MACROBENTHOS OF HAMILTON HARBOUR

TOWARDS A MULTISCALE, SPATIALLY EXPLICIT ANALYSIS OF THE LITTORAL ZONE MACROBENTHOS ALONG THE NORTH SHORE OF HAMILTON HARBOUR

by

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A Thesis
Submitted to the School of Graduate Studies
in Partial Fulfillment of the Requirements
for the Degree
Master of Science

McMaster University

MASTER OF SCIENCE (1995) McMaster University

(Biology) Hamilton, Ontario

TITLE: Towards a Multiscale, Spatially Explicit Analysis of the Littoral Zone Macrobenthos Along Hamilton Harbour's North Shore.

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NUMBER OF PAGES: ix, 79

Abstract

Macrobenthos and macrophytes of the north shore littoral zone of Hamilton Harbour were extensively sampled in late August 1994. Benthic community structure is described, including the presence of several oligochaete and chironomid genera previously unreported in the harbour. Community structure is scale dependent and identifying which spatial scales contribute important structure is a useful step in determining which environmental factors have the greatest impact on the benthic community. This information can be used to plan efficient benthos monitoring programs, and to construct spatially explicit models of the harbour ecosystem. Most of the variation in the data set (approx. 88%) is due to small scale patchiness, probably related to patchiness of the macrophyte community and sediment grain size, as well as biotic processes such as predation and competition. Large scale structure is related to a water depth gradient, probably involving changes in dissolved oxygen concentrations, light attenuation, and sediment grain size. Macrophytes also respond to this gradient. There is little important structuring of the benthos community at intermediate spatial scales. Models of benthic communities in the harbour must deal with spatial pattern effects such as autocorrelation. Additionally, spatial patterns provide information useful for understanding causes of community structure. A method is developed for the spatial pattern analysis of the benthic community data, which allows the simultaneous evaluation of patterns at various scales, with minimal mixing of information between scales.

Acknowledgments

I would like to thank Bob Vanyo for many hours of arduous work sorting and identifying invertebrates. Similarly, I extend my gratitude to Lauren Mansfield for her contribution. Vince Rutter deserves recognition for his help in the field, as does Rick Brown, who transformed sanity-testing afternoons on the harbour into moments of calm contemplation of "kitchen philosophy". Jurek provided an open, friendly workplace, support and encouragement during moments of crisis, and direction when needed. His insights and contributions to my work are valued. Erin Fitzgerald and Catrien Bouwman occasionally assisted in the field and lab, yet it is their friendship I value most; thanks.

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1.0 INTRODUCTION

1.1 General Introduction

It is in the spatial and temporal patterns of species distribution and abundance that community ecologists seek to interpret the natural world. Hence, ecological theory is replete with models which imply spatial and temporal pattern; concepts of predation, competition, parasitism, population growth, dispersal, and migration are but a few examples (Legendre and Fortin 1989). It is therefore interesting that analytical methods which deal specifically with the problems of spatial pattern have been widely available to ecologists only recently (Legendre 1993, Borcard, Legendre and Drapeau 1992). Prior attempts to deal with spatially structured data sets have ignored the spatial structure and its effects on classical statistical analyses.

Classical statistical analyses assume that each observation in a sample is independent of all other observations. This is not the case with spatially structured data. Similar observations tend to aggregate so as to create patches of various sizes, or, in many cases, gradients. Consequently, observations are not independent and it becomes possible to predict the value of an observation at a particular point in space if the values of observations located nearby are known. Since observations are no longer fully independent, it is incorrect to assign each a full degree of freedom when analyzing them statistically. Usually this error is made, however, and tests are liberalized as a result, increasing the chances of rejecting a true null hypothesis (type I error) (Hurlbert 1984). On the other hand, if information concerning the lack of independence between observations (their autocorrelation) is obtained, it may be possible to modify statistical procedures to reduce the risk of making such an error. For example, single factor, non-nested Analysis of Variance (ANOVA) models that take autocorrelation into account have been developed and are available in the literature (e.g. Griffith 1978), although their implementation is not wide-spread.

Although spatial structure can be a nuisance in statistical analyses, it can also be of considerable interest in its own right (Legendre 1993, Levin 1992). Often it is the spatial structure in a data set that will provide clues as to the causes of community structure, such as indicating a pollution point source, a major migration corridor, or perhaps patchy resource availability. In other words, spatial pattern is a functional aspect of ecological communities (Legendre 1993).

Analyzing spatial patterns in large, many-variable ecological data sets is complicated by the fact that often several processes are acting upon the community at different spatial scales. In these instances, if spatial scales of observation are changed, the patterns observed in the data set will also change. Similarly, the patterns derived from an existing data set will often change when analytical procedures with different resolutions are used. These different patterns indicate that different processes become important in defining ecological structure at different spatial scales, leading to the conclusion that patterns at a variety of scales need to be studied in order to gain a good understanding of a particular ecological community.

This thesis presents research towards a multiscale, spatially explicit analysis of the macrobenthos along the north shore of Hamilton Harbour, on the west end of Lake Ontario. Hamilton Harbour is considered an "area of concern" within the Great Lakes Basin due to high levels of conventional pollutants and heavy metals, toxic organics accumulations in fish, contaminated sediments, eutrophication, and overall aesthetic degradation (Hamilton Harbour Remedial Action Plan Team 1992a). A Remedial Action Plan (RAP) for the Harbour has been developed to explain how a comprehensive rehabilitation of the Hamilton Harbour will be undertaken. The report highlights the need for "enhanced wildlife populations [in the Harbour area] through the preservation and rehabilitation of habitat" and "integrated management of fish and wildlife populations throughout the Harbour" (Hamilton Harbour Remedial Action Plan Team 1992b, p.111).

A study of littoral benthos community structure in the harbour is therefore appropriate considering that benthos are an important ecosystem component and provide information concerning long-term ecosystem response to a range of abatement measures (Hamilton Harbour Remedial Action Plan Team 1992b, p.300). Indeed, aquatic ecosystem studies must include benthic ecological processes as one of the various critical components in understanding overall aquatic ecosystem functioning.

The thesis is divided into five sections. Following this introductory section, a detailed description of littoral zone benthos along the north shore of Hamilton Harbour is given, detailing community structure correlated with water depth gradient, sediment trace metal concentrations, macrophyte community structure, and zebra mussel (*Dreissena polymorpha*) abundance. The next section reports on a partitioning of benthic community structure into contributions from five spatial scales of observation, and relates scale dependent structure to habitat descriptors. This section demonstrates that the benthos of the north shore littoral zone exhibits scale dependent structure, and discusses the implications of this structuring for further work on harbour benthos. The third section of this thesis develops a method for the analysis of scale dependent spatial patterns derived from a single multivariate data set, setting the stage for further work on benthos in the harbour. The method is illustrated using a simple simulated data set. The fifth and final section of this thesis provides concluding remarks.

1.2 Clarification of Contribution

Sections two, three, and four of this thesis represent papers prepared for publication by Mark Conrad and Jurek Kolasa. I developed the initial idea for the work reported in these papers. I also am responsible for the sampling design and analysis plans for each paper. Field and laboratory work was carried out by myself, with the assistance of lab mates, two undergraduate students, and several volunteers. Technical and scientific expertise and advice were provided by Jurek Kolasa, as were editorial contributions on the various drafts of the three papers prepared for publication.

2.0 MACROBENTHOS OF HAMILTON HARBOUR'S NORTH SHORE LITTORAL ZONE

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2.0 MACROBENTHOS OF HAMILTON HARBOUR'S NORTH SHORE LITTORAL ZONE

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2.1 Abstract

The macrobenthos of Hamilton Harbour's north shore littoral zone, to a water depth of three meters, was sampled intensively in late August 1994. The most abundant taxon in the benthic community is the zebra mussel, *Dreissena polymorpha*, which comprises approximately 20% of the total benthos count and is most abundant at two meters water depth. *Endochironomus* and *Limnodrilus hoffmeisteri* are the next two most abundant species, respectively. There is no depth effect for total number of chironomids or oligochaetes, although many individual species are significantly more prevalent at certain depths. Habitat quality indices, including an application of the Shannon-Wiener diversity index and two biotic indices, suggest that the littoral zone of the north shore of Hamilton Harbour is "moderately" polluted. Total macrophyte biomass, sediment trace metal concentrations and zebra mussel density are all correlated with total numbers of benthos (excluding zebra mussels) present at a site, with zebra mussels having a strong positive relationship.

2.2 Introduction

Hamilton Harbour is one of the most affected and modified portions of the Great Lakes ecosystem. In 1985, the International Joint Commission outlined its reasons for considering the Hamilton Harbour an "area of concern" within the Great Lakes Basin. These reasons included high levels of conventional pollutants and heavy metals, toxic organics accumulations in fish, contaminated sediments, eutrophication, and overall aesthetic degradation (Hamilton Harbour Remedial Action Plan Team 1992a). The Remedial Action Plan highlights the need for "enhanced wildlife through the preservation and rehabilitation of habitat" and "integrated management of fish and wildlife populations throughout the Harbour" (Hamilton Harbour Remedial Action Plan Team 1992b, p.111). Further, littoral zone habitat rehabilitation and management are indicated as desirable. Benthos is a key component of the littoral zone due to the role it plays in the food web, comprising a major food source for many fishes.

Understanding harbour ecosystem responses to remedial and management actions requires extensive biological knowledge of its various components, including littoral zone benthos. Knowledge of benthos in this region of the harbour, however, is inadequate, particularly in view of the most recent introduction of zebra mussels (*Dreissena polymorpha*). No intensive sampling of the littoral zone benthos in Hamilton Harbour has previously been undertaken. Earlier studies employed designs with widely dispersed sampling sites, useful for harbour-wide benthos mapping (e.g. Johnson and Matheson 1968), or single transect sampling designs aimed at providing depth profiles of benthic community structure (e.g. Hanna 1994). Both of these sampling designs provide useful information for a variety of management issues, but neither provide comprehensive data from the littoral zone

This study attempts to provide a description of harbour littoral zone benthos detailed enough for detection and quantification of future changes resulting from remediation and habitat management decisions. Specifically, we aimed to assess benthos composition, numbers, and spatial trends, particularly in the context of naturally occurring and anthropogenic environmental gradients. The approach we took was an extensive sampling at regular intervals in the littoral zone down to 3m water depth.

2.3 Materials and Methods

Over a two week period in late August 1994, the littoral zone of the north shore of Hamilton Harbour, from Carolls Point to Indian Creek, was sampled using a systematic transect design (Fig. 1). Sample sites were located along twenty-eight transects, each running from shore out into the harbour on a bearing of 150° from true north, with compensation for magnetic declination. Distance between transects alternated between 200m and 300m. Along each transect, three samples were taken at one, two, and three meters water depth, for a total of nine samples per transect.

For each sample, a 23x23 cm (9"x9") Ekman grab was used to capture an approximately constant amount of harbour sediment, along with any macrophytes and algae present within the sampling volume of the grab. A three meter long steel rod, graduated in meters, was attached to the release mechanism of the Ekman. This modification enabled fieldworkers to carefully work the Ekman grab into the sediment at the appropriate water depth before quickly pushing down on the rod, thereby releasing the Ekman grab's jaws. The sediment was washed in a 500 μm nitex mesh net and transferred to plastic specimen cups for storage, while macrophytes and algae were stored in plastic bags. While this method of collecting macrophyte and algal samples is not used in vegetation studies, we considered it adequate for sampling vegetation and benthos from exactly the same location.

In the lab samples were drained and stored in 70% ethanol until being sorted in white trays. Oligochaetes and chironomids were mounted on slides for identification to the genus or species level, whereas most other benthic organisms were identified at lower resolution (Appendix). Unidentified immature oligochaetes were allotted to the identified species at any one site in proportion to their abundance at that site. Unidentified chironomids were also proportionally allotted to chironomid species found at a site. Algae and macrophyte samples were dried for a minimum of 7 days, identified to the lowest level of classification possible given the quality of samples, and weighed to the nearest 0.001g.

To examine the effects of sediment trace metals on benthos distribution, previously collected data (Poulton, Morris and Coakley submitted) were incorporated into the habitat descriptors data set. We used a linear distance weighted interpolation method, with the interpolated values for the point lying closest to each transect being used as values for each site along that transect, since none of the benthos sample sites were located within the lattice of trace metal sample sites. Since the depositional process for trace metals in the harbour does not lead to patchy spatial distributions of sediment trace metal concentrations (rather, gradients are formed), this extrapolation procedure is considered to provide reasonable results (Morris pers. comm.). We use so transformed data for ten sediment trace metals (Table 1).

