THE EFFECTS OF HABITAT SIZE AND ISOLATION ON WETLAND BENTHIC COMMUNITIES

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By

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ABSTRACT

I investigated the effects of habitat fragmentation in terms of spatial scale (enclosures of different sizes) and the degree of isolation (different mesh sizes) on benthic macroinvertebrates in the littoral zone of a shallow lake. I hypothesized that decreasing diversity and increasing temporal variation will occur with decreasing size and increasing isolation of enclosures. This hypothesis was tested by examining spatial and temporal variation (coefficient of variation) among replicate enclosures. Variation in benthic diversity was further examined within and among enclosures. The degree of isolation and habitat size interacted to determine variation of species abundance in the benthic community. Specifically, at higher levels of isolation (plastic enclosures), variance among enclosures of the same and of different sizes was the greatest compared to less isolated enclosures. We also investigated the persistence of benthic macroinvertebrates where persistence is defined as constancy in the number of organisms through time. We hypothesized that persistence is lower in small and more isolated enclosures as opposed to large less isolated ones. We simultaneously tested the hierarchical nature of community persistence as outlined by Rahel (1990) to determine if there is a difference in the assessment of persistence of the assemblage depending on the analytical scale used. There is a possible scale effect at the level of abundance rank since small (1 and 4 m^2) enclosures had lower persistence than large (9 and 16m^2) enclosures. Low persistence in both abundance and abundance rank over time prevented a conclusive test of the hierarchical nature of community persistence. I conclude that it is important for benthic enclosure experiments to be conducted at various spatial and analytical scales and that, where replication is possible, spatial and temporal variation allows a thorough examination of different community responses.

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INTRODUCTION

Complexity in ecology is not so much a matter of what occurs as it is a consequence of how we choose to describe it (Allen and Hoekstra 1992). In identifying ecological patterns and processes, our understanding of ecological phenomena is related to observational scale since different patterns emerge as the scale is changed (Addicott et al. 1987, McArdle et al. 1990, Crowl and Schnell 1990, Rahel 1990, Maguire 1984, Wiens et al. 1987, VerHoef and Glenn-Lewin 1989, Gaston and Lawton 1990, Stiling et al. 1991, Hodda 1990, Hatcher 1989, Allen and Hoekstra 1992, p. xiii, Chesson 1991, pp. 24). Chesson (1991, p. 124) classified three scales including temporal, spatial and population levels. Although spatial and temporal scales of resolution are distinct from each other population scale, or number of individuals, is related to spatial scale since the population size increases as larger areas are measured (Chesson 1991p. 124). Because this relationship exists between population and spatial scale, many researchers examine spatial and temporal scales of resolution with respect to population size as opposed to differentiating them from a population scale (Hodda 1990, Addicott et. al.

1987, Crowl and Schnell 1990, Gaston and Lawton 1990, Hatcher 1989).

Spatial and temporal scales are of both theoretical and practical interest (DeAngelis and Waterhouse 1987, Kolasa 1989). Extrapolation from empirical results on small spatial scales to larger ones has been suggested to determine sizes of conservation refuges (DeAngelis and Waterhouse 1987). Changing the habitat scale can identify constraints of small spatial scale on population sizes (Allen and Hoekstra 1992). For example, patch size may affect small mammal communities in a subdivided successional field because smaller patches contain fewer resources (Foster and Gaines 1991). In practice, spatial and temporal scales need to be appropriate to the question or approach (Barry and Dayton 1991).

> Systems ecologists must be aware of spatial and temporal variability on the scale of the system or compartment of interest. In contrast, the emphasis for community ecologists must relate to processes that control the structure of the community (recruitment, growth, and reproduction) rather than energy flow, and the relevant scale may differ even in the same system. For questions relevant to ecological time frames, consideration must be given to processes responsible for temporal and spatial variations in the recruitment of important species. In contrast, ecologists interested in evolutionary processes must consider scales appropriate to address genome patchiness or population boundaries (Barry and Dayton 1991 p. 302).

Theoretical problems include the existence of spatial heterogeneity (Kolasa and Rollo 1991), nature of persistence (Rahel 1990), and processes of maintenance of community structure at different spatial scales (Virkkala 1991). From a methodological point of view, research that is conducted at various spatial and/or temporal scales allows a better understanding of the patterns and a greater predictability of the processes that create the patterns (Allen and Hoekstra 1992). The converse is also true that

> observation over a particular scale limits our ability to measure variability on other scales. Over short time frames, larger-scale temporal cycles are relatively invariant, whereas short-term fluctuations may be undetectable by observations on a larger scale. For example, seasonal changes in the flux of organic carbon to the sea floor would be undetectable in a week-long study of benthic patterns, but these seasonal cycles would be seen as noise in studies of similar processes from sediment cores encompassing hundreds to thousands of years (Barry and Dayton 1991 p. 302).

Thus it is essential that community patterns be analyzed and interpreted at more than one scale (Rahel 1990).

Different patterns emerge as the spatial scale is changed. For example, when research is conducted at more than one spatial scale, it is possible to identify habitat heterogeneity or the existence of two or more qualitatively different patch types (Addicott et al. 1987, Hodda 1990, Wiens 1989, Kotliar and Wiens 1990, Kolasa and Rollo 1991). Kotliar and Wiens (1990) have developed a conceptual hierarchical model of patch structure with respect to how the organism responds to the habitat. They suggest that natural boundaries of patchiness exist for each organism as opposed to being observer defined (Kotliar and Wiens 1990). The upper boundary is the extent of a species which is the largest scale of heterogeneity to which an organism responds and corresponds to the lifetime home range of the individual. The lower limit of habitat resolution or grain is the smallest scale at which an organism responds to patch structure by differentiating among patches (Kotliar and Wiens 1990). Utilizing organism defined habitat heterogeneity is useful for mobile species when they are directly observed, however, for sedentary species such as plants and benthos, heterogeneity perceived by species must be determined by the observer through sampling at different spatial scales. Heterogeneity can be identified by changes in the patterns of variation among samples (Hodda 1990). For example, Hodda (1990) showed that nematodes have a highly patchy occurrence in space and time by examining small scale stochastic variation between core samples.

Not only do perceptions of ecological patterns change with spatial scale changes so do actual ecological processes. Community persistence, often defined as constancy in some measures of abundance is plagued with controversy over the mechanisms in operation due in large part to differences in the spatial scales examined (Rahel, 1990). Constancy of population density has been viewed as evidence for deterministic mechanisms whereas variations in species abundance is thought to result from stochastic processes (DeAngelis and Waterhouse 1987, Rahel 1990). At smaller spatial scales, those of patch reefs, fish assemblages have been classified as unstable whereas the entire reef assemblage is seen as stable (Sale 1980, Anderson 1981). If we are aware of the scale dependence of our research, we are more likely to gain a broader understanding of the limitations and relevance of a study (Barry and Dayton 1991, pp. 302).

Habitat fragmentation is also scale-dependent. When a habitat is fragmented, patches become smaller and often more isolated by distance from a hospitable surrounding or source pool. Isolation may thus prevent re-colonization or migration of populations and may have detrimental effects on population size or richness. Habitat fragmentation can lead to a point of no return where there is an irreversible decline or random extinction of populations (Loehle 1991). Examples may involve the California condor and carrier pigeon. Stochastic effects associated with small populations (resulting from habitat fragmentation and low population densities) may have contributed to extinction (Loehle 1991 p. 148). Habitat fragmentation is seen as an isolating mechanism among individuals of stream dwelling turtles (Dodd 1990). Irrigation and drainage of water partitions streams in ways analogous to ways oceans separate islands in archipelagoes. Isolated stream populations are then vulnerable to catastrophes without re-colonization (Dodd 1990). Forest clearcutting similarly fragments and isolates populations (Klein 1989). Klein (1989), found that forest fragments had lower diversity, lower density, and smaller beetles than intact forests because there was a potentially desiccating open habitat barrier to migration and reduced food supply within the habitat. Furthermore, isolation is correlated to population densities (Allen and Hoekstra 1992, p. 65). Birds densities can be predicted if patches only allow one territory.

However at larger scales, the degree of isolation, among other factors, is needed to predict bird population sizes (Allen and Hoekstra 1992). These examples illustrate that habitat fragmentation, which reduces the size of land available, is related to isolation and that it may have a large impact on populations (Dodd 1990, Klein 1989, Loehle 1991). Also, isolation ameliorates the predictive value of population studies over large areas (Allen and Hoekstra 1992, p. 65).

Another important scale of resolution that affects our perception of ecological phenomena is the analytical scale. For example, the perception of persistence and stability of an assemblage depends on spatial, temporal, taxonomic, and analytical resolution of the data (Rahel, 1990). Rahel (1990) found that measures of stability could be based on either absolute abundance, abundance rank or presence and absence of species with differing outcomes. He suggests that analytical scales are hierarchically nested whereby the

> assemblage with constant absolute abundances of component species are also stable at lower levels of resolution such as abundance rank or presence-and-absence data. In contrast, an assemblage can be stable at a lower level of resolution (e.g., presence and absence data) but not at higher levels of resolution (e.g., species' abundances or abundance rankings).

By examining different analytical scales, the hypothesis that the perception of persistence depends on the analytical scale used can be tested.

Experimental ecological research at the levels of communities and ecosystems is difficult to carry out

(Jongman, Braak and Tomgeren 1987) although experimental research is necessary to determine patterns and processes which occur at different temporal and spatial scales. The aims of this study are to examine the effects of various spatial scales and degrees of isolation on wetland benthos population and community structure.

Experimental enclosures are used to test hypotheses of spatial scale, enclosure size, isolation or habitat permeability, and persistence. The spatial scale is examined by taking samples at various distances. Enclosure size refers to the physical structure and is compared to determine community level differences of an imposed scale. Because the enclosures allow various organisms to pass or be impeded, the term isolation can be used interchangeably with permeability. Habitat fragmentation encompasses both the size of the enclosure and the degree of isolation or permeability. The persistence, or constancy in some measure of abundance (Rahel 1990) of populations is determined at different analytical scales absolute abundance and abundance rank. Apart from a purely theoretical reason to examine effects of various scales on community dynamics, understanding of trends and regularities may help in interpretation of benthos data collected under various sampling and aggregating regimes.

