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Source: *Journal of the North American Benthological Society*, Vol. 16, No. 1 (Mar., 1997), pp. 263-276

Published by: The University of Chicago Press on behalf of the Society for Freshwater Science

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## Habitat heterogeneity and algal–grazer interactions in streams: explorations with a spatially explicit model

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**Abstract.** We present results from a spatially explicit model that makes predictions about how physical habitat heterogeneity mediates algal–grazer interactions. We simulated the responses of mean algal biomass and variability in the distribution of algae to 2 levels of physical habitat heterogeneity (1 vs. 15 boulders) under 2 velocity regimes (slow vs. fast riffles). Algal growth occurred locally in a spatially explicit grid where local current was specified for each of the  $60 \times 30$  grid cells. Grazer movement and foraging were simulated using an individual-based model, in which the direction and rate of movement of individual grazers were determined at each time step in relation to local current and algal standing crop. Model parameterization was based on field observations, laboratory experiments, and literature review.

In each of the 4 simulations, algae were first allowed to grow in the absence of grazing to near carrying capacity. Neither habitat heterogeneity nor riffle velocity regime had a significant effect on the mean biomass or spatial variability of algae. Next, algae were exposed to 3 simulated grazer densities and the subsequent effects on algal biomass and patchiness were determined after prolonged contact. We performed replicate simulation runs to allow statistical inferences to be drawn about differential responses of algae to the various “treatments.” As expected, mean algal biomass declined in proportion to grazer density. Higher habitat heterogeneity resulted in reduced algal biomass for low and intermediate grazer densities, but only in the slow riffle. Otherwise, the effects of specified grazer densities did not vary between slow and fast riffles. Variability in algal biomass distribution was measured in 2 ways. First, a spatially explicit index of relative patchiness showed a gradual increase under low grazer density but a transient peak followed by decline under moderate and intense grazing pressure, a pattern observed for both slow and fast current regimes. In the slow riffle alone, heterogeneity and grazer density interacted to influence algal patchiness. A second, non-spatially explicit index of variability in algal biomass, the coefficient of variation, increased as grazer density increased regardless of current regime. Higher variability in the distribution of algal biomass tended to be associated with greater habitat heterogeneity, especially in the slow riffle.

The simulations suggested that spatial heterogeneity and ambient current velocity regime mediate algal–grazer interactions. The extent to which grazers crop biomass and create spatial variability in the distribution of algal biomass may depend not only on grazer density but also on the interaction between grazer density, physical habitat heterogeneity, and stream velocity. Given this complexity, empirical approaches to understanding algal–grazer interactions in spatially and temporally heterogeneous stream systems are likely to be greatly augmented by modelling, which allows different environmental conditions and grazer foraging behaviors to be simulated.

*Key words:* heterogeneity, herbivory, patchiness, individual-based model, snails, streams.

By consuming attached algae, benthic herbivores in streams not only directly regulate energy flow to higher trophic levels but may also modify structural habitat features for many non-herbivores in the community (e.g., Hawkins and Furnish 1987, Power 1990, Hart 1992). Numerous studies have established that there are strong interactions among algae and herbivores (reviewed in Feminella and Hawkins 1995), and recent evidence indicates that algal–herbivore dynamics can vary both spatially (e.g., Hart 1992, Creed 1994) and temporally (Feminella and Resh 1990) in streams. But while habitat heterogeneity is thought to be a determinant of

the functional organization of stream ecosystems, stream ecologists have only a rudimentary understanding of how it regulates important biotic processes, such as herbivory.

Research on herbivory has typically been performed under conditions that intentionally reduce heterogeneity (but see Poff and Ward 1992, Palmer 1995), to allow for experimental control of factors influencing algal–grazer dynamics. From these studies, it is clear that nutrient concentrations, light intensity, and local current velocity individually regulate primary production and algal standing crops (e.g., Whitford 1960, Lamberti and Moore 1984, Steinman and Mc-

Intire 1987). Interactions among these variables also commonly influence algal production or biomass, both in laboratory streams (Horner et al. 1983, DeNicola and McIntire 1991, Walton et al. 1995) and in natural streams (e.g., Reisen and Spencer 1970, Poff et al. 1990). It is also evident that grazers respond to algal community structure or biomass, or both, through their distribution and movement, and that they themselves can alter algal productivity, assemblage composition, and biomass (e.g., Lamberti and Resh 1983, McAuliffe 1984, see Feminella and Hawkins 1995). Further, the foraging activity of grazers is subject to constraint by abiotic factors, most notably current, which influences movement rates and microhabitat choice (Vaughn 1986, DeNicola and McIntire 1991, Poff and Ward 1992, 1995). In sum, herbivory in streams is a complex product of both biotic interaction and abiotic constraint, but the effect of environmental heterogeneity on herbivory is not easily approached in empirical studies.

Complex systems not amenable to simple empirical experimentation are often profitably subjected to modelling (Turner and Gardner 1991). Such efforts may afford plausible insight into how algal-grazer interactions change as a function of spatial heterogeneity. Models can be used to make predictions about the relative importance of various controlling variables and to help identify critical empirical experiments.

In this paper, we present a modelling approach that explicitly accounts for spatial heterogeneity in current velocity, an environmental factor known to mediate herbivory. We focus primarily on *simulated* results, but we also use field observational and laboratory experimental data in model parameterization. Our efforts were inspired by observations that heterogeneous streams in the US mid-Atlantic region often support very large populations of the pleurocerid snail *Leptoxis carinata*, which appear to suppress algal biomass in the field. Through observation of individuals in experimental settings, their foraging behavior can be related to environmental constraints such as local current velocity and algal biomass.