2.4 Results

2.4.1 Richness and composition

The 34543 benthic invertebrates collected from the littoral zone of the harbour represent forty-five separate taxonomic groups (Appendix). This is a conservative number since water mites, limpets, bivalves other than zebra mussels, and gastropods other than limpets are identified at taxonomic levels higher than genus. By comparison, only 31 taxa were identified in another recent study (Hanna 1994; data for 1989). This difference may be due to lake zones sampled. Hanna sampled along a transect running from the north shore out into the harbour, with only four sites at water depths of less than eight meters (Hanna 1994). In deeper water, benthic communities in the harbour are dominated by a few oligochaete species, including *Limnodrilus hoffmeisteri*, *Tubifex tubifex*, and *Quistodrilus multisetosus* (Hanna 1994, Johnson and Matheson 1968). Thus, the 1989 transect study provided fewer opportunities to sample sites with higher benthic species richness, and emphasizes the importance of oligochaetes in the benthic community structure of the harbour.

The Chironomidae is the most diverse group of benthic organisms in the littoral zone along the north shore, with a total of twenty-one genera identified, eleven not previously reported as present in the harbour (Table 2).

Oligochaetes are represented by 14 genera, including abundant taxa such as *Limnodrilus hoffmeisteri*, *Limnodrilus cervix*, *Nais* sp., *Stylaria* sp., and *Ophidonais serpentina*. Several other oligochaete taxa have not previously been found in the harbour

(Table 2). The remaining ten taxa include zebra mussel (*Dreissena polymorpha*), the amphipod *Gammarus* sp., water mites of various families, flatworm (*Dugesia tigrina*), isopoda (Asellidae), leeches, bivalves, limpets (Ancylidae), gastropods other than limpets, and dragonflies (in one sample only).

2.4.2 Depth distribution of dominant taxa

Chironomids and oligochaetes are the most abundant group of benthic invertebrates in the littoral zone of the harbour, respectively. As oxygen becomes a limiting factor, oligochaetes tend to dominate in deeper waters of the harbour (Hanna 1994, Johnson and Matheson 1968, Krantzberg and Boyd 1992). Neither group shows a clear depth related trend in the one to three meter water depth range. Based on 1989 data (Hanna 1994), this shift towards dominance of benthos abundance by oligochaetes probably occurs at depths between five and ten meters and therefore does not show up in this study.

The single most abundant benthic invertebrate in Hamilton Harbour in late August 1994 was the zebra mussel, *Dreissena polymorpha* (20% of the total number). No zebra mussels were observed in 1989 (Mongeau 1990, Hanna 1994) and the first observations of juvenile mussels were made in 1991 (Kolasa, *pers. observ.*). The zebra mussel are distributed across the entire north shore from Carrols Point to Indian Creek and are most abundant in the eastern half of the littoral zone. The zebra mussel are highly selective with respect to depth (ANOVA, p=0.017). They are most abundant at a depth of two meters

(62.2% of all zebra mussel), possibly being limited by wave action at shallower depths and by more silty substrate at greater depths (with only 8.7% occurring at three meters.

Among other important species, most show depth preferences. *Endochironomus* (17.5% of all invertebrates) is highly concentrated (92%) at two meters water depth. In addition, *Endochironomus* are also associated with aquatic vegetation. Absence of vegetation at a 3 m depth may explain low densities of (2.5%) at this depth, or may represent a similar response to decreasing dissolved oxygen concentration and light attenuation with increasing depth. However, if all sites are classified, using a k-means clustering algorithm, into two groups, one containing sites with little vegetation, the other containing sites with much vegetation, and this classification is used as a factor in an ANOVA of *Endochironomus* abundance, one does find a significant difference ($p<0.000000$) between the two groups, even when depth is specified as a covariant. Wave action and relatively coarse substrate may inhibit *Endochironomus* populations from attaining high densities at one meter depth in spite of this genus' preference for shallow, and therefore well oxygenated, water (Oliver and Roussel 1983). Another factor which may decrease the number of *Endochironomus*, and other benthic invertebrates, including *Dreissena polymorpha*, is ice "scouring" along exposed portions of the shoreline during winter.

Other abundant chironomids in the harbour's littoral zone include *Paratanytarsus*, *Polypedilum*, *Dicrotendipes*, *Cryptochironomus*, and *Paratanytarsus*. *Polypedilum* abundances are significantly greater at two and three meter depths than at one meter (Tukey's HSD test, $p<0.02$) even though it has been suggested that this genus prefers shallow, well oxygenated sites (Hanna 1994). Even less is known about requirements of *Paratanytarsus* or any of the Tanytarsini tribe species except that they inhabit large, still and flowing bodies of water (Oliver and Roussel 1983) making the interpretation of their presence and abundance difficult. Unlike the previously mentioned chironomids, *Dicrotendipes* is equally abundant at one and two meter depths but shows a significant decrease in numbers at three meters (6.6 % of abundance; Tukey's HSD, $p<0.000023$).

Amongst the oligochaetes, abundant taxa can be separated into two groups. One comprises two pollution tolerant species: *Limnodrilus hoffmeisteri* (dominant) and *Limnodrilus cervix*. The other comprises three naidid taxa: *Nais*, *Stylaria*, and *Ophidonais serpentina*, all of which indicate mesotrophic conditions and are generally associated with macrophytes. Except for *Ophidonais serpentina*, which is significantly more abundant at two meters than the other two depths (Tukey's HSD maximum $p<0.000023$), no other oligochaete showed any significant differences in abundance with increasing depth. Abundance of combined *Limnodrilus* species is about twice that of the naidids, suggesting that the littoral zone, while able to support pollution intolerant species, is still fairly eutrophic.

Gammarus concentrates in shallow water with only 4.1% of its numbers present at three meters water depth. In addition, *Gammarus* is strongly affected by the presence of vegetation (ANCOVA with a two level vegetation biomass factor as the main effect and water depth is the covariant, $p<0.0001$), with more amphipods present at sites with a lot of macrophytic growth. The effect of water depth as covariant was not a surprise because *Gammarus* are restricted to well oxygenated waters (Covich and Thorp 1991). Direct field observations suggest that *Gammarus* are associated with algal biomass ($r= 0.38$, $p<0.05$), which could provide protection from predation.

Not all taxa decline in numbers with depth. The water mites occur at greater densities at two and three meters, with only 7.3% of the total at the one meter depth. They can have significant impact on benthic communities through predation and parasitism on other invertebrates (Smith and Cook 1991).

2.4.3 Indices of habitat quality

The highest values of Shannon-Wiener species diversity index are observed at a depth of two meters, with a significant increase in diversity values from one to two meters (Tukey's HSD, $p=0.03$). Additionally, there is a slight increasing diversity trend from the eastern to western portion of the north shore, and this trend is most pronounced at a depth of one meter (Fig. 2). Surprisingly, there is no significant relationship between benthic species diversity and macrophyte density or richness, or sediment trace metal concentrations, even when depth is used as a covariant.

If compared to an earlier study (Wilhm and Doris 1968), the currently observed diversity values would suggest that most sites (94%) are still moderately polluted (i.e. eutrophic), having diversity values between 1.0 and 3.0. This interpretation may be incorrect, however, as low diversity values may be produced by a variety of causes, including major expansions of populations of invading species such as the zebra mussel.

Specific indicator species may also be used to monitor water or habitat quality. *Limnodrilus hoffmeisteri* and *Limnodrilus cervix* abundances are indicative of high levels of organic enrichment and low dissolved oxygen concentrations, since they are tolerant of eutrophic conditions but are poor competitors for resources in less polluted waters (Jaagumagi 1988). Their relative frequency of occurrence was 82% (*L. hoffmeisteri*), 58% (L. *cervix*), and 87% (when both considered jointly). On the other hand, *Nais*, *Ophidonais serpentina*, and *Stylaria*, are indicative of mesotrophic conditions (Hanna 1994) and are often associated with macrophytes (Brinkhurst 1986). While less abundant than *Limnodrilus* species, the naidids frequency is 60%. The fact that *Limnodrilus hoffmeisteri* and *Limnodrilus cervix* are more common and twice as abundant as naidids, tends to support the classification of the north shore littoral zone as moderately eutrophic.

Finally, total oligochaete densities can be used as an index of water quality (Wright and Tidd 1933). Using this method, sites with less than 1000 oligochaetes per square meter are considered negligibly polluted, sites with mean oligochaete densities of between 1000 and $5000/m^2$ are considered mildly polluted, and sites with means over $5000/m^2$ are considered severely polluted. Accordingly, 86.7% of all sites are considered negligibly polluted, with only eleven of 83 sites having oligochaete densities of greater than $1000/m^2$, none above $5000/m^2$.

2.4.4 Habitat characteristics: macrophytes, trace metal, zebra mussels

The macrophyte community was dominated by *Vallisneria americana*, although *Elodea canadensis*, *Cabomba* sp. and *Potamogeton* sp. were also present, along with five other species, unidentified due to damaged or small size of specimens. Surprisingly, only few significant yet weak correlations ($|r|<0.4$) exist between vegetation diversity (Shannon-Wiener index) and any of the indicator species discussed above. Benthos abundance was significantly correlated with macrophyte diversity, with $r = 0.25$, $p<0.5$ but correlations between macrophyte diversity and benthos diversity were not. Furthermore, ANOVA detected no macrophyte effects when sites were classified according to total macrophyte biomass using a k-means clustering algorithm (with $k=2$).

Correlations are also quite weak between zebra mussel and other benthic species abundances or against total benthos abundance. However, sites with one zebra mussel individual have significantly fewer chironomids and oligochaetes than sites with more zebra mussels (two-way ANOVA, $p<0.0001$). This result seems to support the hypothesis that increasing zebra mussel densities positively affect benthic populations. The primary cause for this increase is the deposition of feces and pseudofeces by the zebra mussel which may be a resource for other invertebrates (MacIsaac et al. 1992, Herbert et al. 1991). This increase is often be complemented by improved water clarity and thus higher local productivity (Herbert et al. 1991).

Frequency distributions of all ten trace metal concentrations in the sediment of the littoral zone are bimodal, suggesting a good separation of sites into two distinct classes (a k-means clustering of sites with respect to all ten trace metals with $k = 2$; Fig.3). Trace metal combined with the macrophyte and zebra mussel data in multi-way ANOVAs provides additional exploratory insights. For instance, when water depth, macrophyte class, and trace metal class are factors in a three way ANOVA of total benthic abundance, all three main effects are significant ($p<0.012$ for all three effects). In other words, the two-way ANOVA with macrophyte class and water depth as factors was confounded by trace metal concentrations in the sediment whose high concentrations are apparently limiting benthic species. Thus, contrary to the initial conclusions both trace metal contamination and macrophyte biomass affect benthic invertebrate abundance even though, taken individually, no effect has been found. Zebra mussel effects on benthos abundances appears to be more important compared to other habitat characteristics. In a three-way ANOVA (macrophyte biomass class, trace metal concentration class, and zebra mussel presence/absence) only the zebra mussel factor is significant (p=0.000001).

2.5 Conclusion

Benthic community structure in the littoral zone of Hamilton Harbour's north shore is clearly dissimilar to the benthos of the rest of the harbour. It is more diverse, appears to respond to heterogeneity in macrophyte community structure, trace metal concentrations, and the presence of zebra mussels. Future changes to these habitat characteristics resulting from fish and wildlife habitat management activities and further expansion of the zebra mussel population, will likely impact the benthic community thereby leading to modifications in the harbour food web, of which benthos, especially in the littoral zone, are an important part. This study provides good baseline information for future monitoring and habitat management assessment activities.

2.6 References

Brinkhurst, R.O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America. Canadian Special Publication of Fisheries and Aquatic Sciences 84. Department of Fisheries and Oceans, Ottawa, Canada.

Covich, Alan P. And James H. Thorp. 1991. Crustacea: Introduction and Pericardia. In: Ecology and classification of North American freshwater invertebrates. eds. Thorp, James H. And Alan P. Covich. Academic Press, San Diego, California.

Hamilton Harbour Remedial Action Plan Team. 1992a. Remedial action plan for Hamilton Harbour stage one report: Environmental conditions and problem definition. second edition. Hamilton, Ontario.

Hamilton Harbour Remedial Action Plan Team. 1992b. Remedial action plan for Hamilton Harbour stage two report: Goals, options and recommendations Vol. 2, Main report. Hamilton, Ontario.

Hanna, M. 1994. Benthic macroinvertebrate community structures in Hamilton Harbour from June to August 1989. National Water Research Institute Contribution No. 93-06. Canada Centre for Inland Waters, Burlington, Ontario.

Herbert, P.N.D. et al. 1991. Demography and ecological impacts of the invading mollusk *Dreissena polymorpha*. Can. J. Fish. Aqu. Sci. 69: 405-409.

Jaggumagi, R. 1988. The in-place pollutants program, Volume V, Part B. Benthic invertebrate studies results. Ontario Ministry of the Environment, Toronto, Ontario.

