Spatial associations between lotic fish, macroinvertebrate prey and the stream habitat: a multi-scale approach

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We adopted a multiscale approach to examine the spatial relations between stream fish, macroinvertebrate prey, and habitat characteristics in a boreal stream. The study site was divided into 279 cells, and abundances of brown trout and Arctic bullhead were quantified at each cell. Depth, water velocity, substrate size and aquatic vegetation were measured, and benthic samples collected, at each quadrat. Shaded contour plots showing the spatial distribution of selected variables within the sample space were produced and fish distributions were superimposed on these plots. High-density patches of trout and bullhead were in separate sections of the riffle, and bullhead were closely associated with their benthic prey, especially semisessile macroinvertebrates. Semivariograms were produced for two variables, water depth and density of semisessile invertebrates. There was spatial dependence, especially in the density data, at lags shorter than 2 metres. Kriging was then used to create maps displaying the spatial patterns of the variables within the sample space. We believe this kind of multi-scale sampling strategy combined with standard geostatistical tools and statistical modeling will prove valuable in the study of aquatic consumer-resource interactions.

Introduction

Habitat models used for predicting the amount of stream habitat suitable for fish are commonly based on four key variables: water depth, water velocity, substrate composition and in-stream cover. It is obvious, however, that habitat selection is also affected by biotic factors, e.g. the presence of competitors and predators and, perhaps most importantly, the availability of food resources. The development of more realistic models has been hindered by the lack of information

about the role of biotic factors in fish habitat selection (Orth 1987, Gore and Nestler 1988). Even observational field studies reporting spatial correlations between stream fishes and their macroinvertebrate prey are conspiciously rare.

It is usually difficult to determine a priori an appropriate scale for a study; thus, it may be advisable to conduct the study, regardless of its objectives, on a variety of spatial scales (Levin 1992, Horne and Schneider 1994, Underwood and Chapman 1996, Cooper *et al*. 1998). Streams are notoriously heterogeneous environments where organisms exhibit patchy distributions on a spatially and temporally variable physical arena. It thus seems obvious that fish-environment relationships, as well as associations between fish species, should be examined across multiple scales. Here, we report the sampling strategy and first results from a field study employing a "landscape approach" to examine habitat selection by stream fishes in relation to spatial variation in physical habitat variables and prey resources.

Material and methods

The field study was conducted in Kuusinkijoki, a third order river in northeastern Finland. The mean discharge of the river is $10 \, m^3 \, s^{-1}$, and it is characterized by wide flow fluctuations. The peak flow (up to $65 \, m^3 \, s^{-1}$) occurs in late May. The average population density of juvenile brown trout (*Salmo trutta* L.) at our study site is $0.80 \, fish \times m^{-2}$, which is considerably more than in other parts of the Oulankajoki system (Huusko and Korhonen 1993). The stream bed is dominated by cobbles and small boulders, interspersed with coarse gravel. The stream bottom is densely covered by aquatic vegetation, mainly *Ranunculus* sp. and aquatic mosses. Brown trout and arctic bullhead (*Cottus poecilopus* Heckel) are the dominant fish species, although other species, especially the European grayling (*Thymallus thymallus* (L.)) and European minnow (*Phoxinus phoxinus* (L.)), also occur in the deepest stream pools.

Our sampling site is located in the Raatekoski rapids (66°17´N, 29°54´E) on the lower course of the river. We delineated a rectangular sampling area of 23 m × 4,5 m, consisting of a grid of 279 cells, each 0.75 m × 0.5 m (Fig. 1). This cell size

was chosen to reduce any disturbance caused by sampling to invertebrates and fish in adjacent cells. We electrofished the entire study area on 13 August 1994 using the point electrofishing method (*see* Moyle and Baltz 1985, Heggenes 1989), and recorded the number of trout and bullheads at each cell. Fish were assigned to one of two size classes (trout: 5–10 cm, 10–15 cm; bullhead: < 5 cm, 5–8 cm). For brown trout, these size classes roughly correspond to age classes 0+ and 1+ (Huusko and Korhonen 1993). To reduce the effects of positive galvanotaxis, we used a DC backpack electroshocker with low voltage (300 V) and a 9-cm-diameter anode. The "fright bias", which may cause displacement of individuals from their original positions, was minimized by the point electrofishing method used to locate fish (e.g., Heggenes 1989).

