sigma}_x \cdot \hat{\sigma}_y}$$

The relationship between mussel community and habitat structure was then quantified and described with Canonical Correlation, using SAS Proc Cancorr (SAS Institute Inc. 1985).

Results

The abundance of all mussel species found (listed in Table 2) varied far less among (diagonal of Table 3)

Table 2. Freshwater mussels (Unionidae) collected in Inner Long Point Bay, Lake Erie.

Species	Abbreviation
Anodonta grandis grandis Say 1829	Ag
Anodonta imbecilis Say 1829	Ai
Elliptio dilatata (Rafinesque, 1820)	Ed
Fusconaia flava (Rafinesque, 1820)	Ff
Ligumia nasuta (Say, 1817)	Ln
Lampsilis radiata siliquoidea (Barnes, 1823)	Lr
Lampsilis ventricosa (Barnes, 1823)	Lv
Proptera alata (Say, 1817)	Pa
Pleurobema coccineum (Conrad, 1836)	Pc
Villosa iris (Lea, 1830)	Vi

Table 3. Dispersion matrix (variances x 10^6 on diagonal; covariances x 10^6 on off-diagonal) of log_{10}-transformed mussel species abundances: Bay spatial scale. Total variance = 0.01265. Species abbreviations as in Table 2. Those species not appearing had zero variability at this scale.

	Ag	Lr	Pa
Ag	1403.1	-83.4	663.0
Lr		11109.6	-729.7
Pa			134.8

than within (diagonal of Table 4) sites. Model II ANOVA indicated that seven of the ten species had 100% of their variability in abundance within sites (site scale structure); only *L. radiata*, *A. grandis*, and *P. alata* had measurable, bay scale structure. Their variability among sites (% $\hat{\sigma}^2_{among}$ = 34%, 13%, and 6% respectively), based on the components of variance estimates, was still less than their within-site variation. In contrast, most of the variation in habitat descriptors was among the sites (Table 4), with within- site variability (Table 5) ranging from 4% (alkalinity) to 26% (pH) of the total variances determined for each of the habitat descriptors.

Scree plots (Cattell 1966) of the eigenvalues from the PCA 's of the mussel abundance data (Fig. 1a) showed the presence of three interpretable gradients at

Table 4. Dispersion matrix (variances x 10^6 on diagonal, covariances x 10^6 on off-diagonal) of log_{10}-transformed mussel species abundances: Site spatial scale. Total variance = 0.05179. Species abbreviations as in Table 2.

	Ag	Ai	Ed	Ff	Ln	Lr	Lv	Pa	Pc	Vi
Ag	9573.2	0.0	0.0	0.0	377.6	2560.0	755.2	-943.9	-377.6	819.3
Ai		3407.4	0.0	0.0	755.2	948.5	0.0	-377.6	0.0	0.0
Ed			2265.5	0.0	0.0	0.0	0.0	0.0 .	0.0	0.0
Ff				1510.3	755.2	-976.0	0.0	0.0	0.0	0.0
Ln					8693.5	-598.4	0.0	-377.5	0.0	0.0
Lr						21244.3	-377.5	1321.5	755.2	819.3
Lv							1510.3	-377.6	-377.6	0.0
Pa								2076.7	755.2	0.0
Pc									755.2	0.0
Vi										755.2

Table 5. Dispersion matrix (variances x 10^6 on diagonal, covariances x 10^6 on off-diagonal) of log_{10}-transformed (except pH) habitat descriptors: Bay spatial scale. Total variance = 0.27264.

	Alkalinity	pH	Ca	Depth	%Sand	LOI
Alkalinity	2868.0	-3092.9	2320.7	-583.6	-16538.1	11693.1
pH		23867.2	-3983.7	-3791.9	24432.5	-19186.4
Ca			2304.9	215.4	-1355.1	9096.8
Depth				11470.4	-9397.1	7864.9
%Sand					148516.6	-101171.0
LOI						83617.8

Table 6: Dispersion matrix (variances x 10^6 on diagonal, covariances x 10^6 on off-diagonal of log_{10}-transformed (except pH) habitat descriptors: Site spatial scale. Total variance = 0.03752.

