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Multiple scales and the relationship between density and spatial aggregation in littoral zone communities

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Understanding the constraints on community composition at multiple spatial scales is an immense challenge to community and ecosystem ecologists. As community composition is basically the composite result of species' spatial patterning, studying this spatial patterning across scales may yield clues as to which scales of environmental heterogeneity influence communities. The now widely documented positive inter-specific relationship between 'regional' range and mean 'local' abundance has become a generalisation describing the spatial patterning of species at coarse scales. We address some of the shortcomings of this generalisation, as well as examine the cross-scale spatial patterning (aggregation and density levels) of littoral-benthic invertebrates in very large lakes. Specifically, we (a) determine whether the positive range-abundance relationship can be reinterpreted in terms of the actual spatial structure of species distributions, (b) examine the relationship between aggregation and density across different spatial scales, and (c) determine whether the spatial patterning of species (e.g. low density/aggregated distribution) is constant across scales, that is, whether our interpretation of a species spatial pattern is dependent on the scale at which we choose to observe the system.

Spatial aggregation of littoral invertebrates was generally a negative function of mean density across all spatial scales and seasons (autumn and spring). This relationship may underlie positive range-abundance relationships. Species that were uncommon and highly aggregated at coarse spatial scales can be abundant and approach random distributions at finer spatial scales. Also, the change in spatial aggregation of closely related taxa across spatial scales was idiosyncratic. The idiosyncratic cross-scale spatial patterning of species implies that multiple scales of environmental heterogeneity may influence the assembly of littoral communities. Due to the multi-scale, species-specific spatial patterning of invertebrates, littoral zone communities form a complex spatial mosaic, and a 'spatially explicit' approach will be required by limnologists in order to link littoral-benthic community patterns with ecosystem processes in large oligotrophic lakes.

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Historically, community ecologists have primarily been concerned with how local biotic interactions affect community structure. As a consequence, much of their research has involved experiments conducted at small spatial scales (Schluter and Ricklefs 1993, Lawton 2000). However, local biotic interactions cannot explain a large proportion of the variation we see in community structure within entire ecosystems, and the local rules of

community assembly are often transient (Lawton 2000). At least some members of the community will operate at a spatial scale greater than that at which research is usually conducted, in terms of both grain and extent (Holt 1993, Underwood and Petraitis 1993). When this happens, ecological information is transferred from one local community to the next, such that local communities are rarely structured independently of larger scale

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processes. Hence, a better understanding of how local communities are structured can only be attained through the consideration of how community members are affected by processes operating at broader spatial scales (Schluter and Ricklefs 1993). More importantly, because the structure of communities impacts upon the functioning of ecosystems (Carpenter and Kitchell 1993, Chapin et al. 1997, Schindler et al. 1997), we must attempt to understand how communities are structured at the ecosystem scale, if we are to provide useful advice to managers (Power 2001, Thompson et al. 2001).

How can we gain an understanding of factors affecting community structure across the broad range of spatial scales that we necessarily need to consider? Community structure is basically the composite result of the spatial patterning of individual community members (Holt 1993). Indeed, spatial and temporal patterning of populations provide the means by which biodiversity is maintained in ecological communities (Tilman 1994, Tilman and Kareiva 1997, Levin 2000). Therefore, a consideration of the spatial patterning of community members at multiple scales may yield important clues as to which spatial scales of ecological heterogeneity influence community structure and function (Levin 1992, Steinberg and Kareiva 1997).

A spatial pattern that is a fairly consistent property of communities is the positive interspecific relationship between 'regional' range and mean 'local' abundance (Lawton 1993, Hanski and Gyllenberg 1997, Gaston et al. 2000). That is, species that have low mean abundances in a region tend to have more restricted ranges in comparison to those species that have higher mean abundances in that region. A number of theories have been presented to explain this relationship (reviewed in Gaston et al. 2000, Lawton 2000). In turn, these theories have provided a framework upon which hypotheses have been built to explain how spatial processes may influence community structure at broad spatial scales (Hanski 1982, Gotelli and Simberloff 1987, Collins and Glenn 1990, 1991, Hanski, et al. 1993, Hanski and Gyllenberg 1993, but see Nee et al. 1991).

In this relationship, range is normally measured as the number of sampling units occupied (presence/absence). When range is measured as occupancy, artefactual positive range-abundance relationships may be generated. For example, if sampling effort is too low, species that occur at lower densities will simply have a higher probability of not being detected than common species, generating a spurious positive abundance-range relationship (Wright 1991). Also, Wright (1991) and Hartley (1998) have demonstrated that when species in an assemblage have the same underlying level of aggregation but different mean densities, random samples from that assemblage will generate a trivial positive relationship between range (occupancy) and abundance. Thus, when range is measured as occupancy,

relationships between range and abundance may be an artefact of the species' mean abundances in the environment and the real spatial pattern of the species in an assemblage may not actually differ.

Moreover, range-abundance relationships are normally interpreted and/or established at a single spatial scale, namely 'regional range' and mean 'local abundance' (but see, for example, Gotelli and Simberloff 1987, Collins and Glenn 1991). One could suggest this interpretation is somewhat ambiguous and limiting for a majority of ecological community types that exhibit structuring across a multiplicity of scales (e.g. invertebrates and plants, Allen and Starr 1982, O'Neill et al. 1986, Collins and Glenn 1991), whereby distinct communities are sub-sets of larger scale species pools, which are in turn assembled from species pools bound by even broader spatial domains (Belyea and Lancaster 1999).