We simulate the response of algal biomass and algal patchiness to 3 factors: habitat heterogeneity, grazer density, and current velocity. Specifically, we simulate 4 "riffles", each of which has either low or high habitat heterogeneity (1 or 15 "boulders") and low or high av-

erage current velocity. Algal growth is simulated in each riffle prior to, and following, the introduction of 3 densities of grazers. The simulations are spatially explicit in that local current is specified at points across the simulated streambed, and algal growth occurs locally in each grid cell. Snail grazing is simulated using an individual-based model (IBM), an approach increasingly employed in ecological research (DeAngelis and Gross 1992, Judson 1994). The IBM allows individual snails to forage according to simple rules that are determined by local algal abundance and current velocity. The algal growth model and IBM are linked together to assess the effect of habitat heterogeneity, snail density, and riffle current speed on mean algal biomass and spatial variability in algal biomass.

## Methods

### *Model grazer*

*Leptoxis carinata* is a dioecious, pleurocerid snail with a 2-y life cycle (Aldridge 1982), during which individual snails can attain a maximum shell length of ca 13 mm. In small streams of the mid-Atlantic region, this species reaches average densities up to 400/m<sup>2</sup>, and field exclusion experiments have shown these snails are able to suppress algal biomass under natural field densities (N.L. Poff, unpublished data). Snails are active from late spring through late autumn; during the remainder of the year they lie dormant beneath stones.

### *Modelling components*

The simulations were conducted by combining 2 modelling approaches. First, a grid model was used to establish levels of physical habitat heterogeneity and to provide a spatially explicit template to keep track of algal biomass. Second, individual snails moved around in this grid according to the movement and foraging rules specified in an IBM. The steps in this combined modelling process are described below.

*Physical habitat heterogeneity.*—We simulated spatially heterogeneous stream environments ("riffles") using a grid model consisting of 1800 cells (30 × 60 lattice), each representing 2 cm on a side (Fig. 1). Two levels of habitat heterogeneity were established by placing 1 "boulder" (22 × 20 cells) or 15 "boulders" (each 8 × 6

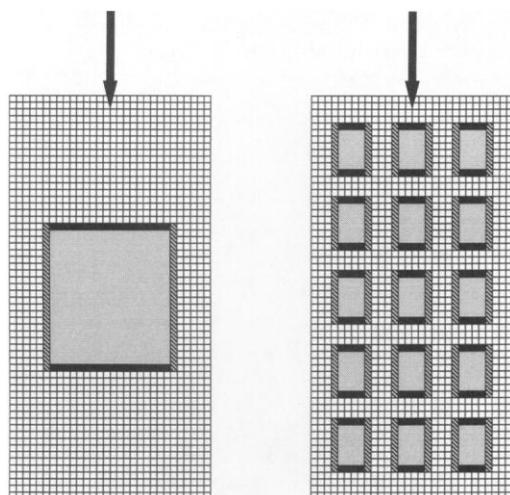


FIG. 1. Schematic of simulated streambed showing low habitat heterogeneity (1 "boulder") and high habitat heterogeneity (15 "boulders") treatments. Each cell in the  $30 \times 60$  grid is 2 cm on a side. Four distinct surfaces (or patch types) are defined for the grid: boulder tops (stippled), lateral sides of boulders (diagonal shading), front and back sides of boulders (black), and streambed area not associated with boulder surfaces (no shading). The arrow shows the direction of streamflow.

cells) on the grid to create local variation in depth and velocity. Four discrete surfaces were specified for each simulated riffle: top of boulder, sides of boulder, front (upstream side) and back (downstream side) of boulder, and non-boulder streambed. The front, sides, and back of the boulders were 1 grid cell (2 cm). The proportion of the 1800 grid cells occupied by boulder tops was held constant in all simulations at 20%, to minimize differences in algal biomass or variability that might arise from areal differences in these surfaces. Total coverage of lateral, front, and back boulder sides combined was 4.4% for the 1-boulder treatment and 20% for the 15-boulder treatment. The difference in coverage by boulder sides is to be expected, since it is not possible to divide a large patch (in this case, 1 boulder top) into many smaller patches without changing the amount of patch edge and/or the patch shape. The choice of precise spatial configuration of substrate surfaces was arbitrary—the purpose of the design was simply to create 2 heterogeneity treatments, which could be used to assess relative effect on algal and grazer response variables.

Slow and fast "riffles" were simulated by defining current velocities for the 4 different substrate surfaces. In the slow riffle, velocities were 20, 15, 5, 5, and 5 cm/s for boulder top, boulder lateral sides, boulder front boulder back, and non-boulder surface, respectively. For the fast riffle, velocities for these respective surfaces were set at 40, 30, 5, 5, and 20 cm/s. Velocities on the front boulder surfaces were set to low values to simulate flow stagnation.

*Algal growth and spatial variability.*—Algal growth was simulated in each grid cell individually as a function of local current velocity. We used the analytical model of Horner et al. (1983, with modifications by Walton et al. 1995), to simulate algal growth in each individual grid cell:

$$\Delta B / \Delta t = K_1 \mu L (k_f + k_{f0}) (B_{\max} - B) - K_2 V^0 \quad [1]$$

where  $B$  is algal biomass,  $K_1$  is a growth coefficient,  $\mu$  is phosphorous uptake rate,  $L$  is a light index,  $k_f$  is a mass transfer coefficient (due to turbulent diffusion),  $k_{f0}$  is a mass transfer coefficient (due to non-turbulent diffusion),  $B_{\max}$  is the maximum supportable algal biomass,  $K_2$  is a scour coefficient, and the term  $V^0$  represents algal loss due to scour as a function of velocity. Coefficient and parameter values generally followed those given by Horner et al. (1983) for a phosphorous level (SRP) of  $10 \mu\text{g}/\text{l}$  and temperature of  $20^\circ\text{C}$  (Table 1). Because our simulated riffles were meant to represent a shallow, shaded stream, we ignored the light index parameter, and we assumed no scour occurred at the relatively low velocities we simulated. However, water velocity is implicitly included in the model because  $k_f$  is a function of the square root of velocity (Table 1). Thus, the final model we used was:

$$\Delta B / \Delta t = K_i (B_{\max} - B) \quad [2]$$

where  $K_i$  is now the combination of  $K_1$ ,  $\mu$ ,  $L$ ,  $k_f$ , and  $k_{f0}$  in equation [1] for each combination of grid cell type (i.e., boulder top, lateral side, front/back, and streambed) and velocity regime. The values of  $K_i$  are given in Table 2.