Johnson, M.G. and D.H. Matheson. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. and Oceanog. 13: 99-111.

Krantzberg, G. And D. Boyd. 1992. The biological significance of contaminants in sediments from Hamilton Harbour, Lake Ontario. Environ. Toxicol. Chem. 11: 1527-1540.

MacIsaac, H.J. et al. 1992. Filtering impacts of larvae and sessile zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Oecologia 92: 30-39.

Mongeau, L. 1990. The accumulation of trace metal pollutants in snails of Hamilton Harbour and its effect on snail community structure. Senior Project thesis (unpublished). Department of Biology, McMaster University. Hamilton.

Oliver, D.R. and M.E. Roussel. 1983. The insects and arachnids of Canada, Part 11, The genera of larval midges of Canada Diptera: Chironomidae. Publication 1746, Agriculture Canada, Ottawa, Ontario.

Smith, Ian M. and David R. Cook. 1991. Water mites. in: Ecology and classification of North American freshwater invertebrates. eds. Thorp, J.H. and A.P. Covich. Academic Press, San Diego, California.

Poulton D.J., W.A Morris and J.P. Coakley. submitted. Zonation of contaminated sediments in Hamilton Harbour as define by statistical cluster analysis. Water Quality Research Journal of Canada.

Wright, S. And W.M. Tidd. 1933. Summary of limnological investigation in western Lake Erie in 1929 and 1930. Trans. Am. Fish. Soc. 63: 271-285.

Wilhm J.L. and T.C. Doris. 1968. Biological parameters for water quality criteria. Bioscience 18:477-481.

Figure 1: Map of Sample Sites Along North Shore of Hamilton Harbour

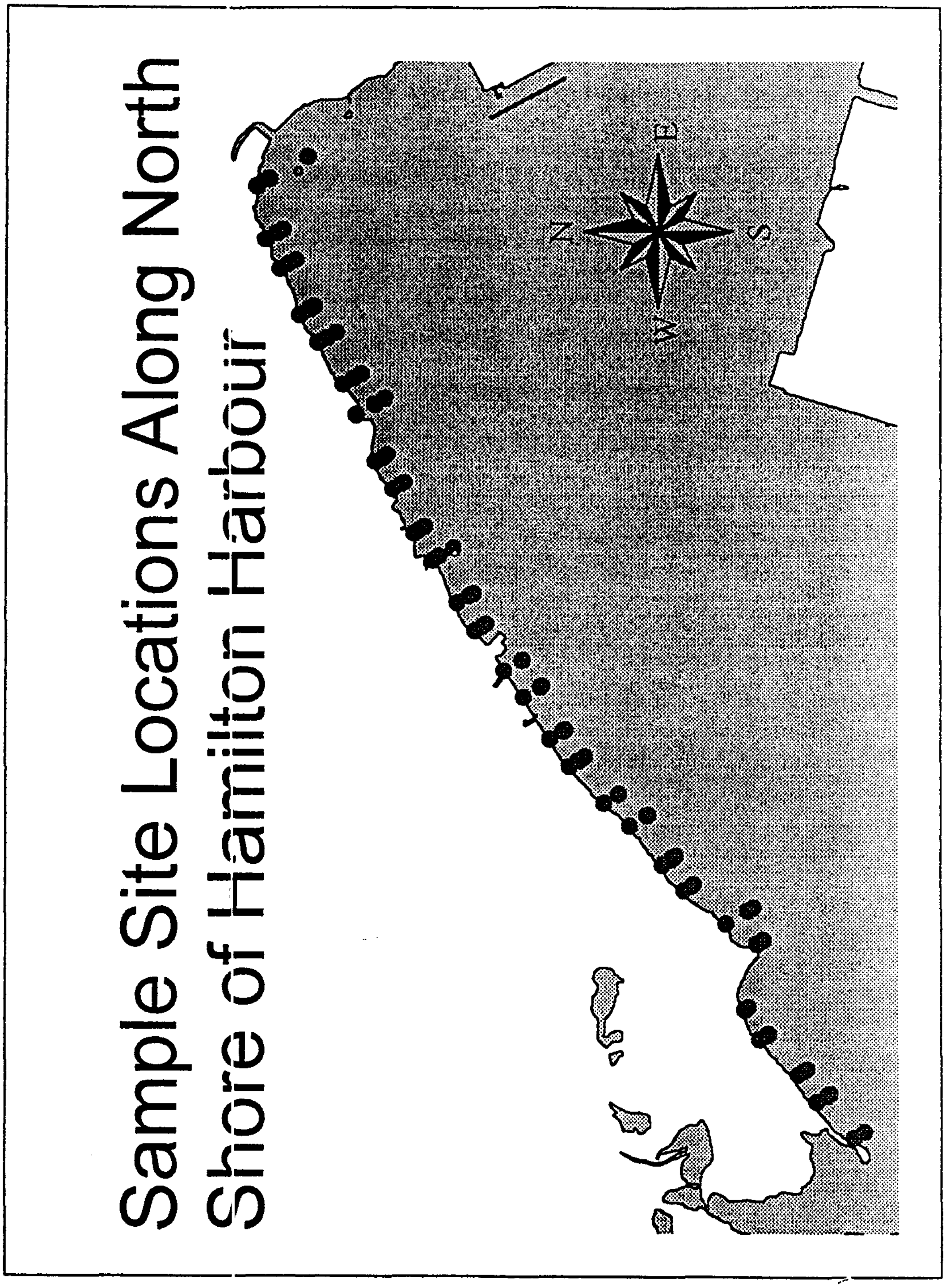


Table 1: Trace Metals Included in Habitat Descriptor Matrix

List of Sediment Trace Metals Included in Habitat Matrix
Aluminum
Cadmium
Cobalt
Copper
Iron
Lead
Nickel
Zinc
Barium
Vanadium

Table 2: Chironomid and Oligochaete Taxa Not Previously Reported in Hamilton Harbour

	Taxa Not Previously Reported in Hamilton Harbour
Chironomids	
	Cladotanytarsus
	Cryptotendipes
	Pagastiella
	Microchironomus
	Stempellina
	Phaenopsectra
	Micropsectra
	Einfeldia
	Pseudochironomus
	Cricotopus
Oligochaetes	
	Limnodrilus maumeensis
	Limnodrilus silvani
	Limnodrilus rubripenis
	Rhyacodrilus falciformis
	Varichaeta pacifica
	Nais sp.

Figure 2: Diversity Index Values for Sampling Transects (East to West Along North Shore of Hamilton Harbour)

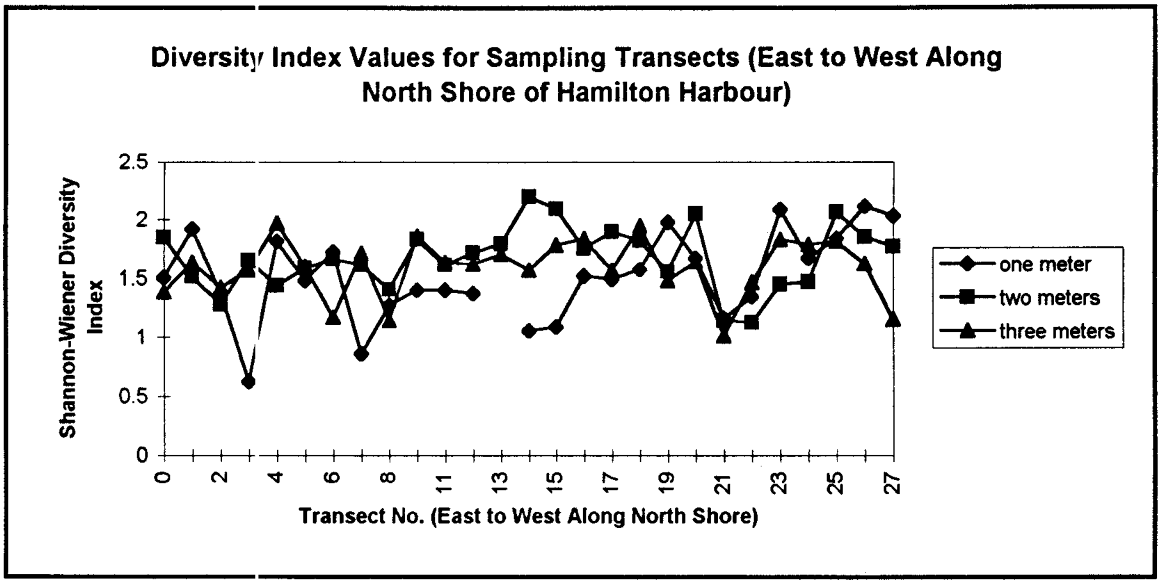
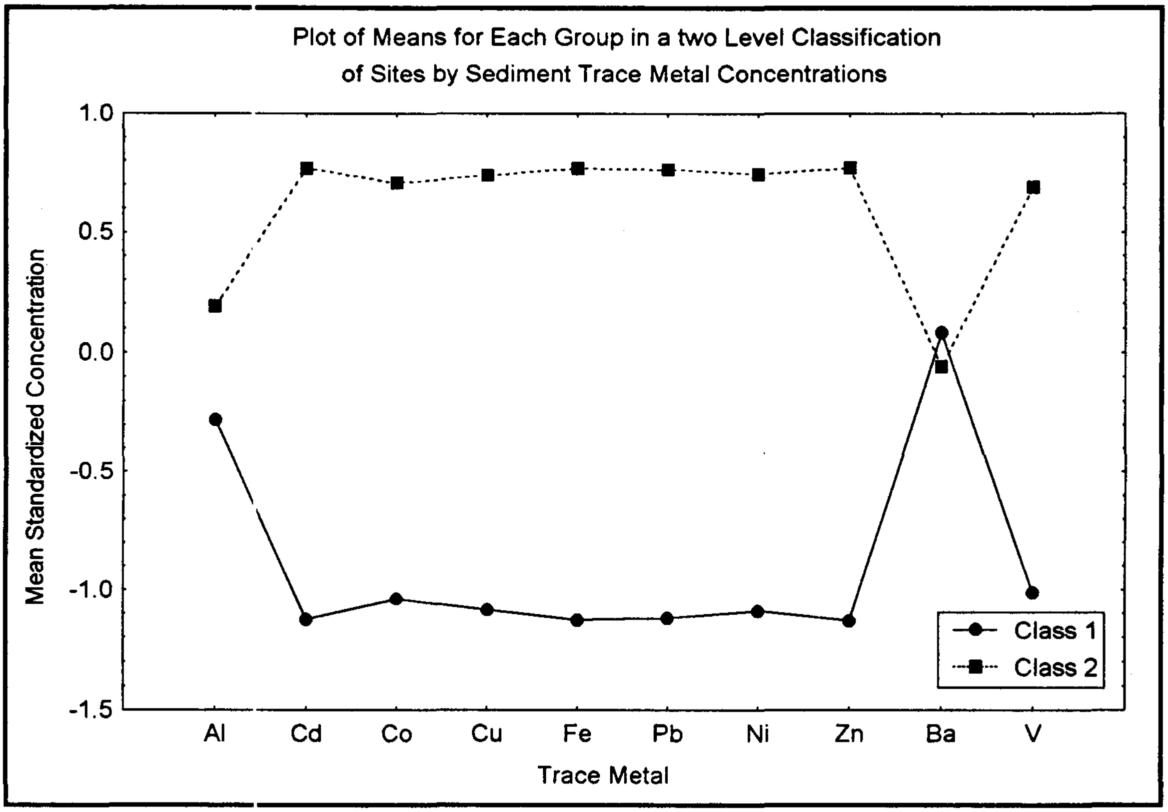


Figure 3: Mean Trace Metal Values for a Two level Classification of Sites by Sediment Trace Metal Concentrations