Habitat size, isolation and dimensions of variation in wetland benthos

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Abstract. We investigated the effects of spatial scale (enclosures of different sizes) and the degree of isolation (habitat permeability) on the benthic macroinvertebrates in the littoral zone of a wetland using enclosures. We hypothesize that lower diversity and greater temporal variation will occur in smaller habitats isolated from the equilibrating influence of the surroundings. This hypothesis was tested by examining spatial and temporal variation (coefficient of variation) among replicate enclosures. Variation was further used to investigate the spatial heterogeneity of benthos (within enclosure variation) and divergence of ecosystems (among enclosure variation). The degree of isolation and habitat size interact in determining variation of species abundance in the benthic community. Specifically, at higher levels of isolation (plastic enclosures), variance among enclosures of the same and of different sizes is the greatest. We conclude that it is important for benthic enclosure experiments with a high degree of isolation to be conducted at various spatial scales and that, where replication is possible, spatial and temporal variation allows a thorough examination of different community responses.

Keywords: isolation, benthic community, scale, hierarchy, variability.

INTRODUCTION

The scale-dependence and hierarchical nature of ecological research are fundamental concepts in designing experiments and drawing appropriate and comparable conclusions from them (Addicott et al. 1987, McArdle et al. 1990, Crowl and Schnell 1990). Current ecological studies have begun to incorporate the concepts that ecological phenomena are scale dependent and that different patterns of species composition emerge as the spatial resolution is changed (Rahel 1990, Maguire 1984, Wiens et al. 1987, VerHoef and Glenn-Lewin 1989, Gaston and Lawton 1990, Stiling et al. 1991, Hodda 1990, Crowl and Schnell 1990, Hatcher 1989). Spatial and temporal scaling can aid in understanding of stochastic or deterministic processes affecting a community (Rahel et al. 1984, Kolasa 1989), stability and persistence (DeAngelis and Waterhouse 1987, Wiens 1990, Rahel 1990, Drake 1991), and patchiness or spatial heterogeneity (Kotliar and Wiens 1990, Kolasa and Rollo 1991) because different processes may occur at different scales (Addicott et al. 1987) and our perceptions are strongly related to the scales we examine (Hatcher 1989, Allen 1990).

Habitat fragmentation can also be viewed as a problem of scale. When a habitat is fragmented, it becomes smaller and often more isolated from a hospitable surrounding or source pool. Habitat fragmentation is seen as an isolating mechanism in stream dwelling species of turtles (Dodd 1990). Irrigation and drainage of water partitions streams in ways analogous to archipelagoes. Isolated stream populations are then vulnerable to catastrophes without re-colonization (Dodd 1990). Forest fragmentation through clearcutting similarly isolates populations (Klein 1989). Klein (1989), found that forest fragments to have fewer species, sparser populations, and smaller beetles compared to continuous forest areas because there was a potentially dessicating open habitat barrier to migration and reduced food supply within the habitat. These examples illustrate that habitat fragmentation, which reduces the size of land available, is related to isolation and that it may have a large impact on populations (Dodd 1990, Klein 1989).

Although Island Biogeography theory has examined both size and isolation using islands of different sizes and distances from a mainland source pool (MacArthur and Wilson 1967), isolation (distance from the mainland) was only considered with respect to equilibrium richness. At smaller spatial scales, in terrestrial and aquatic habitats, direct population effects can also occur. There have been no studies including both factors in aquatic ecosystems. We hypothesized that smaller enclosures will have lower diversity and greater temporal variation of component populations as long as they are significantly isolated from the equilibrating influence of the surrounding habitat (Fig. 1). The goal of this paper is to test this hypothesis experimentally. This study explores spatial scale and isolation simultaneously in a shallow soft-bottom benthic invertebrate community. We focus on density changes across sizes and degrees of isolation and their interaction effects through analysis of variation within and between experimental enclosures.

Species richness, abundance and biomass are often the main measures of population and community structure. Variation in these parameters in space and time can indicate the spatial and temporal heterogeneity of the habitat (Hodda 1990), factors that influence community structure (Hatcher 1989, Pinder and Farr 1987, Bunn et al. 1986) and species interactions such as predation, competition, and mutualism (Barton 1986, Walde and Davies 1987). For example, small-scale stochastic variation among core samples at three spatial scales, indicates that nematodes have a highly patchy occurence in space and time (Hodda 1990). Correspondingly, we examine variation in these parameters at different spatial resolutions. Such an examination is necessary to account for the sources of variation that might affect the test of hypothesis stated earlier. Because we used replicated samples and treatments (see Methods), we assess variation (i) within enclosures as a measure of spatial heterogeneity, (ii) among same-size enclosures of different material to determine if isolation and/or scale affects species diversity or total abundance as hypothesized, and (iii) between different size enclosures to determine the interaction of scale and isolation on population parameters.

STUDY AREA

The study site is Cootes Paradise, a eutrophic wetland in the south-west end of Lake Ontario (Fig. 2a). Dominant plant species include cattails (Typha sp.) and burreed (Glyceria sp.) distributed in a narrow band along the shore. The remaining open water areas have no or few submerged macrophytes. The bottom sediment is soft and consists of fine silt mixed with plant fibers. The depth is uniform throughout the study area (0.8 m in June and decreasing to 0 cm in late September 1991). The wetland receives flow from two rivers and a sewage treatment plant which have been implicated in accelerating eutrophication (Simser 1982). Major benthic vertebrate predators include carp, bullhead catfish, and pumpkinseed sunfish.

MATERIALS AND METHOD

Enclosures of four different sizes (1,4,9,16 m^2) and three levels of permeability (40mm mesh, 2mm mesh, and polyethylene sheet plastic) were arranged in a random design with three replicates of each (Fig. 2b). All enclosures exclude large fish. The 40mm mesh allows the passage of water, small fish, zooplankton and phytoplankton. The 1mm mesh allows the passage of water, zooplankton and phytoplankton only. Plastic enclosures are closed systems with no significant exchange. Controls consisted of demarcated areas of bottom of 1,4,9 and 16 m^2 fully open to animal penetration and water movements.

Samples were taken every other week between June 20 and August 29, 1991. Three core samples were randomly taken from each of the 36 enclosures and controls. The samples were collected with a metal core sampler of 15cm^2 in surface area. Cores were taken to a depth of approximately 10-20 cm.

Samples were washed in the field on 250 micrometer Nitex net, placed in plastic cups and preserved in 70% ethanol. The core samples were mixed with tap water and invertebrates were hand picked. Larval chironomids and oligochaetes were mounted on slides for identification. Biomass was calculated for chironomids by measuring body length and using regression curves of dry weight versus body length developed by Smock (1980).

Statistical analyses were conducted using a software package Statistica from StatSoft.

RESULTS

(i) Effects of treatment on species diversity, richness, abundance and biomassass. We report results with respect to (i) the effects of treatments on benthic invertebrate species richness, abundance and biomass and (ii) patterns of variation in these community parameters. We break down the latter into two levels, within enclosures and among enclosure variation.

In all enclosures, seasonal changes in species abundance were considerable (from 6000 to 15000 individuals per m^2), with abundance increasing towards the end of the summer. The most conspicuous increase coincided with the increased water transparency and decreasing water depth (pers. obser.). Mean species richness within enclosures did not change significantly during the season. Unexpectedly, neither the spatial scale (enclosure size) nor isolation (type of screening material) had a significant effect on species richness and total abundance.

The mean abundance, however, was influenced by interaction of both spatial scale and isolation (ANOVA,F=2.59 $p<0.033$). Individual species responded to treatments with greater sensitivity but we limit this presentation to the community level descriptors only. Mean biomass was lower in 40x40 mm mesh enclosures than in plastic and 2x2 mm mesh isolation treatments (ANOVA, F=3.2 $p<0.0035$). An interaction between size and isolation was also tested after chironomid species were grouped into three or four clusters using Pearson r correlation, single linkage. We found a significant combined effect of system size and system isolation on biomass (ANOVA interaction, F=11.2 $p<0.000$) and on abundance (ANOVA interaction, F=3.36 $p<0.0001$) of chironomids (Fig. 3 a, b).

(ii) Variation

(a) Variation between replicate core samples (within-enclosure variation)

While we found no significant differences in spatial variation expressed as standard deviations of abundance among enclosures of different sizes, there were significant major unexpected differences among control plots (Fig. 4). We had anticipated that the greatest mean distances among individual core samples in large enclosures will influence the variation in these enclosures by reflecting greater potential heterogeneity. We found however that the variation due to within-enclosure sampling error was not affected by the enclosure size. Variation expressed as coefficients of variation showed no significant trend in either enclosures or controls (ANOVA).

(b) Among enclosure variation

variation in time depends on the degree of isolation. A strong temporal increase in the variation of abundance occurs among same sized enclosures (Fig. 5). The greatest temporal increase in variation occurs in plastic (68), compared to 2x2mm mesh (30), and 40x40mm (45) mesh enclosures (Fig. 5). Variation (coefficient of variation) of mean abundances among different sizes of enclosure mean abundances was also influenced by the isolation treatment (Fig. 6a, b). There was significantly greater spatial variation of abundance (coefficient of variation) among more isolated enclosures (plastic) than among more open ones (2x2 mm mesh and 40x40 mm mesh) whrere error bars represent standard error over time (Fig. 6b).

DISCUSSION

(i) the effects of treatments on species diversity, richness, abundance, and biomass

Unexpectedly, there were no effects of either size or isolation on the community level parameters of species richness, Shannon-Werner index of diversity or abundance. We hypothesized that smaller habitats would have lower diversity. Following the predictions of Island Biogeography Theory, (MacArthur and Wilson 1967), we expected the rate of extinction to be higher in small enclosures. It is possible that local extinction did not occur even in the smallest of habitats. Low competition among invertebrates and a rapid re-colonization by midges flying in and depositing new batches of eggs may account for the lack of a substantial response.