After fish sampling was completed, four habitat variables (depth of water, water velocity, substrate size, percent cover of instream vegetation) were measured at each cell. Water depth was measured to the nearest centimeter with a wading rod. Water velocity was measured at 0.6-depth with a Schiltknecht Mini Water type 624 w-m/l flow meter fitted with a 20 mm propeller. Water depth and velocity were determined at the center of each cell. Dominant substrate size and percent cover of submerged vegetation were estimated visually for the entire cell. Substrate was coded according to a modified Wentworth scale, using categories 4–10 (sand to boulder) of the 13 particle size categories in Heggenes *et al*'s (1990) classification.

We used dark-coloured paving bricks (14 × 13 cm) as colonization substrates for benthic invertebrates because, given sufficient colonization time, such bricks will mimic natural stream stones reasonably well (Douglas and Lake 1994). One brick was placed at the center of every other cell three weeks before fish sampling. To reduce the disturbance caused by electrofishing, benthos was sampled one week after the fish sampling. Benthic samples were taken by placing a frame with a net (mesh size 0.25 mm) behind a brick, which was then quickly moved into the net. Invertebrates dislodged from the stone and trapped by the net were included in the sample. Invertebrates were preserved in 70% ethanol in the field and later identified to a feasible (mainly generic) taxonomic

level in the laboratory.

The data were visualized as overlay maps showing the spatial distributions of variables within the sample space. For this, we used a SYSTAT smoothing option (Systat Inc 1992), the Distance Weighted Least Squares (DWLS) smoothing. This method produces shaded contour plots with fill patterns from white (empty) to black (fill) in even gradations, determined by the value of the function at a given cell. The DWLS smoothing fits a contour through a set of points by least squares. As a result, this method produces a locally weighted interpolation surface running through all the measured values in the sample space (McLain 1974).

We also used two geostatistical methods effective in the study of spatial patterns among ecological data: semivariogram and kriging (*see* Rossi *et al*. 1992). Variogram describes spatial dependence between pairs of samples as a function of their distance, *h*, which, given some stationary conditions, is defined as:

$$\text{Var}[z(s + h) - z(s)] \qquad (1)$$

where *z* is the response function and *s* any point within the sample area. Strongest spatial dependence, and smallest variogram values, are usually observed at short lags; samples further apart tend to be spatially less dependent, yielding large variogram values. To illustrate the effectiveness of these methods in describing spatial dependence, we produced omnidirectional variograms (averages over all pairs of data, regardless of their direction) for two variables, water depth and density of semisessile invertebrates. A more detailed analysis, including spatial dependences between different "layers" of the data (e.g., fishes and macroinvertebrates) will appear elsewhere. We produced omnidirectional variograms because our data were isotropic, that is, there were no directional effects in response variables. We applied a spherical variogram model, because it is a standard choice for data displaying diminishing dependence at increasing lags (Cressie 1993: section 2.3.1.). Finally, we created maps of depth and invertebrate densities using the spatial interpolation method of kriging, based on the variogram modeled previously. Kriging provides estimates for unrecorded locations by minimizing the mean squared prediction error (*see* Cressie 1993: chap-
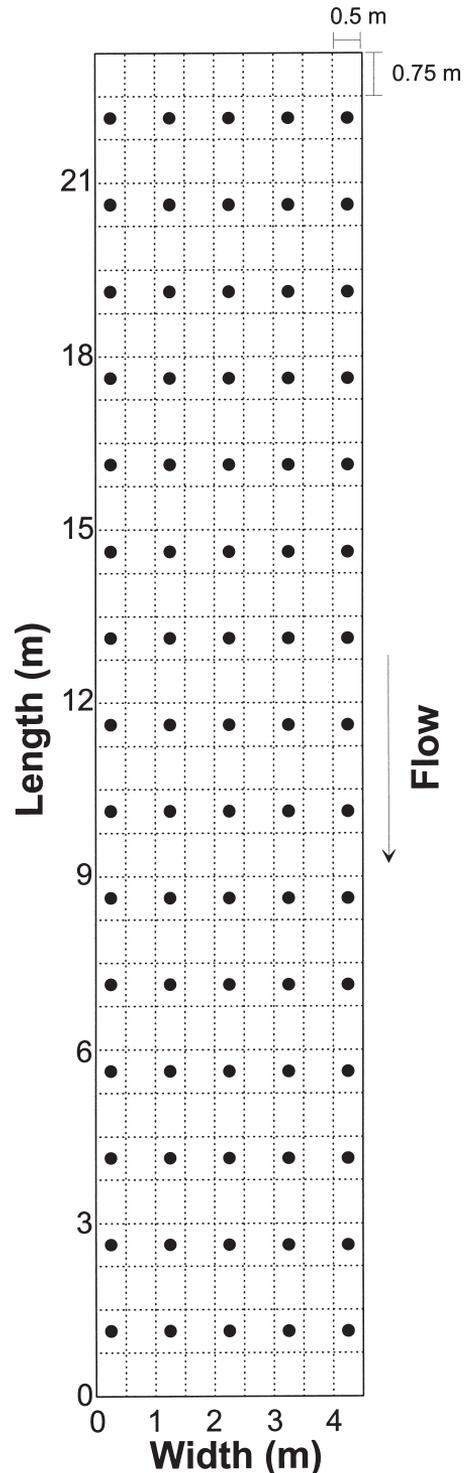
Fig. 1. A schematic presentation of the study section. Black dots denote positions of the colonization substrates used for benthic sampling.