2.7 Appendix: Total Number of Benthic Invertebrates Collected At Each Water Depth

Benthos Taxa	Water Depth (m)		
	1	2	3
Dreissena polymorpha	2029	4347	611
Gammarus sp.	1890	2154	175
Water Mites	178	1003	1241
Dugesia tigrina	1416	352	78
Asellidae	48	2	2
Leeches	94	55	5
Snails	693	718	260
Bivalves other than *D. Poly.*	16	10	41
Ancylidae	23	4	0
Odonata	0	14	0
Unidentified Insects	53	94	92
Chironomids			
Chironomid Pupae	55	256	89
Cladotanytarsus sp.	52	56	88
Chironomus sp.	44	61	49
Polypedilum sp.	75	213	267
Procladius sp.	9	25	63
Cryptochironomus sp.	28	218	294
Dicrotendipes sp.	349	278	44
Cryptotendipes sp.	0	2	0
Parachironomus sp.	55	92	19
Paratanytarsus sp.	800	354	26
Cladotanytarsus sp.	149	164	56
Endochironomus sp.	357	5573	168
Glypotendipes sp.	33	15	13
Pagastiella sp.	12	1	34
Microchironomus sp.	51	29	43
Stempellina sp.	2	0	0
Phaenopsectra sp.	0	2	0
Micropsectra sp.	1	0	0
Tanypus sp.	0	3	3
Einfeldia sp.	3	1	0
Pseudochironomus sp.	3	0	0
Cricotopus sp.	5	4	0
Total Chironomids	2035	7090	1164
Oligochaetes			
Unidentified Immature Oligochaetes	134	119	239
Limnodrilus hoffmeisteri	981	1140	611
Limnodrilus claparedianus	43	39	12
Limnodrilus cervix	310	286	307
Limnodrilus maumeensis	12	26	9
Limnodrilus profundicola	1	2	0
Limnodrilus silvani	2	27	10
Limnodrilus udekemianus	0	2	0
Limnodrilus rubripenis	0	29	8
Quistadrilus multisetosus	0	6	0
Rhyacodrilus falciformis	1	0	0
Varichaeta pacifica	3	0	0
Nais sp.	93	168	137
Ophidonais serpentina	245	628	11
Stylaria sp.	82	297	139
Total Oligochaetes	1901	2757	1479

3.0 SPATIAL SCALE EXPLICIT ANALYSIS OF LITTORAL ZONE MACROBENTHOS IN HAMILTON HARBOUR

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Key words: spatial scale, nested Analysis of Variance and Covariance, Principal Components Analysis, macrobenthos, Hamilton Harbour

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3.0 SPATIAL SCALE EXPLICIT ANALYSIS OF LITTORAL ZONE MACROBENTHOS IN HAMILTON HARBOUR

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3.1 Abstract

Variance/covariance structure of littoral zone macrobenthos and littoral habitat descriptors along the north shore of Hamilton Harbour was partitioned into five spatial scales of observation using nested Analysis of Variance and Covariance. Principal Components Analysis was used to describe community structure at each scale. Benthic community structure in the study area is dominated by small scale patchiness, which makes up about 88 per cent of the total variation in the data set. This is true for dominant species such as *Endochironomus* and *Limnodrilus hoffmeisteri*, as well as for rare species, for whom small scale patchiness is a function of very low abundance. Intermediate spatial scales, ranging from 200m to 2000m along the north shore, contributed little variation to the community, but the largest spatial scale contributed to the overall community structure in the form of a depth gradient, with water mites and *Cryptochironomus* more prevalent at three meters depth, *Dreissena polymorpha* at two meters, and *Gammarus* and *Parachironomus* at one meter. Sediment trace metal concentrations do not have a significant effect on individual benthic invertebrate species, although concentrations do

affect total benthos abundance. Patchy macrophyte community structure and sediment grain size distributions probably influence benthic community structure at scales ranging from one to several hundred meters.

3.2 Introduction

The littoral zone macrobenthos along the north shore of Hamilton Harbour, on the western tip of Lake Ontario, is highly heterogenous and patchy (preliminary observations). Large scale gradients in species composition and abundance might be expected due to strong gradient in harbour morphometry, water currents, and turbidity levels. For example, previous studies established the existence of a water depth dependent gradient in this community (Conrad and Kolasa in prep., Hanna 1994, Johnson and Matheson 1968). Small scale patterns on the order of approximately 1 to $10m^2$, have not been quantified or described at all. Understanding the characteristics of the littoral benthic community is important because the benthos of this region of the harbour are a major source of food for many fish species, and are a component of the harbour ecosystem which will be subject to monitoring and fish and wildlife management activities (Hamilton Harbour Remedial Action Plan Team 1992).

To formally investigate the spatial structuring of littoral zone benthos in Hamilton Harbour, it is necessary to employ data analysis techniques which will not confound large amounts of small scale variation in estimations of larger scale structure. In other words, a spatial scale explicit technique providing independent descriptions of community structure at each scale is required. The need for scale explicit techniques is widely recognized (Allen and Starr 1982, Bailey 1992, Levin 1992, Wiens 1989). This need arises because ecological processes acting upon communities occur at different spatial and temporal scales, and because responses of taxa to an ecological processes can take place over differing spatial and temporal scales (Allen and Starr 1982). A variety of methods to undertake a scale explicit analysis exist, but few of these provide independent partitionings of community structure, and some, such as Noy-Meir and Anderson's (1971) multiscale ordination (modified by Ver Hoef and Glenn-Lewin in 1989), are rather restrictive in terms of the spatial arrangement of sample sites (Bailey 1992). The method used in the analysis reported in this paper does partition community structure according to spatial scale of observation, and does not pool structure from smaller scales in descriptions of larger scale structure. The method was presented by Bailey (1992) in his hierarchical analysis of the freshwater mussel community of Inner long Point Bay, Lake Erie.

3.3 Materials and Methods

Over a two week period in late August 1994, the littoral zone of the north shore of Hamilton Harbour, from Carolls Point to Indian Creek, was sampled using a systematic transect design (Fig 1). Sample sites were located along twenty-eight transects, each running from shore out into the harbour on a bearing of 150° from true north, with compensation for magnetic declination. Distance between transects alternated between 200m and 300m. Along each transect, three samples were taken at one, two, and three meters water depth, for a total of nine samples per transect.

For each sample, a 23x23 cm (9"x9") Ekman grab was used to capture an approximately constant amount of harbour sediment, along with any macrophytes and algae present within the sampling volume of the grab. The sediment was washed in a 500 μm nitex mesh net and transferred to plastic specimen cups for storage, while macrophytes and algae were stored in plastic bags. While this method of collecting macrophyte and algal samples is not used in vegetation studies, we considered it adequate for sampling vegetation and benthos from exactly the same location.

In the lab, samples were drained and stored in 70 per cent ethanol until being sorted in white trays. Oligochaetes and chironomids were mounted on slides for identification to the genus or species level, whereas most other benthic organisms were identified at lower resolution. Unidentified immature oligochaetes were allotted to the identified species at any one site in proportion to their abundance at that site. Unidentified chironomids were also proportionally allotted to chironomid species found at a site. Algae and macrophyte samples were dried for a minimum of 7 days, identified to the lowest level of classification possible given the quality of samples, and weighed to the nearest 0.001 g.

To examine the effects of sediment trace metals on benthos distribution, previously collected data (Poulton, Morris and Coakley submitted) were incorporated into the habitat descriptors data set. We used a linear distance weighted interpolation method, with the interpolated values for the point lying closest to each transect being used as values for each site along that transect, since none of the benthos sample sites were located within the lattice of trace metal sample sites. Since the depositional process for trace metals in the harbour does not lead to patchy spatial distributions of sediment trace metal concentrations (rather, gradients are formed), this extrapolation procedure is considered to provide reasonable results (Morris pers. comm.). We use so transformed data for ten sediment trace metals (Table 1). Benthos, algae and macrophyte data were ln-transformed and standardized to zero mean and unit standard deviation. Trace metal values were standardized.

A nested ANOVA/ANCOVA was employed to partition variability and covariability of all variables, with each level of the nested design corresponding to a smaller aggregation of sample sites. Five spatial scales of observation were created by making the following nested aggregations of samples: 1) all sites at the same water depth are grouped together, 2) sites within each depth are divided into three groups of nine sites, 3) for each depth, each of the three groups is divided into three groups of three sites, for a total of nine groups per depth, 4) sites are not grouped and are compared against each other, and 5) samples within sites are compared (Fig. 2). The ANCOVA procedure used actually partitions covariation of variable pairs, as opposed to the typical procedure of removing covariation via regression and then partitioning residuals. The procedure was performed using SAS PROC NESTED (SAS Institute Inc. 1985). The ANOVA/ANCOVA partitioned variances and covariances (actually correlations, since they were computed for standardized data) are additive which means that they represent fully independent partitionings. Thus, these correlations can be arranged into matrices for each level of the nested design, and each matrix describes community structure occurring at that scale only; community structure occurring at smaller scales is not pooled with structure at larger scales. This method for hierarchical partitioning of community structure according to spatial scale of observation was first applied to benthos by Bailey (1992).

The scale explicit partitioning method described above not only filters the original data set for spatial scale, but also filters out nonlinear structure in the data, since ANOVA/ANCOVA detects and partitions only linear patterns. As a result, it makes little sense to employ ordination methods, such as correspondence analysis, which are designed to handle non-linear patterns. Principal components analysis (PCA), a common multivariate ordination technique for linearly structured data, is therefore used to ordinate benthos and habitat descriptors at each spatial scale of observation. Scree plots were used to evaluate which PCA factors in each ordination should be interpreted; factors comprising the "flat zone" of each scree plot were considered to represent random variation and were excluded. Remaining factors were rotated using a varimax rotation algorithm to improve their interpretability (Wherry 1984).

3.4 Results

3.4.1 Macrobenthic Community

The 34543 benthic invertebrates collected from the littoral zone of the harbour represent forty-seven separate taxonomic groups. This is a conservative number since water mites, limpets, bivalves other than zebra mussels, and gastropods other than limpets are identified at taxonomic levels higher than genus. By comparison, only 31 taxa were identified in another recent study (Hanna 1994; data for 1989). This difference may be due to lake zones sampled; Hanna sampled along a transect running from the north shore out into the harbour, with only four sites at water depths of less than eight meters (Hanna 1994). Deep water sites in the harbour contain few benthic invertebrate taxa, usually dominated by *Limnodrilus hoffmeisteri* and *Tubifex tubifex*, whereas littoral zone sites support many more taxa, most notably the chironomids, which were the most abundant group of organisms. The single most abundant species was *Dreissena polymorpha*, the zebra mussel, which makes up 20 per cent of benthic invertebrates collected. *Endochironomus* and *Limnodrilus hoffmeisteri* were also dominant species. Conrad and Kolasa (in prep.) provide a detailed account of taxa found in the littoral zone of Hamilton Harbour, and readers are referred to this publication for further discussion.

3.4.1.1 Largest Spatial Scale (Water Depth Zones)

At the largest spatial scale of observation, sites of the same water depth are grouped together. When the correlation matrix for this scale is subjected to PCA, the screeplot of eigenvalues indicates only two factors are interpretable. These two factors describe only 17.66 per cent of the variation in the data at this scale, but do provide good separations of the spatial location of depth dependent variation. The first factor gives high positive loadings to taxa most prevalent at three meters depth, including water mites loading = 0.642 and *Cryptochironomus* (loading = 0.630). Large negative loadings indicate taxa most abundant at one meter water depth, including flatworms, leeches, and the chironomid *Paratanytarsus* (loadings = -0.644, -0.417, and -0.417, respectively). In other words, the first axis describes a gradient in benthos phase space which corresponds to a gradient in geographic space. The second factor, as with all PCA factors, also describes a correlational phase space gradient, but this time there is no linear geographic gradient associated with it. All taxa with relatively high loadings on the second factor are more abundant at two meters water depth. These taxa include *Endochironomus* sp., *Ophidonais serpentina* and *Dreissena polymorpha* (loadings = 0.736, 0.592 and 0.575618).

3.4.1.2 Intermediate Spatial Scales (Groupings of Sites)

At the spatial scale of observation corresponding to the second level in the nested ANOVA design, with three groups of nine sites per depth, only one factor is potentially interpretable, the rest having eigenvalues lower than 0.5. This first factor, however, describes a very small 3.8 per cent of variation in the data present at this scale, and does not contain large loadings on any of the taxa. The next smallest scale of observation (nine groups of three sites per depth), allows the computation of three interpretable factors, using the change in screeplot slope as the selection criterion. Each of these factors, however, describes approximately equal portions of the community structure at that scale (for a total of 15.30 per cent of the total structure), which would suggest that none of the factors could be interpreted.

3.4.1.3 Smallest Spatial Scales (Among and Within Individual Sites)

Non-random structure increases at the second smallest scale ("amongst site" scale), as is indicated by the three interpretable PCA factors. Combined, these three factors describe 19.31 per cent of the structure in the correlation matrix. Almost all loadings remain low on all three factors, only *Endochironomus* has a notably high loading, this of 0.607 on the second factor. Three interpretable factors at the smallest spatial scale of observation, the "within site" scale, describe a total of 20.03 per cent of the variation in the correlation matrix. Benthos taxa have higher loadings on these factors than on factors at the amongst sites spatial scale. On the first axis *Limnodrilus hoffmeisteri*, unidentified immature oligochaetes, *Nais*, *Stylaria*, and *Cladotanytarsus* all have relatively high loadings (0.762, 0.509, 0.510, 0.717, 0.689, respectively). *Glypotendipes* loads highly on the second factor (0.480), whereas unidentified immature oligochaetes, *Limnodrilus cervix*, and *Chironomus* load highly on the third factor (0.503, 0.408, and 0.401).