	Alkalinity	pH	Ca	Depth	%Sand	LOI
Alkalinity	122.1	191.8	-22.5	-15.9	-9.9	184.5
pH		8218.8	-217.7	-311.0	-1720.9	126.6
Ca			441.8	72.6	-12.8	704.2
Depth				1664.8	-459.8	536.2
%Sand					11232.6	-156.2
LOI						15844.9

the site scale and only two at the bay scale. The first and subsequent components in the subjectively determined "flat zone" of a Scree plot (PC4 for site and PC3 for bay in Fig. 1a) represent random variation and covariation and should not be interpreted. A 3-dimensional scatter plot of the eigenvectors from PC1-PC3 (Fig. 2) showed the variation in community structure at the two scales. The coefficients from three PC axes are shown in each plot, even though only two gradients were interpretable at the bay scale. This allows visual comparison of this aspect of structure at the two scales. Variables important in defining the various axes will have eigenvector coefficients close to ±1. *L. radiata* dominated the first axis of both the site and bay PCA's, but the second gradient at the bay scale indicated a positive association between *P. alata* and *A. grandis* . The second gradient at the site scale showed a positive association between *A. grandis* and *L. nasuta*. There was no third gradient at the bay scale, while a third axis at the site scale revealed a gradient of varying ratio's of *A. grandis* and *L. nasuta* (*i.e.* their eigenvector coefficients had opposite signs). In summary, from site to site within the bay there was a large amount of variation in *L. radiata* abundance. Independent of this variation, there were positively correlated fluctuations in the abundance of *A. grandis* and *P. alata*. Within a given site, on average, the abundance of L. radiata varied substantially from sub-site to sub-site. Independent of this variation, *A. grandis* and *L. nasuta* positively covaried from sub-site to sub-site while the ratio of their abundances also fluctuated independently.

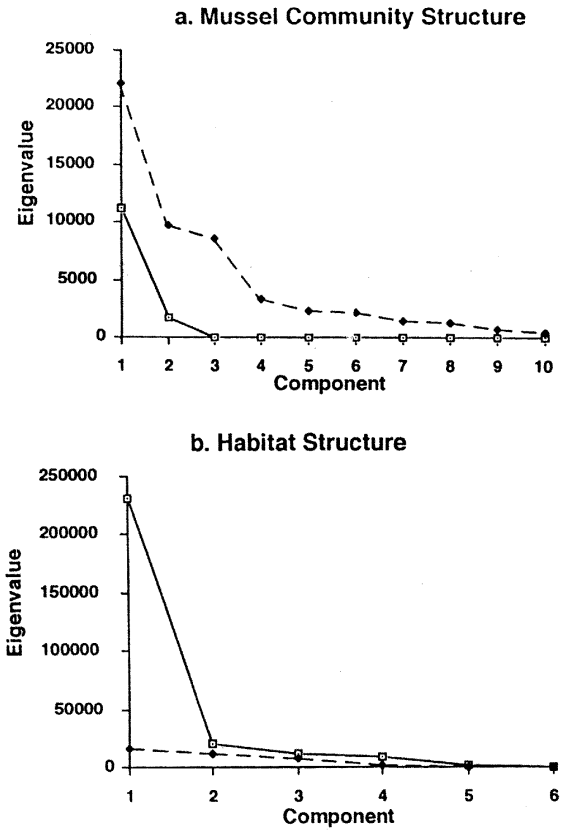

Figure 1. Scree plots (Cattell 1966) from PCA's of a) Mussel Community Structure, and b) Habitat Structure (dashed lines: site scale; solid lines: bay scale). Eigenvalues are multiplied by 10^6 on both plots.

