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Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat

Orlando Sarnelle, Kim W. Kratz, Scott D. Cooper

Department of Biological Sciences, University of California, Santa Barbara, CA 93106, USA

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Abstract. We demonstrated the effect of an aquatic herbivore on the spatial arrangement of benthic algal biomass within artificial stream channels. Transects of ceramic tiles were exposed to a gradient of snail (*Physella*) densities in a 30 d experiment. We observed positive effects of snails on the mean abundance of "overstory" algae (the filamentous chlorophyte *Cladophora* and associated epiphytes), an important benthic microhabitat in streams. Snails altered several aspects of the spatial arrangement of overstory algae. Snails reduced the strength of downstream gradients in overstory biomass, as well as residual variability around these gradients. Geostatistical analysis revealed that snails also reduced the strength of spatial dependence, and so reduced spatial heterogeneity of the overstory, at small scales (<40 cm). As a result, organisms inhabiting the overstory might experience a more fragmented habitat landscape at high snail densities. In addition, snails increased the scale of spatial dependence in understory algal biomass (algae remaining on tiles after overstory was removed) from 10 cm to 40 cm. Consumer effects on the spatial arrangement of a microhabitat argue for the inclusion of feedbacks between the biota and the environment in spatially-explicit models.

Key words: Filamentous algae – Geostatistics – *Physella* herbivory – Spatial dependence – Stream periphyton

Spatial heterogeneity is an important factor mediating ecological interactions. Heterogeneity has been shown to have critical effects on competitive and predator-prey interactions in both ecological models and natural communities (Levin 1976; Wiens 1976; Chesson 1986; Kareiva 1986). Considerably less attention has been directed to effects of ecological interactions on spatial heterogeneity (Gutierrez et al. 1980; Fairweather 1988; Butler 1989; Schneider 1992). For example, the creation of habitat patches by animal activities is widely recognized (Grieg-Smith 1979; Pringle 1985; Forman and Godron 1986), but studies that quantify the effects of animals on landscape patchiness are relatively rare (Johnston and Naiman 1990).

In this paper, we approach the problem of animal effects on spatial heterogeneity from a geostatistical perspective. From this view, we are able to examine heterogeneity as a continuous phenomenon (Palmer 1988), rather than as discrete habitat patches imbedded in a contrasting matrix (Forman and Godron 1986). Our general objective is to examine the effects of an herbivore on the arrangement of continuously-distributed spatial variation in habitat attributes. The arrangement of variation in space has been called environmental *grain* (Pielou 1969), and is distinct from the *intensity* of spatial variation. Intensity is a function of the range of values encountered and is estimated by traditional indices based on sampling variance (Pielou 1969; but see Downing 1991). We report the results of a field experiment demonstrating effects of the herbivorous snail, *Physella* sp., on the spatial arrangement of benthic algal biomass.

Spatial arrangement is a potentially important attribute of environmental variation whose effects on ecological interactions have been little explored (Doak et al. 1992; Milne et al. 1992; Palmer 1992). The arrangement of variation will determine a landscape's continuity (i.e., the proximity of sites having similar values of a habitat attribute) and so should affect the flow of energy and material among sites (Forman and Godron 1986). Similarly, aspects of spatial arrangement, such as the distances between sites containing suitable habitat for organism establishment and the distribution of migration barriers, should influence the flow of dispersing organisms across a landscape (Doak et al. 1992; Johnson et al. 1992; Palmer 1992). Such influences may have effects on coexistence, given the importance of dispersal in spatially-explicit models of predator-prey and competitive interactions (Vandermeer 1973; Pacala 1987).

Continued development of a general theory of ecological heterogeneity is contingent upon a fuller apprecia-

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Correspondence to: O. Sarnelle

tion of scaling issues (Wiens 1989; Levin 1992). Geostatistical techniques provide a means of quantifying scale dependencies in spatial patterns (Palmer 1988; Rossi et al. 1992), but are limited by a requirement for relatively large data sets. Consequently, we chose to perform our experiment using a small invertebrate consumer of stream periphyton to facilitate the collection of large numbers of observations within multiple experimental units.

We quantified consumer effects on the spatial arrangement of benthic algal biomass using the geostatistical technique of variogram analysis. The essence of this technique lies in the concept of spatial dependence, which describes the degree to which sites covary as a function of the distance between them (Palmer 1988; Rossi et al. 1992). Variogram analysis is conceptually similar to the traditional block-size techniques of Pattern Analysis (Greig-Smith 1979), but offers the advantage of describing variation as a *continuous* function of spatial scale (Palmer 1988). As a result, relationships between variation and spatial scale can be analyzed with regression techniques, permitting quantification of critical aspects of spatial arrangement. We used variogram analysis to identify the distances over which response variables were spatially dependent and to estimate the strength of spatial dependence at those scales.

Strong spatial dependence in an environmental variable implies that sites rapidly become more different as the distance between them increases, indicating a more heterogeneous spatial arrangement (Palmer 1988). This "distance decay" is analogous to the concept of pattern, or non-randomness, from Pattern Analysis (Grieg-Smith 1979), and may or may not be associated with an overall gradient running through the study site (Palmer 1988). In contrast, weak spatial dependence is indicative of a variable that is more homogeneous or well-mixed, meaning that high and low values of the variable are more randomly distributed in space. Illustrations of one- and two-dimensional patterns corresponding to varying levels of spatial dependence are presented by Palmer (1988, 1992). Following Palmer (1992), we use the strength of spatial dependence as the operational definition of "spatial heterogeneity" at a particular scale. We define "spatial variability" using a standard index based on sampling variance (standard deviation of log-transformed data). This distinction between heterogeneity and variability has been clearly illustrated by Rossi et al. (1992; their Figs. 1 and 2). We use these terms in these strict senses throughout the remainder of this paper.

Our index of spatial variability requires comment. The standard deviation (SD) of log-transformed data measures variability relative to the mean. This means, for example, that if algal biomass were to be increased by a common factor on all substrates within an experimental unit, our index would be unchanged. We assume that organisms perceive the variability among sites with values of 2, 3 and 5 as being identical to that among sites with values of 20, 30 and 50. In contrast, the SD of raw data is ten times higher in the latter case.