There were significant combined effects of system size and system isolation on mean abundance and chironomid species clusters of biomass and abundance. Species clusters result in a greater resolution of treatment effects. Isolation moderated effects of size on chironomid density to the greatest degree for clusters 3 and 4. In the isolated plastic enclosures, the density of chironomids in clusters 3 and 4 increased with the size of enclosure. This result may reflect a resource constraint at smaller sizes which may give a competitive advantage to these clusters but which is absent in less isolated enclosures. The water passage through 2x2mm and 40x40mm mesh allows phytoplankton and zooplankton movement in and out of these enclosures. Since the diets of some benthic invertebrates in this study are based on a rain of dead phytoplankton and zooplankton (Oliver and Roussel 1983 pp. 20), horizontal flow of resources from the surrounding matrix would mediate the effects of size differences. There is some evidence that when fragmented habitats are linked by hospitable habitat channels or "corridors", the negative effects of isolation can be ameliorated (Laurance 1990). Conversely, habitat fragmentation and the resulting isolation from the surrounding populations has a detrimental effect on populations of dung and carrion beetles in a forest. Forest fragments have sparser populations and fewer species than intact forest because beetles in such fragments are limited by a reduced food supply which is due to extinction of large mammals and primates (Klein 1989). In our case, this reduction in food supply could be due in large part to the negative effects of an impermeable membrane and also increased shade in small enclosures.

The enclosures themselves may provide an increase in habitat complexity due to algae growth. Accordingly, ecological processes in smaller enclosures could be impacted more strongly by the physical structure of the enclosures due to a greater perimeter to surface area ratio (Goodwin Senior thesis 1993). It was found that there are limited effects of the physical enclosure structure on ecological processes occurring within 4m2 plastic enclosures of varying surface perimeter to surface area ratios (Goodwin senior thesis 1993). Although enclosures may amplify resources such as algae compared to control areas, there is no significant difference among enclosure and control means. Furthermore, different sizes of enclosures are probably not significantly affected by different perimeter to surface area ratios.

Biomass provides additional information on species performance since chironomids differ in size according to species and life cycle stages (Oliver and Roussel 1983). Using Pearson's correlation as the basis for this cluster analysis, clusters of species biomass show a size and isolation interaction (Fig. 3b). In the most isolated (plastic) enclosures, the biomass of cluster 1 increases with the size of the enclosure. There is a corresponding increase in the density of most of the species in this group (Fig. 3a, cluster 4). An increase in both density and biomass in larger enclosures may also indicate a resource constraint in smaller enclosures that does not affect other species or less isolated treatments.

(ii) Patterns of variation in community parameters.

The degree of natural variation in macroinvertebrate communities is important to assess the impact of environmental or biotic parameters in structuring communities (Pinder and Farr 1987). Although variation among samples has been seen as a "common problem that typically requires taking replicate samples" (Rahel et al. 1984), when replicate samples are taken the pattern of variation provides valuable information at the community level. Patterns of spatial variation within habitats for example, allows analysis of the spatial heterogeneity or patchiness of the habitat (Hodda 1990). Temporal variation has been used as a measure of community constancy or the stability of the assemblage (Rahel 1990). Most studies of spatial and temporal variation however, do not examine patterns of variation per se nor do they use discrete experimental systems as in this study (Hatcher 1989. Hodda 1990, Wade and Daves 1987, Virkkala 1991). Our hypothesis that smaller isolated enclosures will show the greatest temporal variation combines spatial and temporal components of variation.

(a) Within-enclosure variation

Variation between the three samples in each enclosure was not influenced by the size of the enclosure. This result could be due to two causes, first that the microhabitat is generally homogeneous or that the enclosures are too small to detect a larger microhabitat grain. Heterogeneity or, in this context, the existence of two or more qualitatively different patch types (Addicott et al. 1987), may occur at different scales of resolution or hierarchies (Kotliar and Wiens 1990, Kolasa and Rollo 1991). It may be that natural patches are detectable at a scale larger than 16 square meters, i.e., beyond the enclosure size used.

Outside the enclosures, however, the picture is different. The variation in abundance between samples in 1 and 4 m^2 control plots is low compared to variation in both 9 and 16 m^2 plots. This suggests a natural patch size between 4 and 9 m^2. Because enclosures and controls were sampled in the same way, they should have the same patch size unless enclosures themselves change the microhabitat grain or if there is an outside influence creating patchiness in the control plots later in the season. Because the 40x40 mm mesh enclosures did not differ in water quality (transparency) from open water sites (Kehl thesis 1990) and showed no difference in variation across sizes, enclosures themselves do not account for the lack of invertebrate patchiness. Alternatively, a large benthic predator could account for the patchiness in the open control sites. Common carp, Cyprinus carpio, use the area to spawn and forage. Gut content analysis (unpubl.) has revealed that adult carp, catfish, sunfish and especially juvenile carp consume benthic invertebrates in this study area. Although their present abundance in the marsh is unknown, the presumed densities are high. For example, in 1956 a carp control program yielded 70,000 carp caught by seining over the entire 400 ha wetland (Painter et al. 1989). Carp feeding habits have been implicated in the uprooting of vegetation (King and Hunt 1967, Threinen and Helm 1954) and pitted depressions in a drained soft bottom lake (Cahn 1929). This circumstantial evidence suggests that carp could be creating the patchiness observed in the open sites if their foraging was irregularly spaced.

(b) Variation among enclosures

Some studies have examined variation between locations (Pinder and Farr 1987, Hatcher 1989). Variation among sampling sites has been examined for macroinvertebrate fauna using coefficients of variation (Pinder and Farr 1987) who found a great deal of temporal variation of populations in yearly censuses of river macroinvertebrates. We also used coefficients of variation (COV) in order to compare density variation through time between enclosures of the same and different sizes.

It is apparent that, although there is an increase in the COV of all isolation treatments, the most isolated plastic enclosures show the greatest increase in variation of mean abundance over time (Fig 5) although this result is not significant using ANOVA. This trend indicates that plastic enclosures, irrespective of size diverge from one another to a greater extent than less isolated enclosures. Although the hypothesis that smaller isolated enclosures will show the greatest temporal variation must be rejected for the spatial scales examined, we do not think that this rejection can be made general. The main reason for caution is the small range of spatial scales examined.

Variation among the mean densities of different sizes of enclosures indicates how populations vary independently of each other. The most isolated enclosures show the greatest temporal variation between densities of different enclosure sizes (Fig. 6a, b). Isolation from the equilibrating effects of the surrounding matrix results in a greater divergence of species densities than in less isolated enclosures.

CONCLUSION

The hypothesis that smaller habitats will have lower diversity and greater temporal variation of component populations as long as they are significantly isolated from the equilibrating influence of the surrounding habitat was rejected for the spatial scales and invertebrate community examined. We do not think this rejection can be made general since it is possible that low competition among invertebrates and a rapid re-colonization by midges flying in and depositing new batches of eggs may account for the lack of a substantial response in diversity. Furthermore, greater temporal variation may be evident at other spatial scales than those examined. The second portion of the hypothesis indicates a trend. The isolated plastic enclosures show the greatest (i) increase in variation of mean abundances over time and (ii) divergence of different sizes of enclosure mean abundances compared to less isolated enclosures. Further quantification of the interaction between many spatial scales and different degrees of isolation in aquatic habitats may lead to discovery of a general relationship. Within-enclosure variation in the open sites suggests a natural patch size between 4 and 9 m^2 possibly created by a benthic predator with irregularly concentrated foraging habits.

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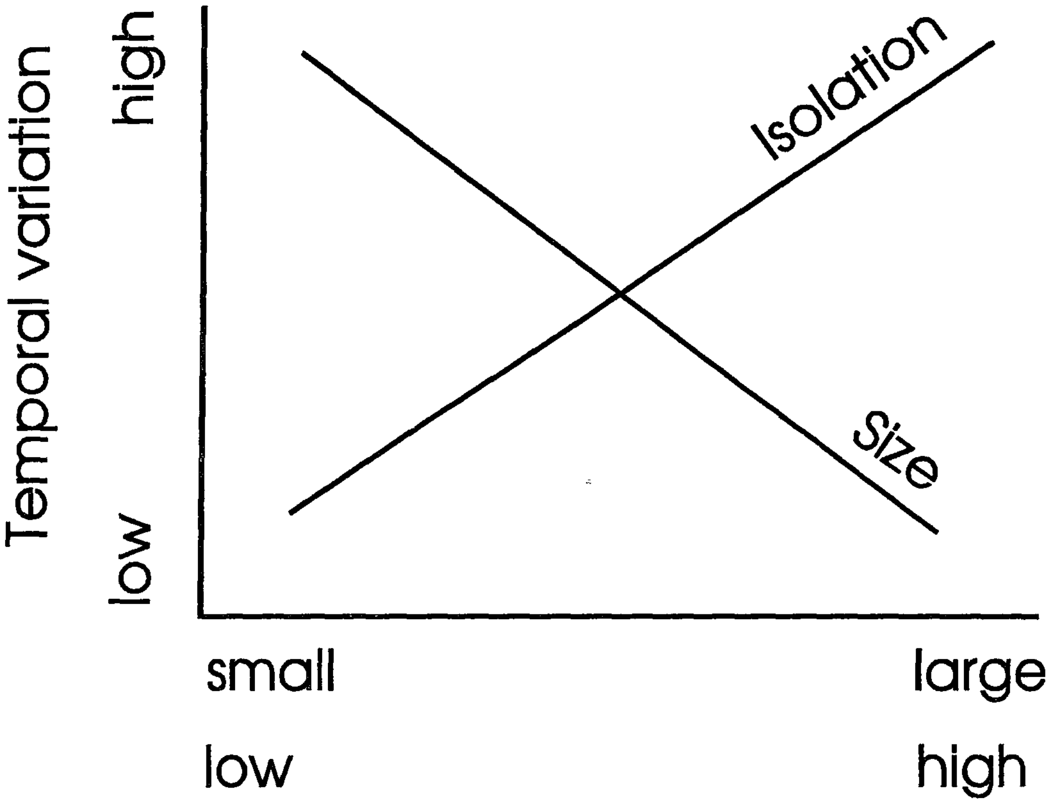

Fig. 1. Predicted decrease in temporal variation with increasing size of the habitat and increase in temporal variation with habitat isolation.