Here, we study the spatial patterning of littoral-benthic macroinvertebrate species inhabiting two large, oligotrophic lakes. There were three objectives to the study: First, we determine whether the now widely documented relationship between occupancy/range and abundance can be reinterpreted in a more spatially informative manner, that is, in terms of the actual spatial structure of species distributions (Hartley 1998). To do this, we examined the relationship between a species' level of aggregation and its mean density within the environment. If occupancy is related to the spatial structure of the species distributions, then we would expect a negative relationship between spatial aggregation and density, as species that are more aggregated would naturally occupy less sampling units in space. Second, as community structure varies along spatial gradients at multiple scales in these large lakes, and the domains of 'local' and 'regional' communities are unknown, we examined the relationship between aggregation and density of littoral-benthic invertebrates across three spatial scales of resolution. Third, we determine how the spatial aggregation and density levels of species change as we narrow in on the centre(s) of their distribution, with finer spatial resolution. In so doing, we examine which spatial scales of environmental heterogeneity may constrain the distribution and abundance of littoral-benthic species. The purpose in studying the cross-scale spatial patterning of species was to assess whether community members all share a characteristic scale of spatial constraint, hence whether the structure of littoral zone communities is constrained by a single, predominant scale of environmental heterogeneity.

Methods

Sample collection and sorting

Sampling was conducted in Lakes Te Anau (417 m deep, 352 km², 520 km shoreline) and Manapouri (444

m deep, 142 km², 170 km shoreline), which border Fiordland National Park in the South Island of New Zealand. These lakes are natural, oligotrophic lakes of glacial origin, with similar bathymetry, physicochemistry, and communities of aquatic plants (Wells et al. 1998) and animals. The sampling locations were nested in a hierarchy of three spatial scales (Fig. 1). Invertebrate samples were collected from six sites in each lake. Within each site, five depths were sampled (0 m, 2 m, 6 m, 10 m, 14 m), and at each depth, three samples 15 m apart were collected. Samples were collected by SCUBA using a Surber sampler modified for completely submersed sampling of a 25 cm² quadrat. This sampler differs from conventional Surber samplers (Merritt and Cummins 1996) in that the mesh bag is readily detached, and the opening of the Surber sampler is much smaller to prevent sample material being washed back out of the detachable bag. This sampler

was designed to take quantitatively comparable samples across the complete range of substrate types in the littoral zones. The top 2 cm of benthos (includes animals, sediment and plants) was removed from a 25 cm² quadrat and washed into a 250 µm mesh bag, after which the bag was rapidly detached, sealed and secured to a dive line for subsequent retrieval. The lakes were sampled in autumn and spring 2000.

Macroinvertebrates were washed through graded sieves and divided into two fractions: those retained by a 1000 µm sieve and those retained by a 250 µm sieve. The 1000 µm fraction was sorted in its entirety, however, a 12.5% sub-sample was sorted for the 250 µm fraction.

Analysis

To ensure our analyses of spatial pattern were robust, only 24 of the 70 taxa recorded in the samples were retained for this analysis; these taxa were all relatively common members of the community, and had a 100% probability of being detected in our total sample size for each lake (see McArdle 1990 for method). Some of the invertebrate taxa included in the analysis (Appendix) are presented as morphospecies because the taxonomy of some New Zealand aquatic invertebrate groups is incomplete (e.g. Oribatid mites).

Spatial aggregation was measured using Lloyd's index, I_L . Aggregation measured this way is a property of the spatial pattern irrespective of density, hence two populations can exhibit the same degree of aggregation even though their densities differ (Pielou 1969, p. 98, Hurlbert 1990). I_L measures how many times more likely it is that two randomly selected individuals will be from the same sampling unit than it would be if the N individuals were distributed randomly among units. For example, if $I_L = 1.5$, then the probability that the two randomly selected individuals are from the same sampling unit is 50% greater than it would be in the case of a random distribution (Hurlbert 1990). Spatial aggregation was calculated among sites, among depths within sites, and among quadrats within depths for each lake in autumn and spring. Whereas quadrats were consistently located 15 m apart, the distance between sites and between depths was variable. Although the distances among sampling locations were variable within spatial scales, the distances between spatial scales were far greater, and we are generally comparing levels of aggregation at scales of metres, tens of metres and kilometres.

To determine I_L , the mean and the variance are calculated across sampling units located within a larger sampling arena. In a nested sampling design, such as the one used here, the sampling units and sampling arenas take on different definitions depending on the spatial scale of interest (Fig. 1). To calculate spatial

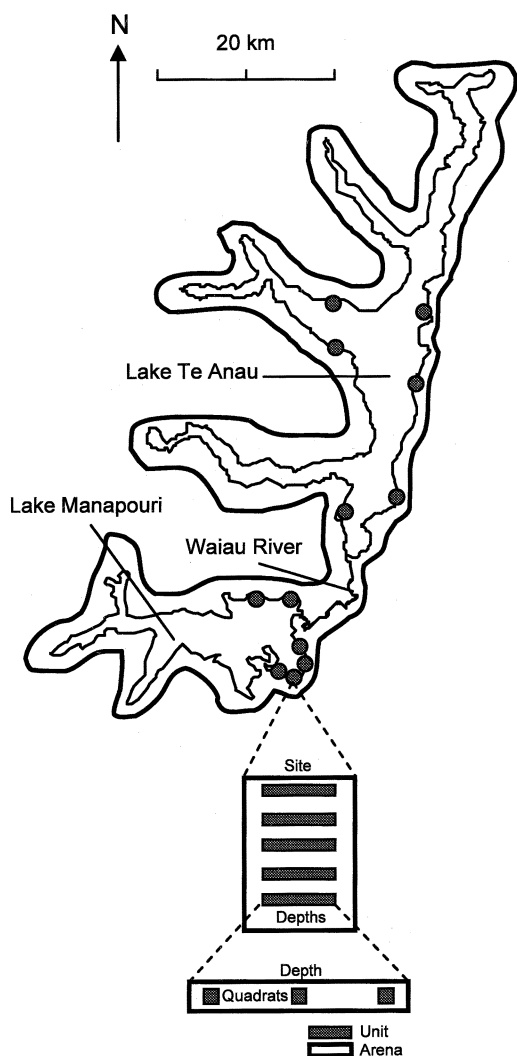


Fig. 1. Site locations and diagram of nested sampling scheme.