According to this equation, algal growth is a positive function of local current and, in the absence of grazers, will reach local carrying capacity in each grid cell. In our simulated riffle, the fastest flows occur on boulder tops; therefore, algal biomass accrues most rapidly on

TABLE 1. Parameters and their values (from Horner et al. 1983 and Walton et al. 1995) used in the algal growth model (equation 1). Values with asterisks were not used in the simulations (see Methods).

Parameter	Definition	Value
$K_1$	Growth coefficient	1.56
$\mu$	Nutrient uptake rate	0.72
$L$	Coefficient of light attenuation	0.04*
$k_t$	Turbulent diffusion	$\sqrt{0.000015}$ if velocity > 15 cm/s 0 if velocity $\leq$ 15 cm/s
$k_{t0}$	Non-turbulent diffusion	0.009
$K_2$	Scour coefficient	0*
$\theta$	Velocity exponent of scour	1*

those surfaces. To determine a reasonable value for  $B_{max}$ , we conducted field experiments in the summer of 1995 in a local stream with high snail density. After 83 d of snail exclusion, algal biomass on initially bare ceramic tiles (as in Poff and Ward 1992, 1995) ranged from 10 to 70 mg/m<sup>2</sup>. For the purposes of modelling, we set  $B_{max}$  for each simulated riffle at 70 mg/m<sup>2</sup> (0.028 g/grid cell or 50.4 g for the entire grid).

Variability in algal biomass was quantified with 2 indices, only one of which is spatially explicit. The Relative Patchiness Index or RPI (Li and Reynolds 1994) measures the contrast in algal biomass between neighboring grid cells. To calculate the RPI, each grid cell was assigned to 1 of 70 categories. The RPI is defined as follows:

$$RPI = 100 \sum \sum E_{ij} D_{ij} / N_b \quad [3]$$

where  $E_{ij}$  is the number of occurrences in the grid where adjacent cells have biomass levels  $i$  and  $j$ ,  $D_{ij}$  is the dissimilarity between levels  $i$  and

$j$ , and  $N_b$  is the total number of grid cell boundaries (see Li and Reynolds 1994 for further details). Elements of the dissimilarity matrix  $D$  were calculated as

$$D_{ij} = |j-i|/70 \quad [4]$$

which ensured that all dissimilarity values ranged between 0 and 1. The RPI essentially measures the average dissimilarity between immediately neighboring cells. It is a spatially explicit measure of heterogeneity because different arrangements of the same biomass levels will yield different RPI values. RPI can range from 0 to 100. Romme (1982) reported RPI values up to 18 for a natural system.

As a second measure of algal variability, we used the coefficient of variation (CV) of algal biomass, calculated as 100 times the standard deviation of the biomass in all 1800 cells divided by the mean cell biomass. This index is not spatially explicit, since different arrangements of

TABLE 2. Parameters and their global (entire grid) and patch-specific values (defined by current velocity) used in the coupled algal-grazer model. For the patch-specific values, the slash separates values for the slow velocity riffle on the left from the high velocity riffle on the right. Parameter values not applicable at a given scale are indicated by dashes.

Parameter	Units	Global value	Patch-specific value			
			Boulder top	Boulder lateral side	Boulder front/back	Non-boulder streambed
Water velocity	cm/s	—	20/40	15/30	5/5	5/20
$K_1$ ( $\times 1000$ )	per 20 min	—	0.459/0.477	0.453/0.469	0.414/0.414	0.414/0.459
$B_{max}$	mg/m <sup>2</sup>	70	—	—	—	—
Snail movement speed	cm/h	6.0 e <sup>-65B</sup>	—	—	—	—
Snail movement direction	none	—	values given in Fig. 2			
Snail functional response	mg/20 min	960 B <sup>2</sup> /(1 + 24,000 B <sup>2</sup> )	—	—	—	—

the same biomass levels do not affect the value of the CV.

*Grazer foraging.*—Snail distribution across the grid was simulated according to the behavior of *individuals*, using an IBM. IBMs may be used under various circumstances (Huston et al. 1988), but they are required when processes are inherently local (i.e., cannot be accurately represented as a spatial average of a random process; Caswell and John 1992). In the IBM the simulated behavior of an individual is drawn from some distribution of responses, rather than treating all individuals as the statistical average of the population. For example, when the movement direction of snails is observed in relation to local current speed or algal biomass, variation among individuals is apparent. Rather than computing the average movement direction of all observed snails, the IBM characterizes the probability distribution of movement rates for all observed snails, draws a value from that distribution, and assigns it to an individual at each time step in the model. Thus, individual behavior is governed according to simple rules, and population level phenomena can be decomposed into the activities of participating individuals (Huston et al. 1988, DeAngelis and Gross 1992, Judson 1994).