Small herbivores in streams have been shown to graze periphyton on primary substrates down to a point where the assemblage is dominated by early successional species of prostrate, tightly adhering diatoms (Sumner and McIntire 1982; Lamberti et al. 1987; Lowe and Hunter 1988; Bronmark et al. 1991; Steinman et al. 1991). In the absence of strong grazing pressure, periphyton assemblages often come to be dominated by upright, loosely-attached "overstory" species (Mulholland et al. 1991; Peterson and Stevenson 1992). This pattern of grazer effect, however, may be altered depending on the history of the assemblage (Dudley 1989; Dudley and D'Antonio 1991; Dudley 1992). If grazers are abundant before filamentous overstory species with strong holdfasts are established, strong herbivory can prevent establishment by these late successional, overstory species (Dudley and D'Antonio 1991). In contrast, if strongly-attached overstory species become established before grazers are abundant, grazers can actually promote overstory abundance and dominance (Dudley 1989; Dudley 1992; but see Feminella and Resh 1991). These contrasting effects of herbivory on filamentous overstory algae can potentially have a strong influence on benthic community structure because patches of these algae constitute an important benthic microhabitat in streams (Dudley et al. 1986; Power 1990; Dodds and Gudder 1992). We introduced grazers in our experiment after filamentous species had begun to establish, and thus were able to examine grazer effects on the spatial arrangement of this microhabitat. Although the conditions of our experiment are somewhat artificial, our primary goal was to show that a consumer could potentially influence spatial dependence in a habitat attribute, an effect that has not previously been documented.

Materials and methods

We established a gradient of *Physella* densities in 12 experimental stream channels situated in Mission Creek, a second-order stream draining a chaparral watershed in Santa Barbara, CA. Our study site had moderate canopy cover. Nutrient concentrations in the stream averaged 0.55 μM soluble reactive phosphorus and 0.77 μM NH_4^+ during the experiment.

Stream channels were rectangular PVC troughs, 6 cm wide by 3 cm high by 270 cm long, that were bolted side-by-side to a plywood sheet using nylon screws. The channels were situated just above the surface of the water and were fed by diverting stream water into a manifold fitted with 12 output ports. Discharge in each channel was maintained at 70–90 ml/s by means of ball valves in each port. Water depth in the channels varied between 1 and 2 cm. Inflow was screened through 500 μm mesh to prevent colonization by larger grazers. The channels were fitted with screens (500 μm) at the downstream end and covered with coarse nylon netting (3 mm mesh) to prevent snail escape. The latter reduced light levels by about 7%. Screens were cleaned and channels were gently flushed with stream water daily to reduce accumulation of sediment and fecal material.

Each channel contained a single transect of 95 unglazed, ceramic tiles (2.3 cm, square, 0.2 cm apart), which acted as substrates for algal attachment. Algae were allowed to colonize the tiles for 16 d prior to the introduction of snails, which was 10 d after we first observed colonization by *Cladophora*, a filamentous chlorophyte with a strong holdfast. Target snail densities were 0, 80, 160, 320, 640, and 1280 mg/m^2 tissue dry mass (0–60 individuals per channel) and were chosen to be within natural densities in local streams (Hemphill and Cooper 1984). Duplicate channels at each density

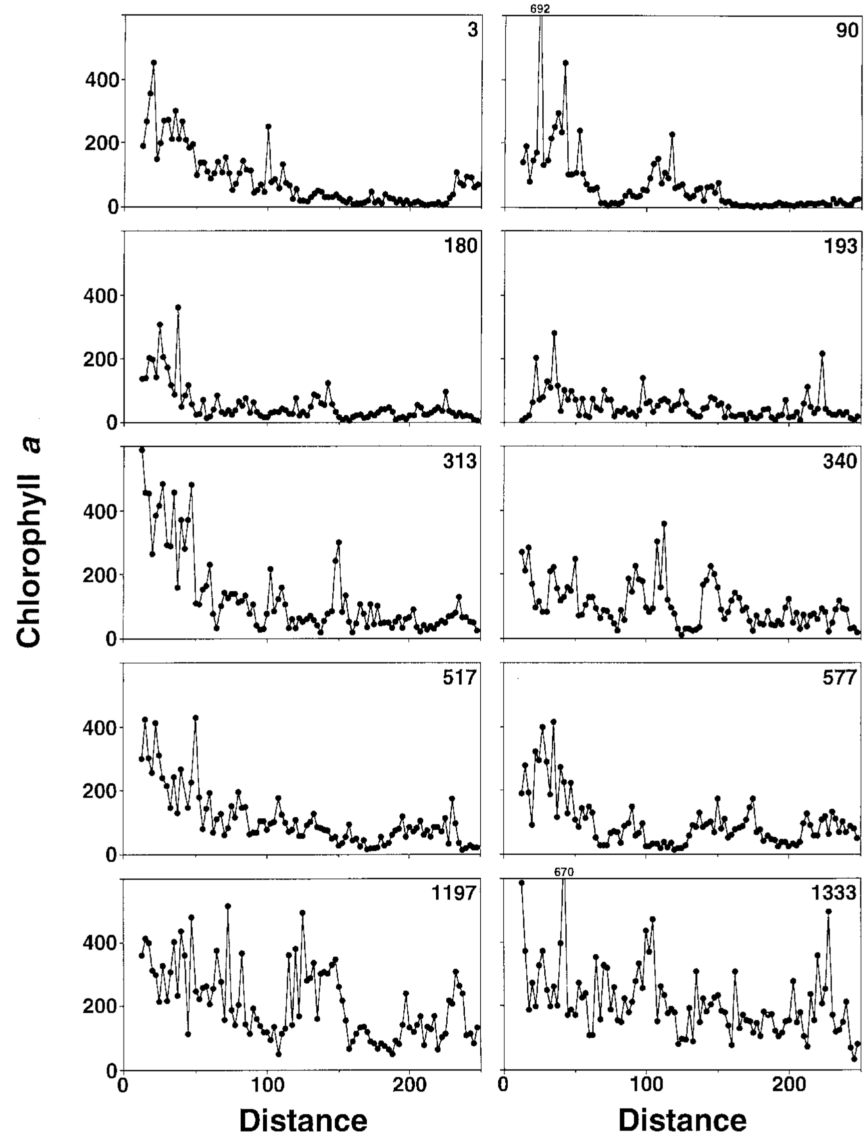

Fig. 1. Biomass of overstory algae (as mg/m^2 chlorophyll *a*) on individual tiles versus distance (cm) from the head of each channel after 30 d exposure to snail grazing. Number in the upper right of each panel is average snail biomass (as mg/m^2 tissue dry mass) over the course of the experiment

were established initially, but two channels did not function properly, leaving 10 experimental units. Dead snails were replaced daily with individuals of similar size.

Physella biomass in each channel was estimated and readjusted to target levels twice during the experiment (on days 13 and 20), by measuring maximum shell lengths (L, in mm) of all snails and applying the following equation for tissue dry mass versus length (Stein et al. 1984): M (mg)$=0.031L^{2.48}$. Snail sizes ranged from 7–12 mm. We looked for effects of snails on response variables with linear and polynomial regression, using snail biomass averaged over the experiment as the independent variable.