ter 3). Variograms were produced with the VarioWin-package (Pannatier 1995), and Surfer for Windows (Golden Software Inc. 1995) was used for kriging.

Results

The contours of water depth and substrate size in relation to the distribution of brown trout are presented in Figs. 2A and B. The overlay maps show the tendency of large trout to occupy the deepest available stream areas with cobble-to-boulder substrates. By contrast, the spatial relations between fish and their prey can not be easily detected from the contour maps (Figs. 3A and B). Microhabitats totally devoid of macroinvertebrates were clearly avoided by fish, but only large bullheads (> 4 cm) showed any aggregation to areas with the highest abundance of benthos, especially semisessile invertebrates (larval stages of blackflies and filter-feeding caddisflies; *see* Fig. 3B). Distribution of trout did not show any obvious relationship with their prey (Fig. 3A).

Both fish species were clearly non-randomly distributed within the sample reach. At the scale of the mapped area, both sculpin and trout seemed to form three or four relatively distinct clusters. It is, however, even more interesting that the two species showed a tendency toward spatial avoidance: high-density aggregations of trout and sculpin were in separate sections of the riffle (Fig. 3A). The two species were located in a same grid cell on only seven occasions, which, considering the high density of fish in the study section, is a remarkably low frequency of co-occurrences.

Omnidirectional semivariogram for water depth presents an example where spatial dependence diminishes with an increasing lag (Fig. 4A). At lags up to two metres, the measurements are spatially dependent (*see also* the kriging map in Fig. 5A). The variogram then levels off (= no spatial dependence). The relatively high nugget value (value at which the curve intercepts the Y-axis) indicates that some unaccounted-for variability is present at scales below the smallest sampling distance (0.5 metres in this case).

For the semisessile invertebrate data, the variogram reaches the sill value, corresponding to no spatial dependence, at about 2.5 metres, in-

dicating relatively strong dependence at lags smaller than that (Fig. 4B). In this case, kriging produced a map with three distinct high-density patches of semisessile invertebrates (Fig. 5B). It must be emphasized, however, that the difference between the model's sill and nugget only represents the proportion of total variation that can be modeled as spatially dependent, based on the available sampling grid. There probably is spatial dependence in densities of invertebrates at lags much shorter than the smallest sampling distance (1.0 m) used in this study. The grid used should thus be dense enough to allow an accurate estimation of the microscale dependence and the nugget. Nevertheless, since different variables vary across different scales, any sampling grid will unavoidably track them to a different accuracy. Stream fishes and benthic macroinvertebrates, for example, can rarely be sampled to the same accuracy with the same grid. Thus, while the measurements of this study are accurate for fish distributions, our grid was not able to uncover the small-scale heterogeneity of invertebrate densities and habitat characteristics. Had these been the main objectives of our study, a denser grid should have been used.