#### *Empirical experiments and observations supporting model parameterization*

We established movement and foraging rules for snails based on a combination of field observations, laboratory experiments, and literature review. Basically, snail movement (rate and direction) and foraging are influenced by algal biomass and current velocity. Previous research on mobile grazers in streams shows that rate of movement may decline with increasing current (Hutchinson 1947, Poff and Ward 1992) and with increasing algal biomass (e.g., Hart 1981, Kohler 1984, Poff and Ward 1992). Further, direction of grazer movement may also be strongly influenced by current speed and direction (Poff and Ward 1992, Hury and Denny 1997). We marked individual *L. carinata* with honey bee tags and observed that mature individuals moved primarily in the upstream direction with a net upstream displacement of 3–4 m/wk. Movement rate appeared to be reduced under higher local velocity (although local algal abundance was not quantified). To

derive better estimates for movement parameters for *L. carinata*, we brought individuals into the laboratory and conducted experiments in a re-circulating flume (see Palmer 1992 for flume description).

In the flume experiments we established 3 levels of algal biomass and 3 levels of current velocity. Ceramic tiles were colonized with algae for several weeks in a nearby unshaded stream. Average algal biomass was measured as chl-*a* (APHA 1985) and determined to be 0.5 mg/m<sup>2</sup> (SD = 0.8, *n* = 5) for the medium and 40 mg/m<sup>2</sup> (SD = 20, *n* = 4) for the high food treatments, respectively. The zero food treatment consisted of uncolonized ceramic tiles. Local velocity was regulated by controlling discharge in the flume. The bottom of the flume was lined with bare tiles so that the upper surfaces of the foraging tiles were flush with the bottom. Velocity in steady flow was measured 13 mm above these tiles (using a Nixon Instrumentation current meter). The average current (*n* = 9) was ca 0, 15, and 30 cm/s for the low, medium and high treatments, respectively.

Mature snails were collected in the field, marked individually with colored honey bee tags, starved overnight, and exposed to 1 of 9 food × current treatments. This process was replicated 3 times for each treatment combination over a 3-d period in late summer 1995. Locations of tagged individuals on the foraging tiles were recorded to the nearest cm at 2-min intervals for up to 30 min per replicate (see Poff and Ward 1992 for a more detailed description of similar methods). Recorded data were later analyzed to characterize the response of movement rate and direction to algal density and current speed.

From our initial field observations, we determined that the snails moved at most 6 cm/h. In the flume we found that snail movement was sensitive to algal biomass but not current speed, in contrast to some other studies (e.g., Poff and Ward 1992). (The lack of response to current speed may have been due to starving the animals before the trials, or to using an insufficient range of current velocities). In the high algal food treatments, snails moved at 40% of their maximum rate in the flume, observed under zero food conditions. Therefore in the model we represented movement rate as a negative exponential function of algal biomass, with a maximum of 6 cm/h and declining to an asymptote

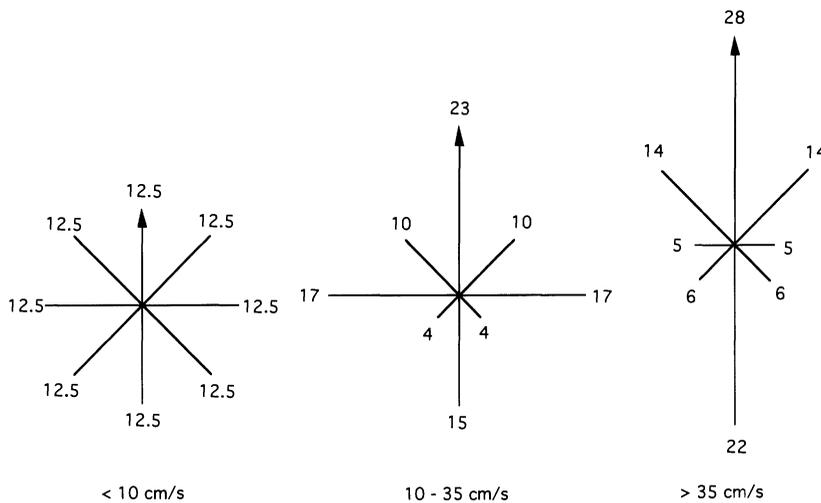


FIG. 2. Rules for snail movement direction as a function of current velocity. Numbers represent percentage of individual snail moves observed in the laboratory flume and hence probability of an individual moving in a particular direction as a function of current. Arrow points upstream.

of 40% of that value (i.e., 2.4 cm/h). Because the simulation time steps represent 20 min, and the grid cells represent 2 cm on edge, the maximum and minimum speeds are equivalent to 1 grid cell/time step and 0.4 grid cell/time step, respectively.

In the flume, movement direction of snails was sensitive to current velocity but not to food level. Movement direction was increasingly oriented in the upstream direction as velocity increased (as in Poff and Ward 1992). We summarized movement direction using a circular distribution divided into 8 categories (Fig. 2). The proportion of movements in each of 8 directions for 3 different current velocity levels was used to determine the probability of an individual snail's movement direction at each time step of the model.

The amount of algal biomass removed by individual snails during movement was not quantified, and the published literature provides scant guidance on what reasonable values might be. Although foraging snails can deplete algae through direct consumption and non-consumptive losses (physical dislodging of algae as snails forage, Lamberti et al. 1987, Scrimgeour et al. 1991), we did not discriminate between these 2 processes. We assumed snails forage according to a Type III functional response (Holling 1959) to allow for the fact that grazers have difficulty removing algal biomass at low algal

densities (cf. Lamberti et al. 1987). We arbitrarily capped total algal removal from a grid cell for each 20-min time step in the model (see below) at 4% of  $B_{\max}$ . We derived this number by estimating that a mature stationary snail can graze a ca 0.16-cm<sup>2</sup> area, and if all algae were removed from that area in a 20-min period, a 4% reduction in algal biomass from the 2 × 2 cm grid cell would result.