On the day before the experiment was terminated, we collected data on snail locations and movements within the channels. We first measured movement rates by tracing the path of randomly-selected snails (1–2 individuals on the overstory, 1–3 on the understory, for each channel) over 2 min, on paper gridded to the same scale as the tiles. The length of these two-minute paths were measured with a map wheel. We then systematically scanned each channel, noting the position of every snail with respect to longitudinal position (tile number), presence on understory versus overstory, and presence on tiles versus sides and bottom of channels. The latter indicated that the tiles were a representative sample of the surfaces visited by snails. Across channels, an average of 29% of the snails were found on tiles (SE=3%; N=9; deleting a channel with only 2 snails that were both found on tiles). By comparison, tiles comprised about 23% of the total wetted surface area available to snails within the channels.

After 30 d of exposure to snails, the filamentous overstory (primarily *Cladophora glomerata* and associated epiphytic diatoms) was collected separately from each tile by manually removing all filaments plus holdfasts with forceps. Samples of understory (algae remaining on the tiles after overstory removal) and overstory algae were stored in a freezer for two weeks prior to chlorophyll analysis. Qualitative microscopic examination indicated that the understory was primarily composed of diatoms although a few basal pads of *Cladophora* remained. Algal biomass was estimated as chlorophyll *a* by spectrophotometry of acidified and unacidified extracts in 90% ethanol (Sartory and Grobbelaar 1986). Overstory filament samples or tiles with understory were placed individually into 50 ml centrifuge tubes and extracted in the dark for 24 h at 4° C. We initially heated all extracts to 78° C for 5 min (Sartory and Grobbelaar 1986), which substantially improved extraction of *Cladophora* pigments.

Analyses of spatial pattern were complicated by a downstream gradient in the biomass of both overstory and understory algae in all channels (Figs. 1 and 2). This algal gradient was associated with a downstream decrease in current velocities, which we measured in each channel by timing the downstream drift of a small, floating plastic sphere (1.5 cm diameter). Average surface velocity across channels decreased exponentially with distance downstream,

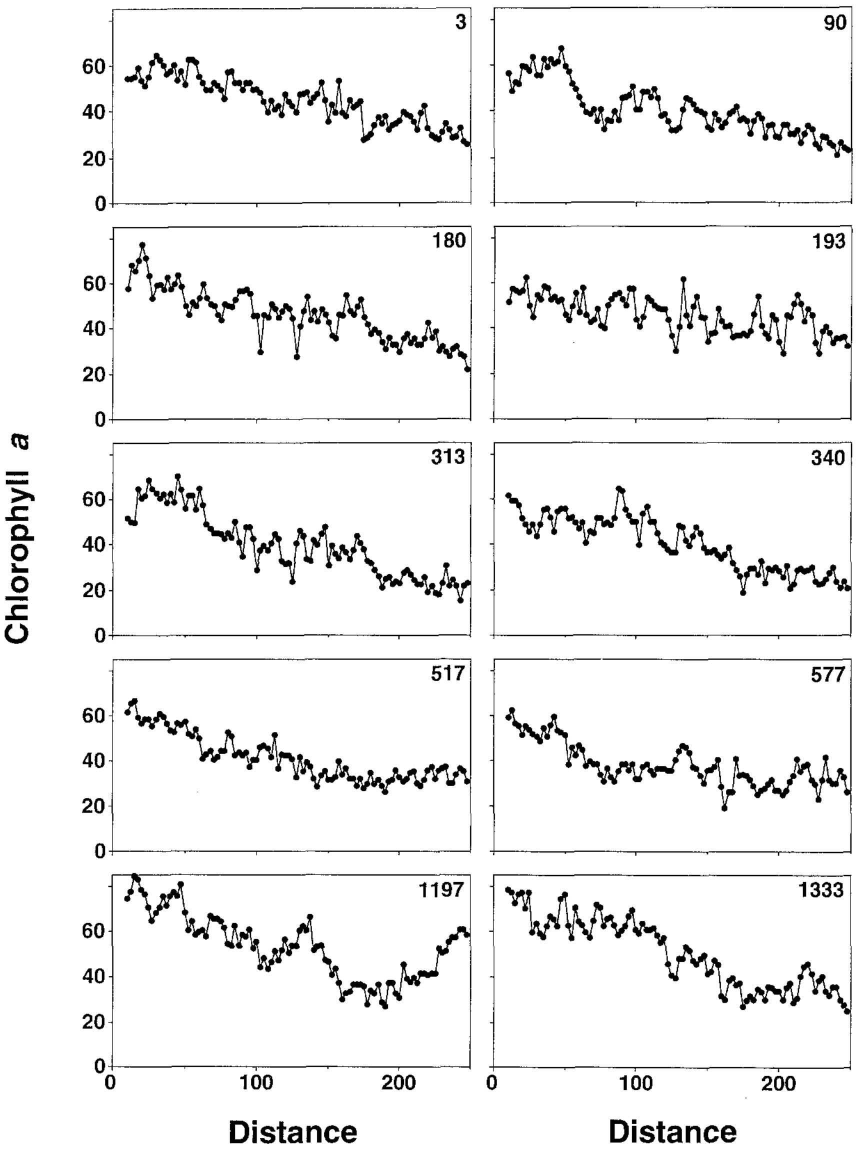

Fig. 2. Biomass of understory algae (as mg/m^2 chlorophyll *a*) on individual tiles versus distance (cm) from the head of each channel after 30 d exposure to snail grazing. Number in the upper right of each panel is average snail biomass (as mg/m^2 tissue dry mass) over the course of the experiment

from 0.17 m/s (SE = 0.016) in the upper 50 cm to 0.07 m/s (SE = 0.003) in the lower 50 cm. In addition to the gradient, overstory biomass was log-normally distributed, and typically showed a decrease in variance with distance downstream within channels (Fig. 1). In contrast, understory biomass within channels was normally distributed, and showed no obvious trends in variance with distance downstream (Fig. 2). To provide stationary series (no trends in local mean and variance) for variogram analyses (Rossi et al. 1992), we fitted linear regressions to understory chlorophyll *a* and log overstory chlorophyll *a* versus distance downstream for each channel, and used the regression residuals in further analyses. This enabled us to examine snail effects on the downstream gradient in periphyton biomass, in addition to effects on spatial dependence not associated with the gradient. The slopes of all these within-channel regressions were significantly less than zero at $P \leq 0.001$.