Discussion

The observation that large trout mainly occupied the deepest stream areas is consistent with the previous finding of Mäki-Petäys *et al.* (1997) for juvenile brown trout in the same stream reach, and this "bigger fish–deeper habitat" relationship has been documented in numerous studies of habitat selection by stream fish (e.g., Bohlin 1977, Power 1987, Harvey and Stewart 1991). By contrast, we found no apparent patterns in the microhabitat selection by Arctic bullhead in relation to physical stream habitat. Instead, large bullhead seemed to prefer areas with high densities of semisessile invertebrates. This may be related to their foraging behavior. Sculpins in general are bottom-feeding, non-visual predators that rely on tactile or hydrodynamic cues for prey detection (Hoekstra and Janssen 1985). Furthermore, there is some evidence that sculpins are size-selective predators, favoring the largest prey types available (Newman and Waters 1984, Englund and Olsson 1997). Net-
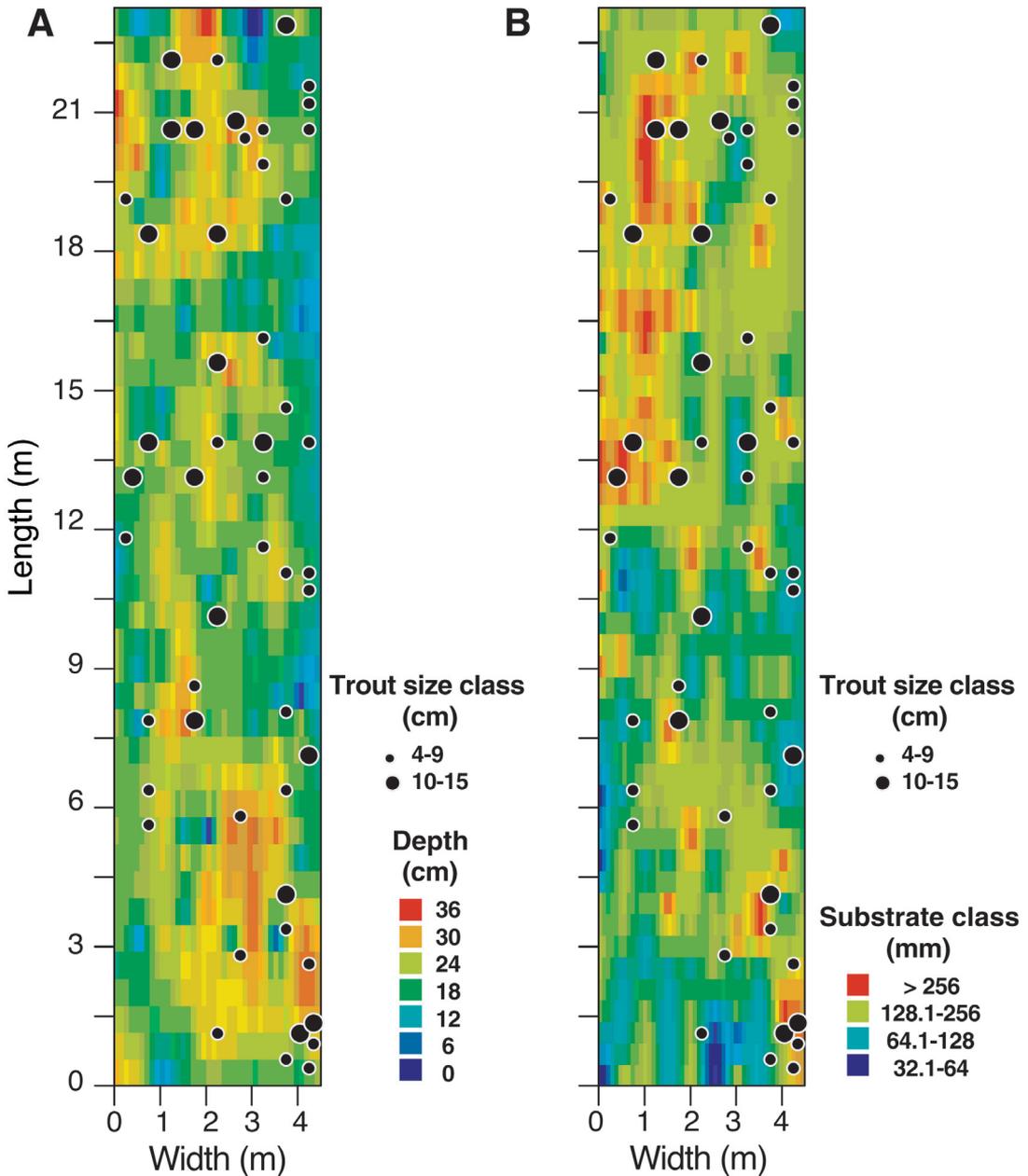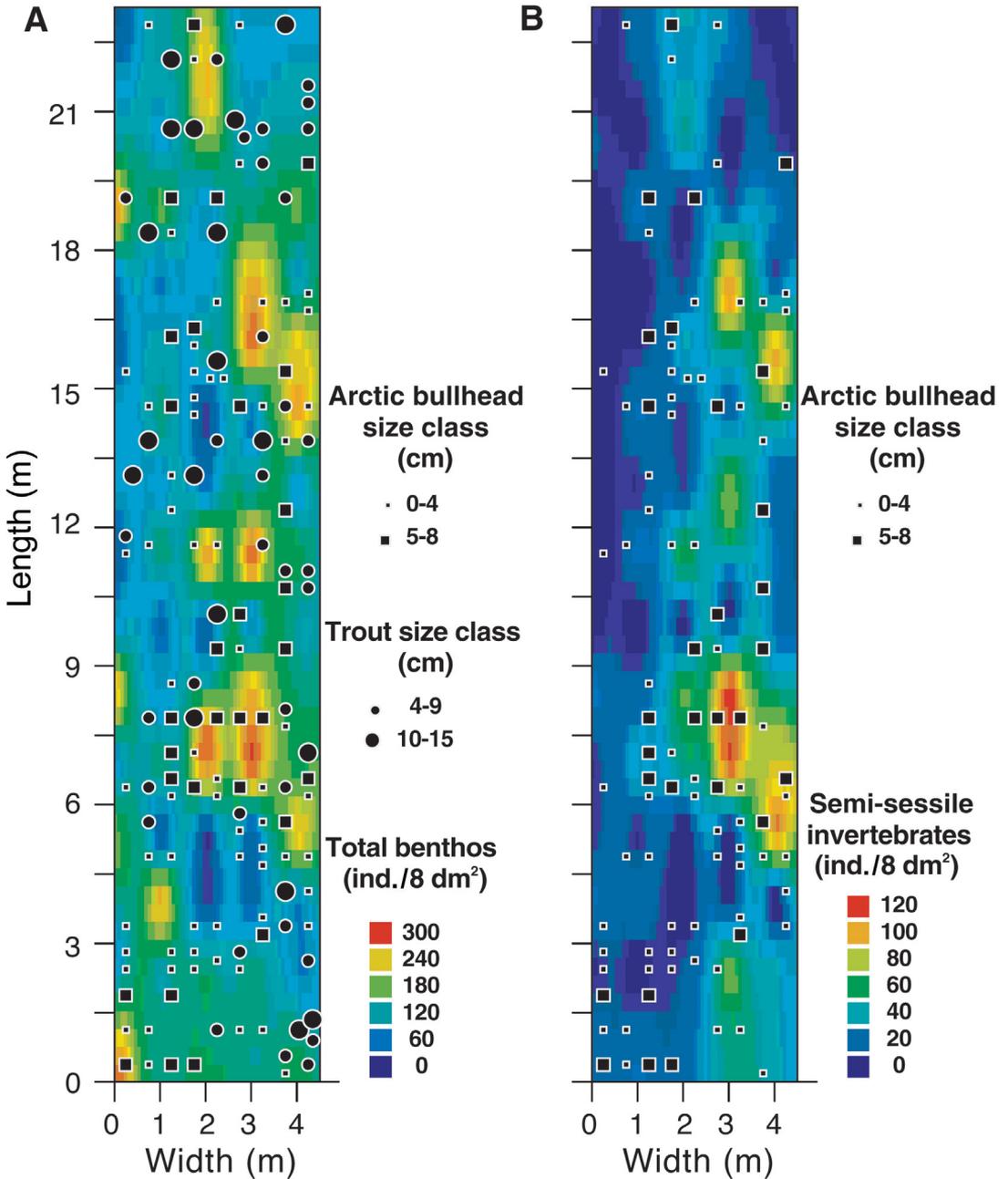
Fig. 2. Overlay maps showing the distributions of brown trout size-classes within the sample space in relation to contour plots of water depth (A) and substrate size (B).