#### *Linkage of model components and empirical data to examine specific questions*

Most model simulations consisted of 2 phases. In the first phase, algae were allowed to grow without grazers, during which time biomass reached ca 70% of carrying capacity. At the start of the second phase, 20, 100, or 500 snails/m<sup>2</sup> were added at random to the grid. During the second phase, the algal and snail components were combined in a single model run in discrete 20-min time steps (see Caswell and Etter 1992 for a general discussion of discrete, spatially explicit models). Each time step consisted of 3 processes, as follows:

- 1) each individual snail assesses algal biomass and current velocity in its grid cell; it then moves in a direction determined probabilistically based on current velocity (see Fig. 2) and at a rate dependent on the algal biomass in the starting grid cell,

2) each individual snail removes algae (up to 4% of  $B_{\max}$ , functional response as described earlier) from the grid cells it encounters during the time step,

3) algae regrow as determined by the algal growth model.

Snails encountering the lateral boundaries of the simulated riffle were reflected away from the boundary. Snails exiting the grid via upstream (or downstream) movement were re-introduced at randomly chosen positions along the downstream (or upstream) edge of the grid to maintain a constant grazer density. Snails did not re-evaluate movement rules within any time interval.

A simulated "day" consisted of 36 time steps (20 min each), and for most model runs phase 1 (algae only) lasted 10 "weeks" and phase 2 (algae plus grazers) lasted 7 "weeks." Mean algal biomass per grid cell, RPI, and CV were calculated once each "day." The simulation model was coded and run using Mathematica (Wolfram Research Inc., Champaign, Illinois); the program code is available from the junior author.

*Model question 1: Does habitat heterogeneity alone influence algal biomass and spatial distribution?*—To address this question, algal biomass was allowed to accumulate over a 70-d period to approach maximum biomass in the absence of grazers. Total algal biomass and biomass variability were calculated as a function of habitat heterogeneity (i.e., 1 or 15 boulders) for both slow and fast riffles.

*Model question 2: Does grazer density interact with habitat heterogeneity to influence algal biomass and variability in algal distribution?*—For each habitat heterogeneity treatment (1 and 15 boulders) and current regime (fast and slow riffles), we applied 3 levels of snail density (20, 100 and 500/m<sup>2</sup>) to determine effects of heterogeneity on algal biomass and variability. These 3 treatments bracket the range of snail densities observed in local streams (N.L. Poff, unpublished data). Snails were added after the 70-d non-grazing period described above and then were allowed to forage for 12 h / d for 49 d in both slow and fast riffles. Three replicates of each simulation run were made, differing only in the initial random seed used. Statistically significant differences among treatments at day 49 were evaluated using *t*-tests.

### *Model sensitivity*

To examine the sensitivity of the model output to parameter estimation, we performed a sensitivity analysis. We systematically varied values for the grazer movement speed and consumption rate parameters by  $\pm 10\%$  of the standard simulation values (cf. Adams and DeAngelis 1987) to determine the percentage change in algal biomass, algal patchiness (RPI), and non-spatial algal biomass variability (CV) after 49 d of grazing under 3 intensities. Changes less than ca 10% would indicate the model is relatively robust to parameter estimation, whereas changes greatly exceeding 10% would indicate high sensitivity and a need for care in parameter estimation. All sensitivity tests were done with the fast velocity regime and 15 boulders.

## Results

### *Model question 1: Does habitat heterogeneity alone influence algal biomass and spatial distribution?*

In the absence of grazers, total algal biomass accumulated at nearly identical rates irrespective of habitat heterogeneity in both slow and fast riffles. After 70 d total algal biomass on the simulated streambed was ca 70% of maximum possible biomass (33.1 mg/m<sup>2</sup> in the slow riffle, 34.6 mg/m<sup>2</sup> in the fast riffle).

Algal biomass distribution varied only slightly with habitat heterogeneity and current regime in the absence of snails when measured with the RPI or CV. In the slow velocity treatment, RPI values were 0.11 and 0.60 for the 1- and 15-boulder treatments, respectively. In the fast velocity treatment, the corresponding RPI values were ca 0.13 and 0.57. For CV, the slow riffle values were 2.37 and 2.57 for the low and high heterogeneity treatments, respectively. In the fast riffle, the corresponding values were 1.18 and 1.74. Compared with the levels of algal variability attained under grazing pressure (see below), all the RPI and CV values were low.

### *Model question 2: Does grazer density interact with habitat heterogeneity to influence algal biomass and variability in algal distribution?*

For both habitat heterogeneity levels and both velocity regimes, 20, 100, or 500 snails/m<sup>2</sup> were added after 70 d of algal growth and allowed

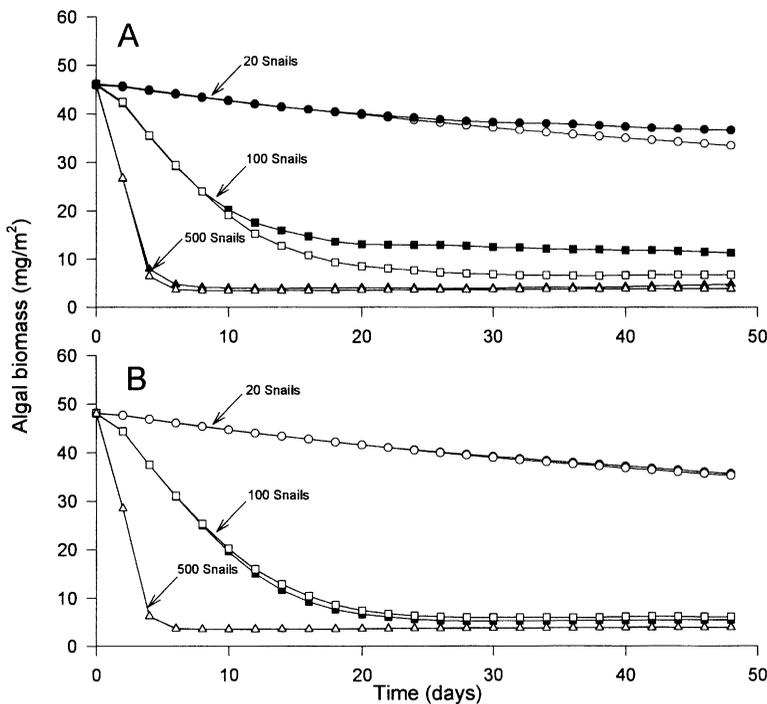


FIG. 3. Time course of simulated mean algal biomass accumulation for (A) slow velocity regime and (B) fast velocity regime under 3 densities of grazers for low (closed symbols) and high (open symbols) habitat heterogeneity conditions.