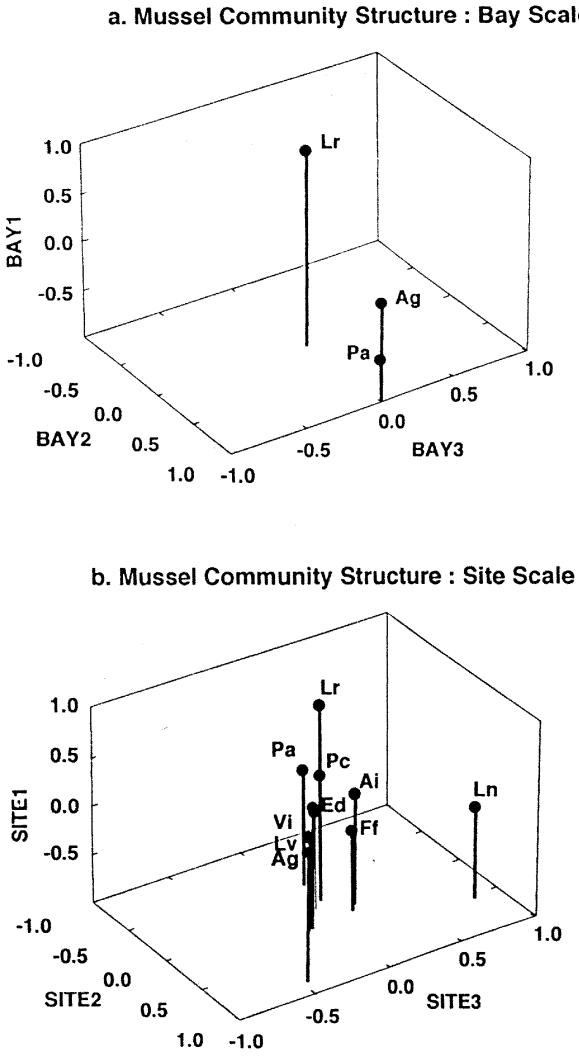

Figure 2. Eigenvectors from the first three principal components of mussel community structure at a) Bay scale, and b) Site scale.

Scree plots showed that habitat structure was limited to one gradient at the bay scale but three at the site scale (Fig. 1b). Normalized eigenvectors (Fig. 3a) indicated an environmental gradient of muddy (high LOI, low %Sand) to sandy sediments among sites in the bay, with higher concentrations of both alkalinity generating anions and calcium in the muddy areas. Once again, three sets of axis coefficients are plotted

for the bay scale to allow comparisons with the site scale. The first principal component accounted for about 85% of the "bay scale" habitat structure, but only 42% of the "site scale". At the site scale (Fig. 3b), there are three independent gradients of variability in LOI (sediment organic content), %Sand (sediment coarseness), and pH of the water respectively.

The relationship between community and habitat structure, quantified using Canonical Correlation, was weak at both spatial scales. The first Canonical R^2 value was higher at the bay (R^2 = 0.47) than at the site scale (R^2 = 0.23), but both were non-significant ($p \geq 0.3$). Redundancies of the first axes were also low for both scales. At the bay scale, CC1 for the habitat descriptors explained only 5% of the structure of the mussel community. CC1 for the mussel species at the same spatial scale explained only 15% of the variance in habitat descriptors. Redundancies were even lower at the site scale. CC1 for the habitat descriptors explained 2% of the mussel variance while the mussel CC1 explained 4% of the habitat structure. Since there was a weak relationship between the community and habitat structure, the coefficients for the canonical axes were not interpreted. However, a few individual correlations between mussel abundance and habitat descriptors were markedly different at the two spatial scales. *A. grandis* was negatively correlated with alkalinity (r =-0.40) and calcium (r=-0.57), and positively correlated with pH (r=0.41), at the bay scale. At the site scale these three correlations were tiny (r_{alk}=-0.06; r_{Ca}=-0.05; r_{pH}=0.02). Similarly, *P. alata* was negatively correlated with depth (r=-0.43) and pH (r=-0.38), and positively correlated with %sand (r=0.41), at the bay scale. At the site scale these relationships were not observed (r_{depth}=0.22; r_{pH}=0.05; r_{sand}=-0.09).