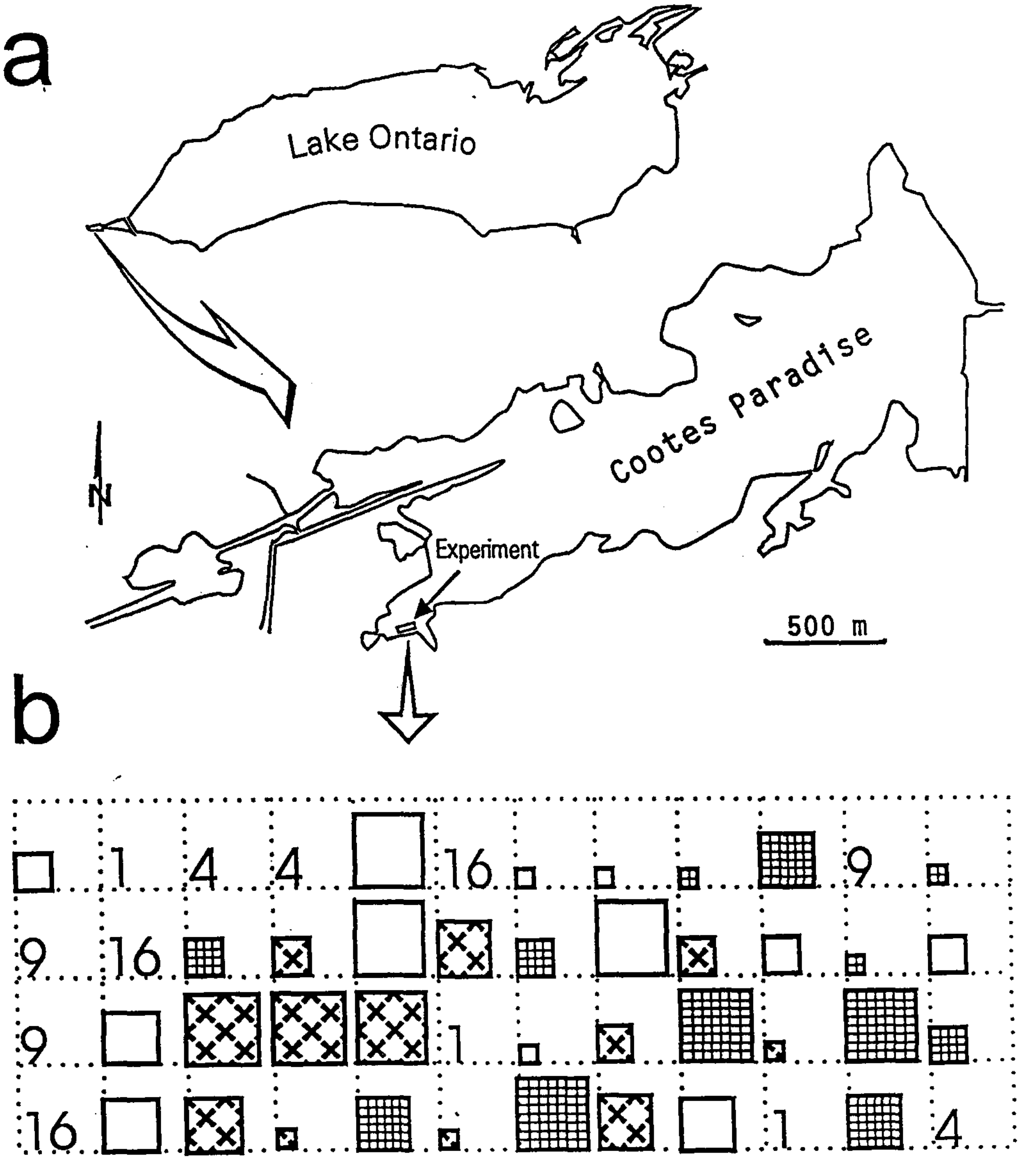

Fig. 2a Study site at the south-west end of Lake Ontario. b Experimental design of enclosures and controls. Numbers represent control plots, solid lines represent plastic enclosures, gridlines represent 2x2mm mesh enclosures and crosses represent 40x40mm mesh enclosures.

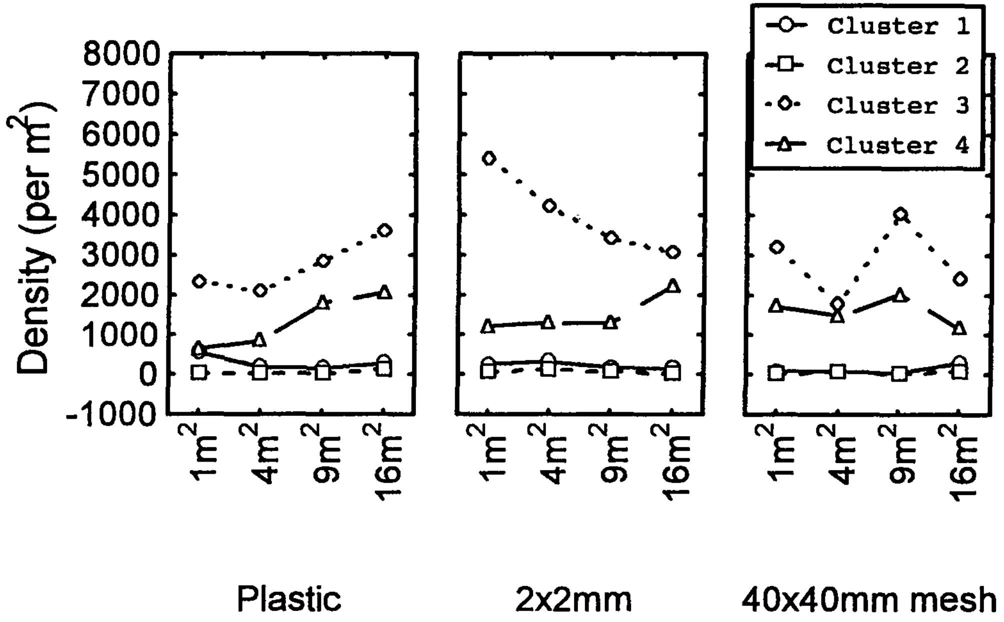

Fig. 3a Effect of isolation and habitat (enclosure) size on density of chironomids in four species clusters using cluster analysis Pearson's r correlation. Cluster 1 includes: *Psectrotanypus* sp., *Chironomus* sp., and *Einfeldia* sp. Cluster 2 includes: *Polypedilum* sp., and *Nanocladius* sp. Cluster 3 includes: *Cricotopus* sp., *Cladopelma* sp., *Cryptochironomus* sp., and *Procladius* sp. Cluster 4 includes: *Dicrotendipes* sp., *Glyptotendipes* sp., *Macropelopia* sp., *Rheotanytarsus* sp., and *Tanypus* sp.

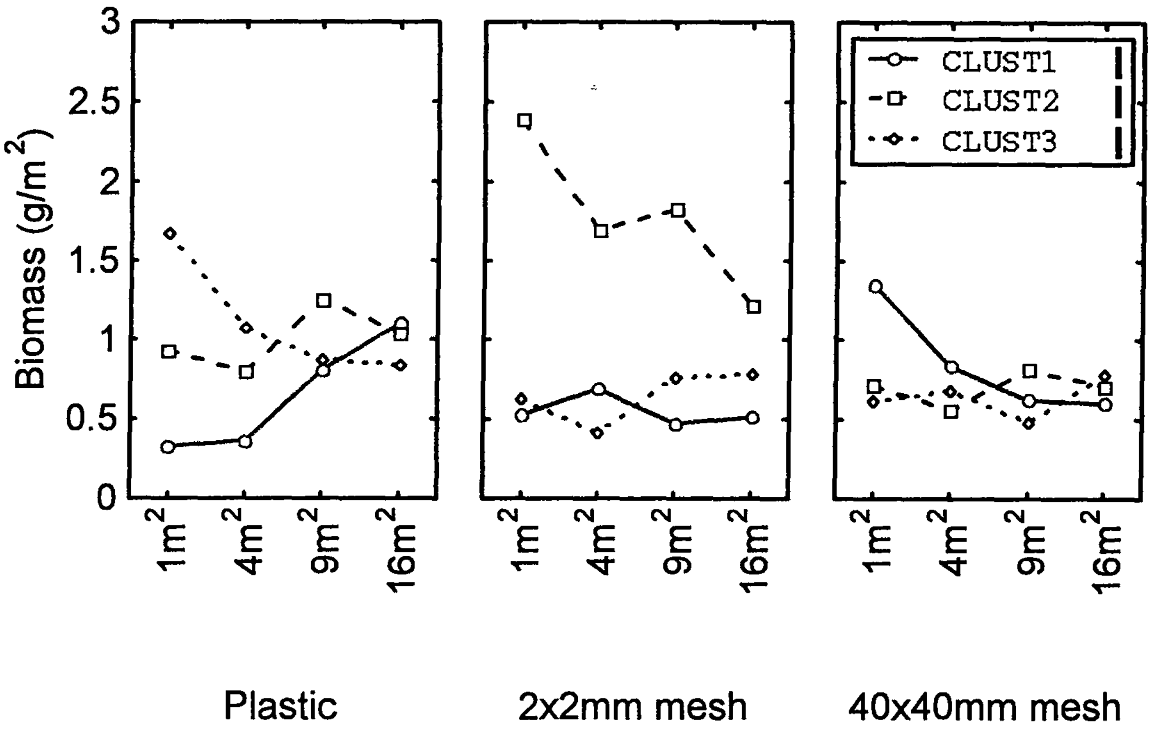

Fig. 3b Effects of isolation and habitat (enclosure) size on biomass of chironomids in 3 species clusters using Pearson's r correlations. Cluster 1 includes: *Tanypus* sp., *Glyptotendipes* sp., *Macropelopia* sp., *Dicrotendipes* sp., and *Polypedilum* sp.. Cluster 2 includes: *Procladius* sp., *Cryptochironomus* sp., *Cladopelma* sp.,*Cricotopus* sp. Cluster 3 includes:*Chironomus* sp.,*Psectrotanypus* sp.,*Einfeldia* sp.,*Nanocladius* sp.,*Rheotanytarsus*sp.