to forage for an additional 49 d. Snail density had clear effects on mean algal biomass for both slow and fast riffles (Fig. 3). In the slow riffle, the low grazing pressure of 20 snails caused a gradual reduction in algal biomass. A density of 100 snails caused a moderate reduction in algae to a minimum after ca. 25 d. Under the highest grazing pressure of 500 snails, algal biomass dropped rapidly to a minimum after only 5 d. Increased habitat heterogeneity increased the magnitude of algal biomass loss in the slow riffle under low and intermediate grazer densities (Fig. 3A), and, based on replicate simulations, these differences were significant after 49 d for 100 snails ( $p < 0.05$ ). In the fast riffle (Fig. 3B), rates of algal loss were similar to those in the slow riffle under each snail density, but were almost unaffected by habitat heterogeneity for any level of grazing.

The spatially explicit RPI varied greatly with grazing intensity for both the slow (Fig. 4A) and fast (Fig. 4B) riffles. In both current regimes, introduction of high and intermediate densities of grazers caused RPI to rapidly increase to a tran-

sient peak value of 13–16 as snails began removing algae from the grid. As small grazing patches began coalescing to larger ones, overall dissimilarity dropped and RPI values declined and leveled out. By contrast, when only 20 snails were introduced, RPI gradually increased over the 49 d grazing period. Additional simulations (to 180 d) showed that RPI values remained at these high values under low grazing intensity in both current regimes.

Habitat heterogeneity contributed to spatially explicit variability in algal biomass under low and intermediate grazing intensities, but only in the slow riffle (Fig. 4A). Differences in RPI values for the 2 heterogeneity levels at day 49 were significant for 100 snails ( $p < 0.05$ ); however, for 20 snails differences were not significant ( $p = 0.12$ ), due to high among-replicate variability and associated low statistical power. With additional replication, the effect of heterogeneity for 20 snails would very likely have been significant. A possible grazer  $\times$  heterogeneity interaction was also observed in the slow riffle, because the effect of high habitat heterogeneity

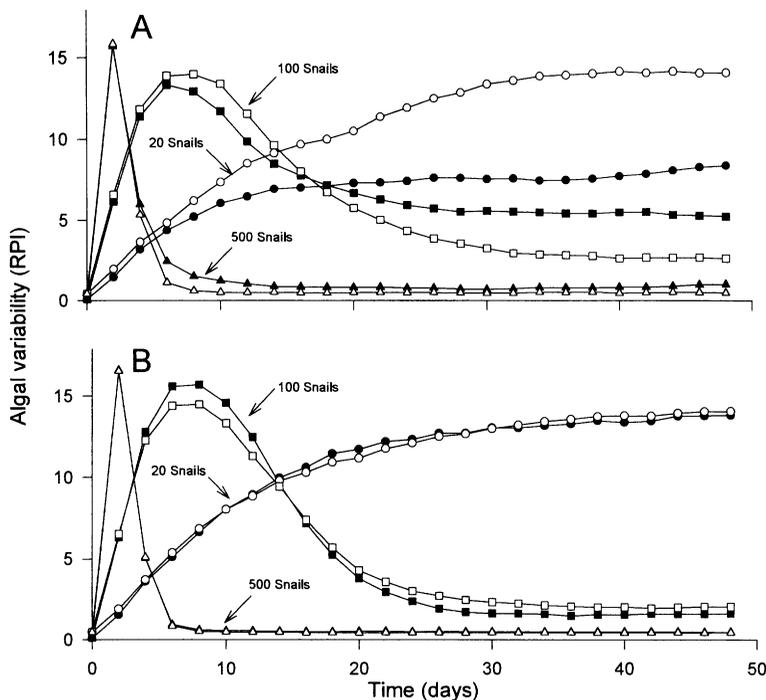


FIG. 4. Time course of spatially explicit variation in distribution of algal biomass (relative patchiness index) for (A) slow velocity regime and (B) fast velocity regime under 3 densities of grazers for low (closed symbols) and high (open symbols) habitat heterogeneity conditions.

was to increase RPI under low grazing pressure and to decrease RPI under intermediate grazing pressure. In the fast riffle, by contrast, the effect of habitat heterogeneity on RPI was minimal for all grazer densities (Fig. 4B).

Variability in algal biomass measured as CV differed from RPI in response to grazing and heterogeneity (Fig. 5). For both slow and fast riffles, the CV increased monotonically to an asymptotic maximum. The greater the snail density, the greater the rate of initial increase and the greater the maximum CV. In the slow riffle (Fig. 5A), high habitat heterogeneity was associated with higher CV for high ( $p = 0.08$ ) and intermediate ( $p < 0.05$ ) grazer densities. By contrast, in the fast riffle, habitat heterogeneity had minimal effect ( $p > 0.5$  in all cases, see Fig. 5B). The different response of algal variability to heterogeneity under intermediate grazing pressure suggests the possibility of a heterogeneity  $\times$  current regime interaction.