aggregation among sites (coarse scale), the sampling units are the sites, and the sampling arena is the periphery of the two lakes (Fig. 1). As the two lakes are located close together (dispersal distances among some sites between lakes are actually smaller than dispersal distances among sites within lakes), and they contain similar environments and invertebrate communities, we pooled the data collected in both lakes, to increase the power of the species-specific aggregation estimates at the coarse scale. To calculate aggregation among depths within sites (intermediate scale), the sampling units are the depths, and the sampling arena is the site (Fig. 1). To calculate aggregation among quadrats (fine scale), the sampling units are the individual quadrats, and the sampling arena is the depth within which the quadrats were located (Fig. 1). Invertebrate densities within sampling units at the coarse and intermediate scales were expressed as means, because they consist of numerous samples nested within those units (Fig. 1).

To improve the validity of comparisons of spatial pattern among taxa at any given scale, we calculated standard errors of our I_L estimates. Replicates were the sampling arenas for each spatial scale (Fig. 1). As we only had one sampling arena for aggregation estimates at the coarse scale (the boundaries of the two lakes pooled; Fig. 1), we used Tukey's Jackknife Method (Sokal and Rohlf 1995) for error estimation at the coarse scale, giving $N = 12$ jackknife estimates of aggregation at the coarse scale. Levels of aggregation could only be calculated for taxa that were present in a sampling arena, so the number of replicates for different taxa at different scales varied, and depended on how aggregated they were at coarser spatial scales. For example, a taxon that is highly aggregated at the coarse scale may only be found at two sites. Hence the level of replication for aggregation estimation at the intermediate scale (among depths within those sites) is $N = 2$. By contrast, a species that is not highly aggregated at the coarse scale may be found at all 12 sites, giving a replication level of $N = 12$ for aggregation estimation for that taxon at the intermediate scale. The same applied for aggregation estimation at the fine scale (among quadrats within depths within sites), where N depended on how many depth-arenas within which that taxon was present, both within and among sites. Such replication imbalance is not ideal, but is an unavoidable consequence of comparing spatial pattern among taxa that exhibit idiosyncratic distributions across scales.

As our scale of resolution becomes finer, sampling arenas from which a taxon is absent are excluded, thereby focusing on the centre(s) of that taxon's spatial distribution at finer scales. This method of analysis enables us to determine how the spatial pattern of invertebrate populations can vary depending on the spatial scale of resolution.

The Pearson product moment correlation statistic (PCS) was used to determine the degree of linear co-

variance between mean density (x) and mean aggregation (y). This was done for both untransformed data and $\ln(x, y + 1)$ transformed data, as the relationship between aggregation and density occasionally had a log-normal shape. To determine the significance of the relationship between density and aggregation, randomisation tests (Manly 1997) were used because of their structural simplicity, and because they make no assumptions about the distribution of variates. The null hypothesis being tested here is that there is no linear relationship between density and aggregation, and that the degree of linear covariance between the two variables, as defined by PCS, is no greater than we would expect by chance alone. In a randomization test, the null hypothesis is true when all possible orders of the data are equally likely to have occurred. Our observed PCS values were compared to a randomization distribution of pcs values generated from 10 000 permutations (reorderings) of x 's with y 's. The P-value is therefore the proportion of pcs values more extreme than our PCS values (Manly 1997).

To examine how aggregation and density levels of individual taxa change across spatial scales we selected a subset of species belonging to the family Chironomidae in autumn, and both chironomids and water mites in spring. Using I_L as a response variable, and 'species' and 'scale' as factors, two-factor ANOVAs were carried out for each lake and season, where the interaction effect (species \times scale) indicated whether aggregation levels of individual species vary in unique ways across spatial scales. To better meet ANOVA assumptions of normality and homoscedasticity, I_L values were either log-transformed ($\ln(x + 1)$), or rank-transformed (Potvin and Roff 1993). All non-chironomid species in autumn, and all non-chironomid and non-water mite species in spring were included in two separate ANOVAs of the same design as that described above to determine whether they exhibited unique variation in aggregation levels across scales.

Results

There was a significant negative relationship between aggregation and density at the coarse and fine scales in autumn and at the intermediate and fine scales in spring (Table 1, Fig. 2 and 3). The removal of the obvious outliers with high aggregation levels in the intermediate-scale (autumn; one outlier, Fig. 2b) and coarse-scale (spring; two outliers, Fig. 3a) plots does increase the degree of negative covariance between variables, but not to the extent that these relationships become significant (Table 1).

The seasonal discrepancies in the nature of the aggregation-density relationship may be due to the relatively small number of species included in our analysis. The

Table 1. Pearson correlation statistics and results of randomisation significance tests for all aggregation-density relationships. Season: a = autumn, s = spring.

Scale (season)	Untransformed		ln(x + 1)-transformed	
	PCS	P	PCS	P
Coarse (a)	-0.47	0.048	-0.57	0.019
Intermediate (a)	-0.01	0.997	0.10	0.727
Fine (a)	-0.69	0.002	-0.72	0.002
Coarse (s)	-0.12	0.627	0.04	0.867
Intermediate (s)	-0.50	0.030	-0.46	0.052
Fine (s)	-0.50	0.028	-0.50	0.033
Intermediate (a) outliers removed	-0.17	0.523	-0.11	0.679
Coarse (s) outliers removed	-0.30	0.250	-0.17	0.513

upper-left portions of Fig. 2b and 3a (also, to a lesser extent 3b) appear particularly truncated in comparison to the other plots. This portion of the plot may normally be filled by the rarer species in the assemblage. A large number of rare littoral zone invertebrate species had to be excluded because their low abundance at all scales meant that we could not accurately document their spatial pattern (McArdle 1990). The 'truncation' of aggregation levels at low densities in Fig. 2b and 3a may be a result of our incomplete data set. More samples would have to be taken to reliably document the spatial pattern of the complete macroinvertebrate assemblage.