3.4.2 Habitat Descriptors

The PCA's on the partitioned correlation matrices for the habitat descriptors successfully described from 44 per cent to 50 per cent of variation at all scales except at the "within site" scale, where only 23.1 per cent of variation was described. Due to high linear correlations between most of the trace metal variables, only aluminum, iron, barium and copper values were used in the analysis.

Differences in habitat descriptors' variation/covariation amongst the three water depths are dominated by algal biomass which has a loading of 0.703 on the first PCA factor. A total of 44.49 per cent of the variation at this largest spatial scale of observation is described by the PCA analysis. Variation and covariation amongst three groups of nine sites is described in the correlation matrix at the next smaller spatial scale. Three factors describe 49.84 per cent of variation at this scale and describe a gradient between algae biomass and *Vallisneria*, an association between aluminum and iron, which can be extended to all trace metals due to their high correlation, and variation in *Potamogeton* When sites are divided into nine groups of three sites, a similar amount of variation is described by the first three factors extracted from the correlation matrix (46.9 per cent). At this scale, gradients between *Elodea* and aluminum, and between *Vallisneria* and barium are described by the first two factors, while the third factor describes variation in *Cabomba*.

Habitat descriptors correlational structure between individual sites and within sites is dominated by macrophyte species, which is a reflection of their small scale patchiness as compared to the greater homogeneity of the trace metal data. Between individual sites, 47.93 per cent of variation is described by three factors. These factors can be interpreted as associations between *Elodea* and *Potamogeton*, and between aluminum and copper concentrations, as well as *Vallisneria* biomass fluctuations between sites. At the smallest observational scale, within sites, 37.56 per cent of variation is described by the first two factors, and can be attributed to variation in *Potamogeton* and *Cabomba* variation, respectively.

3.5 Discussion

Many taxa exhibit most of their variance at the two smallest scales of observation; the average percentage of variation occurring at these two scales combined as up to 87.9 per cent. This indicates that small scale patchiness is the main spatial pattern present in the benthos data set. Of the taxa that exhibit small scale patchiness, very few have high loadings at both "among site" and "within site" spatial scales, with the exception of *Cladotanytarsus*, which has a moderately high loading on the first PCA factor at the "among site" scale (loading = 0.462708) and a high loading at the within site scale (loading = 0.688588). At the "among site" scale, *Endochironomus*, the most abundant chironomid in the littoral zone (Conrad and Kolasa in prep.), exhibits strong patchiness with a loading of 0.607 on the second PCA factor. This contrasts with the most abundant oligochaete, *Limnodrilus hoffmeisteri*, which exhibits most of its patchiness at the "within site" spatial scale, having a loading of 0.762 on the first PCA factor. These observation suggest that some species are patchily distributed at a scale of centimeters to a few meters (random replicates from a boat) and others at the scale of as much as several hundred meters. Rarer species in the data set exhibit patchiness for obvious reasons; they can not be present at many sites if their total abundances are low, especially when lower than the number of sites sampled. Yet, the fact that the most abundant oligochaete and the most abundant chironomid also exhibit fine scale patchiness is a good indication that the presence of rare species is not creating a false impression of small scale patchiness.

The small scale patchiness of benthos is thought to be a consequence of biotic processes such as competition, predation, and dispersal, as well as fine scale habitat heterogeneity. These fine scale habitat factors include sediment grain size changes and macrophyte densities (Barton 1988, Becket, Aartila and Miller 1992). *Potamogeton*, *Vallisneria*, *Elodea*, and *Cabomba* all exhibited small scale patchiness in our data set (relatively high loadings on interpretable PCA factors at the "within site" and "among sites" spatial scales). Additionally, at the "among sites" scale, PCA factors describe two gradients between macrophytes and trace metal concentrations, which may point to an indirect small scale effect of metal concentrations on benthos: metals affect vegetation biomass, which in turn affect benthos abundances.

Although there was structure present in both trace metal concentration and macrophyte biomass data at intermediate spatial scales, indeed this is where most variation in the trace metal variables occurred, there was no appreciable structure present in the benthic community at intermediate scales. This result seems to contradict earlier reports of a significant effect between trace metal concentrations and benthos abundance at a similar spatial scale (Conrad and Kolasa, in prep.), but, in fact, it does not. The previous analysis involved lower taxonomic resolution, since it partitioned total benthos abundance amongst groups of a two level trace metal concentration factor (developed using a k-means clustering algorithm, with k=2). The current analysis makes use of separate correlations between all benthos taxa and trace metals. When, as in the previous analysis, variations of individual taxa where partitioned between the two levels of the trace metal factor, no significant relationships were found. Thus, it is still possible to postulate a relatively weak relationship between trace metal concentrations in the littoral zone of Hamilton Harbour's north shore and benthos community structure. The different results achieved in the two analyses of the same benthos data set draws attention to the point that scale of taxonomic resolution, like spatial (or temporal) scale of observation, also has a definable impact on how community structure is interpreted.

Depth effects on benthic community structure in Hamilton Harbour have been reported in the literature (e.g. Hanna 1994). The most notable changes in community structure begin at approximately eight meters depth, whereas this study did not sample beyond three meters water depth. As a result, depth effects are less pronounced and involve taxa other than those involved at greater depths. For instance, in the most recently reported work on Hamilton Harbour benthos sampled in late August (Hanna 1994), *Limnodrilus hoffmeisteri* and *Tubifex tubifex* become dominant after eight meters depth, whereas in this study, *L. hoffmeisteri* showed no significant response to depth, and *T. tubifex* was not even detected. The taxa most affected by the depth gradient between one and three meters include water mites and *Cryptochironomus*, which are more abundant at three meters water depth, and the amphipod *Gammarus* and the chironomid *Paratanytarsus,* which are most prevalent at shallower depths (Conrad and Kolasa in prep.). *Gammarus* are known to be restricted to well oxygenated sites (Covich and Thorp 1991), and many chironomids generally avoid eutrophic conditions, so it is not surprising to find an inverse relationship between their abundances and water depth in a eutrophic body of water such as Hamilton Harbour.

On the other hand, water mite ecology is very complex (Smith and Cook 1991), precluding simple explanations of their response to depth in the harbour without additional research effort. *Cryptochironomus* are known to prefer coarser substrates than do other chironomids (Oliver and Roussel 1983). Since these coarser substrates are more likely to occur at shallower depths, it is surprising to find this genus more abundant at two and three meters water depth than at one meter, as reflected by the relatively large positive loading on the first factor. *Dreissena polymorpha* are most abundant at the two meter depth, possibly limited at shallower depths by wave action and at deeper depths by more silty substrate which impedes colonization by the mussel (Conrad and Kolasa in prep).

For habitat descriptors, variation between sites at different depths is dominated by changes in algal abundance (loading of 0.703 on the first PCA factor), but it is unlikely that there is a functional relationship between algae biomass and differences in benthos variation amongst depths, with the exception of *Gammarus* abundance, which is moderately correlated with algal biomass ($r=0.38$, $p<0.5$). It is more probable that unmeasured habitat variables correlated with depth are structuring the benthos community at this scale. These factors may include dissolved oxygen concentrations, intensity of wave action, substrate particle size, and water temperature. With the exception of substrate particle size, repeated measurements of these variables would be required for sound ecological interpretation

This hierarchical analysis of littoral zone benthos of Hamilton Harbour reveals that the community is dominated by small scale patchiness and various large scale gradients related to changes in water depth. The second and third levels in the nested

ANOVA/ANCOVA, which correspond to groups of sites covering a spatial range of from 500m to 2000m along the shoreline, contribute little to the non-random structure of the community as a whole, since only 3.8 per cent of the second level and 15.3 per cent of the third level's structure was meaningfully extracted by the analysis. Taxa loadings on the PCA factors at these scales were also quite low, further supporting the claim that benthos taxa in the harbour's littoral zone show little non-random variation at these observational scales. Using PCA to describe structure at particular scales augments simple partitioning of variance/covariance structure, since the community can have a lot of variation/covariation at a particular spatial scale, but this may be dominated by "noise" rather than non-random structure. Selecting interpretable PCA factors essentially partitions structure at each scale into noise and structure components, since all uninterpreted PCA factors are assumed to contain random, or unstructured, variation. Since the correlation matrices at each scale are additive, one possibility is to identify which scales have very large noise components, and then remove this noise from the data set by summing all but the "noisy" correlation matrices and performing PCA on the resulting matrix. In essence, the original data set will have been cleaned or filtered of the effects of community variation/covariation from particularly noisy spatial scales, by eliminating the largely unstructured variation of that scale from the data set. Interpretable factors should therefore describe a greater proportion of the structure in the resulting correlation matrix then would be the case for the initial, unpartitioned matrix. The magnitude of this increased interpretive power depends upon the proportion of total variation occurring at the noisy scale. In this analysis, no notable improvements were achieved using this approach, since the spatial scale eliminated from the analysis did not contain a large percentage of the total variation in the data set (proportion of total variation for individual species averaged 2.9 per cent).

Detection of important patterns at small and large spatial scales, together with the absence of non-random structure at intermediate scales, also has implications for future sampling of benthos in the littoral zone of the harbour. Efficiency of sampling design can be improved by taking samples at more than three depths, perhaps at five sites between one to eight meters water depth, and by collecting more samples at each site. Effort required for these extra samples can be offset by reducing the number of sampling transects along the length of the north shore.

3.6 References

Allen, T.H.F. and T.B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. Chicago University Press, Chicago, Illinois.

Bailey, R.C. 1992. Hierarchical Analysis of Community and Habitat Structure. Coenoses 7(3): 127-135

Barton, David R. 1988. Distribution of some common benthic invertebrates in nearshore Lake Erie, with emphasis on depth and type of substratum. J. Great Lakes Res.14(1): 34-43.

Beckett, David C., Thomas P. Aartila, and Andrew C. Miller. 1992. Contrasts in density of benthic invertebrates between macrophyte beds and open littoral patches in Eau Galle Lake, Wisconsin. Am. Midl. Nat. 127: 77-90.

Conrad, Mark and Jurek Kolasa. in prep. Macrobenthos of Hamilton Harbour's north shore littoral zone.

Covich, Alan P. And James H. Thorp. 1991. Crustacea: Introduction and Pericardia. In: Ecology and classification of North American freshwater invertebrates. eds. Thorp, James H. And Alan P. Covich. Academic Press, San Diego, California.

Hamilton Harbour Remedial Action Plan Team. 1992. Remedial action plan for Hamilton Harbour stage two report: Goals, options and recommendations Vol. 2, Main report. Hamilton, Ontario.

Hanna, M. 1994. Benthic macroinvertebrate community structures in Hamilton Harbour from June to August 1989. National Water Research Institute Contribution No. 93-06. Canada Centre for Inland Waters, Burlington, Ontario.

Johnson, M.G. and D.H. Matheson. 1968. Macroinvertebrate communities of the sediments of Hamilton Bay and adjacent Lake Ontario. Limnol. and Oceanog. 13: 99-111.

Levin, Simon A. 1992. The problem of pattern and scale in ecology. Ecology 73(6): 1943-1967.

Oliver, D.R. and M.E. Roussel. 1983. The insects and arachnids of Canada, Part 11, The genera of larval midges of Canada Diptera: Chironomidae. Publication 1746, Agriculture Canada, Ottawa, Ontario.

Noy-Meir, Imanuel and Derek J. Anderson. 1971. Multiple pattern analysis, or multiscale ordination: Towards a vegetation hologram? In: Patil, G.P., E.C. Pielou and W.E.

Waters, eds, Many species populations, ecosystems, and systems analysis. Stat. Ecol. Ser. 3: 207-231. Pennsylvania State University Press, University Park.

SAS Institute Inc. 1985. SAS User's Guide: Statistics Version 5 edition. Cary, North Carolina.

Smith, Ian M. and David R. Cook. 1991. Water mites. in: Ecology and classification of North American freshwater invertebrates. eds. Thorp, J.H. and A.P. Covich. Academic Press, San Diego, California.

Poulton D.J., W.A. Morris and J.P. Coakley. submitted. Zonation of contaminated sediments in Hamilton Harbour as define by statistical cluster analysis. Water Quality Research Journal of Canada.

Ver Hoef, Jay M. and David C. Glenn-Lewin. 1989. Multiscale ordination: A method for detecting pattern at several scales. Vegetatio 82: 59-67.

Wherry, Robert J. Sr. 1984. Contributions to Correlational Analysis. Academic Press, Orlando, Florida.

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3:385-397.