#### Model sensitivity

Sensitivity analysis for 2 model parameters (grazer movement rate and consumption rate)

showed that model predictions were generally robust (Table 3), because changing the model parameters by  $\pm 10\%$  usually resulted in changes in model output of ca 10% or less. Model output was least variable for parameter changes at low grazer density and most variable for intermediate grazer density. The greatest model sensitivity was observed at intermediate and high grazer densities for RPI (Table 3), which had a low absolute value under these grazing conditions after 49 d (Fig. 4B).

## Discussion

### *Effect of habitat heterogeneity and snail density on algal-grazer interactions*

Our simulations indicate that algal biomass and variability in distribution of algae are influenced by spatial habitat heterogeneity, at both within-riffle (number of boulders) and among-riffle (current regime) scales, but only in the presence of grazers. Without grazers, algae responded similarly to all habitat heterogeneity treatments, apparently because the current ve-

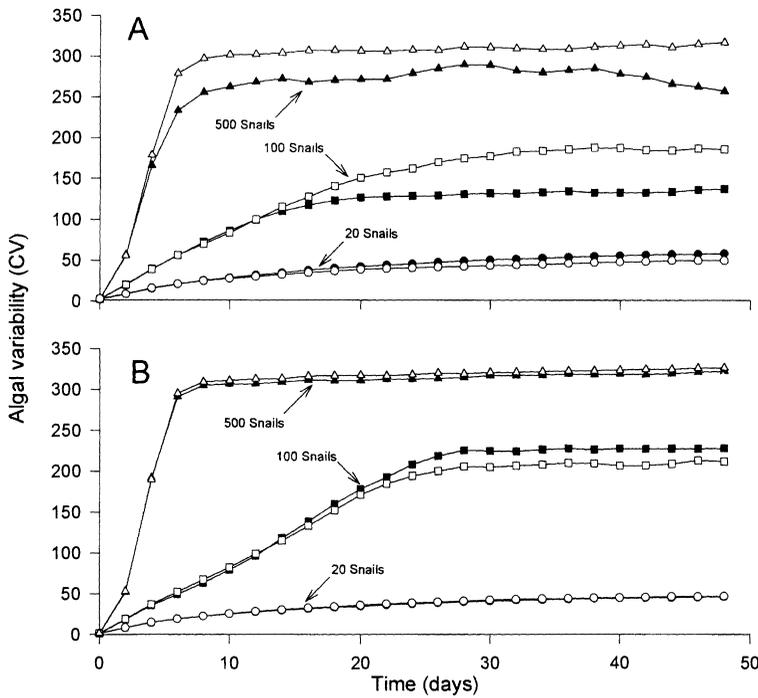


FIG. 5. Time course of non-spatially explicit variation in distribution of algal biomass (coefficient of variation) for (A) slow velocity regime and (B) fast velocity regime under 3 densities of grazers for low (closed symbols) and high (open symbols) habitat heterogeneity conditions.

TABLE 3. Results for sensitivity analysis for 2 model parameters (grazer movement rate and grazer consumption rate) for each of 3 grazer densities after 49 d under fast velocity and high heterogeneity.

Parameter	Graz- er den- sity	% Change in par- am- eter	% Change in output variable		
			Biomass	CV	RPI
Movement rate	20	-10	-0.9	-1.7	1.4
		+10	-0.9	-0.4	4.3
	100	-10	-14.7	11.8	-30.4
		+10	-15.4	12.8	-30.4
	500	-10	-1.3	1.5	-20.0
		+10	-1.3	1.2	-20.0
Consump- tion rate	20	-10	5.7	-13.6	2.8
		+10	-7.1	3.2	8.5
	100	-10	15.8	12.6	-30.4
		+10	15.8	12.2	-30.4
	500	-10	-6.3	1.5	-20.0
		+10	0	1.2	-20.0

locities used in the model were not sufficient to generate algal resource heterogeneity through differential growth rates. Addition of grazers dramatically altered patterns of algal distribution, and these patterns reflected complex interactions between velocity, substrate heterogeneity, and snail density. These findings are consistent with limited empirical research showing that snails grazing in artificial streams can create spatial heterogeneity in algal cover in abiotically homogeneous environments through movement and foraging (Sarnelle et al. 1993).

The constraint imposed by current velocity on grazer movement appears to underlie many of the model predictions. As velocity increased, snail movement direction was increasingly in the upstream direction (Fig. 2). Variation in current was created both within riffles as a function of number of boulders and among riffles as a function of velocity regime. At the among-riffle scale, current regime influenced the extent to which substrate heterogeneity (number of boulders) mediated grazer movement. Specifically, algal biomass and variability in distribution

were sensitive to habitat heterogeneity in the slow, but not the fast, riffle (Figs. 3–5). Thus, the model predicted that the effect of habitat heterogeneity on grazer “control” of algae emerged only when current velocity minimally constrains grazer movement. Exactly how current interacts with habitat heterogeneity to mediate movement is not clear, but our field observations and the work of others on snails (Huryn and Denny 1997), as well as on some other grazers (e.g., caddisflies, Poff and Ward 1992), indicate that snail movement direction is indeed influenced by current magnitude.

Within the slow riffle, the effect of spatial heterogeneity on model predictions also appears to reflect constraint on grazer movement patterns. Under low heterogeneity, 75% of the streambed consisted of non-boulder surfaces, compared to 60% for high heterogeneity. Because this non-boulder substrate was characterized by very slow velocity, snail movement direction was more non-directional in the 1-boulder vs. 15-boulder treatment. The resulting higher biomass in the low vs. high heterogeneity treatment (Fig. 3A), while largely counterintuitive and lacking a simple mechanistic explanation, provides an interesting testable prediction of the model. At the highest snail density, even differences in directional movement were not sufficient to prevent snails from foraging all exposed surfaces, and thus the effect of habitat heterogeneity was obscured (Fig. 3A).