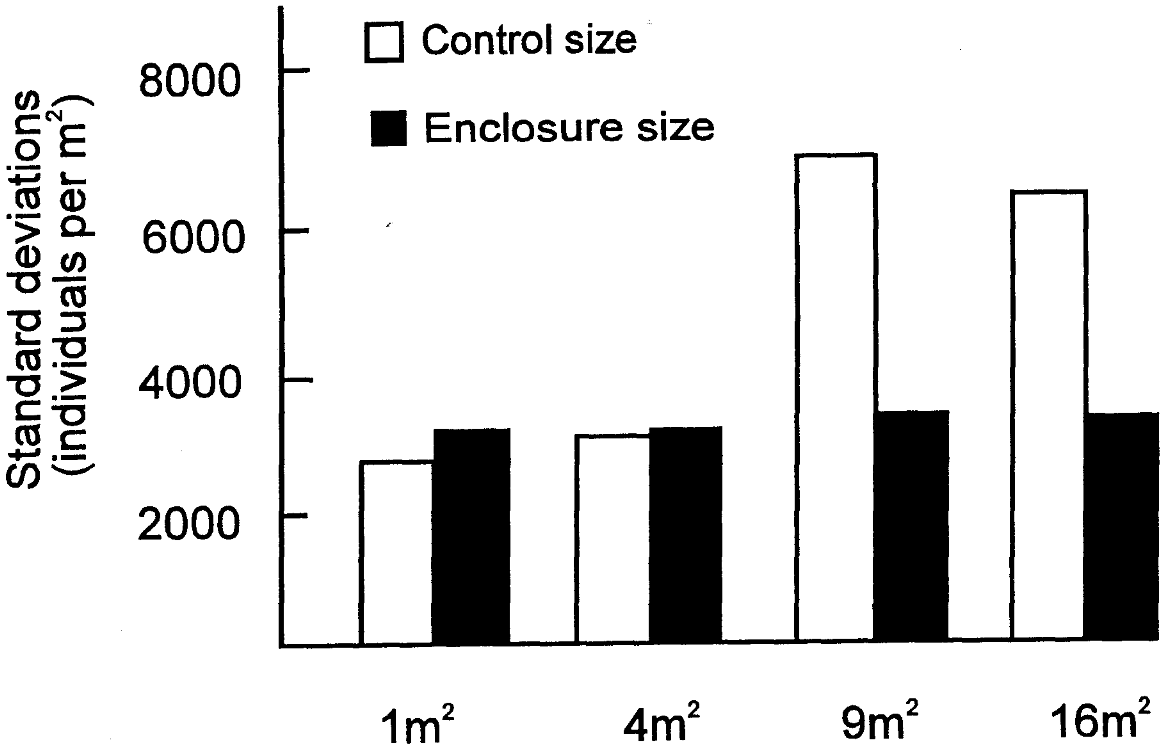

Fig. 4. Variation in benthos density in all isolation enclosures versus controls of different sizes.

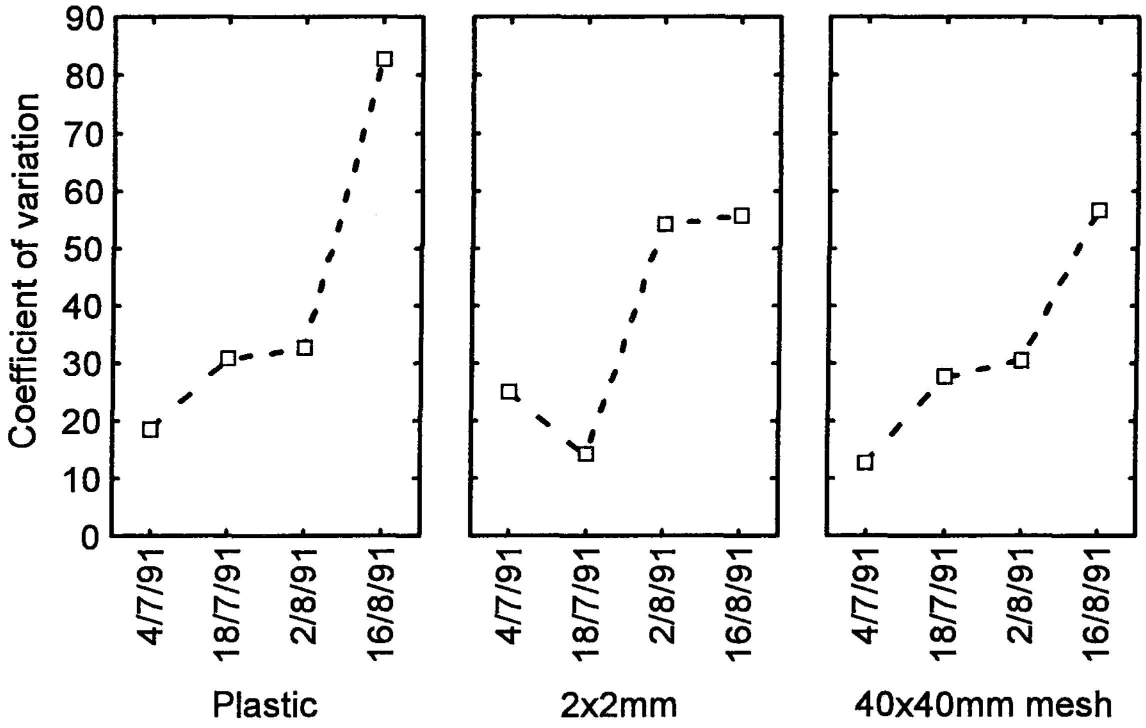

Fig. 5. Effect of isolation on temporal variation in density of benthos calculated among enclosures of the same size. This figure represents the mean of all sizes of enclosures.

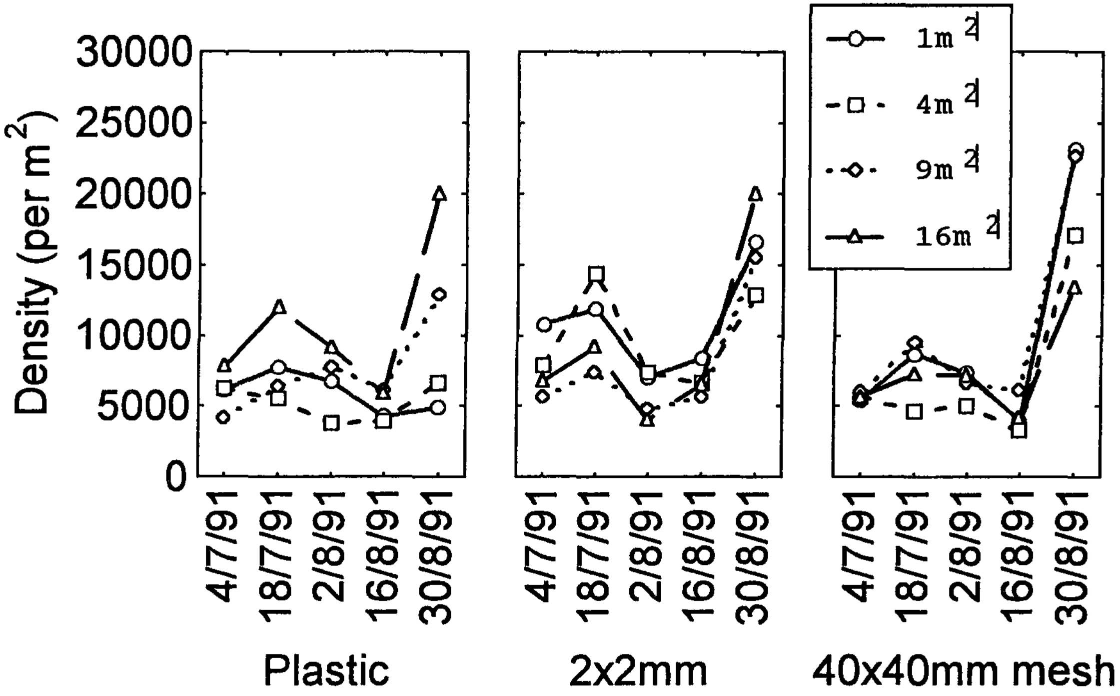

Fig. 6. a Seasonal changes of mean chironomid abundance in enclosures of different degrees of isolation. Different lines represent enclosures of different sizes.