Figure 1: Map of Sample Site Locations Along the North Shore of Hamilton Harbour

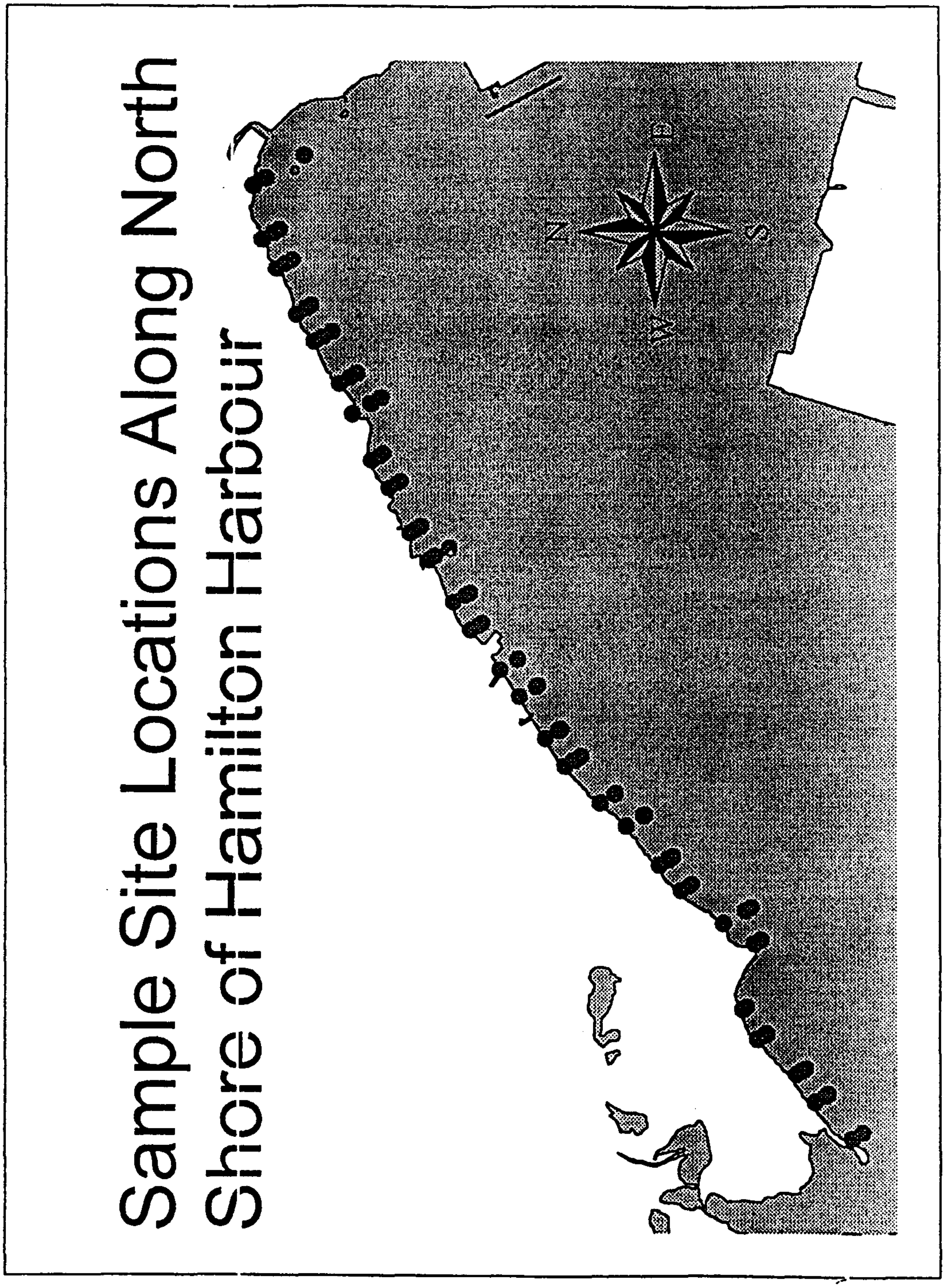
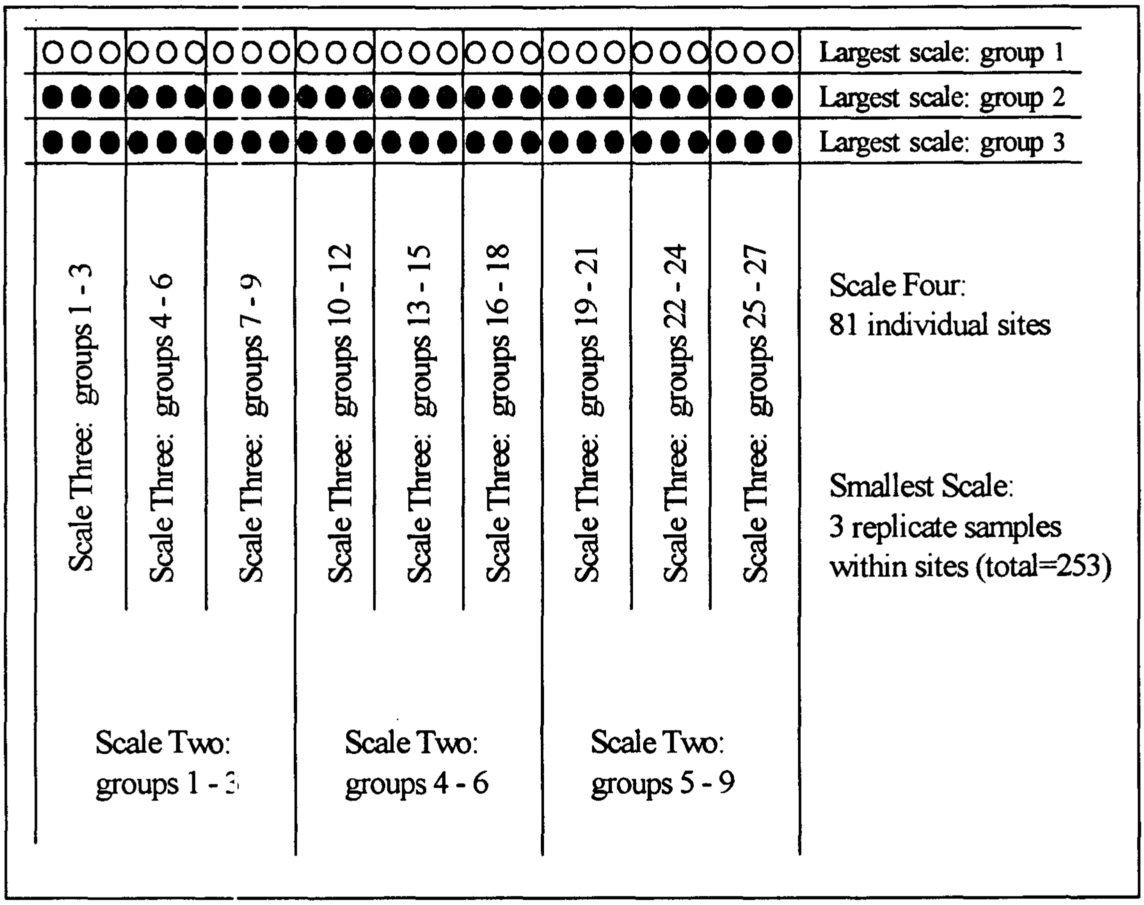


Table 1: Trace Metals Included in Habitat Descriptor Matrix (Highlighted Species used in PCA)

List of Sediment Trace Metals Included in Habitat Matrix
Aluminum
Cadmium
Cobalt
Copper
Iron
Lead
Nickel
Zinc
Barium
Vanadium

Figure 2: Schematic Diagram of Nested Aggregations of Sample Sites Along the North Shore of Hamilton Harbour



4.0 MULTISCALE PATTERN PARTITIONING: A SPATIALLY EXPLICIT APPROACH TO COMMUNITY ANALYSIS

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4.0 MULTISCALE PATTERN PARTITIONING: A SPATIALLY EXPLICIT APPROACH TO COMMUNITY ANALYSIS

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4.1 Abstract

Spatial structure or pattern is an important characteristic of many community level ecological data sets. Spatial patterns can affect standard statistical analyses and can be of ecological significance in their own right. Since spatial patterns are scale dependent phenomena, analytical methods which take into account pattern at a variety of scales simultaneously should be of value. A new method, multiscale pattern partitioning, is introduced for constructing simple, scale specific constituent patterns from large, complex, spatially structured data sets. Nested Analyses of Variance and Covariance are used to partition community structure into separate patterns for user-specified spatial scales of observation. Principal Components Analysis (PCA) is employed to reduce structure at each scale to a few variables describing most of the non-random variation present. PCA factor coefficients for each scale are multiplied by raw data matrices which have been modified to reduce the presence of structure from other scales, thereby providing scale specific spatial patterns of reduced dimensionallity. A simulated data set is used to illustrate the method. This method is an alternative to multiscale ordination, which does

not allow for the construction of constituent patterns, requires spatially contiguous sample sites, and does not provide fully independent partitionings of community structure. Additionally, our method is more appropriate for many community ecology data sets than is spectral analysis, a well known technique for constructing component patterns.

4.2 Introduction

Spatial patterns in nature are obvious; stands of pine trees, herds of ungulates, and schools of fish being three readily visualized examples. These, and most other living entities, are neither uniformly nor randomly distributed in space, but rather exhibit spatial structure such as patches or gradients (Legendre and Fortin 1989). Ecologists have developed many theories incorporating the significance of spatial pattern, including theories of succession, competition and adaptation, to name only a few. Yet, while acknowledging the importance of structure in the spatial domain, ecological models have tended not to give adequate treatment to the ecological role and effects of this structure. In most cases, geographical or relative location of sampling sites is recorded as a matter of good data "housekeeping", but is not factored into ecological analyses of empirical data. Recent advances in the field of landscape ecology have provided insights into the disadvantages of such a situation; many ecological processes seem to be modified or even initiated or terminated, precisely due to the geographical or relative location of the participants (Forman and Godron 1986, Hansen and di Castri 1992). In other cases, the biological processes themselves create spatial patterns (Legendre and Fortin 1989). Given the typical heterogeneous environment, both these factors usually interplay to produce ecological phenomena with complex spatial realizations. Spatial heterogeneity is therefore functional in nature and should be studied for its own sake, not just dealt with as a "nuisance" phenomenon (Legendre 1993).

There is another important reason for incorporating spatial pattern into analysis plans: Legendre and Fortin (1989) clearly outline the detrimental effects of unrecognized spatial patterns in data being analyzed with classical statistical methods. In many cases, spatial autocorrelation can exist between observations, even when random or systematic sampling has been conducted. This autocorrelation reduces the effective degrees of freedom associated with a particular statistical test, thereby leading to a liberalization of the test and dubious conclusions regarding significant differences amongst groups of data (Legendre and Fortin 1989). Employing methods that account for, or even attempt to describe and explain, spatial patterns can both reduce the chances of questionable conclusions and enrich one's understanding of ecological processes.

The problem of spatial pattern in ecology is exacerbated by the fact that ecological process and structure are scale dependent phenomena (Allen and Starr 1982). The patterns observed in nature are often different if observational scales (either spatial and temporal) are changed. By extension, the pattern derived from an existing data set will often change when analytical procedures with different resolutions are employed. These different patterns can indicate that different actors and interactions become important in defining ecological structure at different scales, leading to the conclusion that patterns at a variety of scales need to be studied in order to gain a good understanding of a particular ecological community. Therefore it is necessary to consider analytical methods which take into account both scale and pattern effects during an analysis of community level ecological data sets. This is especially true for large multivariate data sets in which pattern and scale effects may be very difficult to identify using simple graphical procedures.

For these reasons, Noy-Meir and Anderson introduced multiscale ordination as a method to "combine information from all [vegetation] species at all scales to produce an integrated representation of total pattern" - what they called a "vegetation hologram" (Noy-Meir and Anderson 1971). Data from contiguous quadrats are blocked into successively larger sizes, with species covariance matrices constructed for each block size. All matrices are summed to form a covariance matrix representing "total pattern", and this matrix is used to construct factor components using principal components analysis (although a variety of factoring methods could be used). The variation described by each factor can be partitioned amongst all the contributing block sizes, and the factor scores can be plotted and analyzed for spatial pattern effects. Several modifications to this method are discussed by Ver Hoef and Glenn-Lewin (1989), including the use of a local two-term covariance statistic and moving-average filtering of the component score patterns. This method successfully deals with the problem of sampling transect starting position effects, and allows any size of blocking to be used. It does not, however, provide fully independent partitionings of community data structure according to observational scale (i.e. pattern described in the covariance matrices of small blockings is pooled in the matrices of larger blockings). This is viewed as a major shortcoming since community variation "explained" at one scale may be given a second, different explanation at another scale, with neither explanation taking into account its counterpart at the other scale. A fully independent partitioning of community structure would ensure that variation attributed to smaller scales is not pooled within larger scales, eliminating the chance that a particular portion of community structure is explained more times than reason would dictate. It is also difficult to employ this blocking method when sampling sites can not be viewed as being contiguous or are irregularly spaced (Bailey 1992). Finally, the method provides derived component patterns (factor score plots) which <u>combine</u> variation from all scales, rather than providing separate patterns for each observational scale. It is not possible, in this case, to analyze each scale partitioned pattern separately, as one might wish to do.