Variogram analysis is based on the calculation of semivariance (S), which is one-half the average, squared difference between pairs of samples separated by a common distance, or lag (Rossi et al. 1992). To facilitate visual comparison of variograms across channels with widely differing levels of sampling variance (s^2), we present standardized semivariances (S/s^2, Rossi et al. 1992). Standardized semivariances were calculated from product-moment, autocorrelation coefficients (r, Systat 1992) for lags ranging from 2.5 cm (adjacent tiles) to 60 cm, as $S/s^2 = 1 - r$. Over this range, variograms were comparable in shape, consisting of a linear increase in semivariance with lag to an asymptote (Figs. 3 and 4). At the asymptote, semivariance approximates the overall sampling variance of the data (Phillips 1985), so standardized semivariance approaches 1. Occasional dips in semivariance at high lags were considered to be artifacts of chance periodicity (Phillips 1985). These "holes" in the variograms occurred sporadically without relationship to the manipulation, and appear to be largely the product of outliers (Isaaks and Srivastava 1989). Sample sizes for estimates of S/s^2 ranged from 69 (for 60 cm lags) to 94 (for 2.5 cm lags).

We examined two aspects of spatial dependence from these standardized variograms, by fitting rectilinear models of the form:

$$S/s^2 = a + bL, \text{ for } L < L_r$$

$$S/s^2 = a + bL_r \text{ for } L \geq L_r$$

where a and b are regression constants, L is lag, and L_r is lag at the inflection point (piece-wise regression). Parameters were estimated by least squares using Simplex minimization (Systat 1992). L_r is commonly referred to as the Range, which marks the upper extent of the spatial scale over which variation shows spatial dependence. At distances greater than the Range, variation is spatially homogeneous, or randomly arranged. The Range has been used as an estimate of patch size (Sinsabaugh et al. 1991), if one defines

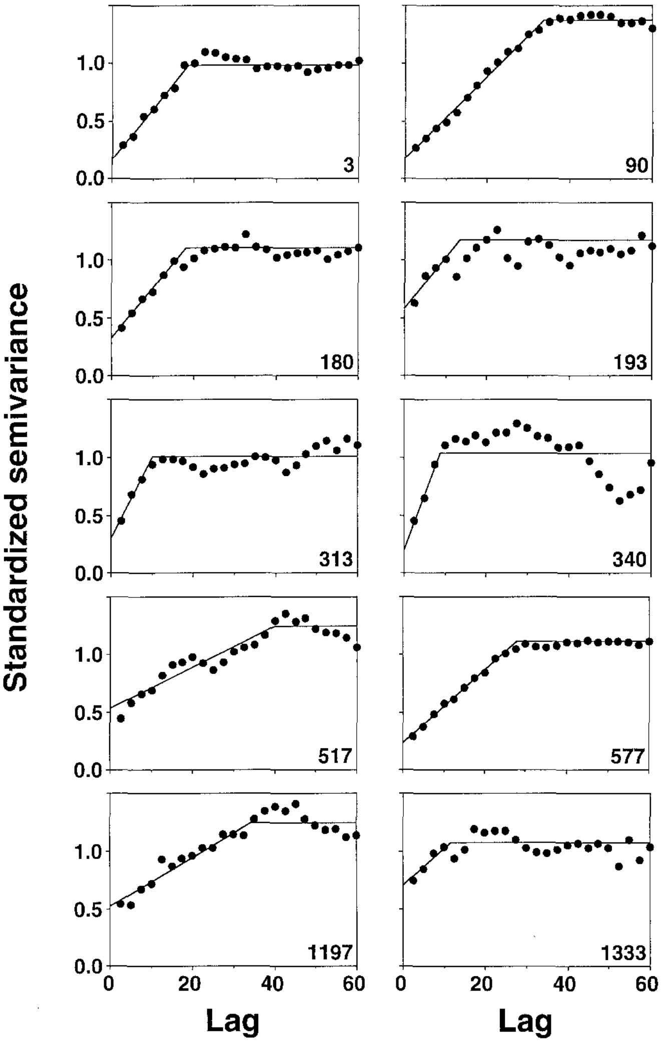

Fig. 3. Plots of standardized semivariance (S/s^2) versus lag (cm) for detrended, log-transformed biomass of filamentous overstory algae (as chlorophyll *a*) in experimental channels. Number in lower right of each panel is average snail biomass (as mg/m^2 tissue dry mass) in each channel over the course of the experiment. Lines fitted by piecewise regression (see text)

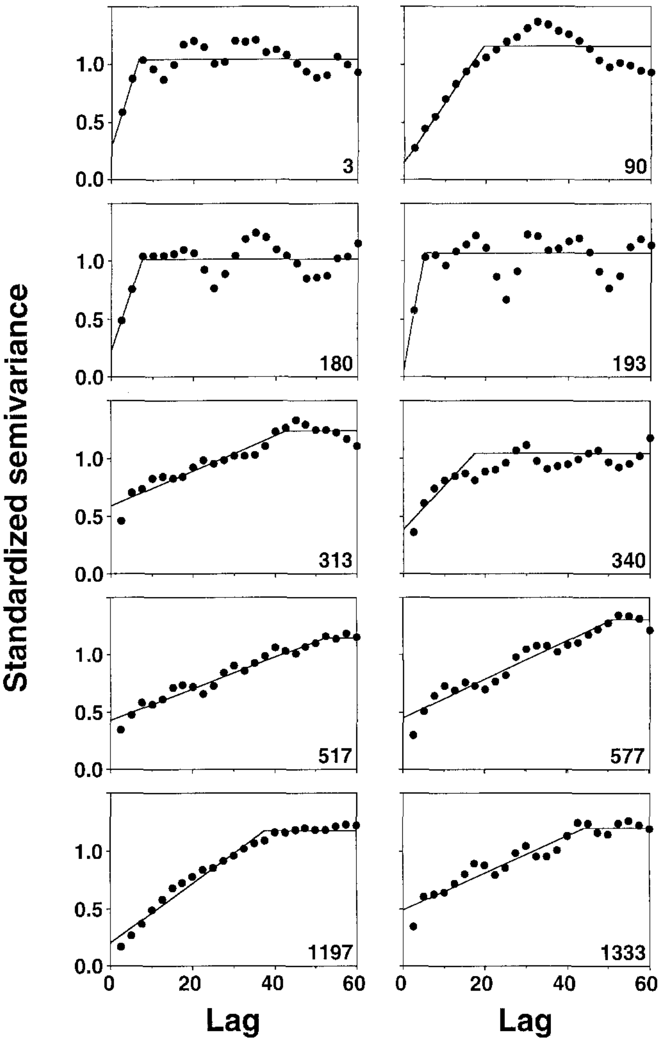

Fig. 4. Plots of standardized semivariance (S/s^2) versus lag (cm) for detrended biomass of understory algae (as chlorophyll *a*) in experimental channels. Number in lower right of each panel is average snail biomass (as mg/m^2 tissue dry mass) in each channel over the course of the experiment. Lines fitted by piecewise regression (see text)

a patch as a set of adjacent sites within which environmental variation is spatially autocorrelated. We avoid specific usage of this criterion because we feel that habitat patches cannot be unambiguously defined without reference to the specific organisms of interest. Definition of a patch would require information about the distances over which such organisms move. For example, mobile invertebrates living on the overstory may move greater distances than epiphytic diatoms, and so may perceive larger patches of the overstory.