spinning caddis larvae are certainly among the largest food items for fish in our study site. These semisessile invertebrates are easy to capture, but they may be too large to be consumed by smaller bullheads. Although these explanations for the spatial relations between bullhead and benthic invertebrates seem plausible, they need to be sup-

ported by behavioral experiments addressing the mechanisms of prey selection in sculpins.

The apparent lack of aggregation by brown trout with their prey may partly result from the methods used to estimate prey availability. Trout is a sit-and-wait predator that hunt visually for drifting prey (e.g., Allan 1981, Grant and Noakes

Fig. 3. Overlay maps showing the distributions of brown trout and Arctic bullhead within the sample space in relation to contour plots of macroinvertebrate density (A), and distribution of bullhead in relation to density of semisessile invertebrates (B).

1986, McIntosh and Townsend 1995). Although there is some evidence that epibenthic feeding may be more common in trout than often thought (Tippets and Moyle 1978, P. Kreivi, unpubl.), a valid description of food availability for stream salmon-

ids may necessitate the quantification of macro-invertebrate drift. For a predominantly drift-feeding fish, benthic samples may give a somewhat biased view of prey availability.

Antipredator behaviours and relative mobil-

ity of prey should always be considered in a study of predator-prey spatial interaction. If spatial dependence is to be found, it should be between fish and semisessile prey (*see* Sih 1984), because more mobile prey types, such as lotic mayflies, may continuously shift their distribution in relation to local predation pressure (Tikkanen *et al*. 1994, Forrester 1995). Thus, from the fish point of view, mayflies and other mobile invertebrates may form ephemeral prey patches which disperse as soon as the predator enters a patch (for a similar interpretation for the lack of aggregation between stonefly predators and their mayfly prey, *see* Peckarsky and Penton 1985).

One of the most intriguing observations of this study was that there seemed to be small-scale inhibition between the two fish species, brown trout and Arctic bullhead. If there really is spatial competition between these species, as previously suggested by Gaudin and Caillere (1990), this could partly explain the near-absence of trout from patches with high densities of semisessile invertebrates. Thus, the spatial interaction between these two species appears highly scale-dependent: inhibition at small to intermediate scales (intraspecific aggregations) vs. coherence at larger scales (whole stream sections; A. Mäki-Petäys, unpubl.).

Previous studies addressing spatial aspects of predator-prey (or, more widely, consumer-resource) interactions in streams have commonly employed areal survey designs with sample plots of a fixed size. If the plots are sparsely distributed, the observations (counts of individuals, measurements of environmental variables) are approximately independent, and standard statistical methods can be used. An often ignored drawback of this approach is that there is usually no a priori information about ecologically relevant scales of interaction. Instead, the size of the quadrat defines the resolution of the study, and true associations between variables may be completely lost, or even worse, artificial associations that do not exist in reality, may emerge. In geostatistics, this is known as "change of support" (e.g., Openshaw and Taylor 1979, Arbia 1989): there is no natural (or "characteristic") scale for a process, or it is different for different processes (e.g., Levin 1992, Horne and Schneider 1994). A multiscale design based on mapped data avoids this bias by considering many different scales si-
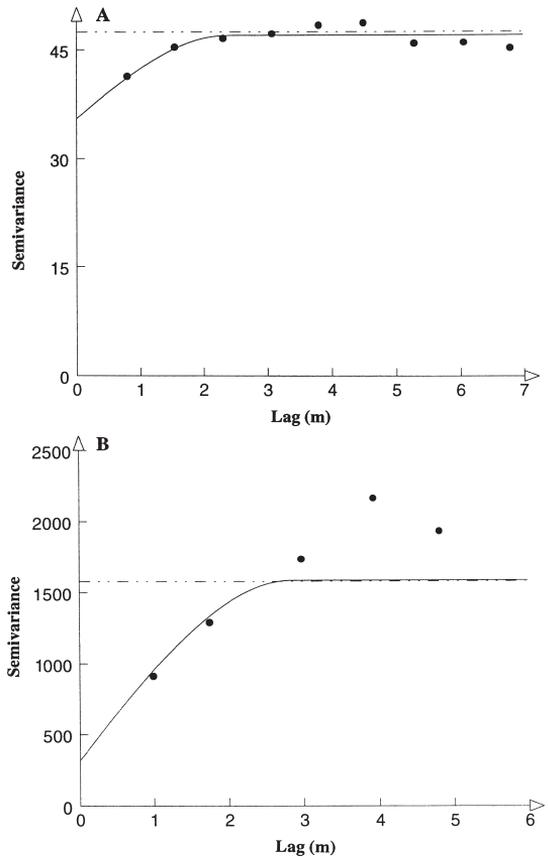
Fig. 4. Omnidirectional, non-standardized variograms for water depth (A) and density of semisessile invertebrates (B), showing semivariance for measurements separated by a common lag as a function of the lag. The horizontal line denotes the overall sample variance for the respective data set.