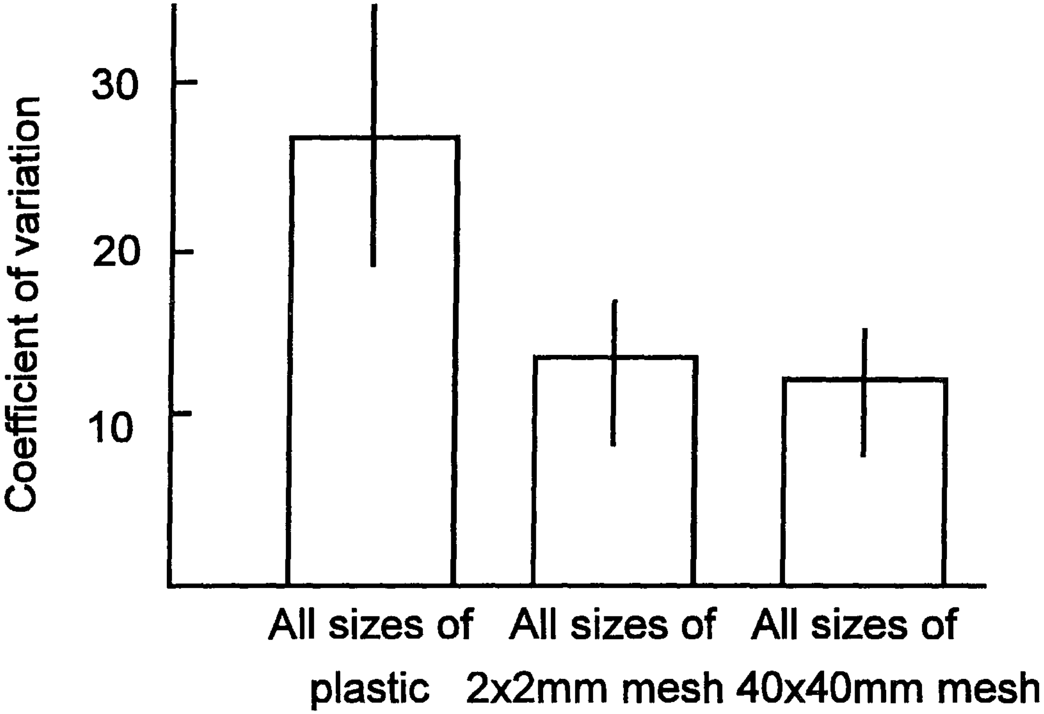

Fig. 6. b The magnitude of variation in enclosures of different degrees of isolation. The error bars represent the standard error calculated over time.

Spatial scale, isolation, and the hierarchical nature of community persistence in wetland benthos

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Abstract. We investigated the effects of spatial scale (enclosure sizes) and the degree of isolation (permeability) on the persistence of benthic macroinvertebrates in the littoral zone of a wetland using enclosures. We hypothesized that persistence is lower in small and more isolated enclosures as opposed to large less isolated ones. We simultaneously tested the hierarchical nature of community persistence as outlined by Rahel (1990) to determine if there is a difference in the assessment of stability depending on the analytical scale used. At the analytical scales of absolute abundance and absolute biomass we used coefficients of variation, a relative measure of variation. At the scale of abundance and biomass rank we examined stability using Kendall's coefficient of concordance. There is a possible hierarchical scale effect at the level of abundance rank since small (1 and 4 m^2) enclosures had lower persistence than large (9 and $16m^2$) enclosures. The most isolated enclosures did not show lower persistence as predicted possibly due to the ability of chironomids to re-colonize by depositing eggs in the enclosures and because the chironomids were not constrained by the lack of horizontal flow of resources. Low stability in both abundance and abundance rank over time prevented a conclusive test of the hierarchical nature of community persistence. Because individual species vary in rank abundance over time in a manner contrary to a hypothetical model of species assemblage, we conclude that this is another scale at which community stability can be examined.

The method of population dispersal relative to the isolation treatment may have influenced the outcome of the study. We suggest that the addition of a top cover on enclosures to prevent immigration would be useful when examining the effects of isolation in benthos.

Keywords: isolation, benthic community, scale, hierarchy, persistence.

INTRODUCTION

Stability or the constancy in the numbers of organisms (Connell and Sousa 1983) is important because it has been viewed as evidence for deterministic community structure, whereas variation in abundance often implies a greater role of stochastic processes in structuring communities (Rahel 1990). According to Connell and Sousa (1983), the measurement of stability requires a disturbing force that either creates a significant change in species abundance or to which the multispecies system can show resistance. This concept of stability invokes a significant outside disturbance being applied to the system which is not always easy to identify. Because an outside force is neither apparent nor directly measurable in some systems, an alternative approach is necessary where one examines stability based on the hierarchical framework of absolute abundance, abundance rank, and presence-absence of species (Rahel 1990). Persistence can be measured by coefficients of variation for absolute abundance data, and Kendall's W for rank abundance data (Rahel 1990).

One general problem with interpretation of ecological data is its scale-dependence (Allen and Hoekstra 1992, Chesson 1991, pp.124, Barry and Dayton 1991,pp.301, Armesto, Pickett and McDonnell 1991,pp.256, Doak et al. 1992). Thus, the perception of persistence and stability of an assemblage depends on spatial, temporal taxonomic and analytical resolution of the data (Rahel, 1990). The size of the habitat is an important consideration because it may have direct effects and because it is related to habitat fragmentation (small habitats in a habitat mosaic are more isolated from each other than continuous areas that make up large ones). Both factors, small habitat size and habitat fragmentation, may negatively influence populations (van Appeldoorn et al. 1992 for review). The size of the habitat fragments and the spatial distance between habitats disrupts animal dispersal (Doak et al. 1992), affects the spatial structure of populations, especially extinctions (van Appeldoorn et al.1992), and affects interspecific interactions in predator-prey and host-parasite models (Reeve 1990, Hastings 1990, Hassell et al. 1991) and in host-parasite empirical systems (Roland 1993, Kareiva 1987). Patch size may affect small mammal communities in a subdivided successional field because smaller patches contain fewer resources (Foster and Gaines 1991). Isolation can also increase the chance of extinction (van Appeldoorn et al. 1992, Geuse et al. 1985, Dodd 1990). For example, stream populations of turtles which are isolated from each other due to habitat fragmentation are vulnerable to catastrophes without re-colonization (Dodd 1990). In many cases, isolation represents distance from a hospitable surrounding (Gottfried 1982, Dickman and Doncaster 1989) or a barrier to migration (Wu et al. 1993, Klein 1989). Isolation measured as distance had an effect on the density and sex ratio of white-footed mice in woodlots (Gottfried

1982). Influences of smaller and more isolated patches occur at different analytical levels of resolution. Some evidence exists that fragmentation reduces persistence at the presence-absence level (Smith 1974, Dodd 1990, van Apeldoorn 1992), and absolute abundance level (Gottfried 1982, van Apeldoorn 1992, Klein 1989).

According to hierarchy theory smaller (lower level) systems, any level of organization from individual to ecosystem and landscape, should be more variable than larger systems (Pickett et al. 1989, Virkkala 1991). This general idea combined with the empirical work mentioned above may be treated as a framework for a testable hypothesis. We use freshwater benthos to examine this issue. Apart from a purely theoretical reason to examine effects of various scales on community dynamics, understanding of trends and regularities may help in interpretation of benthos data collected under various sampling and aggregating regimes.

Biomass provides additional information on species performance and may be another key unit of measurement besides abundance data (Smock 1980). We conducted the study using experimental benthic communities in a soft-bottom wetland connected to Lake Ontario. Since chironomids constituted the main component of benthos in this study and differ in size according to species and stage of development (Oliver and Roussel 1983 pp. 14), it is especially important to consider biomass. Persistence can thus also be measured in terms of absolute biomass and biomass rank.

The specific goal of this paper is to experimentally test the hypothesis that persistence is lower in small and more isolated enclosures as opposed to large less isolated ones and to determine if there is a difference in the assessment of stability in these experimental enclosures depending on the analytical scale used.

MATERIALS AND METHOD

Enclosures of four different sizes (1,4,9,16 m^2) and three levels of permeability or isolation (40mm mesh, 2mm mesh, and polyethylene sheet plastic) were arranged in a random design with three replicates of each (Fig. 1a, b). All enclosures exclude large fish. The 40mm mesh allows the passage of water, small fish, zooplankton and phytoplankton. The 1mm mesh allows the passage of water, zooplankton and phytoplankton only. Plastic enclosures are closed systems with no significant exchange. Controls consisted of demarcated areas of bottom of 1,4,9 and 16 m^2 fully open to animal penetration and water movements.

Samples were taken every other week between June 20 and August 29, 1991. Three core samples were randomly taken from each of the 36 enclosures and controls. The samples were collected with a metal core sampler of 15cm^2 in surface area. Cores were taken to a depth of approximately 10-20 cm.

Samples were washed in the field on 250 micrometer Nitex net, placed in plastic cups and preserved in 70% ethanol. The core samples were mixed with tap water and invertebrates were hand picked. Larval chironomids and oligochaetes were mounted on slides for identification. Biomass was calculated for chironomids by measuring body size and using regression curves of dry weight versus body length developed by Smock (1980). All the analyses were conducted using two levels of analytic resolution. At one level we examine patterns based on abundance and biomass data. At a higher level, similar analyses are conducted using species ranks. At the analytical scales of absolute abundance and absolute biomass we use coefficients of variation, a relative measure of variation. At the scale of abundance and biomass rank we examine stability using Kendall's coefficient of concordance. Statistical analyses were conducted using a software package Statistica from StatSoft.

RESULTS

We organized the presentation of results according to the analytical level of resolution. For each level we compared patterns based on abundance data and/or on biomass.

Abundance/ biomass level

Community stability as measured by coefficients of variation (standard deviation/mean) for absolute abundance was low in all sizes of enclosures. We used coefficients of variation for each species over time and took the average of the values across all species as described by Rahel (1990) and in each enclosure seperately. Coefficients of variation allow measurement of community constancy where low values indicate a more stable assemblage compared to higher values (Rahel 1990). Values of coefficients of variation, which ranged from 105 to 116, were not significantly different between 1, 4, 9 an 16m^2 enclosure sizes when all levels of permeability were pooled (ANOVA). There was also no significant difference in stability measured as coefficients of variation between isolation treatments with enclosure size pooled (ANOVA). The more isolated plastic enclosures showed a lower mean coefficient of variation (COV=105) than the less isolated 2x2 mm (COV=112) and 40 x 40 mm mesh (COV=115) enclosure however this was not significant (ANOVA $p<0.3$). An alternate measure of stability is to examine the change in biomass over time. We tested the stability in biomass through time using coefficients of variation for an average of all chironomid species. The biomass measure was not significantly different between size or isolation treatments (ANOVA).