The strength of spatial dependence over the Range was estimated by calculating a fractal dimension, *D*, from the initial slope (b_l) of log semivariance versus log lag as $D=(4-b_l)/2$ (Burrough 1983; Palmer 1988). We estimated log-log slopes using rectilinear models analogous to those described above. Fractal *D* for a one-dimensional series is bounded between 1 and 2, with low *D* (high slopes) indicating a more heterogeneous spatial pattern (stronger spatial dependence). The conceptual distinction between the Range and fractal *D* is a subtle one: small Ranges indicate complete spatial homogeneity (*D* approaches 2 above the inflection point of the variogram) at all but the smallest scales, while high *D* over the Range (i.e., a relatively flat ascending portion of the variogram) indicates relative homogeneity even at small scales.

Results

We examined the effect of snail density on the following response variables: mean biomass of overstory and understory (calculated for raw data), the slope of the downstream gradient in algal biomass (from regressions of understory chlorophyll and log overstory chlorophyll versus distance downstream), overall spatial variability (as SD of log chlorophyll) which includes variation due to the downstream gradient, spatial variability around downstream gradients (as SD of residuals from regressions of log chlorophyll versus distance downstream), distances over which variation was spatially dependent (as the Range of variograms) and degree of heterogeneity, or strength of spatial dependence, over the Range (as fractal *D*).

The average biomass of overstory algae increased with snail density across channels ($F_{1,8}=47.6$; $P<0.001$; Fig. 5A). This effect was mainly due to an in-

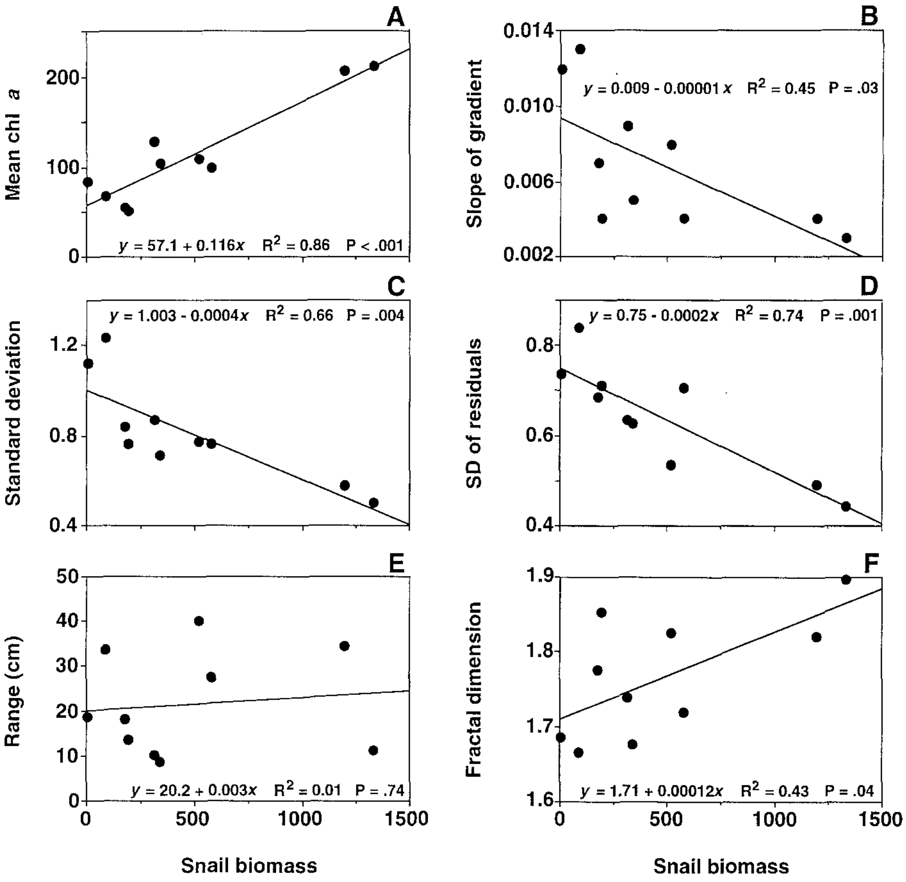

Fig. 5A–F. Relationships across experimental channels between average snail biomass (as mg/m^2 tissue dry mass) and response variables for filamentous overstory algae. (**A**) mean overstory biomass (as mg/m^2 chlorophyll *a*), (**B**) slope of the linear regression of log chlorophyll *a* versus distance downstream, (**C**) standard deviation of log-transformed biomass, (**D**) standard deviation of residuals from the regressions in B, (**E**) geostatistical Range for the variograms depicted in Fig. 3, an estimate of the demarcation between scales at which variation was spatially dependent and spatially independent, (**F**) fractal dimension of spatial variation over the Range