The relationship between aggregation and density is a generally negative triangular one across all spatial scales considered in this study (Fig. 2 and 3). That is, all points do not fall around a single line, but are instead scattered below a trend line describing the upper limit of their distribution in a bi-plot. Conventional abundance-occupancy relationships are also frequently triangular (Lawton 1993, Warren and Gaston 1997). Therefore, abundance or mean density may place the upper limit on the aggregation level of species in an assemblage, but it does not explain all the variance in species' aggregation levels.

To demonstrate how the spatial pattern of closely related species can vary with spatial resolution we have plotted mean level of aggregation against mean density for each spatial scale for chironomid species in autumn (Fig. 4) and chironomid and water mite species in spring (Fig. 5 and 6). ANOVA main effects indicated that there is significant variation in overall aggregation levels among species (irrespective of scale; Table 2), and that there is significant variation in overall aggregation levels among scales (irrespective of species; Table 2). The error term of interest was the taxon \times scale interaction, which was significant in each of the ANOVAs, indicating that individual species may alter their spatial pattern in unique ways across spatial scales (Table 2).

The idiosyncratic changes in spatial pattern across scales are pronounced among chironomid species. In autumn at the coarse scale, *Stictocladus* sp. was relatively rare within the lake, and highly aggregated

among sites (Fig. 4i). Within the sites at which it was found, it was still highly aggregated as it is restricted to particular depths, however, within those depths, it reached some of the highest densities and attained the most even distributions of any assemblage member included in our analyses. Thus, *Stictocladus* sp. was constrained to particular sites and depths, but was randomly distributed within those depths. In spring at the coarse scale, *Paucispinigera* sp. has a moderate mean density within the lake, yet was highly aggregated among sites (Fig. 5f). Within the sites at which it was found, it attained high densities but, unlike *Stictocladus* sp., was only moderately aggregated among depths. Within depths, this species approached a random distribution and was very abundant (Fig. 5f). So *Paucispinigera* sp. was constrained to particular sites, but at those sites was distributed relatively randomly across and within depths. In contrast with *Stictocladus* sp. and *Paucispinigera* sp., *Cladopelma* sp. was almost randomly distributed at the coarse scale, even though it was rare within the lakes. *Cladopelma* became more aggregated among depths at the intermediate scale, and was moderately aggregated on a fine scale (Fig. 4g). So *Cladopelma* sp. may be constrained to certain depths and, to a lesser extent, patches within those depths, but does not appear to be constrained at the coarse scale. *Cricotopus* sp. (Fig. 4b and 5b) exhibited only moderate aggregation at any scale, and that level of aggregation did not appreciably change across spatial scales. Note also that any of the aforementioned species can be present in only one season (e.g. *Stictocladus* sp. Fig. 4i), present in both seasons and have similar patterns across scales in those seasons (e.g. *Chironomus* sp. Fig. 4a and 5a), or have a changed spatial pattern across scales among seasons (e.g. *Tanytarsus* sp. Fig. 4e and 5e).

The water mites also provide an interesting case of cross-scale spatial pattern. *Piona* and Oribatid 1 were almost randomly distributed among sites at the coarse scale, but were highly aggregated among depths within the sites at which they were found, and were also highly aggregated among quadrats within the depths at which they were found (Fig. 6a, b). Hence, the spatial distri-

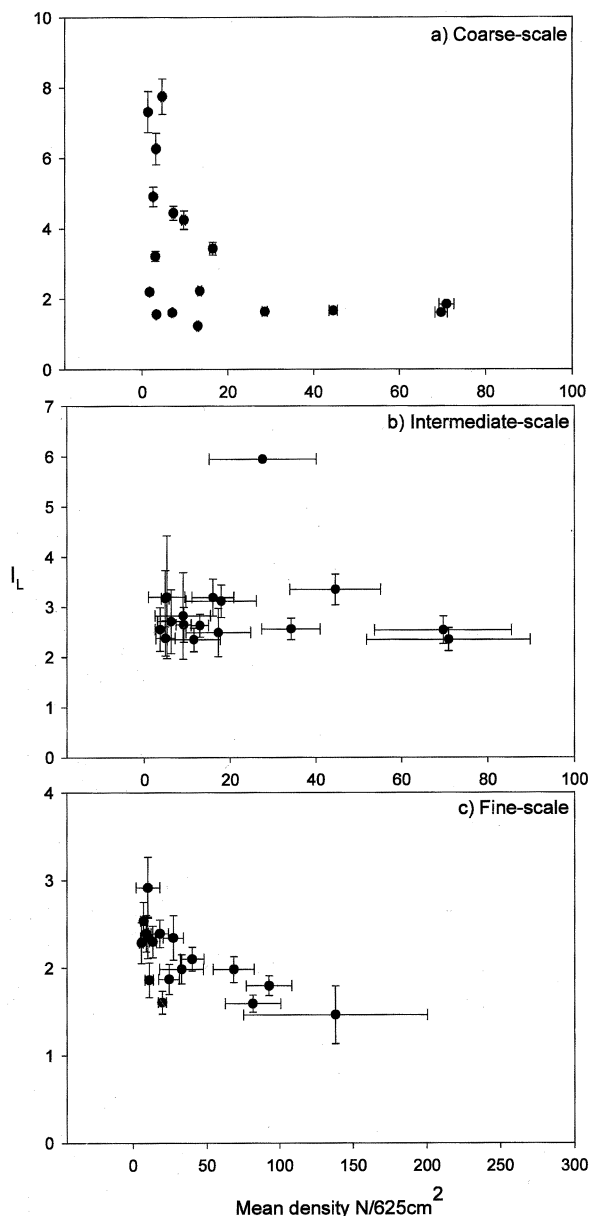


Fig. 2. Mean level of aggregation (I_L) as a function of the mean abundance of common littoral zone invertebrate species at three spatial scales in autumn (both means ± 1 SE).

bution of these species may be constrained by fine and intermediate scale heterogeneity, yet coarse scale heterogeneity places few constraints on their distribution. By contrast, Oribatid 2 was highly aggregated at all spatial scales of resolution, particularly at coarse scales (Fig. 6c).