At this point, the reader may note the similarity between a partitioning of the spatial patterns of community data into several component patterns, and the decomposition of time series data into several component data sets. Indeed, if one views a community level, multivariate data set as being a complex "signal", then the time/spatial series technique of spectral analysis will come to mind as an excellent way to partition the overall pattern into component patterns relating to various spatial scales of observation. Since systems involving interactions taking place at several spatial or temporal scales will often exhibit periodic or nearly periodic behaviour (Platt and Denman 1975), decomposing complex signals into simple cyclical patterns of various frequencies (or scales) should provide interesting results. This has been the case in a variety of marine and aquatic studies. Unfortunately for benthic and terrestrial ecologists, an implied assumption of spectral analysis is that the system being studied does not change from one observation point to another. That is, the presence and character of the important interactions between actors in the system must remain the same from one observation point to another, elsewise simple periodic behaviour (cyclic patterns) will not be exhibited throughout the entire data set, and a spectral decomposition becomes difficult to achieve or spurious.

Since many community level data sets are sampled over spatially heterogeneous environments, this assumption often does not hold. Spectral analysis is therefore of more use at a systems level treatment of ecological problems in which the variables describe system-wide characteristics, integrated over the entirety of a heterogeneous environment (e.g. The CO_2 flux rate of a wood).

Since neither multiscale ordination nor spectral analysis provide an effective means of partitioning spatial patterns of community level data sets into component patterns, a new method is offered in this paper. The method, which we will call “multiscale pattern partitioning” is more appropriate for many community level data sets than is spectral analysis, and avoids some of the perceived shortcomings of multiscale ordination.

4.3 Multiscale Pattern Partitioning

Multiscale pattern partitioning is a simple extension of the work reported by Bailey (1992) in his hierarchical, multiscale analysis of freshwater mussel community structure in Inner Long Bay, Lake Erie. In that study, sample sites are grouped in a nested hierarchy according to spatial location - smaller spatial scale groups nested within larger spatial scale groups. As indicated by Bailey, it is possible, using a nested ANOVA model, to partition the variation for each species in the data set amongst these spatial scales. The largest scale is the area encompassing all sample sites, and the smallest scale is each individual sample site, assuming, of course, that replicate samples were taken at each site. Intermediate spatial scales are created by assigning adjacent sample sites to the same group and then assigning these groups to larger groups, and so on until one all-encompassing group (the largest scale) is formed. The number of spatial scales created is limited by the total number of sample sites in the data set and by grouping decisions based on prior knowledge of the community being studied.

One criticism might be that grouping decisions based on prior knowledge are not very rigorous or objective, yet this can not be helped, nor is the situation improved through the use of formalized grouping algorithms (although these may be employed if desired). Before any sampling takes place, there is, at least in theory, an infinite number of spatial scales of observation available to the researcher. As soon as an experimental design has been established, however, the number of observational scales is effectively limited by the number of sites and their spatial arrangement. There is no way around this situation, for it is impossible to take measurements at an infinite number of locations in time and space, even if it were financially reasonable. If one assumes that researchers usually exercise good judgment in deciding what range of scales are relevant, then a good experimental design may be trusted to deliver enough resolution to allow information from the relevant scales to be analyzed. Since it is at this point in the research program that formalized grouping algorithms might be used, it is misleading to claim that using such algorithms eliminate researcher bias. And since researcher bias is precisely the prior knowledge or good judgment referred to above, the researcher may proceed with the task of assigning sample sites to a series of nested groupings, unfettered by attendant guilt.

At this point, the structure (variation) of each species in the data set has been partitioned according to spatial scale using a standard nested ANOVA model. In a directly analogous fashion, covariance between species pairs can be partitioned amongst nested spatial scales; this is accomplished by calculating, at each spatial scale, sums of products for species pairs, rather than calculating sums of squares for single species (Bailey 1992). The reader should be advised that this procedure does not constitute what is commonly referred to as an analysis of covariance or ANCOVA (Bailey pers. com.). In the later case, covariance is seen as a nuisance to be removed before partitioning variation of the variable under examination, while here we are actually interested in the covariance itself. The computer program SAS PROC NESTED will provide the required partitioning of covariance for species pairs (SAS Institute Inc. 1985). Partitioned variance and covariance values for each species and species pair in the community data set can then be re-organized into scale specific covariance matrices. Each matrix describes the community structure at the spatial scale of the nested ANOVA level to which it corresponds. Since the partitionings are based on sums of squares and sums of products, which are additive, the matrices are fully independent of each other; structure described in one matrix is not described in any other matrix.

At this point, a fully independent partitioning of community structure according to spatial scale of observation has been achieved. Unfortunately, all locational information has been lost in the process, because the raw species by sites data matrix has been replaced by a set of species by species covariance matrices. No spatial pattern can be inferred from these covariance matrices. To reintroduce locational information, common multivariate data analysis techniques are employed. In this paper, we will use principal components analysis (PCA). Bailey (1992) used PCA to reduce the community data set to a few principal components and describe community structure at each spatial scale. Likewise, in multiscale pattern partitioning, PCA reduces the data set and describes it, but the analysis does not end at this point. In order to undertake spatial pattern analyses, component spatial patterns of the structure described by PCA are constructed. To accomplish this, the factor coefficients (eigenvectors) for all relevant principal components (at a particular scale) are multiplied by modified raw data matrices. The modification of the original data matrix involves passing two moving-window "filters" over the data set. The size of the first filter window is the spatial scale of observation of the next highest level to the one for which a pattern is desired. The filter operation is simply the subtraction of the mean value within the window at any one sample site, essentially a centering operation. For example, if structure in a data set has been partitioned amongst three spatial scales of observation, then, when the smallest scale patterns are being constructed, raw data values are centered using a moving window whose size corresponds of the intermediate spatial scale. This operation removes larger scale structure from the data set.

The second modification mitigates the effects of structure at scales smaller than the one for which spatial patterns of principal components are being constructed. In this second instance, the moving-window filter employs an averaging operation, with a window size no larger than the observational scale for which a pattern is being sought. Again, supposing a data set had been partitioned amongst three observational scales, patterns corresponding to the intermediate scale of observation are constructed by passing a centering filter over the raw data with a moving window corresponding to the size of the largest observational scale. Then, an averaging filter with a window size corresponding to the intermediate scale is passed over the data (that is, over the output of the centering filter operation). The resulting modified raw data matrix is then multiplied by the PCA factor coefficients for the intermediate spatial scale, resulting in a spatial representation of the principal components for the intermediate scale.

One drawback associated with using moving filters is that they require data beyond the edge of the study area. This is not a problem when using simulated data, as will be used in this paper, but the logistics can prove difficult when planning a sampling program. Other centering and averaging filters may be considered, such as using stationary instead of moving windows, or successively decreasing the size of the filter window as the edge of the study area is approached, but these methods may provide less realistic spatial patterns.

Trade-offs between required sampling effort and pattern realism remain the researcher's prerogative.

Figure 1 shows the flow of a data set through the various steps of a multiscale pattern partitioning. Upon examination of this flow-diagram, one may ask why we do not simply use the modified raw data matrices themselves as scale specific patterns. The reason is two-fold. First, community level data sets are often very large and cumbersome, with an abundance of variables, and often contain many zero values. Employing PCA as part of the partitioning process avails one of the data reduction and description functionalities which are the raison d'être of multivariate data analysis methods. Indeed, even if the modified raw data matrices were used in a pattern analysis, it is likely that a researcher would want to first describe the patterns using multivariate techniques. Second, the importance of each variable at the various scales is assessed via a fully independent partitioning of the unmodified raw data matrix. We are of the opinion that this method provides a more accurate assessment than would be obtained by applying multivariate techniques to the modified data matrices.

4.4 An Example Using Simulated Data

We now illustrate the use of multiscale pattern partitioning using a simulated data set. This simple data set simulates values for three variables measured at 36 sites along a transect. Although the transect is spatially unidimensional and describes few variables, two- and three-dimensional data sets with large numbers of variables could have been handled with no modification to the methods (save those of graphical illustration). Figure 2 illustrates the simulated data in unmodified form. Following the procedures described above, the structure of the data matrix is partitioned amongst three spatial scales of observation, and PCA factor coefficients are computed for each covariance matrix. In this example, modified raw data matrices are constructed using stationary-window centering and averaging, which produces more obvious, albeit less realistic, breaks between groups of samples at any one scale. and, finally, spatial patterns for the PCA factors are produced at each scale. These patterns are illustrated in Figure 3, along with PCA factors for the raw data set, before it was partitioned.

These figures illustrate the greater amount of information that can be obtained from a spatially structured data set when scale effects are taken into account. The variation in the raw data set is correctly partitioned amongst the four spatial scales, and the principal component patterns do a good job reflecting this partitioning. The PCA factors for the unpartitioned data matrix also does a good job describing the data set, but pools information from all scales. With very large data sets, such a pooling can obscure important information.

4.5 Conclusion

A method for partitioning a complex spatial pattern into simpler, scale specific component patterns has been described in this paper. Of course, this is not an end in itself, but rather an intermediate step towards a scale specific spatial pattern analysis of a community level data set. Thus, once the patterns for each scale have been constructed, they can be subjected to a comprehensive pattern analysis, which might involve an assessment of degree of autocorrelation, and an identification of type of spatial structure (e.g. patches, gradients). Additionally, partial canonical ordinations may be used to "partial out" estimates of pure environmental, combined environmental and spatial, pure spatial, and unexplained source contributions to the overall variance structure at each scale (Borcard, Legendre and Drapeau 1992, Legendre 1993). These source contributions are of interest because they indicate how important different types of ecological processes are in determining community structure at a particular scale. If the pure spatial source contribution is found to be great enough to warrant further consideration, then tests for specific significant ecological relationships can be undertaken, controlling for spatial pattern effects. This is accomplished via partial Mantel tests, as described by Legendre (1993) and Legendre and Trousellier (1988). The authors are applying this type of pattern analysis to a study of the benthos along the north shore of Hamilton Harbour, on Lake Ontario, Canada.

To summarize, many ecological theories imply spatial pattern effects. In addition, spatial pattern effects can "liberalize" many standard statistical tests. Taking pattern effects into account is therefore an important consideration in many community ecology studies. Additionally, spatial patterns are scale dependent phenomena, therefore, an analysis approach that deals with scale and pattern effects is needed. An alternative approach is to construct scale specific principal component factor patterns by multiplying factor coefficients that are scale specific with raw data matrices that have been modified to remove or mitigate the effects of structure from other scales. The gap is thus bridged between spatial pattern and spatial scale analyses. The proposed approach allows fully independent partitionings of community structure into separate covariance matrices for each scale, and gives a set of component factor patterns for each scale, rather than one set of factor patterns spanning all scales. In addition, sites do not have to be viewed as being contiguous, nor must they be regularly spaced. This flexible approach is therefore seen as an improvement over multiscale ordination.

4.6 Reference List

Allen, T.F.H. and Thomas B. Starr. 1982. Hierarchy: Perspectives for ecological complexity. Chicago: University of Chicago Press.

Bailey, R.C. 1992. Hierarchical analysis of community and habitat structure. Coenoses 7(3):127-135.

Borcard, Daniel, Pierre Legendre, and Pierre Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3): 1045-1055.

Forman, R.T.T. and Michel Godron. 1986. Landscape ecology. New York: Wiley and Sons.

Hansen, Andrew J. and Francesco di Castri, eds. 1992. Landscape boundaries: Consequences for biotic diversity and ecological flows. Ecological Studies 92. New York: Springer-Verlag.

Legendre, Pierre. 1993. Spatial autocorrelation: Trouble or new paradigm?. Ecology 74(6): 1659-1673.

Legendre, Pierre and Marie-Josée Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Legendre, Pierre and Marc Troussellier. 1988. Aquatic heterotrophic bacteria: Modeling in the presence of spatial autocorrelation. Limnological Oceanography 33(5): 1055-1067.

Platt, Trevor and Kenneth L. Denman. 1975. Spectral analysis in ecology. Reference not available.

SAS Institute Inc. 1985. SAS User's Guide: Statistics Version 5 edition. Cary, North Carolina.

Noy-Meir, Imanuel and Derek J. Anderson. 1971. Multiple pattern analysis, or multiscale ordination: Towards a vegetation hologram? In: Patil, G.P., E.C. Pielou and W.E. Waters, eds, Many species populations, ecosystems, and systems analysis. Stat. Ecol. Ser. 3: 207-231. Pennsylvania State University Press, University Park.