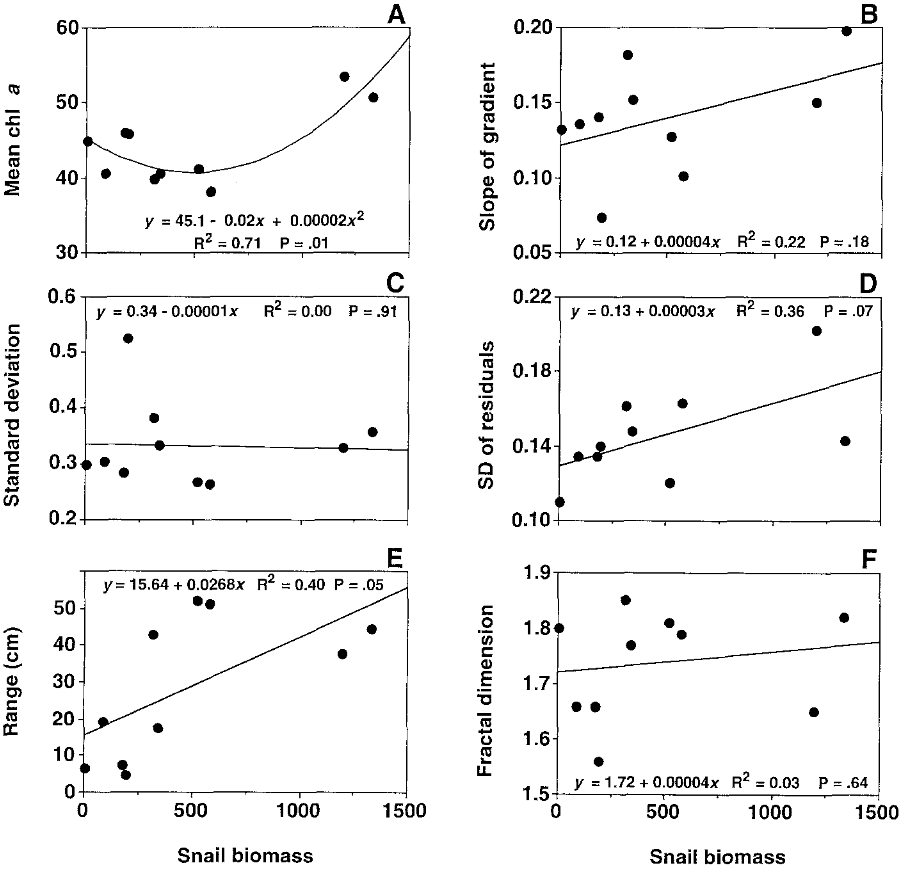

Fig. 6A–F. Relationships across experimental channels between average snail biomass (as mg/m^2 tissue dry mass) and response variables for understory algae. (**A**) mean understory biomass (as mg/m^2 chlorophyll *a*), (**B**) slope of the linear regression of chlorophyll *a* versus distance downstream, (**C**) standard deviation of log-transformed biomass, (**D**) standard deviation of residuals from regressions of log chlorophyll *a* versus distance downstream, (**E**) geostatistical Range for the variograms depicted in Fig. 4, an estimate of the demarcation between scales at which variation was spatially dependent and spatially independent, (**F**) fractal dimension of spatial variation over the Range crease in overstory on downstream tiles (Fig. 1). Consequently, one aspect of this consumer's effect on the arrangement of overstory biomass was to decrease the strength of the downstream gradient ($F_{1,8}=6.6$; $P=0.03$; Fig. 5B). This decrease in gradient contributed to the decrease in overall spatial variability seen with increasing snail density ($F_{1,8}=16.1$; $P=0.004$; Fig. 5C). In addition, snails reduced variability around these gradients ($F_{1,8}=22.9$; $P=0.001$; Fig. 5D).

Snail density had no effect on the Range in the overstory ($F_{1,8}=0.1$; $P=0.74$), despite considerable variation in this parameter among channels (9–40 cm, Fig. 5E). Snails did increase the fractal dimension of overstory variation ($F_{1,8}=5.9$; $P=0.04$; Fig.5F). Thus, snails reduced the strength of spatial dependence, and so decreased heterogeneity, at small scales (less than the Range). This result was not influenced by uncertainty in the estimate of D from variograms with few points describing the ascending limb. Excluding channels where D was estimated from four or fewer values of semivariance (snail densities of 193, 313, 340 and 1333 mg/m^2, Fig. 3) had little effect on the relationship between snail biomass and overstory D (slope$=0.00011$, $R^2=0.49$, $N=6$; see Fig. 5F). We emphasize that this effect on small-scale spatial dependence was independent of the downstream gradient in overstory biomass, since the downstream trend was removed before variogram analysis.

The effects of snail density on understory biomass were in sharp contrast to effects on the overstory. Mean understory biomass was best described as a curvilinear function of snail biomass, with a minimum at moderate snail densities ($F_{2,7}=8.7$; $P=0.01$ for fit of quadratic equation; Fig. 6A). The fit of the quadratic equation was significantly better than that for a positive, linear relationship ($F_{1,7}=7.6$; $P=0.03$ for improvement in fit). Thus, understory biomass was reduced at moderate grazer densities, but was highest at the highest grazer densities (Fig. 6A).

Snail density had no detectable effect on the slope of the downstream gradient, either for raw or log-transformed understory data ($F_{1,8}=2.2$; $P>0.18$ for raw data; Fig. 6B). Likewise, there was no snail effect on overall spatial variability for the understory ($F_{1,8}=0.7$; $P=0.44$; Fig. 6C). Snails had a marginally significant, positive effect on variation around the downstream gradient for the understory ($F_{1,8}=4.4$; $P=0.07$; Fig. 6D), in contrast to the negative effect seen for the overstory (Fig. 5D).

Snails increased the Range over which understory variation was spatially dependent ($F_{1,8}=5.4$; $P=0.05$, Fig. 6E), but had no effect on understory heterogeneity at small scales ($F_{1,8}=0.2$; $P>0.60$, Fig. 6F). Deleting channels with four or fewer values of semivariance describing the ascending limb of the variogram (snail densities of 3, 180 and 193 mg/m^2, Fig. 4), had no effect on the latter result.

Comparisons of D among channels with different Ranges (Figs. 5 and 6, E and F) may present difficulties of interpretation because of differences in the spatial scales over which D was calculated. Re-analysis of the relationship between snail biomass and overstory D for a subset of channels with similar Ranges (9–19 cm) had little effect on the regression parameters (slope$=0.00013$, $R^2=0.45$, $N=6$). Similar re-analyses for the understory data did not uncover any trend in D versus snail biomass. Thus, the effect (or lack thereof) of snails on D was not an artifact of comparing D across different spatial scales.

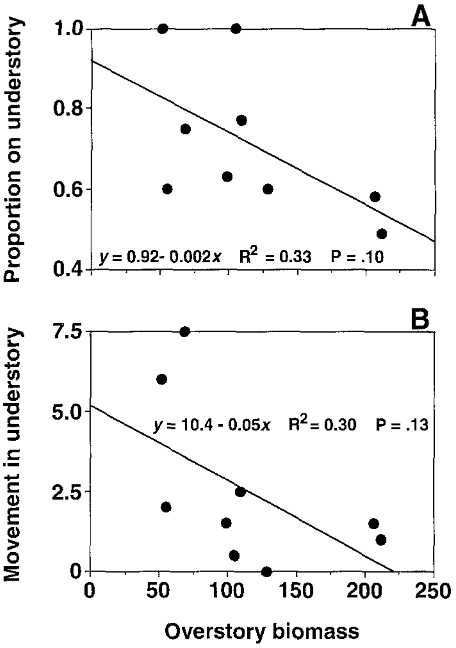

Fig. 7A, B. Across-channel patterns in snail behavior based on observations made at the end of the experiment. (**A**) proportion of snails in each channel that were found on the understory versus average overstory biomass. (**B**) average rate of movement (mm/min) of snails found on the understory versus average overstory biomass (as mg/m^2 chlorophyll *a*)

Observations of snail behavior made at the end of the experiment suggested that: (1) snails were perhaps less likely to be on the understory when overstory biomass was high (Fig. 7A), (2) snails on the understory moved three times slower than those on the overstory (mean rates of movement: 2.5 mm/min, SE$=0.85$ on the understory; 7.6 mm/min, SE$=1.46$ on the overstory; means different by paired t-test, $P=0.01$, $N=9$), and (3) snails on the understory may have moved less with increasing overstory biomass (Fig. 7B).