These results are noteworthy because they suggest that even small differences in spatial habitat heterogeneity can have large consequences for the grazer-mediated patterns of algal resource abundance and distribution. In natural systems, great spatial variation in current velocity is commonplace and is generated by interactions among boulders or smaller roughness elements (e.g., Davis and Barmuta 1989, Hart et al. 1996). Had we simulated this source of hydrodynamic variation, we would likely have found even greater differences between low and high heterogeneity treatments.

Another interesting prediction from the simulations was that qualitatively different patterns of variability in distribution of algal biomass result from using a spatially explicit (RPI) vs. non-spatially explicit (CV) index of variability. RPI generally peaked and declined, while CV rose monotonically (cf. Figs. 4 and 5). For the RPI, there was a transient period where newly

grazed cells of the grid were juxtaposed with completely ungrazed cells, resulting in high average dissimilarity between neighboring cells and peak RPI values. As grazing continued, dissimilarity declined as grazed patches merged and grazed cells became uniformly mixed. This decline occurred for both slow and fast riffles and for high and intermediate snail densities (Fig. 4). Interestingly, under the lowest grazer density, mixing never occurred, suggesting that high patchiness can persist only below some threshold number of grazers regardless of current regime. The CV describes the *amount* of variation without accounting for spatial *arrangement* of that variation. Thus, the CV rose quickly as variation in biomass among grid cells increased due to grazer foraging (Fig. 5). CV rose fastest under high grazing intensity and slowest under low grazing intensity (where the patch “mixing” indexed by the RPI never occurred). After 49 d, predictions of algal variability based on RPI vs. CV were mirror images of one another. While CV is often used as a variability measure, it may be misleading in that it scales inversely with algal biomass, which is used as the divisor in calculating CV. Further, in contrast to the RPI, CV does not account for the spatial arrangement of algal biomass, which may be important to foragers (e.g., if food “patches” are separated by regions of high current velocity that constrain grazer movement). However, calculation of the spatially explicit RPI requires large amounts of data, which are typically unavailable in empirical work.

#### *Modelling approach*

Our intent with this research was to explore the influence of habitat heterogeneity on algal-grazer interactions in streams using a modelling framework. Our model does not describe a particular real-world system; rather, it represents a simplified stream ecosystem lacking many components, e.g., indirect interactions among consumers, algal growth form and species composition, and certain chemical and physical factors. Nonetheless, the model allows us to explore the potential for habitat heterogeneity to mediate algal-grazer dynamics in stream ecosystems, an issue of general interest that has received scant research attention (Feminella and Hawkins 1995). Some aspects of our model were based on existing literature and thus constrained mod-

el outcomes. For example, we expected the model to predict that algal biomass would decline with increasing grazer density, as documented in many previous studies (reviewed in Feminella and Hawkins 1995, but for exceptions see Dudley 1992, Sarnelle et al. 1993). Many model outcomes, however, were unexpected, such as the counterintuitive reduction in algal biomass under high habitat heterogeneity and low grazer density (Fig. 3A) and the possibility of a grazer  $\times$  habitat heterogeneity interaction in algal patchiness in slow riffles (Fig. 4A). These results suggest interesting and possibly rewarding avenues of empirical research. A strength of this modelling approach is that it could be extended to other types of algal-grazer systems in streams. For example, different grazer species could be simulated by modifying fundamental parameters such as consumption rate, movement rate, and movement direction; and the effects of different grazer types on algal biomass and patchiness could be evaluated. Such simulations could be compared to each other and to empirical observations on the effects of grazer type on algal resources (e.g., Steinman et al. 1987).

Modelling approaches can greatly augment empirical research addressed at understanding the importance of heterogeneity in influencing algal-grazer dynamics in streams. Spatially explicit models have received only a little attention in stream ecosystems (e.g., Sarnelle et al. 1993, Bretschko 1995), despite the fact that streams are notoriously heterogeneous and should lend themselves to this modelling approach. A variety of different modelling approaches are possible; however, because algal-grazer interactions are inherently "local" (i.e., they cannot be averaged spatially as the result of random distribution of organisms), an IBM is perhaps the best modelling approach (Caswell and John 1992). Indeed, IBMs are gaining widespread favor among ecologists (DeAngelis and Gross 1992).

Of course, IBMs have their disadvantages as well. Perhaps the most obvious is their need for many equations and parameters, which are best estimated in a well-studied system. It may seem that it would be possible to obtain any desired outcome from an IBM simply by tweaking the individual parameters, but this is generally not true. Any parameter change tends to affect the entire model, often with unexpected effects on

the outcome. In addition, we found that the general characteristics of our model output were robust to most reasonable changes in parameter values (i.e., algal levels always dropped fastest and to the lowest levels under high grazer pressure; they always peaked and declined except under very low grazer density where they remained high, etc.). Formal sensitivity analyses further demonstrated the model's robustness (see Table 3). Thus we agree with Judson (1994), who stated that given the lessons of non-linearity and chaos, IBMs "may be as general as any models can be."

### Acknowledgements

We thank Eric Klineberg and Suzanna Galo Ribblett for diligent assistance in both the field and laboratory. Others providing assistance were Bruce Baker, Art Grinath, Matt Goodman, Tracy Cox, Patrick Ressler, Dwight Courtemanch, Melissa Smith, and Chris Hakenkamp. We also thank Margaret Palmer for use of her flume lab. Special thanks go to Kiimara Baker for her enthusiastic pursuit of snails. Constructive comments from Chris Peterson and two anonymous reviewers improved the final version of the paper.

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Received: 29 January 1996

Accepted: 16 October 1996