Ver Hoef, Jay M. and David C. Glenn-Lewin. 1989. Multiscale ordination: A method for detecting pattern at several scales. Vegetatio 82: 59-67.

Figure 1: Flow of Data Set in Multiscale Pattern Partitioning

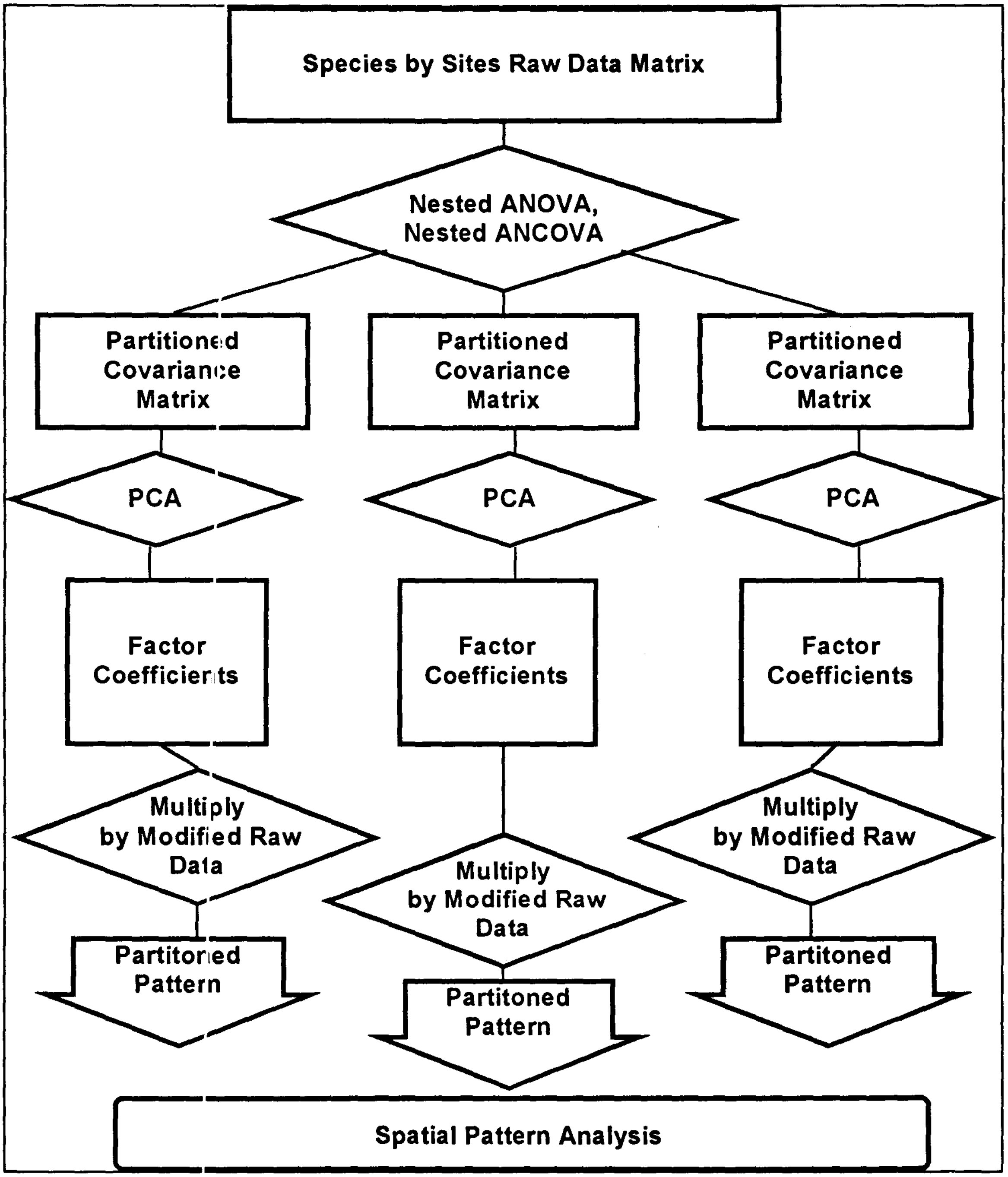


Figure 2: Raw Simulated Data

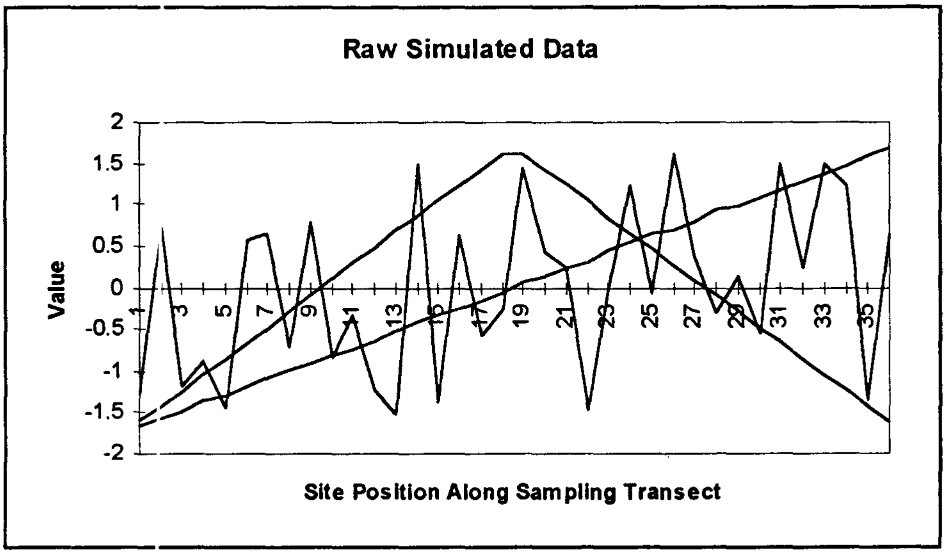
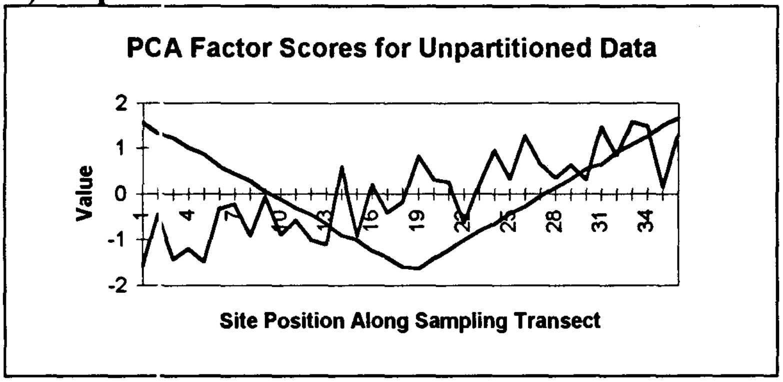
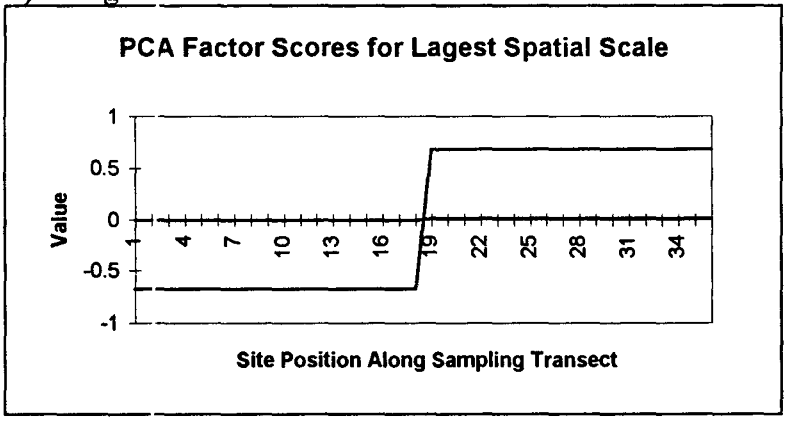


Figure 3: PCA Factor Scores for Unpartitioned and Partitioned Covariance Matrices

A) Unpartitioned



b) Largest Scale



c)Intermediate Scale

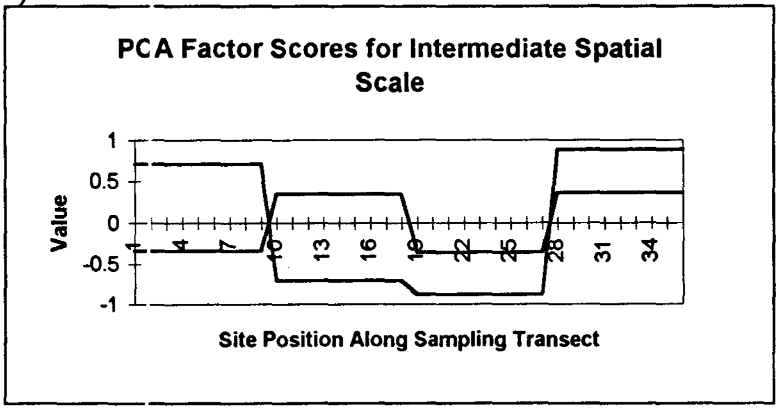
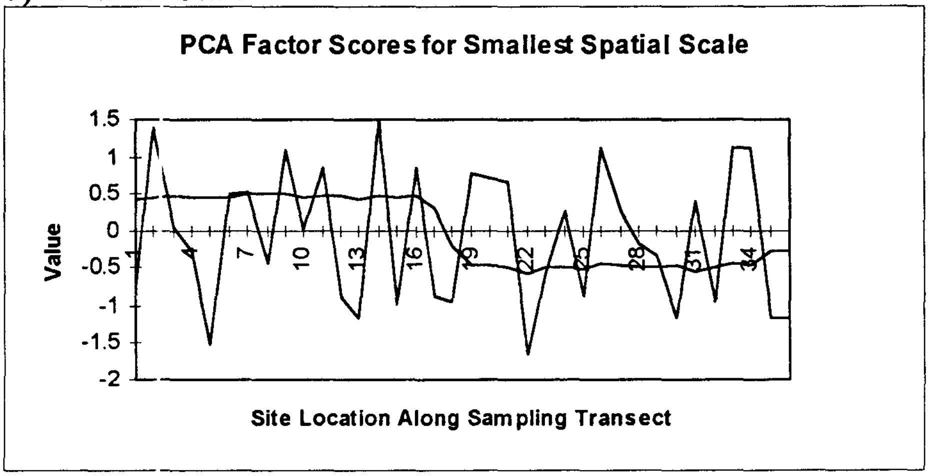


Figure 3 (cont'd): PCA Factor Scores for Unpartitioned and Partitioned Covariance Matrices

d) Smallest Scale



5.0 CONCLUSION

The data set reported in this thesis provides detailed information, previously unavailable, on the benthos of the littoral zone along the north shore of Hamilton Harbour. This fills a knowledge gap which would otherwise impede quantification and prediction of future changes to habitat quality. These changes will result from ongoing human intervention such as habitat management decisions, and from biological influences, including the continued expansion of the *Dreissena polymorpha* population in the harbour. The benthos community exhibits spatial scale-specific structure, the greatest amount of which is present at small scales, manifesting itself as patchiness. Further quantification of scale-specific spatial patterns will be undertaken with the application of the "multiscale pattern partitioning" method to the benthos data. These efforts will provide insights into the functioning of the harbour's benthic community, and are important for the development of spatially explicit models of littoral zone habitat quality in the harbour.

6.0 GENERAL REFERENCES

Borcard, Daniel, Pierre Legendre, and Pierre Drapeau. 1992. Partialling out the spatial component of ecological variation. Ecology 73(3): 1045-1055.

Griffith, Daniel A. 1978. A Spatially adjusted ANOVA model. Geographical Analysis 10(3): 296-301.

Hurlbert, Stuart H. 1984. Pseudoreplication and the design of ecological field experiments Ecological Monographs 54(2): 187-211.

Hamilton Harbour Remedial Action Plan Team. 1992a. Remedial action plan for Hamilton Harbour stage one report: Environmental conditions and problem definition. second edition. Hamilton, Ontario.

Hamilton Harbour Remedial Action Plan Team. 1992b. Remedial action plan for Hamilton Harbour stage two report: Goals, options and recommendations Vol. 2, Main report. Hamilton, Ontario.

Legendre, Pierre. 1993. Spatial autocorrelation: Trouble or new paradigm?. Ecology 74(6): 1659-1673.

Legendre, Pierre and Marie-Josée Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107-138.

Levin, Simon A. 1992. The problem of pattern and scale in ecology. Ecology 73(6): 1943-1967.