Discussion

In the littoral zones of large, oligotrophic lakes the

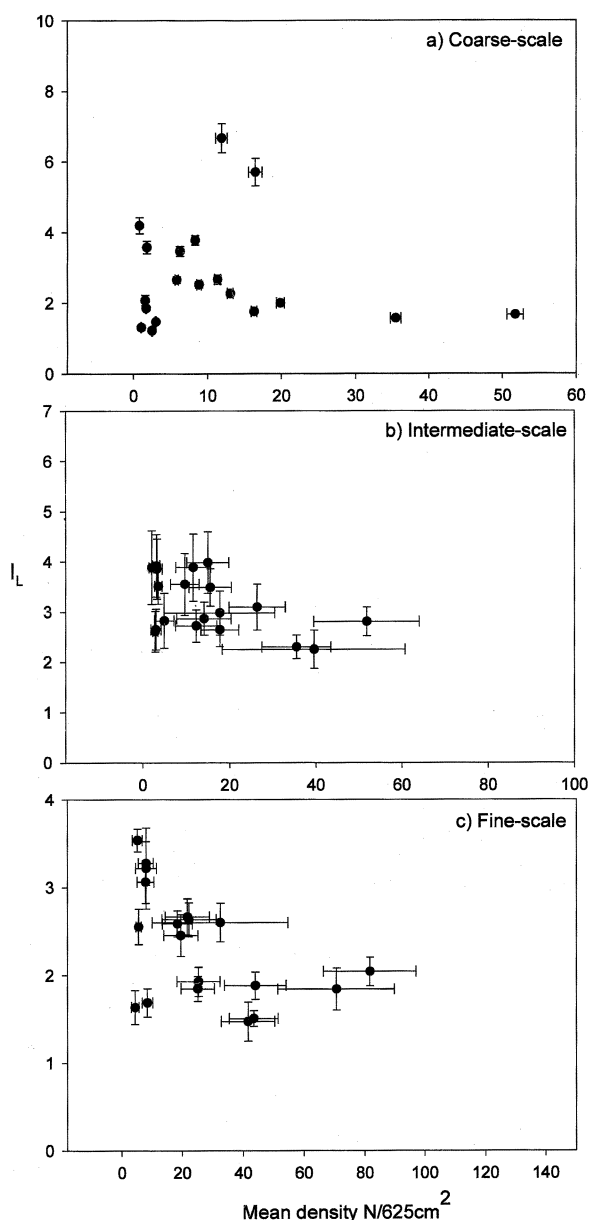
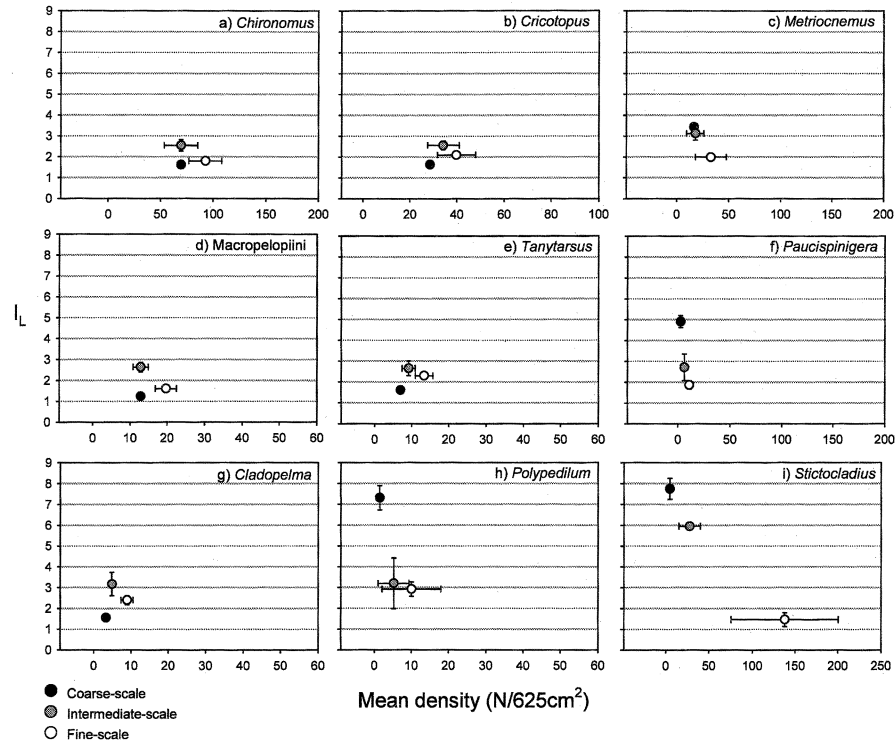


Fig. 3. Mean level of aggregation (I_L) as a function of the mean abundance of common littoral zone invertebrate species at three spatial scales in spring (both means ± 1 SE).

aggregation levels of species appears to be constrained by density, such that species that attain high densities consistently approach a random spatial distribution, whereas species that are rare exhibit more diverse spatial patterns, and are more aggregated on average. This relationship is an analogous, more spatially informative representation of the positive abundance-range relationships, which have recently assumed a prominent place in community ecology (Bock 1987, Hanski et al. 1993, Lawton 1993, 2000, Hanski and Gyllenberg 1997, Gonzalez et al. 1998,

Fig. 4. Mean level of aggregation (I_L) as a function of the mean density exhibited by nine benthic Chironomidae species at three spatial scales in autumn. Note change in x-axis range among plots.