Rank abundance and biomass level

At another analytical scale of resolution, species can be more or less stable in terms of the variation in abundance rank. Kendall's coefficient of concordance (W) ranges from a zero value indicating no concordances through time to a value of one indicating complete concordance (Rahel 1990). The abundance rank differs between small (1 and 4 m^2) and large (9 and 16m^2) enclosure sizes (Fig. 2). Larger enclosures have a higher coefficient of concordance (Kendall's W=0.61) than smaller enclosures (Kendall's W=0.55) (ANOVA $p<0.0225$). There is no difference between isolation treatments for abundance rank, biomass rank, or between size treatments for biomass. In contrast to Rahel's (1990) hypothetical model of species over time where each species shows the same variation in rank or abundance over time, chironomid species have different variation in rank abundance. The dominant species, Procladius sp. had the highest rank abundance (most often ranked #1) and show the least variation in rank abundance over time compared to other species (Fig.3). Procladius sp. is a predaceous chironomid in this assemblage.

DISCUSSION

Spatial scale

We hypothesized that persistence would be lower in small enclosures than in large enclosures. There are no differences between sizes of enclosures for abundance. Foster and Gaines (1991) also predicted that small herbivorous mammals living in a successional field partitioned into different sized patches would persist longer in larger patches. Similarly, densities for three of the four mammals showed that densities did not support the predictions that more individuals would be found on larger patches (Foster and Gaines 1991). There is, however, a difference in the rank abundance measure (Kendall's coefficient of concordance) for chironomid species between small (1 and 4 m^2) and large (9 and 16 m^2) sizes of enclosures. The small enclosures are least stable in terms of species rank as we hypothesized which may indicate a scale effect where the spatial scale of resolution determines the perceived community stability. Abundances vary in all enclosure sizes to a large extent but the rank abundance changes more in smaller enclosures which would seem to indicate a greater effect of succession in smaller enclosures. Whether or not the change in rank represents a directional or predictable change in species composition due to greater competition or predation in smaller enclosures is unclear because it is possible that low competition among invertebrates, a rapid re-colonization by midges flying in and depositing new batches of eggs, and emergence of chironomid larvae may also influence changes in species ranks. According to Cornell and Lawton (1992), a non-interactive community exists where the history of colonization from surrounding region overshadows weak biotic interactions. However,lack of competition,chironomid emergence and depositing of new batches of eggs does not seem to be able to account for the spatial scale effect in any obvious way. Any number of interactions or ecosystem constraints could be operating at smaller spatial scales since hierarchically organized structural constraints may operate on organisms and affect different biological and physical processes at different spatial scales (Virkkala 1991 for review). No specific hypotheses have yet been developed to suggest how these factors could influence the measure we analyze. A predaceous chironomid species, _Procladius_ sp., the most abundant chironomid species in our study, has been found to increase predation in the summer and autumn in an urban reservoir (Bass 1992). Perhaps a combination of competition, predation, and resource constraints occurs at smaller spatial scales and leads to greater fluctuations in individual species. Since there is an effect of the spatial scale on the species rank measure of community stability, the spatial scale, habitat island size or patch size must be considered when drawing conclusions as to the persistence of an assemblage. Monitoring an assemblage over time allows the exploration of the extent to which structure is retained (Sale and Guy 1992).

Isolation treatment

We reject the hypothesis that persistence should be lower in more isolated enclosures for the isolation treatments used. As many studies have indicated, either disruption of dispersal(Doak et al. 1992, Roland 1993), extinction and low re-colonization(van Apeldoorn et al. 1992,Dodd 1990, Dickman and Doncaster 1989) or resource constraints (Foster and Gaines 1991) are results of isolation. For example, isolation also had an effect on re-colonization of woodland patches by wood mice and bank voles (Dickman and Doncaster 1989). This system, however, is different from others in that re-colonization occurs by midges flying in and depositing new batches of eggs, and emigration occurs when chironomid larvae emerge into midges through the open surface of the enclosures. Since there is no barrier to either dispersal or re-colonization, local extinctions did not occur. The more isolated enclosures may improve some resource constraints. It is possible that our treatments might have a protective effect not desirable for the test of the hypotheses above. Since the diets of some benthic invertebrates in this study are based on a rain of dead phytoplankton and zooplankton (Oliver and Roussel 1983 pp. 20), lack of horizontal flow of resources from the surrounding matrix into more isolated enclosures could result in changes in population densities and possibly local extinctions. Chironomid populations were not, however, constrained by food supply in any obvious way nor were they significantly isolated from re-colonization.

Biomass measure

The biomass of benthic invertebrates is a reasonable estimator of productivity (Cole and Weigmann 1983). As such, the biomass is another important estimator of assemblage stability especially when species or developmental stages of organisms differ in size (Oliver and Roussel 1983 pp. 14). Because no trend due to size or isolation is apparent, we conclude that the treatments had no significant impact on productivity.

Analytical scales

Stable assemblages are thought to be influenced more by biotic factors whereas environmental disturbance is seen to account for unstable assemblages (Rahel 1990). Analysis of the abundance and biomass data at two hierarchical scales shows low stability in both absolute abundance and abundance rank. Because there was a low degree of stability at both the analytical scales used, we did not examine presence absence data. Rahel (1990) describes four scenarios: A-where there is no variation in species abundances, B-species abundances vary but ranks remain constant, C-abundances vary to such an extent that species rank varies, and D-variation is so great that ranking and presence and absence of species are unpredictable. Since we measured two hierarchical levels of abundance and rank abundance, this chironomid assemblage at the timescale examined fits into the third category,C, where abundances vary to such an extent that species rank varies. This study only explores seasonal changes within the framework of community persistence. The stability of the assemblage may be different if data is collected over yearly censuses and seasonality is controlled for. We could not test conclusively the hierarchical nature of persistence, where the assemblage can be stable at lower levels of analytic resolution (rank abundance) but not at higher levels of analytic resolution (abundance) (Rahel 1990), since there was a great deal of variation in both measures of stability.

The variation in rank abundance over time was different for each species. This result conflicts with Rahel's (1990) hypothetical model in which all species show the same variation in abundance, abundance rank, or presence absence data. The least variable and most abundant chironomid species is a predator in the assemblage. In addition to understanding community stability at different hierarchical scales, it may be important to identify the individual species variation. The assemblage may be relatively unstable, but it may include a few species that are dominant and have low temporal variation. This is another scale at which persistence or stability can be analyzed. We suggest a need for examining other assemblages, using functional criteria such as trophic level, to determine if a few persistent non-overlapping species of predators exist as in this assemblage of chironomid species.

CONCLUSION

The hypothesis that smaller and more isolated enclosures would show the lowest persistence in absolute abundance or abundance rank was partially confirmed. There was a significant effect of enclosure size at the rank abundance level of analysis which may be due to many factors including resource constraints, competition and predation. The most isolated enclosures did not show lower persistence as predicted possibly due to the ability of chironomids to re-colonize by depositing eggs in the enclosures. This study differs from others in that it has examined isolation with respect to possible resource constraints rather than with respect to dispersal and re-colonization. In similar future studies it might be useful to prevent chironomids from getting access through the top of the enclosures in order to determine if re-colonization is a key factor responsible for the lack of isolation effects. Low stability in both abundance and abundance rank over time prevented the test of the hierarchical nature of community persistence as discussed by Rahel (1990). Furthermore, individual species variation in rank abundance over time appears contrary to a hypothetical model of species assemblage suggested by Rahel (1990). A functional scales based on trophic level is another scales at which stability can be assessed since in this assemblage the most abundant predaceous chironomid varies the least in rank compared to other chironomids. This study confirms the importance of obtaining and analyzing data at many scales of resolution, especially spatial scales.

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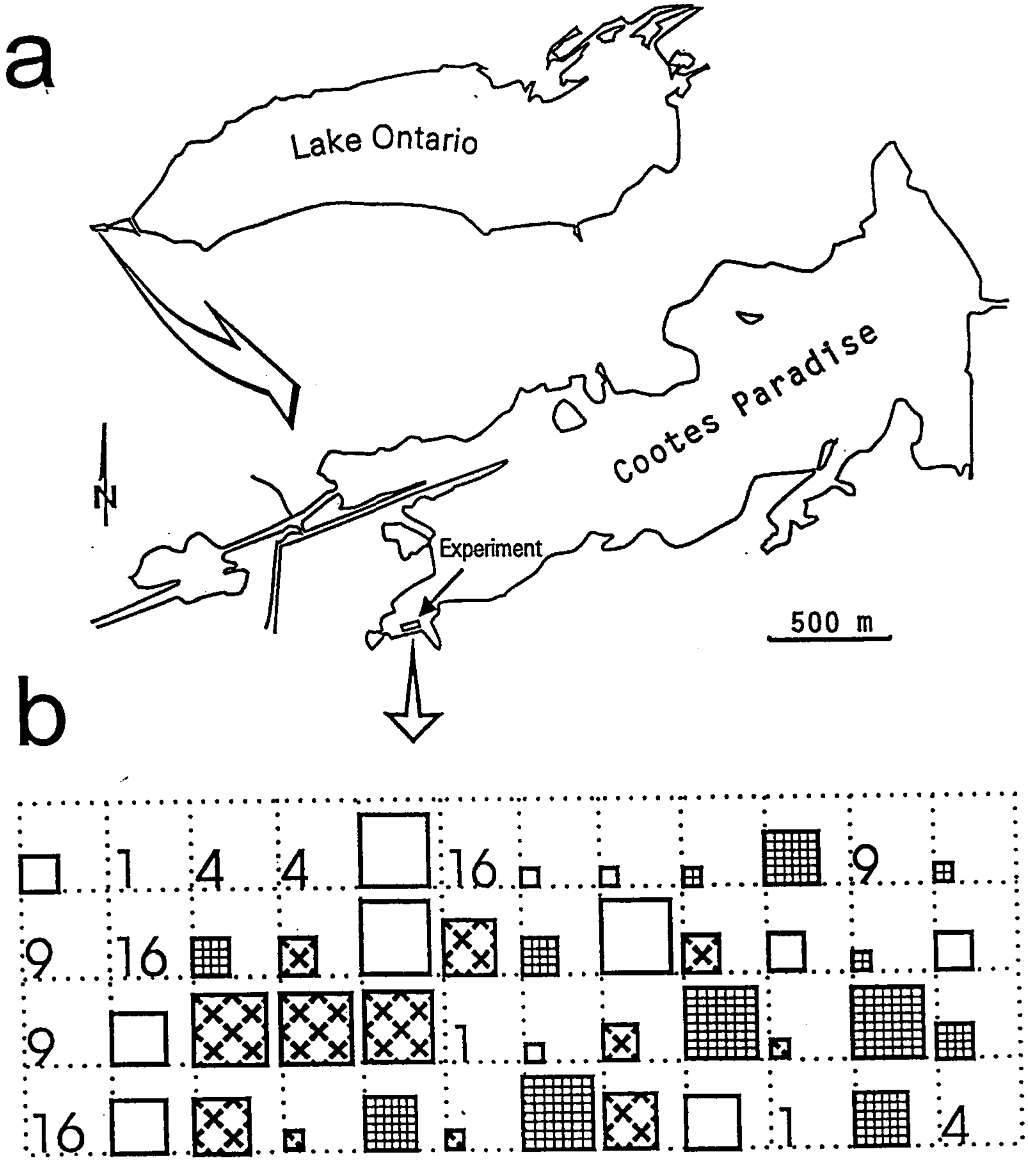