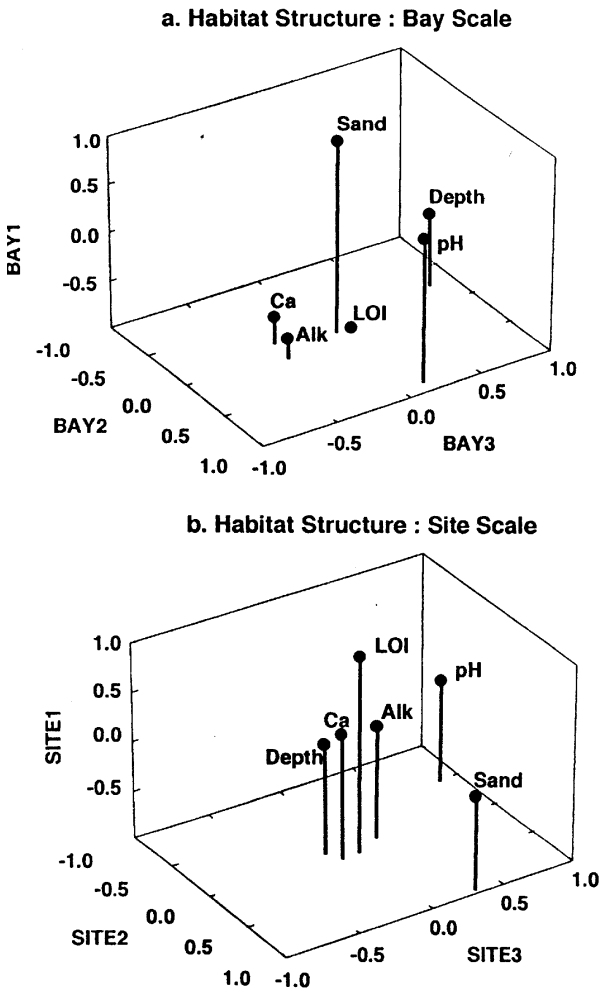

Figure 3. Eigenvectors from the first three principal components of habitat structure at a) Bay Scale and b) Site Scale.

Discussion

Lampsilis radiata, the most abundant mussel in Inner Long Point Bay (Bailey 1988), dominated the community structure at both spatial scales examined. The relationship between the mean and the variance of the density of most organisms is quite strong (Downing 1979), and the importance of a species in contributing to axes of a PCA of the covariance matrix is at least partially due to its own variance. Therefore, it might be argued that *L. radiata* more or less "automatically" dominated the community structure because of its abundance. This may be true at a particular scale, although it does not follow that the great abundance and variation of *L. radiata* should be ignored in either descriptions of or hypotheses explaining the community structure at this scale. It can be shown that high bay-scale abundance and variability does not necessarily cause large site-scale variability, and vice-versa. I carried out simple simulations where I used the observed among-site (bay scale) variability and covariabilty of mussel species while altering values of the within-site (site scale) covariance matrix, and did the pair of PCA's described above. An abundant species may have a relatively constant average site density, and therefore contribute little to a description of structure at the bay scale. However, it may vary substantially among subsites within each site, perhaps correlated with another species or a particular habitat descriptor. It will therefore play a major role in describing community structure at the site scale. The abundant *L. radiata* was an important descriptor of structure at both scales, and it would be interesting to use this approach with other datasets and see if this is a general phenomenon.

Secondary aspects of structure varied at the two scales. The positively correlated fluctuations of *A. grandis* and *P. alata* at the bay scale may indicate similarity in response of the two species to either unmeasured habitat features or biological factors (predation,

parasitism, competition). Interpretation of this aspect of structure should be constrained by the raw data. *P. alata* was only present at three sites, two of which also had *A. grandis* present. *A. grandis* occurred at ten sites without *P. alata*, and there were 28 of the 41 sites where neither species occurred. The secondary and tertiary gradients at the site scale involving *A. grandis* and *L. nasuta* may be explained by a similar suite of hypotheses as the bay- scale gradient described above. Again, these gradients should be interpreted with caution, since they explain much smaller amounts of the community structure at the site scale than the first gradient.