Gaston 1999, Gaston et al. 2000). The relationship is present across the three spatial scales of resolution studied. However, the spatial patterning of individual

species (position of a species within the aggregation-density plots) can change dramatically across scales of resolution.

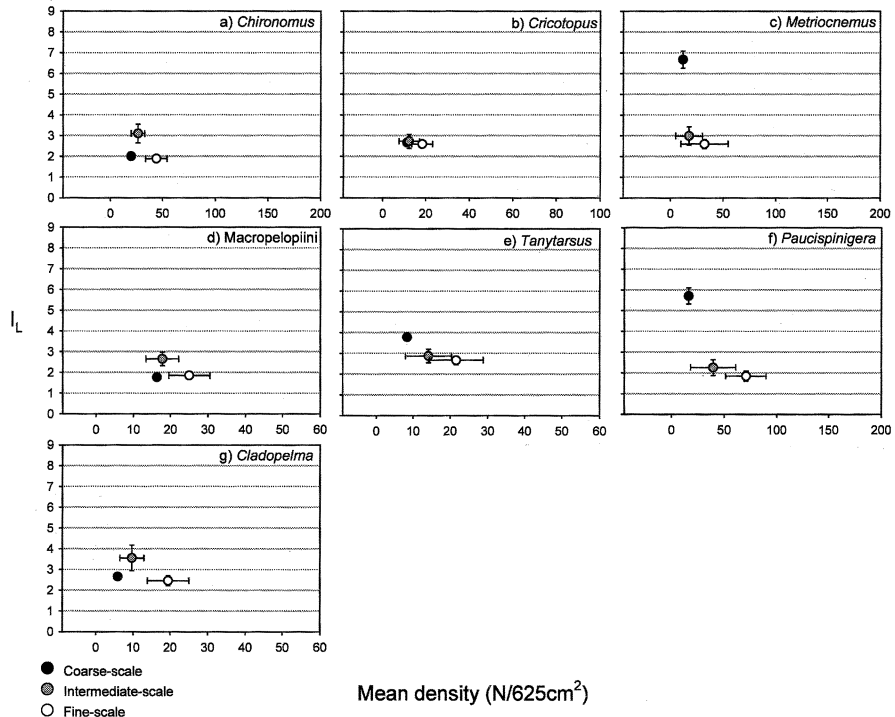


Fig. 5. Mean level of aggregation (I_L) as a function of the mean density exhibited by seven benthic Chironomidae species at three spatial scales in spring. Note change in x-axis range among plots.

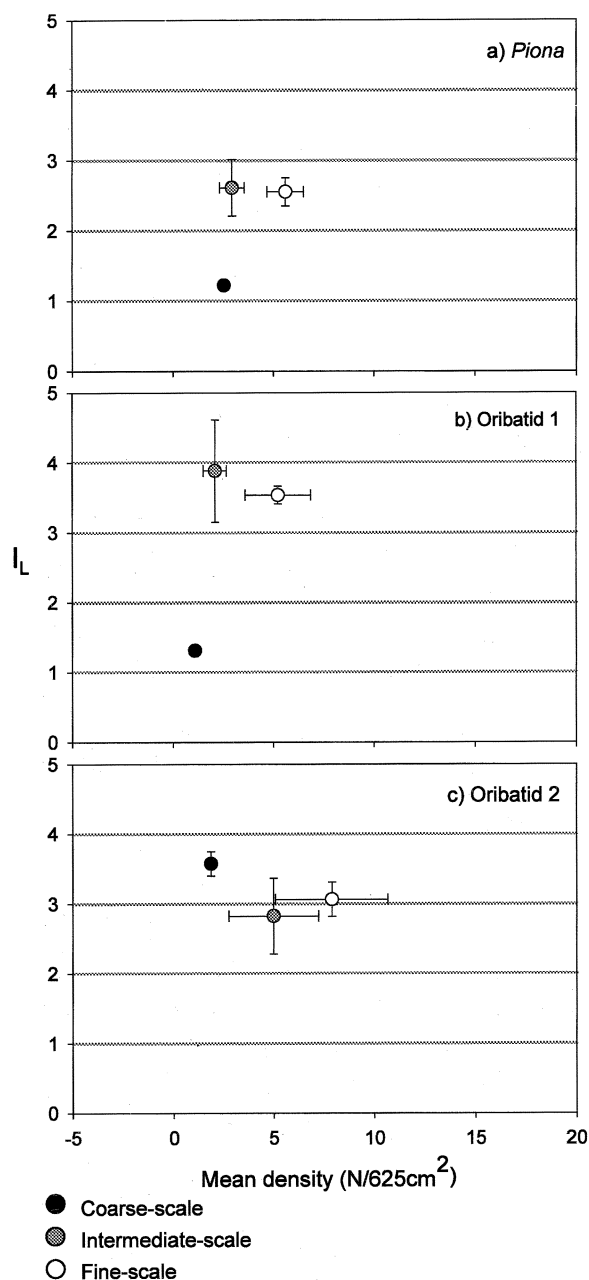


Fig. 6. Mean level of aggregation (I_L) as a function of the mean density exhibited by three water mite species at three spatial scales in spring.

In abundance-range relationships, range is normally measured as occupancy (presence/absence). Measuring range as occupancy provides limited information as to the actual spatial pattern underlying the species' distribution. Measuring range as occupancy can also be problematic in that the smaller ranges documented for rare species may be a simple artefact of the higher probability of not being able to detect that species in a

sample (McArdle 1990, Wright 1991, Hartley 1998). This study demonstrates that rare species, through their aggregated spatial pattern, may fill space less evenly than common species. If rare species are on average more aggregated than abundant species, we would naturally expect them to occupy less sampling units in space, thus, it is probable that such a spatial pattern underlies many of the positive range-abundance relationships documented (see also Taylor et al. 1978).