Discussion

The positive effect of *Physella* density on mean biomass of overstory algae in our channels (Fig. 5A) may have resulted from enhanced growth of established *Cladophora* at high snail densities (see Dudley [1992] for similar effects of larval caddisfly and mayfly grazers on *Cladophora* and Underwood [1991] for similar effects of snails on the macrophyte *Ceratophyllum*). *Cladophora* filaments were tough near their base and firmly attached to tiles (personal observation), so snails may have been unable to remove them. Enhanced growth of *Cladophora* could have been caused by: (1) increased nutrient availability due to release of nutrients from dead snails (see Threlkeld [1987] for the effect of dead fish on phytoplankton), (2) increased nutrient availability due to regeneration from live snails (see [Elser 1992] for the effect of zooplankton regeneration on phytoplankton growth), and/or (3) removal of epiphytes from *Cladophora* filaments by snails (Dudley 1992).

Although there were more dead snails in channels with higher snail densities (per capita mortality averaged 0.015 per day across channels, $SE=0.002$, and was independent of snail density, $P=0.40$), this factor was not likely to have caused *Cladophora* enhancement. We estimated the total amount of N potentially released by live and dead snails in each channel based on total deaths and mean snail biomass in each channel, estimates of *Physella* N egestion (0.6 $\mu g\ N \cdot h^{-1} \cdot mg^{-1}$ ash-free dry mass) and N excretion (0.3 $\mu g\ N \cdot h^{-1} \cdot mg^{-1}$) from Grimm (1988), and assuming that snail tissue is 10% N (Bowen 1966). Assuming that all N in dead tissue and feces was made available to algae by decomposition, the total amount of N released by dead snails over the course of the experiment (range: 2–22 mg N per channel) was only about 10% of that released by live snails (range 16–242 mg N per channel). This estimate is likely high, since we removed dead snails daily. We can say little about the relative importance of nutrient regeneration by live snails versus epiphyte removal, other than to note that soluble reactive phosphorus and NH_4^+ concentrations in the outflow of each channel were not affected by snail density ($P>0.40$). Regardless of mechanism, snail-induced increases in overstory could increase stream-wide diversity of invertebrates by providing more of this diversity-promoting microhabitat (Dudley et al. 1986).

The effects of snail density on mean understory biomass are more difficult to explain. We expected understory biomass to be reduced by snails, based on results from previous studies that have shown strong snail effects on total periphyton biomass (Sumner and McIntire 1982; Lamberti et al. 1987; Lowe and Hunter 1988; Bronmark et al. 1991; Steinman et al. 1991). Some insight into the possible cause of this effect can be obtained by considering the snail distribution and movement data (Fig. 7). Taken together, these data suggest that *Cladophora* filaments may have reduced the ability of the snail population to graze on the understory. As a result, understory algae may have had a partial refuge from herbivory at high snail densities due to the presence of abundant overstory (Figs. 5A and 6A). This would explain the positive relationship between understory and overstory biomass on individual tiles ($y=35.76+0.07x$; $R^2=0.37$; $F_{1,947}=560.1$; $P<0.001$; $N=950$). This refuge effect may be strong, given *Cladophora's* ability to negatively affect the understory (Feminella and Resh 1991), and the ability of snails to reduce periphyton biomass in the absence of established *Cladophora* (Sumner and McIntire 1982; Lamberti et al. 1987; Lowe and Hunter 1988; Bronmark et al. 1991; Steinman et al. 1991). Given the potential complexity of understory responses in our experiment, we emphasize discussion of snail effects on spatial patterns in the overstory.

Snail-induced reduction in small-scale spatial heterogeneity of overstory biomass (Fig. 5F) may be the result of a relatively homogeneous distribution of snail grazing activity within the channels. We suggest that *Cladophora* may establish and/or grow in a spatially-dependent manner over small scales in the absence of grazers. Snails may decrease this heterogeneity by enhancing *Cladophora* growth at randomly-distributed sites. In support of this suggestion, we noted that snails were randomly distributed down the length of channels at the end of the experiment (runs tests for pattern in snail distribution within the four channels with the most snails, null hypothesis of randomness not rejected at $P>0.28$). Randomly-distributed enhancement of *Cladophora* growth could also help explain the decrease in large-scale heterogeneity (the downstream gradient in overstory biomass) caused by snails (Fig. 5B).

The range of fractal dimensions for the overstory encountered among our uniform channels (1.67–1.90; Fig. 5F) was fairly similar to that reported for a set of 42 transects of benthic algal biomass (as chlorophyll *a*) in a natural stream riffle (1.51–1.93; Sinsabaugh et al. 1991), suggesting that the snail effect we saw was not minor relative to natural variation in D. Abiotic factors influencing D would be more variable in natural riffles than in our channels. In contrast, our estimates of the upper limit of spatial dependence (the Range varied between 5 and 52 cm for understory and between 9 and 40 cm for overstory) overlapped, but were generally higher than, the limits estimated by Sinsabaugh et al. 1991 (3–27 cm). We attribute our higher estimates to methodological differences between studies. Sinsabaugh et al. (1991) used the statistical significance of autocorrelations (r) as the criterion for demarcating scales of spatial dependence and independence. Although correlograms are strictly analogous to variograms for stationary data (Rossi et al. 1992), a criterion based on statistical significance will vary among studies due to differences in sampling effort. As a result, we advocate standardized use of the Range to demarcate scales of spatial dependence and independence, because it can be estimated objectively and comparably (by regression) across studies.

Clearly we cannot say whether grazer effects on overstory variability and heterogeneity in these artificial channels are relevant to overstory inhabitants in natural systems. However, our goal was primarily to show that such effects can be demonstrated experimentally. Given that little is known about how specific changes in variability and heterogeneity may affect communities, we offer the following general suggestions regarding the potential implications of our results.