multaneously. An adequate tool for the input, storage, graphical output and preliminary analysis of such data is the Geographical Information System (GIS). GIS-techniques have been extensively used by resource managers for assessing the effects of large-scale land use patterns on aquatic biota, but to our knowledge it has not been applied previously to the analysis of within-stream heterogeneity at the scale of a stream reach (but *see* Cooper *et al*. 1997). In GIS, spatially referenced data for each response variable are stored in separate layers, which can be overlaid to examine the associations, and scales of association, between the variables. In field conditions, uncontrolled variability will always be present. This can to some extent be allowed for by collecting spa-
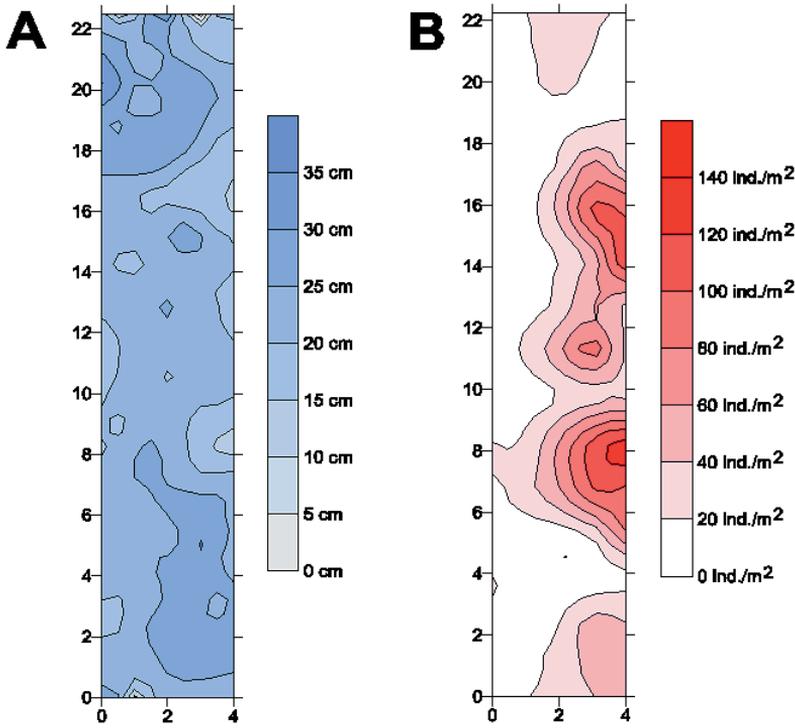
Fig. 5. Maps of water depth (A) and density of semisessile invertebrates (B) within the sample space. The maps were produced using the spatial interpolation method of kriging, based on the variograms modeled earlier (*see* Fig. 4).

tially-referenced data on potentially confounding variables, which are then used as covariates in a GIS. In lotic ecology, it is sometimes possible to map a variable (e.g., the distribution of individuals within a sample space) accurately as a point pattern (*see* Muotka and Penttinen 1994), but in most cases some level of data aggregation is needed. Kriging or other spatial interpolation methods can then be applied to provide estimates for unrecorded locations. The layers describing different response variables may thus be of different forms, but are still subject to visualization in GIS.

The GIS-assisted approach described above consists of the interactive use of a Geographical Information System and statistical modeling to produce effective analytical tools for spatially dependent, multilayered and multiscaled data. We believe such a combination of techniques will prove valuable in the study of spatial heterogeneity in lotic consumer-resource interactions. Since heterogeneity and scale are intimately intertwined in all natural environments (Levin 1992, Dutilleul and Legendre 1993), our approach should also help detect the relevant scales at which different processes operate. As Cooper *et al*. (1997) pointed

out, more studies are needed on the patch-scale dynamics of stream consumers, as well as on the movement patterns of fish and their prey in the heterogeneous stream microlandscapes. Investigation of animal movement patterns across a range of spatial scales may provide a mechanistic link between ecological processes and the spatial heterogeneity of the stream habitat. This approach has proved extremely useful in terrestrial environments (Wiens and Milne 1989, Crist and Wiens 1994, With 1994), and, although tracking of individual stream consumers will in most cases be extremely difficult and labour-intensive, we believe such observations should be pursued whenever possible.

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