Interspecific range-abundance relationships are normally documented at one spatial scale, namely, 'local' abundance and 'regional' occupancy. However, the spatial domain of 'local' and 'regional' processes in relation to any given ecological assemblage is really in the eye of the beholder (Underwood and Petraitis 1993). Lake littoral zone communities provide a good illustration of this. Distinct littoral zone communities may develop among lakes, among large sections of shoreline within those lakes (differing exposures for example), and among depths within those sections of shoreline. This multi-scalar assemblage formation means that if the relationship is to be considered a useful one for community ecologists we must acknowledge space as a continuum and examine the spatial patterning of community members at multiple scales (Hurlbert 1990, Levin 1992). Here we show the negative relationship between spatial aggregation and density is present across three spatial scales in littoral zone invertebrate communities. This indicates that at any given location, we are likely to see a generally negative relationship between spatial aggregation and mean density of species in a community. This relationship may persist irrespective of our spatial resolution, that is, whether that location is an entire lake community, or just a local community within a depth zone at a particular site.

By documenting spatial aggregation in a nested hierarchy of spatial scales the idiosyncratic nature in which the spatial pattern of individual taxa changes across scales may be revealed. This study demonstrates that even closely related species exhibit idiosyncratic changes in spatial patterning across scales. The examples provided herein clearly show that while one species may have strong constraints placed on its distribution at a particular scale, the distribution of a closely related species may be free from constraint on that same spatial scale. As the three points for each species in Fig. 4–6 are simply their respective positions within the aggregation-density plots (Fig. 2 and 3) for each scale and season, we can also see how the position of each species within the aggregation-density plots can be either greatly changed or unaffected by spatial resolution and location.

What is the significance of these spatial patterns to community ecologists? The most obvious implication of the negative functional relationship between spatial ag-

Table 2. Two-factor analysis of variance testing for differences in aggregation levels among littoral zone invertebrate species across three spatial scales in autumn and spring. All I_L values $\ln(x + 1)$ transformed, with the exception of water mite I_L values, which were rank-transformed. *** $P < 0.001$.

Source of error	df	MS	F		df	MS	F
a) Chironomids autumn				d) Other species autumn			
Species	8	1.079	17.019***	Species	7	0.586	8.493***
Scale	2	2.312	36.468***	Scale	2	2.589	37.498***
Species \times scale	16	0.752	11.857***	Species \times scale	14	0.506	7.336***
Error	387	0.063		Error	370	0.069	
b) Chironomids spring				e) Other species spring			
Species	6	0.814	12.452***	Species	7	0.592	9.576***
Scale	2	2.798	42.800***	Scale	2	2.917	47.163***
Species \times scale	12	0.633	9.689***	Species \times scale	14	0.272	4.392***
Error	301	0.065		Error	342	0.062	
c) Water mites spring							
Species	2	5180.553	9.711***				
Scale	2	10178.825	19.081***				
Species \times scale	4	5032.824	9.435***				
Error	99	533.466					

gregation and abundance is that, at a coarse scale, the community will be numerically dominated by just a few relatively uniformly distributed species, and a large proportion of the species appear rare and, on average, more aggregated. However, if we restrict our spatial resolution, and focus on a community within any given section of a lake's littoral zone, we may find a similar negative relationship between aggregation and density, but the structural identity of species, or position of species in the plots, may have changed. Again, if we continue to restrict our spatial resolution to a particular depth within that littoral section, the relationship will persist, but the structural identity of species may continue to change. Essentially, a large proportion of the species in a community may appear relatively rare and aggregated at the scale of entire ecosystems, yet these species are not rare everywhere, and can be numerically dominant, randomly distributed members of particular assemblages at finer spatial scales. It follows then, that because species impact upon the structure and function of communities (Chapin et al. 1997), we are likely to find considerable spatial variation in community structure and function around lake littoral zones. There is a growing body of literature to support the notion that the spatial pattern of species alters ecosystem processes (Menge et al. 1994, Pacala and Deutschman 1995, Power et al. 1996, Tilman and Kareiva 1997, Power and Rainey 2000).

The spatial distributions of closely related species may be constrained by processes operating at different spatial scales. The implication of this is that it is unlikely that any one scale of ecological heterogeneity is responsible for the assembly of littoral zone communities. This interplay between spatial scale and species-specific spatial pattern should result in a complex mosaic of invertebrate community types throughout lake littoral zones, and predicting the spatial distribution of community attributes will require environmental information across a range of spatial scales.

What 'range' of spatial scales should community ecologists consider then? Wiens (1989) rightly asked the question whether domains of scale exist in ecosystems. He defined a domain of scale as a region of the spectrum over which patterns either do not change or change monotonically with changes in scale. He suggested that domains are separated by relatively sharp transitions of dominance by one set of factors to another. The complex idiosyncrasies in spatial pattern that species exhibit across scales raises some doubt as to whether community ecologists can discover discrete domains of scale, within which whole communities are collectively constrained by a characteristic set of factors. If there are a limited number of quantifiable scale domains impacting upon community structure in large lakes, then it is highly likely that the factors in operation at any single domain are only affecting a limited subset of the community. Other members of the same community may be responding to signal(s) sent from other domains.

Aggregation is a crucial determinant of species coexistence and the spatial patterning of species provides the means by which biodiversity is maintained in ecosystems (Ives 1991, Tilman 1994, Sevenster and van Alphen 1996, Pacala and Levin 1997, Krijger and Sevenster 2001). This study emphasizes the multiple spatial scales at which biodiversity is maintained in lake ecosystems. Of particular note, is the very large spatial scale (kilometers) at which littoral zone taxa may aggregate, and the fact that no single spatial scale is responsible for spatial patterning (discussed above). As biodiversity is important in ecosystem functioning and resilience (Naeem and Li 1997, Walker et al. 1999, Tilman et al. 2001), limnologists interested in the role littoral-benthic diversity plays in ecosystem processes of large lakes must consider multiple spatial scales and have a spatially extensive sampling programme.