It is useful to compare a previous analysis of the habitat structure described by this dataset (Bailey 1988) with the present, hierarchical approach. In Bailey (1988), means of habitat data from the sub-sites at a given site were used to do a PCA. This was similar to the bay scale analysis in the present study, but the AMS/m_o and AMP/m_o were used rather than the specific components of variance and covariance for the bay scale (see Table 1). Interpretation of the major habitat axis was the same in both analyses (*i.e.* sand-mud gradient), but the hierarchical technique identified the positively correlated fluctuations of calcium and alkalinity with sediment muddiness not detected by the original analysis. Thus, the hierarchical approach may uncover trends in habitat or community structure which are obscured by pooling scales of structure in the analysis. Of course, the habitat structure at the smaller, site scale was not part of the original analysis (Bailey 1988) of this dataset. The hierarchical, nested technique has revealed structure at this level not previously apparent , and also enabled a direct comparison of its magnitude to that of the bay-scale structure.

Although the species richness of aquatic macrophytes and the other bivalve community in Inner Long Point Bay, the fingernail clams (Sphaeriidae) , are strongly related to the main axis of habitat structure at the bay scale (as calculated in Bailey 1988), little relationship was found at either the bay or site scales between the unionid community and the habitat descriptors used in this study. Possibly other, unmeasured physical or chemical factors could better explain the community structure of the Unionidae in Inner Long Point Bay. Alternatively, as suggested above, biological factors such as predation, spatial variability of the fish hosts of unionid larvae (glochidia), parasite loads or competition may help explain the structure at the spatial scales considered. Only controlled experiments carried out at these scales will elucidate the mechanisms responsible for the patterns observed. I would suggest that only hypotheses to explain the first component axes of community structure be considered experimentally at either scale. The Scree plots were quite liberal in determining what was an interpretable gradient of community structure.

It has recently been asserted that ecological communities must be viewed from a hierarchical perspective (*e.g.* Ricklefs 1987, Addicott *et al.* 1987, Frost et al 1988, Wiens 1989). The specific approaches to looking at communities hierarchically can be broken into three categories, i) hierarchically pooled ordinations (*e.g.* Allen and Star 1982), ii) spatial and temporal autocorrelation (reviewed in Legendre and Fortin 1989), and iii) species abundance curves (*e.g.* Kolosa 1989, Collins and Glenn 1990). The technique of hierarchical, nested analysis described here is a useful addition to this suite of methods, in that it partitions community and habitat structure among different scales in the hierarchy, and allows assessment of both the magnitude and nature of structure at each level. Many applications of the approaches listed above have successively pool variation and covariation at the various scales considered, or require an ad hoc detection of scale- dependent processes from a mixed-scale ordination plot. The hierarchical, nested analysis avoids these problems, but can only detect community and habitat structure, and the relationship between them, at the **s** largest scales considered (see Materials and Methods). Thus, there is still a requirement for the community ecologist to carefully choose a series of spatial or temporal scales of sampling (see Frost *et al.* 1988) which entirely depend on the nature of the community and the goals of the research.

My method of analyzing nested covariance matrices explicitly recognizes the various scales of data collection and community structure. Well-designed observational studies, analyzed in this fashion, will enable ecologists to begin deciphering the complex processes, at many scales, which combine to give a community its rich structure. Such information can then suggest experiments designed at an appropriate single (or set of) spatial and/or temporal scale(s). For example, the nature of the substratum could be varied at a very small (*e.g.* $1m^2$), intermediate (*e.g.* $10m^2$) and relatively large (*e.g.* $100m^2$) scales, and the resulting impact on the mussel community structure at each of these scales could then be compared. The technique neither searches for nor proposes the "correct" scale to study a particular community, since different scales may reveal different processes (chemical, physical, and biological) which help to determine its structure.

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