Physella affected three aspects of overstory spatial patterns: overall spatial variability (Figs. 5C and 5D), the strength of a downstream gradient (Fig. 5B), and the degree of small-scale (<40 cm) spatial heterogeneity (Fig. 5F). For organisms inhabiting the overstory, decreases in spatial variability could reduce the number of competing species able to coexist at equilibrium (Comins and Noble 1985; Pacala 1987; Palmer 1992). Spatial variability in resource abundance can promote coexistence if there is a tradeoff between efficiency of resource use (i.e., the minimum resource requirement) and efficiency with which high-resource patches are located (Brown 1986). Such a tradeoff may exist among stream grazers (McAuliffe 1984; Kohler 1992), suggesting that spatial variability in periphyton might be important in maintaining species diversity. An important issue that remains unresolved is how spatial variability should be measured. In our experiment, snails decreased overstory variability relative to the mean (SD of log-transformed data), but had no detectable effect on absolute variability (SD of raw data; $P = 0.18$). Models and experiments investigating the importance of relative versus absolute spatial variability to species interactions are needed.

Decreases in small-scale heterogeneity might also affect the coexistence of competing species (Palmer 1992), but it is difficult to compare our one-dimensional results to the predictions of Palmer's (1992) model of a two-dimensional landscape. We can say that the overstory was more fragmented at small scales when snails were more abundant. Such fragmentation may have complex effects on coexistence (Palmer 1992). For mobile overstory inhabitants, small-scale changes in habitat heterogeneity would only be potentially relevant to the dynamics of species that move similarly small distances in their lifetimes. These small-scale effects might be more relevant to sessile species living in the overstory. Highly-fragmented (low heterogeneity) habitats may present barriers to the dispersal of colonists across a landscape due to the intermingling of suitable and unsuitable sites (Doak et al. 1992; Johnson et al. 1992; Palmer 1992). For small organisms that reproduce locally, like epiphytic diatoms, effects on colonization could impact local successional trajectories (McCormick and Stevenson 1991). Simulations have shown that the match between dispersal distances and the distances over which variation is spatially dependent (i.e., the Range) can be critical to predictions of competitive coexistence (Comins and Nobel 1985; Pacala 1987). Thus, changes in the Range, which we found for the understory, might have broad implications. In all cases, the issue of relevance to natural communities will only be resolved by conducting manipulative experiments.

The geostatistical techniques we used in this study provide a means of quantifying spatial patterns that are not readily apparent in the data (Fig. 8; Rossi et al. 1992). Viewing habitat variation as a continuous phenomenon, rather than as discrete patches, seems more realistic for many environmental attributes (for example, elevation, nutrient concentrations, light and moisture levels, current speed), and so may provide new insights into how ecological interactions are played out in variable environments. To date, most spatially-explicit models have examined how patchiness in the environment influences interactions among organisms. The demon-

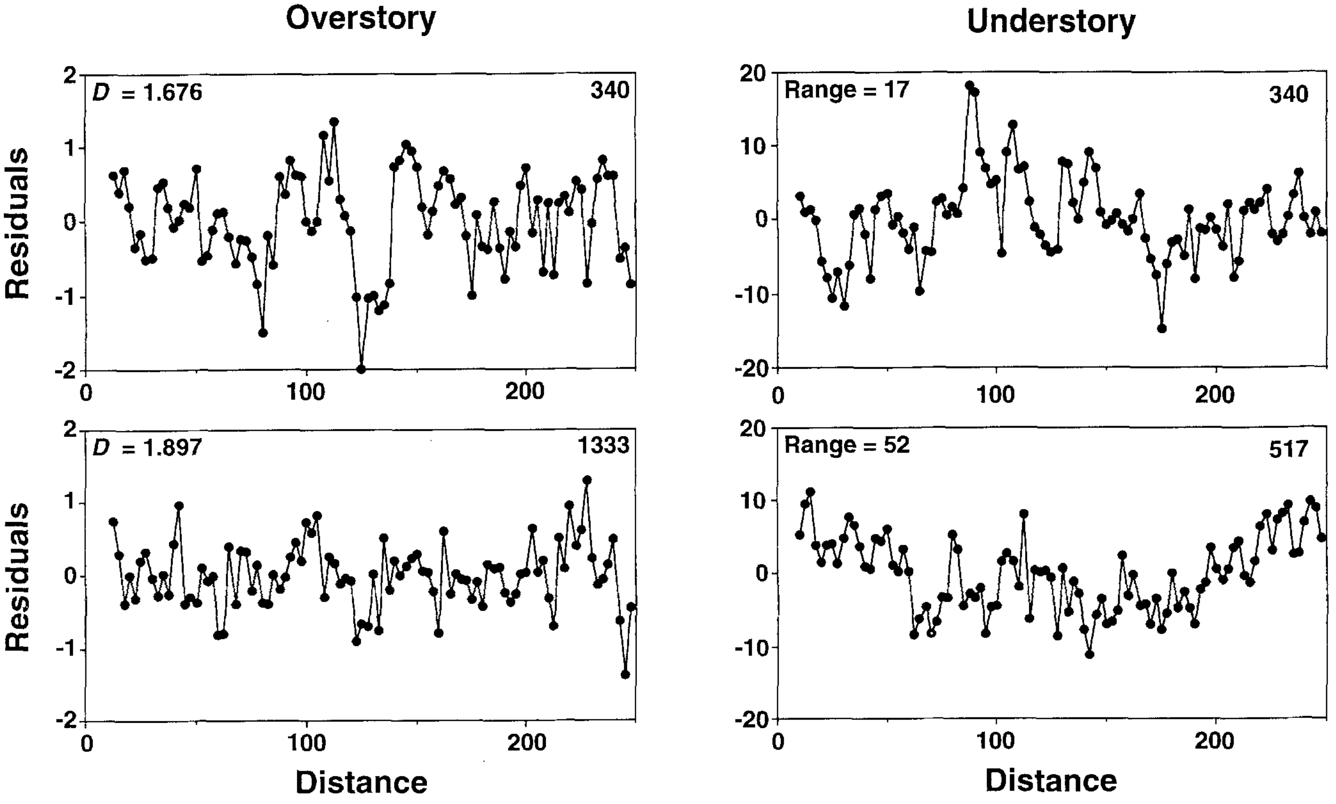

Fig. 8. Examples of data series that were used to calculate geostatistical parameters. The overstory series depict residuals from regressions of log-transformed overstory biomass versus distance downstream for two channels with similar Ranges (9 and 11 cm) but different fractal dimensions over the Range (*D*). The understory series depict residuals from regressions of understory biomass versus distance downstream for two channels with similar fractal dimensions (1.77, 1.81) but different Ranges. Number in the upper right of each panel is average snail biomass (as mg/m^2 tissue dry mass) over the course of the experiment

stration that a consumer can alter spatial dependence in a habitat attribute argues for the inclusion of feedbacks between the biota and the environment in spatial models of communities.

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