In any given community at any given scale, why should rare species fill space less evenly than common species? As the negative aggregation-abundance relationship reported here is an analog of the positive range-abundance relationship, we can infer the same theoretical mechanisms. Hartley (1998) and Wright (1991) demonstrated that a positive range-abundance relationship will be generated when we randomly sample from an assemblage whose members have the same aggregation levels but differ in their mean densities. Although this study explicitly considers the relationship in terms of the actual spatial pattern of assemblage members, hereby discounting this mechanism, we are still left with a great range of theoretical mechanisms to consider (Lawton 2000, p. 82–85). The five most plausible mechanistic explanations of the pattern are centered on issues of niche breadth and resource availability (Brown 1984, Venier and Fahrig 1996, Gregory and Gaston 2000), and population and metapopulation dynamics (Hanski 1982, Maurer 1990, Hanski et al. 1993, Holt et al. 1997, Gonzalez et al. 1998).

As so many mechanisms have been proposed to explain the relationship between spatial aggregation and abundance, and as we know so little about littoral-benthic communities, we feel a discussion of mechanisms that may or may not generate the patterns in the present study is well beyond the scope of this paper. We are currently investigating the role multi-scaled habitat templates play in determining the structure of littoral-benthic communities within large lakes, and these results are forthcoming. However, it is worth mentioning a plausible mechanism given by Lehman and Tilman (1997), that has been overlooked in recent reviews of the abundance-occupancy relationship (Hanski et al. 1993, Holt et al. 1997, Gaston et al. 2000, Lawton 2000).

Lehman and Tilman (1997) showed that even if resources are homogeneously distributed, but species differ in their relative dispersal/competitive abilities, a relationship between spatial aggregation and abundance like the one described here will arise. In a competitive hierarchy, the best competitor cannot be displaced from a site so its distribution is only influenced by its own patterns of mortality and colonization. Because a propagule is more likely to colonise a nearby site, local concentrations of the best competitor arise over space. The next best competitor has its own intrinsic tendency to aggregate, but the environment it perceives is already aggregated (because the best competitor is aggregated it follows that the sites unoccupied by the best competitor are also aggregated). Thus, the next best competitor tends to aggregate in an area that is already aggregated, and hence becomes more aggregated than the best competitor. This tendency to aggregate increases down the competitive hierarchy (Lehman and Tilman 1997, p. 194). Because the best competitors are normally more abundant than inferior competitors,

we would expect a relationship between spatial aggregation and abundance very similar to that documented here. Hence, spatially distributed biotic interactions can be added to the list of potentially generating mechanisms centered on issues of niche breadth, resource availability, and population and metapopulation dynamics.

Concluding remarks

The spatial aggregation exhibited by a species at any given scale of resolution, is not independent of its mean abundance at that scale of resolution. This negative aggregation-abundance relationship may be one of the few general patterns community ecologists can expect real communities to exhibit. However, while the pattern has important implications for community ecology, its causation remains very poorly understood (Lawton 2000). A detailed knowledge of the study community is essential to decipher what mechanisms cause this aggregation-abundance relationship, and whether the mechanisms differ across spatial scales. The current theories of causation are not necessarily mutually exclusive, as some may operate simultaneously (Guo et al. 2000), and some may be complementary across different spatial scales (Collins and Glenn 1991). As the form of the pattern may be scale invariant, but the structural identity of species comprising the pattern may change across scales, ecologists concerned with causative mechanisms must ensure their work is spatially explicit (explicitating spatial scale and location of observation).

Our knowledge of how littoral zone communities are structured across spatial scales is rudimentary. Spatial heterogeneity in community structure transmits spatial heterogeneity in ecosystem processes (Pickett and Cadenasso 1995). How can we manage large ecosystems then if we do not know the magnitude or spatial scales of heterogeneity in the distribution and abundance of organisms within those ecosystems? Indeed, Wiens (2000) suggests that quantification goes a long way towards making the multifarious concept of heterogeneity operational. This study demonstrates that littoral-benthic taxa are gregarious across multiple spatial scales, and that it is unlikely that any single scale of environmental heterogeneity is of primary importance in community assembly. Due to this multi-scale, multi-directional aggregated spatial pattern of community members, the littoral zone undoubtedly comprises a complex mosaic of community types, and therefore poses an immense challenge to limnologists (Lodge et al. 1988, Pickett and Cadenasso 1995). To understand how that mosaic is formed and how it functions, littoral zone research must be multiscaled and spatially explicit. Indeed, such research agendas are now recognized as major priorities for all areas of ecological inquiry (Wu and Loucks 1995, Thompson et al. 2001).

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Appendix: Littoral-benthic invertebrate taxa included in analyses.

Gastropoda
Potamopyrgus antipodarum
 Bivalvia
Sphaerium novaezealandiae
 Chironomidae (Diptera)
 Chironominae
Chironomus zealandicus
Tanytarsus funebris
Paucispinigera approximata
Cladopelma sp.
Polypedilum sp.
 Orthocladinae
Metriocnemus sp.
Cricotopus sp.
Stictocladus sp.
 Tanytopodinae
Macropelopiini sp.

Trichoptera
 Leptoceridae
Oecetis unicolor
 Hydroptilidae
Paroxyethira tillyardi
Paroxyethira hendersoni
 Arachnida
Piona sp.
 Oribatid 1
 Oribatid 2
 Ostracoda
 Ostracoda 1
 Cladocera
Ilyocryptus sp.
 Chydorid 1