Fig. 1a Study site at the south-west end of Lake Ontario. b Experimental design of enclosures and controls. Numbers represent control plots, solid lines represent plastic enclosures, gridlines represent 2x2mm mesh enclosures and crosses represent 40x40mm mesh enclosures.

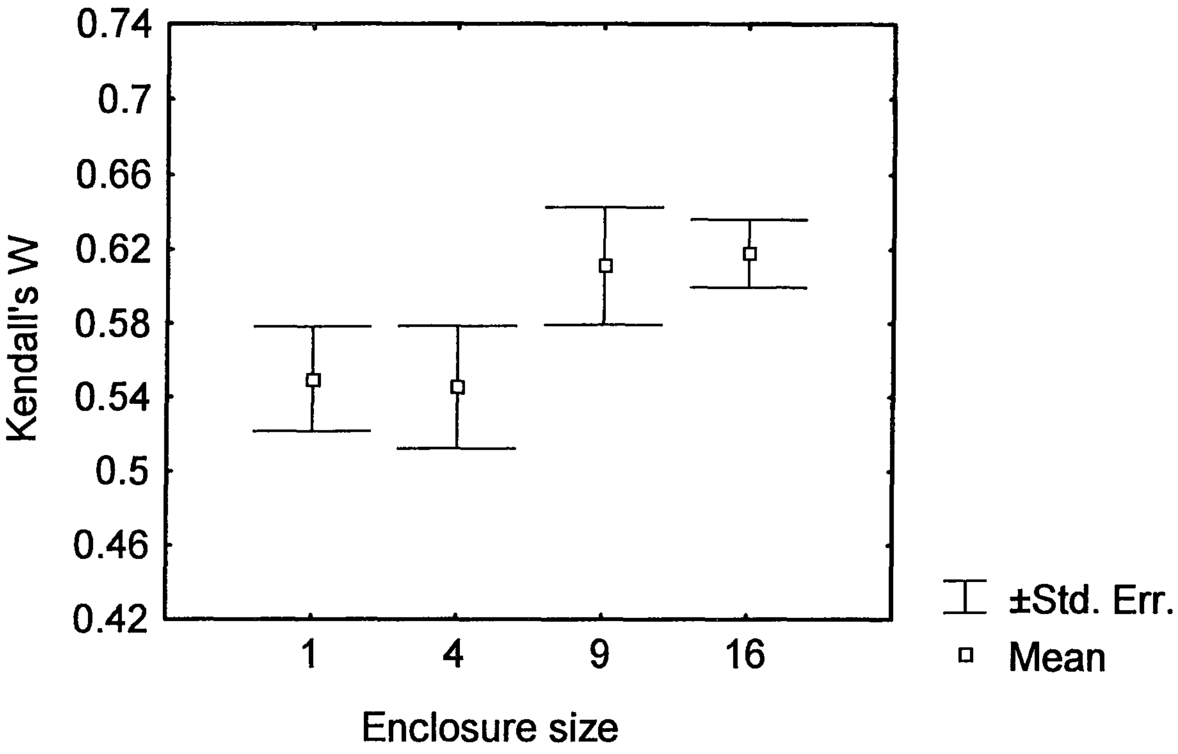

Fig. 2. Kendall's coefficient of variation for different enclosure sizes.

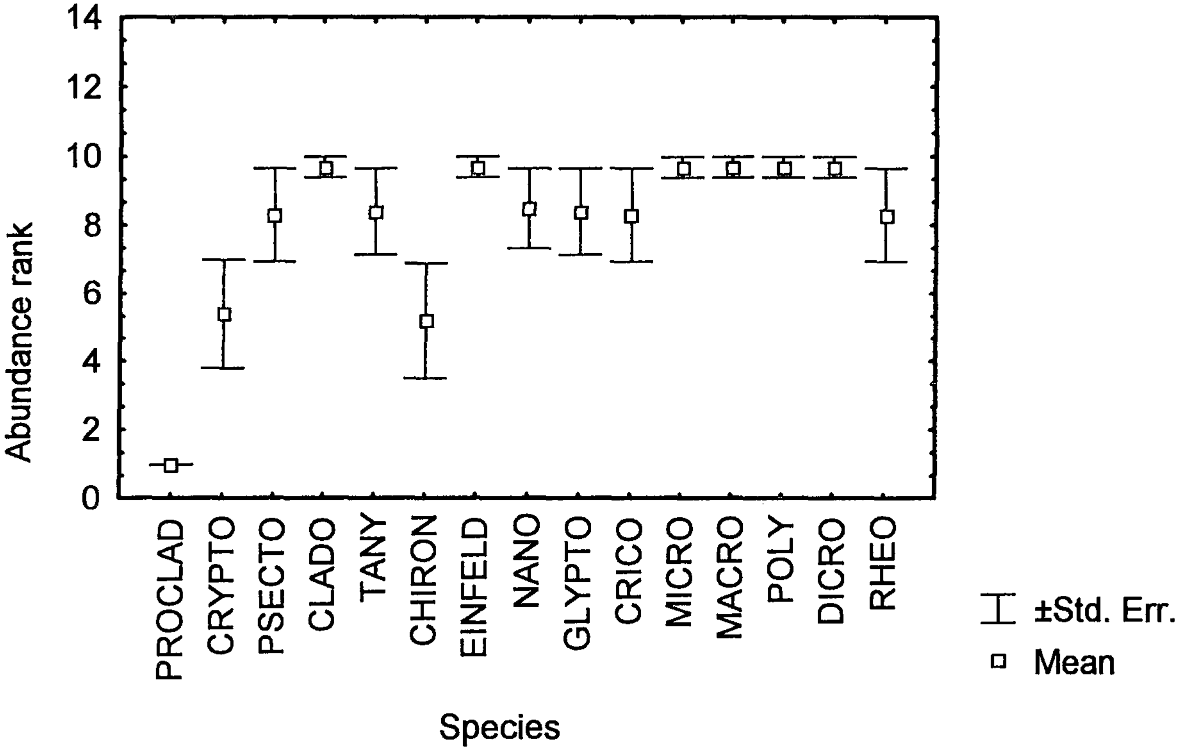

Fig. 3. Abundance rank for different species of chironomids in a $4m^2$ plastic enclosure which shows high abundance rank and low variation in <u>Procladius</u> sp.

CONCLUSION

Different patterns of community structure appear to exist at different spatial scales, degrees of isolation, and analytical scales of resolution in wetland benthos. Only some of the hypotheses on the scale-dependence of ecological patterns withstood the test. The hypothesis that smaller habitats have lower diversity and greater temporal variation of component populations as long as they are significantly isolated from the equilibrating influence of the surrounding habitat was rejected for the spatial scales and invertebrate community examined. Because midges can lay batches of eggs through the open top of the enclosures, and their larvae were not differentially constrained by limited resources, I observed no reduction in diversity due to local extinctions in small enclosures. Other studies which examined larger differences in spatial scales, have showed significant scale effects (Hodda 1990). Thus, I suggest that choosing larger or smaller spatial scales than those examined may reveal greater temporal variation in smaller enclosures. Habitat heterogeneity or the existence of two or more qualitatively different patch types (Addicott et al. 1987, Kotliar and Wiens 1990, Kolasa and Rollo 1991) is another scale effect which I associated with open sites. Within-enclosure variation in the open sites suggests a natural patch size between 4 and 9 m^2. Such a patttern might possibly be created by a benthic predator with irrecularly concentrated foraging habits. Another possible scale effect is between small (1 and 4m^2) and large(9 and 16m^2) enclosures but I do not have an explanation for it. The explanation may possibly involve many factors, including resource constraints, competition and predation.

The most isolated plastic enclosures show the greatest increase in variation of mean abundances over time when same-size enclosures are compared. This indicates that isolated enclosures diverge to a larger extent over time from one another than do less isolated enclosures. Enclosures of different sizes also show greater divergence of mean abundances when they are the most isolated (plastic) compared to less isolated enclosures. The most isolated enclosures did not show lower persistence as predicted. The isolation treatment may not have had an impact on these populations due to the ability of chironomids to re-colonize and lack of food constraint in isolated enclosures. I suggest that it would be useful to prevent chironomids from getting access through the top of the enclosures in order to determine if re-colonization is a key factor in the lack of isolation effects.

The persistence of an assemblage can be determined using different analytical scales of resolution with varied outcomes (Rahel 1990). Stability measures of abundance and abundance rank over time were used to test the hierarchical nature of community persistence. I suggest that individual species variation in rank abundance over time is another important scale at which community persistence can be evaluated. Contrary to a hypothetical model of species assemblage (Rahel 1990), we found some species to be more stable than others. This suggests the comparison of species assemblages should not only be based on an average of all species but should consider the nature of variation of individual species.

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